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Parentage-based tagging improves escapement estimates for ESA-listed adult Chinook Salmon and Steelhead in the Snake River basin

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Abstract

Parentage-based tagging (PBT) is a non-lethal, genetic tagging method that has been successfully applied in hatchery supplemented populations to manage hatchery broodstock and monitor hatchery harvest and straying rates. We show that PBT can also improve the accuracy of escapement estimates by significantly reducing the number of hatchery-origin fish falsely classified as natural-origin. Unlike conventional abundance estimates, which use physical marks and tags to distinguish hatchery individuals from their wild counterparts, PBT identifies origin independent of physical form. We applied PBT to populations of Chinook Salmon (Oncorhynchus tshawytscha) and Steelhead (O. mykiss) which are classified as threatened under the Endangered Species Act and subject to extensive hatchery supplementation efforts. For spawn years 2014-2018, 16,511 adipose-intact Chinook Salmon and 21,953 adipose-intact Steelhead were sampled, and PBT identified 19.6% of returning Chinook Salmon and 8.3% of Steelhead were of hatchery-origin, despite having no physical or mechanical marks. The 90% confidence intervals for escapement estimates of natural-origin Chinook Salmon and Steelhead made with and without corrections using PBT were non-overlapping for nine of ten comparisons indicating that failing to account for unmarked, untagged hatchery-origin fish would result in a significant overestimation of natural abundance.

Introduction

Estimating adult abundance is a central tenet of fish population management as these data are used to set harvest levels, quantify response to management strategies, and monitor population
recovery. The value of adult abundance estimates is limited without some understanding of their accuracy (Ludwig and Walters 1981), as inaccurate estimates can obscure population trends (Muhlfield et al. 2006) and mask stock collapse (e.g., northern Atlantic Cod, *Gadus morhua*; Walters and Maguire 1996). Physical marks and tags are widely used tools to estimate population abundance and have known sources of error including shedding, loss, imperfect detection, changes to life history or behavior, and mortality (Pine et al. 2003). Marks and tags are also used to identify subsets of the overall population, such as hatchery fish released into natural populations. One source of error associated with marking and tagging in hatchery-supplemented populations that remains less explored is what impact hatchery fish without a mark or tag have on the estimation of natural abundance. Given that over 900 hatcheries are operated for natural resource conservation in North America alone (Trushenski et al. 2018), biases associated with misclassifying hatchery-origin fish have broad potential implications.

Parentage-based tagging (PBT) has emerged as an alternative to physical marks and tags that can tag hatchery offspring (Steele et al. 2019) with high rates of accuracy (~100%, Beacham et al. 2017a; Beacham et al. 2019a; 2019b) over large spatial scales (e.g., river basins, Steele et al. 2013; international fisheries, Beacham et al. 2017b). The application of PBT involves generating multi-locus genotypes for a set of parents (e.g., broodstock in a hatchery), which in turn genetically ‘tag’ all resulting offspring (Anderson and Garza 2005). Importantly, genetic tags are permanent and are therefore not subject to shedding or loss as a potential source of recovery error (Palsbøll et al. 1997). Furthermore, the rate at which broodstock in PBT programs are successfully genotyped (i.e., genetic profiles consisting of > 90% non-missing data) is typically very high, resulting in the genetic tagging of near complete hatchery cohorts (e.g., ≥ 95% for tens of millions of offspring; Steele et al. 2019). Whereas the presence of an adipose fin
clip or dorsal fin erosion may be unclear (e.g., partial fin clip/erosion), PBT assignments are unambiguous and nearly all parent offspring relationships are detected when PBT tagging rates are high and large numbers of informative genetic markers are used (≥ 96 single nucleotide polymorphisms; SNPs; Anderson 2010). To date, PBT data have been used to address a wide range of management and research related questions including stock composition in sport and tribal fishery harvest (Byrne et al. 2018), estimation of genetic divergence between hatchery and wild stocks (Venditti et al. 2018), and run-specific life history characteristics (Hess et al. 2016a; see Steele et al. 2019 for a review of PBT applications). Although PBT programs have largely focused on salmon and Steelhead, PBT has also been applied to a number of other species including Pallid Sturgeon (Scaphirhynchus albus) in the Missouri River (Dehaan et al. 2008) and Blueback Herring (Alosa aestivalis) in North Carolina (Evans et al. 2018). Several characteristics of PBT, namely the absence of tag shedding or loss, near-complete detection of all parent-offspring relationships, the nonlethal nature of sampling, and the ability to identify millions of hatchery offspring by sampling far fewer parents make this approach an appealing alternative to conventional tagging programs.

Throughout their range, rates of imperilment among Pacific salmonids (Oncorhynchus spp.) are high with many runs in the United States and Canada being federally protected under the Endangered Species Act (ESA) and Species at Risk Act (SARA). Simultaneously, salmon are subject to extensive hatchery supplementation efforts with billions of hatchery-reared salmon being released on an annual basis (NPAFC 2020). Marks such as an adipose fin clip are widely used to identify hatchery-reared fish including the majority of hatchery released Coho salmon (O. kisutch) produced in southern British Columbia, Washington, and Oregon (~34 million annually) and Chinook Salmon (O. tshawytscha) smolts released in Oregon, Washington and
Idaho (115 million annually) (PSCSFEC 2016). Additional methods of identifying hatchery-released fish include tags (e.g., coded wire tag, CWT) or external marks (e.g., dorsal fin erosion, ventral fin clip), but CWTs are limited in that they are applied to a relatively small proportion of total fish that are released and some external marks may not be equally reliable for all species (Bosakowski and Wagner 1995). Despite massive tagging and marking efforts, salmon and Steelhead may not have a mark or tag because of shedding/loss or because they were knowingly released untagged and unmarked in known or estimated quantities for a variety of purposes (Hand et al. 2010, Matala et al. 2012). Unmarked, untagged hatchery fish are problematic from a management perspective, because if they are erroneously classified as natural-origin, the resulting estimates on natural abundance will be inflated. Such concerns are relevant to a wide range of salmon runs on the Pacific Coast of the United States and Canada where many populations of wild salmon and Steelhead numbers are at historic lows (Gustafson et al. 2007; Heard et al. 2007) and hundreds of millions of hatchery-reared fish are released annually (NPAFC 2020).

