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ARTICLE

Route use of emigrating steelhead in a heavily modified river delta

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Abstract

Objective: Low survival of emigrating salmonid smolts through the interior regions of California's Sacramento–San Joaquin River Delta (hereafter, "Delta") and large-scale water extraction from that region have prompted managers to seek to predict and manipulate smolt route use through the tidal Delta. The local flow variables previously used in modeling are not the metrics used in management. Here, I investigate the predictive utility of variables representing both localized flow conditions and remote management metrics to predict routing of juvenile steelhead *Oncorhynchus mykiss* at two river junctions on the San Joaquin River in the south Delta.

Methods: Individual-based generalized linear models were used with detections of over 4000 acoustic-tagged juvenile hatchery-reared steelhead to relate routing to the presence of a rock barrier, simulated localized flow conditions from a hydrodynamic model, and daily management metrics, including upstream river discharge and water pumping rates elsewhere in the Delta. Models were developed for the first two diffluences encountered by smolts entering the Delta (head of Old River and Turner Cut).

Result: Exclusive use of the management metrics in routing models underestimated the subdaily, tidally dominated fluctuations in fish routing compared to localized flow covariates. The daily rate of water extraction 20–30 km away contributed to use of non-main-stem routes, but the effect was small compared to subhourly flow conditions at the river junctions themselves.

Conclusion: Water resource and fish managers are advised to monitor conditions at the locations of interest rather than depending solely on remote metrics. In the Delta, use of a flow barrier and reduction of water pumping operations when smolts are migrating should be combined with habitat improvement in interior Delta regions to optimize migratory survival through this complex and heavily modified system.

KEYWORDS

acoustic telemetry, estuary, hydrodynamics, route selection, steelhead

INTRODUCTION

Fish migrating through channel networks or past instream structures, such as dams, may encounter multiple possible migration pathways representing a gradient of mortality risks (Skalski et al. 2009; Perry et al. 2010). Managers who seek to maximize population survival need to understand not only the differences in route-specific survival, but also the magnitude and dynamics of variable route use (Salmonid Scoping Team [SST] 2017), either to accurately predict habitat use and migratory survival or to deter use of low-survival routes via management actions (e.g., implement an operable or nonphysical route barrier; Perry et al. 2014). In some settings, natural resource use in one route may prompt managers either to deter fish from using that route or to limit the resource use during times when fish are present. For example, water extractions from a secondary channel may be limited when vulnerable fish are known to be in the area (National Marine Fisheries Service [NMFS] 2009) or more river discharge may be passed over a dam's spillway rather than through the powerhouse during the juvenile salmon migration (U.S. Army Corps of Engineers et al. 2020). Efficient adaptive management requires an understanding of the various time scales on which route use varies to improve the timing of management actions, including daily and subdaily routing fluctuations as well as seasonal patterns in fish presence (Harnish et al. 2023). Also necessary is an understanding of how management actions and resource use influence the use of suboptimal migration routes (Salmonid Scoping Team 2017).

There is a growing body of literature that relates short-term fish routing behavior to localized environmental conditions represented by river flow, current speed, and other hydrodynamic features that coincide with (Dodrill et al. 2022; Holleman et al. 2022) and occur prior to (Goodwin et al. 2023) the behavior under investigation. Other factors shown to be important include time of day (TOD; Swanson et al. 2004; Anchor QEA 2022), fish cross-sectional location (Hance et al. 2020), and fish size (Swanson et al. 2004). Additional work relating route use at dams to operational conditions and management actions has demonstrated that accurate prediction of fish passage routes depends on short-term localized conditions at the time when fish experience them rather than time-averaged, population-level metrics (e.g., daily power generation; Harnish et al. 2023). It is unclear whether knowledge of localized conditions is required for predicting route use at river junctions or in tidal settings, such as river deltas, or whether time-averaged or remote measurements of environmental conditions and management actions (e.g., daily average discharge upstream or daily water pumping rates) are sufficient. This question is particularly relevant in settings where management decisions are based on environmental conditions measured at sites that are remote from the fish routing location.

California's Sacramento–San Joaquin River Delta (hereafter, "Delta"; Figure 1) is an example of a system in which resource managers seek to predict fish routing. Steelhead *Oncorhynchus mykiss* belonging to the Central Valley Distinct Population Segment (DPS) pass through the braided and heavily managed Delta on their emigration to the San Francisco Bay and the Pacific Ocean during the late winter and spring. Population declines resulted in the listing of this DPS as threatened under the Endangered Species Act in 1998 (Lindley et al. 2006); poor juvenile survival through the Delta is thought to be a contributing factor in low population numbers, due in part to higher mortality risk in certain

Impact statement

This research developed a juvenile steelhead routing model that can be used in adaptive management. It highlighted the limitations of common management measures for predicting route use and the importance of monitoring local flow conditions for predictive purposes.

migratory pathways (McEwan 2001; NMFS 2009). Juvenile steelhead from the Southern Sierra Nevada Diversity Group component of the DPS enter the Delta from the San Joaquin River, where they encounter several migration routes to the Delta exit, including a route past two large water-pumping facilities located in the southwestern Delta that extract large quantities of water for municipal and agricultural use elsewhere in the state (up to $28 \times 10^6\,m^3$/day; referred to as water "exports"; Grimaldo et al. 2009). Predation risk near the facilities and risk of entrainment in the pumps and water conveyance canals have prompted efforts to segregate migrating salmonids away from the facilities, including the installation of a temporary rock barrier during the spring at the head (i.e., source) of Old River, the first diffluence on the San Joaquin River that leads to the facilities. However, there are other entries to the interior Delta further downstream, and survival to the Delta exit is particularly low for both steelhead and Chinook Salmon *O. tshawytscha* that leave the main-stem river in the more tidal region downstream at Turner Cut (Figure 1; Buchanan et al. 2021; Buchanan and Whitlock 2022). Thus, an ability to predict route use at several junctions (i.e., diffluences) is needed, both to limit mortality at the facilities and to predict overall migratory survival through the Delta in response to management decisions (e.g., barrier installation; Salmonid Scoping Team 2017). Of particular interest is the extent to which route use is influenced by pumping operations. Although the pumping facilities are located 20–30 km from the junctions on the main-stem river, high pumping (export) rates are anticipated to draw water and fish from the San Joaquin River toward the export facilities. This prediction has been supported by previous hydrodynamic modeling (Cavallo et al. 2013, 2015) but has not been demonstrated in the field.

Previous studies on junctions in the south Delta have characterized short-term behavioral actions in response to changing localized hydrodynamic conditions, including reverse flows from tidal fluctuations and water pumping operations (Anchor QEA 2022; Dodrill et al. 2022; Holleman et al. 2022). However, in a hydrologically complex region like the Delta, fish may experience a given river junction multiple times if they encounter reverse flows, and their preliminary route of entry may differ from

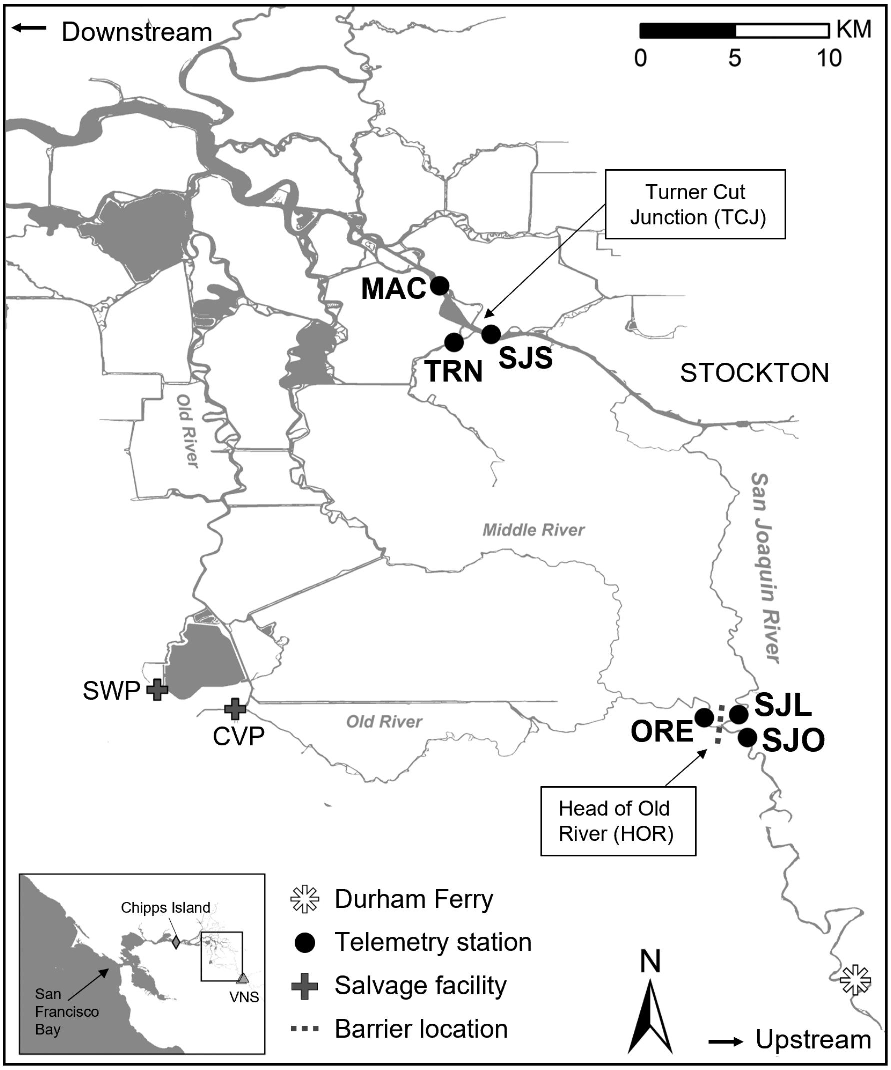

FIGURE 1 The study area in the southern Sacramento–San Joaquin River Delta. The two river junctions modeled are the head of Old River, denoted by telemetry stations SJO, SJL, and ORE; and the Turner Cut junction, denoted by telemetry stations SJS, MAC, and TRN. Marked locations include the release location (Durham Ferry), acoustic telemetry stations, the Vernalis (VNS) river gauging station (inset map), salvage facilities at the water export facilities, and the Delta exit at Chipps Island (inset map). Inset map shows the Delta and San Francisco Bay in the state of California, United States, and the Pacific Ocean; the area depicted in the detailed map is marked with a rectangle. The temporary rock barrier at the head of Old River is marked by the dotted line. Water export facilities are the Central Valley Project (CVP) and State Water Project (SWP).

the final route taken (Perry et al. 2014, 2015). Additionally, predicting survival through the Delta for adaptive management purposes requires relating route use to the metrics available to managers, such as daily measures of pumping rates and river discharge from locations that are at least 20 km away. This investigation is unique in that it examines how final route use depends on hydrodynamic conditions represented both by localized, short-term conditions and by broader-scale management metrics. In addition to characterizing route use for this system, the present work addresses the broader question of whether predicting fish behavior in complex habitats requires knowledge of localized conditions or whether remote or time-averaged measurements are sufficient.

