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RESEARCH

Considerations for the Development of a Juvenile Production Estimate for Central Valley Spring-Run Chinook Salmon

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ABSTRACT

Effective species management depends on accurate estimates of population size. There are, however, no estimates of annual juvenile production for Central Valley spring-run Chinook Salmon ("spring run"), a highly imperiled species in California, making it difficult to evaluate population status and effectively manage key issues such as entrainment of this species at water diversions. In recognition of this critical information gap, we initiated an effort to develop a juvenile production estimate (JPE) for spring run, defined here as an annual forecast of the number of juvenile Central Valley spring-run Chinook Salmon that enter the Sacramento–San Joaquin Delta ("Delta") from the Sacramento Valley. This metric would allow for a more robust scientific assessment of the population, which is needed to effectively manage water to reduce effects on spring run, a key condition of state permit requirements. To help guide this effort, we organized a workshop for stake-holders, managers, and scientists to review some of the key aspects of spring-run biology, examine the management and conservation importance of a JPE, identify knowledge gaps, introduce new tools, and discuss alternative approaches to forecasting the number of spring run emigrating from the Sacramento River drainage and into the Delta. This paper summarizes the spring-run biology, monitoring, and emergent methods for assessment considered at the workshop, as well as the guiding concepts identified by workshop participants necessary to develop a JPE for spring-run Chinook Salmon.

KEY WORDS

INTRODUCTION

Worldwide, cold-water species are threatened by climate change, particularly at the extremes of their distributions (Williams et al. 2015). This is particularly true for salmonids, including some of the most economically and culturally important species in the United States. One of the highest profile species at risk is Chinook Salmon (*Oncorhynchus tshawytscha*) in California's Central Valley. Here, Chinook Salmon occur at the southern-most extent of the species' range and are therefore considered especially valuable for the future adaptive capacity of the species in a warming world. They consist of four distinct runs, named for the season when adults return to freshwater to spawn. Central Valley spring-run Chinook Salmon ("spring run") were once the most abundant run of salmon in the Central Valley, and a major contributor to commercial and recreational fisheries (Yoshiyama et al. 1998). Extant populations, with the exception of Butte Creek, are at historically low population sizes (Figure 1, Table 1; Johnson et al., forthcoming), and the evolutionarily significant unit (ESU) is now listed as threatened under both the California Endangered Species Act (CESA; CDFW 2021) and the Federal Endangered Species Act (Federal Register 2005 37159). While much is known about Chinook Salmon in general, many aspects of the spring-run life history that are important for management and conservation in the Central Valley remain poorly understood (Cordoleani et al. 2020). Perhaps most notably, unlike the endangered Central Valley winter-run Chinook Salmon, there is no annual estimate of the number of spring-run juveniles produced by the remaining spring-run populations in the Sacramento River and its tributaries (O'Farrell et al. 2018). For winter run, a juvenile production estimate (JPE) is calculated annually to determine the authorized level of incidental take associated with the operation of the Central Valley Project (CVP) and State Water Project (SWP) Delta pumping facilities each water year (NMFS 2019). This JPE is defined as the number of the annual cohort of juvenile winter run forecast to enter the Sacramento–San Joaquin Delta (Delta), a legally demarcated region that encompasses the riverine to tidal transition zone (Figure 2; O'Farrell et al. 2018). The lack of this basic metric for Central Valley spring run represents a major knowledge gap critical to managing California's water resources, and the monitoring, research and modeling necessary for producing a spring-run JPE include science critical to the conservation and restoration of spring run.

Recently, this management gap was formally recognized by the CESA Incidental Take Permit (ITP) issued to the California Department of Water Resources (CDWR), which authorizes take of spring run (among other CESA-listed fishes) during long-term operations of the SWP (CDFW 2020). Specifically, the ITP requires the CDWR to develop a method for estimating a spring-run JPE: an annual forecast of the number of juvenile Central Valley spring-run Chinook Salmon expected to enter the Sacramento–San Joaquin Delta ("Delta"). The spring-run JPE will not include San Joaquin River spring-run production because this population is still considered experimental, although the JPE will need to account for San Joaquin spring run at monitoring locations where juvenile populations from the Sacramento and San Joaquin rivers overlap. The JPE is expected to inform minimization measures to manage spring-run losses caused by the SWP operations, and will help guide other required management activities such as the development of a life-cycle model and habitat restoration (e.g., Cordoleani et al. 2020). For similar reasons, a recent federal permit requires the CDWR and the United States Bureau of Reclamation to jointly assess a population performance objective for young-of-year Central Valley spring run (NMFS 2019).

Estimating an annual spring-run JPE is complicated by (1) the broad geographic and geologic range of Central Valley streams that support spring run, (2) the challenge of developing a holistic, coordinated monitoring
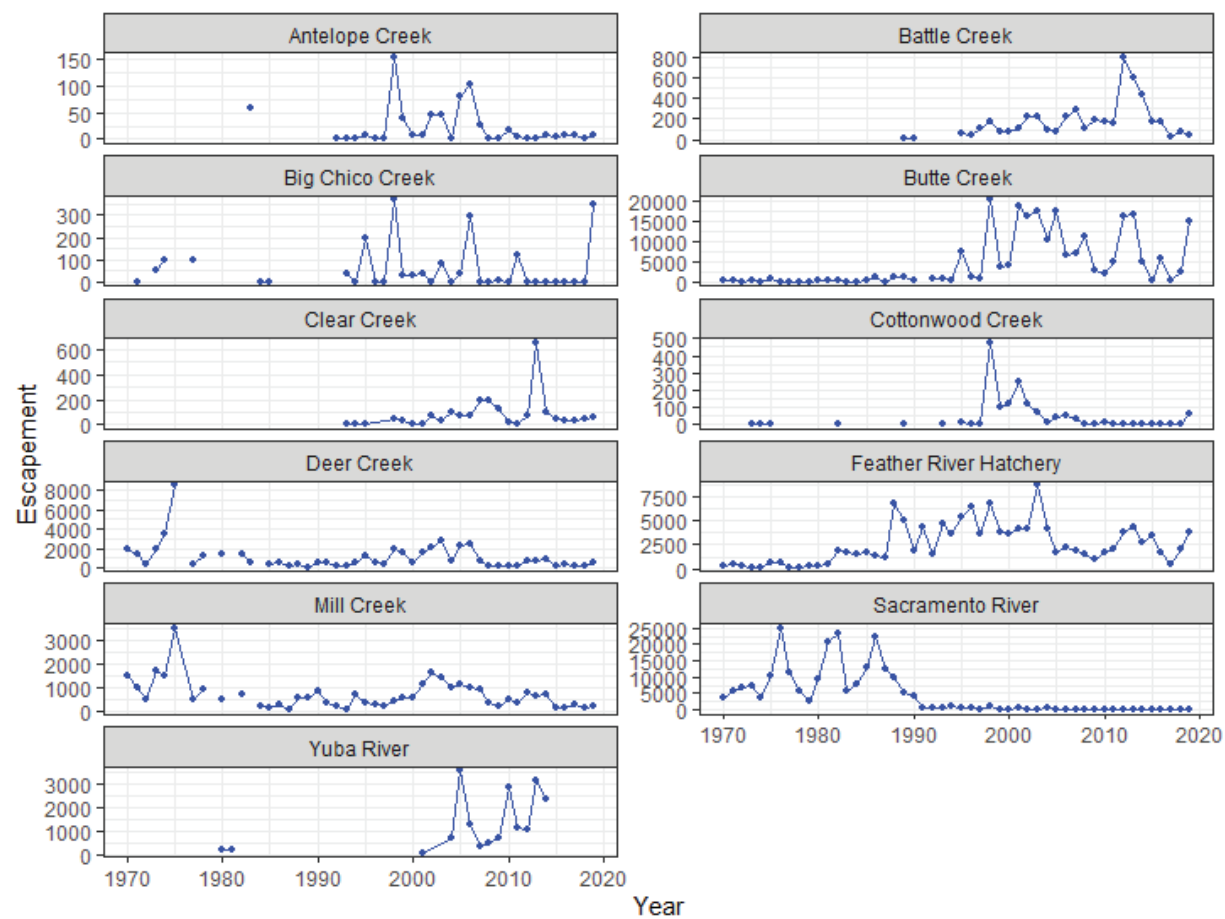
Figure 1 Escapement for Central Valley spring-run Chinook Salmon over time. For Butte Creek populations, the mark-recapture estimates are used beginning in 2001. Beginning in 2009, Red Bluff Diversion Dam estimates of spring-run Chinook Salmon in the upper Sacramento River are recorded '0' in Azat 2020 (modified from Johnson et al., forthcoming).