The Snake River basin, a major tributary to the Columbia River, supports multiple runs of anadromous salmonids including Chinook Salmon and Steelhead (*O. mykiss*). Currently, two Chinook Salmon Evolutionary Significant Units (ESUs) and one Steelhead distinct population segment (DPS) in the basin are listed as threatened under the ESA (Good et al. 2005). Dams constructed on the lower Snake River (Ice Harbor Dam, Lower Monumental, Little Goose, and Lower Granite Dam) have negatively impacted Steelhead and salmon populations in the basin (Raymond 1979; 1988), but provide unique opportunities to enumerate returning adults as all fish use ladders at dam facilities to gain upstream access. The number of adults not harvested by commercial or recreational fisheries that return to their freshwater spawning habitat, also known
as escapement, is currently estimated for Snake River spring/summer Chinook Salmon (hereafter Chinook Salmon) and Steelhead using data collected from window counts and systematic biological sampling at Lower Granite Dam. Window counts provide data on the number and species of fish that escape to the dam and biological sampling at a trapping facility is used to collect biological information from returning salmon and Steelhead (Harmon 2003). Biological data includes observations of marks and tags that are used to indicate whether a fish is of natural or hatchery origin and tissue for genetic analysis which identifies sex (via a sex-linked marker) and genetic stock of origin the within the Snake River basin (Camacho et al. 2019). Window counts and trap data and are then combined to estimate escapement of Chinook Salmon and Steelhead by size, genetic stock, and source of origin: natural or hatchery (adipose clipped and unclipped) (Steinhorst et al. 2017; Camacho et al. 2019). Accurate estimates of escapement for natural-origin salmon and Steelhead basin-wide as well as decomposed by genetic stock and sex is of critical importance to conservation and management efforts (Wainwright and Kope 1999; Chasco et al. 2014; Hess et al. 2014) as these data represent at least two of four key parameters that are presently used to assess salmonid population viability and ESA status (population abundance, growth rate, spatial structure, diversity; McElhany et al. 2000). Many populations of natural-origin Chinook Salmon and Steelhead in the Snake River basin are very small (<100 returning adults; IPTDSW 2020) and ongoing, wide-scale restoration efforts require accurate estimates of escapement to evaluate the program outcomes (NOAA Fisheries 2019).

Additionally, harvest opportunities in the Snake River basin and mainstem Columbia Rivers fisheries are based on escapements levels at Lower Granite Dam (Figure 1). Upwardly biased estimates of escapement stemming from misclassified hatchery fish could allow for the
continued operation of fisheries while numbers of natural-origin fish are below allowable thresholds.

There are several characteristics of Chinook Salmon and Steelhead management in the Snake River basin that make it particularly well-suited for the application of PBT to estimate the source of origin for unmarked, untagged fish. First, returning adults in the Snake River basin are disproportionately of hatchery-origin. The number of hatchery adults returning to the Snake River basin for spawn years 1998-2018 was an average of 3.7 and 5.9 times higher than natural-origin adult Chinook Salmon and Steelhead, respectively (Camacho et al. 2019). Second, although adipose fin clips are the most commonly used mark to identify hatchery-released salmon and Steelhead (Table 1; IDFG Fisheries Management Plan 2019-2024), there are programs that intentionally release unmarked, untagged hatchery fish to supplement natural populations and manage broodstock populations (Tiffan and Connor 2011). Third, other methods of identifying hatchery-released salmonids such as CWTs and external marks (e.g., dorsal fin erosion, ventral fin clip) are used, but these tags are limited in their application (Table 1) and marks may not be equally reliable for all species (Bosakowski and Wagner 1995). External marks such as dorsal fin erosion may occur as a byproduct of the hatchery-rearing environment and have been used as a secondary means to identify otherwise unmarked hatchery-origin Steelhead (Latremouille 2003) but this does not apply for Chinook Salmon. Differences in rearing conditions are thought to be a contributing factor to the lack of dorsal fin erosion observed in Chinook Salmon. Lastly, despite the use of automated trailers for tagging and marking in the Snake River basin which produce high rates of tag retention and completeness, a small portion (<5%) of all processed fish will have either a poor (i.e., <75% of the adipose fin was removed) or missing mark or fail to retain a CWT tag (Hand et al. 2010). Important to note is that many of the characteristics outlined for
Chinook Salmon and Steelhead in the Snake River basin are likely present in other major river systems such as the Columbia River, Sacramento River, and their tributaries.

In an effort to inform management of fisheries, hatcheries, and natural stocks, a PBT program was initiated in the Snake River basin in 2008. Since the inception of the program, adult broodstock (~9,000 spring/summer Chinook Salmon and ~5,000 Steelhead) are sampled annually from each hatchery that releases smolts into the Snake River basin and its tributaries (Steele et al. 2019). Collectively, hatcheries in the Snake River basin release ~20,000,000 smolts each year. The near complete sampling of broodstock has resulted in genetic ‘tagging’ rates of 96.0% and 94.8% for Chinook Salmon and Steelhead smolts, respectively (Steele et al. 2019). In the current study, we applied PBT to adult spring/summer Chinook Salmon and Steelhead returning to the Snake River basin to identify source of origin (hatchery- or natural-origin).

Using biological data and genetic samples collected from adults trapped at Lower Granite Dam, Washington, we quantified the number of putatively natural-origin fish (adipose-intact) without identifying marks (dorsal/ventral fin erosion in Steelhead, ventral fin clip in either Steelhead or Chinook Salmon) or a CWT estimated as hatchery-origin via PBT. We then generated estimates of escapement for adult Chinook Salmon and Steelhead with and without the use of PBT and quantified errors stemming from misclassified source of origin. Finally, we empirically estimated false assignment rates (incorrectly identifying a natural-origin fish as hatchery) by performing parentage analysis on collections of thousands of known natural-origin Chinook Salmon and Steelhead.

Methods
Broodstock sampling from participating hatcheries for genetic tissue is conducted by federal, state, or tribal personnel (Table 1; Figure 1). Importantly, all hatcheries rearing spring/summer Chinook Salmon and Steelhead in the Snake River basin that could have produced returning adults between 2014-2018 (i.e., duration of this study) were being sampled for use in the PBT reference baseline. An approximately 1 cm² clip from the caudal fin of each broodfish was stored on either Whatman chromatography paper (LaHood et al. 2008) or in 1.5 mL microcentrifuge tubes containing 100% non-denatured ethanol.

