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ARTICLE

Improving Abundance Estimates of Spring–Summer Snake River Chinook Salmon for Fisheries Management

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Abstract

The Columbia River basin is home to a run of spring–summer Chinook Salmon *Oncorhynchus tshawytscha* that returns to the Snake River drainage of Idaho, Oregon, and Washington in the Pacific Northwest. Historically, the run was one of the more productive throughout the Columbia River basin. However, Snake River spring–summer Chinook Salmon have experienced declines in abundance due to overfishing, habitat degradation, and dams. Several stocks are listed as threatened under the U.S. Endangered Species Act and are supported by mitigation hatcheries funded by Idaho Power Company, the Lower Snake River Compensation Plan, and the Bonneville Power Administration. To maximize tribal and state harvest of returning hatchery adults, minimize impacts on wild fish, and ensure that enough hatchery fish return to meet broodstock needs, careful fisheries management is required. Since 2008, managers have used hatchery adults, PIT-tagged as juveniles and detected at Lower Granite Dam, to generate adult abundance estimates. In season, these estimates inform state and tribal harvest shares and ensure that broodstock needs are met. Postseason, they provide smolt-to-adult survival and return rates. Since 2012, parentage-based tagging (PBT) has provided an alternative method to estimate stock- and age-specific returns at Lower Granite Dam, since returning hatchery adults sampled at Lower Granite Dam can be assigned to their parents. We compared stock-specific abundance estimates between PIT- and PBT-derived methodologies for return years 2016–2019. Across all years, PIT tag estimates accounted for 65% of the PBT-based estimates at Lower Granite Dam across all age-groups and release sites combined. This underrepresentation across all groups equated to 49,833 fish that were not accounted for in PIT tag abundance estimates. It is clear that PBT-based estimates should aide in-season harvest management and postseason run reconstruction to avoid the known bias of estimates from PIT tags, especially during years of low returns when increased accuracy is critical.

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The Columbia River basin in the Pacific Northwest of the United States spans 668,000 km^2 and supports five species of anadromous salmonids (Johnson et al. 2019), including Chinook Salmon *Oncorhynchus tshawytscha*. Prior to 1890, commercial salmon fishing in the Columbia River was dominated by spring–summer Chinook Salmon (spring–summer indicating timing of return to freshwater) and peaked in 1883 with 19.5 million kilograms caught (Fulton 1968). Construction of Grand Coulee and Chief Joseph dams on the upper Columbia River and the Lewiston Dam on the Clearwater River extirpated many spring–summer Chinook Salmon populations, making the Snake River in Oregon, Washington, and Idaho and its tributaries a major contributor to Columbia River basin spring–summer Chinook Salmon productivity. In fact, the Salmon River, a Snake River tributary, supported 44% of the entire Columbia River basin's spring–summer Chinook Salmon runs during the late 1950s (Fulton 1968; Felts et al. 2019; Johnson et al. 2019). However, precipitous declines in abundance were observed throughout the 1960s and 1970s, caused by a variety of anthropogenic activities (Craig and Hacker 1940).

Hatchery programs have a long history of use throughout the Columbia River basin to offset losses in fish production and impacts to downriver fisheries from the construction and operation of hydroelectric dams. In 1976, the U.S. Fish and Wildlife Service implemented the Lower Snake River Compensation Plan (LSRCP) to mitigate the loss of salmonid productivity from four dams built on the lower Snake River between 1962 and 1976 (USACOE 1983; Nemeth and Kiefer 1999). The LSRCP estimated the number of smolts that should be produced annually to offset the losses that resulted from dam construction and operation. Along with LSRCP-funded programs, additional spring–summer Chinook Salmon smolt production in Idaho is funded through Idaho Power Company (Table 1; Figure 1) as mitigation for the ongoing operation of the Hells Canyon Dam Complex (Brownlee, Oxbow, and Hells Canyon dams) on the Snake River. The Bonneville Power Administration provides funding for the LSRCP and through the Fish and Wildlife Program directed toward fish production.

Accurate abundance estimates are crucial for effective fisheries management. Fish-counting facilities operated at the hydroelectric dams on the Columbia and Lower Snake rivers are used to provide estimates of returning adult salmonids and steelhead *Oncorhynchus mykiss* (anadromous Rainbow Trout). However, for fisheries management and hatchery evaluation purposes in the Snake River basin, a simple counting of hatchery returns at Lower Granite Dam is insufficient because each hatchery has its own escapement goal and fisheries can be stock selective. Therefore, methods that assign adults back to their hatchery of origin are essential for stock-based management and evaluation.

One way of counting and tracing adult offspring back to their hatchery of origin is with passive integrated

TABLE 1. Smolt production and escapement goals per Chinook Salmon hatchery program in Idaho (source: USFWS 2009; Sullivan et al. 2018). COE, Core of Engineers; IDFG, Idaho Department of Fish and Game; IPC, Idaho Power Company; LSRCP, Lower Snake River Compensation Plan; NPT, Nez Perce Tribe; USFWS, U.S. Fish and Wildlife Service. An asterisk (*) indicates hatcheries that do not have escapement goals.

