

Nonlinear survival of imperiled fish informs managed flows in a highly modified river

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Abstract. Water is a fundamental resource in freshwater ecosystems, and streamflow plays a pivotal role in driving riverine ecology and biodiversity. Ecologically functional flows, managed hydrographs that are meant to reproduce the primary components of the natural hydrograph, are touted as a potential way forward to restore ecological functions of highly modified rivers, while also balancing human water needs. A major challenge in implementing functional flows will be establishing the shape of the managed hydrograph so as to optimize improvements to the ecosystem given the limited resources. Identifying the shape of the flow–biology relationship is thus critical for determining the environmental consequences of flow regulation. In California’s Central Valley, studies have found that increased streamflow can improve survival of imperiled juvenile salmon populations during their oceanward migration. These studies have not explored the potential nonlinearities between flow and survival, giving resource managers the difficult task of designing flows intended to help salmon without clear guidance on flow targets. We used an information theoretic approach to analyze migration survival data from 2436 acoustic-tagged juvenile Chinook salmon from studies spanning differing water years (2013–2019) to extract actionable information on the flow–survival relationship. This relationship was best described by a step function, with three flow thresholds that we defined as minimum (4259 cfs), historic mean (10,712 cfs), and high (22,872 cfs). Survival varied by flow threshold: 3.0% below minimum, 18.9% between minimum and historic mean, 50.8% between historic mean and high, and 35.3% above high. We used these thresholds to design alternative hydrographs over the same years that included an important component of functional flows: spring pulse flows. We compared predicted cohort migration survival between actual and alternative hydrographs. Managed hydrographs with pulse flows that targeted high survival thresholds were predicted to increase annual cohort migration survival by 55–132% without any additions to the water budget and by 79–330% with a modest addition to the water budget. These quantitative estimates of the biological consequences of different flow thresholds provide resource managers with critical information for designing functional flow regimes that benefit salmon in California’s highly constrained water management arena.

Key words: California; flow regulation; functional flows; migration; resource management; salmon; survival; telemetry.

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INTRODUCTION

In rivers, natural flow regimes are directly linked with ecological processes that govern the life history of aquatic organisms, and are a major determinant of biodiversity (Bunn and Arthington 2002). Identifying the shapes of flow–ecology relationships is therefore critical for determining the biological consequences of water withdrawal or flow regulation on the ecosystem and to establish well-informed water management rules and recommendations (Rosenfeld 2017). Water resource use and development in watersheds has altered natural flow regimes, which in turn has altered riverine ecosystems, and is generally acknowledged to have considerable negative impacts on native biota (Pringle et al. 2000). As water resources become increasingly overtaxed due to population growth and climate change (Tanaka et al. 2006, Palmer et al. 2008), the task of balancing human and ecosystem needs will become more urgent and politically charged (Arthington et al. 2018). More than ever, objective, science-based approaches are needed for informing the development of water resource allocation targets (Petts 2009).

Few freshwater systems illustrate the management challenges of balancing environmental resources with the restoration of a collapsing ecosystem better than California's Central Valley (CCV) watershed. Here, water is heavily regulated as it supports a multi-billion dollar agricultural economy as well as tens of millions of urban and suburban water users (Speir et al. 2015). The ecosystem is vastly different than it was historically, with many native fish populations diminishing, and increasingly extreme climatic events impacting water availability (Hanak and Lund 2012). Researchers at the nonpartisan Public Policy Institute of California have suggested that restoration of native fish populations and general ecosystem health in the CCV is unattainable under the current regulatory status quo (Mount et al. 2019). These same authors propose that ecosystem-based management of the CCV is a potential way forward. Two key changes would be the adoption of ecologically functional flows (Yarnell et al. 2015, 2020) and an ecosystem water budget. Functional flows are managed hydrographs that are meant to reproduce the primary components of the natural, unimpaired

hydrograph so as to restore related geomorphic, biogeochemical, or ecological functions, while also balancing human water needs. An ecosystem water budget is essentially a water right for the environment: a set amount of water than may be allocated as resource managers see fit to improve the condition of the ecosystem. If these two key changes were implemented throughout the CCV, one of the major challenges will be establishing the shape and magnitude of the managed hydrograph so as to optimize improvements to the ecosystem, given a fixed water budget. A key part of this challenge is predicting the biotic responses to different flow targets.

In the CCV, hydrologic infrastructure and water management have strongly modified the hydrograph of most river systems, including the Sacramento River, resulting in reduced winter and spring discharges (Brown and Bauer 2009). The spring rainfall and snowmelt recession is a critical facet of the CCV Mediterranean-type flow regime, and alterations to this hydrograph strongly affect riverine species which have evolved to use high spring flows resulting from winter and spring rain-fed and snowmelt runoff (Yarnell et al. 2010). Among them, CCV Chinook salmon (*Oncorhynchus tshawytscha*) populations have been particularly impacted by water management in frastructure and altered flow regimes (Yoshiyama et al. 1998, Kimmerer 2008). Of the five historic Chinook salmon populations in the CCV, one has been extirpated, one is listed as endangered, one is listed as threatened, and the other two are listed as Species of Concern under the Endangered Species Act (ESA).

One of the primary impacts of the water management infrastructure and altered flow regimes in the CCV on salmon is the reduction in spring outmigration (i.e., seaward) survival of juvenile salmon (Kjelson et al. 1981, Notch et al. 2020). Importantly, the survival bottleneck at this life stage has significant repercussions throughout the Chinook salmon lifecycle (Michel 2019). Therefore, one vital aspect for implementation of functional flows in the CCV is to assess how they will impact juvenile Chinook salmon during their spring outmigration to the Pacific Ocean. One promising component of proposed functional flows in the CCV is the implementation of spring pulse flows (Yarnell et al. 2015), as these may recreate the ideal outmigration conditions salmon historically benefitted from.

To date, studies have found strong, positive linear relationships between survival and flow in CCV rivers (Kjelson et al. 1981, Zeug et al. 2014, Henderson et al. 2019, Notch et al. 2020). However, when environmental resources are also commercially important for competing needs, this creates a problem: How to allocate limited resources if the only guidance managers have is that more is better for the population or ecosystem process in question? This difficulty often results from the statistical techniques traditionally used by ecologists, which by design only reveal linear relationships between populations or ecosystem processes and the environment. Yet, these relationships are rarely linear (Hunsicker et al. 2016, Rosenfeld 2017), and these nonlinearities can play a critical role in the population or ecosystem dynamics. Several studies have shown that nonlinear responses of ecosystems to environmental resource changes could initiate catastrophic regime shifts and local population extinction events (Scheffer et al. 2001). Therefore, it is important to explore possible nonlinearities between environmental resources and ecosystem processes, with the particular objective of finding information that is more actionable to resource managers. This is especially pertinent to Pacific salmon stocks that are often found in the middle of constrained resource management arenas (Munsch et al. 2020).

We investigated the link between flow variations in the Sacramento River, the primary Chinook salmon river in the CCV watershed, and outmigration survival of juvenile Chinook salmon. We also evaluated hypothetical outmigration survival rates in the context of alternative flow regimes. We addressed the following questions: (1) Is there evidence of nonlinearity in the flow–survival relationship in the Sacramento River? (2) If so, how can knowledge of the nonlinear relationship be used to enact ecologically functional flows that benefit juvenile Chinook salmon? Finally, we weigh the efficacy of two different alternative flow regimes on increasing population-level Chinook salmon outmigration survival rates.

METHODS

Study area

The Sacramento River is the largest river in California and supports the second largest

population complex of Chinook salmon on the U.S. West Coast. However, the Sacramento River has been severely altered from its historic state, with major dams constructed throughout its watershed, extensive water diversions in place for municipal, industrial, and agricultural uses, and diking for flood control and land reclamation. Shasta Reservoir and its downstream forebay Keswick Reservoir are key components in the interface between human alterations and the ecosystem in the Sacramento River. These reservoirs block passage to historic salmonid spawning and rearing habitat upstream and also regulate downstream flow. During all months, the large majority of streamflow in the Sacramento River is regulated by reservoir operations, which alters the seasonal patterns of the natural hydrograph, including the homogenization and reduction of flows during some critical salmon rearing and migration periods (Brown and Bauer 2009), as well as altering other environmental conditions, such as water temperature and turbidity.