Genomic DNA from parental broodstock was extracted using a 96-well plate extraction protocol following manufacturer’s instructions (Nexttec 1-Step DNA Isolation kit, Leverkusen, Germany). Species-specific panels of 95 single nucleotide polymorphisms (SNPs) designed for parentage analysis in Chinook Salmon and Steelhead were used to generate genotypes for all broodstock (Chinook Salmon, Janowitz-Koch et al. 2018; Steelhead, Hess et al. 2016b; additional marker details available on FishGen.net; panel names: Chinook Salmon 96 PBT v5.1 and Steelhead 96 PBT panel v5.1). Since the inception of the Snake River basin PBT program, two protocols have been used for SNP amplification. Initial efforts involved producing genotypes using a TaqMan SNP-assay performed using a Fluidigm 96.96 Dynamic Array IFCs (i.e., chips; detailed in Steele et al. 2013). Beginning in 2015, SNP amplification was switched to the Genotyping-in-Thousands by sequencing (GT-seq) protocol developed by Campbell et al. (2015). This method involves using a high-throughput sequencing platform (e.g., Illumina NextSeq 500) to sequence multiplexed PCR products consisting of 50-500 SNPs per individual. See Campbell et al. (2015) for a breakdown of GT-Seq protocol steps. While marker panels have
been expanded and novel sequencing technologies have been adopted over the course of the Snake River PBT program, the same core suite of 95 SNP markers for PBT have been used since the program’s inception. A sex-specific marker was amplified as part of both Chinook Salmon and Steelhead PBT panels to allow for identification of genetic sex (Brunelli et al. 2008). Following the successful amplification of broodstock genotypes, genetic data were uploaded to a genetic repository (FishGen.net; McCane et al. 2018).

Window counts

The U.S. Army Corp of Engineers conducts window counts on the fish ladder at Lower Granite Dam to enumerate returning adult salmonid passage. The goal of the counting program is to account for at least of 95% of the daily passage of Chinook Salmon and Steelhead and is accomplished using both visual and video counting (Wagner 2007). Visual counts were performed for 16 hours per day (0400-2000 PST), seven days a week throughout the primary migration period (April 1st through October 31st). Video counting using time-lapse video equipment to record fish passage was used in November, December, and March of each year. Visual counts were conducted for 50 min each hour whereas video counts were performed continuously throughout each counting period. Male Chinook Salmon display precocial maturation (i.e., become reproductively mature earlier than females of the same cohort) which includes both jacks and mini-jacks forms. These two life history forms differ in the timing of maturation and time spent in the ocean, with jacks typically being both larger and older. From a management perspective jacks and mini-jacks are classified based on length, but identifying mini-jacks visually can be problematic, and as a result these fish were not included in our
assessment of adult Chinook Salmon. Chinook Salmon were designated as jacks if fish length was between 30 and 56 cm, and mini-jacks were those less than 30 cm based on visual estimation.

Biological sampling and fish trapping operations at Lower Granite Dam

Systematic samples of Chinook Salmon and Steelhead returning to Lower Granite Dam were collected during daily operation of the adult fish trap from 2014 through 2018. Sampling of returning adults was initiated in 2014 to ensure compatibility with our PBT baseline. In other words, because we know the vast majority of hatchery-reared Chinook Salmon and Steelhead return as 3-, 4-, or 5-year old fish, we compared fish sampled in 2014 with our PBT baseline which included all broodstock spawned in 2008 and later. We took this approach to ensure that a failure to assign a fish to the PBT baseline was not due to incomplete sampling of potential parents. The fish trap at Lower Granite Dam is located upstream from the fish counting window in the fish ladder and uses a trap gate to capture a systematic random sample of fish. While the trap is operational 24 hours per day, the sample gate is open four times per hour for a length of time directed by a sample rate. The sample rate is determined using forecasted abundances for target species, runs, rear types, and research projects with associated sample sizes. Adult fish trap operation dates vary annually as a result of environmental conditions or changes to run forecast. For example, trap operations cease or are modified due to high (≥ 21 °C) and low (≤ 0 °C) water temperatures. Additionally, trap operations are reduced seasonally (closed weekends from March 1 to August 17) and modified in-season to accommodate limitations at the trapping facility,
changes to run forecasts, or sample size modifications. Additional trap details can be found in Harmon (2003).

Biological sampling of adult Chinook Salmon and Steelhead were performed by National Marine Fisheries Service (NMFS) and Idaho Department of Fish and Game (IDFG) personnel following standardized sampling methodologies (Ogden 2017, 2018). All fish handled in the fish trap were first anesthetized, examined for external marks and tags, scanned for a CWT (presence/absence), and measured for fork length (FL) to the nearest centimeter. Classification of fish by origin (hatchery or natural) was accomplished using a hierarchical key of internal and external marks/tags (Figure 2). First, fish were inspected for the presence or absence of an adipose fin. Fish with a clipped adipose fin (ad-clipped) or a partial clip and associated healed scar were classified as ad-clipped hatchery fish (hereafter hatchery; H). While the majority of hatchery-origin Chinook Salmon and Steelhead are released as ad-clipped, some are released without receiving an adipose clip (hereafter ad-intact) for supplementation or broodstock management purposes (Table 1). Ad-intact fish were scanned for a CWT and inspected for a ventral fin clip. Ad-intact fish with either (or both) CWT or ventral fin clip were classified as adipose intact hatchery origin (also “hatchery no clip” or HNC). Fin erosion is commonly observed in hatchery-reared fishes (e.g., Latremouille 2003) and dorsal fin erosion has been widely documented for Steelhead in particular (Abbott and Dill 1985; Winfree et al. 1997). Because fin erosion is observed in hatchery-reared Steelhead (Latremouille 2003) but not Chinook Salmon, dorsal fin erosion was only used as a diagnostic mark to identify ad-intact hatchery (HNC) Steelhead. Fish assigned to parents in our PBT baseline via parentage analysis (below) were also flagged as ad-intact hatchery (HNC). Lastly, fish with an intact adipose fin and no CWT, fin erosion/ventral fin clip or PBT assignment were classified as natural origin (N).
At the trap, the above classification scheme was used to identify a fish as natural-origin (N), hatchery (H) or ad-intact hatchery (HNC; Figure 2). In addition to recording length and species information, a genetic sample (a 1 cm² piece of fin tissue) was taken from all ad-intact adults. Fin clips were preserved on either Whatman chromatography paper (LaHood et al. 2008) or in 1.5 mL microcentrifuge tubes containing 95% non-denatured ethanol. After processing, all fish were returned to the fish ladder.

