FEATURE

Parentage-Based Tagging: Reviewing the Implementation of a New Tool for an Old Problem

Craig A. Steele | Pacific States Marine Fisheries Commission, Eagle Fish Genetics Laboratory, 1800 Trout Road, Eagle, ID 83616. E-mail: craig.steele@idfg.idaho.gov

Maureen Hess | Columbia River Inter-Tribal Fish Commission, Portland, OR

Shawn Narum | Columbia River Inter-Tribal Fish Commission, Hagerman Fish Culture Experiment Station, Hagerman, ID

Matthew Campbell | Idaho Department of Fish and Game, Eagle Fish Genetics Laboratory, Eagle, ID

Juvenile Chinook Salmon *Oncorhynchus tshawytscha*.
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Parentage-based tagging (PBT), an innovative and large-scale application of genetic parentage assignments, is transforming how fisheries managers determine the age and origin of sampled fish. PBT is an efficient alternative for mass tagging and has been widely implemented in the Pacific Northwest. While still an emerging technology, PBT is being used to provide information to managers in state, federal, and tribal agencies on the harvest, research, and conservation of Chinook Salmon *Oncorhynchus tshawytscha* and steelhead *O. mykiss* in this region. We review the development of PBT in the Pacific Northwest focusing on the technical and logistical challenges for implementing a regional PBT program. We also showcase recent results and review management efforts that made use of PBT-derived data.

INTRODUCTION

Rarely does a technological approach come along that has the potential to simultaneously advance management, research, and conservation in fisheries. In the past decade a novel idea to genetically "tag" fish was formulated (Anderson and Garza 2006) and has been steadily adopted by fisheries managers in the Pacific Northwest to provide information at a level of detail and precision never before available. This emerging tool, parentage-based tagging (PBT), uses molecular-based approaches to conduct large-scale parentage assignments and has resulted in the unprecedented ability to genetically identify millions of hatchery-origin salmonids. This has in turn provided an opportunity to address a range of research and management questions that were impossible or impractical to achieve using traditional tagging approaches. Parentage analyses can be implemented for wild and natural-origin fish, but here we focus on applications of PBT for hatchery-origin salmonids, which are utilized extensively for fisheries management objectives.

The conception and implementation of PBT was initiated by an increased demand from fisheries managers for precise information on stock contributions to mixed-stock fisheries. Estimating stock composition often begins with the ability to determine the age and origin of a sampled fish and since the 1960s, this was largely achieved in Pacific salmonids using coded wire tags (CWTs; Jefferts et al. 1963). The combination of international agreements and a cooperative infrastructure allowed CWTs to provide essential information on the harvest of salmonid stocks throughout the Pacific Ocean and in terminal fisheries (Nandor et al. 2010). Originally, salmonids receiving a CWT in this region were also adipose-clipped, allowing the straightforward recovery of CWTs through the presence of a visible external mark for each fish with a CWT. By the 1990s, changes in marking policies resulted in adipose clipping of most hatchery-origin fish, regardless if they had a CWT or not. This allowed mark-selected fisheries to target hatchery-origin fish, but also hampered recovery of CWTs because many adipose-clipped fish had to be screened before a single CWT could be recovered. This frequently led to a limited number of CWT recoveries, which could not always meet the informational needs of managers who desired greater certainty of exploitation rates and stock composition at more and finer levels of resolution. A review of the CWT technology in Pacific Salmon *Oncorhynchus* spp. recognized the integral information provided by CWTs, but recommended evaluating alternative methodologies that could provide equivalent information without the drawback of limited tag recoveries (PSC 2005). One feasible alternative identified was PBT, but until recently empirical demonstrations of the approach were lacking.

The principles of PBT are founded on utilizing molecular-based parentage assignments as a large-scale tagging methodology. Parentage assignment is a common genetic tool used in fisheries for examining dispersal (e.g., Planes et al. 2009), supplementation (e.g., Denson et al. 2012), and introgression (e.g., Muhlfeld et al. 2009), but the idea of implementing a parentage-based approach as a large-scale tagging methodology at salmonid hatcheries was only recently envisioned (Anderson and Garza 2006). The ability to handle all fish used for hatchery broodstock (i.e., parents) permits the ability to achieve nearly 100% PBT-tag rates for their offspring. Specifically, when broodstock are handled for artificial spawning at a hatchery a small sample of fin tissue is collected from each individual. Individual tissue samples are genotyped and compiled to create a database of parental genotypes for each hatchery on an annual basis. The genotyping of broodstock essentially "tags" all of their offspring through their DNA. A non-lethal tissue sample from these offspring can be genetically characterized (i.e., tag recovery), and parentage analysis can be completed to assign an offspring to its parents, thereby identifying hatchery stock-of-origin and age of the sampled offspring. Some of the issues associated with physical tags (e.g., tag loss, lethal sampling at recovery, and differential mortality of tagged fish) are eliminated or minimized when PBT is applied as a tagging strategy. An individual carries its genetic tag in its DNA, therefore tag loss only occurs if genotypes fail to be collected in the lab. In addition, these genetic tags can be recovered non-lethally at any life stage by taking a small fin clip, and differential mortality between tagged and untagged fish is eliminated because PBT does not require handling of juveniles before they are released from the hatchery. Furthermore, PBT programs provide valuable research opportunities that physical tags cannot. By tracing individuals back to their parents, PBT opens opportunities for pedigree-based research including evaluation of reproductive success and estimation of heritability for various phenotypic traits.