All of the juvenile winter-run Chinook salmon (ESA endangered status), significant portions of the juvenile spring-run Chinook salmon (ESA threatened status), and juvenile fall/late-fall-run Chinook salmon (ESA species of concern) must navigate a portion of the Sacramento River with several large-scale, and hundreds of small-scale, water diversions. In the late spring, when a large portion of these juveniles outmigrate, natural seasonal reductions in tributary inputs coincide with increases in water diversions; the cumulative impacts of which result in incrementally lower flows in the more downstream reaches, until the confluence with the Feather River, the largest tributary of the Sacramento River (Fig. 1). This pattern is primarily expressed in a region (hereafter “region of interest”) extending from the last major tributary before the Feather River on the upper end, the confluence with Deer Creek (Tehama County, river kilometer [rkm–distance from the Pacific Ocean by way of river] 425), to the Feather River confluence on the lower end (Sutter County, rkm 204; Fig. 2). We presume that detrimental impacts of low flows are primarily expressed in this region, where flows in the late spring are often the lowest of the year. In addition, flows in this region are considerably lower relative to the portions of the Sacramento

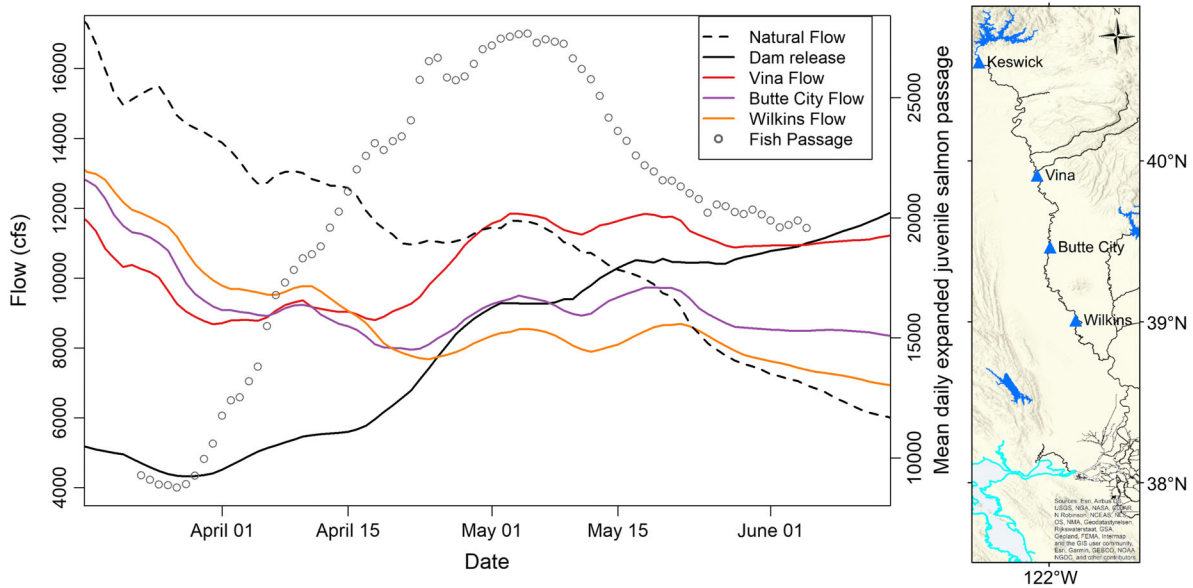


Fig. 1. Mean daily Sacramento River hydrographs for the spring period from 2000 to 2019, (excluding those classified as wet: 2006, 2011, 2017, 2019), mean daily natural hydrograph (dashed line), and mean daily expanded juvenile salmon passage (gray points, data from USFWS Red Bluff rotary screw traps, 38 rkm upstream of the region of interest). Flow levels (in cfs) are plotted through time at several gauges along the river, starting from Keswick gauge (dam release: USGS station number 11370500) on the upstream end to Wilkins Slough gauge (USGS station number 11390500) on the downstream end (color legend inset has gauges listed in order from upstream to downstream). The mean daily natural flow regime is the sum of the full natural flow statistic on the California Data Exchange Center (<http://cdec.water.ca.gov>) for the Bend Bridge (BND) gauging station, along with the daily flow from Mill Creek (USGS 11381500) and Deer Creek (USGS 11383500) gauges. It is therefore representative of the estimated full natural flow entering the region of interest. A 10-d moving average smoothing has been applied to all hydrographs and fish passage data. All stream gauges are operated by either USGS, US Bureau of Reclamation, or California Department of Water Resources.

River upstream and downstream, both of which are not characteristic of historic conditions. The survival rate of acoustic-tagged juvenile Chinook salmon in certain sections of this region is the lowest on the Sacramento River (Michel et al. 2015, Notch et al. 2020).

Study fish and season

The large majority of juvenile Chinook salmon in the Sacramento River rear and outmigrate during the winter or spring months (Fisher 1994). Historically, these seasons typically provided adequate flows and cool water temperatures to allow for juveniles to rear in, and transit through, downstream regions. At present, flows are only occasionally adequate for outmigration or off-channel rearing in most years. This is primarily

due to reduced reservoir releases in order to store water for use in the summer months, after the outmigration window (Sturrock et al. 2020). In the winter and early spring, flows increase in the downstream direction from Keswick to Wilkins Slough until mid-April (Fig. 1), driven by tributary inflows that greatly exceed diversions. After mid-April, there is an inversion in this pattern, and flows are substantially lower at Wilkins Slough compared to Keswick (Fig. 1), resulting from cumulative diversions greatly exceeding tributary inflows during the agricultural irrigation season. It is during this same mid- to late spring period, after the inversion, that a significant portion of natural-origin juvenile salmon outmigrate through this region (Fig. 1). In addition, most CCV juvenile Chinook salmon

