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RESEARCH

Using Life-Cycle Models to Identify Monitoring Gaps for Central Valley Spring-Run Chinook Salmon

Flora Cordoleani,*[1,2] William H. Satterthwaite,[2] Miles E. Daniels,[1,2] Matthew R. Johnson[3]

ABSTRACT

Life-cycle models (LCMs) provide a quantitative framework that allows evaluation of how management actions targeting specific life stages can have population-level effects on a species. The LCM building process is also a powerful tool that can be used to identify data gaps that exist in the knowledge of the target species, and which might strongly influence overall population dynamics. LCMs are particularly useful for species such as salmon that are highly migratory and use multiple aquatic ecosystems throughout their life. Furthermore, they are lacking for threatened Central Valley spring-run Chinook (Oncorhynchus tshawytscha; CVSC). Here, we developed a CVSC LCM to describe the dynamics of Mill, Deer, and Butte creek CVSC populations. We used model construction, calibration, and a global sensitivity analysis to highlight important data gaps in the monitoring of those populations. In particular, we found strong model sensitivity and high uncertainty in various egg, juvenile, and adult ocean life stages' biological processes. We concluded that the current CVSC monitoring network is insufficient to support using a LCM to inform how future management actions (e.g., hydrology and habitat restoration) influence CVSC dynamics. We propose a series of monitoring recommendations—such as the development of an enhanced juvenile-tracking monitoring program, and the implementation of juvenile-trapping efficiency methodology combined with genetic identification tools—to help fill highlighted data gaps. These additional data-collection efforts will provide critical quantitative information about the status of this imperiled species at key life stages (e.g., CVSC juvenile abundance estimates), and create a more comprehensive monitoring framework fundamental for working on the recovery of the entire stock. Furthermore, additional data collection will strengthen the LCM parameterization and calibration process, and ultimately improve the model's predictive performance.

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* Corresponding author email: *flora.cordoleani@noaa.gov*

1 Institute of Marine Sciences,
Fisheries Collaborative Program,
University of California Santa Cruz
Santa Cruz, CA 95060 USA

2 Southwest Fisheries Science Center,
National Marine Fisheries Service, NOAA
Santa Cruz, CA 95060 USA

3 California Department of Fish and Wildlife
Redding, CA 96001 USA

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INTRODUCTION

Life-cycle models (LCMs) are essential tools that are increasingly used in conservation and population management of vulnerable species (Honea et al. 2009; Alldredge et al. 2013; Merz et al. 2013; Hendrix et al. 2017; McGowan et al. 2017). They provide a quantitative framework across all life stages of a species that allows an understanding of how management actions (e.g., habitat restoration, harvest, hatcheries) can have population-level effects on species recovery. Additionally, LCMs can be used to provide recommendations for modifying or implementing new management actions to better achieve conservation objectives, and predict the outcomes of such actions. They can thus be used to support the implementation of an evidence-based adaptive management program—a methodology gaining support in the conservation and resource management community (Franklin et al. 2007; Dahm et al. 2009). This type of analytical framework is particularly valuable for (1) highly migratory species that use multiple habitats across different life stages; (2) species that exhibit non-linear responses to perturbations; and (3) species that are exposed to complex interconnected stressors. Thus, development of a LCM for the management of threatened salmon populations in the California Central Valley (CCV) is worthwhile and timely.

The CCV is a unique ecosystem with a variety of native and endemic inland fishes, including four runs of Chinook Salmon (*Oncorhynchus tshawytscha*), that play a major ecological, cultural, and economic role (Williams 2006). Central Valley spring-run Chinook (CVSC) were once a major component of the combined annual salmon runs, and occupied the headwaters of all major CCV river systems where natural barriers were absent. However, mining activities and the construction of large dams without fish passage have eliminated access to almost all of their historical spawning habitat (only about 20% of their spawning habitat remains accessible; Yoshiyama et al. 2001). Additionally, over- or illegal harvest, habitat degradation (e.g., barriers' construction, water diversions, and water pollution), and the reduction of genetic integrity have negatively affected these fish (CDFG 1998; Yoshiyama et al. 1998; Zeug et al. 2011; NMFS 2014). As a consequence of these activities, only four independent natural populations of the 19 historical populations of CVSC remain (i.e., Butte, Mill, Deer, and Battle creeks; McElhany et al. 2000). CVSC are entirely extirpated from tributaries in the San Joaquin River basin, which represented a large portion of the historic range and abundance of the evolutionarily significant unit (ESU; Fisher 1994; Lindley et al. 2004). They were listed as state and federally threatened species in 1999 (US Office of the Federal Register 1999).

Although supporting healthy CVSC populations has become a central challenge that natural resource managers face, very few studies have assessed how human activities and CCV restoration actions affect the dynamics of CVSC at the population and stock levels. CVSC have a complex life cycle, with cohorts exposed to multiple environmental and anthropogenic stressors (e.g., thermal stress and reduced habitat quality via water diversion) that may affect different life stages in different ways. Non-lethal effects, such as density-dependence, can also propagate to other life stages and influence the overall population dynamics in complex non-linear ways (Grossman and Simon 2019). For a LCM to capture this complexity and evaluate how management actions affect various life stages and overall population dynamics, it requires data and adequate understanding of the multiple biological processes that shape these dynamics. The model-building process itself is an important step that can help identify data gaps that exist in the knowledge of the target species (Fulton et al. 2019). In particular, the development of model equations that represent biological processes can help identify which parameter estimates are lacking. Additionally, the implementation of sensitivity analyses can serve as an important diagnostic tool, by highlighting the governing

parameters in a LCM and quantifying the related uncertainty in the model output (Cariboni et al. 2007; Saltelli et al. 2008).

To enable future use of the LCM for management purposes, the goal of this study was to build a stage-structured LCM, and conduct sensitivity analysis to identify the monitoring gaps and missing data required to properly model CVSC dynamics. We first present the CVSC LCM and the major sources of uncertainty in the model parameterization. We then show how a sensitivity analysis was used to further identify the biological processes that strongly affect CVSC dynamics. Finally, based on the data limitations underlined by the model's construction, calibration, and sensitivity analysis, we provide future monitoring recommendations, and discuss the implications for the use of a LCM in the management of this listed stock.

MATERIALS AND METHODS

Populations of Interest

Of the 19 historic independent populations of CVSC identified by the Central Valley Technical Recovery Team (TRT) only four independent populations—Mill, Deer, Butte, and Battle creeks—remain, warranting a threatened status under the Endangered Species Act (ESA; McElhany et al. 2000). Based on viability criteria developed by Lindley et al. (2007), Mill, Deer and Battle creek populations are considered at moderate risk of extinction; Butte Creek, which is currently the most abundant CVSC salmon population, remains at low risk of extinction (Johnson and Lindley 2016; Figure 1). However, these populations' abundances have continued to decline since the last viability assessment (Azat 2019). The ESU also includes Feather River Hatchery spring-run Chinook (FRHSC) and smaller dependent populations that probably would not have persisted without immigration from other streams (either because they are sink populations or part of a meta-population). However, Feather River fish have been hybridizing with Sacramento River fall-run Chinook (SRFC) stocks since the 1960s (Garza et al. 2008; Clemento et al. 2014) likely because of hatchery practices and spatial constrictions on previously separate spawning distributions created by dams. Although most dependent CVSC populations have experienced continued declines and potential introgression risk as a result of hatchery influence, some streams—such as Clear Creek as well as some San Joaquin River tributaries— have seen signs of

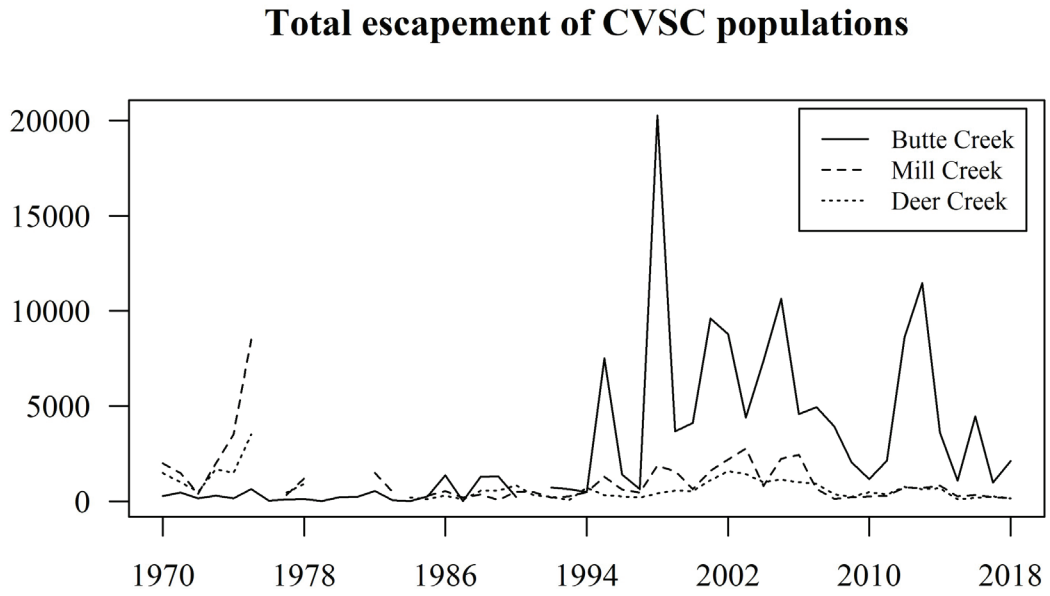

Figure 1 Butte, Mill, and Deer creeks' CVSC adult population abundance from 1974 to 2018 (*Source: Azat 2019*). Butte Creek adult abundance reflects estimates from annual adult snorkel surveys, is the abundance time series used for the model fit.

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spring-running re-population, and could in the future help improve the ESU's spatial and genetic diversity (Johnson and Lindley 2016).

Despite its precarious status, the CVSC ESU has received less attention from the scientific and resource management communities than SRFC, which are heavily supplemented by CCV hatcheries and an important component of California and Oregon's ocean fisheries (Zeug et al. 2012; Merz et al. 2013; Friedman et al. 2019), and Sacramento River winter-run Chinook (SRWC), that which are listed as endangered under the ESA (Botsford and Brittnacher 1998; Winship et al. 2013, 2014; O'Farrell and Satterthwaite 2015; Hendrix et al. 2017). The LCM detailed in the next section focuses on the dynamics of CVSC salmon populations in Mill, Deer, and Butte creeks. We did not include Battle Creek in the model's development because although this population is considered independent it was extirpated for many decades from its historical habitat and only started repopulating in the mid 1990s (Johnson and Lindley 2016). Thus, we lack a long time-series of data, such as spawner abundance, required to fit the model. However, we expect the underlying mechanisms that influence the abundance of these populations through time and space will apply to the other dependent and recovering CVSC populations.