The feasibility of implementing a regional PBT program was tested in the Snake River basin of Idaho, Oregon, and Washington beginning in 2008 (Steele et al. 2013). Since this time it has been adopted as a primary tool by several management agencies for monitoring stock composition of hatchery-origin steelhead *Oncorhynchus mykiss* and Chinook Salmon *O. tshawytscha* in fisheries and escapements (e.g., Hess et al. 2016a). Implementation of a regional PBT program presented several challenges. Collection and analysis of datasets of such magnitude required development of new molecular markers, genotyping techniques, and analytical approaches. Overcoming these hurdles resulted in laying the foundation for a genetic tagging program that has since scaled up beyond its original application in the Snake River basin. Here we review the development, implementation, and application of PBT for fisheries management of salmonids in the Pacific Northwest.

DEVELOPMENT OF PBT—TOOLS AND TECHNIQUES

Molecular Markers

In order for PBT to become a functional tool, several technological complexities had to be resolved. The first was the identification of molecular markers with enough genetic variation to provide accurate parentage assignment even when

thousands of potential parents from different populations across multiple spawn years were analyzed simultaneously. While the characteristics of microsatellites make them well suited for parentage studies (Webster and Reichart 2005), regional implementation of PBT in the Columbia River basin required multiple independent laboratories to annually genotype tens of thousands of samples at the same suite of loci and necessitated the use of a different class of marker. For this reason, SNPs (single nucleotide polymorphisms) were adopted as the marker of choice because they can be screened quickly on genotyping platforms, are easily standardized among laboratories, and have a low genotyping error rate (Morin et al. 2004). SNP discovery efforts have now advanced significantly with the use of restriction associated DNA sequencing technology, which can routinely yield thousands of new SNP loci (Baird et al. 2008; Davey et al. 2011). Studies consistently show that accurate parentage analysis can be conducted with <100 SNPs (Hayes et al. 2005; Anderson and Garza 2006; Hauser et al. 2011; Steele et al. 2013), even when thousands of potential parents across multiple populations are considered. For these reasons, a panel of 95 SNPs was originally adopted for implementation of PBT in steelhead and Chinook Salmon within the Snake River basin (Steele et al. 2011). As implementation of PBT expanded from the Snake River to the Columbia River basin, more SNPs were incorporated to represent variation in the entire range of these hatchery populations. The set of molecular markers used in the current Columbia-basin-wide panel contains 379 SNPs for steelhead and 298 SNPs for Chinook Salmon (Hasselman et al. 2018). Additionally, sex markers based on Y-chromosome sequences (Brunelli et al. 2008) are included for each species in these genotyping panels allowing for confirmation or correction of the phenotypic sex based on the genetic assay. This suite of markers is also integrated into regional Genetic Stock Identification programs that use molecular methods to determine the population of origin for natural-origin fish. The concurrent use of markers for PBT and Genetic Stock Identification applications can achieve complete and accurate stock-specific information for both hatchery- and natural-origin fish (e.g., Hess et al. 2016a, 2016b, 2016c; Beacham et al. 2017, 2018).

Genotyping

The second requirement for PBT to become a functional tool was the development of a cost-efficient genotyping platform. Implementing PBT in the Columbia River basin for Chinook Salmon and steelhead requires approximately 50,000 broodstock fish to be processed annually. Additionally, tens of thousands of samples from offspring are also processed annually by management agencies for analysis and monitoring of various fisheries, escapements, and research studies. Processing this volume of samples required a cost-efficient approach for genotyping. Custom protocols developed for the Illumina® next-generation sequencing platform (Campbell et al. 2015) now provide a low-cost alternative by sequencing SNP loci directly for thousands of individuals at hundreds of SNPs in a single run. This new genotyping approach, called Genotyping-in-Thousands (GT-Seq; Campbell et al. 2015), opened the possibility for agency laboratories to increase their genotyping throughput while minimizing costs on consumable lab supplies. Other high-throughput technologies (e.g., AmpliSeq™ by Ion Torrent) are in use for PBT programs in Canada (Beacham et al. 2017) but GT-Seq has largely been adopted by state, tribal, and academic laboratories processing PBT samples.

Sampling Broodstock

The large number of broodstock samples collected annually also required implementing timesaving approaches for tissue collection and space-saving approaches for tissue storage. Storing tissue in ethanol-filled vials can be relied upon to ensure high-quality DNA, even when stored for long periods of time and evaporation is limited. However, using ethanol-filled vials for large-scale sampling has some challenges. Relying upon vials requires shipping bulky packages, complying with federal regulations for shipping flammable material, and meeting governmental purchasing requirements for alcohol. Archiving tissue in ethanol-filled vials also quickly exhausts storage space, necessitates monitoring of ethanol evaporation, and creates a fire hazard. PBT sampling in the Columbia River basin has since transitioned to an alternative dry storage method that uses absorptive paper to preserve and store samples (LaHood et al. 2008). This method simply requires that fresh tissue from a fin clip is placed on or between sheets of absorptive chromatography paper (Figure 1). One sheet can hold 50–100 samples and occupies considerably less space than an equivalent number of ethanol-filled vials. Once

Figure 1. PBT samples from broodstock are taken as fin clips and placed onto a sheet of Whatman chromatography paper (above). A video demonstrating PBT sampling using the paper is available at https://vimeo.com/134454598. At the lab, the samples are punched with a biopsy tool that removes a small portion for DNA extraction (below). This format of DNA collection significantly reduces storage space of samples and time spent on processing samples.

allowed to dry completely, tissues mounted on the paper yield high-quality DNA and significantly reduce processing timing for sample inventory and DNA extraction. PBT samples are archived by vacuum sealing a single or up to dozens of sheets of paper together to prevent damage from moisture, insects, or rodents.