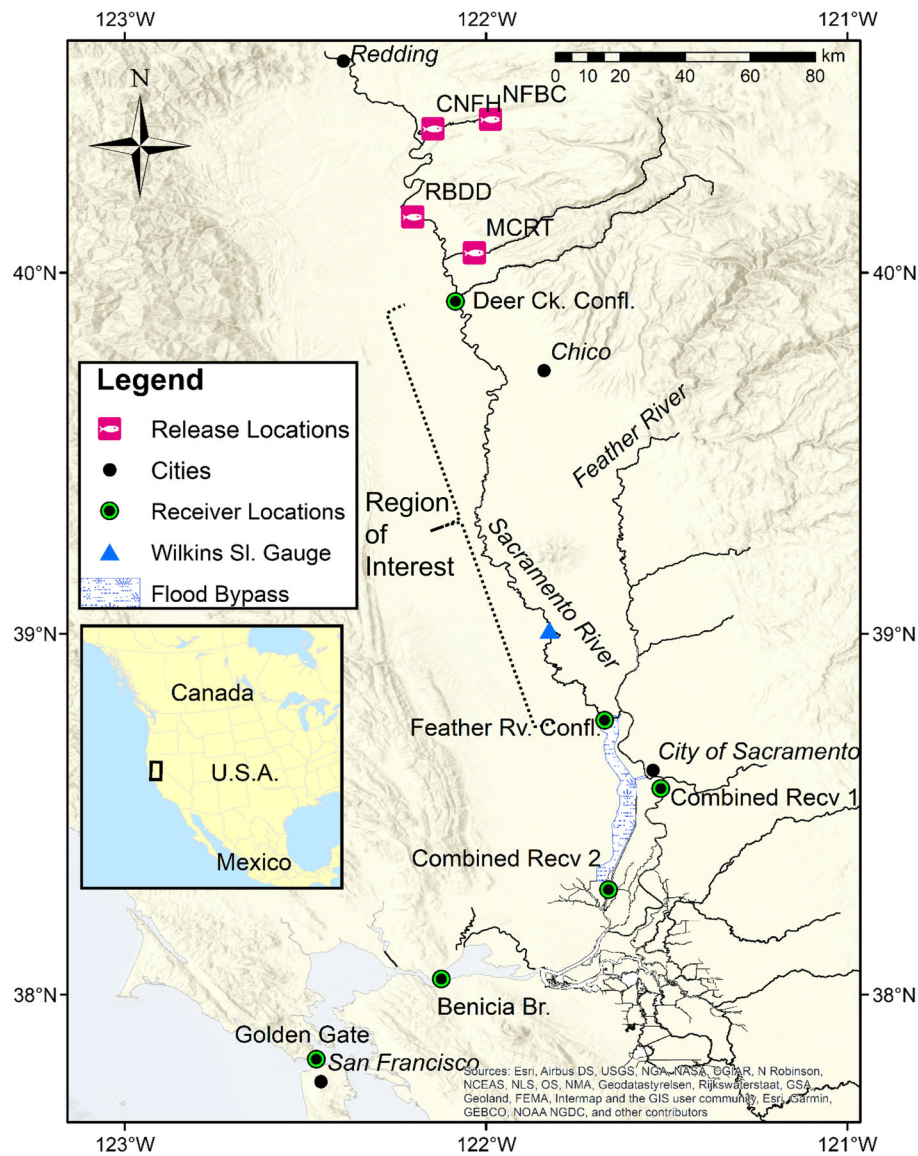


Fig. 2. Study area, release locations, and receiver locations. Region of interest spans from the confluence with Deer Creek to the confluence with Feather River. Release location abbreviations are CNFH, Coleman National Fish Hatchery; NFBC, North Fork Battle Creek; RBDD, Red Bluff Diversion Dam; and MCRT, Mill Creek rotary screw trap.

hatchery releases also peak in spring (Huber and Carlson 2015), during which their outmigration survival rates also appear to be sensitive to flow rates (Zeug et al. 2020).

Acoustic telemetry studies investigating the survival and movement of juvenile salmon in the Sacramento River have proliferated in recent years (Michel et al. 2015, Cordoleani

et al. 2018, Notch et al. 2020). We compiled all the available spring period (15th March–15th June) acoustic tagging data for the Sacramento River and selected fish that were released upstream of the region of interest (above rkm 425): 3402 in total. Of those fish, only fish that were known to have entered the region of interest played a large role in parameterization

of the flow–survival relationship explored in this analysis. Fish that did not appear to survive to the region of interest may have simply not been detected entering the region and therefore play a small role in the parameterization of the flow–survival relationship. The number of fish that were known to enter the region of interest amounted to 2436 acoustic-tagged fish from six different years, including wild and hatchery fish, and fish from three of the four Sacramento River Chinook salmon populations (Table 1).

Acoustic telemetry

Wild fish were collected using rotary screw traps deployed in the Sacramento River and Mill Creek, while hatchery fish were collected from hatchery raceways. Fish were tagged using similar methods across years and populations as described by Deters et al. (2010). Acoustic tags were surgically implanted into the coelomic cavity of the anesthetized fish and closed using one or two interrupted sutures, depending on tag model. Wild fish were allowed to recover in a net pen for approximately 12 h post-surgery and released on-site after sunset. Hatchery fish were allowed to recover for up to 24 h post-surgery and released on-site, or trucked to a release location using an aerated hatchery transport tanker. All release sites were located at least 25 rkm

upstream of the region of interest (Fig. 2), such that by the time fish arrived to the region of interest any potential influences of handling, trucking, or release site on survival should have largely been expressed and should have little to no effect on survival estimates in the region of interest.

All fish were tagged and tracked using the Juvenile Salmon Acoustic Telemetry System (McMichael et al. 2010). Tags were programmed to transmit at three-, five-, or ten-second intervals depending on tag type, enabling them to function for a minimum of 27, 32, and 52 d, respectively. Tag size depended on the study population and ranged in size from 10.5 mm long × 5.2 mm high × 3.0 mm wide to 10.7 mm long × 5.0 mm high × 2.8 mm wide. The transmissions from the tags were detected and the unique tag number recorded by autonomous receivers from different manufacturers (ATS [Isanti, Minnesota, USA], Teknologic [Edmonds, Washington, USA] or Lotek Wireless [Newmarket, Ontario, Canada]). All receiver locations had two or more receivers to maximize detection probability. In an effort to reduce the tag burden in study fish, a maximum 5% tag-to-fish weight ratio was observed. This allowed for fish as small as 75 mm to be tagged and released. Fish tagged ranged from 75 to 120 mm fork length (mean 86.8, standard deviation [SD] 5.8).

Table 1. Wild and hatchery tagged fish groups included in our analysis from 2013 to 2019.

Population	Origin	Year	Release dates	Release location	<i>N</i>	Genetic population origin
Mill Creek	Wild	2013	Mid-April to mid-May	MCRT	48	74% CCV fall-run 26% CCV spring-run
Coleman	Hatchery	2013	Mid-April	CNFH	285	100% CCV fall-run
Mill Creek	Wild	2015	Mid-April to mid-May	MCRT	110	44% CCV fall-run 56% CCV spring-run
Coleman	Hatchery	2016	Early-April to late-April	CNFH	540	100% CCV fall-run
Mill Creek	Wild	2017	Mid-April to late-April	MCRT	24	100% CCV fall-run
Coleman	Hatchery	2017	Early-April to late-April	CNFH	370	100% CCV fall-run
Sacramento River	Wild†	2017	June 6	RBDD	33	100% CCV fall-run
Sacramento River	Wild†	2018	Early-May to early-June	RBDD	207	100% CCV fall-run
Livingston Stone	Hatchery	2019	March 26	NFBC	199	100% Sacramento winter-run
Coleman	Hatchery	2019	April 11	CNFH	140	100% CCV fall-run
Coleman	Hatchery	2019	Late-May	RBDD	480	100% CCV fall-run
Total		2013–2019	Late-March to early-June		2436	

Notes: CCV, California's Central Valley. Release locations are further described in Fig. 2. Genetic population assignments made using protocols outlined in Clemente et al. (2011).

† Fish captured in rotary screw traps in the Sacramento River and tagged were assumed to be wild, although some hatchery fish may have been misidentified and incidentally tagged.

Cormack-Jolly-Seber model

We used the Cormack-Jolly-Seber (CJS) model for live recaptures within Program MARK (White and Burnham 1999) using the RMark package (Laake 2013) in R statistical software (vers. 3.6.1; R Core Team 2019) to estimate survival as well as to assess the fit of different flow relationships with survival. For species that express an obligate migratory behavior such as Chinook salmon, a spatial form of the CJS model can be used, in which recaptures (i.e., tagged fish detected downstream from release) occur along a migratory corridor. The model determines if a fish not detected at a given receiver location was ever detected at any receiver downstream of that specific receiver, thus enabling calculation of maximum-likelihood estimates for detection probability of all receiver locations (p), survival (Φ), and 95% confidence intervals for both (Lebreton et al. 1992).

If a predator consumes an acoustic-tagged salmon and swims downstream past the next receiver location, the CJS model would incorrectly assign that fish as having survived the reach in which it was consumed. In the river above tidal influence, Chinook salmon express obligate anadromy and do not typically travel upstream (i.e., against current) once migration has begun; any movements in the upstream direction are likely predator movements. We therefore used the entirety of detection data available in the Sacramento River for each year (>12 receiver locations per year) to truncate the detection history of each fish to only include detections leading up to the first upstream movement, if one occurred.

We then subset the remaining detection data to only include receiver locations that bookend the region of interest. After release, the first receiver location was at the Deer Creek confluence (rkm 425), at the upstream end of the region of interest. The second receiver location was located just below or above the Feather River confluence depending on the year (rkm 204 or 211, respectively), and therefore, the reach between these receiver locations encompassed the entire region of interest (Fig. 2). We also included additional receiver locations further downstream in the detection history to allow for an estimation of detection probability at the Feather River confluence location. However, during high flow events, such as in 2017 and 2019, a portion of the

Sacramento River spilled into a flood bypass located just upstream of the Feather River confluence (Fig. 2). Since this introduced a secondary migration route, we used a combination of receivers at the end of the bypass (located at Liberty Island, Solano County) and receivers in the mainstem Sacramento River (located at City of Sacramento, Sacramento County) to create a synthetic recapture event in the detection history, ensuring both potential routes were covered. These data were only included in the analysis to better estimate detection probability at the end of the region of interest. Finally, we also used two downstream receiver locations to further improve detection probability estimation, one at Benicia Bridge (Contra Costa County, rkm 52) and at the Golden Gate, the entrance to the Pacific Ocean (rkm 1).