Table 1 Viability metrics for Central Valley spring-run Chinook Salmon ESU independent populations through escapement year 2019. Population size is estimated as the sum of estimated run sizes over the most recent 3 years. Run size is the average of the estimated run sizes for the most recent 3 years (2017-2019). Trend or population growth rate is estimated from the slope of log-transformed estimated run sizes. Catastrophic decline is the largest decline in a single generation over the most recent 10 such ratios. The extinction risk of all independent populations except Butte Creek has increased in 2020 since the previous assessment in 2015 (modified from Johnson et al., forthcoming).

| Independent population	Population size	Run size	Trend (10 years)	Catastrophic decline (%)	Risk of extinction		
					2010	2015	2020
Mill Creek	590	197	− 0.158 (− 0.288, − 0.028)	67.9	High	Moderate	**High**
Deer Creek	956	319	− 0.037 (− 0.191, 0.117)	83.3	High	Moderate	**High**
Butte Creek	17,740	5,913	− 0.059 (− 0.400, 0.283)	76.3	Low	Low	Low
Battle Creek	157	52	− 0.228 (− 0.446, 0.009)	76.5	High	Moderate	**High**
Clear Creek	136	45	0.044 (− 0.266, 0.354)	82.9	High	Moderate	**High**
Feather River Hatchery	6,509	2,170	− 0.026 (− 0.192, 0.140)	45.8	High	High	**High**
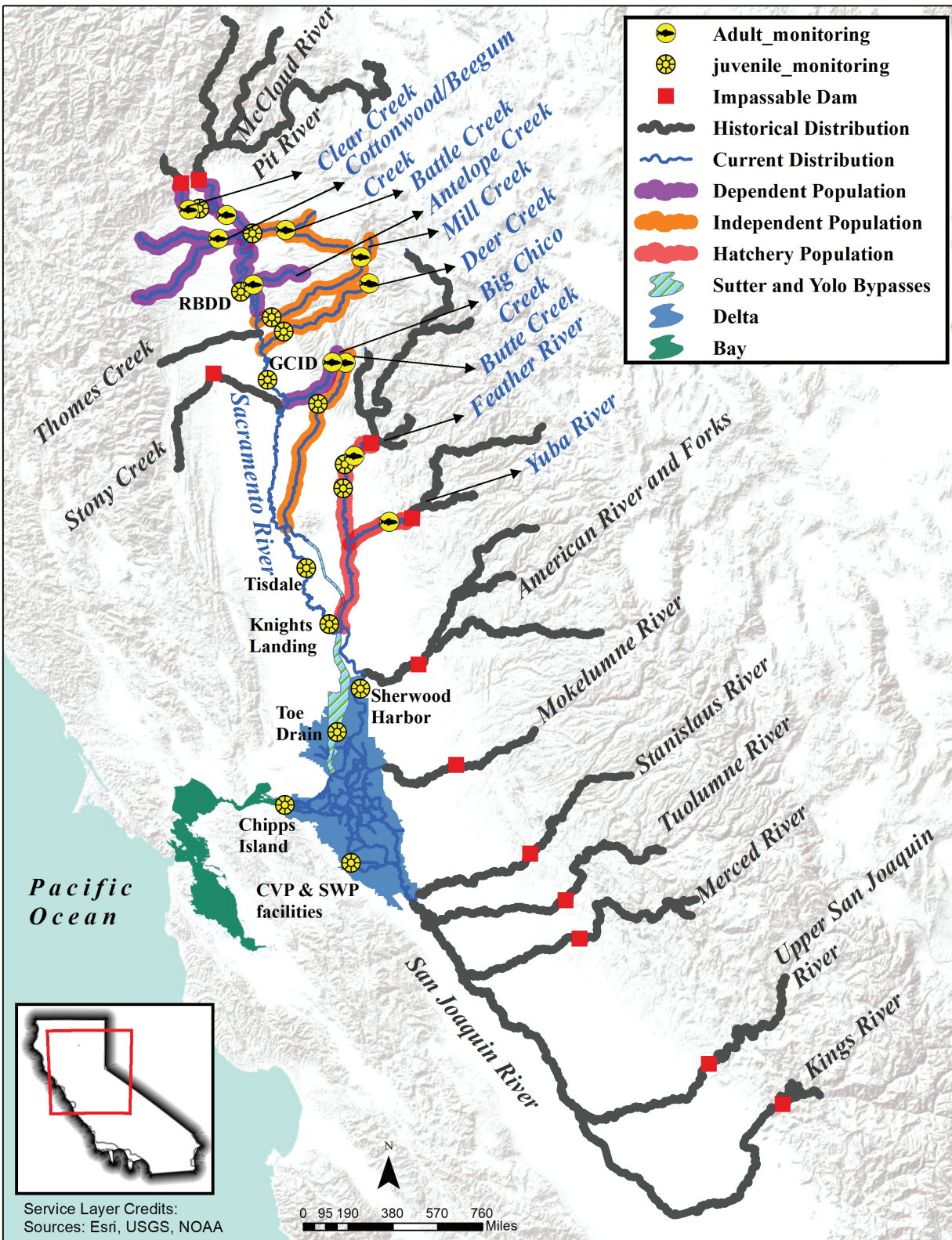
Figure 2 Central Valley spring-run Chinook Salmon populations under consideration for the JPE (i.e., excluding San Joaquin River fish), and current monitoring

framework for generating quantitative estimates of juvenile spring run across their range, (3) multiple life-history variants displayed within and among spring-run streams, and (4) the difficulty of distinguishing juvenile spring run from other co-occurring run types (fall run, late-fall run, and winter run). To assess the current state of knowledge for spring run and launch the spring-run JPE development process, the CDWR and the Delta Science Program held an open workshop in September 2020, soliciting general scientific information on Central Valley spring run and specific input on the challenges and potential approaches for developing a spring-run JPE. Given the high profile of salmon issues in California, the workshop was well-attended by more than 250 participants who represented diverse interest groups, including state and federal agencies, academia, water users, environmental groups, tribal governments, and other organizations and individuals with an interest in salmon and water management. To address the specific challenges outlined above, our workshop was organized around four central themes:

- The state of knowledge of spring-run distribution and life history

- The extent and nature of spring-run adult and juvenile monitoring

- Spring-run genetic and length-at-date identification tools

- Current approaches to producing and using juvenile production estimates (JPEs)

Here, we provide brief reviews of the state of knowledge for these themes and the major findings generated by the workshop: the relevant knowledge gaps and the next steps for producing a spring-run JPE. We expect this information will be of direct use in the development of a spring-run JPE and will support improved science and management for Central Valley Chinook Salmon.