Tracking Families

Depending upon objectives, researchers and managers may wish to assign offspring back to a particular hatchery, a specific release site, or an experimental group. Associating parentage assignment with a release group is straightforward if all progeny for that parental cross were released at the same site. However, dividing progeny produced from a single or multiple families into groups destined for different release sites can reduce the ability to determine an offspring's release site even though it can still be assigned to its parents. In applications where release site information is necessary, adopting PBT often requires a tracking plan to be in place for each family group to prevent mixing of groups destined for different release sites (Figure 2). Whether PBT can serve as an efficient method of tagging for release-site-specific projects depends on the ability of the hatchery to devise a tracking system for family groups from spawning through rearing to release. The extent to which hatcheries must make organizational and infrastructural changes to accommodate tagging with PBT will depend on existing infrastructure, the number of different stocks reared, and the number or complexity of release groups. Through careful planning, the feasibility of tracking discrete PBT-marked groups from eyed egg through smolt release within existing hatchery infrastructure has been demonstrated by at least one state agency (Idaho Department of Fish and Game [IDFG]). To maintain segregation of PBT families, IDFG staff developed loading plans in advance for each stage of the production cycle, working backwards from PBT-specific release sites through raceway loading, adipose fin clipping, vat loading, and egg transfers to the initial spawning of broodstock (Satterthwaite et al. 2015). Even if infrastructure precludes tracking to release site, PBT is still a potentially useful approach. A good example of this situation is the Fall Chinook Salmon program at Lyons Ferry Hatchery in Washington State where tracking is limited by the number and design of rearing facilities. Regardless, PBT is still used to provide information on the proportion of hatchery-origin spawners, adult escapement, estimated proportion of natural-origin broodstock, and age composition of broodstock (Young et al. 2017).

Genetic Tag Rates

Determining a tagging rate for physical tags is usually straightforward and is calculated as the proportion of offspring tagged, but determining the genetic tag rate is different because the parental broodstock, not the progeny, are used to calculate this rate for PBT. If all parents are sampled and all broodstock samples are successfully genotyped, then their progeny are 100% tagged (e.g., all offspring can be assigned back to their parents). The failure to sample or genotype a spawned parent reduces the overall genetic tagging rate. Tagging rates that are < 100% are not problematic for conducting PBT and can be estimated as the proportion of successfully genotyped crosses (e.g., crosses in which both parents were genotyped; Satterthwaite et al. 2015). On average, PBT genetically tags 96.0% of Chinook Salmon smolts and 94.8% of steelhead smolts at facilities in Idaho, Oregon, and Washington where it is implemented (FishGen.net). For comparison, the average tag rate over the past 10 years (2008–2017) for CWTs in those same states was 36.2% for Chinook Salmon and 30.3% for steelhead (RMIS; rmpc.org).

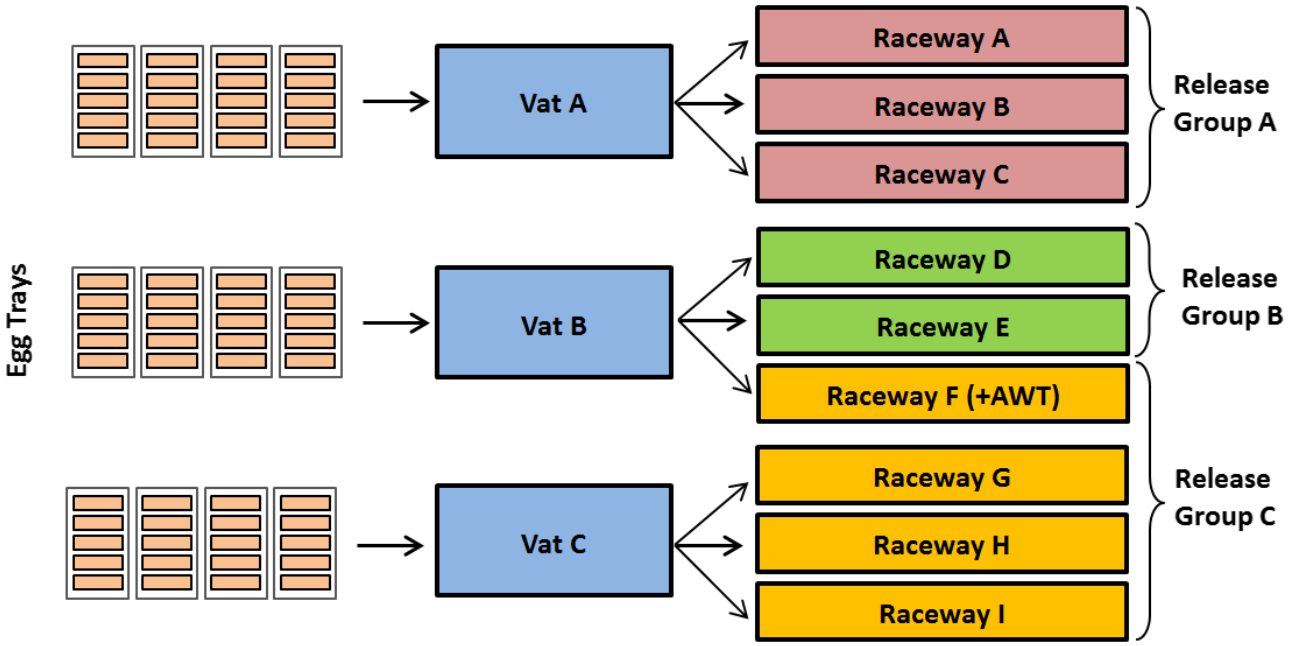

Figure 2. Schematic of a hypothetical loading plan for hatchery fish tagged with parental-based tags. Parentage assignments for fish in release group A can all be assigned back to parents that contributed to this single release location, which is the ideal scenario. Fish in release group B can be assigned to parents that contributed to two release groups (B and C) making it impossible to know if a sampled offspring was part of release group B or C. This can be remedied by applying a differential mark or a blank coded wire tag (e.g., agency wire tag [AWT]) to the offspring in raceway F, thereby allowing release site to be determined for all progeny.

