



Applying the mean free-path length model to juvenile Chinook salmon migrating in the Sacramento River, California

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Abstract Population vital rates, such as stage-specific survival, are influenced by individual behavior and movement patterns. Yet few methods exist to incorporate behavior into predator-prey models, omitting a potentially important source of variability in population dynamics. Here we combine results from an acoustic telemetry study of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) with an existing predator-prey model, called the mean free-path length model, originally presented in Anderson et al. (2005). The model describes the probability of predator-prey encounters as a function of the predator density and the movement patterns of predators and prey. Greater predator densities and greater variation in movement vectors should result in higher predator-prey encounter rates, and lower survival for the prey. Fitting this model to data provides insight into mechanisms of mortality for migrating fishes. Here we estimate model parameters for

two flow conditions in the Sacramento River, California, examining the importance of natural environmental variation in shaping encounters and prey survival. Survival estimates were similar between the high and low flow conditions, yet travel time was slower at lower flows. The model estimates of mean free-path length were lower when compared to those estimated in the Snake River system, corresponding with lower survival. We discuss the value of model parameters estimated from telemetry data in providing a tool for forecasting population-level responses to structural or hydrodynamic modifications in large river systems, and we explore how the XT model can provide insight into nonlinear and threshold-like responses of migratory fish survival to flow.

Keywords Predator-prey · XT model · Acoustic telemetry · Ideal gas law

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Introduction

Population vital rates, such as stage-specific survival, are central to many ecological processes. These rates determine the persistence or extinction of a population and can be influenced by human-alterations to ecosystems, making this a central issue for many topics in natural resource management. There is a long history of modeling survival rate as a result of predator-prey interactions (Leslie 1948; Holling 1959; Arditi and Ginzburg 1989). Classical models continue to be modified and improved, providing new insight into ecological processes and facilitating

improvements in management decisions and our capacity to conserve species and biodiversity (Sabo 2008; Guthery 2013; Sweka and Wainwright 2014; Forrester and Wittmer 2013). One-way population dynamics models can aid in management is through integration with predictive models of physical processes to provide a means of forecasting impacts of alternative management actions.

Modeling of the population dynamics of predators and their prey began in the early twentieth century when Lotka, Volterra, Nicholson, and Bailey proposed the first population models incorporating trophic interactions (Hassell 1978). These predator-prey models drew on the chemical law of mass action, setting population growth rates proportional to the product of the predator and prey densities (Berryman 1992; Anderson et al. 2005). This original formulation was expanded by incorporating elements such as logistic growth (Leslie 1948), predator functional responses (Holling 1959), and spatial heterogeneity (Hastings 1977). Less effort has been dedicated to integrating movement behavior into predator-prey models (but see Gerritsen and Strickler 1977; Werner and Anholt 1993), even though individual-based simulations demonstrate that animal movement patterns can be important in determining encounter rates between predators and prey (Scharf et al. 2006; Hein and McKinley 2013).

To incorporate movement patterns into an analytical model of prey survival, Anderson et al. (2005) drew upon the ideal gas model, which predicts the rate of encounter between gas particles (Hutchinson and Waser 2007). The ideal gas model has been applied to a diverse set of ecological processes, including models of conspecific interactions (van Schaik and Dunbar 1990; Harcourt and Greenberg 2001), gamete encounter rates (Farley 2002), and estimates of species density collected by moving observers (Skellern 1958). Among these diverse applications, it allows the incorporation of predator-prey behavior into estimates of encounter rates (e.g., Gerritsen and Strickler 1977). Anderson et al. (2005) uses the ideal gas model to derive the mean free-path length model. In short, it predicts that predator-prey encounter rates increase at both higher densities of predator and/or prey populations (as in traditional mass action models) *and with greater random movement* of either of the prey or predators. For a prey species with a migratory life-stage, where the prey is much more mobile relative to the predator, this model can be particularly useful in understanding the relative importance of the density of predators versus prey behavior along the migratory path. Additionally, it allows for the extrapolation from movement patterns to

survival expectations, which could be a valuable for evaluating the population-level impacts of altered migration behavior due to in-river modifications.

Here we apply the mean free-path length model to a heavily modified reach of the Sacramento River, California. The model is fit using telemetry data for out-migrating juvenile Chinook salmon (*Oncorhynchus tshawytscha*) recorded along a riverine portion of the migratory path. We estimate the mean free-path length traveled by a juvenile salmon before a predator encounter, as well as the random encounter speed (as defined by Anderson et al. 2005). By applying this model to a linear migratory route and over a finer spatial scale than has been previously done, we expand its applicability. We also highlight opportunities to use estimated model parameters for predictive modeling intended to integrate behavior into mortality estimates used in management planning.

Methods

Mean free-path length model

The mean free-path length model (Anderson et al. 2005) expands upon classic predator-prey models such as the Lotka-Volterra model and its derivatives (Berryman 1992). It describes survival probabilities of a prey species as a function of the density and detection range of predators as well as the movement patterns of predators and prey. From the model we estimate the mean length of an unconstrained (i.e. free) movement path that a prey organism is expected to travel before encountering a predator, referred to as the mean free-path length. Encounter rate is defined as any instance when the movement trajectories of predator and prey pass within the predator's consumption radius. From the model we also estimate the variance in the relative speed between the predator and the prey. In mathematical terms, these movements are quantified using the variation in velocity vectors around the mean vector. We will follow Anderson et al. (2005) and refer to this hereafter as the 'random' encounter speed, while acknowledging that these movements are likely not, in fact, random. More frequent encounters with predators are expected with greater random speeds of the prey relative to the predator. It is important to note that the magnitude of the random movement is determined by both predator and prey swimming behavior. For an ambush predator, the

relative movement is determined by the prey but for a predator that actively searches the environment the relative movement is determined by both individuals.

The model makes two biologically simplifying assumptions by 1) modeling predation as the only source of mortality in the system, and 2) assuming predators have a uniform distribution throughout the habitat. Violations of the assumption of uniform distribution are expected to have a small or non-significant impact on conclusions drawn from the model, because the model characterizes the *average* mean free-path length over all segments of the migratory route. Thus, a heterogeneous distribution of predators does not affect estimates of the average predator densities. For additional details on the derivation of this model see Anderson et al. (2005).

The general form of the mean free-path length model can be simplified for biological situations where prey migrate through a field of resident predators. In this circumstance, the average directional movements of the resident predators are much smaller than those of the migrating prey, allowing us to assume a mean directional predator velocity of zero and a mean directional prey velocity equal to the measured migration speed over a river segment. With these assumptions the model becomes

$$S = \exp\left(-\frac{1}{\lambda} \sqrt{x^2 + \omega^2 t^2}\right) \tag{1}$$

where S is survival, λ is the mean length of the unconstrained path traveled before a lethal predator encounter measured in km, and ω^2 is squared mean speed between the predator and prey measured in km/day. The relative behavior between the predator and prey is then characterized by the root mean squared speed between the predator and prey, i.e., ω . The directional migration distance of the prey between two fixed points is represented by x (km) and t is the time to cover that distance (days). This form is referred to as the XT model because survival depends on the distance x and the travel time t (Anderson et al. 2005). The mean free-path length parameter is $\lambda = 1 \pi \rho r^2$ where ρ is the average predator density and r is the encounter distance at which a predation event occurs.