DISTRIBUTION AND LIFE HISTORY

Current Distribution

Historically, spring run comprised 19 independent populations (McElhany et al. 2000), but the ESU is currently limited to four independent populations, spawning in Battle, Mill, Deer, and Butte creeks (Sacramento River tributaries), and both natural- and hatchery-origin spring run from the Feather River (Figure 2; Williams et al. 2016). Spring run were extirpated from tributaries in the San Joaquin River basin, which represented a large portion of their historic range and abundance (Fisher 1994; Lindley et al. 2004), and approximately 28% of the historic Central Valley salmonid spawning and holding habitat remains accessible (Yoshiyama et al. 2001). The ESU also includes smaller populations that depend on "immigration from other streams" (Lindley et al. 2004). The Battle Creek population was extirpated from its historical habitat and started repopulating in the 1990s (Johnson and Lindley 2016). Clear, Big Chico, Cottonwood, and Antelope creeks and some San Joaquin River tributaries have seen signs of spring-run recolonization (Johnson and Lindley 2016), and spring run have been reintroduced on the San Joaquin River below Friant Dam as part of the San Joaquin River Restoration Program (SJRRP; Figure 2). As explained above, we considered only the Sacramento River populations for calculating a spring-run JPE, and not the San Joaquin tributaries or the reintroduced San Joaquin River population, given their status as an experimental population.

Life History Diversity

Similar to other Chinook Salmon populations, Central Valley ESUs exhibit a diversity of life-history strategies, including run timing, fecundity, spawning location, rearing strategies, migration timing, maturation, and ocean distribution (Healey 1994; Adkison 1995; Bourret et al. 2016; Yoshiyama et al. 1998; Lindley et al. 2004; Williams 2012; Satterthwaite et al. 2018). Spring-run adults migrate, hold, or spawn in the Sacramento River basin from February through October. Juveniles rear in the Sacramento River and its tributaries, Sutter and Yolo bypasses, and the San Francisco Estuary (Delta and bays;
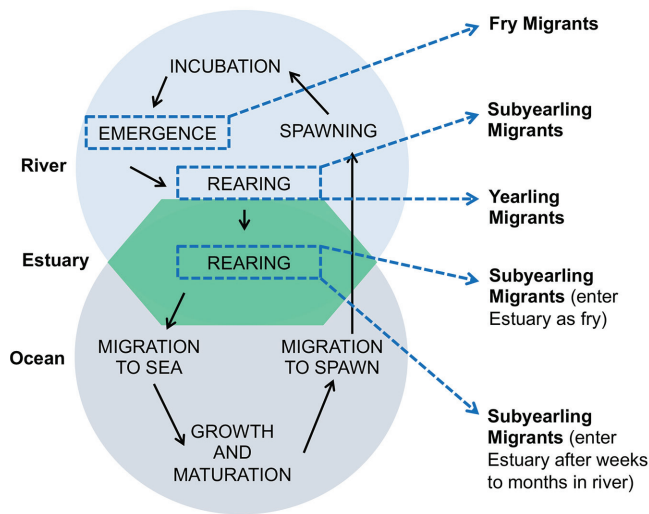
Figure 3 Conceptual depiction of Central Valley Chinook Salmon juvenile life history, emphasizing differences among the timing of fluvial and tidal rearing, and migration to the sea. (*Source: Adapted from Bottom et al. 2009 and Sherman et al. 2017.*)

Figure 2) for 3 to 15 months before out-migrating to the ocean as sub-yearlings during the spring, or they remain in freshwater over the summer and out-migrate the following fall, winter, or spring as yearlings (Cordoleani et al. 2020, 2021b). Thus, juvenile spring run exhibit a wide range in their size, timing, and age at out-migration (Figure 3; Cordoleani et al. 2020).

Our understanding of salmonid life history comes primarily from traditional fish monitoring data, observing the phenology of migration, spawning, rearing, and smoltification. However, studies based on coded-wire tags (CWTs), acoustic telemetry, and otolith microchemistry have provided a more nuanced understanding of life-history diversity. Large-scale CWT fish releases have been used to infer residence time, movement, and survival of salmon release groups for decades (Lyons et al. 2008) at lower cost, and via larger sample sizes than acoustic tags. For example, CWTs placed in late fall-run juveniles as surrogates for spring run and recovered during out-migration from salvage facilities are used to assess effects of water project operations (NMFS 2019). CWTs recovered from adult salmon may be used to describe ocean distribution, reconstruct

spawner age structure, and evaluate the effects of ocean harvest (Satterthwaite et al. 2018). Acoustic tags are more expensive and difficult to implant than CWTs, but enable the fine-scale tracking of individual movement and survival across landscapes where tag-detecting monitors are operated (Cordoleani et al. 2017, 2019; Notch et al. 2020; Singer et al. 2020). Otoliths (calcareous structures in the inner ear) can provide information on fish age, habitat-specific growth rates, duration of freshwater rearing, fish size at out-migration, and migratory histories. Otoliths from adult carcasses recovered on spawning grounds can provide these metrics for successful spring-run escapees (Barnett–Johnson et al. 2008; Johnson et al. 2017; Cordoleani et al. 2021). This is because ratios of environmental strontium vary predictably for many locations across Central Valley watersheds and are incorporated into the daily layers in otoliths, providing a record of their movements across the landscape over their lifetime (Ingram and Weber 1999; Barnett-Johnson et al. 2008). Significant insights into ecology and behavior have been revealed using this approach (Johnson et al. 2016; Phillis et al. 2018; Sturrock et al. 2020; Cordoleani et al. 2021).

Recent work by Cordoleani et al. (2021) revealed the demographic value of yearling spring run to the viability of Mill and Deer creek populations; this may need to be considered in the context of the JPE. For example, during multi-year droughts and ocean heat waves, late yearling migrants that left the freshwater during cooler fall conditions were the only survivors to adulthood. This suggests that the value of yearlings may be disproportionately large under some environmental conditions, and thus the effects of yearling entrainment in the fall may warrant particular consideration. Accounting for diverse spring-run strategies within a JPE will rely on improvements to existing monitoring, which does not fully account for the aspects of spring-run life-history variation pertinent to management. For example, tributary catch data from juvenile monitoring may not identify run or population of origin (i.e., depending on capture location), describe residence time across habitats and life-stages, or account for variation in
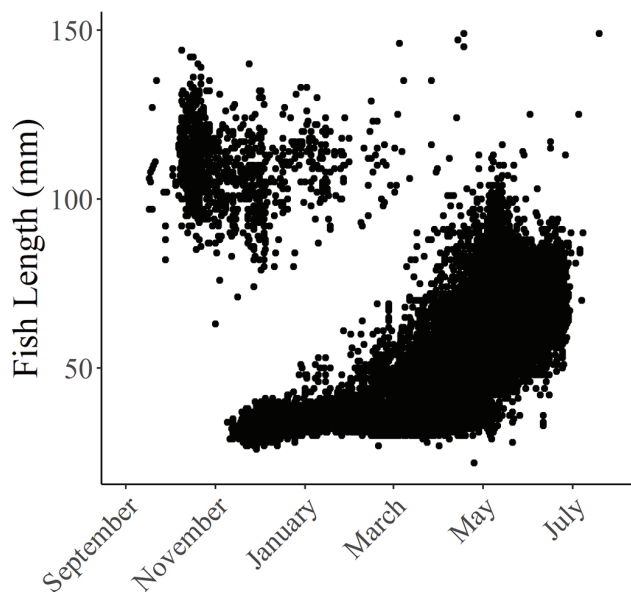
Figure 4 Length and capture date of juvenile Chinook Salmon collected in the Butte Creek rotary screw trap (RST) between 1995 and 2004 (CDFW unpublished data). *Note: the abrupt beginning and end of the RST data may be an artifact of when the sampling gear was deployed and removed.*

migration behavior (Figure 4). While challenging, doing so would provide means to protect life-history diversity and contribute substantially to our understanding of spring-run biology and to conservation efforts.