Flow–survival relationship

Each fish was assigned a value equal to the mean flow over the entire travel time from passing the Deer Creek confluence to first detection at the Feather River confluence. For fish not detected at the Feather River confluence (either due to mortality upstream, or imperfect detection probability; representing 75.3% of all fish), we imputed travel time by creating probability density functions (p.d.f.s) from all known travel times for each tagging group (i.e., rows in Table 1) using kernel density estimation (“density” function in R statistical software). We then imputed travel time by randomly selecting a point along the p.d.f. for that fish’s tagging group. We used flow values from the United States Geological Survey’s (USGS) Sacramento River at Wilkins Slough gauging station (USGS station number 11390500). This location was nearest to the downstream end of the region of interest and represented the minimum flows that fish would experience during the late spring period (15th April and later; Fig. 1).

We created an initial CJS model by grouping fish based on 5% quantile bins of the flows they experienced. These survival groups, parameterized in the model by dummy variables, were allowed to only impact survival estimates of the region of interest (i.e., reach 2: Deer Creek confluence to Feather River confluence, Φ_{reach2}).

To explore nonlinearity in the flow–survival relationship, we employed model selection using

the Bayesian Information Criterion (BIC) to assess the parsimony of different flow–survival modeling structures. We created multiple CJS models that allowed the relationship between flow and survival in the region of interest (reach 2: Deer Creek confluence to Feather River confluence) to take linear, log-linear, polynomial, cubic spline curve, and threshold (i.e., step function) forms. We used flow values for individual fish as individual covariates in the first four model types and as a grouping variable (dummy variable) for the threshold model. We also explored the potential for multiple thresholds in the flow–survival relationship. For all models, detection probability was allowed to vary by receiver location and tagging group. More details on the flow–survival modeling effort can be found in Appendix S1.

Spring pulse flow scenarios and theoretical survival improvements

Where we found strong evidence of a nonlinear flow–survival relationship, we assessed different management strategies that could use this information to improve cohort outmigration survival of salmon in the Sacramento River. We generated two hypothetical implementations of pulse flows during the spring period for the study years (2013–2019). The first implementation scenario allowed for sustained flows that would result in the highest survival rates based on the nonlinear flow–survival relationship. Sustained flows were centered around the average date of peak spring juvenile salmon outmigration (April 19th, based on 2005–2019 expanded juvenile salmon capture data from USFWS's Red Bluff rotary screw traps, https://www.fws.gov/redbluff/rbdd_biweekly_final.html) and scheduled to last as long as possible given the water budget. The second scenario represented an adaptive management implementation of spring pulse flows: Following a substantial increase in daily catch rates at the Red Bluff rotary screw traps, flows were temporarily increased (for four days) to the levels that would result in the highest survival rates based on the nonlinear flow–survival relationship. The maximum number of four-day pulse flow events was enacted given the available water budget. Days with substantial increases in catch rates at the rotary screw traps are proximate estimates of periods of peak

outmigration of juvenile salmon, and we estimated these days to be when both (1) total expanded catch exceeded 10,000 juvenile salmon and (2) the increase was more than one standard deviation over the mean from the previous 10 d. Finally, we used two water budgets for these scenarios: a realized water budget (which consisted of the totality of water released from Keswick Dam during the spring of each year) and an ecosystem water budget, which added 150 thousand acre-feet (TAF) to the realized water budget each year.

We used the expanded combined daily catch of all runs of Chinook salmon for determining peak outmigration triggers. Expansion factors were based on capture efficiency trials operated by USFWS Red Bluff Office, and the resulting expanded total catch numbers represent the total number of fish passing the screw trap at Red Bluff. The rotary screw traps are 38 river kilometers upstream of the region of interest and therefore approximately represent the daily number of fish entering the region of interest during their outmigration. The screw traps are operated continuously, except during the passage of significant numbers of hatchery fish or during storm conditions (B. Poytress, *personal communication*). As a result, some spring sampling days are missing from our study period. Furthermore, some days of significant hatchery fish catches were also removed from the dataset; these days were identified as days when expanded daily catch total surpassed 80,000 fish.

To estimate the realized water budget, we multiplied the sum of the mean daily flow estimates (cfs) from 15th March to 15th June from the Keswick Dam gauge (USGS station number 11370500) by 1.983×10^{-3} to convert to volume (TAF). To benefit outmigrating salmon, the nonlinear flow–survival targets from the most parsimonious CJS model would need to be realized at the Wilkins Slough gauge, so we estimated a daily net change between Keswick Dam and Wilkins Slough. This approximates the net difference between water inputs (tributaries) and water exports (water diversions) between the Keswick Dam and Wilkins Slough at a daily time step. Finally, all alternative flow regimes had three important regulatory constraints: (1) minimum Keswick flows of 3250 cfs (National Marine Fisheries Service 2009 Biological Opinion and

Conference Opinion on the Long-Term Operations of the Central Valley Project and State Water Project: NMFS 2009 BiOp), (2) maximum Keswick flow reduction rate of 15% per day (U.S. Bureau of Reclamation 2008 Central Valley Project Biological Assessment), and (3) no alteration to any daily Keswick releases that were deemed to be for flood control (>20,000 cfs).

We then modeled the impact of the different flow implementation scenarios on cohort outmigration survival of spring-outmigrating juvenile Chinook salmon. We used parametric bootstrapping, where the pertinent logit-transformed survival distribution from the CJS model (given flow levels at Wilkins Slough for that day) was resampled corresponding to the expanded daily total catch at the Red Bluff screw traps. We estimated the mean logit-scale survival from the totality of samples across all days of the spring period, and then re-scaled (inverse-logit transform). For missing daily catch values, we imputed catch using a linear interpolation of the time series. Finally, to provide a baseline for assessing the potential survival gains of each scenario, we estimated the cohort outmigration survival for the status quo (using the observed spring hydrograph in the years 2013–2019).

RESULTS

We found strong evidence of nonlinearity in the flow–survival relationship (CJS model with grouping based on 5% quantile flow bins, Fig. 3). Survival was positively related to flow for values up to 10,000 cfs, followed by a sharp increase in survival near 10,000 cfs, at which point survival asymptotes at approximately 50%.

Out of 724,567 models we tested, the triple threshold models were the most parsimonious, with 12 that were within two BIC points of the top model. We estimated survival parameters and threshold values (4259, 10,712, and 22,872 cfs) from these 12 models using model averaging. The threshold models were substantially better supported than any of the other model types tested ($\Delta\text{BIC} > 29$). Furthermore, these threshold models, as well as all polynomial and spline models, were better supported than the linear, log-linear, and full models ($\Delta\text{BIC} > 146$), indicating strong support of a non-linear flow–survival relationship.

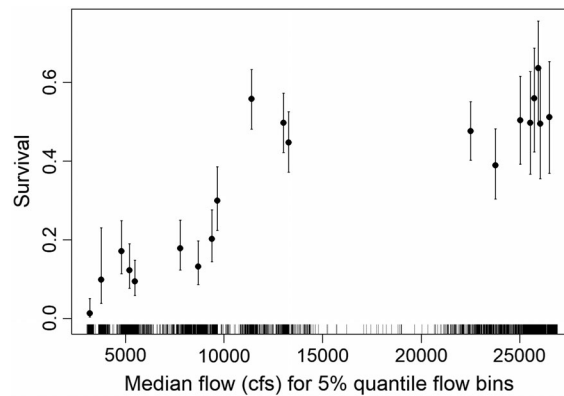


Fig. 3. Survival as a function of flow. Survival estimates (points) with 95% confidence intervals (bars) for groups at 5% quantile bins of experienced flow, plotted at the median value of bins (in cfs) on the *x*-axis. Flow experienced per fish is indicated by vertical tick marks along the *x*-axis.

