



Survival, Travel Time, and Use of Migration Routes by Juvenile Steelhead in a Modified River Estuary

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Received: 4 August 2023 / Revised: 2 January 2025 / Accepted: 22 January 2025

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Abstract

Greater understanding of the survival, travel time, and spatial distribution of juvenile salmonids among migration routes between their natal streams and the ocean is critical to the recovery of these threatened species. In the Sacramento–San Joaquin River Delta (Delta), a highly modified estuary in central California, USA, there is a critical need to evaluate how water management (e.g., water pumping) and environmental factors (e.g., water flow) impact these populations. While management actions can affect some environmental variables in the Delta, only recently have studies begun to uncover associations between these variables and key demographic parameters. In this study, we examine the effects of freshwater flows, water exports, tidal environment, and a temporary barrier on juvenile steelhead (*Oncorhynchus mykiss*) survival, travel times, and migration routing using a multiyear acoustic telemetry dataset and recent advancements in Bayesian multistate mark-recapture modeling. We found that no single covariate explained variation in juvenile steelhead population dynamics across the entire Delta, but that separate regions within the Delta showed association with specific environmental factors.

Keywords Juvenile salmonid survival · Multistate model · Mark-recapture study · Travel time analysis

Introduction

Salmonid populations (family Salmonidae) must navigate multiple challenging environments to complete their life cycle, and much effort has focused on better understanding the factors affecting the survival of salmonid smolts as they migrate oceanward from their natal streams. Although anadromous salmonids have evolved with many of these challenges, such as avian and piscivorous predation, disease, and elevated water temperatures (Thorstad et al., 2012; Warkentin et al., 2022; Yoshiyama et al., 1998), anthropogenic modifications to freshwater hydrology have exacerbated historically existing hurdles and introduced new ones (Molina-Moctezuma et al., 2022; Norrgård et al., 2013; Skalski et al., 2021). A precipitous decline in the abundance

and freshwater spatial distribution of many salmonid populations over the last century can be linked to the construction of dams and other anthropogenic alterations to riverine systems (Atlas et al., 2023; Raymond, 1988; Skalski et al., 2021). This decline, in combination with accelerating climate change (Crozier et al., 2021), has spurred resource managers to reconcile the provision of ecosystem services by modified freshwater systems with the recovery of threatened and endangered fish populations. An understanding of how regulation of the riverine environment affects juvenile salmonid populations at management-relevant spatial and temporal scales is necessary to devise strategies to arrest the decline of, and potentially recover, imperiled salmonid populations.

The Sacramento–San Joaquin River Delta (“the Delta”) is a complex network of distributary channels connecting the San Joaquin and Sacramento rivers with the San Francisco Bay in California, USA. The Delta is intensively managed for multiple competing uses, including recreation, navigation, water conveyance for agricultural and domestic consumption, and native ecosystems. Agriculture in the Central Valley of California contributes significantly to both the economy and domestic food supply, exceeding revenues of \$49 billion in 2020; 17% of irrigated land in

Communicated by Linda Deegan

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the United States is served in part by surface water diverted in the Delta (Gebremichael et al., 2021). Additionally, the California Aqueduct transports freshwater exported out of the Delta at either state or federal export facilities to nearly 20 million Californians for residential use. These demands on this freshwater system, particularly in times of drought, have impacted multiple runs of anadromous fishes historically found in the Delta, including threatened and endangered salmonid populations (Lindley et al., 2007). Freshwater export facilities located in the southwest Delta (Fig. 1) alter the Delta's hydrology by drawing water from river sources away from the ocean (Monsen et al., 2007) while upstream dams alter the annual pattern of freshwater input to the Delta (Munsch et al., 2019). This altered hydrology is hypothesized to affect the oceanward migration of juvenile salmonids by causing them to be entrained at the export facilities, delaying their migration, attracting predators, and degrading water quality (National Marine Fisheries Service, 2009). Actions taken to mitigate these impacts include the installation of temporary barriers to keep juvenile salmonids away from channels leading to the vicinity of the export facilities (Buchanan et al., 2013), as well as collection of juvenile salmonids at the export facilities and transport to

the western Delta (Kimmerer, 2008; Zeug & Cavallo, 2014). The impact of these actions on the survival of migrating salmonid populations is poorly understood, in part because the spatial and temporal scale of existing studies offers only limited insight on intra- and interseasonal variability of the effects (Buchanan et al., 2021; Jahn & Kier, 2020).

Evaluating and improving mitigation efforts requires monitoring impacts of water management on all threatened and endangered populations in the Delta (Eschenroeder et al., 2022; Lindley et al., 2007). In particular, Central Valley steelhead (*Oncorhynchus mykiss*) are listed as threatened under the Endangered Species Act, yet only with the broad adoption of active fish telemetry techniques (i.e., acoustic telemetry) have studies begun to quantify steelhead population dynamics (Buchanan et al., 2021; Eschenroeder et al., 2022). However, estimating demographic parameters in the complex setting of the Delta remains challenging because generally, poor survival of tagged fish combined with many possible migration routes makes it difficult to design studies that can achieve precise estimates at relatively fine spatial scales. Existing modeling results have focused on the associations between survival in large-scale reaches and measures of environmental and operational drivers such as river flow

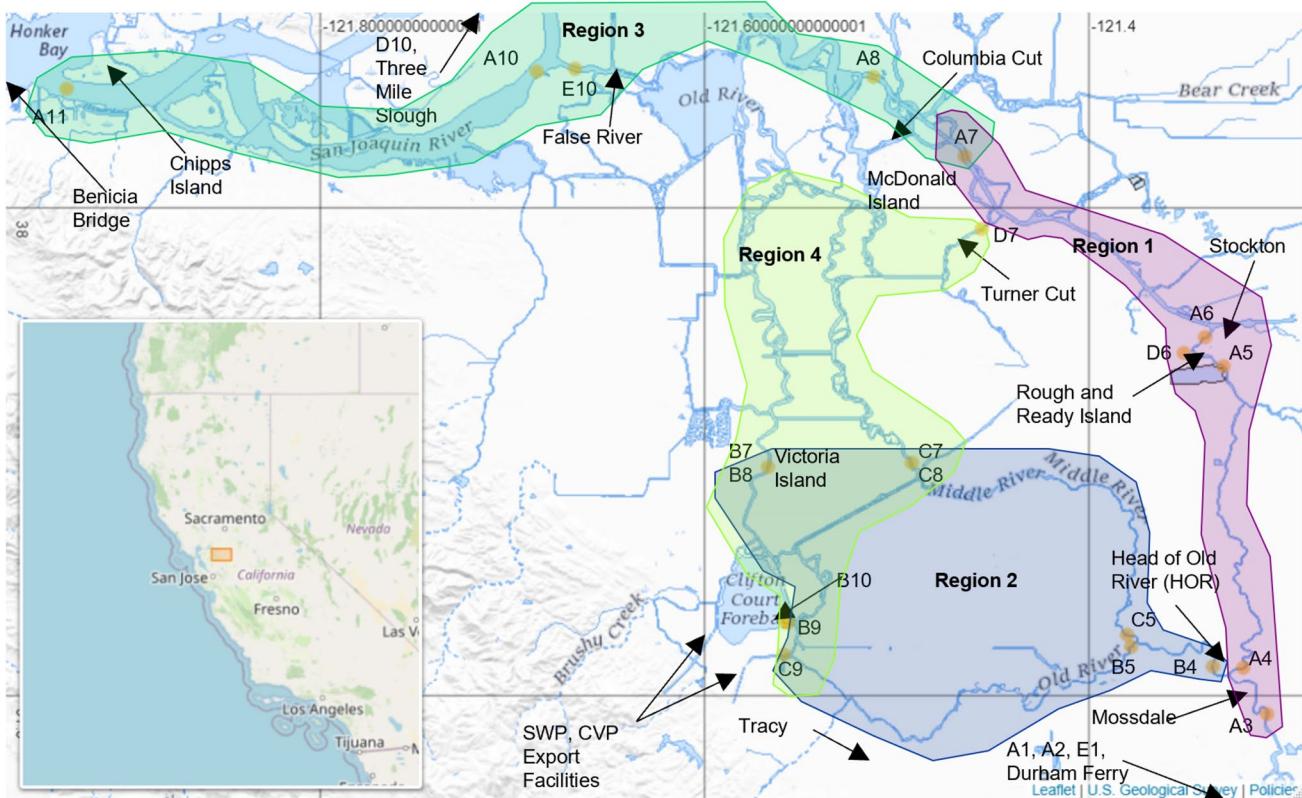


Fig. 1 Map of the study area in the San Joaquin River Delta, northern California, USA, showing fixed acoustic monitoring sites, export facilities, and main river and distributary channels. Tagged juvenile steelhead (*Oncorhynchus mykiss*) were released near Durham Ferry at

the upstream end of the study area (lower right corner). Chippis Island represents the terminus of the Delta at the oceanward end of the study area (upper left corner)

(Buchanan & Whitlock, 2022b; Buchanan et al., 2021), project exports (Tillotson et al., 2022), predation (Brandl et al., 2021; Zeug et al., 2021), and habitat quality (Hause et al., 2022). While these studies have been able to quantify these associations to some extent (e.g., between measures of river flow, the rock barrier installation, and survival; Buchanan et al., 2021), the covariates are summarized over longer temporal scales (multi-day to seasonal averages), and the extent to which the survival relationships vary on smaller spatial and temporal scales is unknown. Many of these studies used traditional “space-for-time” mark-recapture models which typically ignore variation in the travel time of tagged fish (Hance et al., 2020), and as a result, temporal variability in survival and route selection has largely been unexplored. Our analysis was designed to explore these questions in a comprehensive modeling framework and provide guidance to managers faced with supporting these populations through mitigation actions.

In this study, we quantify the association of environmental and operational covariates with demographic parameters of the juvenile steelhead population migrating through the Delta on daily timesteps and at a reach scale. Specifically, we estimate the effects of freshwater flows and water exports on steelhead survival, travel times, and migration routing. We also examine the survival and routing effects of a temporary barrier installed at the Head of Old River (HOR), the first major river junction that diverts fish towards the export facilities or keeps them in the San Joaquin River (Fig. 1). We leverage a multiyear dataset from acoustic-tagged juvenile steelhead from 2011 through 2016, representing a wide range of environmental and operational conditions, in order to quantify these relationships at multiple spatial scales within the Delta. We use recent advancements in Bayesian multistate mark-recapture modeling (Hance et al., 2022) to estimate these relationships at varying spatial scales within a single unified framework.

Methods

Study Area

Because this study focuses on the migration of steelhead entering the Delta from the San Joaquin River basin, the study area includes the mainstem San Joaquin River extending from Mossdale to Chipps Island, along with distributaries including Old River, Middle River, Turner and Columbia cuts, and the area surrounding the state and federal water export facilities near Tracy, California, including the Clifton Court Forebay (Fig. 1). Juvenile steelhead migrating toward the ocean can remain in the San Joaquin River or migrate through one of several distributaries. The HOR has been the site of a seasonal rock barrier installed to prevent steelhead

and juvenile Chinook salmon (*O. tshawytscha*) from entering the Old River corridor. The barrier cannot be installed under high flow conditions. When installed, it includes several culverts that reduce but do not eliminate fish entering the Old River corridor. Fish that enter Old River can remain in that channel westward past the export facilities, as Old River bends northward and rejoins the San Joaquin River. Alternatively, fish can enter the Middle River, migrating northward past Victoria Island, or they can enter one of the two main export facilities (either the State Water Project or SWP, or the Central Valley Project or CVP), where fish protection guidance louvers are used to divert fish to salvage facilities into holding tanks for transport by truck to the San Joaquin River just upstream from Chipps Island (Fig. 1).

