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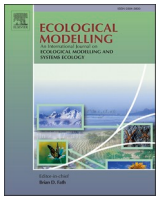

An integrated analysis for estimation of survival, growth, and movement of unmarked juvenile anadromous fish

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ABSTRACT

Managers invest substantial resources to promote recovery of declining anadromous fish stocks. Recovery strategies are manifold and often include management actions intended to stimulate somatic growth, increase in-river survival, and motivate juvenile outmigration during favorable environmental conditions. Evaluating the efficacy of these management actions is difficult, however, because monitoring data that explicitly track individuals from egg deposition to juvenile outmigration are typically lacking. We developed an integrated population model that links two different and often collected types of anadromous fish monitoring data: spawning ground surveys and rotary screw trap juvenile catch data. The integrated model accounts for incomplete detection and uses the two sources of data to estimate juvenile demographic parameters in a multistate framework. We evaluated the model's performance using simulated data under a range of conditions typically encountered in similar surveys. Simulation results indicated that the model estimated juvenile survival, growth, and movement with no-to-minimal bias (i.e., $\geq$ 50 % of simulations $\pm$ 0–0.05). As an example case study, we fit the model to empirical fall-run Chinook Salmon (*Oncorhynchus tshawytscha*) monitoring data collected in California's Central Valley, U.S.A. In doing so, we evaluated the influence of environmental conditions (e.g., discharge, water temperature) and habitat availability on juvenile demographic rates. We demonstrated that through our integrated approach we could estimate state transition probabilities that are typically inestimable for naturally produced, unmarked juvenile fish when using traditional statistical approaches to analyze these types of monitoring data. Furthermore, the structure of our model can serve as a useful foundation for decision-support models within adaptive management programs by directly linking management actions, decision-support-model predictions, and monitoring.

1. Introduction

Managers invest substantial resources to promote recovery of at-risk fish and wildlife species (Mangin et al., 2018). Ecological systems, however, are inherently complex and dynamic, and regularly require managers to make recurrent decisions with incomplete knowledge concerning how these systems might respond to management actions (Regan et al., 2002; Runge, 2013). In such cases, adaptive management, which is a special case of structured decision making, can be used by managers to add structure and transparency to a decision-making process (Clemen, 1996; Williams et al., 2002, 2011; Conroy and Peterson, 2013), reduce uncertainty (i.e., learning by doing; Walters and Holling, 1990), and, in turn, improve future management decision making (Mattsson et al., 2018). Following the adaptive management framework, competing hypotheses related to system dynamics are incorporated using alternative quantitative models, and the support for each hypothesis or model is evaluated by confronting model predictions with monitoring data following the implementation of management actions (Holling, 1978; Walters, 1986; Williams et al., 2002; Nichols et al., 2007; Williams, 2011; Conroy and Peterson, 2013; Mattsson et al., 2018). Managers implementing adaptive management thus require a targeted monitoring program in place that can provide a continuous stream of information on the state of the system being managed (Nichols and Williams, 2006). In practice, monitoring programs needed to compare

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the outcomes of management actions measure responses that are often coarser than decision-support model (DSM) predictions, which complicates the ability to confront model predictions with monitoring data (Nichols and Williams, 2006; Norton and Reckhow, 2008; Lyons et al., 2010; Larson et al., 2013; Jacobsen et al., 2015; Colvin et al., 2018; Williams and Brown, 2018). Importantly, this tends to lead to slower learning.