To estimate parameters of the XT model using the survival and migration speeds from telemetered fish, the model can be converted to a linear form (Anderson et al. 2005) and fit with ordinary least squares regression. For parameter estimation,

regression parameters a and b are related to the model parameters as

$$\lambda = \frac{1}{\sqrt{a}} \quad \omega = \sqrt{\frac{b}{a}} \tag{2}$$

and the linear form of the XT model becomes

$$(\log S)^2 = ax^2 + bt^2 \tag{3}$$

This allows us to estimate parameters a and b , which can then be back-transformed into the biologically meaningful parameters λ and ω . Because neither λ nor ω can take on negative values, the linear model parameters a and b are also constrained to be positive. Therefore, we fit this linear model using a Bayesian framework to allow the use of priors that provide appropriate constraints. We modeled the a and b parameters with uniform priors $[0, 1]$, and modeled the error term using a half-Cauchy prior (location = 0, scale = 1). Models were fit with Hamiltonian Monte Carlo estimation in Stan, via the rethinking package (McElreath 2020) in the R statistical environment. Estimation was completed with four chains, each including 500 warm-up draws and 4000 post-warm-up draws. Successful convergence of models was evaluated by examining the trace plots for stationarity and mixing, and examining values of \hat{R} (Gelman and Rubin 1992).

Study reach

The lower Sacramento River is extensively channelized and controlled by levees and flood bypass channels. The study region was located downstream of the town of Knights Landing, California (river kilometer [rkm] 236.8; 38.800°N, -121.698°W) and continued past the city of Sacramento to Clarksburg, California (rkm 164.8; 38.435°N, -121.524°W). It encompassed the confluence of the Feather River at rkm 223 and the confluence of the American River at rkm 191 (Fig. 1). In extremely dry years tidal influence has been observed as far upstream as the Feather River confluence (Jackson and Paterson 1977), but during more common flow conditions tidal fluctuations are first detectable near the city of Sacramento. During the study, discharge was measured at two long-term environmental monitoring gauges, with one located above the study reach ('Colusa' rkm 326; 39.214°N, -122.000°W) and the other within the study reach, below the confluence of the Feather River with the Sacramento River ('Verona' rkm 221; 38.774°N, -121.598°W). Gauges were operated by US

Geologic Survey and California Department of Water Resources, and the data were accessed through the California Data Exchange Center (cdec.water.ca.gov). At the lower gauge ('Verona') during the water year of 2013 (WY2013), river discharge during the study period ranged from 297 to 1775 m³/s, decreasing from a large pulse event in mid-December (Fig. 2a). In the water year of 2014 (WY2014), river discharge at the same location ranged from 154 to 784 m³/s, encompassing three flow peaks in mid-February, early March, and early April (Fig. 2b). WY2013 was classified as a dry year, while WY2014 was classified as a critically dry year (State Water Resources Control Board 1999), yet both years had distinct peaks in river flow. For the purpose of this analysis, we considered 400 m³/s at the Verona gauge as the partition between high and low flow conditions.

Data collection

Parameters of the XT model were estimated for out-migrating juvenile Chinook salmon in the Sacramento River, using empirical data collected by acoustic telemetry during the winter of WY2013 and WY2014. Juvenile late-fall Chinook salmon were obtained from the Coleman National Fish Hatchery ($N_{WY13} = 614$, $N_{WY14} = 600$) and surgically implanted with ultrasonic tags. Fish above the minimum size threshold of 9.0 cm fork length were selected at random. The mean fork length of all tagged fish was 14.0 cm (SD = 1.7) and mean mass of 31.1 g (SD = 11.4). For those fish released under high and low flow conditions, the mean fork lengths were 13.7 cm (SD = 1.7) and 14.3 cm (SD = 1.6), respectively. Fish were fasted for 24 h prior to surgery, then anesthetized with an aqueous solution of 90 mg/L tricaine methanesulfonate (MS222). Upon reaching stage four anesthesia the fish were weighed, measured, and placed ventral-side up in a surgery cradle where they received a maintenance anesthetic dose of 30 mg/L MS222. A trained surgeon made a small incision into the peritoneal cavity and inserted a tag weighing 0.65 g (Vemco Ltd.; Model V5-1H, 180 kHz) before closing the incision with one or two interrupted sutures. After completion of surgery, fish were held in a small tank until they regained equilibrium, then were transferred to a holding tank for at least 24 h before release. Tags were programmed with a random pulse rate of 25–35 s to reduce tag collisions, resulting in an estimated tag-life of 50 d. They constituted a mean tag burden of 2.9% of fish mass (SD = 1.1%) in WY2013 and 2.1% (SD = 0.6%) in WY2014, following a 5% limit advised to prevent

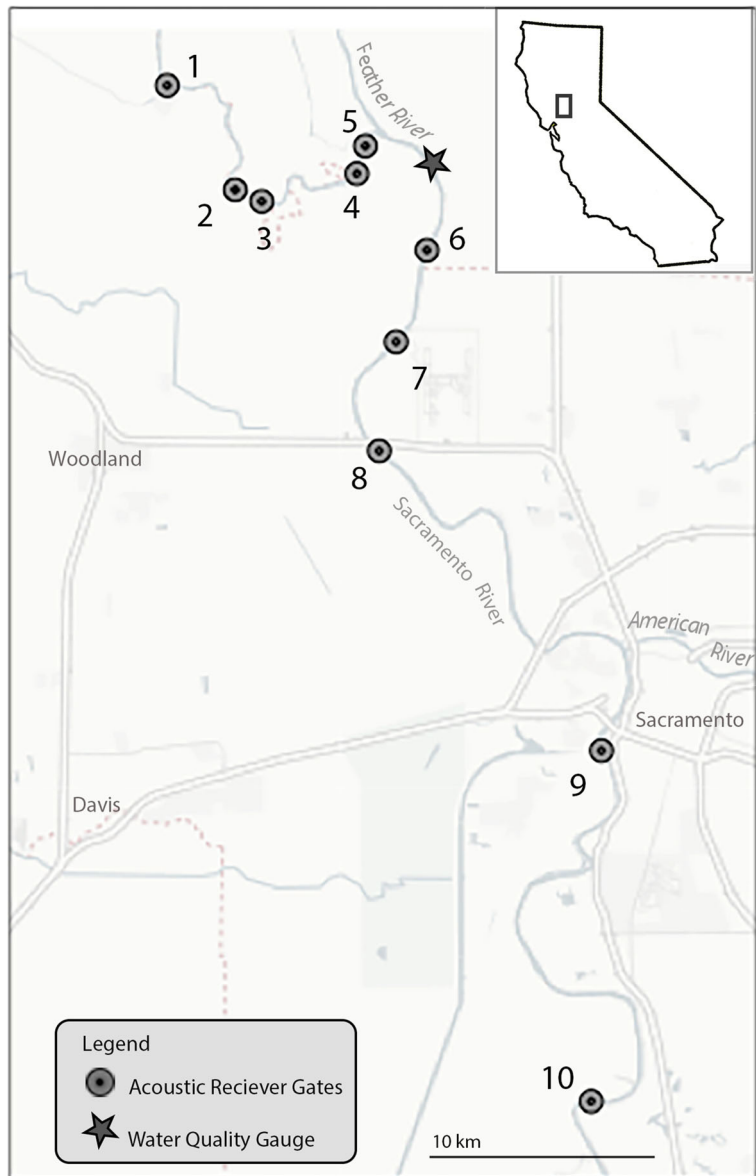
significant tag effects (Adams et al. 1998; Angela et al. 2004). In WY2013 fish were tagged in six groups of approximately 100 and released between December 2012 and March 2013. In WY2014 fish were tagged in four groups of 150 and released during February 2014 (see Appendix 1, Table 2 for details). The release site was located 6.2 km upstream of the study reach (38.853°N, -121.726°W) to allow a period of habituation to the riverine environment prior to entry to the receiver array.