Hatchery	Funding source	Operation	Run timing	Production goal (millions)	Escapement goal	Release river	Site code
McCall	LSRCP	IDFG	Summer	1	8,000	South Fork Salmon	KNOXB
Sawtooth	LSRCP	IDFG	Spring	1.8	19,445	Upper Salmon	SAWT
	LSRCP	IDFG	Spring	1.8	19,445	Yankee Fork Salmon	YANKFK
Clearwater	LSRCP	IDFG	Spring–summer	2.535	11,900	Clear Creek	CLEARC
	LSRCP	IDFG	Spring–summer	2.535	11,900	North Fork Clearwater	CLWHNF
	LSRCP	IDFG	Spring–summer	2.535	11,900	Crooked	CROOKR
	LSRCP	IDFG	Spring–summer	2.535	11,900	Powell ponds	POWP
	LSRCP	IDFG	Spring–summer	2.535	11,900	Red	REDP
	LSRCP	IDFG	Spring–summer	2.535	11,900	Selway	SELWY1
Pahsimeroi	IPC	IDFG	Summer	1	*	Pahsimeroi	PAHP
Rapid River	IPC	IDFG	Spring	3	*	Rapid	RAPH
Kooskia	USFWS	USFWS/ NPT	Spring	0.6	*	Clear Creek	KOOS
Dworshak	LSRCP/COE	USFWS	Spring	1.05–1.65	9,135	North Fork Clearwater	DWORNF

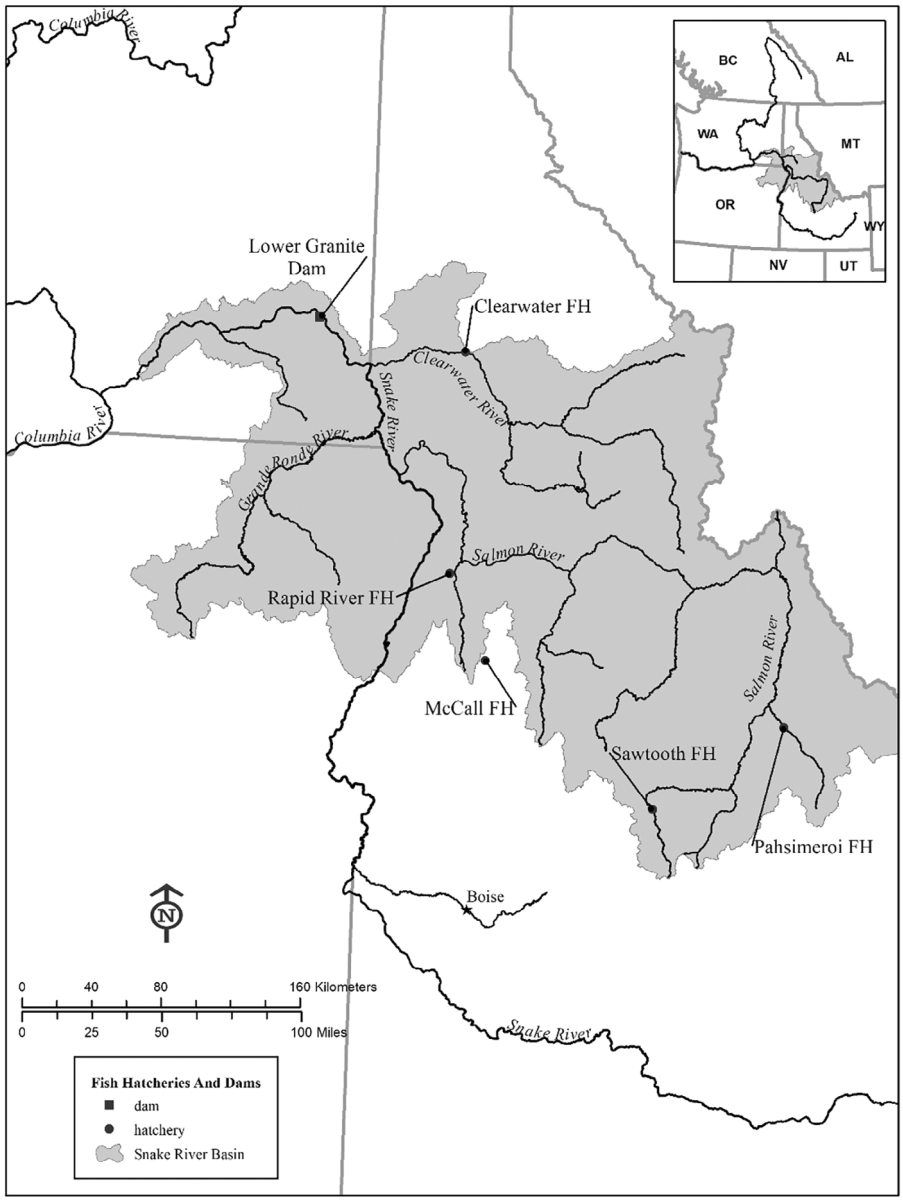

FIGURE 1. Locations of fish hatcheries in Idaho that produce spring–summer Chinook Salmon smolts; FH = fish hatchery.