Steelhead that remain in the San Joaquin River at HOR then migrate northward past the city of Stockton, California, and subsequently have another opportunity to leave the mainstem San Joaquin River at either Turner or Columbia cut. Fish that enter one of these two routes may then migrate either northward to rejoin the San Joaquin River, or southward (upstream) through the Old or Middle River corridors until reaching the export facilities, where they may be collected and transported.

Fish Tagging and Release

From 2011 to 2016, age-1 juvenile steelhead were obtained from Mokelumne River Fish Hatchery in Clements, California. Study fish were surgically implanted with Hydroacoustic Technology (HTI) Model 795 LD acoustic tags in 2011, VEMCO V6-180 kHz acoustic tags in 2012 and 2013, and VEMCO V5-180 kHz acoustic tags from 2014–2016 (Table 1). Tag weight ranged from 0.67 to 1.05 g, and tag burden ranged from 0.2 to 3.8%. Tagging was performed at the California Department of Water Resources (CADWR) Collection, Handling, Transport, and Release Laboratory at the SWP Skinner Fish Protection Facility in 2011 and at the Mokelumne River Fish Hatchery facility in 2012–2016. After tagging, fish were transported by truck to the release

Table 1 Summary statistics for hatchery steelhead (*Oncorhynchus mykiss*) tagged and released at Durham Ferry, California, from 2011 through 2016. Further details can be found in Buchanan et al. (2021). N=number of live-tagged steelhead smolts released each year

Year	N	Release dates	Fork length (mm)	Tag burden (%)
2011	2196	March 22–June 18	277 (149–396)	0.5 (0.2–2.7)
2012	1435	April 4–May 23	234 (115–316)	0.9 (0.3–2.9)
2013	1425	March 6–May 11	212 (115–300)	1.1 (0.4–3.3)
2014	958	April 24–May 24	247 (151–283)	0.5 (0.3–1.2)
2015	1427	March 4–April 25	235 (97–287)	0.5 (0.3–3.8)
2016	1440	February 24–April 30	248 (147–292)	0.5 (0.3–2.2)

site at Durham Ferry, located approximately 20 km upstream of Mossdale, and were held for at least 24 h in the river prior to release. A total of 8881 tagged and released age-1 juvenile steelhead were included in the multiyear dataset for analysis (Table 1). Fish tagging and handling procedures were based on Liedtke et al. (2012). The acoustic telemetry data collected from these fish have been previously analyzed by Buchanan et al. (2021) and are publicly available through the ERDDAP online database (<https://oceanview.pfeg.noaa.gov/erddap/search/index.html?page=1&itemsPerPage=1000&searchFor=FED6yr>).

Acoustic Data Collection and Curation

Fixed acoustic monitoring sites were located at key river junctions and channels of interest throughout the study area. Each monitoring site was composed of one or more acoustic hydrophones arranged to provide complete cross-sectional coverage of the river channel. Monitoring sites were located within each downstream branch at key river junctions to determine routing, at the entrance to both water export facilities, within river channels to determine reach-specific survival and travel time, and at the downstream terminus of the study area at Chipps Island (Fig. 1). Many monitoring sites, including Chipps Island, used two lines of hydrophones (“dual array”) to facilitate estimation of the detection probability. In some years, an additional monitoring site was located downstream of Chipps Island at Benicia Bridge to help estimate detection probability at Chipps Island. With few exceptions, each monitoring site was present in all 6 years of the study. Monitoring site locations did not change significantly from year to year.

Monitoring stations were each identified by a letter and number code (Fig. 1). Letters denoted migratory routes through the Delta as follows: “A” for the mainstem San Joaquin River, “B” for Old River or transport from the State Water Project (SWP), “C” for Middle River or transport from the Central Valley Project (CVP), “D” for other distributaries from the San Joaquin River such as Turner Cut, Threemile Slough, or Rough and Ready Island, and “E” for routes not terminating at Chipps Island such as upstream migration past Durham Ferry or in False River. The numbers correspond to the detection opportunity, with increasing numbers as stations are located further downstream toward the Delta terminus at Chipps Island (Fig. 1). In this way, we distinguish among navigable routes through the Delta, with monitoring stations further dividing routes into discrete river “reaches.” It is these reaches that serve as the fundamental spatial unit through which survival and travel time parameters were estimated.

Raw acoustic detection data were processed and collated into detection events. A detection event was defined by the time of the first and last detection of an individual tag at a

given monitoring site. Repeated detection events at a site were separated by gaps in detection of 30 min or more or by detection at a different monitoring location. Temporally sorted detection events for a given tag then formed the detection history for that tag.

Each detection history was passed through a predator filter to determine the likelihood that detections were the result of an active acoustic tag in the gut of a predatory fish as it passed by a monitoring location (Buchanan & Whitlock, 2022a). The predator filter used residence time near a monitoring location, travel time between monitoring locations, and movements of tags against the prevailing river flow to differentiate behavior between those that resembled juvenile steelhead and those that more closely resembled resident predatory fish such as largemouth bass (*Micropterus salmoides*) or striped bass (*Morone saxatilis*). Each detection event at a given acoustic receiver was run through a set of heuristics or rules based on these metrics, and detection events exceeding a threshold were determined to arise from predation smolts; these and all subsequent detections of the same tag were removed from the dataset. The filter was applied conservatively, and while obvious predator-type detection events were removed, doubtful or uncertain detections were classified as arising from live steelhead smolts. Each year, between 7.3 and 13.9% of detection events were removed via the predator filter. The predator filter construction and application are described in more detail in Buchanan (2018a, 2018b, 2018c), Buchanan et al. (2021), and U.S. Bureau of Reclamation (2018a, 2018b, 2018c).

Once presumed predator detection events had been censored, detection histories were compiled into capture histories for analysis. These capture histories were represented as a 13-letter alphanumeric code for each tagged steelhead, where a letter in the k th digit denoted detection in that lettered route at the corresponding k th telemetry station (Fig. 1). Non-detections were represented by a 0. For example, a capture history of “A00ABC0C00DA0” denotes release at Durham Ferry (A0 in Fig. 1), with subsequent detections at station A3 in the San Joaquin River near Mossdale, station B4 in Old River at HOR, station C5 in Middle River at its junction with Old River, station C7 in Middle River near Victoria Island, station D10 at Threemile Slough, and a final detection at station A11 near Chipps Island (Fig. 1). Each detection at a station represented by a letter in this capture history code was also associated with the time and date of detection, which were used to assign covariates and to inform the travel time model. Although detection histories could include some upstream movement of juvenile steelhead within the study area, the multistate model assumed seaward movement of fish within each route from entry to the Delta at Mossdale to the Delta exit at Chipps Island. Capture histories thus represented a tagged fish’s movement oceanward based on the detection history.

Model Description

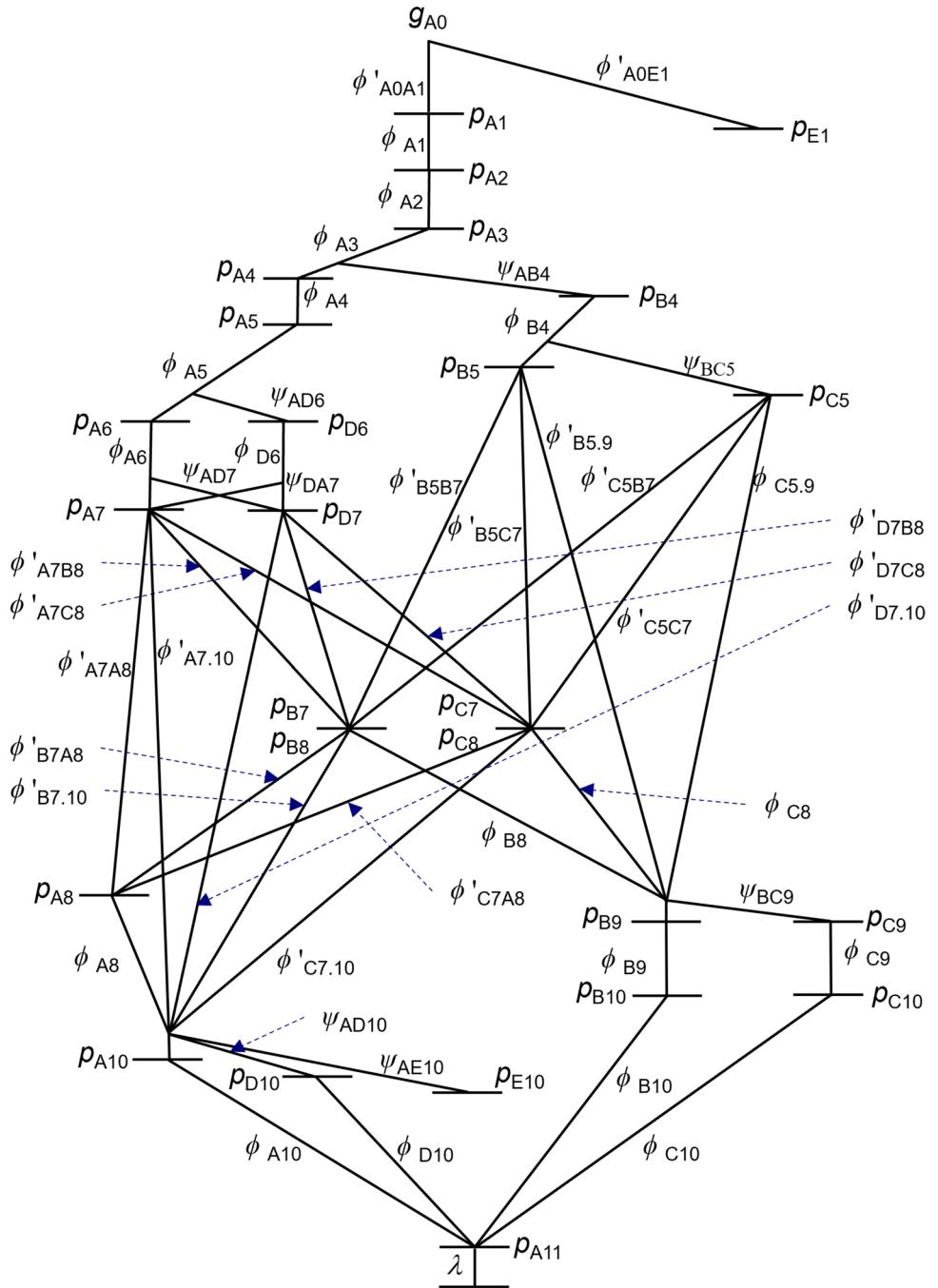
We analyzed capture histories to estimate travel time, routing, and survival parameters in the Delta using a temporally stratified multistate mark-recapture model (TSMS) based on the model developed by Hance et al. (2020) and Hance et al. (2022). As a space-for-time mark-recapture model, the TSMS model assumes unidirectional movement of individuals, such that detections of fish passing monitoring stations form the detection opportunities used to partition survival and travel time estimates among

Fig. 2 Temporally stratified multistate model (TSMS) schematic with states (letters A through E) representing river routes and occasions (numbers 0 through 11) representing detection opportunities (monitoring locations). Estimable survival, routing, transition (joint probability of route and survival), and detection parameters are denoted by the terms ϕ , ψ , ϕ' , and p , respectively. Release at Durham Ferry is denoted by g_{A0} , and the joint probability of surviving and being detected at the last opportunity at Benicia Bridge is denoted by λ

river reaches. Each monitoring station is thus assigned a route which serves as the state in the TSMS model. This approach allows us to translate the layout of monitoring stations in Fig. 1 into a model schematic that identifies parameters to be estimated by the TSMS model (Fig. 2).