Mill and Deer creeks' CVSC populations are very close geographically and genetically; Butte Creek CVSC are considered a genetically distinct population within the ESU (Hedgecock et al. 2001). Mill Creek and Deer Creek, both located in Tehama County, California, are part of the lower Cascade mountain range, with their geomorphological characteristics largely influenced by the volcanic history of the area. Both upper drainages are relatively inaccessible to humans, which has prevented major alteration of the surrounding land, leaving the upper watersheds in a nearly pristine condition (Johnson and Merrick 2012; Figure 2). Butte Creek is located in Butte and Sutter counties, California. The headwaters of Butte Creek originate in the Lassen National Forest, within the Jonesville basin (Figure 2). Because of the presence of a natural, low-elevation migration barrier, Butte Creek has many more miles of low-elevation habitat than Mill and Deer creeks. Therefore, it resides at the climatological margin for CVSC, and remains a favorable habitat because of the Feather River's supplementation of cold water. Water temperatures and flow in Butte Creek's CVSC holding and spawning reaches are managed by PG&E through the DeSabla-Centerville hydroelectric project (Garman and McReynolds 2012). Additionally, Butte Creek connects to the Butte Sink and Sutter Bypass floodplain before flowing into the lower Sacramento River, which provides a unique rearing habitat for Butte Creek CVSC juveniles that is accessible to other Chinook Salmon populations only during large Sacramento River flooding events (CVFMPP 2010).

Model Structure

We developed a LCM to accommodate specific life-history characteristics of CVSC populations. The geographic regions considered in the model—i.e., Mill/Deer/Butte creeks, Sacramento River, Sutter Bypass, Yolo Bypass, Sacramento–San Joaquin Delta (hereafter the Delta), San Francisco–San Pablo Bay (hereafter the Bay), and the ocean—were delimited based on the presence of the different life stages at a given time (Figure 2). The timing of each life stage event, such as adult spawning, is summarized in Figure 3 and is based on existing literature sources (CDFG 1998; Yoshiyama et al. 2001). This spatially explicit stage-structured model follows the movement, survival, and reproduction of CVSC populations at each developmental stage (i.e., egg, fry, subyearling smolt, yearling smolt, sub-adults, spawners) and geographic location throughout their life cycle (Figure 4). Figure 4 displays the transition states of CVSC moving from one life stage in a particular geographic area to the same or another life stage in another geographic area. CVSC dynamics are described at a monthly time-step in the freshwater phase and at a yearly time-step for the ocean phase. The framework of this model also allows habitat information (e.g., freshwater flow and temperature) to be linked to population vital rates (e.g., survivorship or carrying capacity) through empirical and mechanistic relationships.

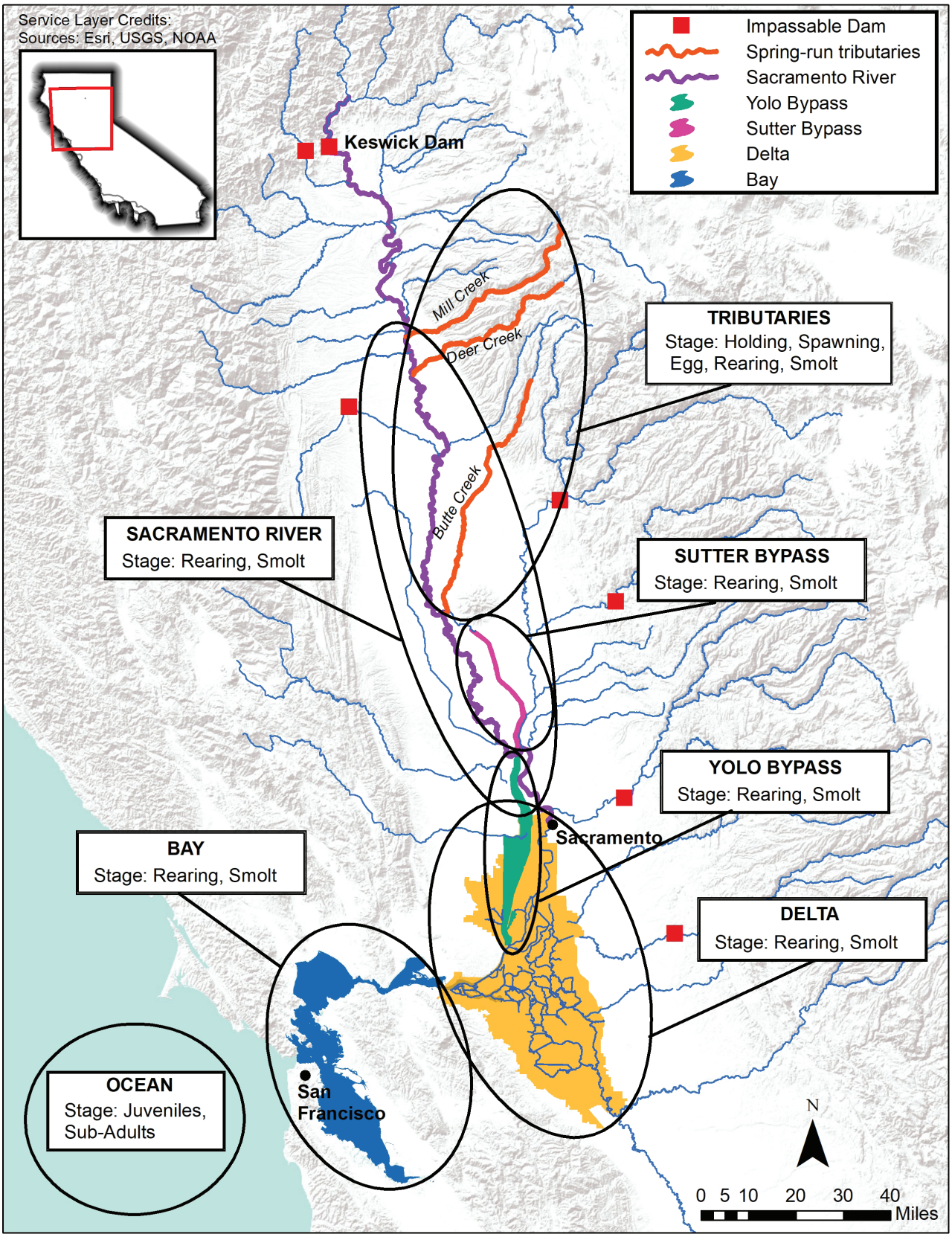

Figure 2 Geographic distribution of CVSC populations at the life stages considered in the LCM

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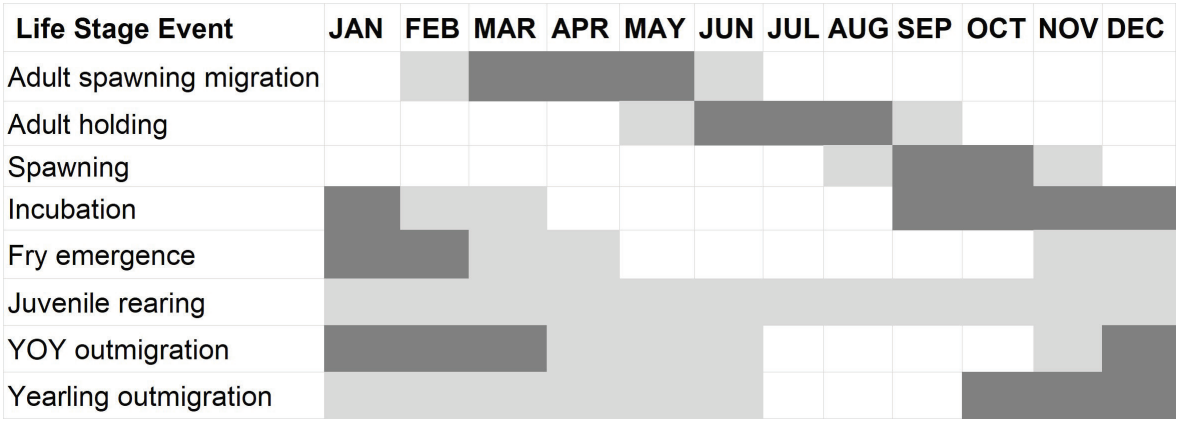

Figure 3 Natural CVSC life history timing. *Light grey boxes* show the entire timing window for each life stage event and the *darker grey boxes* show the event peak timing. YoY = Young-of-the-Year which corresponds to juveniles that outmigrate from the natal tributary as fry or sub-yearling smolts and enter the ocean within their first year. Yearling juveniles are fish that spend an entire year in the natal tributary before outmigrating to the ocean in the following fall, winter and spring.

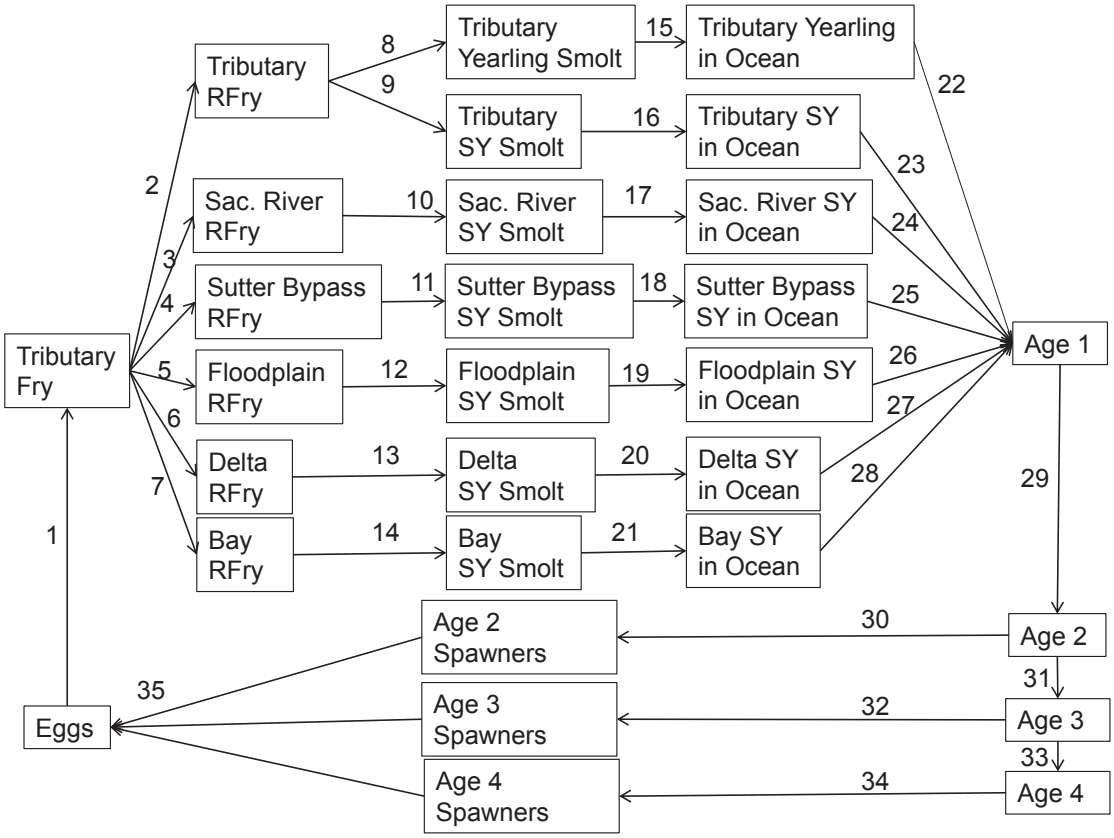

Figure 4 CVSC LCM schematic. The *numbered arrows* represent the transition states describing the probable success of CVSC moving from one life stage in a particular geographic area to the same/or another life stage in another geographic area. RFry = rearing fry, SY = subyearling.