transponder (PIT) tags. Since the early 1990s, state, federal, and tribal entities in the Snake River basin have inserted PIT tags into the body cavity of hatchery Chinook Salmon smolts to monitor juvenile outmigration and adult returns through the Snake River and Columbia River hydrosystem (Skalski 1998; Williams et al. 2005). At Lower Granite Dam, all returning wild and hatchery-origin anadromous fish pass through 22 PIT tag detectors installed throughout the fish ladder (Morrisett et al. 2019). Beginning in brood year 2006, the Idaho Department of Fish and Game (IDFG) began increasing the number of tagged hatchery spring–summer Chinook Salmon smolts to investigate the feasibility of estimating postseason adult returns and smolt-to-adult returns (SARs) by hatchery, release site, and age. Over time, PIT tag data has become useful for updating run projections, run status, and harvestable shares and for ensuring broodstock needs would be met. While it was assumed that PIT tags would provide robust abundance estimation, research within (Cassinelli and Rosenberger 2011) and outside (Knudsen et al. 2009) the Snake River basin indicated that returning PIT-tagged adult Chinook Salmon were producing underestimates of abundance seemingly due to PIT shedding or tagging related mortality.

Another method of tagging hatchery-origin fish is parentage-based tagging (PBT), first described in

Anderson and Garza (2005) as full parental genotyping, whereby hatchery broodstock are genotyped at a set of molecular markers (e.g., single nucleotide polymorphisms [SNPs]). Adult progeny of these broodstock are systematically trapped at Lower Granite Dam, where biological data and fin clips are collected from a subsample. Fin clips are genotyped for the same markers as the broodstock from all hatcheries and parentage is inferred based on the genotypes (Anderson and Garza 2006). Since 2008, all Chinook Salmon broodstock spawned in Idaho hatcheries have been genotyped for PBT analysis (Steele et al. 2013). Beginning in return year 2012, IDFG began investigating the utility of PBT sampling and assignments for estimating the abundance of spring–summer Chinook Salmon returning to hatcheries in the Snake River basin (Steele et al. 2019).

In this study, we compared spring–summer Chinook Salmon hatchery abundance estimates from PIT tag and PBT return data from years 2016–2019 and describe how estimates from these two data sources differ. These were the first years that we could expect to assign returning hatchery fish back to release groups via PBT, making comparison with the PIT-tag-based abundance estimates possible. Sufficient tracking data (which maternal parent contributed to which release group) was lacking in earlier years. We also provide recommendations for improving future management of this important resource.

METHODS

Passive integrated transponders.— The entire smolt production from each hatchery is divided and released at several different sites each year. Smolts are PIT-tagged during the fall, 4–6 months prior to release the following spring by experienced crews that travel to all anadromous fish hatcheries in Idaho to PIT-tag Chinook Salmon and steelhead. The smolts are approximately 30 fish per pound at the time of tagging. Posttagging, all Chinook Salmon mortalities collected by hatchery staff are scanned for PIT tags in order to adjust the actual tagging rate at release. At most fish hatcheries in Idaho, tags shed into raceways during the remainder of the rearing cycle cannot be recovered or enumerated. Each release group has its own PIT tag rate. Only a small proportion of smolts (an average of 3.8% in this study) from each hatchery release group are PIT-tagged. When these fish are detected as adults, an expansion rate is applied based on the abundance of their initial release group. This study included 2,211 PIT-tagged adult hatchery returns to Lower Granite Dam from 2016 to 2019, corresponding to migration years 2013–2018 from seven different Idaho hatcheries (https://www.ptagis.org/). All fish returning to Lower Granite Dam before August 18 (the first day of fall run) and with ocean ages (the number of years spent in the ocean) above 0 were included.

Parentage-based tagging.— Every adult fish that makes it upstream to Lower Granite Dam passes through the fish ladder equipped with a trap that is operational 5 d of the week from March through August 17, and 7 d a week until the trap closes in late November. Within this seasonal window, a systematic random sample of migrating fish, both tagged and untagged, is diverted into the trap where biological and genetic data are taken. A certain number of times per hour, both untagged and PIT-tagged fish are sampled (Ogden 2019), constituting the PBT trapping rate. Our PBT analysis focused on spring–summer Chinook Salmon adult returns sampled at Lower Granite Dam from 2016 to 2019 and parents of these fish, which were spawned in years 2011–2016. Prior to spawn year 2015, all tissue preservation, DNA extraction, and SNP genotyping of broodstock and adult returns were performed as in Steele et al. (2016). In subsequent years, we adopted the genotyping-in-thousands by sequencing (GTseq) technique developed by Campbell et al. (2015). Details of development and improvement of the SNP panels developed by Columbia River Inter-Tribal Fish Commission (CRITFC) and IDFG used in this study (CRITFC–IDFG Chinook Salmon 96 PBT v5.1 and CRITFC–IDFG Chinook GTseq v3.0 299) and accessing the data sets in the public database, FishGen.net (McCane et al. 2018), can be found in Hargrove et al. (2020b). The GTseq laboratory methods closely followed Campbell et al. (2015), except for the following modifications. In the second PCR step, we used New England Biolabs Hot Start *Taq* 2X Master Mix. In the bead size selection step, the washes were performed with 80% ethyl alcohol. The purified and size-selected libraries were eluted from the Ampure XP beads with 17 µL of TE buffer with 0.1 µM EDTA (low TE; Thermofisher). The libraries were then quantified using a Qubit High Sensitivity kit (Thermofisher) and diluted to 4 nM. Up to 50 libraries were combined and sequenced on the Illumina NextSeq 500 housed at Eagle Fish Genetics Lab. Depending on the number of libraries sequenced at a time, we used NextSeq 500/550 v2 high-output 75-cycle or NextSeq 500/550 v2 mid-output 150-cycle sequencing kits (Illumina). In either case, single end sequencing was performed for 79 cycles. Once libraries were sequenced, data were run through in-house quality control pipelines to ensure that there was no contamination, sample failure, or duplication and a random number of samples were rerun to ensure genotype calls match (Delomas et al. 2019). Genotypes of the 9,830 broodstock baseline and adult returns used in this analysis can be found at FishGen.net, data set ID #20210320. Adult returns were PBT-assigned to hatchery broodstock using SNPPIT (Anderson 2012) as described in Hargrove et al. (2020a) and assigned to their corresponding hatchery release group.