MONITORING PROGRAMS

State and federal resource agencies and their contractors currently monitor spring run at multiple freshwater and estuarine sites, including critical life-stage monitoring of adult escapement and spawning, and juvenile out-migration. These existing long-term monitoring programs provide ongoing and historical data useful to developing a JPE approach and calculating an annual JPE, although we expect that some additional monitoring will ultimately be required. Below, we describe programs for adult and juvenile monitoring; a discussion follows of one of the most critical needs: accurate methods for run identification.

Adult Monitoring
Spring-run adult monitoring currently includes (1) estimating the number of adults that have successfully returned to the spawning ground (escapement); (2) monitoring summer holding and pre-spawn mortality, spawner spatial distribution, and spawn timing; and (3) estimating successful spawning through redd or carcass surveys (Table 2). Spring-run escapement inventories in the upper Sacramento River basin have been conducted sporadically since the 1940s, but were incomplete, inconsistent, and not replicable (Bergman et al. 2012). Since the early 1990s, there has been an effort to standardize sampling methods to provide consistent and reproducible spring-run adult escapement estimates (Cordoleani et al. 2020); however, there are still substantial uncertainties.

The National Marine Fisheries Service (NMFS) uses the escapement survey data to conduct viability assessments and a status review update every 5 years for the spring-run ESU using the criteria established in Lindley et al. (2007; Table 1). Results from the most recent analysis suggest that the viability of the Central Valley spring-run ESU has deteriorated since the 2015 assessment (Williams et al. 2016), primarily as a result of initially low population sizes and subsequent catastrophic declines in abundance (Johnson et al., forthcoming). Using data through 2019, all spring-run populations—with the exception of Butte Creek—had weakening viability metrics, placing them at a high risk of extinction (Table 1). The largest effects are likely due to the freshwater drought conditions and unusually warm ocean conditions experienced by this cohort (Johnson et al., forthcoming).

Adult Monitoring and JPE Development
Given that spring-run adults reach the spawning grounds several months before spawning, there are obstacles to collecting adult monitoring data, including accurately assessing mortality that may occur during the summer holding period. For instance, if abundance estimates come only from adult sampling performed during their upstream migration in the spring or early summer (e.g., video monitoring downstream of the spawning

Table 2   Adult spring-run Chinook Salmon monitoring. Note that "Escapement" corresponds to the number of adults that have returned to the spawning ground. Feather River Hatchery production is not included in this table. Spring-run adult escapement estimates are available from: *https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=84381&inline*

Watershed	Monitoring method	Variable measured	Sampling efficiency estimate	Tissue sampling	Otolith sampling	References
Upper Sacramento River	Aerial redd survey	Escapement	No	No	No	Killam 2019
Clear Creek	Snorkel, redd, and carcass surveys; video monitoring	Escapement and successful spawner estimates, summer holding/spawning distribution	Yes (partially)	Yes	Yes	Bottaro and Chamberlain 2019
Cottonwood Creek	Snorkel survey and video monitoring	Escapement	No	No	No	Killam 2019
Battle Creek	Fish trapping/sorting; video monitoring; snorkel and carcass surveys	Escapement and successful spawner estimates, summer holding/spawning distribution	Yes	Yes	Yes	Bottaro and Earley 2020
Antelope Creek	Snorkel survey and video monitoring	Escapement	No	No	No	Killam 2019
Mill Creek	Redd survey and video monitoring	Escapement and successful spawner estimates, summer holding/spawning distribution	No	No	Yes	Killam 2019
Deer Creek	Snorkel survey and video monitoring	Escapement, summer holding/spawning distribution	No	No	Yes	Killam 2019
Big Chico Creek	Snorkel survey	Escapement, summer holding/spawning distribution	No	Yes	Yes	Garman and McReynolds 2009
Butte Creek	Carcass and snorkel surveys; infrared fish counter	Escapement and successful spawner estimates, summer holding/spawning distribution	Yes	Yes	Yes	Garman and McReynolds 2009, 2012
Feather River	Carcass Survey, Adult Angling/ Telemetry study	Escapement (combined with fall run), summer holding/spawning distribution	No	No	Yes	CDWR 2011
Yuba River	Carcass and redd surveys; infrared fish counter	Escapement, summer holding/spawning distribution	No	No	Yes	YRMT 2013, PSMFC 2015

reach), failure to account for adult mortality upstream could result in an overestimation of spawner abundance and of the total number of eggs produced. Accounting for pre-spawning mortality using pre-spawning carcass surveys or redd counts will likely add complexity and cost to existing long-term monitoring.

A second challenge is estimating sampling efficiencies at counting stations. In most of the spring-run watersheds with video or infrared counting stations, sampling efficiency and sampling uncertainty are not evaluated. Methods for assessing and handling these sources of error range from no assessments to the use of multiple

complementary methods (e.g., video monitoring and redd surveys) and statistical tools (e.g., mark-recapture modeling; Link and Barker 2005; Bromaghin et al. 2013).

In some watersheds, the difficulty of distinguishing between spawning spring-run and fall-run adults—as well as overlap between spring-run and fall-run spawning in space and time—complicate accurate visual counts of adult spring run. In the Yuba River, adult passage data are used to develop a statistical model that helps define a demarcation date between the spawning of the two runs upstream of Daguerre Dam. However, model improvements have been

suggested and are ongoing to better separate spring-run and fall-run adults. In Clear Creek, a weir is used to separate migrating spring-run and fall-run spawners (NMFS 2016). Some level of spawning overlap is sometimes observed in Mill, Deer, and Butte creeks, which can add uncertainty to redd counts or carcass surveys.

Fish length and sex information are necessary to better estimate the number of eggs produced per spawner each year, and egg-to-fry survival from spring-run streams would be necessary to estimate a fry-equivalent production index as has been used for the winter-run JPE (O'Farrell et al. 2018). Length and sex data can only be collected accurately when carcasses are recovered, which could be challenging in some spring-run streams where carcass recoveries are rare due to low retention or difficult-to-access spawning reaches, low returning adult numbers, or insufficient monitoring funding.

Other Considerations

Additional adult sampling is performed in some spring-run watersheds to obtain biological and environmental information that could also be important for the development of a JPE. For example, current carcass otolith sampling in Mill, Deer, Butte, Clear, and Battle creeks, as well as the Feather River could be used to study successful spring-run juvenile rearing and migration strategies (Sturrock et al. 2020; Cordoleani et al. 2021). Environmental factors such as water temperature and flow are also monitored in many of the spring-run watersheds, and can be used to evaluate habitat suitability for holding, spawning, and egg incubation. Reaches where environmental monitoring takes place include Cottonwood, Antelope, Clear, Mill, Deer, and Battle creeks, as well as the Yuba and Feather rivers (Figure 1).

Juvenile Monitoring

The goals of current spring-run juvenile monitoring include: (1) quantifying relative juvenile salmon abundance, (2) obtaining raw counts and error estimates from select tributaries, and (3) collecting juvenile salmon life-history information such as out-migration timing and size distribution (Table 3). Juvenile monitoring is mainly performed using rotary screw traps (RSTs) downstream of the spawning reaches in spring-run tributaries (USFWS 2010) or by using trawls or beach seines at key locations along the migratory corridor (e.g., in the Sacramento River and Delta). Currently, juvenile abundance estimations are performed in very few spring-run watersheds and are unavailable at locations along the migratory corridor because of the challenges identified below.

Juvenile Monitoring and JPE Development

To expand raw juvenile capture numbers to total abundance estimates, trap efficiency studies are needed for multiple seasons and conditions. Efficiency trials typically consist of marking and releasing sampled fish upstream of the trapping location to assess recapture rates. Unfortunately, only a few spring-run watersheds currently conduct trap efficiency trials at the levels necessary to reliably expand estimates. Challenges to calculating sampling efficiency include not sampling enough juvenile salmon and frequent high-flow events in unregulated tributaries (e.g., Butte, Mill, and Deer creeks) that hinder sampling and efficiency testing when many juveniles are out-migrating. Surrogate fish, such as hatchery fall-run or spring-run juveniles, could be used for efficiency tests in some of these streams. Additionally, an approach similar to the one currently implemented for juvenile winter run at Chipps Island, which uses paired CWT and acoustic-tagged hatchery fish, could be used to generate efficiency and abundance estimates for spring run (described in Johnson et al. 2017).