In order to better understand model fit across the range of potential flow thresholds, for each flow value tested in the threshold models, we estimated the mean BIC of all models that included that flow value as one of its thresholds (Fig. 4). With similar results to the model selection exercise, models with flow thresholds around 4259, 10,712, and 22,872 cfs had strong support (i.e., lower mean BIC). We labeled these minimum (4259 cfs), historic mean (10,712 cfs), and high (22,872 cfs). The historic mean threshold had highest support of the three thresholds

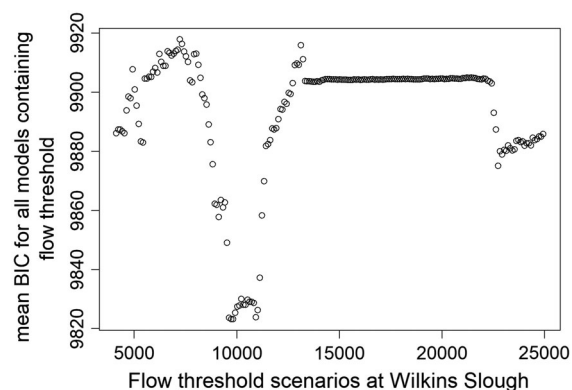


Fig. 4. Mean BIC scores per threshold value as a function of flow. A lower BIC value indicates a stronger supported model.

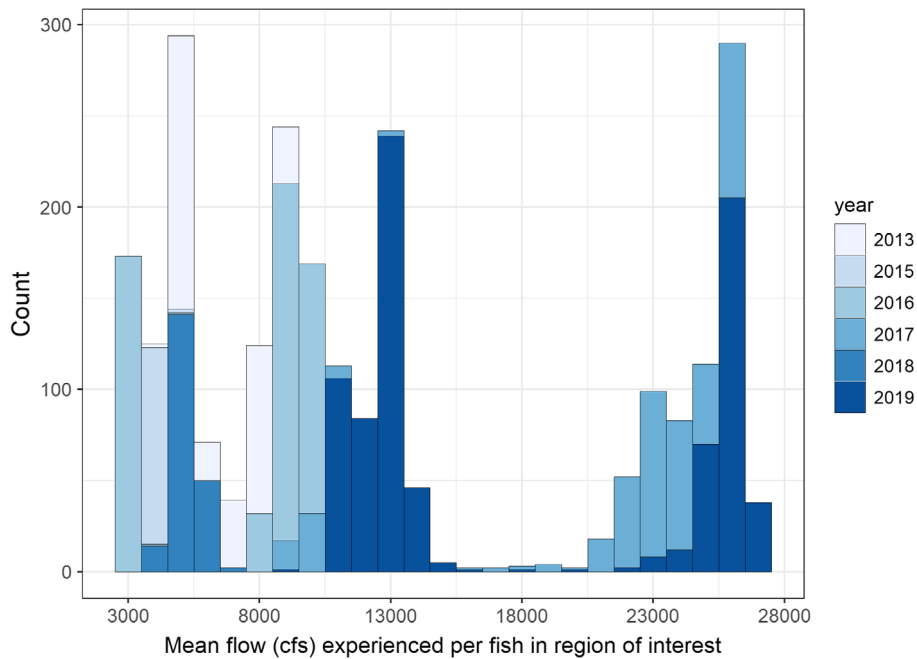


Fig. 5. Frequency of flow values used in analysis by year. Values are mean flow (cfs, as measured at Wilkins Slough gauge), both empirical and imputed, for all fish. Flow bin sizes are 1000 cfs, and bar colors indicate the relative number of fish by year for each flow bin.

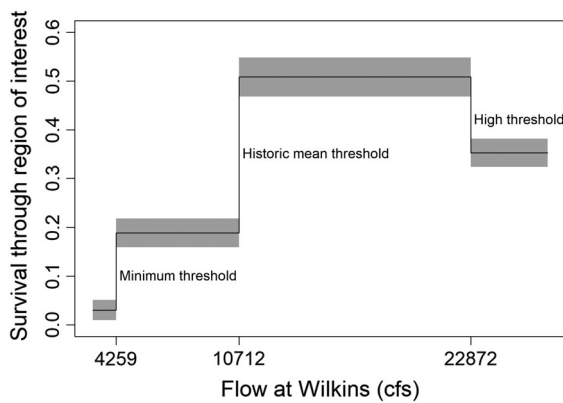


Fig. 6. Thresholds of predicted survival as a function of flow at Wilkins Slough. Predictions are based on the model averaged parameters from the most parsimonious triple threshold models, with mean thresholds at 4259, 10,712, and 22,872 cfs, with 95% confidence intervals (gray fill).

(Fig. 4). Few fish experienced flow values between approximately 14,000 and 21,000 cfs (Fig. 5), and therefore, model fit did not vary significantly with thresholds found in this range.

We used model averaged parameter estimates to predict survival for the range of flow values (Fig. 6). There was a 6.3-fold increase in survival from flows below 4259 cfs (0.03) to flows between 4259 and 10,712 cfs (0.189). There was a 2.7-fold increase in survival from flows between 4259 and 10,712 cfs to flows above 10,712 cfs (0.508). Overall, there was a 16.9-fold increase in survival from flow below 4259 to flows above 10,712 cfs. Finally, survival decreased above the 22,872 cfs threshold to 0.353. Survival was significantly different between groups, with non-overlapping 95% confidence intervals. The 22,872 cfs threshold may be an artifact of lower detection efficiencies associated with fish utilizing additional high flow migration routes with less receiver coverage.

We compared modeled cohort outmigration survival rates among five different water release scenarios for five water years with the modeled survival rates for actual flows (Fig. 7). Water years 2013 (dry), 2014 and 2015 (critical), and 2016 and 2018 (below normal) represent three classes of water supply scarcity in the Sacramento River Basin (<http://cdec.water.ca.gov/re>

portapp/javareports?name=WSIHIST). For dry year 2013 and below normal years 2016 and 2018, the three alternative scenarios using the available water budget resulted in survival rate increases ranging from 55% to 98%, while the scenarios with an additional 150 TAF resulted in survival rates increases ranging from 79% to 119%.

For critical years 2014 and 2015, the realized water budgets were not sufficient to allow for the alternative release scenarios, beyond just maintaining flows above the low flow threshold for as long as possible (resulting in survival rate increases of 83% and 132%, respectively). Scenarios using an additional 150 TAF resulted in survival rate increases ranging from 130% to 330%.

DISCUSSION

Streamflow is a master variable in stream ecology, influencing biological and physical habitat characteristics, and if not managed properly, flow alteration can be a serious threat to freshwater ecosystems. Yet, water management decisions continue to be poorly informed by environmental research (Davies et al. 2013, Horne et al. 2016). In the Sacramento River Basin, surface water demands exceed supplies in all but the wettest years (Grantham and Viers 2014), and there is a pressing need to optimally allocate those limited resources to meet management objectives, including ecosystem benefits. We identified threshold responses in salmon outmigration survival across a range of observed instream flow rates. These relationships are valuable tools for updating water management practices aimed at balancing competing demands. Applying our minimum threshold (4259 cfs) as a lower critical flow boundary for spring flows could result in a 6.3-fold increase in outmigration survival. Flows above the historic mean threshold (10,712 cfs) could provide an additional 2.7-fold increase in survival. Flows above this threshold could be enacted when the resources are available, especially if coordinated with hatchery releases or peak wild salmon migration periods. All else being equal, these survival gains could result in concomitant increases in adult escapement. These modeled survival benefits justify the need to identify ways to exceed these flow thresholds

more consistently and for longer periods during the spring months.