The TSMS model is defined in terms of the following parameters:

- ϕ_{qjsy} is the probability that a tagged fish alive in route q at detection opportunity j on day s of study year y survives to the next detection opportunity.



- α_{qjsty} is the probability that a tagged fish in route q passing detection opportunity j on day s of study year y will arrive at detection opportunity $j + 1$ on day t , given that the fish survived to detection opportunity $j + 1$.
- ψ_{qrkty} is the probability that a tagged fish initially in route q will enter route r immediately prior to detection opportunity k on day t of study year y .
- ϕ'_{qjrkst} is the probability that a tagged fish in route q departing detection opportunity j on day s of study year y survives and transitions to route r at detection opportunity k .
- P_{rkty} is the probability that a tagged fish in route r arriving at detection opportunity k on day t of study year y will be detected.

As we define the model here, ψ represents the transition from one route to another immediately preceding the next available detection opportunity. This leads to a natural interpretation of the model parameters in cases where telemetry stations (detection opportunities) are located in either channel immediately downstream of a river junction (e.g., HOR; Fig. 1). In these cases, survival occurs before routing, and ψ therefore represents the proportion of surviving fish entering each channel. In contrast, given the layout of the acoustic telemetry network, some reaches encompass junctions located a considerable distance upstream of the downstream reach boundaries. This layout introduces possible bias into estimates of ψ owing to the potentially differential survival in reaches seaward of the unmonitored junction. For example, fish departing telemetry station B5 (Old River at its junction with Middle River) can next be detected at either

B7, C7, B9, or C9 (Old or Middle River at Victoria Island, the radial gates outside of the Clifton Court Forebay, or the CVP gate, respectively; Fig. 1). In this example, a significant portion of the survival process occurs after the junction and may differ among destinations. Thus, for these reaches, we estimate ϕ' , defined as the joint probability of traversing a particular route and surviving along that route from one detection opportunity to the next. Our model is constrained so that $\phi_{qjsty} = \sum_{rk} \phi'_{qjrkst}$; in other words, the sum of all joint transition and survival probabilities from a given departure location estimates the overall survival from that detection opportunity to all possible destination detection opportunities. For pure transition probabilities not involving joint probability of survival (ψ), the model constrains all such available transitions from a departure location to sum to 1. We additionally enforce the constraint that α_{qjst} sums to 1 across all possible t , so that all surviving fish must arrive on some day between day s and day T (the final day of the study year).

The TSMS model makes use of two intermediary parameters, λ and χ :

λ_{qjrkst} is the probability that a tagged fish, departing detection opportunity j in route q on day s of study year y , will next be detected at detection opportunity k in route r on day t (Hance et al., 2022) where one or more monitoring stations may occur between detection opportunities j and k . Thus the λ parameter integrates over all possible survival, travel time, route selection, and detection probabilities at intervening sites between any two monitoring stations. The following equation defines λ in cases where ϕ' is in the final reach:

$$\lambda_{qjrkst} = \begin{cases} \phi'_{qjrkst} \alpha_{qjsty} \psi_{qrkty} & \text{fork} = j + 1 \\ \sum_{w=1}^R \sum_{u=s}^T \lambda_{wjrk-1suy} (1 - p_{wk-1uy}) \phi'_{wk-1rkuy} \alpha_{qk-1uty} \psi_{wrkty} & \text{fork} > j + 1 \end{cases} \quad (1)$$

where $w \in \{1, \dots, R\}$ is the set of available routes at a detection opportunity, and $k - 1$ represents the detection opportunity immediately preceding k . For cases where ϕ' is in the final reach, replace ϕ'_{qjrkst} with ϕ_{qjsty} and drop the outer summand over w .

χ_{qjsty} is the probability that a tagged fish, having been detected at detection opportunity j in route q on day s of study year y , will not be detected again during the study

period. Like λ , the χ term integrates over all possible mortality, missed detection, route selection, and travel time probabilities from the last monitoring station at which a fish was detected to the study terminus. When there is more than one possible route immediately after departing detection opportunity j in route q , χ must sum over the ϕ' parameters from that station; otherwise, no outer summand is needed since only a single ϕ term is available when departing that station:

$$\chi_{qjsty} = \begin{cases} \sum_{w=1}^R \left((1 - \phi'_{qjwksy}) + \phi'_{qjwksy} \sum_{u=t}^T \alpha_{qjsty} \left[\sum_{v=1}^R (\psi_{wvkt} (1 - p_{vkuy}) \chi_{vkty}) \right] \right) & \text{for } \phi'_{qjrkst} \\ (1 - \phi_{qjsty}) + \phi_{qjsty} \sum_{u=t}^T \alpha_{qjsty} \left[\sum_{v=1}^R (\psi_{qvkt} (1 - p_{vkuy}) \chi_{vkty}) \right] & \text{for } \phi_{qjsty} \end{cases} \quad (2)$$

The λ and χ parameters operate on pairs of monitoring stations at which consecutive detections are recorded and monitoring stations where the last detections are recorded, respectively. As such, they provide a link between the latent ϕ , ϕ' , α , ψ , and p parameters and the data and are defined on the scale of the observed capture histories. Thus, the observed data likelihood takes a multinomial form and is the product of each λ or χ term raised to the power of the observed number of fish with the relevant capture history (Hance et al., 2022).

Covariates

To investigate the effect of environmental factors on the steelhead population migrating through the South Delta, we modeled the survival, travel time, routing, and joint survival-transition probabilities as a function of several covariates. Juvenile steelhead migrating seaward through the San Joaquin River and the Delta may be affected by freshwater flows, water exports through state and federal facilities, and fluctuating tides. In addition, a temporary barrier at HOR can affect access to this route. Because flows at Vernalis are representative of freshwater flow through much of the upper mainstem San Joaquin River and have been used to represent freshwater flow into the South Delta in other studies (Buchanan et al., 2021), we

used the daily, tidally filtered flow at the USGS gaging station at Vernalis, California (gage number 11303500, U.S. Geological Survey, 2021) as reported in the Dayflow dataset (<https://data.cnra.ca.gov/dataset/dayflow>) from 2011 through 2016 from the date of first juvenile steelhead release in that year to 120 days after (the maximum date of the study period for that year). Because project water exports draw significant portions of freshwater flow in the Delta, we wanted to assess whether exports affected local flows within the Delta enough to alter juvenile steelhead migration timing or survival. Therefore, we measured the effect of project water exports using the combined total daily raw export rate from the state and federal water projects as reported in Dayflow (the sum of columns “SWP” and “CVP”). The Old and Middle River index (OMR) is used by managers as a measure of the river environment in the portion of the Delta close to the export facilities where frequent reverse flows occur, reflecting both tidal influences and water pumping operations at the export facilities. This daily index is calculated using a formula designed to closely track the sum of flows in the Middle and Old Rivers near Victoria Island. We defined the OMR measure used in our analysis as the sum of the daily flows at the two USGS gaging stations in Old and Middle Rivers nearest Victoria Island (Fig. 1, gage numbers 11313315 and 11312674, U.S. Geological Survey, 2021). Finally,

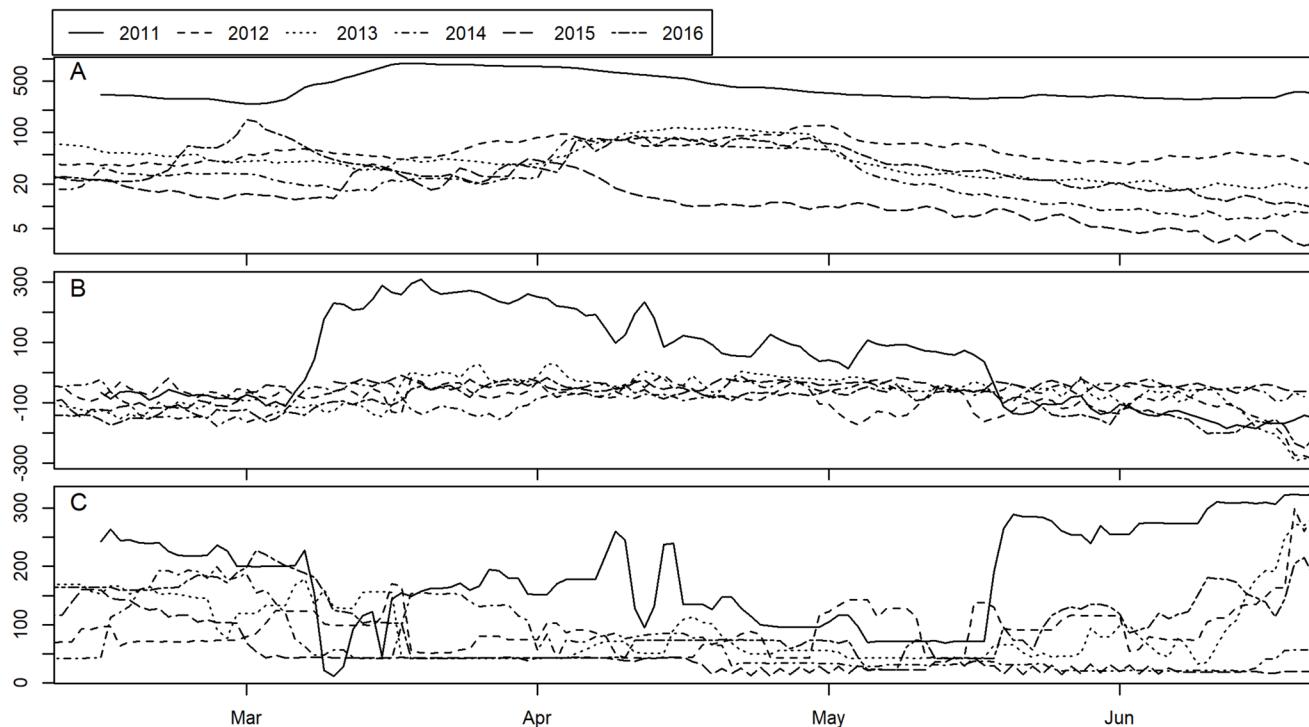


Fig. 3 Daily San Joaquin River flow at Vernalis (A, log scale), Old and Middle River index (OMR) flow (B), and total exports (C) in cubic meters per second from February to July 2011–2016

we used an indicator variable to denote the status of the temporary barrier at HOR (1 = barrier present, 0 = barrier absent). The HOR barrier was present in the spring during 4 of the 6 years of our study. All covariates used were reported as daily measures (Fig. 3), matching the daily stratification of the capture histories, and the covariate value assigned to an individual's transit through a reach was the value measured on the day of entry into that reach.