Estimating fry-to-smolt survival and smolt passage survival from natal streams to the Delta will be especially helpful in the development of a spring-run JPE; however, spring-run fry survival estimates are difficult to obtain. Most young-of-the-year migrants are too small for acoustic tags, and CWT programs large enough to calculate fry survival rates are not practical in most spring-run streams. One exception is Feather River Fish Hatchery, where 100% of spring-run Chinook Salmon juveniles are tagged with CWTs at the hatchery before being released

Table 3 Juvenile spring-run Chinook Salmon monitoring. FL = fork length, W = weight, K = condition factor; RST = rotary screw trap, CWT = coded wire tag, GCID = Glenn-Colusa Irrigation District, FRH = Feather River Hatchery, CVP = Central Valley Project, SWP = State Water Project.

Watershed	Monitoring Method	Years of operation	Season of operation	Variable measured	Traits measured	Tissue sampling	References
Clear Creek	RST	1998–present	November–June	Production, outmigrant size & timing	FL – W – K	Yes	Schraml et al. 2020
Sacramento River–Balls Ferry	RST	1996–1999	October-September	Production, outmigrant size & timing	FL	No	---
Cottonwood Creek	None	---	---	---	---	---	---
Battle Creek	RST	1998–present	November–June. Restarting year round in 2020	Production, outmigrant size & timing	FL – W – K	Yes	Schraml and Earley 2020
Sacramento River–Red Bluff Diversion Dam	RST, telemetry study	1995-2000 2002–present	January– December	Total abundance, outmigrant size & timing, smolt survival	FL	Yes (during the fall period)	Poytress et al. 2014
Antelope Creek	None	---	---	---	---	---	---
Mill Creek	RST, telemetry study	1996–2010	November– June	Relative abundance, outmigrant size & timing, smolt survival	FL	No	Johnson and Merrick 2012, Notch et al. 2020
Deer Creek	RST, telemetry study	1994–2010	November–June	Relative abundance, outmigrant size & timing, smolt survival	FL	No	Johnson and Merrick 2012
Sacramento River–GCID Hamilton City	RST	1991–2009 2013–present	January– December	Relative abundance, outmigrant size & timing	FL	No	Coulon no date
Big Chico Creek	RST	1999–2003	November–May	Relative abundance, outmigrant size & timing	FL	No	Garman and McReynolds 2009
Butte Creek	RST, CWT and telemetry study	1995–present	October–June	Relative abundance, outmigrant size & timing, smolt survival	FL	No	Garman and McReynolds 2009, Cordoleani et al. 2019
Sacramento River–Tisdale	RST	2010–present	October–June	Relative abundance, outmigrant size & timing	FL – K	As needed	Purdy and Coulon 2013
Sacramento River–Knights Landing	RST	1995–present	Aug/Sept–June (since 2015)	Relative abundance, outmigrant size & timing	FL – W	Yes (since 2017)	Julienne 2016
Feather River	RST, beach seining, snorkel survey, CWT and telemetry study	1998–present	November / December–June	Production, outmigrant size & timing, disease monitoring, smolt survival (FRH fish)	FL	Some	CDWR 2019
Yuba River	RST	1999–2009	October–June	Relative abundance, outmigrant size & timing	FL – W	No	YRMT 2013
Sacramento River–Sherwood Harbor	Trawl	1988– present	Year-round since 1994	Relative abundance, outmigrant size & timing	FL	Yes	Barnard et al. 2015

Table 3 *continued*

Watershed	Monitoring Method	Years of operation	Season of operation	Variable measured	Traits measured	Tissue sampling	References
Yolo Bypass	RST, fyke trap, beach seine, telemetry study	1998–present	January–June (RST), September–June (fyke), year-round (seine)	Relative abundance, outmigrant size & timing, spatial distribution, smolt survival	FL	Yes	Schreier et al. 2018
Delta – various locations (e.g., Chipps Island)	Trawl	1976–present	Year-round since 1996	Relative abundance, outmigrant size & timing	FL	Yes	Barnard et al. 2015
Delta - various locations	Beach Seine	1970–present	Year-round since 1995	Spatial distribution	FL	No	Barnard et al. 2015
Delta - CVP and SWP facilities	Salvage facilities	1968–present	Year-round	Outmigrant size & timing, fish count	FL	Yes	---

in the river, with roughly half of them released in March at 65-70 mm and the other half in April at 85-90 mm (2021 in-person conversation between FC and J. Kindopp, unreferenced, see "Notes"). If enough of the smaller tagged Feather River juveniles released in March are recovered in the Delta, this information could help in estimating in-stream fry survival. However, there are likely hatchery effects and environmental differences in other spring-run tributaries and the upper Sacramento River, and fry-size individuals are typically smaller than those released at the Feather River hatchery (< 40 mm). Additionally, Passive Integrated Transponder (PIT) tags could be used to mark and track parr-size juveniles in the spring-run streams to help gain insight into fry-to-smolt survival.

Smolt survival studies using acoustic telemetry have provided estimates of smolt-sized spring-run survival through their migratory corridor (Cordoleani et al. 2017, 2019; Notch et al. 2020; Singer et al. 2020). However, most of the spring-run tagging studies occurred during the last California drought period, and recent winter-run tagging studies show that survival varies greatly across the range of hydrological conditions and Water Year types (Hance et al. 2021). Furthermore, because of the small number of tagged fish in some of these studies and their release over a short time-period, spring-run smolt survival estimates through (or to) the Delta were associated with large error margins and based

on a limited portion of the out-migration season (a study of acoustic-tagged, late-fall run is an exception, see Michel et al. 2015).

Other Considerations

Additional monitoring efforts in some spring-run watersheds could also help the development of an accurate spring-run JPE. For example, a study on disease prevalence and the effect on juvenile health and out-migration success has been conducted in the Feather River (Lehman et al. 2020 and references therein). Juvenile tracking studies of both wild and hatchery spring run, using CWTs or acoustic tags, can also provide valuable information, such as (1) movement and presence of juveniles from various size classes (e.g., fry, sub-yearling, or yearling) at key locations and time-periods (e.g., in the Delta during opened Delta Cross Channel gate period); and (2) sub-yearling migration routes throughout the Central Valley.

Securing reliable funding for the implementation of long-term acoustic telemetry studies throughout the Central Valley could help provide better smolt survival estimates to the Delta for spring-run populations. Arguably, all challenges and uncertainties for both adult and juvenile monitoring could be at least partially addressed with greater funding. One of the future challenges to spring-run JPE development will be to determine the most efficient use of limited resources, including their application to

a monitoring program that contributes best to a robust JPE.

RUN IDENTIFICATION

As noted above, run identification is one of the biggest challenges in the development of a spring-run JPE. Migrating juvenile spring-run Chinook Salmon occur in a mixed population of the four salmon runs in the Central Valley and are morphologically indistinguishable from these other runs. In most watersheds, sampled juveniles are assigned to run based on capture date and fork length (i.e., length-at-date (LAD) criteria; Harvey et al. 2014). However, LAD discrimination operates under two assumptions: juvenile salmon of different runs hatch during segregated periods of the calendar year, and all juvenile salmon grow at a constant rate. These criteria have been shown to produce inaccurate results for spring run when compared to genetic identification (Harvey et al. 2014; Johnson et al. 2017). Therefore, in locations where both fall run and spring run are found (e.g., the Sacramento, Feather, and Yuba rivers; Delta; flood bypasses), spring-run juvenile abundance estimates frequently include fall-run fish and/or exclude misclassified spring-run fish as a result of the overlap in size and out-migration timing.