Parentage analysis

Genotypes for returning adult Chinook Salmon and Steelhead sampled at Lower Granite Dam were generated following the same procedures for the PBT baseline (outlined above). We removed individuals missing greater than 10% of the total SNP panel prior to downstream analysis but not duplicate genotypes. Because genetic samples are taken from every adipose-intact Chinook Salmon and Steelhead entering the trap facility, we encountered small numbers of duplicate genotypes each year from fish that ascended the dam multiple times and were sampled on more than one occasion. We did not remove duplicate genotypes because fish that fallback and subsequently reascend Lower Granite Dam are not removed from the window count but are assumed to be equal in number as fish that fallback over the dam but never reascend (Camacho et al. 2019). Parentage assignment in trios (both parents and one offspring) was performed using the likelihood-based algorithms within SNPPIT (Anderson and Garza 2005; Anderson 2010) using a per-allele genotyping error rate of 0.5%. A genotyping error rate was calculated annually for each broodstock collection, and across all spawn years the genotyping error rate was 0.42% and 0.66% for Chinook Salmon and Steelhead, respectively. Chinook Salmon and Steelhead
from the Snake River basin display a diversity of life-history strategies which includes varied freshwater residence time and number of years spent at sea (Narum et al. 2007; Campbell et al. 2012). To account for variation in life histories in our PBT analysis, we included broodstock from multiple brood years that could have potentially produced returning adults. Hatchery-reared adult Chinook Salmon and Steelhead predominantly return as 3-, 4-, and 5-year olds (Delomas et al. 2019), and as a result returning adults sampled at Lower Granite Dam were compared against broodyears 3+ years prior to their return. Each year of returning adults was compared against the PBT baseline independently. Parentage assignments with a LOD score (log of odds) \( \geq 14 \) were retained to minimize false positive and false negative assignments as this criteria has been shown to produce assignments that concur with hatchery spawning records (Hess et al. 2016b). Among retained parentage assignments we checked for discrepancies between the phenotypic/genotypic sex of parents as well as assignment to unexpected brood years to ensure the accuracy of inferred parent-offspring relationships. Unexpected brood years would be those that fall out of the known age distribution for hatchery-reared Chinook Salmon and Steelhead (e.g., <2 or >5 years of age).

Returning adults were ultimately decomposed by rearing type as either hatchery (H), natural-origin (N), or adipose-intact hatchery (HNC). We used results from parentage analysis to estimate the rearing type of natural-origin fish. In other words, the expectation was that natural-origin fish would fail to assign to hatchery broodstock. Returning adults that were confidently assigned to hatchery broodstock were identified as hatchery-origin and flagged as HNC to denote the sample represented an unmarked, untagged hatchery fish.

To test whether PBT would falsely identify natural-origin fish as hatchery-origin (false positives) we performed parentage analysis using separate collections of wild individuals that are used for genetic stock identification (GSI) in the Snake River basin and thus should not assign to
hatchery parents in the PBT baseline. The GSI baselines included representative samples from 31 of 34 extant Chinook Salmon populations in the Snake River basin and all extant populations of Steelhead (Vu et al. 2015). The Chinook Salmon GSI baseline consisted of 30 collections totaling 4,356 adult and juvenile samples and the Steelhead GSI baseline contained a total of 5,967 individuals from forty-five collections. Our sample collections included rivers managed exclusively for natural populations as well as rivers with ongoing supplementation efforts. As a result, our evaluation of false assignment rates included a range of populations with varied degrees of relatedness to hatchery-released fish which may increase the chances of assigning a fish to non-parent relative (e.g., Ford and Williamson 2010). Approximately 75% of the collections in our GSI baselines contained two or more sets of samples taken through time with the most recent collections being from 2013. We report the false assignment rate (natural-origin fish falsely assigned as hatchery) as the number of fish from our GSI baseline that were matched to parents in our PBT collections.

Adult escapement by origin

A conceptual model describing the integration of results from PBT analysis into escapement bias estimation can be found in Figure 2. Daily window counts recorded at Lower Granite Dam were assumed to represent the daily aggregate escapement for Chinook Salmon and Steelhead. Count data were downloaded from the Fish Passage Count website (http://www.fpc.org/).

The Salmonid Composition Bootstrap Intervals (SCOBI) function (https://github.com/mackerman44/SCOBI; Steinhorst et al. 2017) in R (R Core Team 2019) was
used to estimate adult escapement at Lower Granite Dam with 90% confidence intervals. Briefly, this package combines the daily window or video counts with adult trap sample data on a temporally stratified basis to account for changes in the trapping rate and run characteristics through time. The spawn year for each species is divided into strata ("statistical weeks") with each stratum defined as a week or a series of adjacent weeks with sufficient trap numbers (n ≥100) to adequately estimate proportions. In some instances, adjacent strata were not combined if sample sizes were above the minimum number or if there were gaps in sampling (e.g., winter trap shutdown during the Steelhead migration). Each stratum started on Monday and ended on Sunday. Escapement by stratum was estimated by multiplying the window or video counts by the trap proportions. The total escapement to Lower Granite Dam was the sum of escapement estimates from each stratum, which equals the total window count for the spawn year. In essence, the stratum proportions were weighted by stratum run size of all fish from each species as counted at the window or by video. Assumptions included: 1) window counts represented true abundance, and 2) proportions were constant within each stratum.

We generated two separate estimates of total escapement for hatchery- and natural-origin fish. In both instances, fish were decomposed by rearing type [hatchery (H), natural-origin (N), and adipose-intact hatchery (HNC)] (Figure 2). In the first estimation scenario, total escapement was decomposed by rearing type omitting any information gained via PBT analysis [i.e. HNC fish detected only by PBT were treated as natural-origin fish; Figure 2]. In the second scenario, total escapement was decomposed by rearing type where the HNC category was informed via PBT results. In both scenarios, escapement estimates were generated by multiplying the trapping proportions of each rearing type for each stratum by the window count for that stratum and summing over the season. A parametric bootstrap was used to find confidence intervals on the
estimated escapement of the different categories (scenario 1: H, N, and HNC without PBT; scenario 2: H, N, and HNC with PBT) (Steinhorst et al. 2017). The parametric bootstrap used the number of adults trapped in each stratum along with the estimated multinomial proportions for rearing type in that stratum to produce bootstrap pseudo-values for numbers of fish by rearing category. These were converted to pseudo-proportions by stratum and multiplied by weekly window counts to produce bootstrap estimates of totals by rearing type. The bootstrap estimates were ordered and the $\alpha/2$-th and (1- $\alpha/2$)-th ordered values provided the one-at-a-time confidence intervals associated with each rearing type. All confidence intervals were generated for the spawn year total rather than for individual strata. We assessed the impacts of applying PBT techniques on escapement estimates by comparing credible confidence intervals of escapement estimated with and without the use of PBT.

**Results**

**Chinook Salmon**

A total of 16,511 adipose-intact Chinook Salmon were sampled at Lower Granite Dam across spawn years 2014 – 2018 (Table 2), with an average of 3,302 fish sampled per year (range: 2,062 - 4,514, S.E. = 530). The average number of adipose-intact Chinook Salmon identified as natural-origin based on inspection during biological sampling at Lower Granite Dam (i.e., without PBT results) was 2,929 fish per year (range: 1,754 - 4,081, S.E. = 493). On average, PBT identified an additional 649 Chinook Salmon per year (range: 255 - 907, S.E. = 107) as hatchery-origin that would have been falsely classified as natural-origin otherwise.
Detection of coded wire tags were the primary method of identifying Chinook Salmon as hatchery-origin without the use of PBT, with only a small fraction classified using physical marks (Figure 4A).