In this paper, I present a statistical investigation of final route use at the first two Delta junctions encountered on the San Joaquin River by using 6 years of acoustic telemetry data from hatchery-reared juvenile steelhead that were released upstream. I report release group-level estimates of route use and explore associations with a variety of covariates representing hydrodynamic and operational conditions on two spatiotemporal scales. Of particular interest are (1) the degree to which the management-relevant covariates can be used to predict route use, (2) the effect of water export operations on route use, and (3) how the relationships depend on the presence of the Old River barrier. Localized conditions were represented by subhourly hydrodynamic model predictions of river discharge ("flow") and its decomposition into net flow, tidal flow, and flow proportions (flow splits). Operational (i.e., management) covariates were the daily measures of river flow into the Delta ("Delta inflow"), water export rates, and the ratio of inflow to exports. Also considered were the presence of the barrier, fish size, and TOD.

Several hypotheses were addressed in response to management needs and preconceived ideas of the determinants of route use at river junctions. The primary hypothesis under consideration was that fish routing is determined largely by localized flow conditions represented by net flow from upstream, tidal flow, and flow proportion at the junctions (i.e., the proportion of flow moving downstream in the main-stem exit of the junction). The possibility that fish simply follow the flow was represented by the flow proportion in the junction exits. Fish were expected to be more likely to select the main-stem route when the flow proportion in that leg was higher, when net flow entering the junction from upstream was higher, and on an ebb tide.

A second hypothesis was that metrics used in water operations management could be used to predict fish routing at both junctions—in particular, daily rates of water export pumping at the two facilities in the southwestern Delta and the daily inflow to the Delta measured at Vernalis, California. Fish were expected to be more likely to enter the interior Delta route when daily export rates were higher and when Delta inflow was lower. The effect of exports on fish routing was expected to be stronger at the upstream junction (head of Old River) because of its proximity to the export facilities and because the tidal flow is stronger at the downstream junction (Turner Cut; Cavallo et al. 2013). Managers are also interested in the relationship between the ratio of Delta inflow to exports (inflow : export [IE] ratio) and routing, with the hypothesis that fish are more likely to stay in the main-stem river route when the IE ratio is higher.

Finally, larger fish were expected to be more likely to remain in the main-stem San Joaquin River route at both junctions because their larger size was expected to enable them to maneuver in faster water flow and to require fewer evasive actions in response to predators and thus be less likely to enter the interior Delta involuntarily (Swanson et al. 2004). Time of day was included to account for differences in visual cues and predator evasion actions that might affect fish routing (Holleman et al. 2022).

STUDY AREA

The Delta is the upstream component of an inverted tidal estuary that connects the rivers of the Central Valley of California to a series of bays leading to the Pacific Ocean (Figure 1). The Delta drains an area of nearly 3000 km^2 and provides drinking water and agricultural water for 25 million Californians. The head of Old River and the Turner Cut junction are in the south Delta, a region bounded to the east and north by the San Joaquin River and to the south and west by Old River. Two large water-pumping facilities, parts of the federally owned Central Valley Project (CVP) and the State Water Project (SWP), are located off Old River (Figure 1). Fish from the San Joaquin River enter the Delta from the south. At the head of Old River, they may either continue migrating northward in the San Joaquin River or they may enter Old River. Those fish that enter Old River may navigate through the channels of the interior Delta (i.e., off the main-stem San Joaquin River) to eventually rejoin the San Joaquin River upstream of the Delta exit (Chipps Island). Alternatively, Old River fish can enter the water pumping facilities, where they may be salvaged and trucked around the rest of the Delta. Fish that remain in the San Joaquin River at the head of Old River may either (1) migrate to the Delta exit wholly within the San Joaquin River or (2) exit the San Joaquin River for the interior Delta through any of several channels leaving the San Joaquin River north of the city of Stockton, California. Turner Cut is the first of these channels (Figure 1). Fish that enter Turner Cut may migrate northwest to the Delta exit or may navigate southwest through the Delta to the water export facilities.

The interior Delta consists of a collection of natural and man-made channels, agricultural tracts isolated from the water channels by dikes, and tidal lakes formed by tracts that were flooded when dikes failed. Hydrodynamic patterns in the south Delta are largely influenced by Sacramento River inflow from the north, San Joaquin River inflow from the south, tidal forces, water export operations, and the presence of the rock barrier at the head of Old River. The combination of tides and water exports can result in flow reversals throughout large swaths of the south Delta, depending on the amount of water entering from upstream and whether the barrier at Old River is installed. A large community of predatory fishes resides in the interior Delta and at the entrances of the water export facilities (NMFS 2009; Loomis 2019; Michel et al. 2020). Additionally, emigrants entering the facilities may evade salvage and be entrained in the water conveyance canals or lost to predation within the facilities (Grimaldo et al. 2009). Thus, effort has been expended to prevent fish from entering the interior Delta and the facilities, either by installation of the rock barrier at the head of Old River or by restriction of water export rates in the spring when migrating salmonids are present. The barrier includes several culverts that allow for some passage of both water and fish. It is installed during the spring in most years but cannot be installed in wet years. No barrier has been installed at Turner Cut or at other downstream connections to the interior Delta.

In the absence of exports and the barrier, river flow enters the head of Old River from upstream and splits either into the San Joaquin River or Old River. In low-flow years, river flow may reverse under flood tide and enter this junction from downstream (i.e., from regions closer to the Delta exit); low flows combined with high exports may result in water flow being directed down Old River coming from both upstream and downstream in the San Joaquin River. The barrier prevents most water from entering Old River and limits the extent of reverse flows in the San Joaquin River.

Flow direction and magnitude at the Turner Cut junction are largely determined by the tidal cycle (Cavallo et al. 2013). During outgoing tides, river flow enters the Turner Cut junction both from upstream in the San Joaquin River and from the interior Delta and exits the junction downstream in the San Joaquin River. On incoming tides, flows reverse in both channels and flow enters the interior Delta via Turner Cut from downstream in the San Joaquin River. More flow is predicted to enter the interior Delta via Turner Cut under conditions of high export rates.

METHODS

Field study methods

Each spring from 2011 to 2016, between 958 and 2196 yearling juvenile steelhead reared at the Mokelumne River Fish Hatchery were surgically implanted with microacoustic transmitters and released in the San Joaquin River at Durham Ferry, located approximately 25 km upstream of the head of Old River. Details on acoustic telemetry technology, surgery, and fish transport and release are provided by Buchanan et al. (2021). Tagged steelhead were monitored after release using 26–44 telemetry stations each year, consisting of fixed-site acoustic hydrophones and receivers. A subset of the full network of telemetry stations was used in this analysis—specifically those installed directly upstream (SJO station) and downstream of the head of Old River in both the San Joaquin River (SJL station) and Old River (ORE station) and directly upstream (SJS station) and downstream of the Turner Cut junction in both the San Joaquin River (MAC station) and Turner Cut (TRN station; Figure 1). Placement of the telemetry stations depended on channel geomorphology and site access; the distances between the river junctions and their respective telemetry stations were approximately 0.7 km for SJO, 0.8 km for SJL, 1.1 km for ORE, 0.4 km for SJS, 3.2 km for MAC, and 1.2 km for TRN. Each station comprised from two to six hydrophones arranged in parallel lines across the channel to ensure complete coverage of the channel and to provide the data structure necessary to estimate route-specific detection probabilities. The SJO station was not installed in 2011, and the SJS station was not installed in 2011, 2012, or 2014.

Covariates

Covariates were selected to represent either (1) localized hydrodynamic conditions (“local”) that were hypothesized to indicate forces acting on juvenile steelhead as they experienced the river junctions or (2) remote conditions that are relevant to water resource management (“management”; Table 1). A third, catch-all category (“fish”) consisted of nonhydrodynamic covariates, including fish size, the presence of the barrier at the head of Old River, and TOD. Management metrics consisted of the daily average measures of Delta inflow at Vernalis and export pumping rates at the CVP and SWP, which were extracted from the California Department of Water Resources' (CDWR) Dayflow database (https://water.ca.gov). Time-varying localized flow conditions were represented by net flow, tidal flow, and flow proportion, which were derived from simulations by the UnTRIM (Unstructured Tidal, Residual, Intertidal, and Mudflat) Bay–Delta hydrodynamic model (described below; MacWilliams et al. 2015; Anchor QEA 2022) for the locations of the telemetry stations marking the junction entrance or exit; see Supplemental Materials (in the online version of this article) for more details. Modeled flow was simulated on a 90-s time step and as a tidally averaged measure (dual-pass, 24.83-h rolling average) and was provided by Anchor QEA (personal communication).

The UnTRIM Bay–Delta model (MacWilliams et al. 2015) is a three-dimensional hydrodynamic model of the San Francisco Estuary, including the Delta, that was developed using the UnTRIM hydrodynamic model (Casulli and Zanolli 2005). The UnTRIM Bay–Delta model has previously been applied in multiple studies in the estuary; see MacWilliams et al. (2015) for a description of the model and a partial listing of model applications. The model simulates a variety of measures of hydrodynamic and environmental conditions throughout the Delta at subhourly time steps using several data types: bathymetry data throughout the Delta and downstream bays; daily Delta inflow data from the Sacramento and San Joaquin rivers and other tributaries; daily water export and intake flows from water project operation facilities throughout the Delta; data on evaporation, precipitation, and local wind speed; and operation of several hydrodynamic control gates and temporary barriers (MacWilliams et al. 2015). More information on the implementation of the UnTRIM Bay–Delta model is available from Anchor QEA (2022).