The LCM equations were parameterized based on information from existing monitoring data and scientists' knowledge, or, when those were not available, were based on information from other spring-run Chinook populations or other CCV runs such as winter- or late-fall run Chinook (see Table A1 in Appendix A for LCM parameter value details). Based on the respective populations' resemblances and dissimilarities, we used the same parameterization for the Mill and Deer creeks' populations, and we used a separate parameterization for the Butte Creek population. We then combined the dynamics of both Mill and Deer creeks' and Butte Creek's populations and simulated them within a single model to allow for the integration of population interactions that might occur for some life stage processes (e.g., density-dependent juvenile migration). The LCM was built on R version 3.4.1 (R Development Core Team 2015).

Egg to Emerging Fry

Central Valley spring-run Chinook juveniles emerge from the gravel between November and April. The first transition equation represents the survival of eggs to emerging fry in the natal reaches, during those months:

$$TributaryFry = Eggs * S_{eggs} \quad (1)$$

where $TributaryFry$ = emerging fry in natal tributary, $Eggs$ = eggs produced in the natal tributary, and S_{eggs} = egg survival rate during incubation.

There is currently no estimation of Mill, Deer, and Butte creeks' egg-to-fry survival, and we assumed that survival in those watersheds was similar to survival values found for Yuba River spring-run Chinook Salmon (Stillwater Sciences 2013).

Rearing to Migrating Juvenile

CVSC juveniles exhibit a wide variety of migrating and rearing strategies. They will either (1) migrate out of the spawning habitat soon after emergence as fry and rear for a few months in downstream habitats, such as the mainstem Sacramento River and the Sutter Bypass, or (2) rear in their natal habitat and outmigrate as subyearling smolts during the winter and spring, or (3) stay an entire year in the natal reaches and outmigrate as yearling smolts the following fall, winter, or spring (CDFG 1998). Juveniles will thus spend from 3 to 15 months in freshwater before outmigrating to the ocean (Figure 3). Each of these strategies is represented in the LCM.

Equations 2 to 7 describe the dispersal of emergent fry from the natal reaches to the different rearing habitats, and the associated survival during the rearing phase in each of these habitats. Incorporated in the LCM are rearing dynamics based on density-dependent movement out of habitats (Beverton-Holt function; Equations 2-7). The emergent fry are therefore split between residents that stay in a habitat, and migrants that are forced—as a result of habitat saturation—to move downstream to find a suitable habitat to rear in.

$$ResFry_i = \frac{S_i * (1 - m_i) * N_i}{1 + \frac{S_i * (1 - m_i) * N_i}{K_i}} \quad (2\text{-}7)$$

$$MigrFry_i = S_i * N_i - ResFry_i$$

where $ResFry_i$ = resident fry in the ith habitat, $MigrFry_i$ = migrant fry from the ith habitat, S_i = fry survival rate in the ith habitat, N_i = pre-transition abundance in the ith habitat, m_i = migration rate without density dependence in the ith habitat, K_i = rearing carrying capacity of the ith habitat, and i = index denoting Tributary (2), Sacramento River (3), Sutter Bypass, (4) Yolo Bypass (5), Delta (6), or Bay (7) (same i values used among the following model equations).

Very little is known about Butte, Mill, and Deer creeks' CVSC fry survival and movement, mainly because of their small size and the difficulty of tracking them through their rearing and migratory corridor. Therefore, fry survival rates in the tributaries (S2), the Sacramento River (S3), the Sutter and Yolo bypasses (S4, S5), the Delta (S6), and the Bay (S7) were based on survival estimates used in models studying the dynamics of spring-

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run Chinook Salmon from the Pacific Northwest (Lestelle et al. 2004), the Yuba River (Hendrix et al. 2014), and SRWC (Hendrix et al. 2017).

The density-independent migration rates (m_i) were estimated using rotary screw trap (RST) data collected at different locations along the CCV. We calculated the proportion of fry-size fish (< 50 mm) passing through the trap each month. Several sources of uncertainty were related to those estimates: (1) because of the lack of RST efficiency estimates, we assumed that the raw count numbers were a good proxy for juvenile abundances and followed the same temporal trend; (2) because of uncertainties in juveniles' population origins, other CCV Chinook populations' juveniles might have been included in some of those estimates; and (3) when trapping data for a given region were not available, we assumed it was similar to another LCM region's value, based on our knowledge of the system.

The monthly rearing capacities of the Sacramento River (K_3), Sutter Bypass (K_4), Yolo Bypass (K_5), Delta (K_6), and Bay (K_7) were calculated using a series of habitat-specific models that relate habitat quality to a spatial capacity estimate for rearing juvenile Chinook Salmon. Habitat quality was defined uniquely for each habitat type (Sacramento River, Delta, etc.) to reflect the different habitat attributes (see Appendix B for rearing capacity estimation details). Rearing capacities in the natal tributaries (i.e., Butte, Mill, and Deer creeks; K_1) could not be estimated using the same methodology because of the lack of topographic data in these streams. We assumed a constant monthly rearing capacity of one million.

Equations 8 to 14 model the monthly probability of smoltification that both CVSC subyearling and yearling juveniles undergo before migrating to the ocean:

$$YearlingSmolt = P_{Yearling} * RFry_{Tributary} * S_{Yearling} \quad (8)$$

where $YearlingSmolt$ = yearling smolts in the natal tributary, $RFry_{Tributary}$ = rearing fry in the tributary, $P_{Yearling}$ = proportion of fry that follow a yearling (as opposed to subyearling) life history, and $S_{Yearling}$ = oversummer natal tributary's yearling smolt survival rate.

Although yearling smolt outmigrants are assumed to be an important CVSC juvenile life history strategy, especially in Mill and Deer creeks (Johnson and Merrick 2012), there is currently no information on their oversummer survival in the tributaries. Therefore, $S_{Yearling}$ was based on survival estimates of yearling spring-run Chinook Salmon from the Pacific Northwest (Lestelle et al. 2004), which assumed that similar watershed conditions were observed for those two regions in the summer months.

The timing of smoltification of CVSC subyearlings begins in January, with a majority of subyearling smolts outmigrating from April to May (CDFW unpublished RST data):

$$SubyearlingSmolt = P_{Smolt} * RFry_i \quad (9\text{-}14)$$

where $SubyearlingSmolt_i$ = subyearling smolts in ith rearing habitat, $RFry_i$ = rearing fry in ith rearing habitat, P_{Smolt} = monthly smolting probability, and $P_{Smolt,t} = Z_t$, where $0 < Z_1 < Z_2 \ldots < Z_t < 1$ to ensure that the probability of smolting increases over months. The monthly smolting probabilities ($Z_1,\ldots,Z_6$) were estimated to coincide with CVSC tributaries' RST data and the assumption that all fry have smolted by June ($Z_6 = 1$).

Equations 15 to 21 model the survival of smolts from the different rearing habitats to the ocean:

$$YO = P_{YearlMigr} * YearlingSmolt * S_{15} \quad (15)$$

where YO = yearling smolts in the ocean, $PYearlMigr$ = monthly yearling smolt migration probability to the ocean, and S_{15} = survival rate of migrating yearling smolts to the Golden Gate.

$$SO_i = S_i * SubyearlingSmolt_i \quad (16\text{-}21)$$

where SO_i = subyearling smolts from ith rearing habitat in the ocean, S_{16} = subyearling smolt survival rate from natal tributary to the Golden Gate, S_{17} = subyearling smolt survival rate from Sacramento River to the Golden Gate, S_{18} = subyearling smolt survival rate from Sutter Bypass to Golden Gate, S_{19} = subyearling smolt survival rate from Yolo Bypass to the Golden Gate, S_{20} = subyearling smolt survival rate from the Delta to the Golden Gate, and S_{21} = subyearling smolt survival rate from Chipps Island to the Golden Gate.

Subyearling smolt survival rates were broken into survival segments such as:

$$S_{16} = S_{16a} * S_{16b} * S_{16c},$$

$$S_{17} = S_{17a} * S_{17b} * S_{17c},$$

$$S_{18} = S_{18a} * S_{18b} * S_{18c},$$

$$S_{19} = S_{19a} * S_{19b},$$

$$S_{20} = S_{20a} * S_{20b},$$

where S_{16a} = tributary subyearling smolt survival rate, S_{17a} = Sacramento River subyearling smolt survival rate, S_{18a} = Sutter Bypass subyearling smolt survival rate, S_{19a} = Yolo Bypass subyearling smolt survival rate, $S_{16b} = S_{17b} = S_{18b} = S_{20a}$ = Delta subyearling smolt survival rate (i.e., from Sacramento to Chipps Island), $S_{16c} = S_{17c} = S_{18c} = S_{19b} = S_{20b}$ = Bay subyearling smolt survival rate (i.e., from Chipps Island to the Golden Gate).

Yearling smolt survival to the Golden Gate (S_{15}) and subyearling smolt survivals in the tributaries (S_{16a}), Sacramento River (S_{17a}), Sutter and Yolo bypasses (S_{18a}, S_{19a}), and Bay (S_{20b}) were based on survival estimates from multiple acoustic telemetry studies that used Coleman National Hatchery late fall-run (used as a proxy for CVSC yearling smolt because of similar size at outmigration in the fall); Livingston Stone Hatchery winter-run; and natural Butte and Mill creeks' fall-run and spring-run Chinook Salmon juveniles (Michel et al. 2015; Cordoleani et al. 2019; Notch et al. 2020).