Estimates of natural-origin, adult Chinook Salmon escapement calculated using SCOBI without PBT were higher than those with the use of PBT across all spawn years (mean = 21,357, range: 8,647 – 36,416, S.E. = 5,636; Table 3). Incorporating PBT results, the average number of natural-origin adults escaping to Lower Granite Dam across spawn years 2014 – 2018 was 16,735 (range: 5,793 - 30,338, S.E. = 4,674). The greatest difference in escapement estimates made for Chinook Salmon was for spawn year 2017 in which the percent change between estimates (with and without PBT) was 35.9%. The 90% confidence intervals for escapement were non-overlapping for all five years examined.

Parentage analysis using natural-origin Chinook Salmon from the genetic baseline collection identified a false assignment rate of 0.09%. Specifically, four natural-origin fish from a total of 4,356 individuals tested were assigned to a hatchery parent pair when compared against 46,296 potential parents. On a per-comparison basis, this is a false positive rate of 2.2 x 10^-7.

Steelhead

A total of 21,953 adipose-intact Steelhead were sampled at Lower Granite Dam from spawn years 2014 – 2018 (average: 4,391 per year; range: 2,975 – 5,047; S.E. = 365; Table 2). The mean number of adipose-intact Steelhead identified as natural-origin based on biological sampling at Lower Granite Dam (i.e., without PBT results) was 3,087 fish per year (range: 2,537 – 4,735; S.E. = 364). On average, PBT detected an additional 366 hatchery-origin Steelhead
annually (range: 164 – 800; S.E. = 116) that would have been falsely classified as natural-origin otherwise (Figure 3B). Hatchery-origin Steelhead identified without the use of PBT were identified using marks, fin erosion (e.g., dorsal fin erosion) and coded-wire tags (Figure 4B). The observation of marks other than coded wire tags was much more common for Steelhead than for Chinook Salmon.

Estimates of escapement for adult natural-origin Steelhead calculated with and without the use of PBT were less variable than for Chinook Salmon (Table 3). Natural-origin escapement estimates generated without PBT were higher than those with the use of PBT across all spawn years (mean = 28,725; range: 11,484 – 48,691; S.E. = 6,519). Incorporating outputs from PBT, the average number of natural-origin adults escaping to Lower Granite Dam across spawn years 2014 – 2018 was 26,275 (range: 10,717 – 45,789; S.E. = 6,312). The largest percent change between escapement estimates made with and without the use of PBT occurred in spawn year 2017. Failing to account for unmarked, untagged hatchery-origin fish (no PBT) resulted in a difference of 20.8% in the estimate of returning escapement that year. The 90% confidence intervals of Steelhead abundance estimated with and without PBT were non-overlapping for four of the five years examined.

Parentage analysis of natural-origin juveniles and adults compared against the PBT baseline identified a false assignment rate of 0%. No natural-origin fish from a total of 5,967 individuals tested were assigned to a hatchery parent pair.

Discussion
Estimates of salmonid escapement play a fundamental role in management and conservation and have been traditionally inferred using count data. A fundamental assumption of counting methods is that natural-origin fish can be accurately differentiated from their hatchery-produced counterparts using marks and tags, and we show this assumption is not entirely valid. While significant portions of hatchery-origin fish are currently identified using marks and tags, we have demonstrated that PBT is a complementary method that provides an independent line of evidence to differentiate hatchery- and natural-origin fish. We applied PBT to estimate the source of origin for over 38,000 adipose-intact Chinook Salmon and Steelhead in the Snake River basin and identified more than 5,000 of these fish were of hatchery-origin and would not have been detected otherwise. Importantly, estimates of natural escapement made with and without the use of PBT were significantly different, and the extent of bias in these estimates varied as a function of year and species. The use of PBT to estimate source of origin has widespread applications including captive broodstock programs as well as many river systems across the West Coast of North America where salmon and Steelhead runs are at historic lows and returning adults are disproportionately of hatchery-origin.

The application of PBT to identify source of origin for individuals lacking marks or tags is not unique, and there are several examples of such use in both resident (Dehaan et al. 2008; Campbell et al. 2019) and anadromous freshwater fishes (Hauser et al. 2006; Seamons et al. 2012). For example, recovery efforts for endangered Pallid Sturgeon in the Missouri River include the use of a captive breeding program to compensate for low or non-existent levels of natural recruitment (Dehaan et al. 2008). Although physical tags such as CWT and Floy tags have been used to track hatchery produced Pallid sturgeon, Dehaan et al. (2008) identified a number of juveniles using PBT that were presumed to be natural-origin due to the absence of
tags that were actually hatchery-origin. While this and other studies have shown that PBT can be used to estimate source of origin, our study is novel in that we have applied PBT to inform escapement estimation at a large, basin-wide scale for near entire runs of federally protected salmon and Steelhead. The application of PBT as described here could be transferred to other salmon and Steelhead runs (e.g., winter run Chinook Salmon in the Sacramento River, lower Columbia salmon and Steelhead), captive breeding programs (e.g., Burbot, *Lota lota*; Campbell et al. 2019), and fisheries where the determination of hatchery and naturally produced individuals is necessary for conservation or management efforts (e.g., Blueback Herring, Evans et al. 2018).

There are several examples from the Snake River basin that highlight how reducing bias in escapement using PBT can directly benefit conservation and management efforts. For instance, escapement estimated at Lower Granite Dam using PBT is incorporated into run reconstruction models along with survival and movement probabilities to estimate the abundance, disposition (e.g., harvested, survived), and spatial distribution of spawning adult Steelhead in the Snake River basin (Stark et al. 2016). Results from these models are used by National Oceanic and Atmospheric Administration (NOAA) Fisheries to evaluate the status and performance of the Snake River Steelhead Distinct Population Segment (NWFSC 2015). Additionally, population-level estimates of abundance and genetic diversity generated using escapement at Lower Granite Dam along with passive integrated transponder (PIT) tag data have been submitted to NOAA Fisheries for upcoming Status Reviews for Snake River Chinook Salmon and Steelhead (IPTDSW 2020). In both of the above modeling approaches, failing to account for unmarked, untagged hatchery-origin fish would lead managers to conclude that natural-origin populations were higher than the actual escapement (*Table 3*). In addition to
informing viability assessments, escapement estimates of natural-origin adults are used to
manage fisheries which operate on hatchery-origin salmon and Steelhead in the Snake River
basin. Fisheries which adversely impact ESA-listed species are regulated by permits issued by
the National Marine Fisheries Service (NMFS), and Critical Abundance Thresholds are used to
minimize impacts on natural-origin adults and direct in-season management decisions (ESA
sections 4(d) and 10(a)). In the case of Chinook Salmon in the Upper Salmon River in 2018, low
numbers of returning natural-origin adults led fisheries managers to significantly reduce the
operation of Chinook Salmon fisheries to minimize bycatch of natural-origin adults (Chris
Sullivan, Anadromous Fisheries Program Coordinator, Idaho Department of Fish and Game,
personal communication). In this case, upwardly biased estimates of abundance could have
allowed for the expanded operation of fisheries despite critically low numbers of natural-origin
fish. The above examples illustrate how escapement estimates are used to assess the recovery of
listed stocks and how a reduction in escapement bias using PBT uses the best available science to
make informed decisions.