High flows promote favorable outmigration conditions for Chinook salmon juveniles, resulting in increased survival to the ocean (Connor et al. 2003, Smith et al. 2003). We identified an optimal threshold of 10,712 cfs, which we labeled historic mean, as it is similar to the long-term average of natural spring flow conditions under which Chinook salmon have evolved in this system (Fig. 1). One potential mechanism for this threshold is high flows typically increase water turbidity, which may aid juveniles in evading predators (Gregory and Levings 1998). Alternatively, it is known that outmigrating juveniles move at higher speeds with higher flow (Berggren and Filardo 1993), limiting their exposure time to predators and other hazards. Movement speeds and survival rates of wild Chinook salmon juveniles in this section of the river are strongly correlated (Notch et al. 2020). Therefore, to determine whether movement speeds may be one of the mechanisms driving the 10,712 cfs threshold, we conducted a post hoc analysis of fish travel times through the region of interest as grouped by the flow threshold boundaries. A Kruskal–Wallis test indicated significant differences in travel time distributions between the groups ($P < 0.001$), and a Dunn's multiple comparison test indicated that travel times for fish experiencing flows between 10,712 and 22,872 cfs were significantly shorter than for fish experiencing all other flow levels (Fig. 8).

Flow levels above the historic mean threshold represent normal spring time flows under natural runoff and streamflow conditions up until approximately 15th May (Fig. 1). Yet, from 1993 to 2019 such flows were only achieved in 37% of days during the 15 April–15 May peak outmigration period, and only 10% of days in below average water years (Fig. 9), and were even less likely to occur later in the spring (Fig. 10). In late spring (after approximately 15 April), tributary flows subside and demand for agricultural water deliveries increase dramatically, a combination that creates progressively diminished instream flow in downstream reaches (Fig. 1). Sturrock et al. (2020) found that under current water management regimes, the low flows and high water temperatures that occur in the late spring are selective forces against the later-migrating smolt

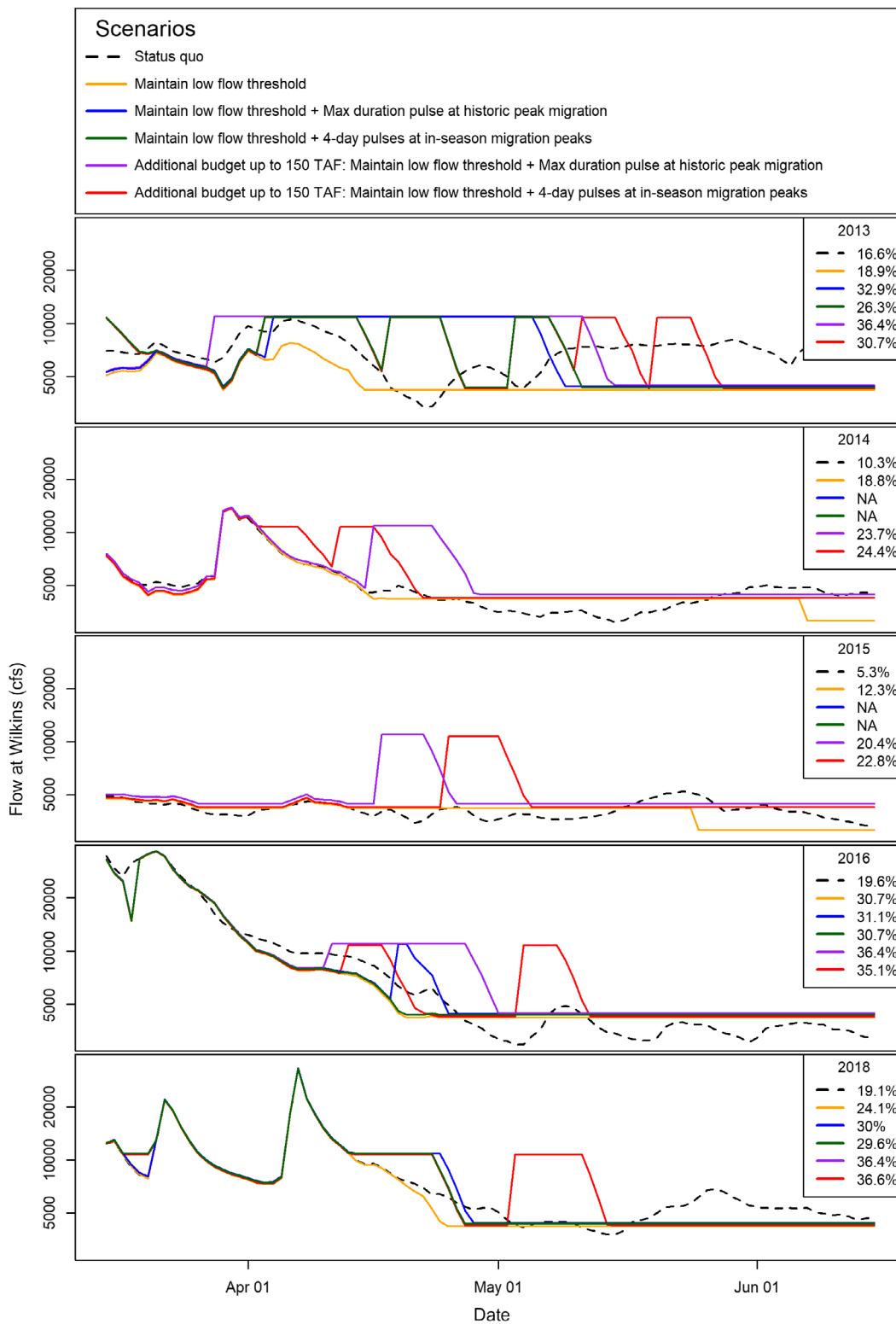


Fig. 7. Alternative flow scenario hydrographs using the flow–survival nonlinearities found in this study. Predicted cohort spring outmigration survival based on flow scenarios and daily fish passage at Red Bluff rotary

Fig. 7. Continued

screw traps are depicted in figure legends. Scenarios for 2017 and 2019 water years are not depicted, as wet conditions in those years precluded the need for pulse flows. In the historic drought years of 2014 and 2015, pulse flows were not possible based on realized water budget (NA for respective survival estimates in legend).

juvenile life-history type (>75 mm fork length [FL]). The implementation of spring pulse flows above the 10,712 cfs threshold could be a powerful tool to restore functional parts of the natural flow regime during critical periods of the salmon life history, and ultimately, the increased heterogeneity of flows may promote increased population diversity.

The mechanism driving the lower flow threshold (4259 cfs) is unclear. Anecdotal observations indicate that under certain low flow conditions, sections of the Sacramento River may have increased habitat heterogeneity, in particular with regard to pools and riffles where predator ambush habitat is likely created (C. J. Michel, *personal observation*). Flow influences other important environmental variables, such as water temperature, that might also have nonlinear

relationships with survival. Because temperature and flow are highly correlated (flow and temperature experienced for these fish as measured at Wilkins Slough had a Pearson's correlation coefficient of 0.93) and flow is the most persistent driver of survival in the CCV (Henderson et al. 2019, Notch et al. 2020), we did not include temperature in this analysis. At very low flows during the latter end of the spring period, water temperature in the lower Sacramento River can approach the thermal tolerance of juvenile Chinook salmon. For fish outmigrating during flows lower than the low flow threshold, mean water temperature experienced was 19.9°C (0.5 SD) as measured at the Wilkins Slough gauge. At this temperature, salmon health and vulnerability to predation can be affected and ultimately lead to lowered survival (Marine and Cech 2004, Miller et al. 2014, Lehman et al. 2017, Michel et al. 2020). During most years, spring outmigration flows are above the lower threshold, and these unfavorable conditions are usually only observed during years of drought (e.g., 1994, 2013–2015; Fig. 10). However, in recent years, spring flows below this lower threshold have occurred in years of near average precipitation (i.e., 2016, 2018; Fig. 10), likely resulting from a complex suite of factors, including reservoir management strategies for conserving cold water for endangered winter-run Chinook salmon, and increasing water deliveries for out-of-stream uses during the summer months.