Subyearling smolt survival in the Delta (S_{20a}) reflects output of the enhanced particle tacking model (ePTM) developed at the Southwest Fisheries Science Center, Santa Cruz (California) to simulate movement and survival of juvenile Chinook Salmon moving through the Delta (Sridharan and Byrne 2015). The ePTM is based on the Delta Simulation Model II Particle Tracking Model (DSM2 PTM) developed by the California Department of Water Resources (CDWR), and adds juvenile salmon swimming behavior and predation mortality to the DSM2 PTM. In brief, the ePTM simulates juvenile salmon movement through the Delta, and juvenile survival is estimated for each time-step and each node of the Delta grid based on hydrological conditions at the node and the probability of encountering predators (see Hendrix et al. 2017 for details). Since the ePTM was primarily developed for the SRWC LCM, we adapted it for this study to estimate Delta subyearling smolt survival rates for the time-period when CVSC smolts were found in the Delta (i.e., from January to June).

Freshwater Juvenile to Ocean Sub-Adult

CVSC juveniles enter the ocean as subyearling smolts during the first year of their life or as yearling smolts the following year. Although yearling smolt migration to the ocean spans 2 calendar years Y and Y+1, we considered that yearling and subyearling smolts are part of a single fish cohort that turns to Age-1 fish if smolts survive ocean entry:

$$Age1_{Yearling} = S_{22} * YO \quad (22)$$

where $Age1_{Yearling}$ = Age-1 yearling-origin fish, and S_{22} = yearling smolt survival rate from ocean entry to Age-1 fish.

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$$Age1_i = S_{23-28} * SO_i \quad (23\text{-}28)$$

where $Age1_i$ = Age-1 subyearling-origin fish from ith rearing habitat, and $S_{23\text{-}28}$ = subyearling smolt survival rates from ocean entry to Age-1 fish from different habitats (Figure 4).

Because no data exist on Butte, Mill, and Deer creeks' yearling early ocean survival (S_{22}), and because of size similarities between late fall-run and spring-run yearling juvenile Chinook during their ocean outmigration, we assumed that S_{22} was equal to the first year of ocean survival rate used in a cohort analysis conducted on Coleman National Hatchery late fall-run and FRHSC (Cramer and Demko 1996). Additionally, we assumed that the survival of subyearling juveniles during the early ocean phase ($S_{23\text{-}28}$) depended on food availability in the Gulf of Farallones, based on results from Wells et al. (2017) who found a relationship between salmon survival in the Gulf of the Farallones and March upwelling (upwelling index found at *https://www.pfeg.noaa.gov/products/PFELData/upwell/monthly/upindex.mon*). We also hypothesized that subyearling smolts that reared in the tributaries, Sacramento River, and Sutter and Yolo bypass habitats (considered to be "good" rearing habitat) had the same gulf survival. Subyearling smolts from the Delta and Bay habitats (considered to be "poor" rearing habitat) had survival probabilities that were reduced slightly from those of the "good" rearing habitat to reflect lower-quality rearing conditions, which could lead to smaller smolt size at ocean entry (McGurk 1996; Satterthwaite et al. 2014) and affect ocean entry survival:

$$logit(S_{23\text{-}28,good}) = b0.23\_28 + b1.23\_28 * UpMarch$$

$$logit(S_{23\text{-}28,poor}) = b0.23\_28 + b0.23\_28.add + (b1.23\_28 + b1.23\_28.add) * UpMarch$$

where $S_{23\text{-}28,good}$ = ocean entry survival rate for subyearling smolts that reared in "good" rearing habitats (i.e., Tributary, Sacramento River, Sutter Bypass, and Yolo Bypass), $S_{23\text{-}28,poor}$ = Ocean entry survival rate for subyearling smolts that reared in "poor" rearing habitat (i.e., Delta and Bay), and $UpMarch$ = March upwelling index.

Finally, the total number of Age-1 fish was obtained by combining Age-1 subyearling- and yearling-origin fish: $Age1 = Age1_{Yearling} + Age1_i$.

Ocean to Spawning Adult

Sub-adult CVSC will stay in the ocean for 1 to 3 years before returning to freshwater to spawn. Although there is no targeted ocean fishery for CVSC salmon populations, they are harvested mainly at Age-3 and Age-4 in the mixed-stock Chinook fisheries off California and Oregon. West Coast ocean Chinook fisheries are not stock-selective, except to the extent that regulations on timing, location, and minimum size limits can affect the relative impacts on different stocks (Satterthwaite et al. 2018). The main stocks harvested off California and southern Oregon are Central Valley and Klamath River fall-run (Satterthwaite et al. 2015). Yearly sub-adult CVSC mortality from natural or anthropogenic causes while in the ocean is modeled by Equations 29, 31, and 33:

$$Age2 = Age1 * S_{29} \quad (29)$$

where $Age2$ = Age-2 ocean fish, and S_{29} = Age-1 to Age-2 ocean survival rate.

$$Age3 = Age2 * (1 - M_2) * S_{31} \quad (31)$$

where $Age3$ = Age-3 ocean fish, M_2 = Age-2 fish maturation rate, and S_{31} = Age-2 to Age-3 ocean survival rate.

$$Age4 = Age3 * (1 - M_3) * (1 - I_3) * S_{33} \quad (33)$$

where $Age4$ = Age-4 ocean fish, M_3 = Age-3 fish maturation rate, I_3 = Age-3 fish harvest rate, and S_{33} = Age-3 to Age-4 ocean survival rate.

CVSC adults leave the ocean as sexually immature fish during the spring and ascend to the highest accessible elevations of CCV rivers

where spring run-off conditions provide suitable water temperatures (< ~ 21 °C; Williams 2006) for adult CVSC to mature throughout the summer before spawning in the fall. Equations 30, 32, and 34 estimate the cumulative survival of adults during their migration to the natal reaches and their maturation stage:

$$Age2Spawner = Age2 * M_2 * S_{30} * S_{prespawn} \quad (30)$$

where $Age2_{Spawner}$ = Age-2 fish spawning in the natal tributary, S_{30} = survival of Age-2 fish to the spawning ground, and $S_{prespawn}$ = adult fish holding/pre-spawning survival in tributaries during summer months.

$$Age3Spawner = Age3 * M_3 * (1 - I_3) * S_{32} * S_{prespawn} \quad (32)$$

with $Age3_{Spawner}$ = Age-3 fish spawning in the natal tributary, and S_{32} = survival of Age-3 fish to the spawning ground.

$$Age4Spawner = Age4 * (1 - I_4) * S_{34} * S_{prespawn} \quad (34)$$

where $Age4_{Spawner}$ = Age-4 fish spawning in the natal tributary, I_4 = Age-4 fish harvest rate, and S_{34} = survival of Age-4 fish to the spawning ground.

Direct estimates of CVSC ocean harvest rates (I_3 and I_4) are not available for most years covered by our study. We assumed that the effects of ocean fisheries on Age-3 CVSC were equal to ocean effects calculated for Age-3 SRWC from the same brood year (BY) because of similarly small size-at-age and the returning of mature adults in spring, before the most intense pressure from ocean fisheries in a given calendar year. We assumed that the effects of ocean fisheries on Age-4 CVSC equaled the arithmetic mean of the SRFC adult ocean harvest indices (as a result of broadly similar size and spatial distribution) calculated for fishing years corresponding to BY+3 and BY+4. For SRFC, harvest rate calculations for fishery year Y span from September 1 of calendar year Y-1 to August 30 of calendar year Y. Thus, for maturing CVSC returning in spring (nominally May 1; Grover et al. 2004) of calendar year Y, their last year in the ocean partially exposes them to fisheries that correspond to fishery year Y (from September 1 of calendar year Y-1 through April 30 of calendar year Y) and partially to fisheries that correspond to fishery year Y-1 (May 1 through August 30). Ocean harvest rate estimates were obtained from the Pacific Fishery Management Council (PFMC 2018), with earlier harvest rate estimates for SRWC obtained from O'Farrell and Satterthwaite (2015). SRFC ocean harvest indices were calculated as total ocean harvest divided by the Sacramento Index (PFMC 2018, their Table II-1). Annual harvest rate estimates are summarized in Table A2.

Additionally, even though Grover et al. (2004) used 3 years of coded wire-tagged (CWT) Butte Creek data to try to estimate CVSC Age-2, –3, and –4 maturation rates, because of the low number of ocean CWT recoveries during those years and the limited number of years studied, the exact maturation schedule of wild CVSC populations—along with its degree of variability—remains unknown. We combined Grover et al. (2004) cohort reconstruction results and additional Butte Creek CWT data from adults recovered in the spawning ground between 2001 and 2010 to estimate CVSC Age-2 and Age-3 maturation probabilities (M_2, M_3). Finally, because Butte Creek Age-5 CWT recoveries have occurred in ocean fisheries but not in carcass surveys, we did not include Age-5 fish in this model, and considered that all Age-4 fish remaining in the ocean a given year had to reach maturation (i.e., $M_4 = 1$).

Wild CVSC adult survival from the ocean to the spawning ground (S_{30}, S_{32}, S_{34}) is also unknown. Mortality from harvest during the migration to adult spawning phase was ignored in the model because there are currently no legal CVSC freshwater fisheries in Butte, Mill, and Deer creeks. Thus, survival for this life stage event was assumed to be high, and similar to the survival of migrating Chinook Salmon adults from the Pacific Northwest (Lestelle et al. 2004).

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In Butte Creek, large pre-spawning mortality events have been observed and linked to elevated water temperature in the holding/spawning reaches during the summer months (Garman and McReynolds 2012). Therefore, Butte Creek adult pre-spawning survival ($S_{prespawn}$) was modeled using the temperature-dependent survival relationship developed by Thompson et al. (2012):

$$logit(S_{prespawn}) = b0.prespawn + b1.prespawn * T$$

where T = monthly water temperature in Butte Creek holding and spawning pools.

Because no pre-spawning mortality assessments exist for the Mill and Deer creeks' populations, we assumed that limited mortality could occur as a result of water temperature stress, predation, and adult poaching risks ($S_{prespawn}$=0.9).

To close the life cycle loop, Equation 35 describes the production of eggs by Age-2, Age-3, and Age-4 spawners:

$$\begin{aligned} Eggs = (&V_{age\,2} * Age2Spawner * Fec_{age\,2} \\ &+V_{age\,3} * Age3Spawner * Fec_{age\,3} \\ &+V_{age\,4} * Age4Spawner * Fec_{age\,4}) / \\ (1 + (&V_{age\,2} * Age2Spawner * Fec_{age\,2} \\ &+V_{age\,3} * Age3Spawner * Fec_{age\,3} \\ &+V_{age\,4} * Age4Spawner * Fec_{age\,4}) / K_{sp}) \end{aligned} \quad (35)$$

where $Eggs$ = eggs produced in natal tributary, $Vage_j$ = fecundity rate of Age-j female fish, Fec_j = Age-j proportion of female, and K_{sp} = spawning carrying capacity.