Abundance model.— The numbers of returning adults from each release group were estimated separately with

PIT tag data and with PBT data using Bayesian models. With the PIT tag data, fish were detected as returning adults in the adult fish ladder at Lower Granite Dam. The tag rate (calculated at the time of tagging) was considered known and detection efficiency at Lower Granite Dam was assumed to be 100% (Keefer et al. 2014). The number of tagged returning adults from a given release group was modeled as a binomial random variable, with success probability being the tagging rate and the number of trials being the total number of returning adults from that release group. A minimally informative prior for the log of the total number of returning adults was used: a normal distribution with mean 0 and variance of 10^3.

For the PBT data, our analysis was based on the model described by Delomas and Hess (2020) for hatchery-origin fish. Genotyping rates were calculated as the proportion of crosses with both parents successfully genotyped (Satterthwaite et al. 2015; Steele et al. 2019). Return years were divided into strata with a minimum of 50 genotyped fish and a minimum time duration of 1 week.

In Idaho hatcheries, approximately 85% of hatchery Chinook Salmon are released with their adipose fins clipped or removed for visual identification purposes (Belnap et al. 2021). However, some hatchery fish are misclipped or are intentionally left unclipped for management purposes. Because sampling rates differ between adipose-clipped (all hatchery origin) and adipose-unclipped (mostly wild origin) Chinook Salmon, the proportion of fish that had a clipped adipose fin was estimated per stratum. The number of trapped fish with clipped adipose fins was considered a binomial random variable with the number of trials equal to the total number of trapped fish per stratum and the success probability equal to the true proportion of fish with a clipped adipose fin. A minimally informative prior was used for the true proportion of fish with a clipped adipose fin: a beta(0.1, 0.1) distribution. The proportions of fish with clipped and unclipped adipose fins per stratum from each release group were then estimated separately to account for the differential subsampling and genotyping rates based on adipose fin status. The number of trapped fish per stratum from each release group was treated as a multinomial random variable with probabilities for each release group being the product of the true proportion per stratum represented by a release group and its tagging rate. A minimally informative prior for the true proportions was used: a Dirichlet distribution with pseudocounts of 0.1 for release groups that were observed in the given stratum and pseudocounts of 0 for release groups that were not observed in the given stratum. Strata were combined by multiplying the estimated proportions of the run made up by each release group and the window count for that time period and summed (Steinhorst et al. 2017; Delomas and Hess 2020). The daily window count data for Chinook Salmon at Lower Granite Dam from January 1 to August 16 for years 2016–2019 can be found on the Fish Passage Center Web site (Columbia Basin Fishery Agencies and Tribes 2019).

Both the PIT-tag-based and PBT-based abundance estimate models were specified in JAGS (Plummer 2003) and fit using the R package rjags. The Markov chain–Monte Carlo algorithm was run with a burn-in of 1,000 iterations followed by 20,000 iterations used for inference. Convergence was assessed by visually inspecting traces. The means of the posterior samples were taken as the point estimates. Because individual release groups as defined by PIT tags and PBT were only partially overlapping, estimates for release groups were summed into 72 pools that represented identical groups of fish (Supplemental Table 1 available in the online version of this article). Estimated numbers of returning adults in each pool were then compared between the two methods. Upper and lower 90% credible intervals were calculated for each abundance estimate across pools.

To further compare abundance estimates between the two tagging methods, we calculated the ratios of the smolt-to-adult survival estimates (quasi-SARs) from PIT tag data and PBT data from our 2013–2018 migration year cohorts by dividing our PIT-based and PBT-based abundance estimates per migration year by the total smolt release from that year. We included data from all six migration years, even though not all fish from those migration years had returned to Lower Granite Dam by the end of the 2019 season. Therefore, our quasi-SAR estimates are not analogous to SARs used by Bonneville Power Administration's Comparative Survival Study (Tuomikoski et al. 2009) and other fisheries agencies. These quasi-SARs are intended to compare our two methods within this restricted data set.

Parentage-based tagging rate validation.—Each PBT release group has its own expected tag rate, based on the sampling and genotyping success of the broodstock. The assignment success of the returning adults back to those release groups is the realized tag rate. If assignment success is lower than expected, the PBT tag rate is biased high, which would result in underestimates of abundance. To evaluate PBT tag accuracy, we used the maximum likelihood method in the R package fishCompTools (Delomas and Hess 2020) to estimate what proportion of the broodstock from hatcheries described in this study (spawn years 2016–2019) are offspring of previous years' broodstock.