PBT currently requires a sample from both parents but the possibility of conducting PBT using single-parentage assignments is being considered. Implementing single-parentage analysis would require the development of analytical tools with rapid computational speed and genotyping of a requisite number of loci with high exclusionary power (it is hypothesized that 200 to 500 SNP loci may be adequate [Satterthwaite et al. 2015]), but this would increase genetic tagging rates that consistently approach 100% because only one of the two parents in each cross would need to be genotyped.

Analysis

An early hurdle for implementing PBT was the development of the analytical ability to efficiently conduct parentage analyses with large-scale datasets. Previously available likelihood-based analysis methods could not efficiently handle datasets when parental genotypes numbered in the tens of thousands and simpler Mendelian incompatibility-based methods required overly large numbers of markers to be accurate (Anderson and Garza 2006). The program SNPPIT was developed to make improvements upon existing likelihood-based methods and introduces several novel computational approaches for parentage assignment with SNPs (Anderson 2010).

Data Storage

The final condition for making PBT a functional tagging tool was to make parental genotypes publicly available so that any laboratory or agency can access the data for assigning parentage to their own samples. A genetic data repository (FishGen.net) was designed to house SNP and microsatellite data and may also be used to house any finalized datasets used in publications (McCane et al. 2018). Researchers interested in sampling fish tagged with PBT will need to genotype their samples at the same loci as the parents, but can then compare their data to those in the publically available parental database. This online database is freely accessible and serves as a central repository of parental broodstock genotypes for steelhead and Chinook Salmon PBT projects in the Columbia River basin and potentially across their geographic range.

IMPLEMENTATION OF PBT—BASELINES AND RECOVERIES

Baselines

Implementing PBT is essentially a two-step process. The first step is the sampling and genotyping of parental broodstock, which can be thought of as the tagging stage (i.e., genotyping the parents tags their offspring). The final assemblage of parental genotypes is commonly referred to as a PBT baseline. Creating a PBT baseline is critical because without these parental genotypes the recovery of a PBT tag cannot occur. Thus, much emphasis has been placed on the complete and consistent collection of genetic samples from hatchery broodstock. The early implementation of PBT in the Snake River basin achieved coverage with the annual sampling of broodstock at a handful of steelhead and Chinook Salmon spawning facilities. Sampling at hatcheries was expanded as PBT gained momentum and baselines are now available for most Chinook Salmon and steelhead hatcheries in the Columbia River basin (Figure 3; Tables 1 and 2). Current efforts are underway to ensure all hatcheries in the region are sampled so that a complete PBT baseline for the entire Columbia River basin will be available. PBT baselines for Chinook Salmon and steelhead are expanding beyond the Columbia River basin and efforts lead by state and tribal agencies are being made to coordinate broodstock sampling at hatcheries in the Puget Sound in

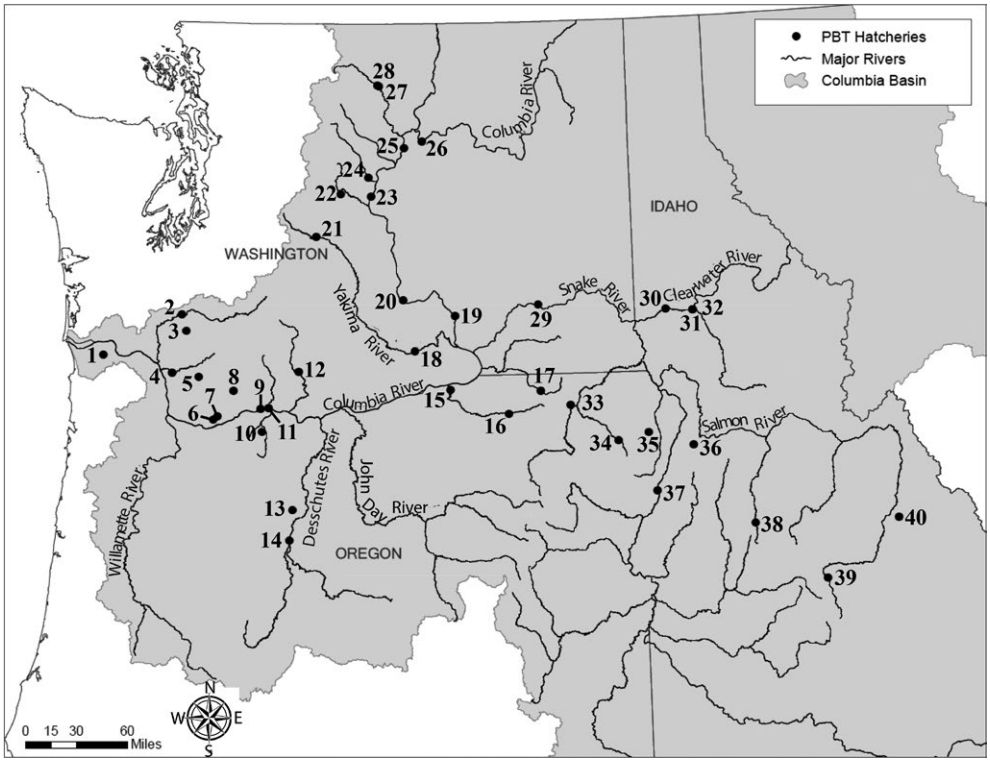

Figure 3. Locations of hatcheries in the Columbia River basin that are participating in sampling of Chinook Salmon and/or steelhead broodstock for parental-based tagging (PBT). Numbered locations correspond to identifiers in Tables 1 and 2.

Table 1. Hatcheries participating in sampling of Chinook Salmon broodstock for parental-based tagging. Sampling began in 2008 with spring/summer Chinook in the Snake River basin and has expanded to most hatcheries in the Columbia River basin.