TABLE 1 Covariates that were evaluated in individual-based steelhead route use probability models or that were used to derive other covariates. Model categories are localized hydrodynamic conditions (local [L]), management (M), or other (fish [F]). Stations are telemetry stations, water export facilities, or river gauging stations (see Figure 1). Junctions include the head of Old River (HOR) and Turner Cut junction (TCJ). "When" indicates the time of measurement (entrance = estimated or observed fish departure time from the junction entrance telemetry station; exit = observed fish arrival at the junction exit telemetry station). Sources are the California Department of Water Resources' Dayflow database (Dayflow; https://data.cnra.ca.gov/dataset/dayflow) and the UnTRIM (Unstructured Tidal, Residual, Intertidal, and Mudflat) Bay–Delta model (UnTRIM; MacWilliams et al. 2015; Anchor QEA 2022). Water flow covariates that are marked with an asterisk (*) were used to derive other covariates but were not used directly in route modeling. CVP, Central Valley Project; SWP, State Water Project; TA, tidally averaged; VNS, gauging station at Vernalis, California.

Symbol	Type	Category	Station(s)	Junction	When	Time scale	Unit	Source
Q_{SJO}, Q_{SJL}, Q_{ORE}	Water flow*	L	SJO, SJL, ORE	HOR	Both	90 s	m^3/s	UnTRIM
Q_{SJS}, Q_{MAC}, Q_{TRN}	Water flow*	L	SJS, MAC, TRN	TCJ	Both	90 s	m^3/s	UnTRIM
nQ_{SJO}	Net flow	L	SJO	HOR	Entrance	TA	m^3/s	UnTRIM
nQ_{SJS}	Net flow	L	SJS	TCJ	Entrance	TA	m^3/s	UnTRIM
tQ_{SJO}	Tidal flow	L	SJO	HOR	Entrance	90 s	m^3/s	UnTRIM
tQ_{SJS}	Tidal flow	L	SJS	TCJ	Entrance	90 s	m^3/s	UnTRIM
pQ_{SJL}	Flow proportion	L	SJL, ORE	HOR	Exit	90 s	Unitless	UnTRIM
pQ_{MAC}	Flow proportion	L	MAC, TRN	TCJ	Exit	90 s	Unitless	UnTRIM
E_{CVP}	Export rate	M	CVP	Both	Exit	Daily mean	m^3/s	Dayflow
E_{SWP}	Export rate	M	SWP	Both	Exit	Daily mean	m^3/s	Dayflow
Q_{VNS}	Delta inflow	M	VNS	Both	Entrance	Daily mean	m^3/s	Dayflow
IE	Inflow : export (IE) ratio	M	VNS, CVP, SWP	Both	Entrance	Daily mean	Unitless	Dayflow
B	Barrier at the HOR	F		Both	Exit		True, false	
L	Fork length at tagging	F		Both	Entrance		mm	
TOD	Time of day	F		Both	Entrance		Day, night, crepuscular	

The primary variable simulated from the hydrodynamic model was the total rate of water flow through a cross section of the channel (water flow [Q]; m^3/s) at the junction telemetry stations, simulated both on a 90-s time step and as a tidally averaged measure. Direction of water flow was represented by the sign (positive = toward the Pacific Ocean; negative = away from the Pacific Ocean) of the simulated metric. The 90-s flow measure was decomposed into a measure of net flow (nQ; m^3/s) and tidal flow (tQ; m^3/s). Additionally, the 90-s flow proportion exiting the junctions was derived from the model output. Flow proportion (pQ; unitless) represented the fraction of the flow exiting the junction downstream into the main-stem San Joaquin River branch and was used to assess the hypothesis that juvenile steelhead follow the bulk of the river flow. More details on the construction of the derived covariates are provided in the Supplemental Materials.

Remote effects of hydrodynamics and water project operations were considered both in response to concern about the potential for water export operations to draw fish into the interior Delta and to represent conditions that are subject to manager control. Management metrics included the following covariates: the daily measure of export rates from the SWP and CVP facilities (E_{SWP} and E_{CVP}; m^3/s), the daily average of San Joaquin River discharge into the Delta measured at the VNS gauging station near Vernalis (27 km upstream of the head of Old River; Delta inflow [Q_{VNS}]; m^3/s), and the daily ratio of Delta inflow to the combined (SWP + CVP) export rate (IE ratio; unitless).

Although the presence of the rock barrier at the head of Old River (B) represents a management action, its status was placed in a separate category of covariates because of its expected dominating influence on the routing of both fish and flow at the head of Old River. The barrier covariate was defined as an indicator variable assigned as "true" if the tag was detected at the river junction's telemetry stations on or between the day of closure during barrier installation in April and the day of breach during barrier removal in June

(Table 2). The barrier may influence routing either directly by blocking entry into the Old River route (for fish that fail to find the culverts) or indirectly by influencing the response to other potential drivers, such as flow or exports. Other covariates considered were TOD (day, night, or crepuscular period, where the crepuscular period was the 30 min prior to sunrise or the 30 min following sunset) and fork length (L) at tagging (Table 1).

Covariates were measured at either the (upstream) entrance or the (downstream) exit of the junction, as described below. Although emigrants entered the junctions from upstream, several investigations have observed juvenile salmonids exhibiting behaviors such as holding, foraging, and lateral movement in these junctions, suggesting that some migrants experience conditions at the downstream edge of the junction before their final route fate is determined, whether by active choice or by passive dispersal in response to flow patterns (Anchor QEA 2022; Dodrill et al. 2022; Holleman et al. 2022). Additionally, neither junction is in a purely riverine region with unidirectional flow, so both downstream and upstream forces are important components of the hydraulic conditions within the junction.

Net flow and tidal flow were modeled at the entrance of the junction at the time of fish arrival. Net flow represented the conditions that the fish experienced as they approached the junction from upstream. Higher net flow may encourage fish to migrate along one riverbank rather than the other such that they are likely to enter the route closest to them upon junction entry. Tidal flow was also measured at the junction entrance to provide the full flow components at that location. Flow proportion was modeled at the location of the acoustic receiver station in the main-stem exit of the junction (i.e., SJL or MAC) at the time that the fish exited the junction.

TABLE 2 Dates of closure (during installation) and breach (during removal) of the annual temporary rock barrier at the head of Old River and the number of detections at the head of Old River receivers (SJL and ORE; see Figure 1) between closure and breach. "NA" indicates that no barrier was installed during the specified year.

Year	Closure	Breach	Number of detections
2011	NA	NA	NA
2012	Apr 1	Jun 4	787
2013	NA	NA	NA
2014	Apr 8	Jun 9	433
2015	Apr 3	Jun 1	161
2016	Apr 1	Jun 1	424

Delta inflow, IE ratio, and TOD were measured at the time of fish entrance to the junction. Daily export rates were measured at the time of fish exit of the junction because the expected mechanism by which exports may influence fish routing is by "pulling" them into the route that is more directly connected to the export facilities (i.e., the interior Delta route). The barrier at the head of Old River was also measured at the time of junction exit because its expected primary routing mechanism is through a partial physical blockade of the Old River route; it may also affect hydrodynamic conditions upstream (i.e., closer to the junction entrance), but that effect was expected to be smaller than the blockade effect. Although the barrier status was measured at the junction exit, the status was identical whether measured at the junction entrance or exit for over 99.8% of all records; thus, the results were robust to the timing of the barrier status measurement.

Statistical methods

Data processing and parameter estimation

The raw acoustic telemetry data were processed by the U.S. Geological Survey (USGS; Sacramento, California, office) to remove false detections and then were transferred to the University of Washington (UW) for analysis. A behavior-based predator filter (Buchanan and Whitlock 2022) was implemented to remove detections of potential predators after consuming study fish. The detection data for each release group were analyzed in a multistate mark–recapture model (Buchanan et al. 2018) to estimate route use probabilities at the Old River and Turner Cut junctions concurrently with route-specific survival and conditional detection probabilities at the telemetry stations. More details on data processing, the predator filter, the mark–recapture model, and estimates of route-specific survival are available from Buchanan et al. (2021) and a series of annual reports (Buchanan 2018a, 2018b, 2018c; U.S. Bureau of Reclamation [USBR] 2018a, 2018b, 2018c).

Individual-based route use models were developed for both the head of Old River and the Turner Cut junction. Detections used in fitting the model for each junction were restricted to those tags that were last detected either at one of the two telemetry stations marking the downstream exit of the river junction or at stations further downstream; steelhead detection histories that terminated upstream of the junction were omitted even if they were previously detected within the junction. Additionally, records were restricted to fish that entered the junction from upstream or from the other leg of the junction; this was done to avoid chance detections of fish that had returned partway upstream after previously exiting the junction. Fish fate within the junction (i.e., final route use at the junction) was determined by the telemetry station where the final downstream-directed detection event occurred; fish direction was inferred from the complete pattern of detections through the full study area from the Durham Ferry release site to Chipps Island. Time-varying covariates were measured at the time step nearest either to the end of the tag's final detection event at the junction's upstream entrance receivers or to the start of the tag's final detection event at the downstream exit receivers (Table 1; Supplemental Materials).

Route use model

Individual-based generalized linear models with Bernoulli errors and a logit link were developed for use of the mainstem San Joaquin River route at both the head of Old River and Turner Cut (McCullagh and Nelder 1989). For both junctions, five model sets were constructed representing different collections of covariates: a null model that included only the effect of the barrier at the head of Old River (for the head of Old River junction) or only the intercept (for the Turner Cut junction; "null"), a model that included the barrier as well as fork length at tagging (L) and TOD of arrival at the junction (fish), a model that included the terms from the fish model as well as the variables representing localized environmental conditions (local), a model that included the terms from the fish model as well as the variables representing management metrics (management), and a model that included all variables ("combined"). Collections of covariates with variance inflation factors (VIFs; Kutner et al. 2004) greater than 10 were omitted. In most cases, pairs of covariates with high levels of pairwise correlation ($|r| > 0.70$) were also omitted; the exception was if the covariates represented different types of metrics (e.g., management versus local) and had VIFs less than 10.

For the head of Old River junction, the effect of the barrier was included in all models (including the null model) because it provided a direct physical mechanism for influencing route use (i.e., partial blockade of the Old River route). Additionally, for that junction, interaction effects were included between the barrier and all variables except flow proportion and tidal flow, for which values were expected to already reflect the physical effect of the barrier on localized hydrodynamic conditions. Thus, for the head of Old River, the general form of each model considered was analogous to the following example, which uses one covariate (x_1) for which the effect was constant regardless of the barrier status and one covariate (x_2) for which the effect depended on barrier status,

$$\text{logit}(\psi_i) = \beta_0 + \tau_0 B_i + \beta_1 x_{1i} + \beta_2 x_{2i} + \tau_2 x_{2i} B_i \quad (1)$$

for individual i, where β_0 is the intercept when the Old River barrier is absent, τ_0 is the adjustment to the intercept when the barrier is present, β_1 is the effect of covariate x_1 regardless of barrier status, β_2 is the effect of covariate x_2 when the barrier is absent, τ_2 is the adjustment to the effect of covariate x_2 when the barrier is present, and B_i is an indicator variable of barrier installation. Models that included any number of nonbarrier covariates were considered. Modeling assumptions are identified in the Supplemental Materials. For the Turner Cut junction, the effect of the Old River barrier was omitted from the null model because the mechanism by which the barrier might influence route use was indirect via an influence on the amount of river flow moving down the San Joaquin River between the head of Old River and Turner Cut. Additionally, the possibility of barrier interaction effects was assessed by the change in Akaike's information criterion corrected for small sample size (AIC_c) calculated for the combined model with and without interaction effects with all covariates except flow proportion and tidal flow.