We examined all covariates for collinearity, and with the exception of the HOR barrier status, we found that all covariates exhibited at least moderate correlation with one another. Thus, we did not include any two covariates in the same model and instead chose to model their effects on travel time, survival, and routing separately. For a given model and associated covariate, we modeled survival as:

$$\text{logit}(\phi_{qjy}) = \beta_{0qj} + \beta_{1qj}X_{sy} + \beta_{2qj}\text{HOR}_{sy} \quad (3)$$

where q indexes route, and j indexes detection opportunity for each survival reach; β_{0qj} is the logit-intercept of survival, β_{1qj} is the effect of a given covariate on survival, X_{sy} is the covariate chosen for a given model on day s of study year y , β_{2qj} is the effect of HOR barrier status on survival, and HOR_{sy} indicates status of the HOR barrier on day s of study year y . Note that β_{2qj} was set at 0 for all reaches except those in the vicinity of the HOR barrier (see Table S1). The transition probability ϕ' is defined as a function of covariates in the same way as ϕ . Because by definition ϕ' was only estimated in reaches where survival was inseparable from route entrainment, we denote intercepts and covariate effect slopes with β_{0qrk} and β_{1qrk} respectively, as for survival but with the addition of r and k subscripts to denote the destination route and station (Table S1).

Travel time in each reach was modeled as the probability of arriving at the downstream monitoring station on a given day t . This probability, α_{krty} , was estimated hierarchically by fitting a lognormal kernel to the daily arrival probabilities:

$$\log\left(L\left\{p_{rkty}^A, p_{rkty}^B | n_{rkty}^{AB}, n_{rkty}^B, n_{rkty}^A\right\}\right) \propto n_{rkty}^{AB} p_{rkty}^A p_{rkty}^B + n_{rkty}^B \left(1 - p_{rkty}^A\right) p_{rkty}^B + n_{rkty}^A \left(1 - p_{rkty}^B\right) p_{rkty}^A \quad (8)$$

where p_{rkty}^A and p_{rkty}^B are the conditional probabilities, given detection at a dual array, of being detected at the first or the second array, respectively, and n_{rkty}^{AB} , n_{rkty}^B , n_{rkty}^A are the numbers of individuals at a location on a given day that were detected at both arrays, not detected at the first array but detected at the second, or detected at the first array and not detected at the second, respectively. The probabilities of detection on each of the dual arrays were linked back to the

$$\alpha_{qjsty} \propto \frac{1}{t - s + 0.5} e^{\left(\frac{-(\log(t-s+0.5)+\mu_{qjsty})^2}{2\sigma_{qjy}^2}\right)} \quad (4)$$

where μ_{qjsty} represents the log of the mean travel time for departure day s and σ_{qjy} represents the log of the variance in travel times, constrained to be constant across all departure days s . By defining the log mean travel time as conditional on the daily strata, we could then link μ_{qjsty} to daily covariates:

$$\mu_{qjsty} = \gamma_{0qj} + \gamma_{1qj}X_{sy} + \gamma_{2qj}\text{HOR}_{sy} \quad (5)$$

With X_{sy} denoting daily covariates, HOR_{sy} denoting HOR barrier status, and γ_{2qj} set to 0 for the same reaches as for survival above (Table S1).

Migration routing at key junctions was allowed to vary daily as a function of covariates as well. The probability of entrainment into a given branch of a river junction was defined as follows:

$$\text{logit}(\psi_{qrkty}) = \zeta_{0qrk} + \zeta_{1qrk}X_{ty} + \zeta_{2qrk}\text{HOR}_{sy} \quad (6)$$

similar to survival above and where ζ_{2qrk} set to 0 for all junctions except those noted in Table S1.

Finally, detection probabilities at each monitoring station were also allowed to vary daily as a function of covariates and were defined on a logit scale similar to survival:

$$\text{logit}(p_{rkty}) = \xi_{0rk} + \xi_{1rk}X_{ty} \quad (7)$$

Some monitoring stations were not present in some years of the study. For these stations, during these years, the detection probability was set to 0. Additionally, many monitoring stations were composed of dual arrays which allowed us to specify an auxiliary dual array detection model, leveraging additional information to inform detection probability. The auxiliary likelihood, which assumes independence of the "A" and "B" arrays within each dual array, was defined as follows:

$$\text{overall detection probability at a location through the equation } p_{rkty} = 1 - \left(1 - p_{rkty}^B\right)\left(1 - p_{rkty}^A\right). \quad (8)$$

We fit three separate models to the capture history data, with each model incorporating one of the following covariates into the survival, travel time, and routing relationships described above: (1) flows at Vernalis, (2) exports at the state and federal facilities, and (3) Old and Middle River flows. Each model included the effect of the

HOR barrier on survival and travel time in reaches in the vicinity of HOR, as well as routing at that junction. Each model also included the effects of Vernalis flow on detection probability at each monitoring station.

Given differences in hydrological patterns across the Delta (e.g., directional flow and tidal patterns), we expected different covariates to better explain demographic parameters in different regions of the Delta. Therefore, we present model results by focusing on four major regions within the Delta. These regions were selected based on anticipated covariate effects: (1) the upstream portion of the mainstem San Joaquin River (Fig. 1 (A3 to A7)) where flows were primarily unidirectional, (2) the Old and Middle River corridors from HOR to either of the water export facilities or to monitoring stations near Victoria Island (Fig. 1, (B4 to B7/C7/B9/C9)), (3) the downstream portion of the San Joaquin River from Turner Cut to Chippis Island (Fig. 1 (A7 to A11)) where flows were primarily tidally reversing, and (4) the portion of the Delta composed of the route from Turner Cut back through the Old and Middle River, where fish swam against oceanward flows to arrive at the water export facilities (Fig. 1 (D7 to B9/C9)).

We coded our model in the Stan programming language (Carpenter et al., 2017). Continuous covariates (Vernalis and OMR flows, and total exports) were standardized by subtracting the mean and dividing by the standard deviation. All prior distributions for estimated parameters were weakly informative, which have been shown to improve efficiency and reduce type I error rates (Lemoine, 2019). In particular, priors for parameters with a logit-link function such as those relating to survival, entrainment, and detection probabilities (β , ζ , and ξ from Eqs. 3, 6, and 7) were assigned Student's t distributions with 7 degrees of freedom and standard deviation of 1 for slope terms and 2 for intercept terms. We assigned standard normal prior distributions to the log-transformed mean and variance terms of the travel time parameters (γ and σ from Eqs. 5 and 4). We ran the models with four independent chains for 500 warmup iterations and 500 sample iterations for a total of 2000 posterior samples for each model (no thinning was performed). Model results showed evidence of well-mixed and converged chains, with all Rhat values < 1.02 and over 95% of parameter Rhat values < 1.01 . All parameter Bulk Effective Sample Sizes (Bulk ESS) were greater than 450.

Results

Our analysis showed that juvenile steelhead survival, travel time, and routing probabilities through the San Joaquin River and the Delta varied significantly by

year and by region within the Delta. Environmental and operational covariates explained some of this variation, although the extent to which particular covariates explained these parameters also varied depending on the region within the Delta. In particular, both survival and travel time varied most substantially with Vernalis flows in the upstream mainstem San Joaquin River and with Old and Middle River flows in the Old and Middle River corridors (Regions 1 and 2 below, respectively). Both the region from Turner Cut upstream through Old and Middle River toward the export facilities (Region 4) and the downstream, tidally influenced San Joaquin River (Region 3) displayed more uncertainty in relationships between travel times, survival, and covariates. The temporary barrier at HOR was associated with variation in survival and travel time in both the riverine reaches of the San Joaquin and the Old and Middle Rivers. Below, we describe our findings in more detail, first by highlighting selected examples of fine-scale, reach-specific travel time results, followed by results grouped by region of the Delta. We then present summary metrics of survival, travel time, and migration route probability for each main route through the Delta from Mossdale to Chippis Island.

Selected Reach-Specific Travel Time Estimates

Travel time slope parameter estimates for reaches in the mainstem San Joaquin were largely negative for reaches upstream of Turner Cut, with slopes in the Vernalis flow model ranging from -0.140 ($\gamma_{1,1,4}$; 90% credible interval (CI) -0.183, -0.098) between A6 and A7 to -0.323 ($\gamma_{1,1,1}$; 90% CI -0.395, 0.265) between A3 and A4. Downstream of Turner Cut, this trend was muted, with Vernalis flow slope parameters in the Vernalis flow model for travel times between A7 and A8 ($\gamma_{1,1,5,1,6}$) and between A8 and A10 ($\gamma_{1,1,6}$) estimated near zero. However, in the farthest downstream reaches in the San Joaquin, there was again a negative association between Vernalis flow and travel time, with slope parameters between A10 and A11 ($\gamma_{1,1,8}$; -0.102, 90% CI -0.125, -0.078) and between D10 and A11 ($\gamma_{1,4,8}$; -0.146, 90% CI -0.221, -0.070) estimated below zero (Table S1; Fig. 1). These estimates indicate an association between increased Vernalis flow and reduced travel time through nearly the entire length of the mainstem San Joaquin River within the Delta. A similar trend was seen with OMR flows, although slope parameter estimates for the model including Vernalis flows were generally more negative for reaches in the San Joaquin River than were parameter estimates for the same reaches in the OMR flow model (Table S1). Travel time slope parameters for the model including exports were negative for the uppermost reaches of the San Joaquin River and near zero downstream of the city of Stockton (Table S1; Fig. 1).

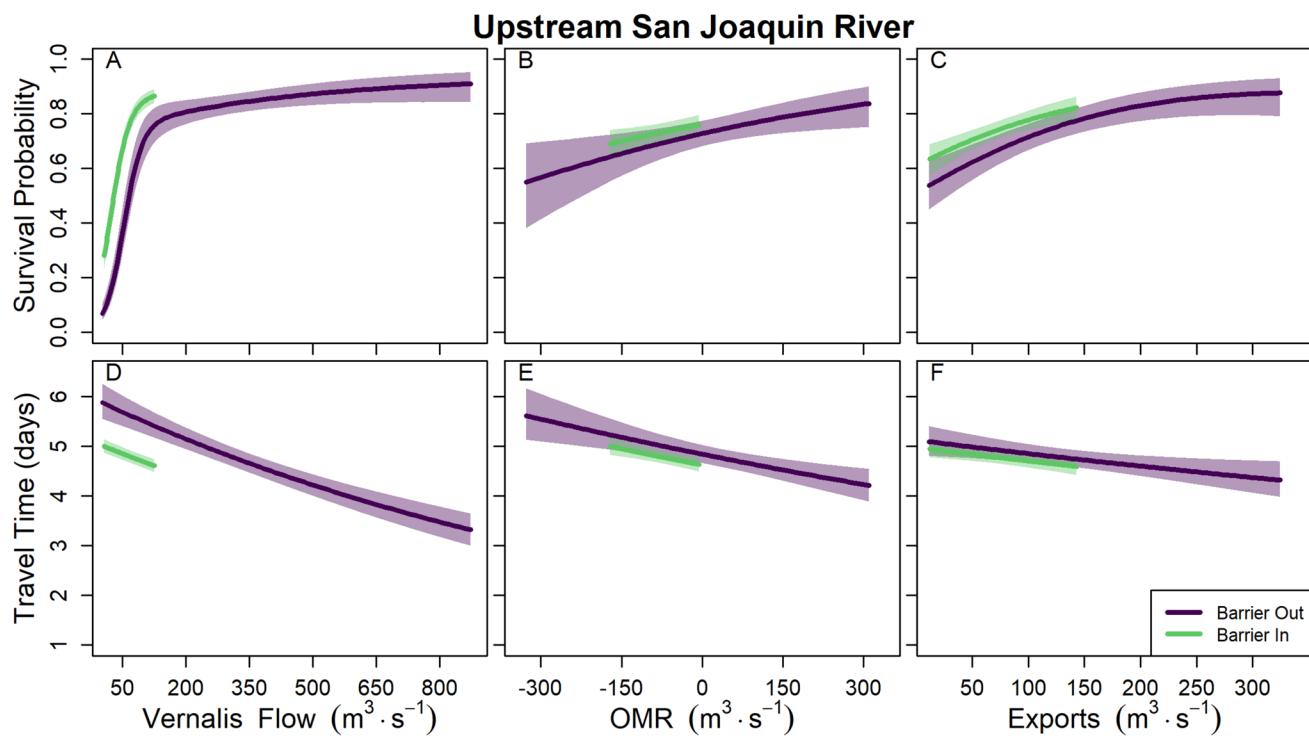


Fig. 4 Predicted juvenile steelhead (*Oncorhynchus mykiss*) survival (A–C) and travel time (days; D–F) in the San Joaquin River corridor from Mossdale to Turner Cut as a function of three covariates modeled: Vernalis flow (A and D); Old and Middle River index (OMR) flows (B and E); and total exports (C and F). Shaded regions repre-

sent 90% credible intervals. Median predictions and credible intervals are plotted over the range of observed covariates during the study period when the Head of Old River (HOR) barrier was either present or absent