Hatchery/facility broodstock	Map num.	Run type	Year									
			2008	2009	2010	2011	2012	2013	2014	2015	2016	2017
Clearwater Fish Hatchery	32	Spring	X	X	X	X	X	X	X	X	X	X
Clearwater Fish Hatchery (Powell Facility)	32	Spring	X	X	X	X	X	X	X	X	X	X
Dworshak National Fish Hatchery	31	Spring	X	X	X	X	X	X	X	X	X	X
Lookingglass Fish Hatchery—Catherine Creek stock	33	Spring/summer	X	X	X	X	X	X	X	X	X	X
Lookingglass Fish Hatchery—Grande Ronde River stock	33	Spring	X	X	X	X	X	X	X	X	X	X
Lookingglass Fish Hatchery—Imnaha River stock	33	Spring/summer	X	X	X	X	X	X	X	X	X	X
Lookingglass Fish Hatchery—Looking-glass Creek stock	33	Spring	X	X	X	X	X	X	X	X	X	X
Lookingglass Fish Hatchery—Lostine River stock	33	Spring	X	X	X	X	X	X	X	X	X	X
Lyons Ferry Fish Hatchery	29	Spring	*	*	*	*	X	X	X	X	X	X
Lyons Ferry Fish Hatchery—Tucannon River stock	29	Spring	X	X	X	X	X	X	X	X	X	X
Lyons Ferry Fish Hatchery	29	Fall	*	*	*	X	X	X	X	X	X	X
McCall Fish Hatchery—Johnson Creek stock	38	Spring/summer	X	X	X	X	X	X	X	X	X	X
McCall Fish Hatchery	38	Spring	X	X	X	X	X	X	X	X	X	X
Nez Perce Tribal Fish Hatchery	30	Fall	*	*	*	X	X	X	X	X	X	X
Nez Perce Tribal Fish Hatchery	30	Spring	X	X	X	X	X	X	X	X	X	X
Pahsimeroi Fish Hatchery	40	Spring	X	X	X	X	X	X	X	X	X	X
Rapid River Fish Hatchery	36	Spring	X	X	X	X	X	X	X	X	X	X
Sawtooth Fish Hatchery	39	Spring	X	X	X	X	X	X	X	X	X	X
Big Creek Hatchery	1	Fall	*	*	*	*	*	*	*	X	X	X
Carson National Fish Hatchery	8	Spring	*	*	*	*	X	X	X	X	X	X
Chief Joseph Hatchery	26	Spring	*	*	*	*	*	*	X	X	X	X
Chief Joseph Hatchery (Integrated)	26	Summer	*	*	*	*	*	X	X	X	X	X
Chief Joseph Hatchery (Segregated)	26	Summer	*	*	*	*	*	X	X	X	X	X
Cowlitz Salmon Hatchery	2	Spring	*	*	*	*	*	*	*	**	**	**
Cowlitz Salmon Hatchery	2	Fall	*	*	*	*	*	*	*	**	**	**
Eastbank Fish Hatchery	23	Spring	*	*	*	*	*	X	X	X	X	X
Eastbank Fish Hatchery	23	Summer	*	*	*	*	X	X	X	X	X	X
Entiat National Fish Hatchery	24	Summer	*	*	*	*	*	X	X	X	X	X
Kalama Falls Fish Hatchery	4	Spring	*	*	*	*	*	*	*	**	**	**
Kalama Falls Fish Hatchery	4	Fall	*	*	*	*	*	*	*	**	**	**
Klickitat State Fish Hatchery	12	Spring	X	X	X	X	X	X	X	X	X	X
Leavenworth National Fish Hatchery	22	Spring	*	*	*	*	*	X	X	X	X	X
Speelyai Hatchery	5	Spring	*	*	*	*	*	*	*	**	**	**
Little White Salmon National Fish Hatchery	9	Fall	*	*	*	*	*	X	X	X	X	X
Little White Salmon National Fish Hatchery	9	Spring	*	*	*	*	*	X	X	X	X	X
Methow State Fish Hatchery	27	Spring	*	*	*	*	X	X	X	X	X	X
Parkdale Fish Facility	10	Spring	*	*	*	*	X	X	X	X	X	X
Priest Rapids Hatchery	20	Fall	*	*	*	*	X	X	X	X	X	X
Round Butte Fish Hatchery	14	Spring	*	*	*	*	X	X	X	X	X	X
Ringold Springs State Hatchery	19	Fall	NA	NA	NA	NA	NA	NA	NA	NA	X	X

(Continues)

Table 1. (Continued)

Hatchery/facility broodstock	Map num.	Run type	Year									
			2008	2009	2010	2011	2012	2013	2014	2015	2016	2017
Spring Creek National Fish Hatchery	11	Fall	*	*	*	*	*	*	*	X	X	X
North Toutle Hatchery	3	Fall	*	*	*	*	*	*	*	**	**	**
Three Mile Falls Dam, Umatilla River[a]	15	Fall	*	*	*	*	X	X	X	~	~	~
South Fork Walla Walla Facility	17	Spring	*	*	*	*	X	X	X	X	X	X
Washougal Hatchery	6	Fall	*	*	*	*	*	*	*	**	**	**
Warm Springs National Fish Hatchery[b]	13	Spring	*	*	*	*	X	X	X	~	~	~
Wells Fish Hatchery	25	Summer	*	*	*	*	X	X	X	X	X	X
Winthrop National Fish Hatchery	28	Spring	*	*	*	*	*	X	X	X	X	X
Yakima Nation Prosser Hatchery	18	Fall	*	*	*	*	X	X	*	X	X	X
Levi George/Cle Elum (Integrated)	21	Spring	*	*	*	*	X	X	X	X	X	X
Levi George/Cle Elum (Segregated)	21	Spring	*	*	*	*	X	X	X	X	X	X

X: Broodstock genotyped; ~: Chinook broodstock sampled/spawned at another hatchery and genotyped; *: Broodstock not sampled; **: Broodstock sampled, tissues archived until funding identified for processing; NA: Stock discontinued/non-existent.