Global models were developed for each set of covariates (fish, local, management, and combined) that included all main effects and all relevant barrier interaction effects, as described above. All subsets of each global model were fitted; to maintain a consistent interpretation of regression coefficients across competing models, models were excluded if they incorporated main effects but not barrier interaction effects for the fish, management, and net flow covariates at the head of Old River. Individual models were ranked using AIC_c, and model weights were computed using the change in model AIC_c (ΔAIC_c) relative to the top-ranked model following the methods of Burnham and Anderson (2002). A prediction model was constructed for each suite of covariates using model averaging based on the model weights via the MuMIn package in R version 4.3.1 (Bartón 2022; R Core Team 2023). Model fit was assessed using the area under the receiver operating characteristic curve (AUC; Nam and D'Agostino 2002); AUC values greater than 0.7 were considered acceptable (Hosmer and Lemeshow 2000). The relative importance of each individual covariate was measured by the sum of the AIC_c weights over all subsets of the global combined model that included the covariate. Effect sizes were estimated from the combined prediction model, and asymptotic 95% confidence intervals were calculated from the adjusted standard errors (SEs; Burnham and Anderson 2002).

Model predictions were computed from the local, management, and combined model sets by averaging the predictions from individual models within each model set using model weights (Burnham and Anderson 2002). The relationships between route use and the top covariate from both the local and management suites of covariates were depicted graphically by plotting model predictions across a range of values for those covariates; other covariates were set to their mean observed value for these plots. Route use was predicted with and without the barrier for the head of Old River junction and for both a wet year and a critically dry year (water year types) for the Turner Cut junction, where the water year type was represented by the mean Delta inflow and net flow values entering the junction during the 2011 study (wet year) and the 2013–2015 studies (critically dry years); the Turner Cut predictions were made with the barrier installed at the head of Old River for the critically dry years and with the barrier absent for the wet year. Finally, predictions from the local, management, and combined models were compared to assess the gain in predictive value provided by including local hydrodynamic variables rather than the more readily available management metrics. Hindcast predictions were computed for the first 4 days of May 2011 and April 2015. These time periods were selected to represent the middle of the tagging study during a wet year when the barrier at the head of Old River was not installed (2011) and the days before and after the barrier was closed during installation in a critically dry year (2015).

RESULTS

San Joaquin River discharge entering the Delta (Delta inflow) was markedly higher throughout the 2011 study than during the later study years, and 2013–2015 were classified as "critically dry" by the CDWR (https://cdec.water.ca.gov; Figure 2). Daily export rates at the CVP during the study ranged from 0 m^3/s in March 2011, April 2013, and April 2014 to approximately 113 m^3/s in June 2011 and May 2012 (Figure 3). Daily export rates at the SWP during the study ranged from 0 m^3/s in March 2011 and May 2014 to approximately 198 m^3/s in July 2011. Export operations were higher and more variable outside of the spring migration. The Old River barrier was installed in 2012 and 2014–2016 and was present for between 37% (2015) and 98% (2012) of tag detections at the head of Old River during those years. Descriptions of the observed covariate values are provided in the Supplemental Materials.

Head of Old River junction

Detections of 4774 acoustic-tagged steelhead were observed at the SJL and ORE telemetry stations composing the head of Old River junction, with nearly equal proportions selecting the San Joaquin River route (SJL station; 53%) and the Old River route (ORE station; 47%). Sample sizes from each release group ranged from 59 (April 2015) to 423 (April 2016). Detection probabilities for tagged fish present at the telemetry stations were mostly 1.0 ($\widehat{SE} = 0$) and were greater than 0.95 for all except two release groups (Table 3). Estimated probabilities of selecting the San Joaquin River route at this junction ranged from 0.08 ($\widehat{SE} = 0.02$) in March 2013 to 0.97 ($\widehat{SE} = 0.01$) in May 2012.

There was evidence of extreme multicollinearity when Delta inflow (Q_{VNS}), net flow at the junction entrance

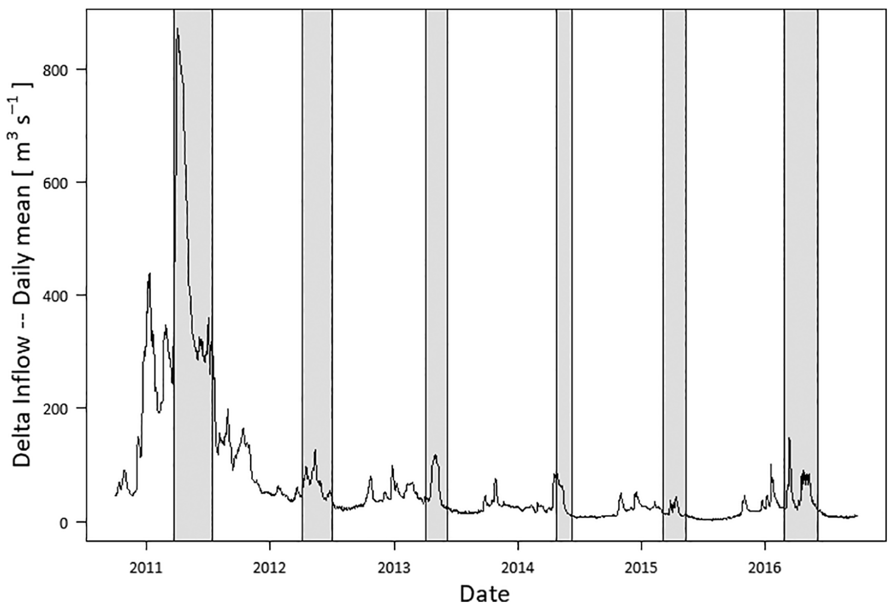

FIGURE 2 Daily mean Delta inflow rate from the San Joaquin River, measured at the VNS gauging station near Vernalis, California, 2011–2016 (i.e., source of the covariate Q_{VNS}). Gray shading indicates the dates when acoustic-tagged steelhead were detected at the head of Old River junction or the Turner Cut junction. Delta inflow data are from the California Department of Water Resources' Dayflow database (https://data.cnra.ca.gov/dataset/dayflow).

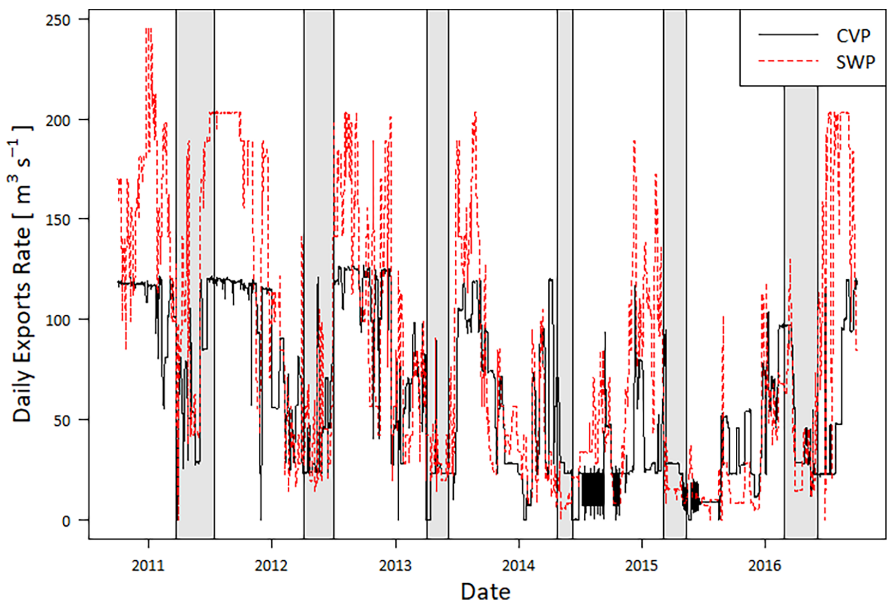

FIGURE 3 Daily water export rates from the Central Valley Project (CVP) and State Water Project (SWP), 2011–2016. Gray shading indicates the dates when acoustic-tagged steelhead were detected at the head of Old River junction or the Turner Cut junction. Daily export rate data are from the California Department of Water Resources' Dayflow database (https://data.cnra.ca.gov/dataset/dayflow).

(nQ_{SJO}), and the IE ratio were used together in the routing models. As a result, the Delta inflow covariate was retained in place of the localized net flow and IE ratio covariates for the head of Old River junction. Detailed multicollinearity results are provided in the Supplemental Materials.

The presence of the barrier at the head of Old River was strongly associated with selection of the San Joaquin River route at that junction (ΔAIC = 2346) and was included as a factor in all models. With the barrier effect accounted for, the null model had an AUC value of 0.816 (Table S1 available in the Supplemental Materials), indicating a moderate to high level of discrimination even before accounting for effects of fish characteristics, localized hydrodynamic conditions, or management metrics (Hosmer and Lemeshow 2000). Including fish size, TOD, and either management or local covariates increased the AUC to 0.903 or higher values. The SJR flow proportion (pQ_{SJL}), Delta inflow (Q_{VNS}), and L were included in all models that received positive weight in the model selection protocol (total weight = 1.0; Table 4). Exports at the SWP (E_{SWP}) and TOD also had high total weights (≥0.782), whereas exports at the CVP (E_{CVP}) and tidal flow (tQ_{SJO}) contributed little to the route use model at the head of Old River (total weight ≤0.241). Effect sizes from the combined prediction model also indicated that the largest effects were from the SJR flow proportion, Delta inflow when the barrier was absent, and fork length when the barrier was present (Figure 4). However, there was large uncertainty in the effect of TOD, and the estimated effect of SWP exports was small compared to the uncertainty estimate.

The combined model (i.e., all covariates) predicted higher use of the main-stem San Joaquin River route when either the San Joaquin River flow proportion (pQ_{SJL}) or Delta inflow (Q_{VNS}) was higher (Figure 5). For both covariates, the largest increase in main-stem route use was predicted when the barrier was absent. This was expected due to the partial physical blockade of Old River entry that was provided by the barrier.