Sensitivity Analysis

Before we calibrated the model, we conducted a global sensitivity analysis to evaluate the relative influence of different model parameters on the projected model outputs. From an ecological perspective, such an analysis can help identify the life stage events that contribute most to influencing overall population dynamics. Using a global (rather than local) sensitivity analysis is advantageous because it accounts for the effects of interactions between different parameters, and it does not assume a linear relationship between the parameters and state variables (Cariboni et al. 2007; Saltelli et al. 2008). Parameter value ranges were generated using the Latin Hypercube Sampling function (LHS; function "lhs" from the "pse" package in R) (McKay et al. 1979), a stratified sampling-without-replacement method often selected to perform sensitivity analysis of complex non-linear models such as the LCM developed here (Chalom and Prado 2012). We assumed that each parameter followed a normal probability density function, with a mean equal to the initial parameter value listed in Table A1. A standard deviation (SD) of 0.85 was used for every parameter, to account for large uncertainty in existing parameter estimates, except for the Thompson et al. (2012) temperature model parameter for which SD was obtained from the 95% CI values reported, and for the fecundity rate parameters ($Fecj$) where we assumed that SD = 300 for Fec_{age2}, and SD = 500 for Fec_{age3} and Fec_{age4}. Partial rank correlation coefficients (PRCCs) for the series of adult abundances generated under different parameterizations were estimated to assess the model's sensitivity to each parameter variation. PRCCs provide a measure of the strength of an association, that could be non-linear, between a parameter and the model output (Marino et al. 2008). The closer the PRCC value is to –1 or 1, the stronger the parameter's influence on the model's output. A negative sign indicates that the parameter is inversely proportional to the adult abundance measure. We looked at the influence of every parameter described in the model structure section (Table A1), besides the habitat-specific rearing and spawning capacities, and the ePTM subyearling smolt Delta survival estimates obtained from collaborators. Because of the way capacity and smolt Delta survival parameters are included in the model, a separate sensitivity analysis would be required to study their influence on the model's dynamics, and a direct comparison of both sensitivity analyses was beyond the scope of this study.

We also performed a post-calibration sensitivity analysis to assess whether changes in parameter

values related to the calibration process led to a significant change in the LCM's sensitivity results. We implemented the same methodology as presented for the pre-calibration sensitivity analysis. We used the initial parameter values found in Table A1, except for the parameters that were estimated during the model's calibration (see section below), for which we used the new estimations.

Model Calibration

This LCM was used as a hindcast model. When forced with historical habitat conditions (e.g., monthly varying flow, water temperature, annual coastal upwelling) and harvest rates, it reflects historical trends and spatial patterns in CVSC adult abundance. For each population, we calibrated the model by fitting the adult abundance predictions to available spawner abundance observations from 1985 to 2009 (Azat 2019). During the model's calibration, we estimated only a set of 11 parameters identified during the pre-calibration sensitivity analysis to strongly influence population dynamics (Table 1, "Value" column). We fixed the rest of the model parameters to initial values (Table A1). We assumed that the spawner abundance followed a log-normal likelihood distribution, and we estimated the parameter values by maximizing the likelihood of observing the spring-run adult abundance indices. We parameterized the model using a general-purpose optimization method with a simulated anneal optimization algorithm to avoid local minima (function "optim" with the "SANN" method in R; Kirkpatrick et al. 1983). Finally, we compared spawner abundance observations to the model predictions obtained with the estimated parameters.

Additionally, because only spawner abundance data are currently available to calibrate this multi-stage model, and studies in other systems have shown that observations at multiple points in the life cycle could increase the performance of population models (e.g., Rivot et al. 2004; Winship et al. 2014), we hypothesized that the LCM's calibration would improve with the addition of a juvenile abundance time-series. To test this hypothesis, we decided to work with simulations of stock-specific Chipps Island CVSC juvenile trawl data. Chipps Island is a key location in the Central Valley for Chinook Salmon monitoring where mid-water trawling has been conducted since 1976 to gain information about juvenile Chinook Salmon emigrating from the Delta to the Pacific Ocean (USFWS 2010). However, we could not use actual Chipps Island juvenile data because of inconsistency in counts reported during the years of interest (e.g., counts combining fall-run and spring-run fish [USFWS 2010]), and run misclassification as a result of the use of length-at-date criteria (Pyper et al. 2013a). Therefore, juvenile abundance of CVSC entering the Bay were generated from a log-normal distribution ("rlnorm" function in R) with a mean value equal to the mean predicted Bay juvenile abundance obtained from the LCM, using the initial parameter values reported in Table A1 and a standard deviation equal to Chipps Island trawl efficiency estimate (Pyper et al. 2013b). A second calibration was then performed by fitting the LCM simultaneously to annual spawner abundances and to the simulated monthly Bay juvenile abundances, where spawner and juvenile abundances were given equal weights in measuring fit. The same set of parameters were estimated by maximizing the joint likelihood distribution of spring-run adult and juvenile abundances (Table 1, "Value with Chipps data" column). Although this exercise has some limitations, because Bay juvenile LCM prediction was used to generate the juvenile abundance time-series, we believe the results can be used to qualitatively assess the potential benefit of having additional data sets for the LCM's calibration.

RESULTS

Parameter Sensitivity Analysis

During the pre-calibration sensitivity analysis, the highest sensitivity for Butte Creek dynamics was linked to the parameters of the temperature-dependent adult pre-spawning survival relationship (PRCC value greater than 0.4; Figure 5A). The Butte Creek population was also observed to be:

- sensitive to Age-2 fish survival in the ocean, egg to fry survival, subyearling smolt survival

https://doi.org/10.15447/sfews.2020v18iss4art3

Table 1 Parameter estimates from the optimization algorithm when only adult abundance data are used for model fit ("Value" column), and when Chipps Island juvenile abundance are also used for model fit ("Value with simulated Chipps data" column). (**A**) Butte Creek population. (**B**) Mill/Deer creeks' population. See Table A1 in Appendix A for parameter description.

A

Parameter	Value	Value with Chipps data
S.eggs.BC	0.97	0.89
S.tributary.BC	0.99	0.87
S.16a.BC	0.99	0.27
S.18.a	3.5e-04	6.9e-03
S.SmoltBay	0.68	0.32
b0.23_28	0.97	0.96
b1.23_28	6.6e-04	0.75
S.29	0.14	0.89
S.31	0.99	0.95
M.3	0.40	0.62
S.30,S.32,S.34	0.97	0.73

B

Parameter	Value	Value with Chipps data
S.eggs.MDC	0.99	0.99
S.tributary.MDC	1	0.99
m.river.MDC	0.03	0.82
S.16a.MDC	0.99	0.59
S.SmoltBay	0.99	0.03
b0.23_28	0.81	0.92
b1.23_28	0	0.50
S.29	0.05	0.95
S.31	0.99	0.99
M.3	0.99	0.98
S.prespawn.MDC	0.71	0.90

in the tributary and in the Bay, early-ocean survival in the Gulf of Farallones (PRCC values greater than 0.2; Figure 5A) and

- somewhat sensitive to Age-3 fish survival in the ocean, rearing fry survival in the tributary, Age-3 maturation rate, adult survival from ocean to spawning ground, and subyearling smolt survival in the Sutter Bypass (PRCC values greater than 0.1; Figure 5A).

The highest sensitivity for Mill and Deer creeks' dynamics was linked to egg to fry survival, Age-2 fish survival in the ocean, and the tributary's density-independent fry migration rate (PRCC values greater than 0.4; Figure 5B). The Mill and Deer creeks' population was also observed to be:

- sensitive to subyearling smolt survival in the tributary, rearing fry survival in the tributary, subyearling smolt survival in the Bay, Age-3 fish survival in the ocean, early-ocean survival in the Gulf of Farallones, Age-3 maturation rate, adult pre-spawning survival, adult survival from the ocean to spawning ground, and monthly yearling smolt migration probability to the ocean (absolute PRCC values greater than 0.2; Figure 5B).

- somewhat sensitive to Delta fry survival, Sacramento River's density independent fry migration rate, the probability of becoming a yearling, and yearling smolt survival in the tributary and to the ocean (absolute PRCC values greater than 0.1; Figure 5B).

All those parameters correlated positively with the model's output—other than for Mill and Deer creeks' fry migration to the Sacramento River, where higher adult abundance was correlated with a lower migration to the Sacramento River. This suggests that increased rearing in Mill and Deer creeks' tributary rather than in downstream habitats might improve overall population resiliency.

Most of the parameters that were identified to influence the LCM dynamics in the pre-calibration sensitivity analysis were found to influence the post-calibration LCM dynamics