RESULTS

Passive Integrated Transponders

All PIT-tagged adult hatchery spring–summer Chinook Salmon returns detected at Lower Granite Dam PIT arrays in years 2016–2019 were traced back to their respective release groups. The 2,211 Chinook Salmon used

for this study came from 136 different PIT release groups and seven hatcheries spanning years 2013–2018. Release years 2014 and 2016 yielded the most adult returns over the span of the study, owing to release groups from Rapid River, Clearwater, and McCall hatcheries.

Parentage-Based Tagging

A total of 39,187 adult Chinook Salmon were trapped at Lower Granite Dam in years 2016–2019 from the end of March to August 17, the cutoff date of the spring–summer run (Table 2). Of those, 19,260 were biologically sampled and successfully genotyped at 95–299 SNPs. These genotyped returns were compared with SNP genotype databases (baselines) of hatchery broodstock from previous years. Of the trapped and genotyped spring–summer Chinook Salmon, 7,466 did not assign to the PBT baseline and 1,964 did assign but belonged to groups not included in this study. This left 9,830 hatchery-origin, spring–summer Chinook Salmon that assigned back to PBT release groups from brood years 2011–2016 that were selected for this study. Additionally, PBT tag rates (proportion successfully genotyped) were very high, ranging from 0.94 to 1.00 (Supplemental Table 2).

Abundance Model

The models produced 72 comparisons (pools) between PIT-based abundances and PBT-based abundances per return year and 288 comparisons across all years. Figure 2 includes comparisons where the PBT-based abundance estimates were below 2,000 per return year to better visualize error bars and points above and below the diagonal line. Supplemental Figure 1 (available in the online version of this article) includes all comparisons per return year. When considering only the nonzero comparisons, 80.8% of the PBT-based estimates were higher than PIT-based estimates. In all years, the single pool with the largest abundance was from Rapid River release groups (Supplemental Figure 1; Supplemental Table 3). Rapid River hatchery was the top contributor to the PIT-tag-based abundance estimates in three of four adult return years, with Clearwater Hatchery the top contributor in return year 2018 (Figure 3A). In all return years considered for the PBT-based estimates, Rapid River hatchery fish were most abundant (Figure 3B).

The release groups represented in this study contained approximately 70.5 million smolts total (Supplemental Table 4). Across all migration years, the percentage of smolts that return as adults (quasi-SARs) from PBT-based estimates were 1.3–2 times higher than those calculated using PIT-tag-based estimates (Table 3). Note that in order to compare between PIT-tag-based and PBT-based estimates, it was necessary to use incomplete cohorts for four of the six migration years. Therefore, quasi-SARs reported do not necessarily reflect complete cohorts.

The relationship between the difference in PIT-tag-based and PBT-based abundance estimates and release group size in age-4 fish is shown in Supplemental Figure 2. We chose to limit this comparison to only age-4 fish because this is the age at which the majority of fish return and thus allows the most direct comparison between release group size and estimation differences. We expressed the difference between the two estimates as a proportion of the total smolt release size. The majority of the differences between PIT-tag-based and PBT-based abundance estimates were negative (PIT-tag-based estimate lower than PBT-based estimate) and almost all pools with larger PIT-tag-based estimated abundance had relatively small release group sizes.

TABLE 2. Numbers of spring–summer Chinook Salmon adult returns to Lower Granite Dam used in PBT analysis. Each year's returns were split into fish with the adipose fin clipped (LGRA) or unclipped (LGRU), with unclipped fish comprised of both wild and hatchery components. The "Ots" in the sample group names refers to *Oncorhynchus tshawytscha*, and the numbers, 16–19, refer to the year they were sampled (S). Other column headings are as follows: Trapped = the number of hatchery fish trapped at Lower Granite Dam, Genotyped = the subset of trapped fish that were subsampled and successfully genotyped, Sp-Su hatchery = subset of genotyped fish that were successfully assigned to spring–summer hatchery broodstock parents.

Sample group and total	Return year	Trapped	Genotyped	Sp-Su hatchery
OtsLGRA16S	2016	9,887	2,470	2,102
OtsLGRU16S	2016	4,529	4,476	994
OtsLGRA17S	2017	7,881	1,997	1,785
OtsLGRU17S	2017	2,062	2,055	542
OtsLGRA18S	2018	6,179	2,019	1,683
OtsLGRU18S	2018	2,270	2,259	475
OtsLGRA19S	2019	4,761	2,373	1,943
OtsLGRU19S	2019	1,618	1,611	306
Total		39,187	19,260	9,830

Parentage-Based Tagging Rate Validation

We estimated the proportion of broodstock that were parents of the adult returns from this study that successfully assigned to broodstock from previous years in our baseline in order to uncover a possible source of bias in PBT-based abundance estimates. The results from the PBT rate validation estimated that 1.7–2.9% of the hatchery broodstock were not accounted for through PBT tag rate expansion (Supplemental Table 5).