When implemented on hydrodynamic and operational data from early May 2011, the management-only model generated lower predictions of the probability of taking the San Joaquin River route when compared to the local and combined models during the nighttime, although the differences were within the margin of error (Figure 6A). The predictions from the local-only model were in most cases slightly greater than the predictions from the combined model. The predictions in early May 2011 varied between 0.48 and 0.58, indicating stable routing during this period of high discharge (Delta inflow = 439–544 m^3/s) and without the barrier installed.

The hindcast predictions of San Joaquin River route use for early April in the critically dry year of 2015 demonstrated more variability, ranging from 0.02 (night, with no barrier installed) to 0.98 (day, with barrier installed), both from the combined model (Figure 6B). The barrier closure occurred on April 3 in 2015, and the predicted probability of taking the San Joaquin River route was considerably higher after the barrier was installed, particularly for the management-only model. The perceived barrier effect from the local and combined models was less extreme, especially during times when the flow in the San Joaquin

TABLE 3 Release dates, number of steelhead released at Durham Ferry (N_{Rel}) and detected at the head of Old River (HOR) junction (N_{HOR}) and the Turner Cut junction (TCJ; N_{TCJ}), estimates (standard errors in parentheses) of the probability of selecting the San Joaquin River (SJR) route (ψ) at the HOR junction and TCJ, and estimates of the probability of detection (P) at junction exit telemetry stations for release groups of acoustic-tagged juvenile steelhead. Telemetry stations include SJL, ORE, MAC, and TRN; see Figure 1 for station locations. Values without standard errors were estimated at exactly 1.00; "$n=0$" indicates no detections at the junction or telemetry station.

Year	Release dates	N_{Rel}	N_{HOR}	N_{TCJ}	$\hat{\psi}_{SJR\_HOR}$	$\hat{\psi}_{SJR\_TCJ}$	$\hat{P}_{SJL}$	$\hat{P}_{ORE}$	$\hat{P}_{MAC}$	$\hat{P}_{TRN}$
2011	Mar 22–26	479	304	159	0.52 (0.03)	0.91 (0.02)	0.95 (0.02)	0.86 (0.03)	1.00 (0.00)	1.00
	May 3–7	474	232	110	0.51 (0.03)	0.68 (0.04)	0.91 (0.03)	0.95 (0.02)	0.99 (0.00)	1.00
	May 17–21	478	223	94	0.49 (0.03)	0.76 (0.04)	0.95 (0.02)	0.99 (0.01)	1.00 (0.00)	1.00
	May 22–26	480	242	116	0.53 (0.03)	0.68 (0.04)	0.97 (0.02)	0.99 (0.01)	1.00 (0.00)	1.00
	Jun 15–18	285	96	34	0.52 (0.05)	0.50 (0.09)	1.00	1.00	0.89 (0.10)	1.00
	2011 total	2196	1097	513	0.51 (0.02)	0.72 (0.02)	0.95 (0.01)	0.95 (0.01)	0.98 (0.01)	1.00
2012	Apr 4–7	477	327	217	0.94 (0.01)	0.77 (0.04)	1.00	1.00	1.00 (0.00)	0.58 (0.11)
	May 1–6	478	308	242	0.97 (0.01)	0.77 (0.03)	1.00	1.00	0.97 (0.02)	1.00
	May 18–23	480	166	139	0.92 (0.02)	0.63 (0.04)	1.00	1.00	1.00 (0.00)	1.00
	2012 total	1435	801	598	0.94 (0.01)	0.72 (0.02)	1.00	1.00	0.99 (0.00)	0.86 (0.04)
2013	Mar 6–9	476	288	0	0.08 (0.02)	$n=0$	1.00	1.00	$n=0$	$n=0$
	Apr 3–6	477	306	9	0.12 (0.02)	0.56 (0.17)	1.00	1.00	1.00	1.00
	May 8–11	472	306	17	0.16 (0.02)	0.67 (0.11)	1.00	1.00 (0.00)	1.00	1.00
	2013 total	1425	900	26	0.12 (0.01)	0.61 (0.10)	1.00	1.00 (0.00)	1.00	1.00
2014	Mar 26–29	474	137	0	0.09 (0.02)	$n=0$	1.00	1.00	$n=0$	$n=0$
	Apr 24–27	480	338	257	0.96 (0.01)	0.69 (0.03)	1.00	1.00	1.00	1.00
	May 21–24	478	89	16	0.88 (0.03)	0.87 (0.08)	1.00	1.00	1.00	1.00
	2014 total	1432	564	273	0.64 (0.01)	0.78 (0.04)	1.00	1.00	1.00	1.00
2015	Mar 4–7	480	162	10	0.19 (0.03)	0.80 (0.13)	1.00	1.00	1.00	1.00
	Mar 25–28	478	210	54	0.41 (0.04)	0.91 (0.04)	1.00	1.00	1.00	1.00
	Apr 22–25	469	59	23	0.80 (0.05)	0.74 (0.09)	1.00	1.00	1.00	1.00
	2015 total	1427	431	87	0.46 (0.02)	0.82 (0.05)	1.00	1.00	1.00	1.00
2016	Feb 24–27	480	193	15	0.12 (0.02)	0.60 (0.13)	1.00	1.00	1.00	1.00
	Mar 16–19	480	365	63	0.23 (0.02)	0.71 (0.06)	1.00	1.00	1.00	1.00
	Apr 27–30	480	423	362	0.96 (0.01)	0.75 (0.02)	1.00	1.00	1.00 (0.00)	1.00
	2016 total	1440	981	440	0.44 (0.01)	0.69 (0.05)	1.00	1.00	1.00 (0.00)	1.00

TABLE 4 Total weight of steelhead route use models that included individual covariates for the head of Old River (HOR) junction and the Turner Cut junction (TCJ). CVP, Central Valley Project; SWP, State Water Project.

Covariate	HOR	TCJ
Barrier at HOR (B)	Included in all models	0.284
Net flow at entry (nQ)	See Q_{VNS}	1.000
Tide (tQ)	0.241	1.000
Flow proportion (pQ)	1.000	1.000
Delta inflow (log scale) (Q_{VNS})	1.000	0.786
Exports at CVP (E_{CVP})	0.177	1.000
Exports at SWP (E_{SWP})	0.802	0.255
Fork length (L)	1.000	0.293
Time of day	0.782	0.377

River branch of the junction was negative (i.e., $pQ_{SJL}=0$; Figure 6B). There was little difference between the predictions from the local model and the combined model, and the largest differences were seen before the barrier was installed.

Turner Cut junction

In total, 1937 steelhead were detected at the telemetry stations composing the Turner Cut junction over the 6 years of the study: 1449 at the San Joaquin River station (MAC) and 488 at the Turner Cut station (TRN). Release-specific sample sizes varied widely (0–362) throughout the study. Detection probabilities were mostly estimated at 1.0 ($\widehat{SE}=0$) and were greater than 0.95 for all except three release groups (Table 3). Estimated probabilities of selecting the

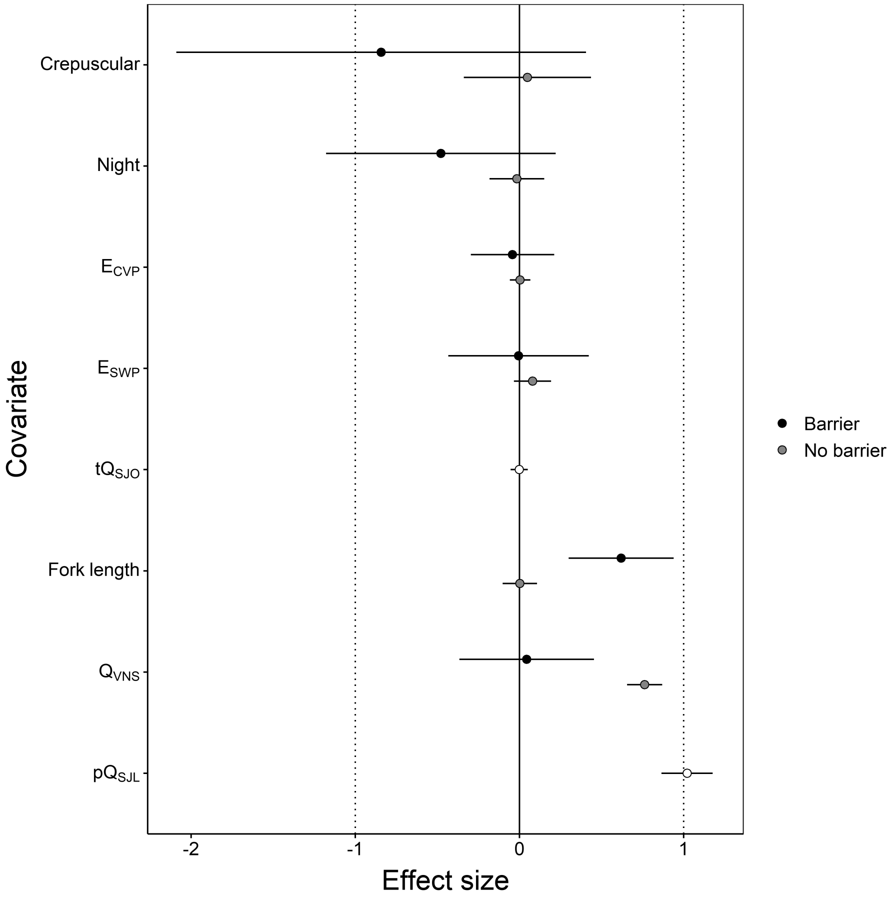

FIGURE 4 Estimated standardized effect sizes and asymptotic 95% confidence intervals from the prediction model for steelhead route use at the head of Old River. The response variable is the use of the San Joaquin River route. All models included the effect of the Old River barrier. All variables except flow proportion and tidal flow were included with an interaction effect with barrier. Positive flow is directed downstream. "Night" and "crepuscular" define time-of-day effects in relation to the baseline setting "day." Vertical dashed lines indicate effect sizes of ±1 standard deviation. "Barrier" defines covariate effects in relation to the baseline setting "no barrier" (i.e., the added effect of barrier on the covariate effect size). Covariate symbols are defined in Table 1.