As an improvement to the LAD approach, Bayesian probabilistic modeling based on genetic confirmation of run identification is under development (2020 email conversation between BH and N. Hendrix, unreferenced, see "Notes"). The probabilistic approach has a similar construct to the original LAD approach in that it relies on the fork length and sample date of a juvenile salmon to assign a run but may assign more than one run for a given juvenile salmon, along with a probability for each run assignment (Figure 5). The assignment probabilities will be based on genetic identification of catch from the preceding years of monitoring, and updated regularly throughout a migration season as new genetic identifications become available. In addition to genetic information, variables such as geographic area, flow, and temperature may be
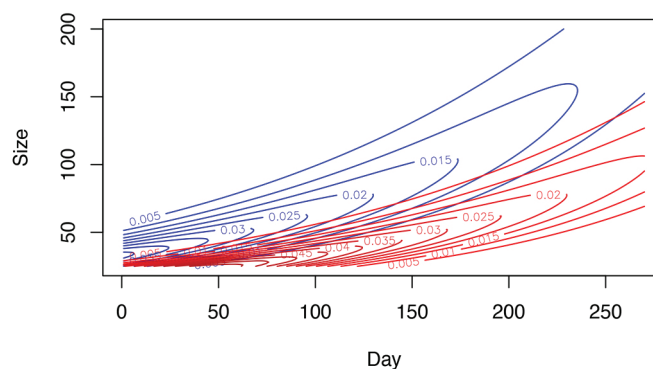

Figure 5   Conceptual depiction of probabilistic length-at-date (PLAD) juvenile salmon size ranges for two runs (*Source*: N. Hendrix, unreferenced, see "Notes").

incorporated into the probabilistic assignment model.

All salmon runs were originally and primarily defined by phenotypic differences among adult Chinook Salmon run-timing and spawning periods, not by differences in genetic composition or morphology. To use genetics to differentiate between salmon runs, adult salmon samples displaying different run-timing phenotypes are collected throughout each run's geographic range and genotyped to serve as a genetic baseline. Salmon of unknown run origin can then be genetically assigned a probability of belonging to a run by comparison with the baseline (Figure 6).

The appropriate genetics test for differentiating among Central Valley salmon populations varies, depending on the needs and conditions of a specific application. These needs include the biological question at hand, logistical requirements, and the number of genetic markers needed to achieve a desired level of identification accuracy (Meek et al. 2019; Thompson et al. 2020). Primary among biological questions is the type and level of population differentiation required, such as determining a fish's genetic run type (e.g., spring run) vs. also needing tributary-of-origin information (e.g., spring run from Butte Creek). In general, finer-scale population resolution will require more genetic markers and have higher costs. Once these parameters are defined, a geneticist can work with managers to determine
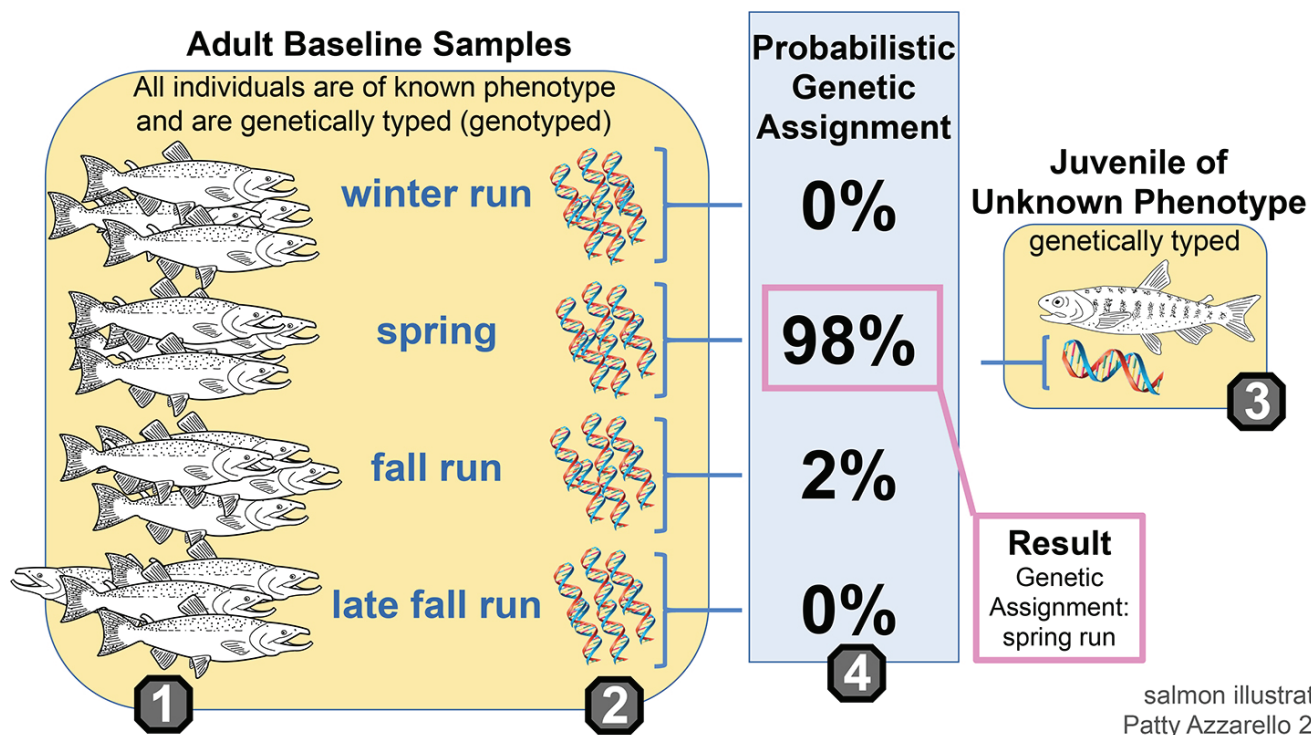
Figure 6   The basic steps in the process of genetic identification of a salmon of unknown origin include (1) collecting tissue samples from a larger number of adult salmon of known run type, called the baseline samples; (2) analyzing the genetic composition of the baseline samples at specific locations (genetic markers) in the salmon genome; (3) analyzing the genetic composition of the unknown salmon at those same genetic markers; and (4) comparing the unknown salmon genetic composition to the baseline samples to derive a probabilistic assignment.

the most appropriate available techniques and develop an approach or explain the trade-offs of different potential approaches.

Until recently, the ability to differentiate among Central Valley salmon populations required reproductive isolation, due to either spatial or temporal segregation during spawning. However, advancements in salmon genetics have identified single nucleotide polymorphisms (SNPs) located around and within an adjacent pair of genes—GREB1L and ROCK1—that are unique to early-migrating (i.e., spring run and winter run) vs. late-migrating (i.e., fall run and late-fall run) phenotypes, even in populations with interbreeding between runs (Prince et al. 2017; Narum et al. 2018; Thompson et al. 2020). Individuals that display intermediate timing for their migration phenotype (i.e., adults that migrate later than most early-migrating salmon but earlier than most late-migrating individuals)

are often heterozygous for SNPs in this region, and contain alleles from both migratory timing phenotypes (Thompson et al. 2019).

As previously mentioned, assignment accuracy of current genetic tests varies, depending on the level of differentiation a test was designed to resolve, which in turn depends on the purpose, cost, and other constraints that were considered in the design of the test. If the objective is to distinguish spring run from other runs, or to distinguish between the four Central Valley runs, a high degree of accuracy can be obtained with low cost (Meek et al. 2019; Thompson et al. 2020). Fine-scale differentiation within a run, such as assignment to tributary origin (not a requirement of the ITP but potentially useful for conservation and management purposes), however, will likely be associated with higher costs per individual sample and may become prohibitive for large sampling programs.