DISCUSSION

Our results demonstrate that PIT tags can underestimate hatchery Chinook Salmon abundance estimates, sometimes by a large margin. In 80% of 288 comparisons comprised of over 9,000 genotyped and 2,000 PIT-tagged

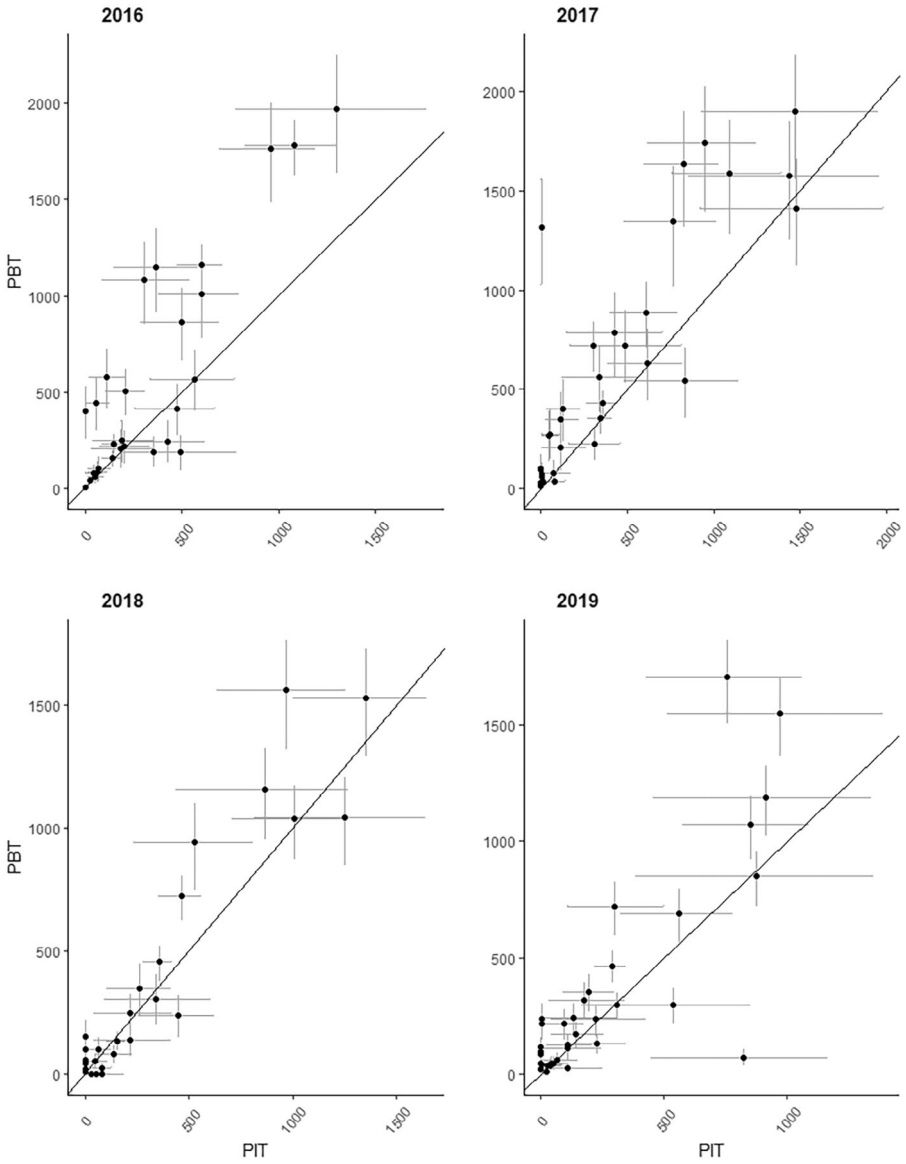

FIGURE 2. Comparisons of PIT-tagged-based abundance estimates and PBT-based estimates below 2,000 from the Bayesian model for hatchery spring–summer Chinook Salmon adult return years 2016–2019. Each point represents one pool of hatchery release groups of spring–summer Chinook Salmon and is a ratio of the PIT-based point estimate of the mean of the posterior sample (*x*-axes) to the PBT-based point estimate of the mean of the posterior sample (*y*-axes) from the Bayesian model. Upper and lower 90% credible intervals for both estimates are present on each point. The diagonal line through the origin represents equal PIT and PBT estimates. Only abundance estimate comparisons that were <2,000 are represented. See Supplemental Figure 1 for all comparisons per year.

adult returns over 4 years, PBT-based abundance estimates were larger than PIT-tag-based estimates. Previous observations of PIT-tagged returns, even before implementing PBT, were lower than expected in most return years, which would lead to a downward bias in abundances based on PIT tag counts. In 2012, the first year IDFG implemented PBT as a tool for Chinook Salmon abundance estimates, final PIT-tag-based abundance estimates were 88.7% of PBT-based estimates (Cassinelli et al. 2013). Since then, PIT-tag-based estimates have underestimated abundances of hatchery Chinook Salmon with respect to PBT-based estimates with a few exceptions. For release-specific abundance estimates of <1,000 individuals, PIT-tag-based estimates have been observed to both under- and overrepresent PBT-based estimates, though the magnitudes of overestimation are smaller (Supplemental Figure 2; Sullivan et al. 2018). In the current study, almost all instances where PIT-tag-based estimates were larger than PBT-based estimates were for small release groups. This suggests that they are the result of