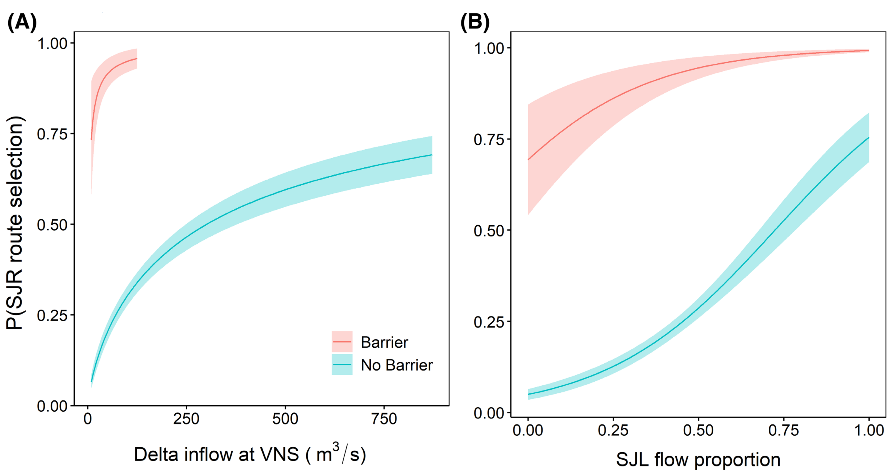

FIGURE 5 Predicted probability (with asymptotic 95% confidence bands) of steelhead selecting the San Joaquin River (SJR) route at the head of Old River (SJL and ORE telemetry stations) as a function of (A) daily average Delta inflow at Vernalis (Q_{VNS}) and (B) the instantaneous SJR flow proportion (pQ_{SJL}) at the head of Old River for the prediction model using all covariates. Predictions were computed for the daytime using the studywide means of all other covariates ($L = 245$ mm; $tQ_{SJO} = 4.6\ m^3/s$; $pQ_{SJL} = 0.48$; $Q_{VNS} = 81.5\ m^3/s$; $E_{CVP} = 48\ m^3/s$; $E_{SWP} = 53\ m^3/s$; covariate symbols are defined in Table 1) with the Old River barrier present (red line) or absent (blue line). Higher values of pQ_{SJL} denote that a higher proportion of flow exiting the junction is directed downstream in the SJR.

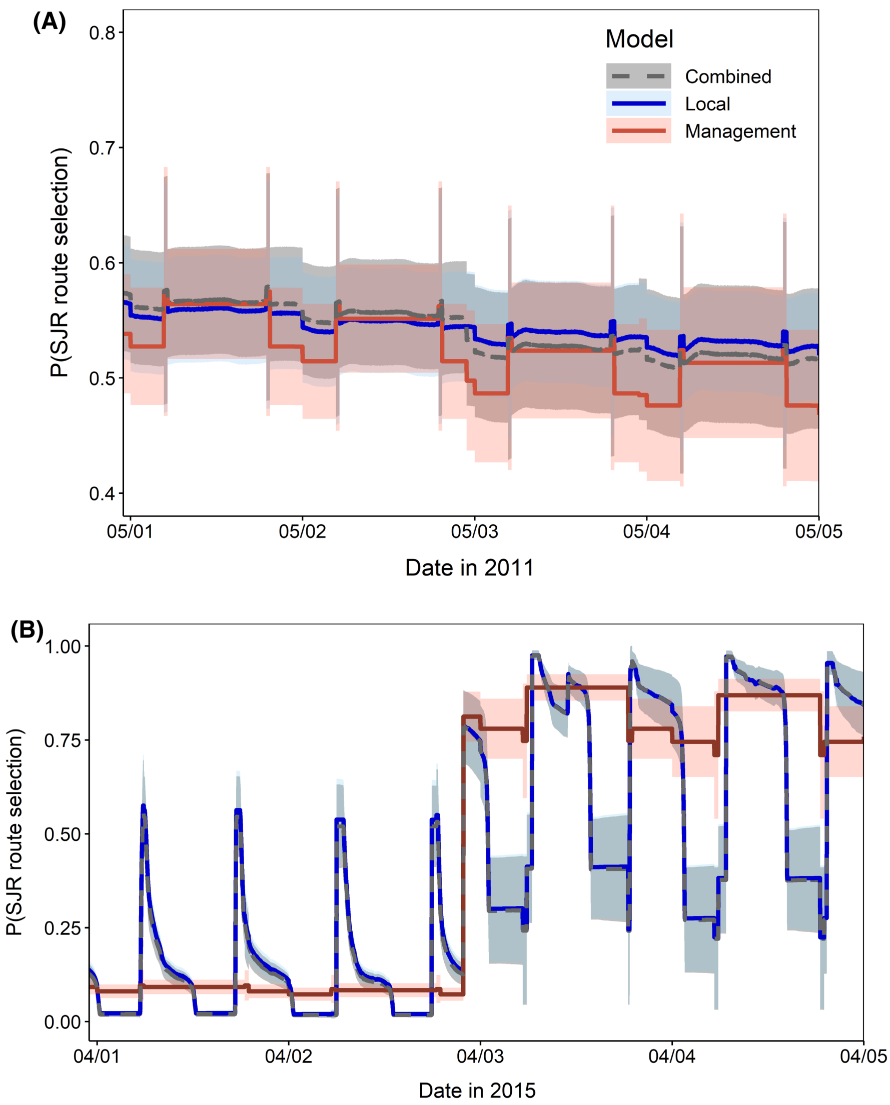

FIGURE 6 Hindcast prediction of the probability of steelhead selecting the San Joaquin River (SJR) route at the head of Old River junction for 4 days in (A) May 2011 and (B) April 2015. Shaded regions represent 95% prediction intervals. Predictions were made using the observed or modeled conditions during the time period for a fish with a fork length of 245 mm (average across the study at that junction) and from the local (blue), management (red), and combined (black) models.

San Joaquin River route ranged from 0.50 ($\widehat{\mathrm{SE}}=0.09$; June 2011) to 0.91 ($\widehat{\mathrm{SE}}\leq 0.04$; March 2011 and late March 2015).

The local covariates at the Turner Cut junction demonstrated the tidal nature of the habitat (Figure S3 available in the Supplemental Materials). The IE ratio was dropped from modeling because of its high correlation with Delta inflow. Detailed descriptions of the multicollinearity results are provided in the Supplemental Materials.

Use of barrier interaction effects in the global model increased the AIC_c, so only main effects of the barrier were considered in the Turner Cut models. The null, fish, and management models of route use at the Turner Cut junction all had poor fit to the data (AUC $\leq$ 0.624; Table S1), whereas the local and combined models had high AUC values ($\geq$0.863), indicating that route use depended on localized conditions that were poorly represented by remote management metrics and fish characteristics. All three localized measures (net flow at entry [nQ_{SJS}], tidal flow [tQ_{SJS}], and San Joaquin River flow proportion [pQ_{MAC}]) were included in all supported models (i.e., total model weight = 1.0) from the model selection protocol for Turner Cut, as was the daily average export rate at the CVP (E_{CVP}; Table 4). Although Delta inflow (Q_{VNS}) was highly correlated with net flow entering this junction ($r=0.86$; Figure S4), Q_{VNS} received a lower total model weight (0.786). Exports at the SWP (E_{SWP}), the barrier at the head of Old River, L, and TOD all contributed little to the route use model at the Turner Cut junction (total weight $\leq$ 0.377).

Effect sizes from the combined prediction model indicated higher probabilities of remaining in the San Joaquin River at Turner Cut for fish that arrived at the junction

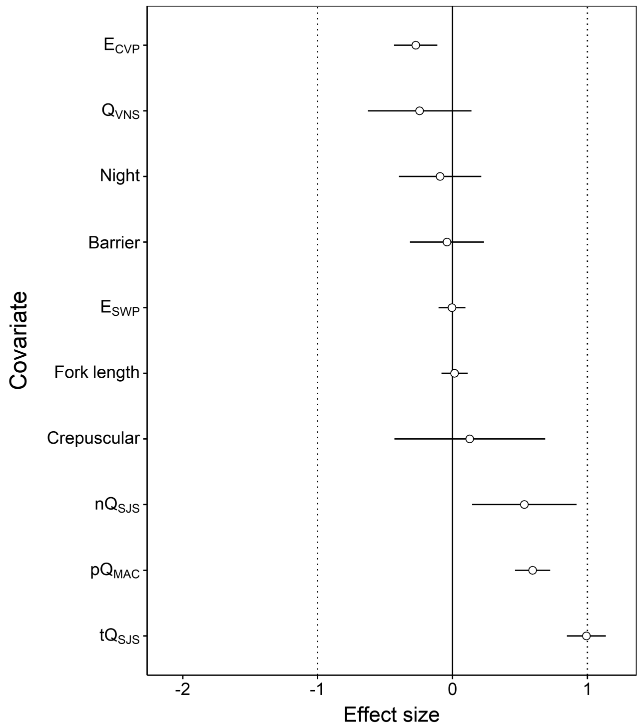

FIGURE 7 Estimated standardized effect sizes and asymptotic 95% confidence intervals from the prediction model for steelhead route use at the Turner Cut junction. The response variable is the use of the San Joaquin River route. Positive flow is directed downstream. "Night" and "crepuscular" define time-of-day effects in relation to the baseline setting "day." Vertical dashed lines indicate the effect sizes of ±1 standard deviation. Covariate symbols are defined in Table 1.

on an outgoing tide, with higher positive net flow, and with lower CVP exports (Figures 7 and 8). There was no indication of an effect of SWP exports or TOD on route use (Figure 7). Examination of model predictions demonstrated wide variation in route use across the range of tidal flow at the upstream entrance of the junction (tQ_{SJS}), with a considerably smaller effect of net flow and river discharge from upstream (represented by water year type in Figure 8A). The range of route use predictions in response to changes in CVP exports was small compared to the effect of tidal flow (Figure 8B).

The hindcast predictions for early May 2011 from the management model exhibited considerably lower variability than the predictions from the local and combined models (Figure 9A). The daily fluctuations in route use predictions from the local and combined models demonstrated the influence of the tidal forces at the Turner Cut junction, all of which were omitted from the management model. Although the local and combined predictions generally had good agreement for this period in 2011, the slight overestimation of steelhead use of the main-stem river route from the local model compared to the combined model for May 3–5 reflected the added influence of CVP exports included in the combined model. The maximum difference between the predictions of the combined model and the two submodels was 0.74 for the management model and 0.15 for the local model. The predictions for early May 2011 varied between 0.08 and 0.95.