Rapid portable genetic testing tools, first developed in 2017 for human disease detection during outbreaks, are being adapted for ecological applications, including rapid, sensitive, and accurate fish genetic identification (Baerwald et al. 2020). Essentially, these tests search for the presence of a specific DNA nucleotide sequence in a sample of genetic material, such as a swab taken from the mucus of a juvenile salmon. These tests can be carried out anywhere (e.g., field, salvage facility, or laboratory), with minimal equipment and training, and results are returned in as few as 30 minutes. Once a specific test has been developed, test production is very low-cost.

One challenge that has been identified is the need to differentiate Sacramento from San Joaquin spring run at the salvage facilities. Both are early-migrating populations, and because Feather River Fish Hatchery spring run are the source stock for reintroduced San Joaquin spring run, there has been insufficient reproductive isolation to segregate stocks. Several identification approaches have been suggested, relying on tagging or initial genetics tracking based on parentage assignment. Any identification solution will have to balance required population resolution, cost, turn-around time, and acceptable levels of identification uncertainty.

POTENTIAL MODELS FOR A SPRING-RUN JUVENILE PRODUCTION ESTIMATE

Juvenile production estimates previously developed for other salmonids can serve as a model for a spring-run JPE. Of these, several forms of the Central Valley winter-run Chinook Salmon JPE (Oppenheim 2014; Poytress et al. 2014;

Voss and Poytress 2017; O'Farrell et al. 2018) offer a particularly useful starting place for reviewing alternative JPE models, including "demographic" versus "direct" methods, improved survival estimates, and statistical procedures to estimate error.

The 2014 JPE model (Table 4, Scenario 1) used a demographic approach to determine both the number of winter run passing Red Bluff Diversion Dam (RBDD) and the probability of survival as these fish moved from the RBDD to the Delta. To estimate the number of winter run passing RBDD, adult escapement was multiplied by viable egg production and then by survival from eggs to juvenile passage at RBDD. Egg-to-RBDD passage survival was calculated as the "…mean of the time-series of the ratios of juveniles passing RBDD (the Juvenile Production Index, JPI) divided by the adult carcass survey adjusted for fecundity data and pre-spawning mortality" (Anderson et al. 2014). Subsequent RBDD-to-Delta survival was estimated from late fall-run acoustic tag studies and a single (weighted) winter-run study. The use of late fall-run studies was expected to overestimate survival but was necessary at the time because only 1 year of winter-run acoustic tag studies had been conducted. Anderson et al. (2014) summarize two alternative approaches to Scenario 1 (Table 4) that result in substantially lower JPEs: Scenario 2 uses a survival estimate from RBDD to the Delta (S2, Scenario 2) based on the winter-run data only; Scenario 3 couples this reduced S2 with a direct estimate of the JPI (the number of juveniles passing RBDD). The JPE results from these three methods differ substantially, depending on both the survival estimates used and the application of real-time

Table 4 Summary results from three winter-run JPE models, including basic model elements and input data, modified from Anderson et al. (2014). RBDD = Red Bluff Diversion Dam. Note that S1 for Scenario 3 has been calculated from the JPI and the viable egg estimate.

Scenario	Adult escapement (AE)	Viable eggs per adult (E)	Viable egg estimate	Survival to RBDD (S1)	Juveniles passing RBDD (JPI)	Survival RBDD to Delta (S2)	Number of juveniles entering Delta (JPE)
1. NOAA method	5,958	2,755	16,411,348	0.27	4,431,064	0.27	1,196,387
2. WR S2	5,958	2,755	16,411,348	0.27	4,431,064	0.16	708,970
3. JPI & WR S2	5,958	2,755	16,411,348	0.15	2,485,797	0.16	397,726

monitoring data (Table 4). Cyril Michel observed that, at present, the winter-run JPE uses survival estimates from acoustic tagging studies from prior years that regularly differ substantially from the year in question (2021 email conversation between PN and C. Michel, unreferenced, see "Notes"). The advent of real-time acoustic telemetry and more nuanced models that link survival to flow and temperature, however, have the potential to provide more reliable annual predictions of survival (e.g., Hance et al. 2021).

O'Farrell et al. (2018) compared three other methods for estimating winter-run juvenile production, all based on a model structure similar to that of Oppenheim (2014). These models use the estimated number of fry-equivalent units (JPI) observed from rotary screw trap (RST) data at the RBDD, modified by two survival estimates: fry-to-smolt survivorship and survival of out-migrating smolts between RBDD and the Delta (Table 5). All three models use direct estimation of fry-equivalent passage, albeit with some differences; this reduces the uncertainty of starting with estimates of egg-to-fry survival. Method 1 was used for the 2018 winter-run JPE and provided a point estimate for production but no error estimate (Table 5). By incorporating survival estimates from a mark-recapture model, Method 2 accounts for observation error—a critical improvement on Model 1—and was used to calculate the JPE in 2019, 2020, and 2021. Method 3 differs from the other methods by using Bayesian modeling to produce a JPE with credible intervals that reflect observation error for abundance and

survival estimates, and by including an estimate of process error for RBDD-to-Delta survival. Although the process error estimate for RBDD-to-Delta survival accounts for year-to-year natural variability, it does not account for the influence of environmental variables on that process error, such as flow or temperature (O'Farrell et al. 2018).

Together, these winter-run JPE modeling cases highlight some of the options and challenges that will occur in the development of a spring-run JPE. A key consideration for any model is the initial abundance estimate to be modified by various production or survival parameters. Selecting an input abundance estimate close in time or life-stage to the model end point should reduce observation and process error that affect the resulting JPE. For the winter-run model, this logic supported the post-2014 shift from using a demographic approach that relying on adult escapement as the starting point for JPE calculations to using an estimate of fry-equivalent passage at RBDD based on direct observations. For spring run, to provide the starting point for calculating a JPE, the equivalent would require spring-run out-migrant abundance estimates derived from out-migration monitoring on tributaries or in the mainstem Sacramento River, rather than demographic estimates derived from adult passage, carcass surveys, or redd counts.

Unfortunately, winter run differ from spring run in ways that may preclude a spring-run JPE based on direct measurement of out-migrant abundance: First, all winter run are produced upstream

Table 5 Estimates used to forecast the 2018 winter-run JPE. For Method 3, the estimates are the means of the distribution for each factor (modified from O'Farrell et al. 2018, Table 4). RBDD = Red Bluff Diversion Dam, JPI = juvenile production index, JPE = juvenile production estimate.

	Method		
	1	2	3
Juveniles passing RBDD (JPI)	545,132	606,039	606,794
Fry-to-smolt survival	0.5900	0.4725	0.4733
RBDD-to-Delta survival	0.5129	0.4378	0.4721
Methodological differences	Point estimate; no error estimation	Accounts for observation error	Mean and variance estimates; accounts for observation and process error
JPE	164,963	125,378	135,472

of RBDD, many river miles from the point of Delta entry; spring run are produced from at least seven Sacramento River tributaries each year, and a large proportion of this production comes from the Feather River, a short distance upstream from the location of Delta entry. This precludes establishment of an out-migration monitoring station far enough upstream of the Delta to derive a direct abundance estimate that would account for all spring-run production before the majority of spring run have entered the Delta. Second, the majority of winter-run juveniles pass RBDD well *before* the January 1st regulatory deadline, allowing sufficient time for producing a winter-run JPE. The majority of spring-run out-migration, however, typically occurs *after* the January 1st regulatory deadline in the ITP for producing a spring-run JPE. These characteristics of the Sacramento River spring-run population may necessitate a spring-run JPE model that uses a demographic approach based on abundance estimates of a life-stage that occurs before juvenile out-migration. Such a demographic approach would still benefit from— or may require—direct out-migration abundance measurements to support estimation of pre-migration demographic parameters (e.g., egg production and fry survival), and each year's direct measurement of out-migration abundance could also be used later in the year to "true up" the January 1st JPE.