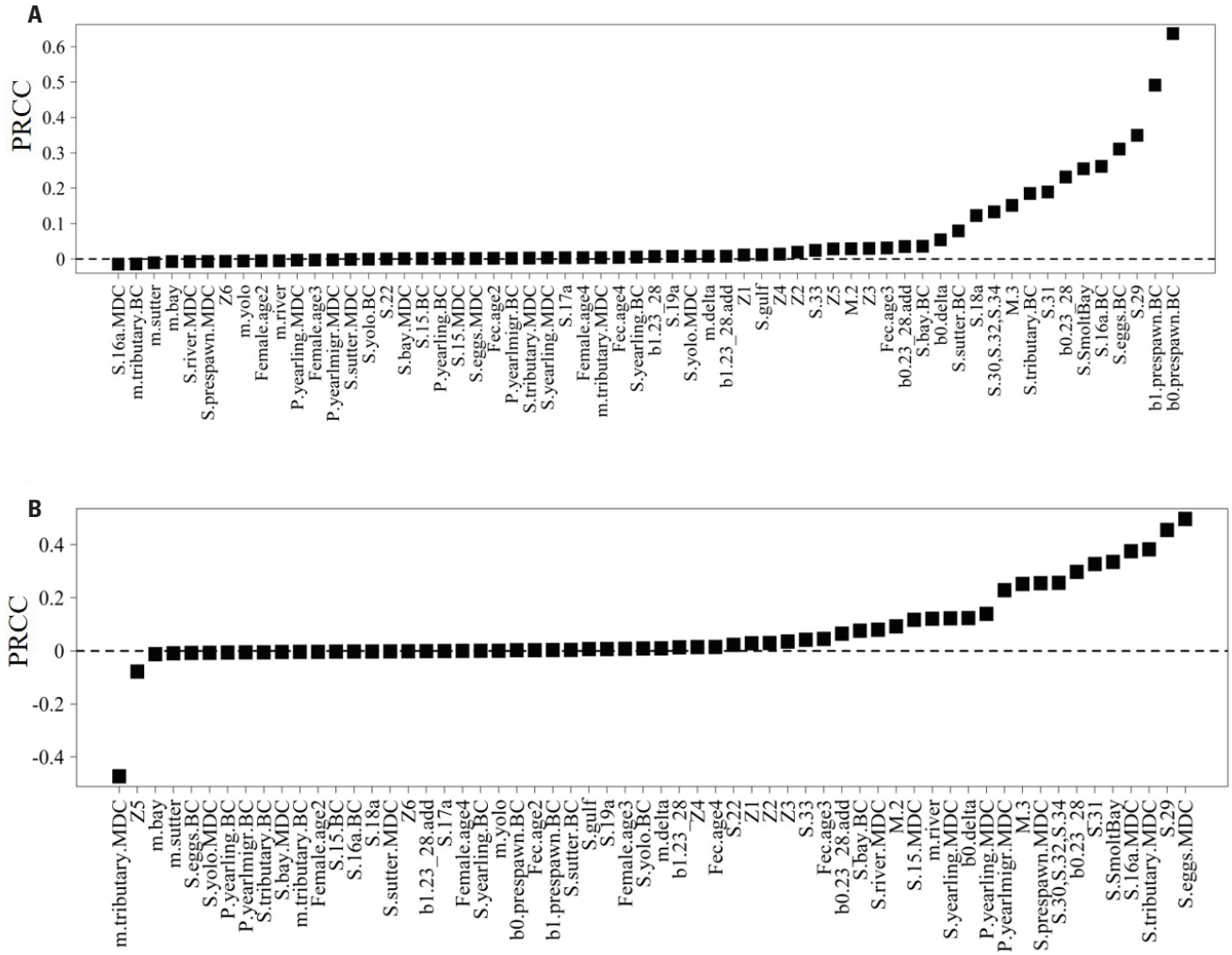

Figure 5 Pre-calibration global sensitivity analysis results. (**A**) Butte Creek population PRCC values for each LCM parameter. (**B**) Mill/Deer creeks' population PRCC values for each LCM parameter. The closer the absolute value of the PRCC value is to 1 the stronger the parameter's influence on the model output. See Table A1 in Appendix A for parameter description.

as well (Figures 6A and 6B). However, we found some parameters, in particular those that were estimated during calibration—such as egg-to-fry survival, rearing fry survival in the tributary, subyearling smolt survival from the tributary to Sacramento, and Age-3 ocean survival rates—to be less influential after calibration. A few parameters—such as Butte Creek fry migration rate, Mill and Deer creeks' yearling smolt survival during the summer months, yearling smolt ocean outmigration probability, and survival rate—had a higher influence on the LCM's population dynamics after calibration. Those pre- and post-calibration differences highlight the potential role of parameter correlation in redirecting some of the model's sensitivity from one parameter that had a decreased influence on the model after calibration to another likely correlated parameter. For instance, we found that Butte Creek fry migration rate, which is likely correlated to rearing fry survival rate, had a greater effect on population dynamics during the post-calibration sensitivity analysis, while the estimated rearing fry survival rate had a lesser effect on it. Moreover, these pre- and post-calibration differences emphasize the importance of reducing parameter estimation uncertainty to improve model robustness.

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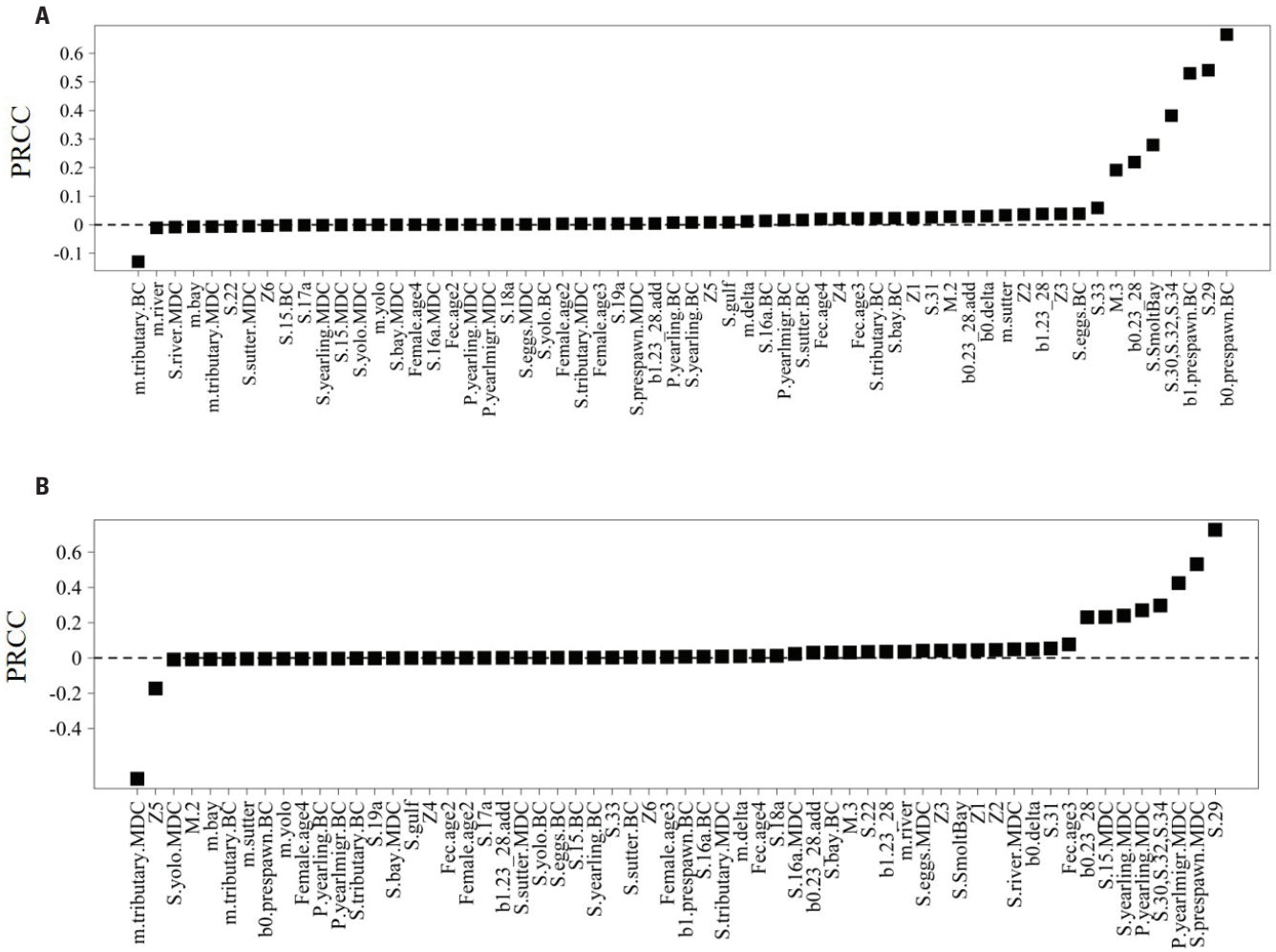

Figure 6 Post-calibration global sensitivity analysis results. (**A**) Butte Creek population PRCC values for each LCM parameter. (**B**) Mill/Deer creeks' population PRCC values for each LCM parameter.

Model Performance

Overall, the fitted LCM was able to capture the general Butte Creek spawner dynamics observed (Figure 7A and 7B). However, the model was not able to capture the high number of spawners produced in 1995, 1998, and 2005, and it largely overestimated the spawner abundances in 2003 and 2007. The model fit to Mill and Deer creeks' spawner dynamics was acceptable overall; however, in some instances it seemed out of phase with the observations (Figure 8A and 8B). The model largely overestimated abundance in 2001, 2004, 2009, and it largely underestimated abundance increases in 1990, 1999, and 2005.

When we fit the model to adult abundance only, some of the estimated parameters had values very close to boundaries (parameter values close to 0 or 1). However, our addition of a juvenile abundance time-series for the model's calibration allowed it to obtain a more realistic combination of estimated parameter values (see Table 1 for comparison). Although the juvenile data used here might not be the most realistic reflection of the accuracy and precision of data that might be collected in practice, and was generated under the assumption that our model structure was appropriate, this exercise showed how having an additional calibration checkpoint could create more constraints on parameter estimation and improve the model calibration.

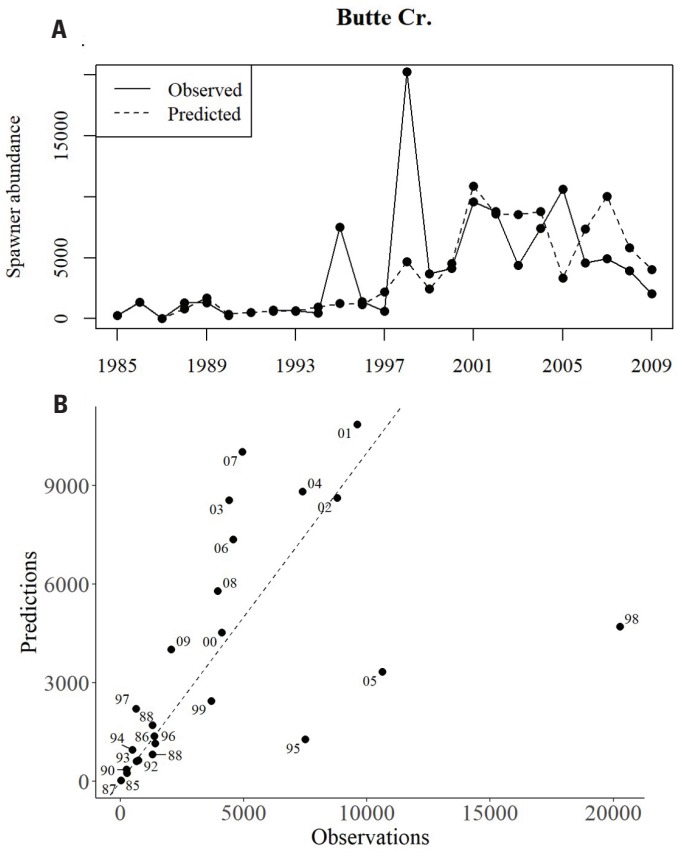

Figure 7 (**A**) Observed and predicted Butte Creek CVSC annual spawner abundance time series. (**B**) Predicted versus observed Butte Creek CVSC annual spawner abundance. Each dot represents a given escapement year (yy).