The application of PBT is particularly relevant in systems where hatchery management
objectives are complex, such as the Snake River basin. Specifically, there are a number of
programs that intentionally release hatchery-origin smolts without marks or tags for various
purposes. In the South Fork Clearwater River, the Lower Snake River Compensation Program
(LSRCP) operations have included the release of hundreds of thousands of unmarked, untagged
Steelhead smolts from Dworshak Fish Hatchery to reestablish stocks that were nearly extirpated
by since razed dams (e.g., Harpster Dam; Stiefel and Leth 2012). For Chinook Salmon, fish from
the McCall Fish Hatchery have been used in an ongoing supplementation program operating on
the South Fork Salmon River (Matala et al. 2012), and many of these releases had no
distinguishing marks or tags. Additionally, egg box programs, in which hatchery-cultured eggs are placed into in-stream incubators (LSRCP 2019), have been used in tributaries of the Salmon River to reestablish extirpated populations (Conley et al. 2020). It is worth noting that unmarked, untagged fish could also be the byproduct of tag loss, imperfect tag detection, fin misclipping rates, or some combination thereof, and that these factors may vary by hatchery. In contrast, we have demonstrated that PBT assignments are highly accurate; false positive assignment rates were <0.1% for Chinook Salmon and zero for Steelhead, which are in line with previous empirical evaluations (Steele et al. 2013).

In applying PBT to determine the source of origin for adult Chinook Salmon and Steelhead sampled at Lower Granite Dam, we noted that the proportion of adipose-intact adults identified via PBT as hatchery-origin varied by both species and year. A greater number of adipose-intact Chinook Salmon were identified as hatchery-origin using PBT relative to Steelhead, and this discrepancy was driven by the identification of hatchery-origin Steelhead using an additional mark. Specifically, dorsal fin erosion, has been widely documented in Steelhead (Abbott and Dill 1985; Winfree et al. 1997, Latremouille 2003) but not Chinook Salmon. As a result of this species-specific mark, PBT was responsible for identifying a far greater number of hatchery-origin Chinook Salmon without a mark or tag than Steelhead (Table 2). That we observed annual variation in the number of unmarked, untagged adults identified as hatchery-origin via PBT was not surprising. There are a number of factors likely to influence how many unmarked, untagged fish are detected by PBT, and changes in hatchery release numbers may be the most likely culprit. Production goals at many hatcheries are dictated by mitigation agreements (e.g., LSRCP Annual Operation Plans; https://www.fws.gov/lsnakecomplan/Reports/AOPreports.html), but the numbers of smolts
released tagged and untagged varies as a function of broodstock availability and low return years may restrict outplants for different programs. Variation in PBT tag rates might also affect detection rates; however, tag rates across spawn years were consistently high (≥ 95%; Table 1) suggesting this was an unlikely source of error. Lastly, it is possible that systematic errors may influence detection rates, such as changes in equipment, personnel, or operating procedures at Lower Granite Dam.

Cost-effectiveness is an important consideration associated with using PBT data to correct for escapement estimation. For example, an estimate of misclassification could be derived using clipping and marking rates from different hatcheries; however, rather than use an approximation that may fail to account for error (i.e., true releases that differ from estimated values for a variety of reasons), PBT directly quantifies misclassification rates. Alternatively, an average correction factor could be applied based on existing estimates derived from PBT. We argue there are several benefits to performing PBT on an annual basis. First, the number of hatchery-origin adults detected using PBT alone varied by year (Table 2), implying that an average value may fail to reflect true abundance. Second, and most importantly, is that PBT applied at Lower Granite Dam to estimate source of origin is just one of many applications for this technology. Specifically, PBT in the Snake River basin has supplied information on stock-specific patterns of migration and abundance (Hess et al. 2016a; Hess et al. 2016b), demographic effects of supplementation programs (Janowitz-Koch et al. 2018), estimation of genetic divergence between hatchery and wild stocks (Venditti et al. 2018), and hatchery contributions to reproduction in the wild (Hinrichsen et al. 2016). Furthermore, PBT has been used extensively to monitor hatchery-specific contributions to recreational and tribal fisheries occurring in the Snake and Columbia River basins (Byrne et al. 2018; also reviewed in Steele et al. 2019). Lastly,
advancements in sequencing technologies (e.g., GT-seq; Campbell et al. 2015) have significantly reduced costs associated with genotyping (consumable cost of approximately $4 USD per sample for GT-seq; Campbell et al. 2015) implying that costs associated with these programs may continue to decline (Satterthwaite et al. 2015).

The methods used in the current study to estimate escapement and assign individuals as hatchery or natural-origin are not without their limitations. Namely, our analyses assumed that between physical marks, CWTs, and PBT, all hatchery-origin fish were detected when trapped at Lower Granite Dam. This assumption leads to an overestimation of the number of natural-origin fish because not all hatchery-origin fish are ultimately detected. However, the bias associated with failing to identify all hatchery-origin fish is expected to be negligible at Lower Granite Dam because our PBT tag rates were high (≥ 95% across hatcheries and years) and we used a combination of marks and tags (dorsal fin erosion, CWT, and PBT) to identify hatchery-origin fish. Furthermore, the accuracy of our parentage assignments was high. False positive rates for our data set were 0.09% and 0% for Chinook Salmon and Steelhead, respectively, both of which were in line with predicted rates based on simulated datasets (0.005%, Anderson 2010). Furthermore, false negative rates are expected to be less than 0.1% (Anderson 2010), although they may be higher in instances with large numbers of unsampled parents (~3%, Steele et al. 2013). In systems where PBT tag rates are much lower and only PBT is used to identify hatchery-origin fish, this bias is expected to be higher (e.g., at Bonneville Dam on the Columbia River; Hess et al. 2020). Methods have been developed (Delomas and Hess, in review) to correct for this bias, and can be used to provide an estimate of the number of natural-origin fish in scenarios where the number of untagged fish is higher.
In conclusion, we have shown that PBT can be applied at a basin-wide scale to estimate the source of origin for unmarked, untagged fish and the resulting data can be used to inform both conservation and management efforts by reducing bias in estimates of escapement. While PBT is a complementary tagging method to conventional techniques, it offers several advantages including the ability to nonlethally sample at recovery, the ability to overcome tag loss/shedding and imperfect tag detection as a source of uncertainty, and the lack of a need to handle juveniles (Steele et al. 2019). Moving forward, the application of PBT in conjunction with genetic stock identification (GSI) techniques will continue to serve as indispensable management tools in the Snake River basin and beyond to conserve populations of Chinook Salmon and Steelhead.