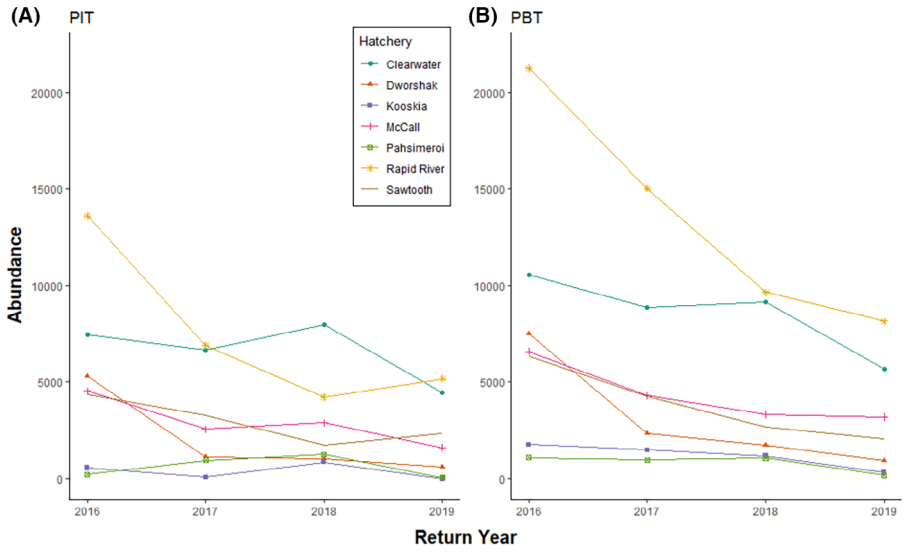

FIGURE 3. Graphs of **(A)** PIT-tag-based abundances and **(B)** PBT-based abundances from each hatchery per return year of spring–summer Chinook Salmon.

TABLE 3. Smolt-to-adult comparisons (quasi-SARs) per migration year between PIT-tag-based abundance estimates and PBT-based estimates.

Migration year	PIT abundance	PBT abundance	Smolt release	PIT SAR %	PBT SAR %	%PIT/PBT SAR
2013	4,417	5,895	10,192,863	0.0433	0.0578	74.9
2014	27,981	45,060	12,280,052	0.2279	0.4421	51.5
2015	18,175	31,856	10,845,267	0.1676	0.3125	53.6
2016	25,755	37,155	12,247,969	0.2103	0.3645	57.7
2017	12,713	17,532	11,725,144	0.1084	0.172	63.0
2018	2,830	4,208	13,239,652	0.0214	0.0413	51.8

sampling variation, which is larger for smaller populations as they have fewer PIT and PBT detections. Unfortunately, when populations are small, errors in abundance estimates have the potential for larger negative consequences, such as overharvest of an imperiled stock or premature fishery closures.

Uncertainty and errors in sampling and tag rates are what lead to inaccurate abundance estimates, but sources and magnitudes are different between the two methodologies. For PIT-tag-based methods, detection rates are at or near 100% because all fish passing through the ladder at Lower Granite Dam are interrogated by 22 PIT tag arrays regardless of whether they enter the adult trap. Keefer et al. (2014) reported a general detection efficiency of >99% at Lower Granite Dam, suggesting that PIT detector failure is not likely to affect abundance estimates. Since a small fraction of smolts from each hatchery release group receives PIT tags and the rate of tag loss is unknown, tagging rate uncertainty and sampling variation are the major sources of error in PIT-tag-based abundance estimates.

If PIT-tagged fish lose their tags at some point in their lives prior to Lower Granite Dam detection or are subject to increased mortality rates as compared with untagged fish, the estimates of abundance based on PIT-detected fish will tend to underrepresent the true return numbers. Previous studies indicate that PIT tag retention rates can vary widely. In PIT-tagged Atlantic Salmon *Salmo salar* kept in captivity, a high tag retention rate (91%) was observed over 1.5 years with no spawning activity (Foldvik and Kvingedal 2018). Tag insertion in the body cavity versus dorsal musculature in Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* and Rainbow Trout led to a 20% lower retention rate, and of those, a 30% reduction in tag retention in egg laying females (Mamer and Meyer 2016). In Idaho hatchery operations, PIT tags are inserted into the body cavities of smolts. Data from a double marking study conducted by the IDFG estimated the PIT tag shed rate for hatchery spring Chinook Salmon released from the Powell Satellite Facility on the Clearwater River to be 12.5% in those returning in 2009 and 30.6% in 2010 returns, though

sample sizes were small (Cassinelli and Rosenberger 2011).

In addition to tag shedding, PIT-tag-associated mortality can lead to subsequent underestimations of abundance. A study of captive Rainbow Trout over 2 years demonstrated a nearly 2% mortality above non-PIT-tagged fish in two of three raceways (Hill et al. 2006). In a larger-scale study on hatchery spring Chinook Salmon released into the wild over 5 years, the mortality of PIT-tagged fish was 4–33% (mean = 10%) higher than untagged fish (Knudsen et al. 2009). However, a study of PIT tag size and fish size influences on mortality in age-0 Chinook Salmon over 28 d resulted in survival rates of 97.8–100%, with no discernable influence of fish size at insertion or PIT tag size (Tiffan et al. 2015). Variability within and across release groups, sexes, and sizes makes measuring PIT tag retention rates and applying a correction to PIT tag abundance estimates time consuming and costly. During a preliminary assessment of our data, we attempted to model PIT tag loss with our data, but sample sizes were too small to produce meaningful estimates. However, using PBT to estimate abundance has provided a cost-effective solution.