This monitoring-modeling mismatch is typified in California's Central Valley, where large-scale restoration efforts are ongoing to recover declining Chinook salmon (*Oncorhynchus tshawytscha*) stocks (Merz et al., 2013). The current management strategy is largely focused on manipulating conditions in freshwater environments (e.g., increase or enhance spawning and rearing habitats, implementing pulse flows, reducing predator contact points) aimed at increasing the number of naturally produced adult anadromous fishes in the Central Valley (Central Valley Project Improvement Act [CVPIA], 1992). Since 2013, a group of stakeholders known as the Science Integration Team (SIT) have regularly met to participate in the structured decision-making process to identify management objectives and candidate actions, develop DSMs, and evaluate restoration strategies to help inform decisions made by the U.S. Bureau of Reclamation (USBR) and U.S. Fish and Wildlife Service (USFWS). Peterson and Duarte (2020) describe the Chinook salmon DSMs developed by the SIT and the approach the SIT used to prioritize restoration actions and information needs that ultimately informed the implementing agencies' near-term restoration strategy. Importantly, they found that DSM predictions, and therefore the perceived optimal management actions, were heavily influenced by assumptions regarding juvenile growth, survival, and movement. This finding is consistent with other systems that use DSMs to evaluate tradeoffs in management actions for anadromous fishes (Peterson et al., 2022; Beechie et al., 2023; Chen et al., 2023).

Thus, a need is evident for a reliable, cost-efficient method to estimate demographic rates for naturally produced juvenile Chinook salmon that can be integrated into adaptive management frameworks to reduce uncertainty and improve management decision making. However, monitoring data that explicitly track naturally produced individuals from egg deposition to juvenile outmigration are often cost-prohibitive and difficult to obtain (Merz et al., 2013; Payton and Som, 2021). Tagged hatchery fish are often used as a proxy for naturally produced fish (Bellinger et al., 2015; Goertler et al., 2016). Yet, hatchery fish are known to differ substantially from their wild counterparts in terms of juvenile survival, morphology, and behavior (Taylor, 1986; Berejikian, 1995; Hill et al., 2006; Wessel et al., 2006; Tiffan and Connor, 2011; Beamish et al., 2012; Brown et al., 2013; Christie et al., 2016; Salvanes, 2017; Pinter et al., 2018). Population monitoring of naturally produced Chinook salmon in the Central Valley has focused on three separate efforts: (1) rotary screw trap deployments to estimate outmigrating juvenile fish abundances, sizes, and timing of outmigration; (2) trawl surveys to estimate outmigrating juvenile fish abundances, sizes, and timing as they transition into the San Francisco Bay-Delta; and (3) spawning ground surveys to estimate adult escapement and in some locations, pre-spawn mortality and spawning adult sex ratios. Although these data provide information on changes to fish populations following implementation of management actions, there is not a direct link between these population metrics and the parameters of interest (e.g., growth, survival, and movement).

We therefore developed a new parameterization of an integrated population model that links spawning ground survey data and juvenile rotary screw trap capture data to estimate juvenile salmon demographic parameters of interest. Our objectives were to (1) describe the structure and assumptions of our model framework; (2) evaluate the model adequacy by fitting it to simulated data under a range of environmental and habitat conditions; and (3) provide an example application by fitting the model to empirical Chinook salmon monitoring data collected in California's Central Valley.

2. Methods

2.1. Model description

The model tracks individuals from egg deposition to juveniles leaving a stream segment and assumes spawning and juvenile outmigration occur over multiple months. Furthermore, to match the SIT's Chinook salmon DSMs (i.e., Peterson and Duarte, 2020), the model operates at a monthly time step, incorporates three size classes for juvenile fish, and assumes all surviving juveniles in the last month outmigrate. However, these settings can easily be modified to match other use cases. The model relies on the availability of rotary screw trap capture data with sufficient capture efficiency trials to track changes in juvenile abundances by month and size class. The model relies on spawning ground survey data to estimate adult returns, sex ratios, and prespawn mortality. Furthermore, the model requires information on redd size, fecundity (i.e., the number of eggs per redd), egg-to-fry survival, and spawning habitat availability. The model assumes transitions from the three size classes in each month are instantaneous; that transition probabilities are only related to the state at time t; that transition probabilities are static or that variation in these parameters can be captured with the use of covariate information; that emigration (and death) is permanent; and that growth is unidirectional (i.e., big fish cannot become medium-sized fish).