Of the models we tested, the threshold models had strongest support, possibly because they allow for a sharp transition between survival levels as a result of small changes in flow across some ecologically important value. For example, exceeding a given threshold can lead to river bank overflow, which activates seasonal floodplains, providing juvenile salmon an alternative downstream migration route. This is the hypothesized mechanism for the high threshold (22,872 cfs): Tisdale Weir, within the region of interest, overtops at approximately this flow value, allowing fish to enter the Sutter Bypass. Survival decreased at flows above this

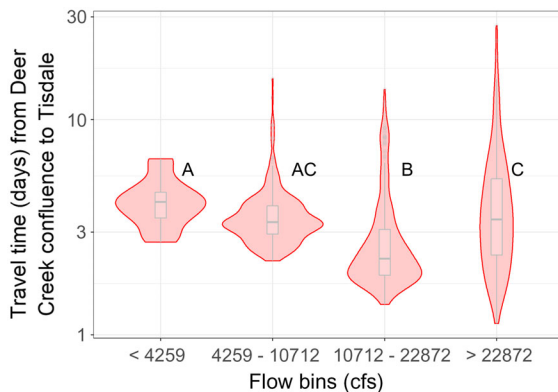


Fig. 8. Distribution of fish travel times (log-scale) through the area of interest as a function of flows experienced with respects to the flow thresholds. Travel time is calculated for fish detected both at Deer Creek confluence and at Tisdale (rkm 269), representing the upper 74% of the region of interest. Travel times to the end of the region of interest (Feather River confluence) were not used as too few fish remained in the <4259 cfs group to accurately represent travel times for that group. Letters within the plot frame indicate significant differences between travel time distributions from a Dunn's multiple comparison test, at the 0.05 level.

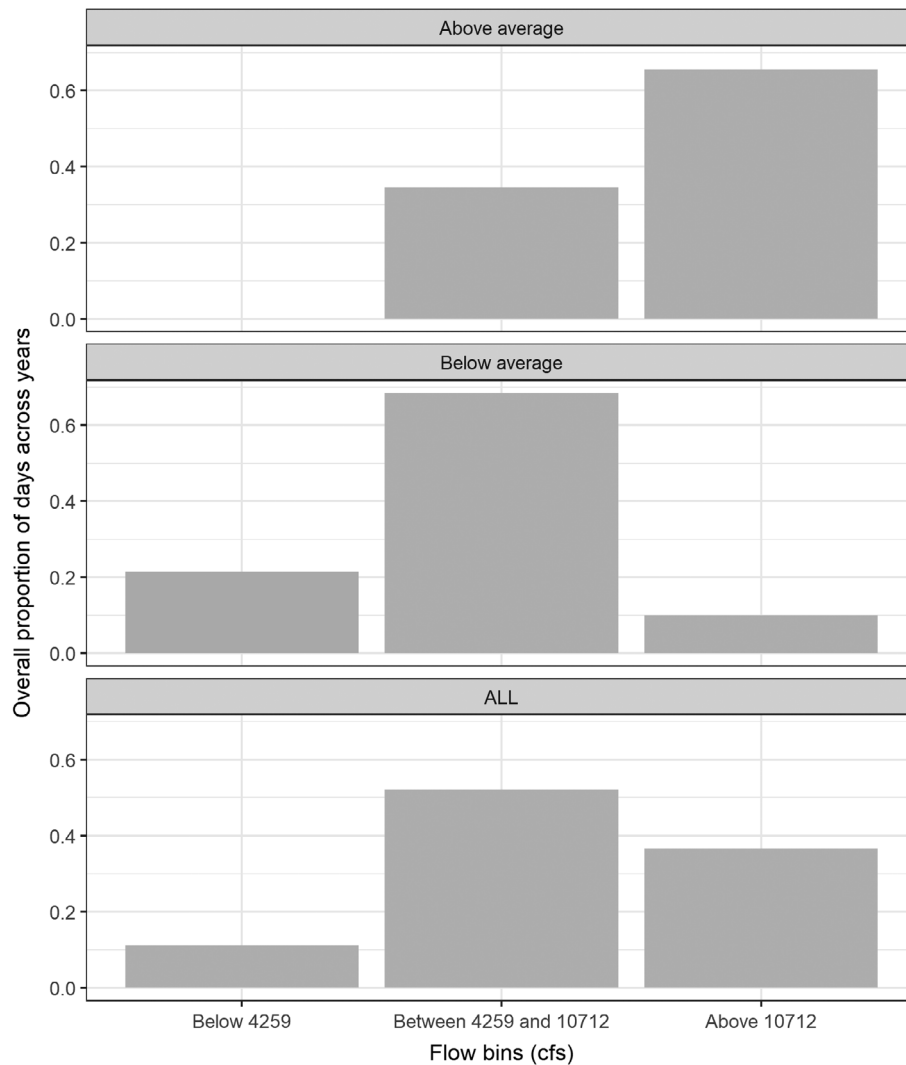


Fig. 9. Proportion of daily flows at Wilkins Slough that fall below, between, or above the two lower flow thresholds from 15th April to 15th May period from 1993 to 2019, split out by above average (i.e., wet and above normal) and below average (i.e., below normal, dry, and critically dry) water years, according to the Water Year Hydrologic Classification Index for the Sacramento Valley (<http://cdec.water.ca.gov/reportapp/javareports?name=WSIHIST>).

threshold, which could be evidence that fish utilizing this alternate route experienced decreased survival compared to fish remaining in the Sacramento River. While flood bypasses are generally considered to be high-quality rearing habitat for juvenile salmon (Sommer et al. 2001), there is little known about the relative survival of fish utilizing these habitats. Travel times for fish above the high threshold were significantly higher and are more widely

distributed than for fish just below this threshold (Fig. 8), with fish taking up to 27 d to transit the region of interest. These slower moving fish may have been delayed as a result of spending time on floodplains, and their increased exposure time to potential stressors may explain their decreased survival in comparison to fish just below the high threshold that could not access the floodplains. This is consistent with the results of a similar study