Region 1: Upstream San Joaquin River

Reaches within the upper, riverine portion of the San Joaquin River exhibited relatively high survival and shorter travel times than more seaward reaches, with estimated median travel times from Mossdale to Turner Cut ranging from approximately 3 to 5 days and estimated survival ranging from around 0.3 to 0.9 over the range of covariates observed during the study (Fig. 4). Among covariates modeled, San Joaquin River flow at Vernalis showed the strongest relationship with survival and to a lesser degree travel time (Fig. 4), with slope coefficients consistently centered away from zero for most reaches in this region (Table S1). Increasing San Joaquin River flow at Vernalis was strongly associated with an increase in survival and a decrease in travel time through the region, while OMR flows and exports showed similar, although weaker, relationships with survival and travel time (Fig. 4). While exports can affect the flow split at the HOR and thus the remaining flow in the mainstem San Joaquin River downstream of the HOR, the apparent “export effect” in the upper San Joaquin River may be largely due to higher San Joaquin River flows which are often correlated with higher exports. The presence of the HOR barrier was associated with decreased travel time and increased survival

through this region across the range of San Joaquin River flow at Vernalis (Fig. 4).

Region 2: Old and Middle River Corridors (Downstream Transit)

For fish traveling oceanward from HOR within the Old and Middle River corridors, median travel time predictions from the upstream end of the region at the HOR to one of the endpoints, either in the Old or Middle River near Victoria Island or at the SWP or CVP export facilities, ranged from 3 to 8 days and predicted survival ranged from 0.6 to 0.9 across the observed range of covariates (Fig. 5). Travel time in this region was most strongly associated with OMR flows (Fig. 5), although the trend in travel time depended on which route fish were traversing. For fish traveling to either of the export facilities in the southwest of the Delta (HOR to CVP/SWP), increased OMR flow was associated with increasing travel times, whereas for fish traveling through the Old and Middle Rivers northward past Victoria Island (HOR to OR4/MR4), travel times decreased as OMR flows increased. All three covariates displayed strong associations with at least some of the transition probabilities in this region (Table S1). While these transition probabilities are

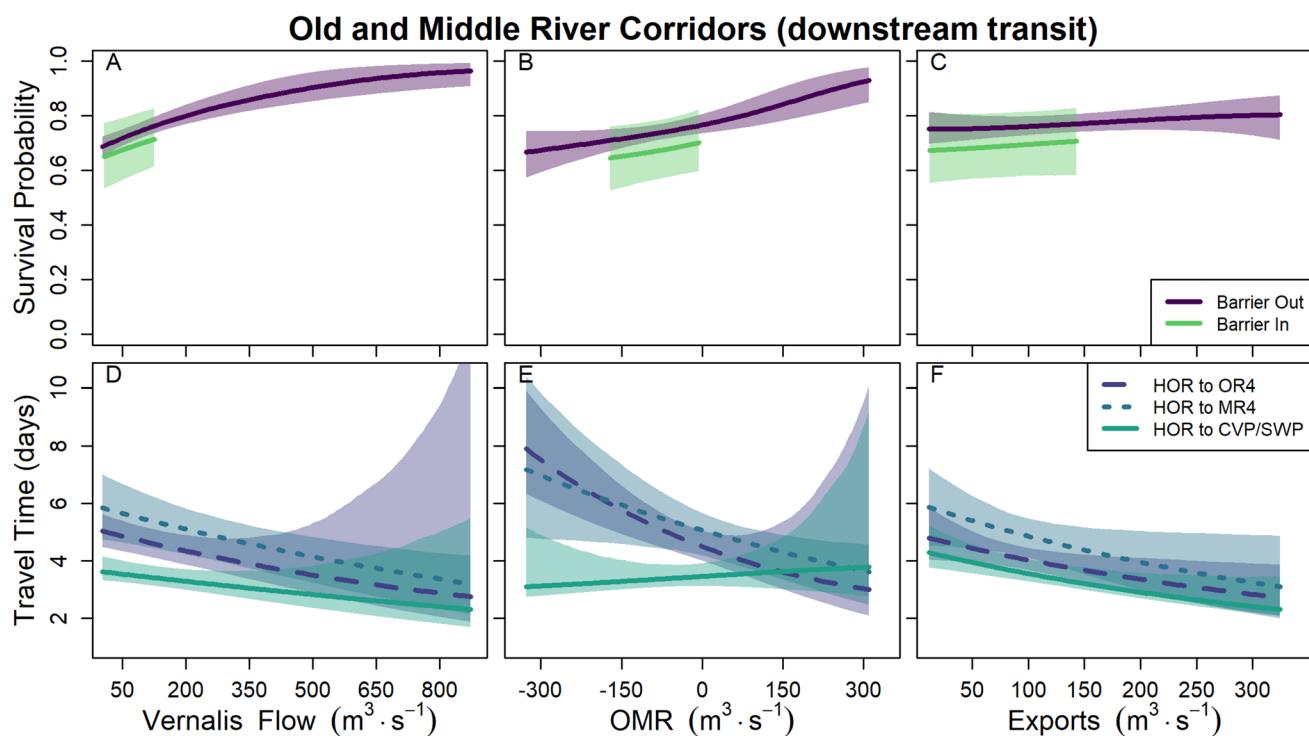


Fig. 5 Predicted juvenile steelhead (*Oncorhynchus mykiss*) survival (A–C) and travel time (days; D–F) in the Old and Middle River corridors from the Head of Old River to either the export facilities or Victoria Island as a function of three covariates modeled: Vernalis flow (A and D); Old and Middle River index (OMR) flows (B and E); and total exports (C and F). Survivals are shown for Head of Old River

(HOR) barrier present and absent status, while travel times are shown for barrier absent only. Solid, dashed, and dotted lines represent travel times from the HOR to either the federal or state export facilities (CVP/SWP), Old River at Victoria Island (OR4), and Middle River at Victoria Island (MR4), respectively. Shaded regions represent 90% credible intervals

defined as the joint probability of traversing and surviving a particular reach, survival in this region is calculated by summing the transition probabilities to each of the stations denoting the downstream boundary of the region. Thus, although each transition probability was strongly associated with exports because the transition to the export facilities showed a positive association and the transition past Victoria Island a negative association with exports, overall survival in the region was not strongly associated with exports, presumably because the transition probability relationships offset one another (Fig. 5, Table S1). Overall survival in this region appears more strongly associated with OMR flows and Vernalis flows, increasing as these flows increased (Fig. 5).

Region 3: Downstream San Joaquin River

Survival predictions within reaches in the lower, tidally dominated portion of the San Joaquin River were slightly lower than in the upstream San Joaquin River, ranging from about 0.5 to 0.8, while the median predicted travel time from McDonald Island to Chipps Island was consistently around 4 days across the range of observed covariates (Fig. 6). The remarkably consistent travel time predictions, as well as

travel time slope coefficients estimated near zero, indicate no strong association between any of the covariates and travel time in this region. Survival, on the other hand, was positively associated with OMR flows, with survival from McDonald Island to Chipps Island increasing with increased OMR flows (Fig. 6, Table S1).

Region 4: Old and Middle River Corridors (Upstream Transit)

Predicted transition probabilities from Turner Cut to the export facilities were relatively low, ranging from 0.2 to 0.4 across the observed range of covariates (Fig. 7). However, because fish could also transition from Turner Cut directly to Chipps Island, these transition probabilities are not directly comparable to survival estimates in other regions. Transition probabilities showed a slight positive association with exports, with more fish departing Turner Cut predicted to arrive at the export facilities as exports increased (Fig. 7). This association was likely driven largely by transition via Middle River, with the two slope coefficients on transition probabilities via this route in the export model both having 90% credible intervals greater than 0 ($\beta_{1,3,6}$ and $\beta_{1,4,5,3,6}$,

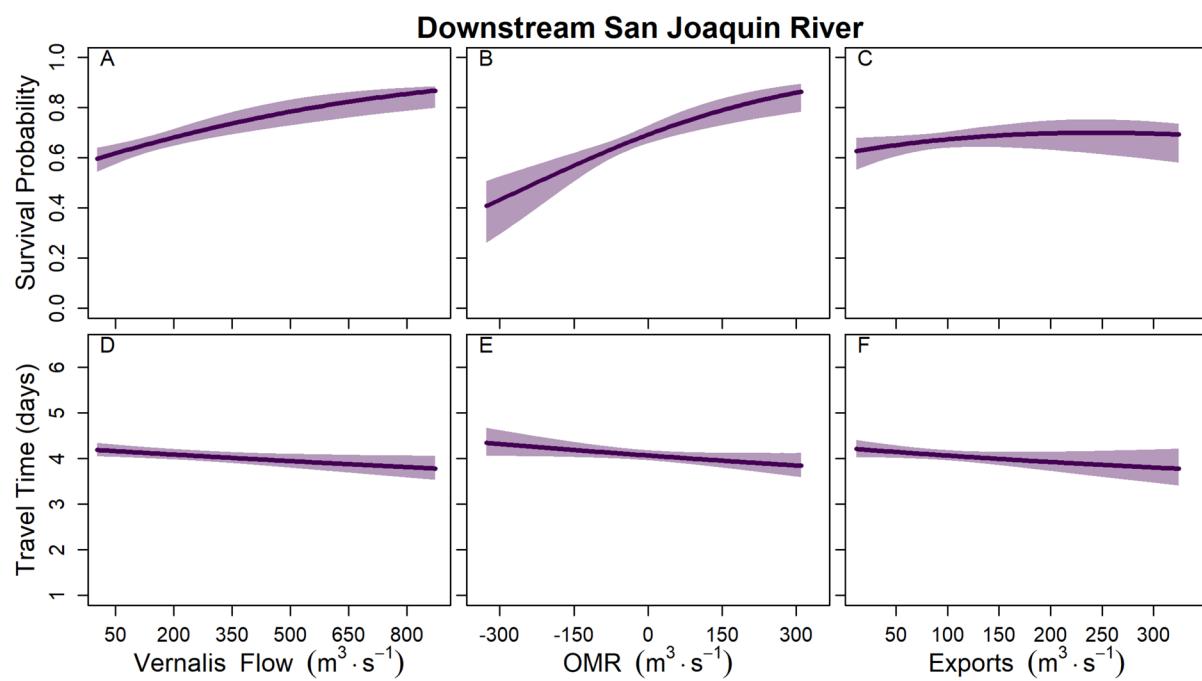


Fig. 6 Predicted juvenile steelhead (*Oncorhynchus mykiss*) survival (A–C) and travel time (days; D–F) in the San Joaquin River corridor from McDonald Island to Chipps Island via the San Joaquin River as a function of three covariates modeled: Vernalis flow in thousands of

cubic feet per second (kcfs; A and D); Old and Middle River index (OMR) flows (B and E); and total exports (C and F). Shaded regions represent 90% credible intervals