The integrated model is comprised of a juvenile production submodel, a juvenile outmigrant submodel, and the integration of these submodels (Fig. 1). The juvenile production submodel uses adult carcass counts, estimated sex ratios, and estimated prespawn mortality to calculate the number of adult females that potentially produced viable redds. Notably, prespawn mortality occurs when adult Chinook salmon reach the spawning grounds but perish before reproducing (Bowerman et al., 2016). The model considers superimposition (i.e., when late spawners construct their redds on top of previously constructed redds; Merz et al., 2013; Bowerman et al., 2016) by truncating the estimated redds based on the availability of spawning habitat and the assumed redd size. Finally, the submodel estimates juvenile production as the product of the number of viable redds, the assumed fecundity, and the assumed egg-to-fry survival. The juvenile outmigrant submodel estimates juvenile outmigrant abundances based on the rotary screw trap catch data and the estimated trap efficiencies using a state-space model. The model then integrates these submodels using a multistate framework, where individual fish transition based on survival, growth, and

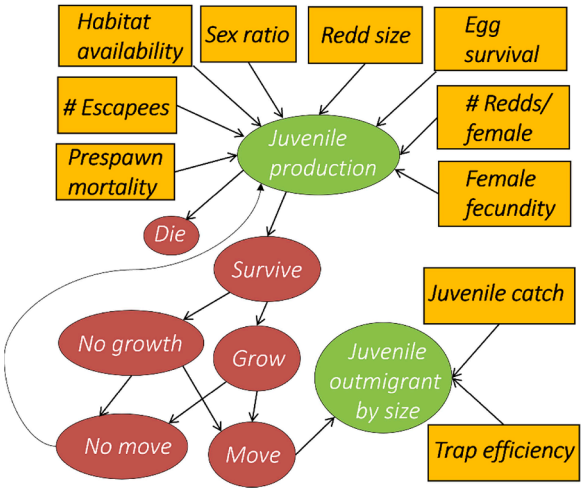

Fig. 1. Conceptual diagram of the integrated population model showing data needed (yellow boxes), the estimated transition probabilities (red ellipses), and the juvenile production submodel (where the model starts) and juvenile outmigrant submodel (green ellipses). Temperature, discharge, and habitat availability can be included as covariates for trap efficiency, survival, and growth nodes.

then movement each month. The submodels and their integration are described in more detail below.

2.1.1. Juvenile production submodel

In the juvenile production submodel (which is the starting point for the model), we assumed adult escapement, i.e., adults migrating from the Pacific Ocean, were Poisson distributed each year (t) because carcass surveys were count data.

$$escapees_t \sim Poisson(\#\ adult\ returns_t) \tag{1}$$

We calculated the number of redds each year as the minimum of either the number of surviving adult females on the spawning grounds or the maximum possible number of redds limited by spawning habitat availability and redd size.

$$redds_t = \min(\ ((escapees_t \times sex\ ratio_t),\ spawning\ habitat_t \div redd\ size), 0)\ \times\ (1 - prespawn\ mortality_t) \tag{2}$$

The total number of juveniles produced was then a product of the number of redds, fecundity, and egg survival rate.

$$N_{juveniles,\ t} = redds_t \times fecundity \times egg\ survival \tag{3}$$

2.1.2. Juvenile outmigrant submodel

We used a state-space model for the juvenile outmigrants submodel. Here, we used the Poisson approximation of a binomial process due to the very large number of juveniles produced. Catch data for month (i) and year (t) were Poisson distributed, i.e., count data, with a mean as the product of the number of fish of a given size class (out_{size}) and monthly trap efficiency ($p_{realized}$):

$$Catch_{size\ i,\ t} \sim Poisson(out_{size\ i,\ t} \times p_{realized\ i,t}) \tag{4}$$

where efficiency trial data are used to estimate monthly trap efficiency as:

$$p_{realized\ i,\ t} = p_{i,t} \times proportion\ monitored_{i,t} \tag{5}$$

where p is the daily trap efficiency for tagged fish at the screw trap and *proportion monitored* is the proportion of the month that the trap was open and operational.