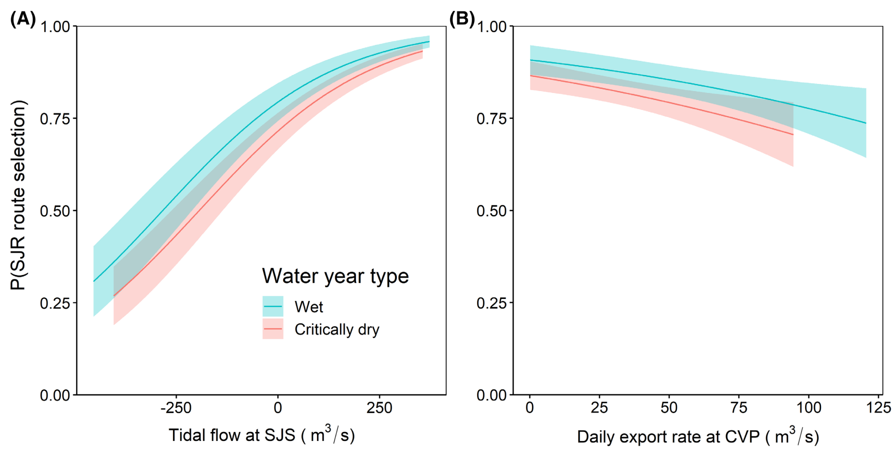

FIGURE 8 Predicted probability (with asymptotic 95% confidence bands) of steelhead selecting the San Joaquin River (SJR) route at the Turner Cut junction (MAC and TRN telemetry stations) as a function of (A) 90-s tidal flow at the entrance to the junction (tQ_{SJS}) and (B) the daily average export rate at the Central Valley Project (E_{CVP}) for the prediction model using all covariates. Predictions were computed for the daytime using the average values of Delta inflow (Q_{VNS}) and net flow (nQ_{SJS}) for 2011 (wet year type; $Q_{VNS} = 703\,m^3/s$, $nQ_{SJS} = 205\,m^3/s$) and 2013–2015 (critically dry year type; $Q_{VNS} = 49\,m^3/s$, $nQ_{SJS} = 46\,m^3/s$). The barrier at the head of Old River was assumed to be absent for the wet year type and present for the critically dry year type. All other covariates used their studywide means ($L = 251$ mm; $tQ_{SJS} = 99\,m^3/s$; $pQ_{SJL} = 0.7$; $E_{CVP} = 45\,m^3/s$; $E_{SWP} = 50\,m^3/s$; covariate symbols are defined in Table 1). Tidal flow is greater than 0 for an ebb tide and less than 0 for a flood tide.

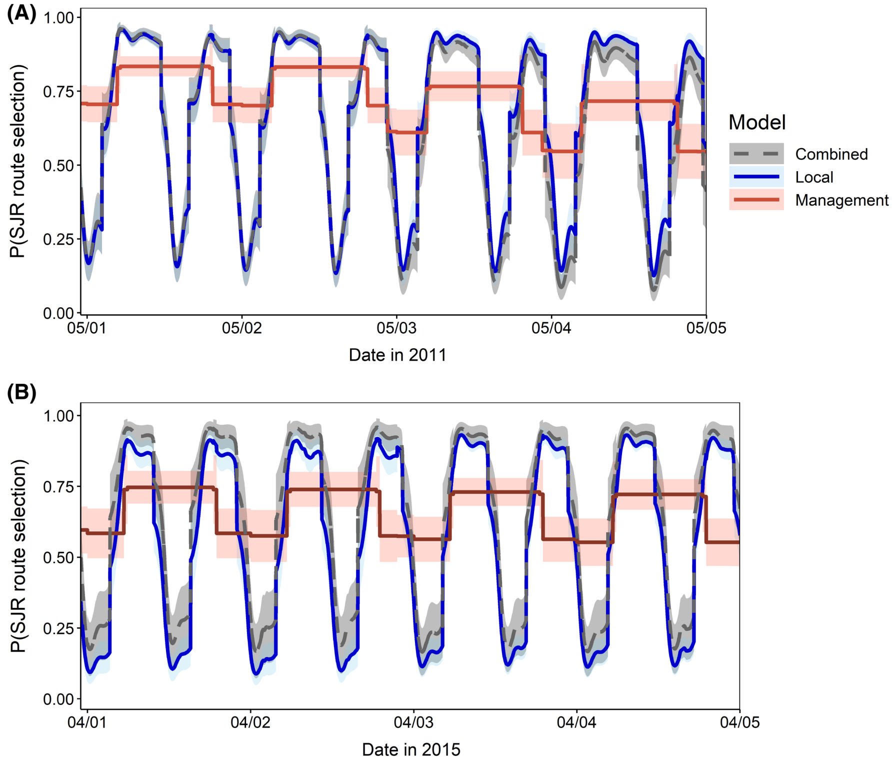

FIGURE 9 Hindcast prediction of the probability of steelhead selecting the San Joaquin River (SJR) route at the Turner Cut junction for 4 days in (A) May 2011 and (B) April 2015. Shaded regions represent 95% prediction intervals. Predictions were made using the observed or modeled conditions during the time period for a fish with a fork length of 251 mm (average across the study at that junction) and from the local (blue), management (red), and combined (black) models.

The hindcast predictions for early April in the critically dry year of 2015 demonstrated patterns similar to those for 2011, with the management model predictions of main-stem route use underestimating the highest predictions and overestimating the lowest predictions from the local and combined models (Figure 9B). However, the local model consistently predicted a lower probability of using the main-stem route compared to the combined model for 2015. The early April 2015 export rate at the CVP ranged from 28.01 to 28.09 m^3/s—considerably lower than the early May 2011 CVP export rate (50.5–105.0 m^3/s)—and the lack of an adjustment for exports would not have resulted in a lower estimate of main-stem route use, given the negative estimated effect of CVP exports overall. However, without the Delta inflow and export variables, the perceived barrier effect was larger and the estimated intercept was lower in the local model than in the combined model, which may have accounted for the underestimation by the local model compared to the combined model in early April 2015. The difficulty in interpreting the differences among the models highlights the challenges of causal attribution in a system where covariates are correlated, even when efforts have been made to reduce the effect of multicollinearity.

DISCUSSION

This study investigated the ability to predict routing of juvenile steelhead in a heavily modified tidal river delta, where large-scale water extraction and landscape changes have contributed to a survival gradient across different migratory pathways. I found that accurate prediction of routing depended on knowledge of localized flow conditions at the times when fish were present at the river junctions. The monitoring of flow conditions and water management operations at locations that were at least 20 km away provided some information on route usage but did not replace the predictive capabilities provided by localized information. Depending only on the metrics of remote conditions that are commonly used in water management in the region resulted in underestimation of the subdaily fluctuations in route usage. This pattern was most apparent at a tidally dominated river junction (Turner Cut), although it was also observed at a more riverine junction (head of Old River) during low water years. The use of a temporary rock barrier at the head of Old River was the most effective factor in determining route use there, but it had no discernible effect on route use at Turner Cut, located 30 km downstream. Emigrating steelhead were predicted to use the main-stem river route if they entered a river junction on an ebb tide or when net river flow or flow proportion in the main-stem junction exit was higher. River discharge that was measured 20–57 km upstream provided no additional predictive ability and was a poor replacement for local flow measures at Turner Cut. The daily rate of water export pumping at sites 20–30 km away contributed to the use of non-main-stem routes, but the effect was small compared to subhourly flow conditions at the junctions themselves.

The hypothesis that fish routing can be predicted by the management metrics was predicated on the expectation that upstream conditions and remote water operations affect hydrodynamic conditions at river junctions situated 20–57 km away, as predicted by previous hydrodynamic modeling (Cavallo et al. 2013). Both that hypothesis and the hypothesis that local flow conditions affect fish routing rest on the assumption that fish follow the flow. The movement of small fish through rivers and estuaries is often treated as passive drifting with the current in particle-tracking models (e.g., Sridharan et al. 2018). In such a framework, any effect of active swimming behavior is negligible in comparison to hydrodynamic forces, and prediction of routing at junctions can be effected via a sufficiently precise characterization of velocity forces (i.e., the critical streakline, or the boundary of the water velocity field leading to the off-main-stem route) and the cross-sectional distribution of fish as they approach the river junction (Hance et al. 2020; Harnish et al. 2023). The mechanism by which remote management actions or conditions may influence fish routing is then limited to the hydrodynamic influence of the action on the water velocity field in the junction (e.g., the “pull” of downstream exports) or on the cross-sectional approach distribution. The latter may occur if salmonid smolts tend to favor one side of the channel under high-flow conditions either because of refuge from high current speed or because off-channel rearing habitat becomes available during high flows. The cross-channel fish distribution at upstream locations may persist to downstream river junctions if shoreline conditions are favorable or if high flows deter the lateral movement required to cross the midchannel current (Hance et al. 2020; Holleman et al. 2022).

As an alternative to depicting fish as drifting particles, several researchers have observed active swimming behavior by salmonid smolts at river junctions in this system and elsewhere (Holleman et al. 2022; Goodwin et al. 2023). Holleman et al. (2022) performed two-dimensional tracking of acoustic-tagged spring Chinook Salmon smolts at the head of Old River and observed a variety of behaviors, including both positive and negative rheotaxis and lateral movement from one side of the channel to the other. This study occurred during a dry water year, and it is possible that the diversity of behavior would be lower in a high-flow setting because of the greater energy required to swim against the flow (Swanson et al. 2004). Nevertheless, the larger steelhead smolts in this study may have been better able to respond actively to changing conditions than the smaller salmon smolts in the study by Holleman et al. (2022; average fork length of smolts: 77 mm [their study] versus 245 mm [present study]). Goodwin et al. (2023) also observed a range of behaviors among Chinook Salmon smolts at the diffluence of Georgiana Slough from the Sacramento River. Using a fish cognition model, they demonstrated that fish movement in the junction depends not only on current hydrodynamic conditions, but also on flow conditions and fish behavior from the recent past (i.e., memory). This finding allows for a complex routing mechanism of upstream discharge that is independent of localized flow conditions.

Several investigations have explored the use of flow proportion to model fish routing at river diffluences under the rubric of fish following the flow (e.g., Cavallo et al. 2015; Perry et al. 2015; Romine et al. 2021). Perry et al. (2015) observed a positive relationship between routing and flow proportion but found that the probability of using the non-main-stem route for yearling Chinook Salmon smolts tended to be lower than the proportion of river flow entering that route; in other words, the relationship was not 1:1. Spill proportion is an analogous metric in dam passage studies, and Harnish et al. (2023) similarly found a relationship between spillway routing of fish and water flow that was positive but not 1:1. The possibility of fish exactly following the flow proportion depends on the distribution of the fish across the channel as they enter the junction, such that the prediction of route use by individual fish requires knowledge of when they are present and what part of the channel they are using (Hance et al. 2020; Harnish et al. 2023). However, if smolts typically move downstream on ebb tides and seek refuge or hold during flood tides (e.g., via selective tidal stream transport; Forward and Tankersley 2001; Bennett and Burau 2015), then the results here can be used to predict a range of probabilities of entry to the interior Delta via Old River or Turner Cut.