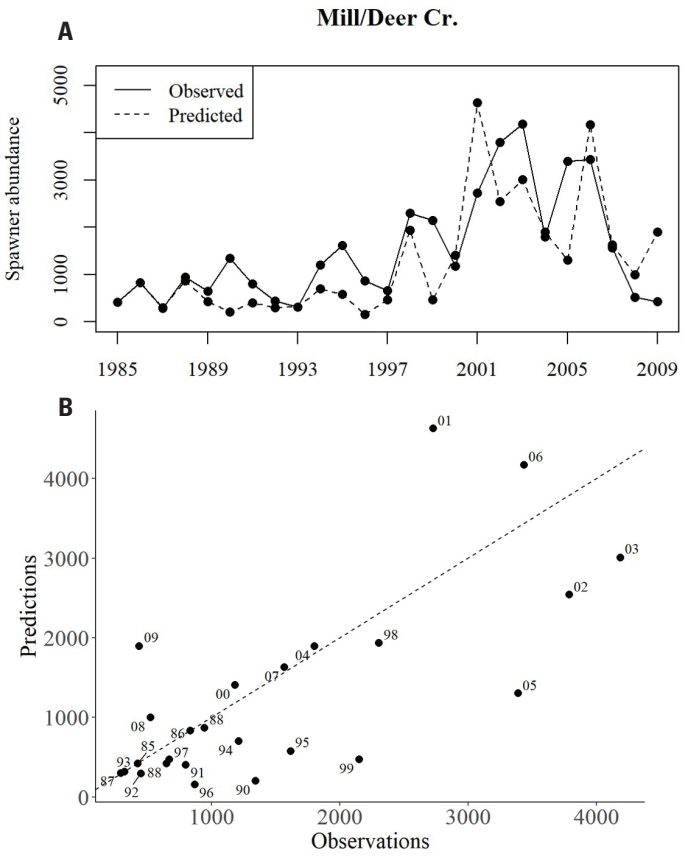

Figure 8 (**A**) Observed and predicted Mill/Deer creeks' CVSC annual spawner abundance time series. (**B**) Predicted versus observed Mill/Deer creeks' CVSC annual spawner abundance. Each dot represents a given year (yy).

DISCUSSION

Monitoring Recommendations

Based on what we learned from the model's construction, calibration, and sensitivity analyses results, we propose potential monitoring recommendations that we believe would help fill important data gaps, with the goal to improve the LCM fitting performance, as well as to deepen our understanding of CVSC dynamics.

Juvenile Abundance Estimates

The results from the simulation exercise suggested the importance of juvenile abundance estimation at key locations, such as Chipps Island, to improve the LCM's calibration. Studies in other systems have also shown how observations at multiple points in the life cycle can increase the performance of population models; for example, through allowing state-space models to integrate multiple sources of information (e.g., Rivot et al. 2004; Winship et al. 2014). However, CVSC juvenile abundance estimation is currently a critical key data gap in the monitoring of those populations, and juvenile production estimate (JPE) was recently identified as an important metric to be developed to assess how the long-term operation of the State Water Project (SWP) in the Delta influenced CVSC populations (CDFW 2020). The juvenile production estimate of fish entering the Bay could also help with estimating the smolt-to-adult-return index, which is often used to tease apart the effect of freshwater versus ocean conditions on salmon population dynamics (Petrosky and Schaller 2010; Michel 2019).

https://doi.org/10.15447/sfews.2020v18iss4art3

Even though Chipps Island trawls provide important information on the timing of when CVSC juveniles exit the Delta and enter the Bay (USFWS 2010), none of these monitoring programs report population-level abundance estimates for CVSC juveniles or other CCV Chinook runs. The expansion of catch to absolute estimates of abundance depend on adequate estimates of gear efficiency. Pyper et al. (2013b) found that varying estimates of trawl efficiency at Chipps Island can significantly affect abundance estimates. Currently, no robust approach for estimating trawl efficiency allows catch data to be expanded to abundance measures. Furthermore, the stock identification of the sampled fish at each location is based on the length-at-date (LAD) criterion, which was shown to be inaccurate for spring-run fish compared to genetic identification (Pyper et al. 2013a). Poor LAD stock identification arises from mixing salmon runs as a result of their overlapping dynamics in time and space. Sacramento River fall-run Chinook juveniles are commonly misclassified as CVSC, and this LAD inaccuracy leads to an overestimate of CVSC juvenile counts. To generate accurate trawl efficiency estimates and abundance estimates of juvenile SRWC at Chipps Island, a study proposed by Johnson et al. (2017) is currently in progress that combines CWTs, acoustic-tagged (AT) hatchery fish, and genetic stock identification (GSI). This approach could simply be extended to assessing CVSC juvenile abundance by estimating trawl efficiency for the CVSC juvenile's outmigration time window, and using the same GSI approach to identify the presence of CVSC stocks. Similarly, to estimate the CVSC JPE for Delta entrance, the hybrid design study currently developed for Chipps Island trawl efficiency could also be extended to the Sacramento trawl site at Sherwood Harbor, because this location constitutes a good Delta entrance checkpoint (Barnard et al. 2015).

Finally, to collect CVSC juvenile outmigration size and timing information, Butte, Mill, and Deer creek RSTs have been operated by the California Department of Fish and Wildlife (CDFW). Although the RST is still in place in Butte Creek, annual juvenile monitoring in Mill and Deer creeks terminated in 2010, and RSTs are now used opportunistically for acoustic telemetry studies. During years when the RST was in place, trap efficiency tests were not performed because of high winter flow fluctuations, and the limited ability to consistently catch sufficient numbers of test fish for recapture trials, especially in Mill and Deer creeks (Johnson and Merrick 2012). Therefore, CVSC juvenile catch data from Butte, Mill, and Deer creek RSTs could not be extrapolated to juvenile abundance estimates. To obtain natal tributary JPE estimates, a RST trap efficiency protocol—like the ones developed in other CVSC tributaries (e.g., Clear Creek and Battle Creek; Schraml et al. 2020; Schraml and Earley 2020)—would need to be implemented in Butte, Mill, and Deer creeks. Additionally, because it has been suggested that yearling juveniles effectively avoid RSTs, because of their larger size and swimming abilities, evaluating size-specific trap efficiency would also be important, to make sure that yearling abundance is properly assessed.

Subyearling Smolt Freshwater Survival

The sensitivity analyses identified subyearling smolt survival in various CCV regions (e.g., the natal reaches and the Bay) as important parameters that influence both Butte as well as Mill and Deer creeks' population dynamics. With new advances in acoustic tagging technology (smaller tags, longer battery life), biotelemetry has become a well-established tool in estimating movement and survival rates of Central Valley hatchery Chinook Salmon smolt-sized juveniles (Michel et al. 2013, 2015; Perry et al. 2010, 2013). Recently, acoustic tagging experiments have also been performed on wild CVSC smolt populations from Mill Creek (for the period 2013-2017; Notch et al. 2020) and Butte Creek (2015-2017; Cordoleani et al. 2018, 2019). However, it is appropriate to highlight certain caveats from those two studies: (1) tagging occurred during the last California drought period and likely do not represent the suite of hydrological conditions and water-year types CVSC juveniles experienced during the modeled years, (2) because of the small number of tagged fish detected exiting the Delta and entering the Bay, smolt survival estimates for this region were associated with large error

margins, and (3) Butte Creek juveniles were tagged in the Sutter Bypass, therefore survival estimates in the upper Butte Creek watershed are not available and might differ from the ones found for the Bypass. Consequently, expanding the CVSC short-term acoustic tagging projects to a long-term acoustic monitoring program, which would spatially include upper Butte Creek (e.g., trapping and tagging could be done at the Parrot Phalon Diversion Dam RST; Garman and McReynolds 2009), would help to assess the survival of CVSC smolts more accurately along their entire migratory corridor and across various hydroclimatic conditions. Additionally, combined with the development of a systematic water quality monitoring program (i.e., water temperature, flow, turbidity, toxin/pathogen concentrations), and localized predation impact studies, especially at in-river structures (Sabal et al. 2016), the influence of each environmental/biological stressor on smolts' survival could be more clearly identified, providing insights on observed inter-annual survival variance. Furthermore, real-time detection of the tagged fish throughout their migratory path could serve the adaptive management of CCV water operations, while protecting migratory CVSC juveniles (Klimley et al. 2017).

Fry and Yearling Movement and Survival, and Rearing Habitat Capacity in the Natal Tributaries

Rearing fry and yearling survivals in the natal tributaries were also identified as strongly affecting population dynamics in Butte, Mill, and Deer creeks in the pre- or post-calibration sensitivity analysis. Fry survival estimates are more difficult to obtain than smolt survivals, because of their small size. However, the use of passive integrated transponder devices (PIT tags; Gibbons and Andrews 2004) to mark and track parr-sized juveniles (fish >50mm) in the spring-run tributaries could help gain insight into the survival of smaller fish in the natal reaches. Yearling juveniles could also be PIT-tagged in their natal tributaries, which would provide valuable missing information on their survival over summer. This would also allow important information on juvenile movements within those reaches to be collected, and improve estimation of the density-independent fry migration rates from the tributaries to downstream habitat, as well as the yearling smolt ocean outmigration probabilities—parameters which were also found to affect CVSC population dynamics. Additionally, the ongoing miniaturization of electronic tags and the development of acoustic micro-tags, such as the Eel/Lamprey acoustic tag (ELAT; Fischer et al. 2019), will likely allow even smaller Chinook Salmon juveniles to be tagged in the near future, and will help to further improve estimation of fry survival.

During construction of the model, we were not able to accurately estimate juvenile rearing capacity in natal tributaries, because of a lack of bathymetric data among other data sources. Accurate evaluation of CVSC tributary rearing capacity is of great importance, because it guides density-dependent fry movement in the LCM, which could play an important role in fry dynamics. Two primary factors used to estimate the rearing capacity are water depth and velocity experienced in the stream network over space and time (Rosenfeld et al. 2011). To estimate water depth and velocity, hydraulic models such as the Hydrologic Engineering Center's River Analysis System (HEC-RAS) can be used to simulate channel characteristics under varying flow conditions at different locations in a stream network. A main component required to run hydraulic models is accurate channel geometry information. Currently, channel geometry information for CVSC tributaries is lacking, and this lack prevents estimating habitat capacity at the desired temporal and spatial scale using hydraulic models. Typically, channel geometry can be gathered by ground-based methods, such as cross-sectional surveys using total stations, or by remote-sensing methods, such as aerial-based bathymetric light-detection and ranging (LiDAR), or, more recently, using unmanned aerial vehicles (UAVs) equipped with sensors such as multi-spectral cameras and using methods such as photogrammetry (Legleiter et al. 2009; Tamminga et al. 2014). While ground-based survey methods are traditionally inexpensive and relatively easy to implement for short reaches of a stream (e.g., less than a few kilometers),

https://doi.org/10.15447/sfews.2020v18iss4art3

conducting ground-based survey methods for CVSC tributaries over tens of kilometers may present challenges associated with access to private land, difficult working terrain, high costs, and time. However, bathymetric LiDAR and UAVs also have relevant limitations; these include cost and reduced accuracy when characterizing areas with deep water, depending on factors such as turbidity, water aeration, and others that affect the scattering and adsorption of LiDAR-emitted wavelengths received by other sensors (Kinzel et al. 2012; Tamminga et al. 2014). Therefore, a hybrid approach using both ground- and remotely-based observations may be necessary to characterize the channel geometry of CVSC tributaries at the desired scale, as has been done elsewhere (Kinzel et al. 2012). A hybrid approach would also provide additional information valuable to managing CVSC. For example, the UAV approach with a true color sensor can acquire sub-meter resolution images of habitat metrics related to salmon habitat, such as distribution of exposed large woody debris and gravel bars in a stream network. Similarly, the ground-based survey associated with the hybrid approach could be used as an opportunity to characterize additional features of the CVSC tributaries related to salmon habitat use, such as substrate composition and identifying areas of high- and low-quality habitat for rearing and spawning.