[a]Spawned at Little White Salmon Hatchery in 2015–2016 and at Ringold Springs in 2017.

[b]Spawned at Little White Salmon Hatchery starting in 2015.

the state of Washington and along the West Coast. The establishment of a PBT program in Canada has also begun and baselines for Coho Salmon *O. Kisutch* (Beacham et al. 2017) and Chinook Salmon (Beacham et al. 2018) at many hatcheries in British Columbia are also available. The effort to coordinate annual sampling and genotyping of all broodstock at these facilities is not insignificant and these responsibilities are largely covered by state, provincial, and tribal genetics labs in the region that work collaboratively to select informative molecular markers, genotype broodstock, and distribute the resulting baselines.

Recoveries

The second step of the two-step process is recovery of the PBT tag by sampling, genotyping, and assigning an offspring back to its specific parents in the broodstock. The recovery of these tags can occur as soon as the offspring can be sampled. In order to conduct parentage analysis, the offspring must be genotyped using the same molecular markers as the adults. Most evaluations and analysis of offspring involve some collaborative interaction with one of the regional genetic labs associated with a fisheries management agency to ensure concordant data are generated and standardized analyses are conducted.

A variety of research and monitoring projects are already underway that sample offspring tagged with PBT from the Columbia River basin. Juveniles are sampled at screwtraps, bypass facilities at dams, or from trawls to estimate timing of outmigration and evaluate differences in survival. Returning adults are sampled along their migration routes at fish passage facilities at dams and at terminal fisheries in order to determine stock-specific run timings and monitor stock compositions of harvest. Hatchery-origin adults are even sampled as carcasses on the spawning ground to estimate hatchery influence on wild populations. Ultimately, the adult offspring are sampled as broodstock at their facility of origin and genotyped to tag the next generation. This final sampling opportunity can be used to estimate stray rates between facilities, relative reproductive success of family groups, and heritability of physical traits.

APPLICATIONS—PBT IN FISHERIES MANAGEMENT

Since its introduction, PBT sampling of hatchery broodstock has been implemented for steelhead, as well as Chinook, Coho, and Sockeye Salmon *O. nerka* in California, Idaho, Oregon, Washington, and British Columbia. We have chosen to showcase a series of studies that make use of PBT for steelhead originating from the Snake River basin in the Pacific Northwest of the United States. This region was the first to adopt the technology in 2008 to supplement, and in some cases, replace the existing CWT program to interrogate mixed stocks for a variety of research and management purposes. We provide examples of six projects that originate from state, federal, and tribal agencies positioned to utilize PBT. Details of sampling methodology, results and interpretation can be found in the respective citations. The studies we reference share a common theme in that they all took samples from adult hatchery steelhead, which returned to the Columbia River basin in 2012/2013. This group of returning adults comprised 3-, 4-, and 5-year-old fish that were produced as offspring from spawn years 2010, 2009, and 2008, respectively, thereby providing the first PBT assignments for all cohorts present in a migration returning from the ocean. This returning group of fish was independently and non-lethally sampled by various researchers and managers in multiple major sport and tribal fisheries, at several dams, and in a study on the use of a thermal refuge during migration (Figure 4; Hess et al. 2016c). A review of these studies makes it apparent that PBT not only excels at its original purpose of estimating contributions of various hatchery stocks in mixed-stock assemblages, but also allows a variety of research questions to be investigated.

There is not a large steelhead fishery in the marine environment, thus no effort was made to sample this group of adults while in the ocean. However, once these hatchery-origin steelhead entered freshwater they encountered a number of fisheries. The first was a sport fishery in the lower Columbia River (Figure 4A) where over two-thirds of the harvest was attributed to stocks tagged with PBT (Byrne et al. 2014b). Next, the returning adults passed over Bonneville Dam where they were sampled to assess stock escapement into the Columbia

Table 2. Hatcheries participating in sampling of steelhead broodstock for parental-based tagging. Sampling began in 2008 in the Snake River basin and has expanded to most hatcheries in the Columbia River basin.

Hatchery/facility broodstock	Map num.	Run type	Year									
			2008	2009	2010	2011	2012	2013	2014	2015	2016	2017
Dworshak National Fish Hatchery	31	Unknown	X	X	X	X	X	X	X	X	X	X
Little Sheep Creek Facility	35	Summer	X	X	X	X	X	X	X	X	X	X
Lyons Ferry Fish Hatchery—Touchet River stock	29	Summer	*	X	X	X	X	X	X	X	X	X
Lyons Ferry Fish Hatchery[a]	29	Unknown	*	X	X	X	X	NA	NA	NA	NA	NA
Lyons Ferry Fish Hatchery—Grande Ronde River stock	29	Summer	X	X	X	X	X	X	X	X	X	X
Lyons Ferry Fish Hatchery—Tucannon River stock	29	Summer	*	X	X	X	X	X	X	X	X	X
Lyons Ferry Fish Hatchery—Wallowa stock	29	Summer	*	*	*	*	*	*	*	X	X	X
Oxbow Fish Hatchery	37	Summer	X	X	X	X	X	X	X	X	X	X
Sawtooth Fish Hatchery	39	Summer	X	X	X	X	X	X	X	X	X	X
Sawtooth Fish Hatchery—East Fork Salmon River stock	39	Summer	X	X	X	X	X	X	X	X	X	X
Sawtooth Fish Hatchery—Squaw Creek stock[b]	39	Summer	X	X	X	X	X	X	X	X	X	X
Pahsimeroi Fish Hatchery	40	Unknown	X	X	X	X	X	X	X	X	X	X
Wallowa Fish Hatchery	34	Summer	*	X	X	X	X	X	X	X	X	X
Eastbank Hatchery	23	Summer	*	*	*	*	X	X	X	X	X	X
Methow Hatchery (Twisp)[c]	27	Summer	*	*	*	*	*	X	X	X	X	~
Parkdale Fish Facility	10	Winter	*	*	*	*	X	X	X	X	X	X
Round Butte Fish Hatchery	14	Summer	*	*	*	*	*	X	X	X	X	X
Skamania Hatchery	7	Summer	*	*	*	*	*	X	X	X	X	X
Skamania Hatchery	7	Winter	*	*	*	*	*	X	X	X	X	X
Minthorn Springs	16	Summer	*	*	*	*	X	X	X	X	X	X
Wells Hatchery	25	Summer	*	*	*	*	*	X	X	X	X	X
Wells Hatchery—Okanogan stock	25	Summer	*	*	*	*	*	X	X	X	X	X
Wells Hatchery—Omak stock	25	Summer	*	*	*	*	*	X	X	X	X	X
Wells Hatchery—Methow stock	25	Summer	*	*	*	*	*	X	X	X	X	X
Winthrop National Fish Hatchery	28	Summer	*	*	*	*	X	X	X	X	X	X