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FIGURE CAPTIONS

Figure 1. A map of the Snake River basin displaying fish hatcheries (FH) where spring/summer Chinook Salmon (Oncorhynchus tshawytscha) and Steelhead (O. mykiss) broodstock were sampled as part of a parentage-based tagging program. Biological samples (including genetic tissue) were collected from returning adult Chinook Salmon and Steelhead at Lower Granite Dam, Washington. This map was created using ArcGIS Desktop 10.6.1. Data sources included USGS Geographic Names Information System (GNIS) and US Census 2000 for towns, states and provinces, Idaho Department of Fish and Game (IDFG) and SteamNet for fish hatchery and dam locations, and USGS and IDFG 1:100,000 scale hydrography for stream data. Snake River subbasin data were derived from USGS Hydrologic Units.

Figure 2. A conceptual model illustrating decomposition of adult Chinook Salmon (Oncorhynchus tshawytscha) and Steelhead (O. mykiss) sampled at Lower Granite Dam by rearing type. Fish were placed into one of three categories (natural-origin, adipose-intact hatchery, and hatchery) using a combination of physical marks, tags, and positive hits to a
parentage-based tagging (PBT) baseline. Dorsal fin erosion was only used for steelhead (STHD).

The box highlighted in red indicates the subset of returning adult fish that are adipose-intact and identified as hatchery-origin using PBT.

Figure 3. A) The number of adipose-intact adult Chinook Salmon (*Oncorhynchus tshawytscha*) and B) Steelhead (*O. mykiss*) sampled at Lower Granite Dam, Washington, that were identified as natural-origin, hatchery-origin using physical marks or tags (Mark/Tag), or hatchery-origin using parentage-based tagging (PBT).

Figure 4. A) The proportion of adipose-intact adult Chinook Salmon (*Oncorhynchus tshawytscha*) and B) Steelhead (*O. mykiss*) determined to be hatchery-origin based on coded wire tags or marks. Marks included fin clips (e.g., left ventral) in either Chinook Salmon or Steelhead and dorsal fin erosion in Steelhead only. The yellow bars are relatively high for Steelhead since dorsal fin erosion is a common mark to identify hatchery-origin fish for this species, but it is not an effective mark for Chinook Salmon.
A map of the Snake River basin displaying fish hatcheries (FH) where spring/summer Chinook Salmon (\textit{Oncorhynchus tshawytscha}) and Steelhead (\textit{O. mykiss}) broodstock were sampled as part of a parentage-based tagging program. Biological samples (including genetic tissue) were collected from returning adult Chinook Salmon and Steelhead at Lower Granite Dam, Washington. This map was created using ArcGIS Desktop 10.6.1. Data sources included USGS Geographic Names Information System (GNIS) and US Census 2000 for towns, states and provinces, Idaho Department of Fish and Game (IDFG) and SteamNet for fish hatchery and dam locations, and USGS and IDFG 1:100,000 scale hydrography for stream data. Snake River subbasin data were derived from USGS Hydrologic Units.

215x279mm (300 x 300 DPI)
A conceptual model illustrating decomposition of adult Chinook Salmon (*Oncorhynchus tshawytscha*) and Steelhead (*O. mykiss*) sampled at Lower Granite Dam by rearing type. Fish were placed into one of three categories (natural-origin, adipose-intact hatchery, and hatchery) using a combination of physical marks, tags, and positive hits to a parentage-based tagging (PBT) baseline. Dorsal fin erosion was only used for steelhead (STHD). The box highlighted in red indicates the subset of returning adult fish that are adipose-intact and identified as hatchery-origin using PBT.
A) The number of adipose-intact adult Chinook Salmon (*Oncorhynchus tshawytscha*) and B) Steelhead (*O. mykiss*) sampled at Lower Granite Dam, Washington, that were identified as natural-origin, hatchery-origin using physical marks or tags (Mark/Tag), or hatchery-origin using parentage-based tagging (PBT).
A) The proportion of adipose-intact adult Chinook Salmon (*Oncorhynchus tshawytscha*) and B) Steelhead (*O. mykiss*) determined to be hatchery-origin based on coded wire tags or marks. Marks included fin clips (e.g., left ventral) in either Chinook Salmon or Steelhead and dorsal fin erosion in Steelhead only. The yellow bars are relatively high for Steelhead since dorsal fin erosion is a common mark to identify hatchery-origin fish for this species, but it is not an effective mark for Chinook Salmon.
Table 1. A list of fish hatcheries with spring/summer Chinook Salmon (CHNK) and Steelhead (STHD) broodstock sampled as part of the Snake River basin parentage-based tagging (PBT) program, estimated smolt releases for release years 2009-2015 (source: Regional Mark Information System (RMIS) database), PBT tag rates for spawn years 2008-2014, marks and tags used to identify releases. All facilities have been sampled for PBT annually since 2008, with the exception of Wallowa Fish Hatchery that began sampling 2009. * denotes stocking data was unavailable for 2011-2012 and ** denotes that not all broodstock in 2008, 2009, 2010 were sampled. Values in parentheses represent standard error among annual PBT tag rates. States are abbreviated as follows: ID = Idaho, OR = Oregon, WA = Washington.