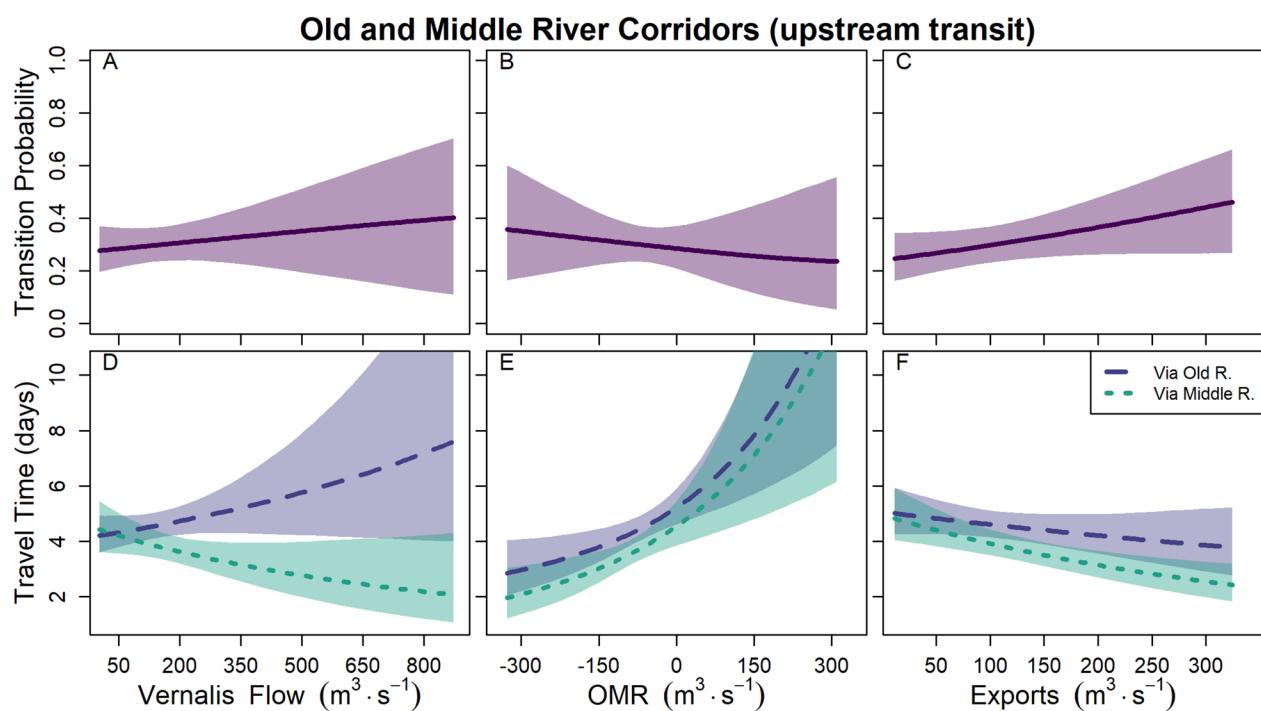


Fig. 7 Predicted juvenile steelhead (*Oncorhynchus mykiss*) transition probabilities (A–C) and travel time (days; D–F) in the Old and Middle River corridors for fish traveling upstream from Turner Cut to the export facilities as a function of three covariates modeled: Vernalis

flow (A and D); total exports (B and E); and Old and Middle River index (OMR) flows (C and F). Dashed and dotted lines represent travel times from Turner Cut to CVP/SWP via Old River and Middle River, respectively. Shaded regions represent 90% credible intervals

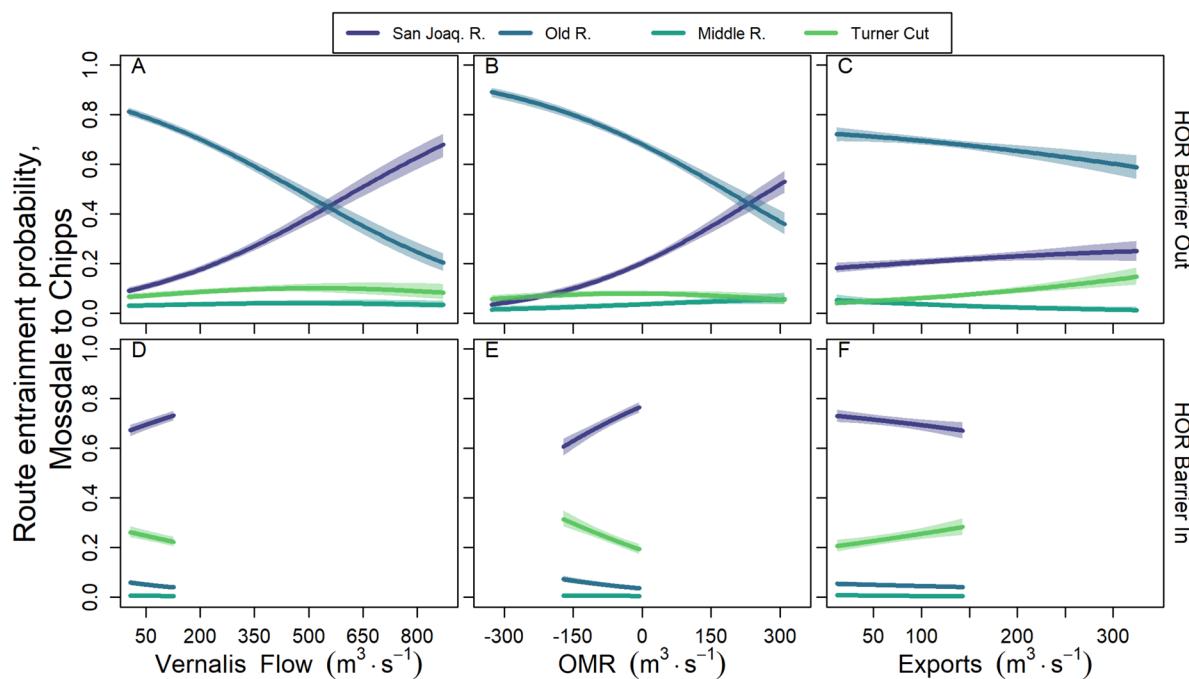


Fig. 8 Predicted juvenile steelhead (*Oncorhynchus mykiss*) migration routing probabilities as a function of covariates in the San Joaquin River Delta. Probabilities represent the predicted proportion migrating through major routes within the Delta, from Mossdale to Chipps Island. Major routes include remaining in the San Joaquin River at

both junctions with Old River and Turner Cut, entering and remaining in Old River, entering Middle River, and entering Turner Cut. Migration routing probabilities are shown for both Head of Old River (HOR) barriers in (A–C) and out (D–F). Shaded regions represent 90% credible intervals

Table S1). Changes in exports showed little association with travel times through this region, relative to OMR and Vernalis flows. Instead, OMR flows showed the strongest association, with travel times from Turner Cut to the export facilities ranging from 2 to over 10 days across the range of observed OMR flows, increasing as OMR flows increased (Fig. 7).

Route-Specific Delta-Wide Summary Parameters

Although the presence of the HOR barrier had a large effect on routing probabilities among the major migration routes through the Delta, the San Joaquin River route and Old River route were the most heavily traveled by juvenile steelhead regardless of HOR barrier status (Fig. 8). The Middle River route and Turner Cut route were much less frequently used (Fig. 8). When the HOR barrier was absent, the Old River route had the highest proportion of steelhead migration, with the San Joaquin River route second. When the HOR barrier was present this pattern reversed, with San Joaquin River first and Old River second (Fig. 8). The presence of the HOR barrier was also associated with decreased usage of the Turner Cut route. The Middle River was used by relatively few fish regardless of barrier status (Fig. 8). When the barrier was in, changes in route migration patterns were most strongly associated with Vernalis flows. When the barrier

was out, both Vernalis and OMR flows were associated with large changes in route usage (Fig. 8). As freshwater San Joaquin River flow at Vernalis increased, a higher proportion of steelhead were predicted to migrate through the mainstem San Joaquin River and a lower proportion through the Old River. This pattern was similar regardless of HOR barrier status (Fig. 8).

Overall survival estimates through the Delta from Mossdale to Chipps Island increased as each of the three covariates increased, though the strongest association was with Vernalis flows. This positive association between survival and covariates was seen in both overall survival as well as within each of the major migration routes (Fig. 9). Survival was highest for fish remaining in the San Joaquin River and lowest for fish either migrating through Middle River or entering Turner Cut.

Discussion

Although recent studies have begun to uncover relationships between environmental drivers and demographic parameters of Central Valley steelhead and Chinook salmon (*O. tshawytscha*), many questions remain unanswered. For steelhead, survival through the Delta has been found to vary with river flows at Vernalis (Buchanan & Whitlock, 2022b; Buchanan