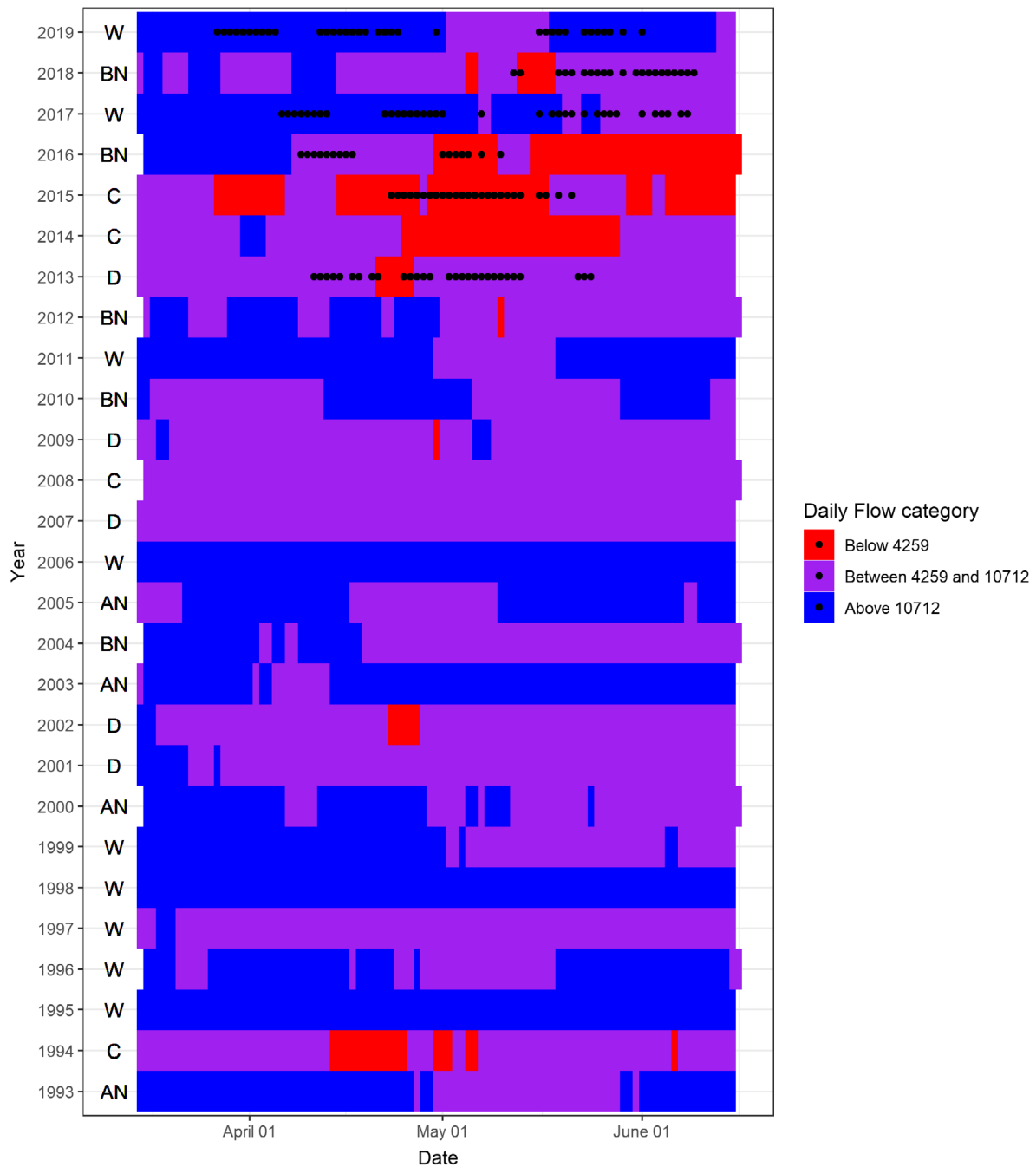


Fig. 10. Classification of flow values into the below 4259 cfs, between 4259 and 10,712 cfs, and above 10,712 cfs categories for each day of the spring outmigration period (15th March–15th June) for the years 1993–2019. Flow values are as measured at USGS Wilkins Slough gauging station on the Sacramento River. Black points represent days when acoustic-tagged fish were entering the region of interest. Text within box indicates the Water Year Hydrologic Classification Index for the Sacramento Valley (<http://cdec.water.ca.gov/reportapp/javareports?name=WSIHIST>); year type codes are W, wet; AN, above normal; BN, below normal; D, dry; and C, critically dry.

where survival per day was similar between release groups that traveled through a floodplain compared to those that traveled through the mainstem river, and yet due to longer travel times through the floodplain, the floodplain groups experienced overall lower survival rates (Pope et al. 2018). It should again be noted that the detection probability of fish utilizing the bypass route is likely lower, which could be a confounding driver of the high threshold.

The alternative flow regimes indicated that substantial survival gains over the status quo were possible by leveraging the thresholds we identified. These flow scenarios lead to increases in annual outmigration survival ranging between 57% and 130% without additions to the water budget and increases ranging from 79% to 330% with a modest 150 TAF addition to the water budget (Fig. 7). There were no clear and consistent differences in survival between the historic peak migration pulse flow scenario and the four-day adaptive pulse flow scenario, whether with the realized water budget or with the additional environmental water budget. We included an additional scenario where flows mimicked the status quo hydrograph, but flows were not allowed to dip below the minimum threshold, which alone led to substantial gains in survival in the Critical Dry water years 2014 and 2015 (Fig. 7). Adaptive pulse flow scenarios may be preferable to a single-pulse, fixed calendar date scenario in ways not measured in this study. For example, the adaptive implementation will be more responsive to hydrologic or biotic nuances of a given year and promote more diversity in outmigration timing.

Our analysis is consistent with many studies concluding that flow is a strong driver for Chinook salmon smolt spring outmigration survival. This period of time coincides with peak hatchery releases and peak natural-origin outmigration of fall-run Chinook salmon, the stock that supports an important commercial and recreational fishery, as well as peak outmigration of ESA threatened wild spring-run Chinook salmon smolts from Sacramento River tributaries. Spring-run Chinook salmon populations historically spawn at high elevations and therefore experience slower growth rates and delayed outmigration timing compared to other Chinook salmon populations (Yoshiyama et al. 1998). This delayed

outmigration timing makes them particularly vulnerable to low flows in the late spring. Further, these late outmigrants are subject to asynchronous flow conditions between natal streams (when their initial downstream migration is triggered by snow melt or spring freshets in the tributary) and the mainstem Sacramento River, where they experience periods of low managed flows. Restoring the functionality of the spring flow regime during wild smolt outmigration is a critical step toward promoting sustainable fisheries (Jager and Rose 2003), as well as restoring a threatened population of salmon.

Other CCV native fish species may require different flow conditions during the spring, potentially creating water management conflicts. For example, high flows and cold water from dam releases may have detrimental impacts on threatened green sturgeon (*Acipenser medirostris*) in the Sacramento River (Zarri et al. 2019). Similarly, endangered winter-run Chinook salmon rely on cold water released from Shasta Reservoir during egg development in the summer, which is contingent on water operations that allow sufficient cold water availability in Shasta Reservoir for the summer months (Martin et al. 2017). Increasing spring flows for the benefit of fall-run and threatened spring-run Chinook salmon requires carefully balancing the needs of other protected species in the Sacramento River.

Our study focused on the flow–survival relationship for the smolt outmigration life history, as it was based on acoustically tagged fish, and tag size constraints precluding the tagging of smaller juveniles. However, other juvenile life-history types, namely fry and parr (approximately <55 mm and 55–75 mm FL, respectively), are important contributors to CCV Chinook salmon populations (Sturrock et al. 2020). While higher winter and spring flows also benefit fry and parr life histories (Sturrock et al. 2015, 2020), the flow thresholds defined in this study are for smolt outmigration and are likely not directly compatible with fry and parr life histories, which need flows appropriate for rearing. In addition, wild smolts were underrepresented in this analysis due to the difficulty in capturing adequately sized individuals for tagging, and the results we present are likely driven largely by survival dynamics of hatchery fish. Nonetheless, targeting ecologically functional flows that mimic the

shape of the historic flow regime under which these fish evolved should also benefit these other populations and promote life-history diversity.

Our study identifies key thresholds in the flow–survival relationships that can help water and fisheries managers evaluate trade-offs associated with different water management options that are, by law, supposed to balance instream and out-of-stream management objectives. We recommend that future studies attempt flow experiments to verify that migrating salmon would benefit as predicted from managed flow augmentation (such as pulse flows). It is likely that such pulse flows will engendered larger cohort-wide survival gains than predicted here: Flow pulses are known to promote juvenile Chinook salmon to initiate their downstream migration (Sykes et al. 2009), allowing a larger portion of the population to take advantage of the associated improvements in survival. Courter et al. (2016) used managed flow releases in the Yakima River, Washington, to show the positive impact of increased flow on Chinook salmon smolt survival, which was then used to implement a minimum flow target. Experimental pulse flows may also help decouple the mechanisms driving increased survival, because increased flows through reservoir releases may not affect temperature and turbidity the same as storm-related flow increases. Ultimately, functional flows in CCV should include a spring pulse flow component that mimics the characteristics of spring freshets and snowmelt events of a natural flow regime. These will benefit outmigrating smolts and also engender many other benefits to the ecosystem (Poff et al. 1997, Kiernan et al. 2012).

This is timely research as the frequency of drought events is predicted to increase in the CCV, creating additional stress to already vulnerable salmon populations (Yates et al. 2008). Munsch et al. (2019) showed a truncation of fish size and outmigration timing of juvenile Chinook salmon from the Sacramento River during warmer springs, which could lead to lower ocean survival. This highlights the influence of climate change on salmon species phenology and dynamics and the need for new flow management policies that include the potential impacts of future climate warming. In the Sacramento River, finding functional flows that could simulate ecologically critical aspects of the natural

spring flow regime, especially in increasingly common dry water years, is a critical step in ensuring the resiliency of juvenile Chinook salmon and other native fish species into the 21st century.

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DATA AVAILABILITY

The data that support the findings of this study are openly available from the National Oceanic and Atmospheric Administration's ERDDAP data server at: https://oceanview.pfeg.noaa.gov/erddap/tabledap/FED_JSATS_detects.html. The authors report no conflict of interest.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3498/full>