Detections of the tagged out-migrants were obtained from an array of 10 gates created by 41 hydrophone receivers (Vemco Ltd., Model VR2W 180 kHz) with two to five receivers in each gate. The receivers covered a reach 74.3 km in length, located in the lower Sacramento River (Fig. 1). Significant river features (e.g., river confluences) and the quality of local acoustic environments were considered when determining gate locations, and the number of receivers needed at each gate to achieve high detection efficiency. The number and design of receivers within each gate was informed by prior range testing and by the width and depth of the local site. At most gates, four receivers were arranged in a square with two on each side of the river. When the river was wider than 150 m, a fifth receiver was placed in the center of the square. Receivers were affixed approximately 1 m above the river bed on rigid, custom-made mounts. The mounts were held in place with 41 kg weights attached to shore via stainless steel cables for retrieval purposes.

Data analysis

Before analysis, the detections of tagged Chinook out-migrants were filtered to remove false detections that can occur when multiple tags emit overlapping signals or when environmental conditions mimic acoustic tag signals. Tag detection histories were also examined to identify and remove tag detections received after the tagged juvenile Chinook had potentially been consumed by predatory fish. Possible predation events pose a common challenge in telemetry of prey species (Romine et al. 2014) and to our knowledge no solution has been prescribed when working only with detections of tag presence. We defined a likely predation event as any instance where a tag moved upstream against the current >1 km, and did not resume out-migratory behavior. This criterion assumes that juvenile salmon rarely move upstream (Steel et al. 2001), while mobile predators found in the Sacramento River often do (Kynard and Warner 1987; Harvey and Nakamoto

Fig. 1 Map of the study reach in the Central Valley of California. Gates of acoustic telemetry receivers, identified here by number, were deployed throughout 74.3 km of the lower Sacramento River, California. Tagged juvenile Chinook salmon from Coleman National Fish Hatchery were released above the study reach in the winters of water years 2013 and 2014, and subsequently detected during their out-migration. Within the study reach, river discharge and water quality were recorded at the ‘Verona’ gauge, indicated on the map with a star



1999). When upstream movement events were identified, the tag detection record was truncated at the point where the upstream movement began. This approach is similar to those used by other researchers conducting telemetric survival studies (Perry et al. 2010; Buchanan et al. 2013).

Prior to fitting the XT model, probabilities of survival through each reach of river between pairs of consecutive receiver gates (hereafter ‘inter-gate reach’) were estimated for each release group using Cormak-Jolly-Seber (CJS) estimation within the package ‘marked’ (Laake et al. 2013) in R (R Core Team 2020). Models allowed

detection probabilities to vary by receiver gate and by release group. Survival estimates and detection probabilities are presented in Appendix 2 (Tables 3 and 4). We examined the correlative relationships between survival within each inter-gate reach and the distance of the reaches, as well as mean passage time through the reaches. For high and low flow conditions, bivariate linear models were used to estimate the relationship between the log-transformed estimates of survival and distance traveled or mean travel time. Distance and travel time were centered and scaled to aid in comparison of the two predictors.

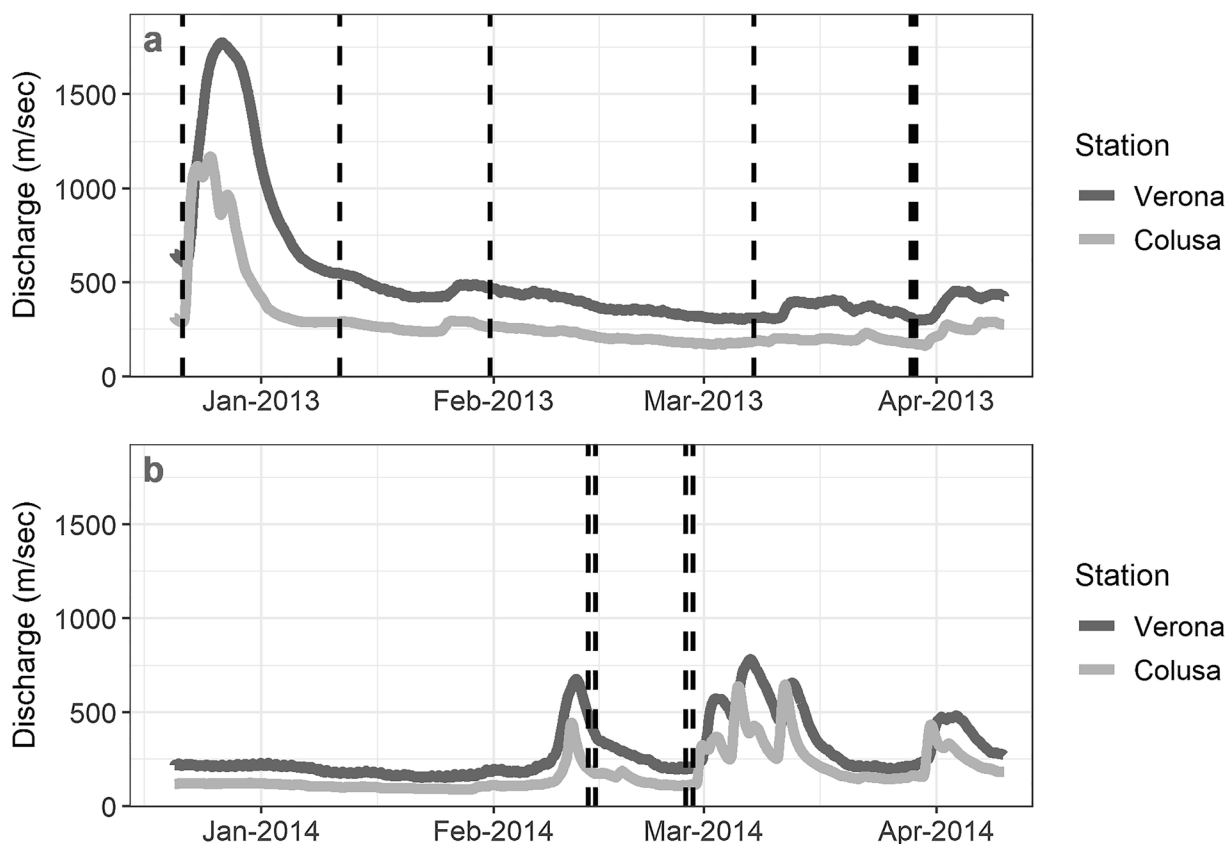


Fig. 2 River discharge during the study periods. Hydrograph of discharge (m^3/s) in the Sacramento River, California, measured at long-term gauging stations at Colusa above the study area (light gray line; 39.214°N , -122.000°W) and at Verona below the confluence of the Feather River (dark gray line; 38.774°N , -121.598°W). Hydrographs correspond with study periods during

water year 2013 (a) and water year 2014 (b). Vertical dotted lines indicate dates of releases of tagged juvenile Chinook salmon. Fish released at river discharges greater than $400 \text{ m}^3/\text{s}$ were considered as the high flow group, while those below that threshold were placed into the low flow group