| Species | Hatchery                        | State | Estimated smolt releases | PBT Tag rate | % Adipose clip only | % Adipose clip + CWT | % CWT only | % Unmarked, untagged |
|---------|---------------------------------|-------|--------------------------|--------------|---------------------|-----------------------|------------|---------------------|
| CHNK    | Clearwater Fish Hatchery        | ID    | 18,236,270               | 92.5 (4.2)   | 64.2                | 18.1                  | 12.5       | 5.2                 |
|         | Dworshak National Fish Hatchery | ID    | 16,540,425               | 98.3 (0.5)   | 86.3                | 9.3                   | 0.0        | 4.4                 |
|         | Lookingglass Fish Hatchery      | OR    | 7,825,548               | **65.5 (10.9)| 30.6                | 53.3                  | 10.9       | 5.2                 |
|         | Lyons Ferry Fish Hatchery       | WA    | 19,683,331              | 95.0 (1.4)   | 1.4                 | 40.8                  | 28.2       | 29.6                |
|         | McCall Fish Hatchery            | ID    | 7,963,158               | 98.4 (0.4)   | 69.5                | 14.4                  | 15.9       | 0.1                 |
|         | Nez Perce Tribal Fish Hatchery  | ID    | 21,240,334              | 97.4 (0.7)   | 1.2                 | 21.4                  | 53.0       | 24.5                |
|         | Pahsimeroi Fish Hatchery        | ID    | 7,491,780               | 98.6 (0.3)   | 73.8                | 16.8                  | 9.1        | 0.2                 |
|         | Rapid River Fish Hatchery       | ID    | 21,932,061              | 98.1 (0.6)   | 95.4                | 4.6                   | 0.0        | 0.0                 |
|         | Sawtooth Fish Hatchery          | ID    | 10,208,307              | 99.4 (0.4)   | 72.8                | 12.7                  | 14.2       | 0.3                 |
| STHD    | Dworshak National Fish Hatchery | ID    | 16,500,445              | 95.6 (2.1)   | 55.6                | 15.4                  | 14.7       | 14.3                |
|         | Lyons Ferry Fish Hatchery       | WA    | 1,512,089               | 98.0 (0.8)   | 75.4                | 23.1                  | 0.1        | 1.4                 |
|         | Oxbow Fish Hatchery             | OR    | 4,604,423               | 92.8 (1.3)   | 90.9                | 9.1                   | 0.0        | 0.0                 |
|         | Pahsimeroi Fish Hatchery        | ID    | 12,052,253              | 94.9 (2.3)   | 84.4                | 14.0                  | 0.0        | 1.7                 |
|         | Sawtooth Fish Hatchery          | ID    | 9,548,969               | 99.4 (0.2)   | 75.5                | 14.4                  | 0.0        | 10.1                |
|         | Wallowa Fish Hatchery           | OR    | *1,485,525              | 95.2 (1.7)   | 64.1                | 30.1                  | 2.3        | 3.5                 |
Table 2. The number of adipose-intact spring/summer Chinook Salmon (*Oncorhynchus tshawytscha*) and Steelhead (*O. mykiss*) sampled at Lower Granite Dam, Washington, for estimation of annual escapement. Genotypes of returning adults were compared to a parental baseline of hatchery broodstock to estimate source of origin (hatchery or natural) using parentage-based tagging (PBT). Additional sources of information to classify source of origin include coded wire tags (CWT) and ventral fin clips/dorsal fin erosion (Fin). The final column indicates the number of adipose fin intact Chinook Salmon and Steelhead that were determined to be natural-origin based on all possible marks.

| Species         | Spawn Year | Genotyped | PBT | CWT | Fin | Total # natural-origin fish |
|-----------------|------------|-----------|-----|-----|-----|----------------------------|
| Chinook Salmon  | 2014       | 4,514     | 667 | 428 | 5   | 3,414                      |
|                 | 2015       | 3,135     | 731 | 220 | 1   | 2,183                      |
|                 | 2016       | 4,530     | 907 | 543 | 1   | 3,079                      |
|                 | 2017       | 2,062     | 683 | 154 | 0   | 1,225                      |
|                 | 2018       | 2,270     | 255 | 515 | 1   | 1,499                      |
| Steelhead       | 2014       | 4,547     | 217 | 295 | 558 | 3,477                      |
|                 | 2015       | 4,808     | 247 | 303 | 296 | 3,962                      |
|                 | 2016       | 5,047     | 402 | 287 | 23  | 4,335                      |
|                 | 2017       | 4,576     | 800 | 441 | 273 | 3,062                      |
|                 | 2018       | 2,975     | 164 | 240 | 198 | 2,373                      |
**Table 3.** Model estimates of total escapement of natural-origin spring/summer Chinook Salmon (*Oncorhynchus tshawytscha*) and Steelhead (*O. mykiss*) entering the Snake River basin made with and without the application of PBT to determine source of origin among adipose-intact returning adults (outputs from SCOBI). Window counts represent the raw number of all adults passing the observation window at Lower Granite Dam. LCI and UCI correspond to lower and upper 90% confidence intervals on estimates of escapement. Escapement difference and the percent change columns display the inflated proportion of returning natural-origin adults without the use of PBT. Values in the escapement difference column marked with an asterisk represent years in which the 90% confidence intervals for escapement estimates with and without PBT were non-overlapping.

| Species          | Spawn Year | Window Count | Without PBT | With PBT | Escapement difference | Percent Change |
|------------------|------------|--------------|-------------|----------|-----------------------|----------------|
|                  |            |              | Escapement  | LCI      | UCI                   | LCI            | UCI            |               | Escapement difference | Percent Change |
| Chinook Salmon   | 2014       | 114,673      | 36,416      | 35,576   | 37,299                | 30,338         | 29,569         | 31,071        | 6,078*            | 16.7%            |
|                  | 2015       | 132,432      | 31,109      | 30,249   | 31,968                | 23,409         | 22,610         | 24,194        | 7,700*            | 24.8%            |
|                  | 2016       | 81,753       | 21,577      | 21,101   | 22,051                | 16,752         | 16,312         | 17,183        | 4,825*            | 22.4%            |
|                  | 2017       | 48,192       | 9,037       | 8,734    | 9,339                 | 5,793          | 5,537          | 6,043         | 3,244*            | 35.9%            |
|                  | 2018       | 42,232       | 8,647       | 8,344    | 8,953                 | 7,382          | 7,105          | 7,669         | 1,265*            | 14.6%            |
| Steelhead        | 2014       | 108,154      | 26,797      | 26,003   | 27,623                | 25,355         | 24,557         | 26,163        | 1,442             | 5.4%             |
|                  | 2015       | 165,591      | 48,691      | 47,637   | 49,725                | 45,789         | 44,753         | 46,816        | 2,902*            | 6.0%             |
|                  | 2016       | 136,150      | 36,985      | 36,258   | 37,739                | 33,936         | 33,221         | 34,657        | 3,049*            | 8.2%             |
|                  | 2017       | 101,826      | 19,668      | 19,209   | 20,136                | 15,576         | 15,171         | 15,991        | 4,092*            | 20.8%            |
|                  | 2018       | 74,097       | 11,484      | 11,154   | 11,832                | 10,717         | 10,387         | 11,052        | 767*              | 6.7%             |