Given that a spring-run JPE approach will likely include some kind of demographic approach based on a life stage or stages that occur many months before juveniles are expected to enter the Delta, there will likely be increased sources of both observation and process error compared to the JPI-based winter-run JPE. For this reason, we expect that it would be advisable to design a spring-run JPE and related monitoring and survival studies that account for major sources of both observation and process error. This would require out-migrant monitoring and monitoring efficiency studies across a range of environmental conditions. Because currently available historical data will probably not allow estimation of major sources of error, the spring-run JPE approach adopted at the end of 2024 should include a plan

for future updates to the modeling approach and for the monitoring necessary to estimate and reduce observation and process error. For life-stages, parameters, and conditions not currently accounted for in the historical monitoring data, we expect that this will require at least 5 and more reasonably 10 years of new monitoring to support updates in model design.

Like RBDD-to-Delta survival estimation for earlier winter-run JPEs, spring-run survival estimates will need to rely initially on surrogate survival estimates from winter-run acoustic studies. Even after spring-run survival studies are numerous enough to end reliance on surrogate studies, a spring-run JPE will need to contend with the difference between the size of acoustic tag study fish and the comparatively small size at which most spring run exit their natal tributaries. Besides the possible remedies described above under Juvenile Monitoring and JPE Development, this issue could be resolved with acoustic studies using smaller tags and fish, or by demographic approaches that estimate survival by comparing abundance estimates at different life stages, similar to the winter-run JPE approaches before 2014.

DISCUSSION

Next Steps for the Development of a Spring-Run JPE

The intent of developing a JPE is to provide a tool for use in making management decisions to address several challenging issues (see Sommer 2020). Most obvious among these challenges are minimizing the effect of water project operations. Less obvious, perhaps, but also important are developing recovery efforts for spring-run Chinook Salmon, including restoration and conservation of natal and rearing habitat, quantitative evaluation of restoration actions, refining hatchery operations, and continued management of ocean fisheries. The background information, guiding concepts, and expert input produced by the workshop will continue to contribute to the development of a spring-run JPE. To move forward quickly and efficiently to develop a JPE, we describe below some of the

major information needs and processes we expect to address.

Structured Decision-Making

Developing a JPE will require substantial information, and to address management needs there are likely to be major trade-offs in approaches. A major recommendation from the workshop was to use a Structured Decision-Making approach to guide initial monitoring, analyses, and applications (Gregory et al. 2012). Structured Decision-Making will help selection of special studies and major new monitoring (see sections below) that reduce critical JPE uncertainty. The process will clearly articulate the fundamental objectives of the JPE approach, and highlight trade-offs between targeted levels of JPE uncertainty, potential constraints, and stake-holder concerns. Structured Decision-Making will also provide an objective and transparent process for weighing JPE options and selecting the most suitable approach, which will in turn inform longer-term monitoring needs (Lyons et al. 2008). This approach will rely on information gathered from some of the elements described below.

Historical Data

Preliminary quantitative JPE models can be developed based on estimated abundance at key salmonid life stages and locations: (1) adult escapement estimates or redd counts; (2) juveniles produced in tributaries; (3) juveniles out-migrating from tributaries; and 4) juveniles as they enter the Delta. We anticipate that the spring-run JPE will ultimately depend on abundance estimates from at least one life stage in multiple locations, survival estimates for passage to the Delta, and some measure of associated errors. For example, there is already some information from previous acoustic telemetry studies, CWT releases, escapement surveys, RST surveys, and genetic results that could be used to inform initial JPE approaches. Preliminary models, tested with historical data, will allow initial comparisons of model estimates and model uncertainties across JPE approaches, identify primary sources of uncertainty, and provide direction for special studies to reduce that uncertainty.

Additions to Existing Programs

To refine the JPE approaches, there is clearly a need to improve existing information sources. Rather than initiate totally new surveys at the outset of the JPE development period, it is more efficient to supplement or modify established programs that track demographic life stages that would (1) serve as primary input variables in the preliminary models referenced above; (2) allow estimation and reduced uncertainty of key transition parameters; or (3) provide estimates of error that can be used in a JPE directly, or guide the trial and selection of alternative data sources. Examples of these include the judicious application of data from surrogate runs or species; collecting relevant data on adult abundance, survival, and fecundity; estimating and improving sampling efficiency; and expanding genetic and life-history testing. Data on the behavior, growth, and survivorship of surrogate fish may be used where information on spring run is unavailable or questionable. For example, except for Clear Creek, egg-to-fry survival rates are not known for spring run. For other spring-run tributaries, egg-to-fry survival of fall-run could be used where the data exist until spring-run monitoring data are available to estimate this parameter. Because it is not feasible to conduct comprehensive sampling in all tributaries, we plan to focus initially on selected indicator streams. Lessons learned from these initial efforts will be used to inform whether and how to sample in other tributaries, and will allow early parameterization of JPE models.

Special Studies

In addition to the use of historical data and the expansion of existing monitoring programs, the spring-run workshop identified new research as a third tier of work necessary for the development of a JPE. Developing genetic approaches to successfully identify spring-run salmon at multiple locations in the system will be essential to the JPE program. Other examples in this category include studies to understand variation in migration timing and telemetry estimates of reach-specific survival. We anticipate that many of these elements will be guided by initial modeling and Structured Decision-Making, and

may require substantial planning, permits, and shifting of effort from other trial monitoring.

Guiding Concepts

The September 2020 workshop led to several guiding concepts applicable to the development of the JPE. Many of these topics are consistent with previous reviews of monitoring needs to support management (e.g., Johnson et al. 2017):

Maintain Focus on Entrainment Management. As a driving element in the ITP, the JPE aims to minimize entrainment of spring run at the SWP, and annual estimates could be used to inform protective management measures to this end. That said, we expect that JPE forecasts, and the monitoring and research conducted to support the JPE, will benefit other important management and conservation efforts. We also note that JPE development and its application are distinct from management decisions made in response to JPE forecasts.

Multiple Tools Will Be Necessary. The JPE program will rely on multiple monitoring efforts, experiments, models, and analyses. These reflect the complex life history and the geographical diversity of the spring-run range, as well as a variety of data sources and technical tools. The goal is to apply the best tools to the problems for which they are most suited.

Redundancy. Partially provided by the application of multiple tools, redundancy in monitoring programs and analytical strategies will improve statistical power, help to identify and manage sources of error, and provide alternatives in the case of catastrophe (e.g., the loss of a RST).

Comparability. Multiple JPE approaches should be comparable during the research and development phase, and later during implementation. Comparisons may focus on scientific, logistical, or management variables, depending on the need, and will facilitate program development and lead to a robust product.

Progressive Approach. Refining early season estimates as data become available will allow an annual JPE to respond to changing conditions. Similarly, data from successive years should be used to improve JPE models as additional life-history and survival data are gathered.

Adaptive Developmental Process. The process of developing the JPE should reflect short-term priorities while allowing sufficient flexibility to incorporate the results from initial research and monitoring into developing and refining the JPE.

CONCLUSIONS

To ensure that a spring-run JPE meets permitting, management, and conservation needs, the timely production of an annual JPE is going to be critical, and will likely require (1) the application of multiple tools to meet minimum standards for accuracy and precision, (2) redundant methods to provide an internal check on results and to safeguard against monitoring errors, and (3) a progressive approach that provides for early estimates each year to be refined as additional data become available. The current state of knowledge for spring-run distribution and life history provides an adequate starting point for developing a JPE, but the findings of this workshop and the ensuing discussion indicate that additional monitoring, the development and application of improved methods for run identification, and a modeling approach that incorporates key sources of uncertainty and accounts for the unique biology and ecology of Central Valley spring-run Chinook Salmon will be necessary for a spring-run JPE that supports improved science and management of this threatened species.

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