The mean migration speed (distance traveled over mean group travel time) of each release group was calculated for the entire study reach (gate 1 to gate 10) as well as through each inter-gate reach. It is important to note that this method uses only surviving fish, and thus assumes the speed over ground of fish which did not survive was the same as those which did. An alternative method is to impute travel times for non-surviving fish (Perry et al. 2018). For the current analysis, we believe a simpler approach is reasonable because survival through the inter-gate reaches was high, and therefore even if survival was correlated with travel time the effect on the mean group speed should be small.

We also described differences in reach-specific survival and migration speeds by flow group. The effect of flow group on survival was evaluated by fitting nested CJS models with and without flow group as a covariate,

while allowing the detection probability to vary by both gate and release group. The resulting models were compared using AIC metrics to determine whether flow group contributes important explanatory value to the model. The effect of flow group on overall migration speed (Gate 1 to 10) was evaluated with a linear mixed model, using release group as a random effect.

To parameterize the XT model from the empirical telemetry dataset, we used the telemetered movement (reach distance, mean travel time) and CJS estimated survival metrics for each unique combination of inter-gate reach and release group, as described above. Then, using these three metrics, we fit the linear model (Eq. 3) with Bayesian methods to constrain the model parameters to be positive. We note that using the survival estimates from the CJS model in this way does not allow us to propagate uncertainty in the survival estimates

through to the linear model fitting, resulting in an underestimate of model variance. For the purposes of this work, we elected to remain consistent with the methods presented in Anderson et al. (2005), yet note that future methodological advances to propagate uncertainty would be valuable.

In the original work by Anderson et al. (2005), groups of fish were released in separate headwater streams and detected again at a shared site downstream, resulting in many unique reaches defined from the headwater release sites to the final detection location, with a variable proportion of the migratory route shared among release groups. Due to the single linear out-migration path considered in this study, and its relatively short distance as compared to the routes considered in Anderson et al. (2005), we elected to evaluate survival separately across consecutive reaches and among release groups. While this may retain elements of autocorrelation (non-independence of survival estimates), it is analogous to conducting mark-recapture studies to estimate survival across sequential captures of tagged individuals. To explore whether this non-independence may interact with the reach lengths to lead to spurious results, we also conducted a sensitivity analysis by fitting the model using five different reach definitions. All new inter-gate reach groupings provided similar results, suggesting the general results and conclusions don't change with changes in spatial resolution. See [Online Resource](#) for further details.

In addition to describing survival as a function of predator density and predator-prey movement patterns, the XT model allows us to describe the relationship between survival and prey migration speed. By replacing travel distance x with the product of migration speed and time Ut , Eq. (1) becomes

$$S = \exp\left(-\frac{x}{\lambda} \sqrt{1 + \left(\frac{\omega}{U}\right)^2}\right) \quad (4)$$

Based on Eq. (4), the relative importance of prey migration speed U depends on the random movement of the predators and prey represented by ω . The non-linear effect of the ratio U/ω on S is visualized as a curve with a positive slope (concave down), approaching an asymptotic level of survival when the directional migration speed U is much larger than the random speed ω ($U/\omega \gg 1$). The survival at the asymptote depends upon the mean free-path length λ and the migration distance x . Under asymptotic conditions, small changes in either U

or ω affect survival very little. However, as the ratio U/ω approaches one, small changes in either speed affect survival more strongly. Thus, after fitting the XT model with the telemetered movement data, we also explored the relationship between survival and the ratio of the median directional migration speed U (from gate 1 to gate 10) to the random speed ω as estimated from the model.

Results

Telemetry data

Of the 605 and 600 fish released in water years 2013 and 2014 respectively, 575 (95%) and 587 (98%) were detected by at least one receiver within the array. While the probability of detecting a tag at a given receiver gate fluctuated, the receiver gates had detection efficiencies greater than 0.90 during all but a few occasions (see Appendix 2, Table 4). At those receiver gates with lower detection probability, it appears that missing receivers or fluctuating environmental conditions contributed to temporarily impaired detection ability.

The process of filtering tag detections identified 45 (7.4%) instances in WY2013 where tags initially moved downstream in a manner typical for out-migrating Chinook salmon, but then reversed direction and moved upstream for distances between 1.3 and 72.0 km with a mean ground speed of 0.61 m/s (SD = 0.23). A majority (93%) of these instances occurred during the two releases at the end of March, coinciding with the annual upstream spawning movement of striped bass (*Morone saxatilis*) in the Sacramento River (Moyle 2002). It appears likely that the upstream portion of these tracks occurred after the juvenile salmon was consumed by a predatory fish, and thus these portions were removed from the analysis. Similarly, in WY2014 we identified 46 (7.7%) instances where tags moved upstream more than 1.3 km and never resumed out-migration. These tags moved upstream with a mean ground speed of 0.31 m/s (SD = 0.16), and were relatively uniformly distributed across the releases (Feb 12 to Feb 26, 2014).

Migration speed and survival

The XT model describes the relationship between survival, migration time, and migration distance. When these relationships were examined in bivariate linear regression with

standardized predictors, we saw that both time and distance had significant relationships with the log-transformed survival estimates (all $p < 0.001$), within both flow conditions showing stronger relationships between survival and distance than between survival and time (Fig. 3). In the high-flow releases, this difference was more pronounced ($\beta_{distance} = -0.90$, $SE = 0.06$; $\beta_{time} = -0.57$, $SE = 0.10$), whereas in the low flow releases the relationships between the two variables and survival were more similar ($\beta_{distance} = -0.92$, $SE = 0.07$; $\beta_{time} = -0.80$, $SE = 0.14$). For both flow conditions there was more variance in the relationship between survival and time ($R^2_{high-flow} = 0.44$, $R^2_{low-flow} = 0.43$) than in the relationship between survival and distance ($R^2_{high-flow} = 0.84$, $R^2_{low-flow} = 0.81$).