We assumed the number of recaptures of tagged fish at the rotary screw trap came from a binomial distribution, i.e., number of successes in n trials as:

$$Number\ of\ recaptures_{i,\ t} \sim Binomial(p_{i,\ t}, Number\ of\ tagged\ fish\ released_{i,t}) \tag{6}$$

Similar to all other rotary screw trap estimators, this submodel assumes that fish outmigration during days monitored are representative of days not monitored, fish markings are not lost or overlooked when trapping, and traps are monitored long enough for all marked fish to outmigrate to accurately estimate trap efficiencies.

2.1.3. Integrated population model

We integrated the juvenile production and juvenile outmigrant submodels to estimate survival ϕ, movement ψ, and growth γ (Table 1). We used multinomial logistic regression to model monthly growth transitions for small fish, which allowed them to transition to medium and large fish or stay the same size class. Furthermore, we used logistic regression to model monthly growth transitions for medium fish, which allowed them to transition to large fish or stay the same size class. Fish then transition from small to medium, small to large, or medium to large, or stay the same size and then either outmigrate (move), stay in the natal tributary (not move), or die with associated probabilities (Table 1). For example, the probability of small-sized fish that grew to medium and stayed in the natal tributary at time $t + 1$ is the probability small fish survive × (1 - the probability small fish move) × the probability small fish transition to medium-sized fish (Table 1). We used logistic regression to model monthly survival and movement probabilities for the three size classes.

2.2. Model evaluation

We conducted simulations to evaluate the accuracy of our model. We simulated juvenile production and outmigrant rotary screw trap data for one season (i.e., 6 months) at high and low values for seven sets of parameters in the model. Each scenario was simulated for 250 iterations resulting in 32,000 simulated datasets to evaluate our model. We simulated low (0.5 mm/day) and high (1 mm/ day) growth rates per day based on research along the lower San Joaquin River (Zeug et al., 2019), lower Sacramento River (Sommer et al., 2001), and laboratory experiments (Perry et al., 2015). We further assumed a coefficient of variation in growth among fish at 60 % (Peterson and Duarte, 2020). We also simulated low and high small fish monthly survival within observed ranges in the Sacramento River (Marine and Cech, 2004) and model calibrations (Peterson and Duarte, 2020; probability = 0.6, 0.8). Movement rates of small fish were based on model calibrations (probability = 0.15, 0.25; Peterson and Duarte, 2020). We assumed trap efficiency was moderate to high (0.15, 0.30; Thedinga et al., 1994; Montgomery et al., 2007; Tattam et al., 2013; Silva and Bouton, 2015). Adult escapement values (2000 and 3000) were based on adult escapees estimates from carcass surveys and redd count surveys (CDFW, 2023), and the proportion of the time the trap was operating was based on real data or assumed perfect (0.8, 1; Montgomery et al., 2007; Tattam et al., 2013; Silva and Bouton, 2015). Redd area was simulated using a gamma distribution, a flexible distribution for positive outcomes with shape = 7.30 and scale = 0.462 based on field data collected on the Mokelumne River, California and spawning habitat area was assumed as either 2024 (low) or 4049 ha (high), which are within the range observed for Central Valley tributaries (CDFW, 2023). We simulated data for the juvenile production submodel assuming prespawn mortality was zero, sex ratio was 50:50, fecundity was 5500 eggs per redd, and egg-to-fry survival was 0.51 as described below. We assumed prespawn mortality was zero

Table 1
Integrated model transition probability matrix representing ϕ = survival, ψ = movement, and γ = growth. n = the number of estimated juveniles, s = small, m = medium, and l = large juveniles. γ_{sm} = growth from small to medium, γ_{sl} = growth from small to large, γ_{ml} = growth from medium to large, $trib_{t+1}$ = number of that size fish in the natal tributary at the next time step (month), out_{t+1} = number of fish outmigrating (moving), dead = number of fish that died.