X: Broodstock genotyped; ~: Broodstock sampled and/or spawned at another hatchery and genotyped; NA: Stock discontinued/non-existent; *: Broodstock not sampled.

[a]Discontinued in 2013.

[b]Stock renamed "Upper Salmon B-run" and transferred to Pahsimeroi hatchery in 2013.

[c]Spawned at Winthrop NFH starting in 2017.

River (Figure 4B), which revealed over 80% of samples were genetically tagged with PBT (Hess et al. 2014). The returning adults next passed through a tribal fishery (Figure 4C), where a sample of harvested adipose-clipped adults reflected similar proportions observed at Bonneville Dam (Byrne et al. 2014b). During the summer period of the migration, returning adults are known to seek thermal refugia in cooler tributaries, such as the Deschutes River of Oregon (Figure 4D), where these adults were sampled (Hess et al. 2016c) to determine the origin of out-of-basin hatchery fish during their upstream migration. The returning adults were sampled again as they passed through another sport fishery in the lower Snake River (Figure 4E) where nearly 100% of the sampled harvest was assigned with PBT (Byrne et al. 2014b) before crossing their final dam (Lower Granite; Figure 4F), where they were sampled again to estimate escapement into terminal sport fisheries (Warren et al. 2015). The adults finally returned to their hatchery of origin where they were genetically sampled and spawned as broodstock to produce the next generation of steelhead tagged with PBT.

A consistent pattern from these steelhead studies show that most samples originated from hatcheries in the Snake River basin where PBT sampling of broodstock parents was implemented. This is not surprising given that production of steelhead from Snake River basin hatcheries is intended to provide fishing opportunities and that ~70% of steelhead smolts released during this time in the entire Columbia River originated from the Snake River Basin (Fish Passage Center; fpc.org), which practically ensures their detection in downriver samples. It is also not surprising that as the migration was sampled closer to the source of these hatcheries, a larger proportion of stocks were found to originate from these hatcheries until nearly 100% of the sample comprised stocks tagged