Partitioning the data into the high and low flow groups resulted in different travel times over the entire reach (gates 1–10), with a median travel time of 1.4 days (interquartile range: 1.3–1.7 days) for the high flow group and 2.7 days (interquartile range: 1.8–4.6 days) for the low flow group. The corresponding median migration speeds were 61 and 32 cm/s respectively. A linear mixed model constructed to evaluate differences in migration speed between flow groups indicated that migration speeds (cm/s) were significantly faster at higher flows ($\beta_{high-flow} = 23.4$, $SE = 6.5$, $p = 0.007$). In contrast, the CJS estimated survivals between gates 1–10 were similar at 0.69 ($SE = 0.02$) and 0.67 ($SE = 0.02$) for high and low flow groups respectively. Comparison of CJS models fit with and without flow group as a covariate showed this was not a valuable predictor for survival, with a slightly lower AIC score for the model without flow group ($\Delta AIC = 1.5$). Survival estimates for each inter-gate reach indicated that much of this mortality occurred in the lower reaches (downstream of gate 8).

XT model

Using empirical measurements of juvenile salmon movement speeds and survival probabilities, we estimated mean free-path lengths of 159 and 154 km under high and low flow conditions, respectively (Fig. 4a and Table 1). We estimated random encounter speeds of 2.3 and 3.5 cm/s under high and low flow conditions, respectively (Fig. 4b and Table 1). We also explored the ratio of downstream migration speed to the random encounter speed (U/ω), and saw differences between years (Fig. 5). The mean U/ω under high flows was 24.3 while the mean U/ω under low flows was only 9.1.

Discussion

The data set of telemetered juvenile salmon, released in two years and partitioned into high and low flow groups, revealed that travel time over the total study region (73.4 km) were different by a factor of two: 1.4 days at high flow versus 2.7 days at low flow. However, the survivals of the two groups were essentially equal at 0.68. These results present a challenge for classical survival models which predict survival exponentially declines with time. This conundrum is of importance because the paradigm that flow augmentation will increase juvenile salmon survival by decreasing travel time has a long and controversial history (Berggren and Filardo 1993; Williams and Matthews 1995). Resolving this disconnect between the flow-survival paradigm and new observations is important because efficient use of water and sufficient allocation of water to stressed fish populations are both critical objectives in water-limited environments such as the California Central Valley.

To this end, we note that our survival estimates for juvenile Chinook salmon in the lower Sacramento River are similar to findings for juvenile Chinook salmon in other large rivers along the west coast of North America. The survival rate ($S = 0.59$ per 100 km) is comparable, or slightly lower, than those estimated for survival of Chinook hatchery releases migrating through the Thompson-Fraser river system in British Columbia, Canada in three separate years (0.70, 0.58, 0.64 per 100 km; Welch et al. 2008) and for juvenile Chinook salmon migrating from multiple hatcheries to the tailrace of Lower Granite Dam in the Lower Snake River in the Pacific Northwest, USA (range: 0.77–0.86 per 100 km; Muir et al. 2001). It is important to note that the study region evaluated here covers only a portion of the Sacramento River, and other work in the watershed suggests this region generally has higher survival than reaches farther up-river or in the estuary (Michel et al. 2015; Henderson et al. 2019).

Additionally, as with this study, the flow-survival hypothesis is not consistently supported for migrating juvenile salmon in the Columbia River watershed (Miller and Sims 1984; Williams and Matthews 1995; Giorgi et al. 1997). Some studies have shown that flow alone has little effect on survival of juvenile Chinook during migration (e.g.: Zabel et al. 2008). However, in the Snake River, increased flow and corresponding decreased temperature were found to be correlated with increased survival of migratory fall Chinook salmon (Connor et al. 2003). Other studies have demonstrated

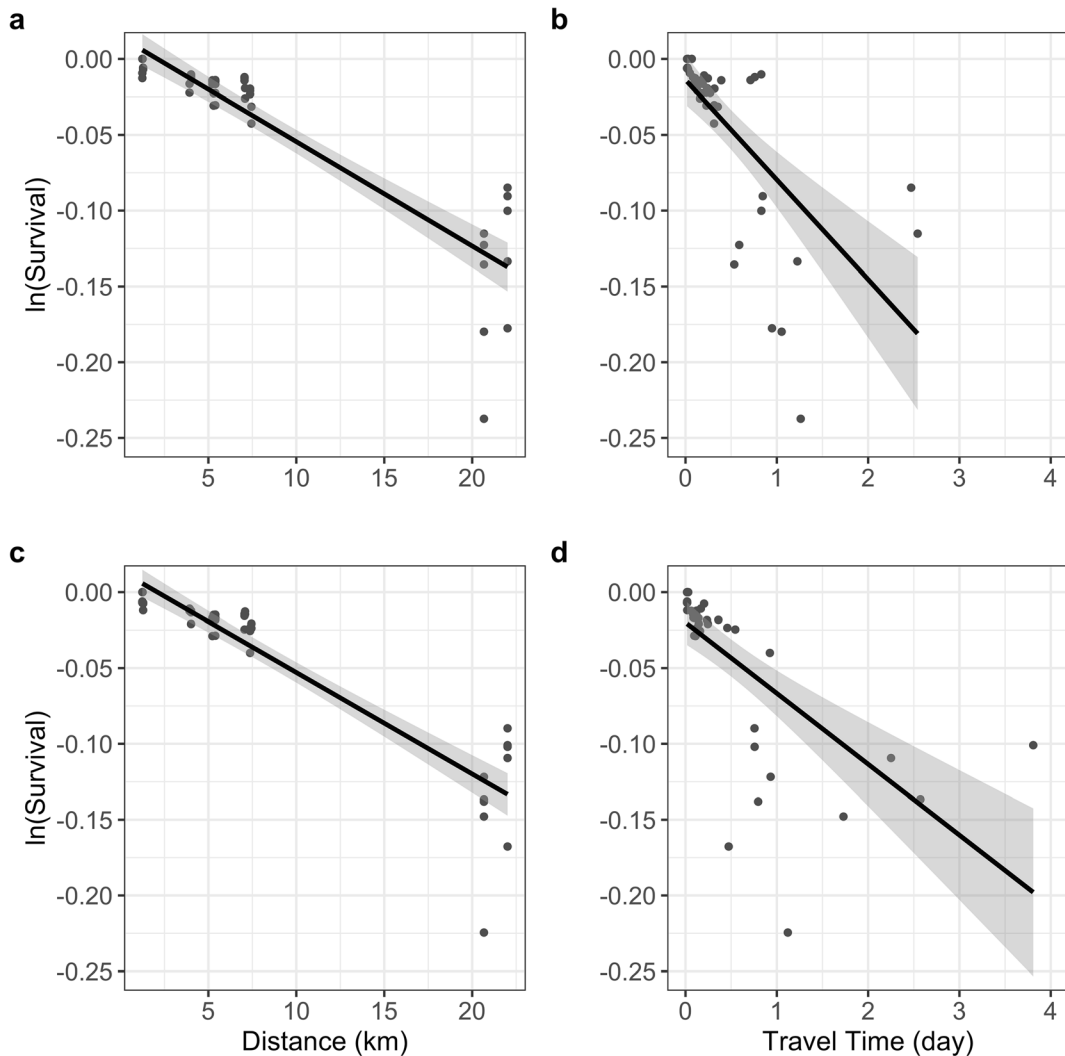


Fig. 3 Bivariate relationships between survival and migration distance (km) or survival and migration time (days) for the low flow group (**a, b**) and the high flow group (**c, d**). Survival is log transformed then standardized, with a mean of -0.042 and a standard deviation of 0.055 . Predicted relationship and 95%

confidence interval shown from a bivariate linear model. All slopes were significantly different from zero ($p < 0.01$). The sampling units are the unique combinations of release group and river reach (between consecutive receiver gates)

variability in flow-migration survival relationships (Smith et al. 2003; Courter et al. 2016).