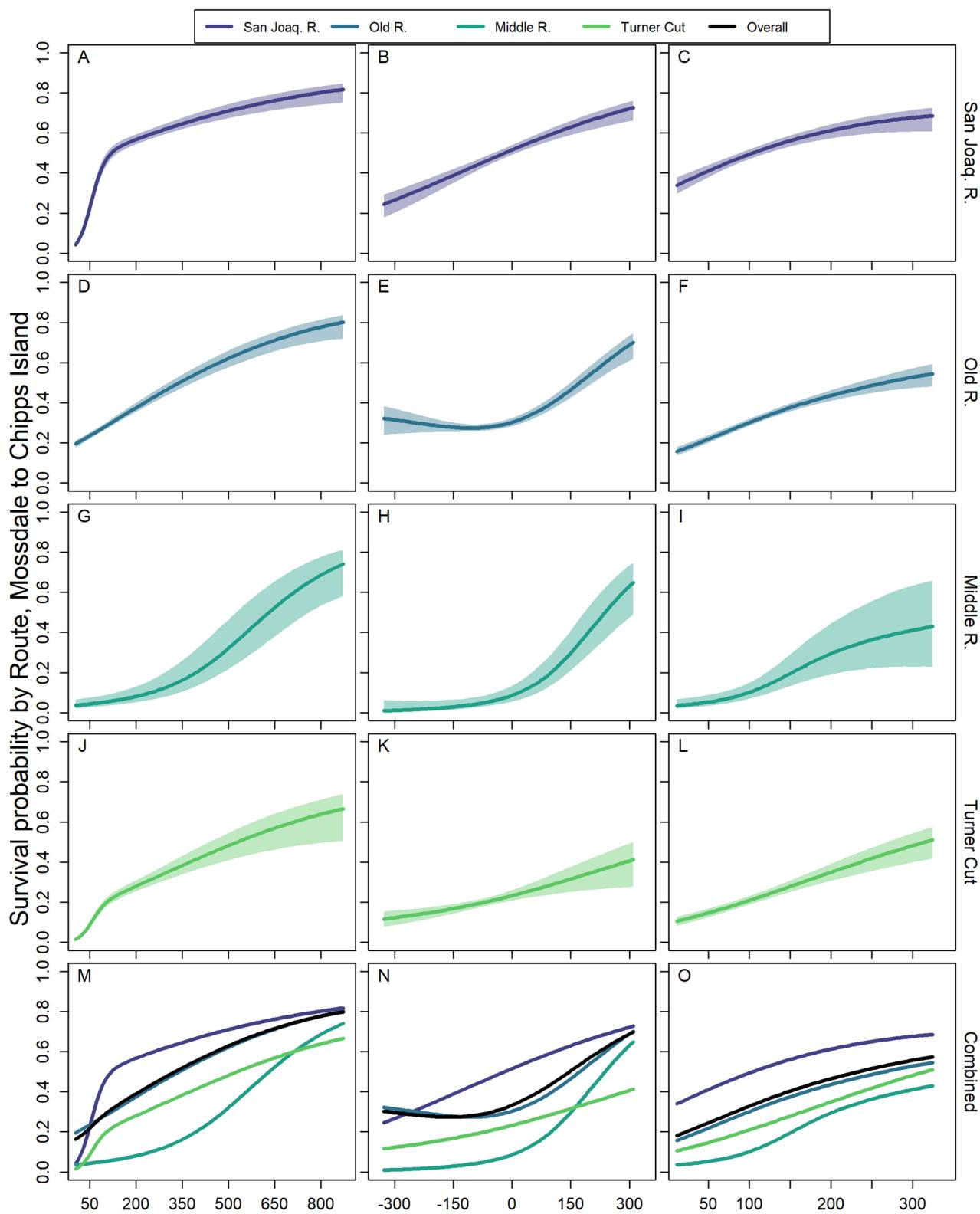


Fig. 9 Predicted overall juvenile steelhead (*Oncorhynchus mykiss*) survival as a function of covariates from Mossdale to Chipps Island by major migration route and for all routes combined as a function of covariates

et al., 2021), and large flow-pulse water releases have been hypothesized to improve Chinook salmon survival through the Delta (Wohner et al., 2022). Tillotson et al. (2022) used a machine learning approach to quantify a link between exports and entrainment risk for both Chinook salmon and steelhead. Hause et al. (2022) explored linkages between Chinook salmon survival through the Delta and spatial variability in habitat quality. The magnitude of predation of juvenile salmon migrating through the Delta has been assessed through experimental trials (Zeug et al., 2021) and genetic testing (Brandl et al., 2021). While these and other studies have begun to uncover linkages between environmental and operational covariates and juvenile salmonid survival at the Delta-wide scale, relatively little is known about how these covariates affect migration routing, travel times, and survival at finer scales such as those found for juvenile Chinook salmon migrating through the Delta from the Sacramento River to the north (Hance et al., 2022; Perry et al., 2018).

We found that patterns in population dynamics for juvenile steelhead migrating through the San Joaquin River and the Delta are complex and vary depending on the region within the Delta and which covariates are modeled. Our results largely agree with and build upon other recent studies of Central Valley salmonid populations showing spatial variability in the factors associated with survival (Buchanan & Skalski, 2020; Buchanan et al., 2021; Hause et al., 2022). While no single covariate explained variation in juvenile steelhead population dynamics across the entire Delta, summarizing relationships over major regions within the Delta revealed how covariate relationships varied along a riverine to tidal gradient. For example, freshwater San Joaquin River flow at Vernalis is more representative of the hydrologic conditions within the upper reaches of the mainstem San Joaquin River than in the deltaic, narrow, tidal channels of the Old and Middle River corridors. Thus, it is unsurprising that both survival and travel times within the upper San Joaquin River showed strong associations with Vernalis flow while survival and travel time in the lower Old and Middle Rivers did not. Conversely, project exports could be expected to most heavily alter hydrology within the vicinity of the export facilities. Indeed, where the export covariate showed the strongest association was for steelhead migrating toward the export facilities from Turner Cut. That predicted survival and travel time in the San Joaquin River, far from the export facilities, did not vary substantially when exports changed was likewise an intuitive finding, although it is difficult to fully separate the effects of exports from those of freshwater inflow due to collinearity of these variables. Each of Vernalis flow, project exports, and OMR flows could be seen as explaining some variation in steelhead migration and survival, depending on the region of the Delta.

Even within a region, association with survival, transition probability, or travel time sometimes showed conflicting results depending on which route fish transit. Steelhead smolts that enter Old River at its head might subsequently follow the Old or Middle River northward, or they might instead migrate toward the export facilities in the southwest of the Delta. For steelhead migrating northward along the Old and Middle River corridors, increasing OMR flows guide fish oceanward, with decreasing predicted travel times as a result. For steelhead migrating toward the export facilities, it is lower OMR flow that results in an environment where those fish arrive more quickly (Fig. 5E). This type of contrast in trends between covariate and predicted travel time is also seen for steelhead migrating through Turner Cut (Fig. 7D) southward toward the export facilities. Increased Vernalis flows lead to increased travel times for steelhead migrating via Old River but decreased travel times for those migrating via Middle River. Such conflicting relationships can lead to muted overall trends as the opposing relationships within different routes cancel each other out when summarized over a region. This may be one reason why previous studies have had difficulty in teasing apart the underlying relationships motivating trends in travel time and survival.

Our model structure, which stratifies capture histories into daily strata and allows for missing covariates (i.e., if a fish is not detected as it passes a station, a time-varying covariate value cannot be assigned for that reach), played a key role in our ability to uncover relationships between environmental and operational variables and reach-specific travel time and survival parameters. Recent advances in Bayesian modeling techniques allow missing covariates to be assigned in the context of a complete data likelihood (CDL), for instance when fish are not detected passing monitoring stations (Muthukumarana et al., 2008). Further modeling advances extended this approach to a multistate framework (Perry et al., 2018), but found that the CDL approach was computationally expensive. Converting the CDL to an ODL through stratification of travel times in both a CJS (Hance et al., 2020) and multistate (Hance et al., 2022) framework couples similar predictive power with a greatly reduced computational burden by assigning covariates based on day (strata) of entry to a reach for detected individuals and analytically integrating the likelihood over all possible strata for missing detections. Prior to the development of these approaches, analyses relied on either virtual releases, or else aggregated individual fish into release groups to uncover these linkages, which does not leverage the full power of the individual data. This may be one of several reasons why linking covariates to reach-specific demographic parameters has been so challenging in the Delta.

Although our analysis advances the understanding of juvenile steelhead migration dynamics, inferences are

limited to some extent due to the complex nature of the channel network in the Delta. In space-for-time multistate mark-recapture models, transitions among states are typically assumed to occur just before a monitoring opportunity in order for survival and routing probabilities to be separately estimable. When this is the case, the state is common to both routes until just before the subsequent detection opportunity, and so a single survival dependent on the state at entry is estimated (Arnason, 1973). When it is not, there are two survivals to estimate along with the transition probability, overparameterizing the model. Instead, in these circumstances, the joint probability of entering a state and surviving between detection opportunities is estimated. Not only is this joint probability difficult to interpret biologically, but it also can preclude our ability to summarize survival over particular regions of interest. Although we can sum over transition probabilities to estimate survival from an entry point to all possible exit points, often research questions center on a specific pathway within that region. In the Delta, there are too many channels to feasibly monitor to capture all possible routes migrating fish can traverse.

Additional factors related to Central Valley juvenile steelhead transiting the Delta environment present further challenges to estimating population parameters. The Delta is a predator-rich environment, and sometimes acoustic tags implanted in steelhead will be detected while in the gut of a piscivorous predator (Buchanan & Whitlock, 2022a). Determining which detections are legitimately of live steelhead and which are of predators requires applying sophisticated techniques to telemetry data before capture histories are compiled. Adding to the complexity, juvenile steelhead can exhibit a wide range of migratory behaviors, some of which can appear similar to those of predator species in the data. Careful consideration is necessary to avoid attribution of mortality by the model to the wrong reach, and failure to account for the possibility of predator detections in this region will almost certainly lead to biased survival estimates. The ability to precisely identify the timing and location of predation events is a promising area of current research necessary for improved precision of inference for Central Valley steelhead (Buchanan & Whitlock, 2022a). Further, linking environmental and operational covariates to demographic parameters is made more difficult by the ways in which many of the covariates widely considered most important in explaining these relationships often covary. Because freshwater export facilities typically pump more during periods of higher flows, and because those exports can drive hydrology in their vicinity, including the OMR flow index, these three variables are usually tightly linked. To separate these effects from one another, researchers will need to observe greater variability in operational data, preferably in the context of randomized, experimental trials. In all studies, sample size, release timing, and receiver monitoring configuration should

be motivated by a clear and focused articulation of specific research questions, including the spatial and temporal scales over which inference is desired. In addition, an appropriate statistical mark-recapture model can overcome some of these challenges to a degree by leveraging as much information as possible from the acoustic data.

While we believe our analysis uncovers some previously unquantified relationships between juvenile steelhead survival and environmental drivers in the Delta, there remain unanswered questions ripe for future research. The three main covariates we modeled displayed too high a degree of collinearity for more than one at a time to be included in a given model, and as such our ability to perform model selection is limited. Further, we found that different covariates seemed to explain more variation in survival and travel time within different regions of the Delta. A rich set of models combining these covariates in various ways deserves further exploration. For example, Bayesian model averaging techniques might be employed in order to arrive at a unified model using different covariates in different regions commensurate with their importance. Alternatively, researchers might assemble such a unified model or models using expert opinion, although some degree of subjectivity is inherent in this approach. Additionally, other covariates widely considered important to steelhead population health may be modeled using our approach, such as temperature and fish size.

Our findings of relationships between changes in the environment juvenile steelhead encounter during their migration and population survival can be used to better inform management actions in several ways. For example, because Vernalis flows exhibited the strongest association with survival in the mainstem San Joaquin River, actions aiming to guide steelhead into that channel may reduce the effects of exports on overall survival. Conversely, once steelhead enter the interior Delta via HOR, the slope parameters on transitions from B5 to B7, C7, or B/C9 suggest that survival to Chipps Island is higher for fish that enter the export facilities and are transported relative to those that migrate northward via Old and Middle Rivers (Table S1), and further, that this survival may increase with increasing exports.

The importance of linking juvenile steelhead population dynamics in the San Joaquin River Delta with environmental and operational covariates cannot be overstated. The suite of actions that can be taken by managers to improve the survival of this threatened species is constrained by competing demands on limited resources. By understanding how management actions are variably associated with steelhead population survival in different regions of the Delta, managers may be able to tailor these actions to optimize benefit to both steelhead and human populations. Our study provides key insights into detailed multiscale patterns of juvenile steelhead migration and survival.

Disclaimer

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12237-025-01493-5>.

Funding Funding for this study was provided by the National Marine Fisheries Service, Western Region (Interagency Agreement No. NMFS-2020-WCRO-028).

Data Availability Data are available at <https://oceanview.pfeg.noaa.gov/erddap/search/index.html?page=1&itemsPerPage=1000&searchFor=FED6yr>.