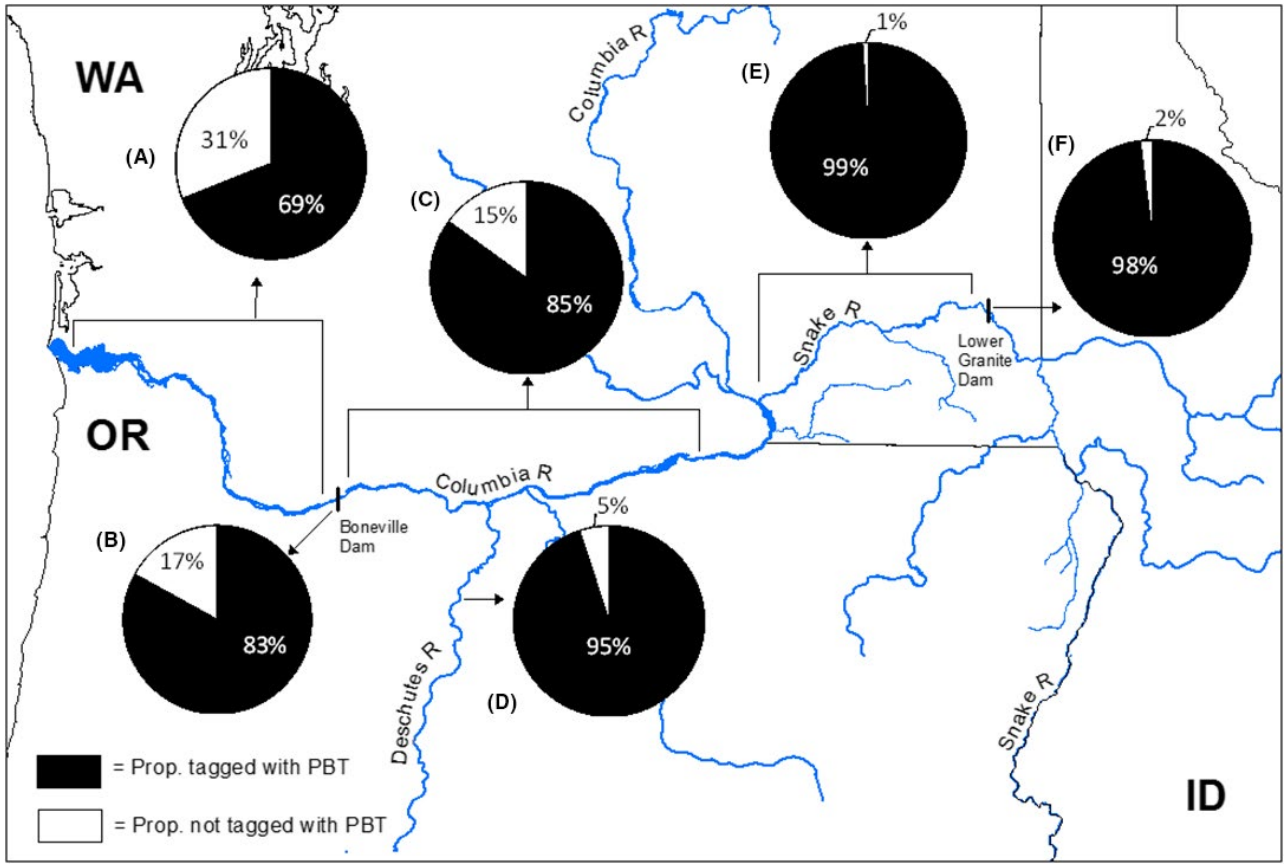

Figure 4. Location and results of independent projects that sampled returning adult steelhead in the Pacific Northwest during the 2012/2013 return migration. Projects include **(A)** a sport fishery in the lower Columbia River below Bonneville Dam (Byrne 2014b), **(B)** escapement at Bonneville Dam (Hess et al. 2014), **(C)** a tribal fishery in the mid-Columbia (Byrne et al. 2014b), **(D)** a study examining origin of out-of-basin hatchery fish during migration in the Deschutes River of Oregon (Hess et al. 2016c), **(E)** a sport fishery in the lower Snake River (Byrne et al. 2014b), and **(F)** escapement at Lower Granite Dam (Warren et al. 2015). Details of results and origin of fish identified with parental-based tagging (PBT) can be found in the respective citations.

with PBT. The 1–2% of unassigned fish likely originated from out-of-basin hatcheries where PBT was not implemented at that time.

The studies mentioned here represent only a portion of the recent publications making use of PBT. In addition, PBT is being used to identify stock composition of hatchery Chinook Salmon in sport fisheries in Idaho (Sullivan et al. 2015, 2016); identifying unclipped hatchery-origin fish in steelhead fisheries (Byrne et al. 2014a, 2014b, 2015, 2016); identifying hatchery-origin kelts (Matala et al. 2016); characterizing run timing of hatchery stocks (Hess et al. 2016b); and estimating proportion of hatchery-origin spawners on spawning grounds (Hinrichsen et al. 2016; Young et al. 2017). Ongoing studies also make use of PBT to evaluate origin and reproductive success of stray steelhead (Smith et al. 2016) and to manage endangered Sockeye Salmon (Peterson et al. 2014). PBT has also been implemented at some California hatcheries where it was used to examine life history and trait heritabilities of steelhead (Abadía-Cardoso et al. 2013). Groundwork is also being laid to implement PBT at Chinook Salmon hatcheries in California (Clemento et al. 2011). Implementation of PBT is also becoming an international endeavor. In British Columbia, Canada, several proof-of-concept studies were completed to pave the way for using PBT in sampling Coho (Beacham et al. 2017) and Chinook (Beacham et al. 2018) Salmon in ocean fisheries.

Even though PBT is frequently used by managers to gather information about hatchery-origin fish, it also plays a role in the conservation of wild stocks. Identifying unclipped hatchery-origin fish with PBT improves abundance estimates of wild Endangered Species Act-listed steelhead and Chinook Salmon stocks (Ackerman et al. 2014, 2016). The proportion of hatchery-origin fish that appear to be natural-origin can be significant and recent estimates from the Snake River basin indicate that 9.2% of outmigrating steelhead juveniles and 21.7% of returning adults that appeared to be of natural origin were actually unmarked hatchery-origin fish (Powell et al. 2018). Thus, PBT will likely become an instrumental tool for refining estimates of natural-origin stocks by allowing putative natural-origin fish to be screened with a PBT baseline.

CONCLUSION

The role of molecular methods in fisheries management has reached a milestone and PBT represents a paradigm shift in how we age and identify hatchery-origin fish. PBT is still an emerging technology but this genetic approach can now provide equivalent or superior levels of information as traditional physical tags in many situations. The level of infrastructure and interagency agreement lags far behind that of the long-established programs for physical tags; nonetheless, some agencies have adopted it as the method of choice for

informing estimates of stock composition in the Snake and Columbia river basins. PBT continues to gain momentum and there is increased awareness and interest in expanding its application. Whether PBT will be adopted as a coordinated coast-wide approach that replaces the existing CWT system depends largely upon the economic and infrastructural considerations for such a program (Hankin et al. 2015). The most recent economic assessment evaluating the implementation of a coast-wide PBT program (Satterthwaite et al. 2015) indicates that overall cost effectiveness could be achieved if low-cost genotyping methods were applied (e.g., GT-seq; Campbell et al. 2015). Low-cost genotyping has since become common and largely removes economic barriers for PBT applications (e.g., Hess et al. 2016a; Beacham et al. 2017). However, there are remaining infrastructural needs that must be addressed to support a coast-wide PBT program including a database query system similar to that used for CWT (e.g., Regional Mark Information System), a coast-wide sampling system, and a committee to oversee the program. PBT is not currently positioned to replace the coast-wide use of CWTs but recommendations are to continue its development and evaluation (NPCC 2013) and to reassess the merits and costs of implementing a coast-wide PBT-based system (Hankin et al. 2015).

The Pacific Northwest is moving toward a future where all hatchery-origin steelhead and Chinook Salmon will be genetically tagged. PBT may complement or replace other tagging methods, depending on the management goals, but it should be viewed as another tool for managers dealing with the complexity of salmonid fisheries and the potential for finer-scale management if desired. Hatcheries in the Pacific Northwest provide a significant proportion of the harvest for salmon and steelhead in commercial, tribal, and sport fisheries (Mahnken et al. 1998; Naish et al. 2007) and PBT provides a relatively efficient alternative for mass tagging this fishery resource.

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