When we compare the XT model parameter estimates from this study to those from Anderson et al. (2005) in the Lower Snake River, we see that the mean free-path lengths estimated for the Sacramento River, 154 and 159 km, are substantially shorter than those estimated in the Snake River, which ranged from 354 to 917 km. However, the random encounter velocities estimated in the Sacramento River, 2.3 and 3.5 cm/s under high and low flow conditions, respectively, are within the range of those estimated across multiple years in the Snake River

(0 to 9.9 cm/s). These parameter differences suggest that lower survival in the Sacramento River (this study and Perry et al. 2010), versus the Snake River (Muir et al. 2001) may be due to a greater density of predators rather than differences in salmon migratory behavior.

The XT model offers a possible explanation for the disconnect between migration survival, travel time, and flow by describing predator prey interactions in terms of the mean free-path length traveled by a migrating prey before encountering a predator as well as both the predator and prey movement behavior. When predators are relatively stationary and prey migrate directly through the

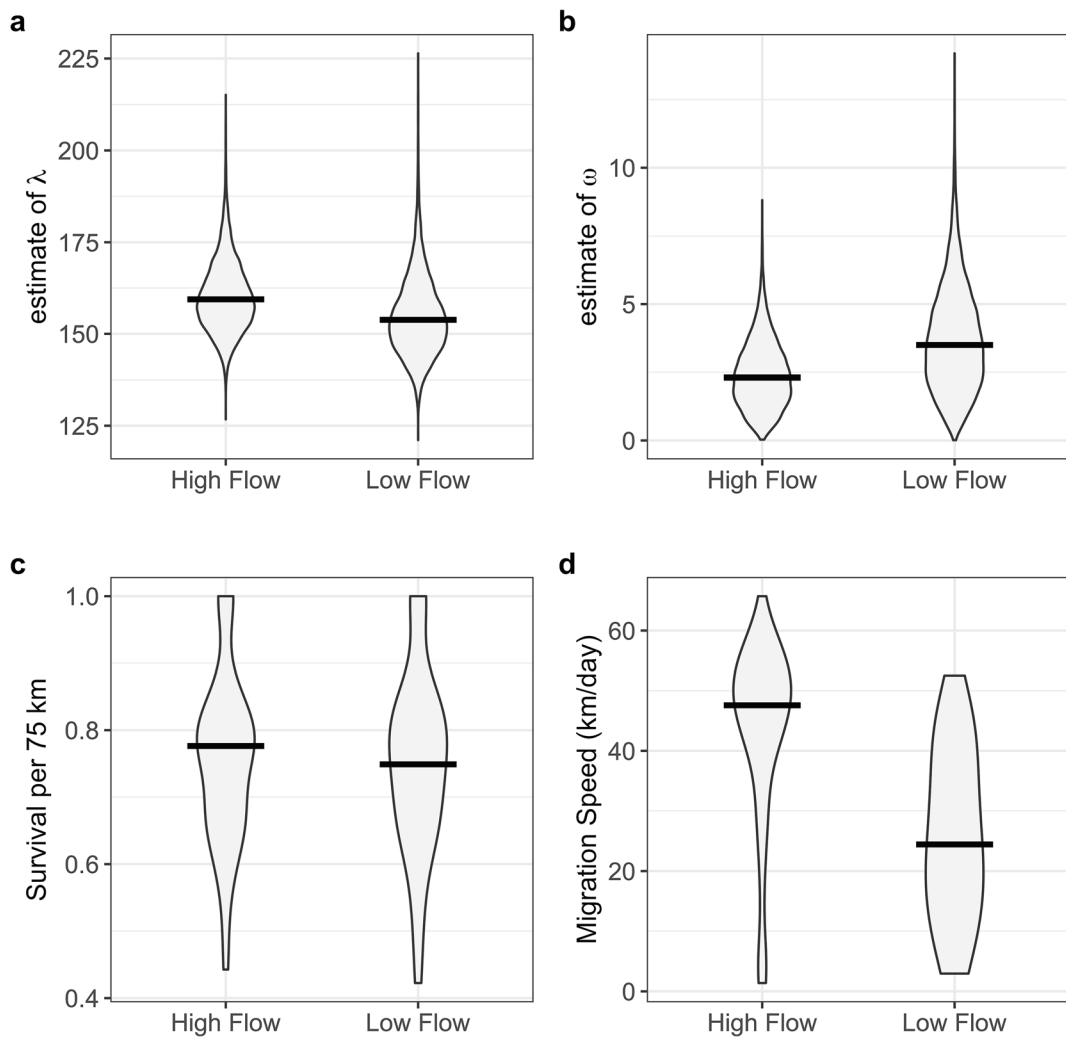


Fig. 4 Comparison of model parameters and associated confidence limits for the XT model, estimated for two years: Mean free-path length (λ) in km (a), and random encounter speed (ω) in cm/s (b). Posterior distributions of parameters are shown, with a thick line indicating maximum a priori estimates. To provide context,

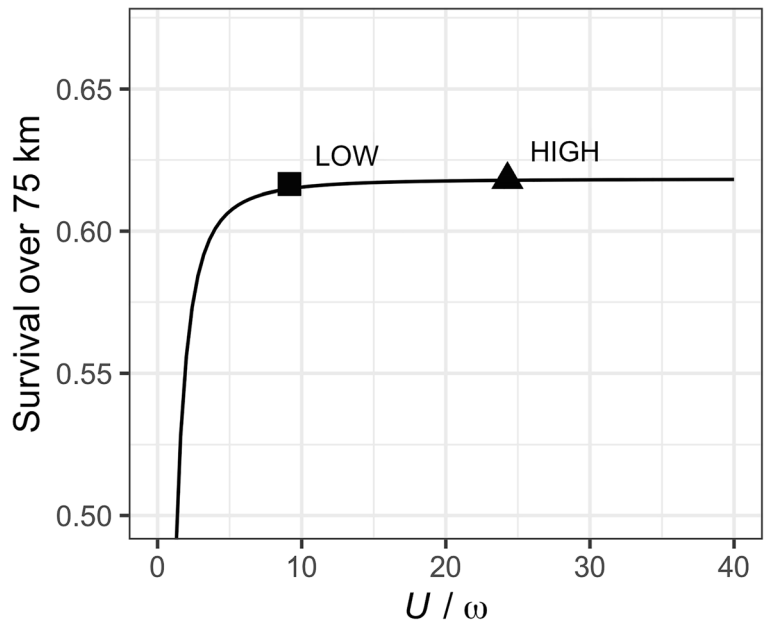
we also show medians (thick line) and distributions of survival (as estimated per inter-gate reach per release) standardized to the distance of 75 km (c), and migration speed over ground from Gates 1 to 10 (d)