References

- Arnason, A. N. (1973). The estimation of population size, migration rates and survival in a stratified population. *Researches on Population Ecology*, 15, 1–8.
- Atlas, W. I., Sloat, M. R., Satterthwaite, W. H., Buehrens, T. W., Parken, C. K., Moore, J. W., Mantua, N. J., Hart, J., & Potapova, A. (2023). Trends in Chinook salmon spawner abundance and total run size highlight linkages between life history, geography and decline. *Fish and Fisheries*, 24, 595–617.
- Brandl, S., Schreier, B., Conrad, J. L., May, B., & Baerwald, M. (2021). Enumerating predation on Chinook salmon, Delta smelt, and other San Francisco Estuary fishes using genetics. *North American Journal of Fisheries Management*, 41, 1053–1065.
- Buchanan, R. A., & Skalski, J. R. (2020). Relating survival of fall-run Chinook salmon through the San Joaquin Delta to river flow. *Environmental Biology of Fishes*, 103, 389–410.
- Buchanan, R. A., & Whitlock, S. L. (2022). Diagnosing predation tags in telemetry survival studies of migratory fishes in river systems. *Animal Biotelemetry*, 10, 1–23.
- Buchanan, R. A., & Whitlock, S. L. (2022). Understanding salmon migration dynamics in a data-limited environment. *North American Journal of Fisheries Management*, 42, 1111–1133.
- Buchanan, R. A., Skalski, J. R., Brandes, P. L., & Fuller, A. (2013). Route use and survival of juvenile Chinook salmon through the San Joaquin River Delta. *North American Journal of Fisheries Management*, 33, 216–229.
- Buchanan, R. A., Buttermore, E., & Israel, J. (2021). Outmigration survival of a threatened steelhead population through a tidal estuary. *Canadian Journal of Fisheries and Aquatic Sciences*, 78, 1869–1886.
- Buchanan, R. A. (2018a). *2014 six-year acoustic telemetry and steelhead study: Statistical methods and results*. Technical report to the US Bureau of Reclamation. Available from <https://www.cbr.washington.edu/papers>. Accessed 1 Aug 2023.
- Buchanan, R. A. (2018b). *2015 six-year acoustic telemetry and steelhead study: Statistical methods and results*. Technical report to the US Bureau of Reclamation. Available from <https://www.cbr.washington.edu/papers>. Accessed 1 Aug 2023.
- Buchanan, R. A. (2018c). *2016 six-year acoustic telemetry and steelhead study: Statistical methods and results*. Technical report to the US Bureau of Reclamation. Available from <https://www.cbr.washington.edu/papers>. Accessed 1 Aug 2023.
- Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., & Riddell, A. (2017). Stan: A probabilistic programming language. *Journal of Statistical Software*, 76(1), 1–32. <https://doi.org/10.18637/jss.v076.i01>
- Crozier, L. G., Burke, B. J., Chasco, B. E., Widener, D. L., & Zabel, R. W. (2021). Climate change threatens Chinook salmon throughout their life cycle. *Communications Biology*, 4, 222.
- Eschenroeder, J. C., Peterson, M. L., Hellmair, M., Pilger, T. J., Demko, D., & Fuller, A. (2022). Counting the parts to understand the whole: Rethinking monitoring of steelhead in California's Central Valley. *San Francisco Estuary and Watershed Science*, 20(1). <https://doi.org/10.15447/sfews.2022v20iss1art2>
- Gebremichael, M., Krishnamurthy, P. K., Gebremichael, L. T., & Alam, S. (2021). What drives crop land use change during multi-year droughts in California's Central Valley? Prices or concern for water? *Remote Sensing*, 13, 650.
- Hance, D. J., Perry, R. W., Plumb, J. M., & Pope, A. C. (2020). A temporally stratified extension of space-for-time Cormack–Jolly–Seber for migratory animals. *Biometrics*, 76, 900–912.
- Hance, D. J., Perry, R. W., Pope, A. C., Ammann, A. J., Hassrick, J. L., & Hansen, G. (2022). From drought to deluge: Spatiotemporal variation in migration routing, survival, travel time and floodplain use of an endangered migratory fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 79, 410–428.
- Hause, C. L., Singer, G. P., Buchanan, R. A., Cocherell, D. E., Fangue, N. A., & Rypel, A. L. (2022). Survival of a threatened salmon is linked to spatial variability in river conditions. *Canadian Journal of Fisheries and Aquatic Sciences*, 79, 2056–2071.
- Jahn, A., & Kier, W. (2020). *Reconsidering the estimation of salmon mortality caused by the state and federal water export facilities in the Sacramento-San Joaquin Delta* (p. 18). San Francisco Estuary and Watershed Science: San Francisco Estuary.
- Kimmerer, W. J. (2008). Losses of Sacramento River Chinook salmon and delta smelt to entrainment in water diversions in the Sacramento–San Joaquin Delta. *San Francisco Estuary and Watershed Science*, 6(2). <https://doi.org/10.15447/sfews.2008v6iss2art2>
- Lemoine, N. P. (2019). Moving beyond noninformative priors: Why and how to choose weakly informative priors in Bayesian analyses. *Oikos*, 128, 912–928.
- Liedtke, T.L., J.W. Beeman, and L. Gee. 2012. A standard operating procedure for the surgical implantation of transmitters in juvenile salmonids. U.S. Geological Survey Open-File Report 2012-1267
- Lindley, S. T., Schick, R. S., Mora, E., Adams, P. B., Anderson, J. J., Greene, S., Hanson, C., May, B. P., McEwan, D., & MacFarlane, R. B. (2007). Framework for assessing viability of threatened and endangered Chinook salmon and steelhead in the Sacramento–San Joaquin Basin. *San Francisco Estuary and Watershed Science*, 5(1). <https://doi.org/10.15447/sfews.2007v5iss1art4>
- Molina-Moctezuma, A., Stich, D. S., & Zydlewski, J. D. (2022). Effects of dam-induced delays on system-wide survival of Atlantic salmon smolts during high-flow, high-survival years in the Penobscot River, Maine, USA. *Canadian Journal of Fisheries and Aquatic Sciences*, 79, 2237–2250.
- Monsen, N. E., Cloern, J. E., & Burau, J. R. (2007). Effects of flow diversions on water and habitat quality: Examples from California's highly manipulated Sacramento–San Joaquin Delta. *San Francisco Estuary and Watershed Science*, 5(3). <https://doi.org/10.15447/sfews.2007v5iss5art2>
- Munsch, S. H., Greene, C. M., Johnson, R. C., Satterthwaite, W. H., Imaki, H., & Brandes, P. L. (2019). Warm, dry winters truncate timing and size distribution of seaward-migrating salmon across a large, regulated watershed. *Ecological Applications*, 29, e01880.

- Muthukumarana, S., Schwarz, C. J., & Swartz, T. B. (2008). Bayesian analysis of mark-recapture data with travel time-dependent survival probabilities. *Canadian Journal of Statistics*, 36, 5–21.
- National Marine Fisheries Service. (2009). *Endangered Species Act Section 7 Consultation: Biological opinion and conference opinion on the longterm operations of the Central Valley Project and State Water Project*. National Marine Fisheries Service. Available from <https://www.fisheries.noaa.gov/resource/document/biological-opinion-and-conference-opinion-long-term-operations-central-valley>. Accessed 1 Aug 2023.
- Norrgård, J. R., Greenberg, L. A., Piccolo, J. J., Schmitz, M., & Bergman, E. (2013). Multiplicative loss of landlocked Atlantic salmon *Salmo salar* L. smolts during downstream migration through multiple dams. *River Research and Applications*, 29, 1306–1317.
- Perry, R. W., Pope, A. C., Romine, J. G., Brandes, P. L., Burau, J. R., Blake, A. R., Ammann, A. J., & Michel, C. J. (2018). Flow-mediated effects on travel time, routing, and survival of juvenile Chinook salmon in a spatially complex, tidally forced river delta. *Canadian Journal of Fisheries and Aquatic Sciences*, 75, 1886–1901.
- Raymond, H. L. (1988). Effects of hydroelectric development and fisheries enhancement on spring and summer Chinook salmon and steelhead in the Columbia River Basin. *North American Journal of Fisheries Management*, 8, 1–24.
- Skalski, J. R., Whitlock, S. L., Townsend, R. L., & Harnish, R. A. (2021). Passage and survival of juvenile salmonid smolts through dams in the Columbia and Snake Rivers, 2010–2018. *North American Journal of Fisheries Management*, 41, 678–696.
- Thorstad, E. B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A. H., & Finstad, B. (2012). A critical life stage of the Atlantic salmon *Salmo salar*: Behaviour and survival during the smolt and initial post-smolt migration. *Journal of Fish Biology*, 81, 500–542.
- Tillotson, M. D., Hassrick, J., Collins, A. L., & Phillis, C. (2022). *Machine learning forecasts to reduce risk of entrainment loss of endangered salmonids at large-scale water diversions in the Sacramento-San Joaquin Delta* (p. 20). San Francisco Estuary and Watershed Science: California.
- U.S. Geological Survey. 2021. USGS water data for the Nation: U.S. Geological Survey National Water Information System database. Accessed August 1, 2021, at <https://doi.org/10.5066/F7P55KJN>.
- USBR. (2018a). *NMFS Biological Opinion RPA IV.2.2: 2011 six-year acoustic telemetry steelhead study*. Contributions by Buchanan, R. A., Israel, J. A., Brandes, P., and Buttermore, E. US Bureau of Reclamation Bay–Delta Office. Final Report 14 May 2018. <https://www.usbr.gov/mp/bdo/docs/2011-six-yr-acoustic-telemetry-steel-head-report.pdf>. Accessed 1 Aug 2023.
- USBR. (2018b). *NMFS Biological Opinion RPA IV.2.2: 2012 six-year acoustic telemetry steelhead study*. Contributions by Buchanan, R. A., Brandes, P., Israel, J. A., and Buttermore, E. US Bureau of Reclamation Bay–Delta Office. Final Report 16 May 2018. <https://www.usbr.gov/mp/bdo/docs/2012-six-yr-acoustic-telemetry-steel-head-report.pdf>. Accessed 1 Aug 2023.
- USBR. (2018c). *NMFS Biological Opinion RPA IV.2.2: 2013 six-year acoustic telemetry steelhead study*. Contributions by Buchanan, R. A., Brandes, P., Israel, J. A., and Buttermore, E. US Bureau of Reclamation Bay–Delta Office. Final Report June 2018. <https://www.usbr.gov/mp/bdo/docs/2013-six-yr-acoustic-telemetry-steel-head-report.pdf>. Accessed 1 Aug 2023.
- Warkentin, L., Parken, C. K., Bailey, R., & Moore, J. W. (2022). Low summer river flows associated with low productivity of Chinook salmon in a watershed with shifting hydrology. *Ecological Solutions and Evidence*, 3, e12124.
- Wohner, P. J., Duarte, A., Wikert, J., Cavallo, B., Zeug, S. C., & Peterson, J. T. (2022). Integrating monitoring and optimization modeling to inform flow decisions for Chinook salmon smolts. *Ecological Modelling*, 471, 110058.
- Yoshiyama, R. M., Fisher, F. W., & Moyle, P. B. (1998). Historical abundance and decline of Chinook salmon in the Central Valley region of California. *North American Journal of Fisheries Management*, 18, 487–521.
- Zeug, S. C., & Cavallo, B. J. (2014). Controls on the entrainment of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) into large water diversions and estimates of population-level loss. *PLoS ONE*, 9, e101479.
- Zeug, S. C., Beakes, M., Wiesenfeld, J., Greenwood, M., Grimaldo, L., Hassrick, J., Collins, A., Acuña, S., & Johnston, M. (2021). Experimental quantification of piscivore density and habitat effects on survival of juvenile Chinook salmon in a tidal freshwater estuary. *Estuaries and Coasts*, 44, 1157–1172.

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