Egg-to-Fry Survival

Egg-to-fry survival was also found to affect both Butte and Mill/Deer creeks' population dynamics during the pre-calibration sensitivity analysis, and has also been reported as a limiting factor for the recovery of spring-run Chinook population in other systems (e.g., Honea et al. 2009). However, there is currently no estimation of egg-to-fry survival in those tributaries, and the estimate for the LCM parameterization was based on survival values from spring-run Chinook Salmon from the Yuba River, which experience different hydrologic, water temperature, and gravel-permeability conditions (Stillwater Sciences 2013). Additionally, the effect of elevated temperature on the CVSC per-adult egg production and survival in the gravel is unknown. Yet, it has been shown that exposure to elevated temperature critically undermines SRWC embryo survival (USFWS 1999; Martin et al. 2017). Therefore, although water temperatures recorded in the spring-run tributaries are not typically as high as in the SRWC spawning grounds, a warming climate and drought events that could become more intense and regular could strongly affect CVSC egg-to-fry survival. Estimation of this parameter across several years and different hydroclimatic conditions is thus necessary.

One way to obtain those estimates would be to implement an approach similar to the one used at Red Bluff Diversion Dam (RBDD) to calculate the SRWC JPE. The SRWC egg-to-fry survival rate at RBDD (a key location for this population) is back-calculated using the spawner abundance estimates from redd and carcass surveys, the estimated number of eggs produced by spawner, and the fry-equivalent abundance estimate at RBDD, which depends on the fry-to-smolt survival and the smolt survival from the spawning ground to RBDD (O'Farrell et al. 2018). As previously mentioned, no tributary CVSC JPE currently exists, and to obtain a fry-equivalent abundance estimate in Butte, Mill, and Deer creeks would require a trap efficiency protocol to be implemented. Additionally, fry-to-smolt and smolt survivals in the tributaries would also need to be estimated by, for instance, developing a multi-year PIT tagging and telemetry acoustic study, as suggested in the previous section.

Adult Pre-Spawning Survival

Based on the sensitivity analysis results, adult pre-spawning survival is another factor that strongly influences the dynamics of both Butte and Mill/Deer creeks populations. Warm water has been shown to exacerbate a number of salmonid diseases (e.g., columnaris, furunculosis, *Ichthyophthirius* infection, external fungal infections, and enteric redmouth disease; CDFG 1998), and can seriously reduce Butte Creek adult pre-spawning survival during the summer months (Garman and McReynolds 2012). A pre-spawning carcass survey monitoring program developed for Butte Creek since 2003 has allowed the estimation of pre-spawning mortality and

the dynamics of spawner abundance during the summer months. However, future funding for this program is currently uncertain (2019 email between C. Garman and F. Cordoleani, unreferenced, see "Notes"). Additionally, since 2012 for Mill Creek and 2014 for Deer Creek, video monitoring has been used to estimate the number of adults entering the tributaries in the spring and summer, and to compare with the total escapement numbers estimated from the redd and snorkel survey counts performed during the spawning season (Killam 2019). However, to obtain an accurate estimate of pre-spawning survival, additional managerial emphasis and funding should be directed to redd/spawner surveys on Mill and Deer creeks. Furthermore, water temperature monitoring in the different holding and spawning reaches of the stream needs to be developed and combined with long-term pre-spawning monitoring programs to develop a robust temperature-dependent pre-spawning survival model for each extant CVSC population.

Ocean Survival, Harvest and Maturation Rates

Age-1, -2 and -3 ocean survival rates in the absence of fishing (i.e., the inverse of natural mortality), as well as Age-3 maturation rates, were also among the parameters identified in the sensitivity analysis for their important influence on Butte and Mill/Deer creeks population dynamics. Although sub-adult natural mortality rates in the ocean are difficult to estimate for salmon and often simply assumed (but see Allen et al. 2017), cohort reconstructions are routinely used for some stocks to estimate juvenile natural mortality (e.g., Kilduff et al. 2015). Additionally, harvest rates for CVSC populations were unknown for most of the modeled years, and values had to be assumed based on other stocks. Furthermore, because Age-4 effects are likely substantially higher than Age-3 effects, the overall effects of ocean fisheries are highly sensitive to uncertain maturation schedules. Although the maturation rate of spring-run Age-2 fish is assumed to be very low, and CVSC adults mainly return to spawn at Age-3 and Age-4 fish, the exact maturation schedule of wild CVSC populations is unknown. Therefore, a better assessment of early survival in the ocean and sub-adult ocean harvest effect on CVSC, through cohort reconstruction and maturation rate estimation, is the first step toward being able to tease apart the role of natural versus human-related ocean mortality on their dynamics.

We propose here two, potentially complementary, routes. First, FRHSC cohort reconstruction could be performed, accompanied by ongoing research into the suitability of hatchery fish as proxies for the effect of fishing on natural CVSC (Satterthwaite et al. 2018). Ocean harvest of FRHSC could be calculated based on CWT recoveries reported in the Regional Mark Processing Center (*www.rmis.org*). Coordinated CWT sampling of ocean harvest is carried out coastwide for both commercial and recreational fisheries; however, catch of FRHSC is not routinely calculated from these data. Routine cohort reconstructions (similar to O'Farrell et al. 2012a) could therefore be conducted for FRHSC, allowing calculation of age-specific exploitation rates. In the absence of better information, year-specific FRHSC exploitation rates could be assumed to also apply to natural-origin CVSC, although this should be done with caution (Grover et al. 2004; Satterthwaite et al. 2018). Cohort reconstructions applied to FRHSC would also allow for maturation rates to be directly estimated, although there is evidence that maturation rates differ between natural and hatchery-origin fish (Sharma and Quinn 2012). However, there is limited information available to test this assumption for CVSC, and no strong evidence for differences has been found (Satterthwaite et al. 2018).

Second, GSI can identify most natural-origin CVSC, although FRHSC are assigned to the "Central Valley Fall" reporting group along with Sacramento and San Joaquin fall-run and Sacramento late-fall-run Chinook (Clemento et al. 2014). Previous GSI studies allowed calculation of natural-origin CVSC harvest in particular times, locations, and fishery sectors (e.g., Bellinger et al. 2015; Satterthwaite et al. 2015), but GSI data have not been (and are not currently being) collected as part of a coastwide sampling scheme that covers all relevant times, areas, and fishery sectors.

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Thus, GSI sampling could be expanded to cover the entire coast (or at least throughout California and Oregon where it appears most CVSC are caught; Satterthwaite et al. 2013; Bellinger et al. 2015) with representative sampling in all times, areas, and fishery sectors. Since CVSC make up only a small portion of the catch (Bellinger et al. 2015; Satterthwaite et al. 2015), sample sizes would need to be large (Allen-Moran et al. 2013). Comprehensive GSI sampling would enable total natural-origin CVSC catch (exclusive of FRHSC) to be calculated, but estimating age-specific exploitation rates would also require aging (e.g., through scale reading) of genetically identified CVSC, as well as accurate and age-specific estimates of CVSC escapement over the entirety of the CVSC genetic reporting group (O'Farrell et al. 2012b). Alternatively, if it is confirmed that GSI can separate Butte Creek CVSC from the remainder of CVSC populations with high accuracy, cohorts could be reconstructed based on Butte Creek CVSC harvest and escapement alone. Cohort reconstructions applied to natural-origin CVSC would also allow for maturation rates to be directly estimated, and thus provide important context for understanding the relative effect of harvest on different age classes.

CONCLUSION

Providing scientific data and modeling results in a format that stimulates constructive dialog among scientists, resource managers, and stakeholders can be challenging, but is an important step for the recovery of threatened CVSC ESU. The CVSC LCM described in this paper represents a valuable scientific framework that was used here to highlight key data needs required to improve management of CVSC populations. While we developed the model, we realized that targeted monitoring of the remaining CVSC populations is somewhat limited, and insufficient to support robust model predictions of CVSC populations' responses to potential management or restoration actions. The only strong quantitative data set identified were adult spawner estimates in the natal tributary; juvenile production estimate, a metric broadly used to study salmon population dynamics (Hendrix et al. 2017; Johnson et al. 2017), was not available for this stock. Additionally, various biological processes, with high modelling uncertainty, were found to influence CVSC population dynamics. In particular, very little is known about the egg, juvenile, and adult ocean life-stage dynamics. The lack of some key stage-specific data might be in part because of a combination of factors, including:

- small adult population abundances (Azat 2019),
- the difficulty in accessing remote spawning habitat in some of the natal tributaries and trapping juveniles during high-flow conditions (Johnson and Merrick 2012),
- the difficulty in visually distinguishing spring-run from fall run juveniles because of very similar length-at-date (Pyper et al. 2013a), and
- the limited information on—and analysis of—sub-adult ocean dynamics related to the lack of active fishery management for this stock (Grover et al. 2004; Satterthwaite et al. 2018).

However, despite these limitations, we believe that the additional monitoring and data-collection efforts identified in this paper could be successfully implemented, and help create a more comprehensive monitoring framework fundamental for working on the recovery of the entire ESU. More specifically, this will provide critical quantitative information about the status of this imperiled species at key life stages (e.g., stock-wide juvenile abundance estimates), and would help deepen our understanding of CVSC dynamics. Ultimately, this would also help strengthen the model parameterization and calibration process, which could improve the LCM prediction performance—a necessary step if this model is to be used for future management purposes, such as to evaluate the effect of Delta water operations on CVSC population abundance. Furthermore, some of the monitoring recommendations highlighted in this paper, such as a basin-wide acoustic tagging survival study

and the incorporation of genetic run identification in juvenile sampling, were also previously identified for the monitoring and management of the SRWC population (Johnson et al. 2017), and have already been partially or entirely implemented. Therefore, extending similar monitoring frameworks for CVSC populations could provide unique multi-stock tools for the management of CCV salmon.

Finally, structural model improvements could be considered in the future. For instance, by incorporating a hatchery component into the current model, the influence of FRHSC on different life stages of the natural-origin populations—such as the competition for juvenile rearing habitat and adult straying to other CVSC tributaries—could be further assessed. Moreover, a Bayesian framework could be used to calibrate the model, which might help improve parameter estimation and model fit, and to quantify and communicate the uncertainty of model outputs.

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NOTES

Clint Garman, California Department of Fish and Wildlife. 2019. Email conversation between Clint Garman and Flora Cordoleani regarding the future of Butte Creek pre-spawning carcass survey monitoring.