Table 1 Mean free-path length model parameter estimates and confidence limits. Values estimated from survival and migration speeds calculated for each release and each inter-gate reach of telemetered juvenile Chinook salmon. Mean free-path length (λ) in km. Random encounter speed (ω) in cm/s. Upper (ucl) and lower (lcl) confidence limits are calculated as the 90% density

region of the Bayesian posterior distributions. Mean (SD) flow and median migration speeds are also shown for reference. Flows were measured at the Verona gauge when each group was released, and averaged across five releases within a flow group. Migration speeds are calculated using travel times of all fish from Gate 1 to Gate 10

Flow Condition	Mean free-path length (λ)			Random encounter speed (ω)			Mean flow (m ³ /s)	Median migration speed (cm/s)
	λ_{lcl}	λ	λ_{ucl}	ω_{lcl}	ω	ω_{ucl}		
High	146	159	177	0.6	2.3	5.0	562 (82)	60.7
Low	139	154	174	0.9	3.5	7.6	240 (110)	32.0

Fig. 5 Survival estimates as a function of the mean migration speed U and random encounter speed ω . The curve indicates the non-linear relationship between survival and the ratio of U/ω predicted by the XT model. The asymptotic value of survival is a function of the mean free path length and the distance traveled – this figure is plotted using the predicted mean free-path length (156 km) and approximate length of the study reach (75 km). The points indicate the location along the curve corresponding with the median observed migration speed U and ω for each flow group



river, the rate of encounter depends on the distance between predators. Thus, survival over a fixed distance is independent of the mean migration velocity U , and thus also travel time T , of the prey. The XT model predicts that as long as the relative random speed between predator and prey is small, as expressed by $U/\omega \gg 1$, then as shown in Fig. 5 survival is independent of T , or U , and therefore should also be independent of flow because T is shorter in a high flow environment. However, if flow also affects the random encounter speed, a different response is possible. The model estimated parameters for our study indicate that as flow decreased, ω increased by 50% and U decreased by 50%, resulting in the ratio U/ω dropping from 24 in the high flow conditions to 9 in the low flow conditions. This shift is significant because the upper threshold for the region of declining survival is $U/\omega < 10$ (Fig. 5). So in low flow condition the effect of flow on survival was at the threshold of being substantial.

The XT model describes this threshold-like response as a function of both predator foraging and prey migration behaviors; with decreasing flows, predator and prey random speeds might increase while downstream prey migration speed decreases, reducing U/ω . To the best of our knowledge, this dual effect of flow has not been considered. To explore the interactions, assume the prey random speed does not change with flow yet predator feeding behaviors are determined by the energetic cost of foraging, and thus their movement patterns may vary with flow. The prevailing theory suggests that refuge foraging,

such as ambushing prey from a velocity refuge, should dominate in high flows while freestream foraging, in which the predator swims in the flow, should dominate in low flows (Ross and Winterhalder 2015). In the lower reaches of the Sacramento River (the study region), the habitat is channelized with a relatively smooth bottom, such that the primary velocity refuge may be the bottom boundary layer. Observations from the fishing community support the idea that in the tidal regions of the river striped bass, a significant predator of juvenile Chinook salmon, follow the theory of energetic efficiency (personal communication, Jack Naves, contributor to FishSniffer.com); during ebb tides the predators are caught frequently near the bottom boundary layer while during flood tides they are caught higher in the water column. Due to the limited refuge availability in this system, the distinction between refuge and freestream zones might be minor and thus increases in ω at low flow could reflect an increase in the predators' search speed for prey. Increases in ω at low river flows (not tidal cycles) may also represent a switch in local predator community, as conditions become favorable for species specializing in freestream search versus refuge foraging strategies.

At low flow, an increase in ω might also be attributed to changes in the prey migration behavior. We assume lower flow conditions reduce the passive transport speed of migrating juveniles, contributing to the 50% decrease in mean migration velocity. When passive transport is

reduced, a consistent level of random movement behavior will result in a greater relative random encounter speed, potentially accounting for the 50% increase in random encounter velocity we saw in this study. Similar responses have been documented for actively swimming larval fish (Codling et al. 2004; Glas et al. 2017), and juvenile salmon (Morrice et al. 2020). However, it is important to note that in our study the lower flow conditions all occurred later in the migration season, corresponded with warmer water temperatures, and were experienced by larger fish (see Appendix 2). These additional variables may also be driving the change in movement pattern.

Because the data and model do not resolve the individual effects of flow on predators and prey, we are confined to three essential points. First, flow can change both the prey and predator behaviors in complex ways. Second, these changes did not significantly affect fish survival in migration, and third due to the relationship of survival and the ratio U/ω we expect survival would dramatically decrease at some flow slightly below the low flow conditions observed in this study.

In addition to shedding light on the mechanisms of predation during migration, the XT model may have strategic use as a tool for management planning. Physical changes to river corridors can have indirect effects on migration survival. It is becoming more common for extensive hydraulic modeling to be conducted prior to the implementation of major in-river structural alterations, as these alterations can change hydrodynamic fields and resulting advection of migrating fishes. Parameters from the XT model could allow the translation of fish behavior models, build upon high resolution hydrodynamic models (Goodwin et al. 2006), into estimates of survival in areas of interest. When used in this context it would be important to note the inability to propagate uncertainty from survival estimations into the XT model, and thus uncertainty in the parameter estimates may be underestimated. Even with this caveat, the XT model may provide managers with estimated relative survival benefits, allowing evaluation of alternative actions.

In summary, the XT model incorporates prey movement patterns into a classic predator-prey models. Due to the biological basis of the model, its parameters can potentially suggest when certain management actions, such as managed flow releases or structural alterations, might be most effective in improving migratory survival. We also find that the model parameters are relatively robust to variability in the environment, in particular the

mean free-path length. Thus, we suggest parameters estimated using the existing data may provide a first order extrapolation to broadly similar conditions in other years. We emphasize that, as is implicit in the model, different responses of the predators and prey to flow can produce highly nonlinear responses of survival to flow. This nonlinearity and its threshold-like nature is implicit its model's name; survival depends on distance traveled, X , in linear systems such as rivers and on residence time T in oscillatory systems such as estuaries. Furthermore, we anticipate the transition between responses also depends on the foraging strategies of predators in the environments. Thus, while the XT model introduces additional dimensions and uncertainty in river management, it offers an intuitive and relatively simple framework in which to view possible outcomes of management actions from the river continuum to the estuary.

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Authors' contributions B.M., A.S., and D.S. oversaw and assisted in data collection. D.S. conceived the original idea. A.S. conducted the data processing, analysis, and drafted the manuscript. J.A. provided extensive review of and additions to the manuscript. All authors discussed the results and contributed to the final manuscript.

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Compliance with ethical standards

Conflicts of interest/completing interests The authors have no relevant financial or non-financial interests to disclose.

Ethical approval All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted, as authorized by the Institutional Animal Care and Use Committee, UC Davis, protocol number 17208.