The roles of Delta inflow and net flow on route use in the south Delta have been uncertain. Previous hydrodynamic modeling and release-level analysis of Chinook Salmon telemetry data predicted that salmon were more likely to use the Old River route than the San Joaquin River route at that junction when Delta inflow was high (Cavallo et al. 2015). Similarly, Dodrill et al. (2022) predicted a higher tendency of juvenile Chinook Salmon to move toward the Old River route when net flows were high at the head of Old River. Nevertheless, this study predicted a lower probability of using the Old River route when either Delta inflow or net flow was high. This is consistent with the findings of Anchor QEA (2022), in which a small increase in steelhead movements toward the San Joaquin River route was observed under conditions of higher net flow at the head of Old River. However, the present investigation found that variation in Delta inflow accounted for a smaller portion of the variability in route use than the instantaneous flow proportion, and Anchor QEA (2022) similarly reported a stronger effect of tide than of net flow on downstream movements. Regardless of the impact of Delta inflow variation at the head of Old River, changes in Delta inflow had little apparent effect on steelhead route use at Turner Cut, consistent with previous predictions for salmon (Cavallo et al. 2015). Net flow in the main stem at Turner Cut was associated with route selection there but had a lower effect than tidal flow.

The most effective driver of route use at the head of Old River was the temporary rock barrier that was installed in the spring during some years to limit access to the upper reaches of Old River. When the barrier is installed, fish are much more likely to select the San Joaquin River route over Old River. However, the barrier cannot be installed when Delta inflow exceeds 141.6 m^3/s (5000 ft^3/s), and it is costly to install and to later remove each spring. There has also been concern about the effects of barriers in the south Delta on threatened Delta Smelt *Hypomesus transpacificus* in the central Delta (U.S. Fish and Wildlife Service [USFWS] 2023). Furthermore, there has been no evidence that a survival benefit is accorded to juvenile fall-run Chinook Salmon by remaining in the San Joaquin River at the head of Old River (Buchanan and Whitlock 2022), and the survival differences between these two routes have been equivocal for steelhead as well (Buchanan et al. 2021). Thus, the barrier has not been installed in recent years. However, for both steelhead and salmon, there is evidence that the presence of the rock barrier has sufficient effect on hydraulics to improve survival in the upper reaches of the San Joaquin River route, presumably by preventing San Joaquin River water from entering Old River and instead causing it to move downstream in the San Joaquin River (e.g., survival difference of ~0.1 due to the barrier between the head of Old River to Turner Cut for steelhead in 2016 [Buchanan et al. 2021] and up to ~0.4 for Chinook Salmon in dry years [Buchanan and Whitlock 2022]). Thus, the barrier and its effects remain of interest to managers due the potential survival benefit gained from the barrier's effect on flow (i.e., increased San Joaquin River flow).

This investigation found no evidence that the Old River barrier affected route use for steelhead that arrived at the Turner Cut junction. Considering the distance between the head of Old River and the Turner Cut junction (30 km), it is unsurprising that the barrier had no strong effect on route use there. The total population effect of the barrier is not limited to its fish guidance capability at the head of Old River, however, if fish that are diverted from entering the interior Delta via Old River instead enter it via Turner Cut. This can happen even without a barrier effect on route use at Turner Cut if more fish arrive at that junction when the barrier is installed upstream because they were deterred from entering Old River or because the barrier diverted additional flow down the San Joaquin River. In the north Delta, Perry et al. (2014) observed that some juvenile late-fall-run Chinook Salmon avoided entering the interior Delta via the Delta Cross Channel when an operable gate blocked access only to enter the interior Delta just downstream via Georgiana Slough. Although the Old River barrier is relatively far from Turner Cut, the improved survival probability in the San Joaquin River from the head of Old River to Turner Cut when the barrier is installed raises the question of whether the barrier results in more fish entering the Delta at Turner Cut. This possibility is of special concern because although there is little difference in route-specific survival between the San Joaquin River route and the Old River route, the Turner Cut route has considerably lower survival than the San Joaquin River through the lower river and Delta (Buchanan et al. 2021). Preliminary analysis found no effect of the Old River barrier on the joint probability of arriving at the Turner Cut junction and selecting the Turner Cut route (results not shown). However, a full sensitivity analysis of through-Delta survival to barrier effects under different conditions is recommended. These results will be an important component of such an investigation.

The role of exports in influencing route use is of particular interest to regional water managers. This study found only moderate evidence of an effect of SWP exports on steelhead entry into Old River in the absence of the barrier, and the effect was small compared to local flow covariates. However, CVP exports were strongly associated with a small increase in use of the Turner Cut route regardless of barrier status. Reducing exports when emigrants are present in the San Joaquin River may improve total survival through the Delta, although the small effect on routing makes it unlikely that changes to export operations alone will be sufficient for population recovery.

A related management metric of interest to managers is the IE ratio. Allowable export rates are set based on target IE ratios that are defined for different water year types (e.g., dry versus wet years), and managers seek to understand how survival through the Delta is related to this metric. In the present investigation, the IE ratio was omitted from modeling because of its high correlation with Delta inflow. Additionally, because different combinations of inflow and export conditions can be represented by the same IE ratio, it is difficult to assign mechanisms by which an observed IE ratio value might influence routing (Salmonid Scoping Team 2017). Typically, more explanatory power is gained from using Delta inflow and exports as covariates separately rather than combined in their ratio.

Fork length and TOD were included in the modeling at both junctions. Larger fish have been observed to exhibit a greater ability to move laterally or against the flow (Swanson et al. 2004), and salmon smolts have been observed engaging in more lateral movement during the day at the head of Old River (Holleman et al. 2022). In this investigation, larger fish were more likely to remain in the San Joaquin River at Old River, but only when the barrier was installed. Fish entering the head of Old River junction during dawn, dusk, and night were predicted to have a higher probability of entering Old River when the barrier was in place, but there was large uncertainty in the effects. Neither fish size nor TOD was associated with fish routing at Turner Cut. However, use of a wider range of fish sizes might have detected a different effect.

The steelhead used in this investigation were yearling hatchery-reared smolts and may have had different responses to barrier and flow conditions than wild fish or smaller fish (Murphy et al. 2011). The Central Valley DPS is dominated by hatchery fish (Huber et al. 2024), but steelhead exiting the San Joaquin River are naturally produced. Determining management policies based entirely on observations of hatchery-reared smolts that are large enough to bear an acoustic tag risks a failure to protect the natural population if habitat or survival differences exist between wild and hatchery juveniles. Wild fish may be smaller and more subject to flow patterns than hatchery fish (Hill et al. 2006). If so, the effect of net flow, tidal flow, and flow proportion may be greater for wild fish than for hatchery fish, especially if they are less able to move laterally across the critical streakline. Additionally, potential differences in habitat or shoreline use between hatchery and wild fish limit direct inferences of these results to wild steelhead (Hill et al. 2006). Ideally, wild fish would be used in the tagging studies targeting their management (Murphy et al. 2011). However, small population sizes make the direct study of wild fish challenging, and it is expected that hatchery steelhead serve as a better surrogate for wild steelhead than hatchery Chinook Salmon, which have been used as surrogates in the past (Murphy et al. 2011).

The management objective of keeping migrating smolts out of the interior Delta arises from the highly modified environment, pumping facilities, and low survival in that region. However, Old River historically was the primary route for both water and salmonids entering the Delta from the south (Erkkila et al. 1950), and the Delta's tidal marshes formed an important rearing habitat for young salmonids (Moyle et al. 2010). Attempting to keep emigrants in the main-stem San Joaquin River overlooks the historical and ecological significance of the alternative routes and may increase population risk by reducing phenotypic diversity (Hilborn et al. 2003). An alternative to focusing on route manipulation is habitat restoration in the interior Delta to improve survival for native fishes, which would promote rearing and survival of younger life stages as well as smolts.

Several recommendations for Delta managers arise from this work. First, because steelhead have a higher probability of using the interior Delta route at Old River when discharge from upstream is lower, managers are advised to install the barrier during low-flow years to keep fish in the San Joaquin River. There is no barrier option at Turner Cut, however, where survival is notably lower for fish that enter the interior Delta. Furthermore, the covariates with the strongest support at that junction were measures of local tidal flow, which are not subject to manager control. However, there was a small export effect at Turner Cut, and limitation of exports when smolts are expected in the lower San Joaquin River would help to limit interior Delta entry at Turner Cut and to lower the risk of entrainment in the pumping facilities for fish that do enter Turner Cut. Additionally, because the cross-sectional distribution of fish as they enter the junction is expected to be especially important at Turner Cut due to the higher flows in that region (Hance et al. 2020), upstream habitat restoration that favors the eastern and northern sides of the San Joaquin River may encourage smolts to use those sides of the channel as they approach Turner Cut and thus remain in the San Joaquin River (Holleman et al. 2022). Finally, because the control of fish routing at Turner Cut and other tidal junctions further downstream is highly likely to be imperfect, managers should aim to improve survival in the interior Delta, both by limiting exports when fish are migrating through the lower river and by reducing habitat that is favored by predators (Conrad et al. 2016; Young et al. 2018).

Questions of management are inherently local in nature, and the recommendations above are specific to water resource managers in the Delta. However, some lessons can be gleaned on a broader scale for use with water or fish managers in other urban or industrial estuaries. The first is to monitor conditions where they are needed. Measurement of conditions only at remote locations for use in predictions elsewhere risks degrading predictive capabilities, especially for tidal or other settings in which conditions fluctuate on a subdaily or subhourly basis. Established management metrics may need to be augmented to represent more local conditions. This applies in problems of dam passage as well as in tidal areas. Additionally, considering the effect of factors that are outside of management control (e.g., tides) is important for accurately characterizing the expected benefit of actions that are available (e.g., exports). This is necessary for yielding unbiased estimates of potential effects and for managing the expectations of proposed actions. Finally, effective conservation requires examining the potential efficacy of different approaches locally within the system. If the ability to manipulate routing away from low-survival regions is poor, then it may make more sense to devote limited resources to improving route-specific survival than to attempt to control routing. The question of conservation priorities is especially relevant for threatened species in highly modified and dynamic environments that support human and aquatic populations alike.

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CONFLICT OF INTEREST STATEMENT

The author declares no conflict of interest.

DATA AVAILABILITY STATEMENT

Data that support the findings of this study are available from the author upon reasonable request.

ETHICS STATEMENT

This study consisted of analysis of existing data, and there were no applicable ethical guidelines.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.