Tagging rates for PBT have the potential to reach 100% if all broodstock spawned in a given spawn year are successfully genotyped and females are tracked from spawning to release. Often <100 SNPs are needed to trace offspring back to their hatchery of origin (Steele et al. 2019). However, tag rates of 100% are rarely realized due to inadvertently failing to sample all broodstock during spawning, poor sample preservation, and/or genotyping failures in the genetics lab. These are examples of known errors that are incorporated into tagging rates, which can still lead to accurate abundance estimates. However, if unknown errors are introduced into the abundance estimation process, this would lead to either over- or underestimation of abundances, depending on the error. For example, if genetic samples are not taken from broodstock during hatchery spawning, that would lead to an artificially inflated tag rate and an underestimation of abundance, if offspring from those parents return to Lower Granite Dam and are sampled. The PBT tag rate validation demonstrated that 1.7–2.9% of the hatchery broodstock were not offspring of previous years broodstock in Snake River basin hatcheries. We suggest that this discrepancy was due to occasional wild fish and/or out-of-basin strays used as broodstock across brood years 2016–2019 (Supplemental Table 5). If this suggestion is incorrect, and the slight discrepancy is due to error in the tag rates, it would imply that the PBT-based estimates underestimate true abundance by a few percent.

The vertical 90% credible interval bars in Figure 1 demonstrate uncertainty around PBT-based abundance estimates, but they are generally smaller than the horizontal intervals around the PIT-based abundance estimates. Nevertheless, given the high PBT rates in this study and in general, genotyping failures and undetected or unsampled broodstock rarely happen (Supplemental Table 2). This means that any error or bias in PBT tag rates will have a limited effect on the accuracy of the estimates.

Adjustments to PIT-tag-based abundance estimates using PBT assignments have influenced management decisions for sport and tribal fisheries in Idaho. Harvest share decisions are made yearly, based on projected escapement to Lower Granite Dam minus the broodstock need. The resulting harvestable surplus is split equally between the tribal and nontribal fisheries. Approximately midway through the adult migration at Lower Granite Dam, a PBT analysis is performed. Harvest shares may be adjusted depending on the disparity between the PIT and PBT estimates. In return year 2018, a midseason PBT adjustment more than doubled harvest opportunities to sport anglers and tribal fishers for the terminal fisheries on the Rapid River. That year the harvest share for the Rapid River stock, the largest contributor to Idaho harvest, increased from 537 to 1,374 (+128%) adult Chinook Salmon. Conversely, in return year 2019, the Rapid River fishery harvest share decreased for the first time as a result of the in-season PBT adjustment from 1,164 to 651 (−56%). This adjustment ensured that managers met broodstock collection goals.

The utility of PBT technology for addressing a multitude of conservation and management questions has been demonstrated in a variety of salmonid species in Idaho (Steele et al. 2013, 2019) and in additional species throughout the western United States and Canada (Evans et al. 2018; Beacham et al. 2019). Outside of the Pacific Northwest, feasibility studies of PBT have been conducted on varied species such as Florida Largemouth Bass *Micropterus floridanus* (Zhao et al. 2018) and greenlip abalone *Haliotis laevigata* in Australia (Arbon et al. 2021). Parentage-based tagging has been implemented in a Largemouth Bass *M. salmoides* hatchery system in North Carolina (Hargrove et al. 2022) as well. The advantages of PBT include reducing the handling of juveniles in hatchery before release, no tag shedding, and pedigree-based research beyond PBT (Steele et al. 2019). We encourage managers overseeing hatchery supplementation programs for other species, both inside and outside of North America, to consider the use of PBT technology when concerns related to tag shedding, tag-related mortality, or tag detection are suspected sources of bias.

Nevertheless, PIT tags are vital tools for a variety of estimates as well, such as conversion rates between dams, smolt survival during downstream migration, and travel time estimates of smolt migration (Sullivan et al. 2018). Furthermore, PIT tags are currently the only means of assessing release site- and age-specific abundance

throughout the migration season ("real time"), whereas the genotyping for PBT analysis currently occurs only midseason and at the end of season. Passive integrated transponder tag technology is an invaluable tool for managers to assess several metrics of fish abundance and population health, but unaccounted for error in abundance estimates based solely on PIT-tagged returns can lead to large underestimations of hatchery returns and smolt-to-adult returns (quasi-SARs in this study). Past program reviews have indicated that the LSRCP rarely has met spring–summer Chinook Salmon mitigation goals in the Snake River basin (ISRP 2011, 2014). The increased accuracy PBT provides to SARs estimates is crucial for effective management, especially for sustained, historically low runs. As such, we recommend that managers continue to use PBT analyses for estimating abundance and SARs of returning hatchery Chinook Salmon in the Snake River basin.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.