Appendix 1

Six groups of acoustically tagged Chinook salmon were released into the Sacramento River, California across two study years. Fish tracks were truncated if movement patterns indicated predation of tagged smolt; detections after initiation of a prolonged upstream movement (>1 km) were removed. Long-term environmental data

obtained from monitoring gauges located above study reach, termed ‘Colusa’ (39.214°N, –122.000°W), and within study reach below confluence with Feather River, termed ‘Verona’ (38.774°N, – 121.598°W). Release groups were classified into a high flow group if the mean discharge at Verona upon release was >400 m³/s. Water temperature was recorded at Verona.

Table 2 Release information for acoustically tagged juvenile Chinook salmon

Water Year	Release group	Flow group	Release date	Mean discharge (m ³ /s) @ Colusa	Mean discharge (m ³ /s) @ Verona	Mean water temp. (°C)	N release	N alive at Gate 1	N truncated tracks
2013	1	High	12/20/2012	331.3	662.6	8.2	94	76	0
	2	High	1/10/2013	288.8	552.2	7.9	100	99	0
	3	High	1/30/2013	269.0	484.2	9.1	100	97	1
	4	Low	3/6/2013	181.8	305.8	12.3	100	94	2
	5	Low	3/27/2013	181.2	331.3	15.0	108	107	15
	6	Low	3/28/2013	179.0	322.8	15.7	102	100	27
2014	1	High	2/12/2014	258.8	628.6	12.3	150	148	31
	2	High	2/13/2014	201.0	484.2	12.9	150	146	37
	3	Low	2/25/2014	111.3	119.6	14.3	150	148	22
	4	Low	2/26/2014	111.6	119.1	14.0	150	143	12

Appendix 2

Survival of telemetered juvenile Chinook salmon (Table 3), and detection efficiency of acoustic receiver

gates (Table 4), and associated standard errors. Salmon were released in multiple groups 6.2 km upstream of the initial receiver gate (Gate 1). Boldface indicates detection efficiency below 0.90.

Table 3 Survival (SE) from Cormack-Jolly-Seber estimations

Water Year	Release Group	Flow Condition	Release Date	Survival (SE)									
				Gate 2	Gate 3	Gate 4	Gate 5	Gate 6	Gate 7	Gate 8	Gate 9	Gate 10	
2013	1	High	12/20/2012	0.98 (0.06)	1.00 (0.00)	0.97 (0.07)	0.99 (0.03)	0.96 (0.09)	0.98 (0.05)	0.97 (0.08)	0.80 (0.41)	0.85 (0.33)	
	2	High	1/10/2013	0.98 (0.21)	1.00 (0.00)	0.98 (0.24)	0.99 (0.10)	0.97 (0.33)	0.99 (0.18)	0.98 (0.23)	0.86 (1.59)	0.90 (1.25)	
	3	High	1/30/2013	0.99 (0.06)	1.00 (0.00)	0.98 (0.08)	0.99 (0.03)	0.98 (0.10)	0.99 (0.06)	0.98 (0.07)	0.87 (0.49)	0.90 (0.39)	
	4	Low	3/6/2013	0.99 (0.03)	1.00 (0.00)	0.99 (0.04)	0.99 (0.02)	0.98 (0.05)	0.99 (0.03)	0.99 (0.04)	0.89 (0.29)	0.92 (0.22)	
	5	Low	3/27/2013	0.99 (0.03)	1.00 (0.00)	0.99 (0.04)	0.99 (0.02)	0.98 (0.05)	0.99 (0.03)	0.99 (0.04)	0.88 (0.28)	0.91 (0.21)	
	6	Low	3/28/2013	0.99 (0.02)	1.00 (0.00)	0.98 (0.03)	0.99 (0.01)	0.98 (0.04)	0.99 (0.02)	0.98 (0.04)	0.87 (0.21)	0.90 (0.16)	
2014	1	High	2/12/2014	0.99 (0.04)	1.00 (0.00)	0.99 (0.05)	0.99 (0.02)	0.98 (0.06)	0.99 (0.03)	0.99 (0.04)	0.89 (0.30)	0.91 (0.24)	
	2	High	2/13/2014	0.97 (0.06)	1.00 (0.00)	0.97 (0.07)	0.99 (0.03)	0.96 (0.10)	0.98 (0.05)	0.97 (0.09)	0.79 (0.45)	0.84 (0.36)	
	3	Low	2/25/2014	0.98 (0.05)	1.00 (0.00)	0.98 (0.06)	0.99 (0.02)	0.97 (0.08)	0.98 (0.04)	0.98 (0.07)	0.84 (0.38)	0.87 (0.30)	
	4	Low	2/26/2014	0.99 (0.03)	1.00 (0.00)	0.98 (0.04)	0.99 (0.02)	0.98 (0.05)	0.99 (0.03)	0.98 (0.05)	0.87 (0.28)	0.90 (0.22)	

Table 4 Detection efficiency (SE) from Cormack-Jolly-Seber estimations

Water Year	Release Group	Flow Condition	Release Date	Detection Efficiency (SE)									
				Gate 2	Gate 3	Gate 4	Gate 5	Gate 6	Gate 7	Gate 8	Gate 9	Gate 10	
2013	1	High	12/20/2012	1.00 (0.00)	0.99 (0.04)	1.00 (0.01)	0.99 (0.07)	0.97 (0.22)	0.94 (0.35)	0.96 (0.27)	0.99 (0.05)	0.99 (0.05)	
	2	High	1/10/2013	1.00 (0.00)	0.98 (0.14)	0.99 (0.04)	0.96 (0.24)	0.88 (0.72)	0.81 (1.09)	0.86 (0.81)	0.97 (0.18)	0.96 (0.29)	
	3	High	1/30/2013	1.00 (0.00)	0.99 (0.03)	1.00 (0.01)	0.98 (0.05)	0.93 (0.16)	0.88 (0.27)	0.91 (0.18)	0.98 (0.03)	0.98 (0.08)	
	4	Low	3/6/2013	1.00 (0.00)	1.00 (0.02)	1.00 (0.00)	0.99 (0.03)	0.98 (0.08)	0.97 (0.14)	0.98 (0.1)	1.00 (0.02)	1.00 (0.02)	
	5	Low	3/27/2013	1.00 (0.00)	1.00 (0.01)	1.00 (0.00)	1.00 (0.02)	0.99 (0.05)	0.99 (0.09)	0.99 (0.06)	1.00 (0.01)	1.00 (0.02)	
	6	Low	3/28/2013	1.00 (0.00)	1.00 (0.01)	1.00 (0.00)	1.00 (0.02)	0.99 (0.06)	0.98 (0.11)	0.98 (0.07)	1.00 (0.01)	1.00 (0.02)	
2014	1	High	2/12/2014	1.00 (0.00)	0.99 (0.07)	1.00 (0.02)	0.98 (0.12)	0.94 (0.37)	0.89 (0.57)	0.92 (0.44)	0.99 (0.1)	0.98 (0.08)	
	2	High	2/13/2014	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	
	3	Low	2/25/2014	1.00 (0.00)	1.00 (0.03)	1.00 (0.01)	0.99 (0.05)	0.98 (0.14)	0.96 (0.23)	0.97 (0.17)	0.99 (0.04)	0.99 (0.03)	
	4	Low	2/26/2014	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	0.99 (0.01)	0.98 (0.02)	0.99 (0.02)	1.00 (0.00)	1.00 (0.00)	

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