$$\begin{bmatrix} n_{s,trib} \\ n_{m,trib} \\ n_{l,trib} \\ n_{s,out} \\ n_{m,out} \\ n_{l,out} \\ n_{dead} \end{bmatrix}_{t+1} = \begin{bmatrix} \phi_s(1-\psi_s)\left(1-(\gamma_{sm}+\gamma_{sl})\right) & 0 & 0 & 0 & 0 & 0 & 0 \\ \phi_s(1-\psi_s)\gamma_{sm} & \phi_m(1-\psi_m)(1-\gamma_{ml}) & 0 & 0 & 0 & 0 & 0 \\ \phi_s(1-\psi_s)\gamma_{sl} & \phi_m(1-\psi_m)\gamma_{ml} & \phi_l(1-\psi_l) & 0 & 0 & 0 & 0 \\ \phi_s\psi_s\left(1-(\gamma_{sm}+\gamma_{sl})\right) & 0 & 0 & 1 & 0 & 0 & 0 \\ \phi_s\psi_s\gamma_{sm} & \phi_m\psi_m(1-\gamma_{ml}) & 0 & 0 & 1 & 0 & 0 \\ \phi_s\psi_s\gamma_{sl} & \phi_m\psi_m\gamma_{ml} & \phi_l\psi_l & 0 & 0 & 1 & 0 \\ 1-\phi_s & 1-\phi_m & 1-\phi_l & 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} n_{s,trib} \\ n_{m,trib} \\ n_{l,trib} \\ n_{s,out} \\ n_{m,out} \\ n_{l,out} \\ n_{dead} \end{bmatrix}_t$$

during simulations for simplicity. Fecundity and egg-to-fry survival estimates were calculated from data collected on the Mokelumne River, California and American River, California respectively. We also assumed that rotary screw trap efficiency is the same across size classes for simplicity. In practice, differences in trap efficiency across size classes can be estimated in the model with sufficient size-specific efficiency trials to account for known size bias in capture rates (Tattum et al., 2013).

We used JAGS (Plummer, 2012) and R (R Development Core Team, 2021) via the R package *rjags* (R software, 2021) to fit our integrated model to the simulated data (see Supplemental Material for R code). We used diffuse normal distributions (mean = 0, SD = 0.368) for priors for logistic regression model intercepts and coefficient estimates. We initiated three Markov chains with a 20,000-sample burn-in and adaptation and evaluated output from an additional 200,0000 MCMC updates from each chain with a thinning rate of four. We summarize posterior distributions of estimated parameters (i.e., ϕ, γ, ψ) with their mean and 95 % credible interval (Gelman et al., 2014) using the MCMCvis package (Youngflesh, 2018). We confirmed chain convergence with the potential scale reduction factor ($\widehat{R} < 1.1$) for all simulations and visual inspection of trace and density plots from sample simulations of the posterior distributions of all top-level stochastic nodes (Gelman et al., 2008; Royle et al., 2014).

2.3. Case study

2.3.1. Clear creek background

Clear Creek is a west side tributary of the Sacramento River in the California Central Valley (Fig. 2). The Clear Creek watershed below Whiskeytown Dam covers ~127 km^2 and receives supplemental water from a cross-basin transfer between Lewiston Lake in the Trinity River watershed and Whiskeytown Reservoir in the Sacramento River watershed (Early et al., 2013). The upper reach flows south from Whiskeytown Reservoir for ~16.3 rkm and the lower reach heads in an easterly direction to the Sacramento River for ~13.2 rkm. There are no hatcheries on Clear Creek, so the lower reach only supports naturally produced fall and late-fall Chinook salmon and other species that represent the foothills fish community. The average daily discharge in Clear Creek is approximately 5.1 m^3/s (U.S. Geological Survey [USGS], 2022).

2.3.2. Monitoring data

We analyzed data for brood years 1998–2021 when the rotary screw trap in the lower Clear Creek was consistently operated and carcass surveys were performed. We obtained yearly fall run adult Chinook salmon escapement estimates for lower Clear Creek from Azat (2023). Prespawn mortality is generally low for fall run in Clear Creek (1990–2017 mean: 0.57 %, range 0–2.07 %) so we assumed that it was zero. Male-to-female sex ratio during this same time period averaged 53 % (+/- 7 %), so we assumed a 50/50 sex ratio for years in which these data were not collected (2018–2021). Spawning habitat availability

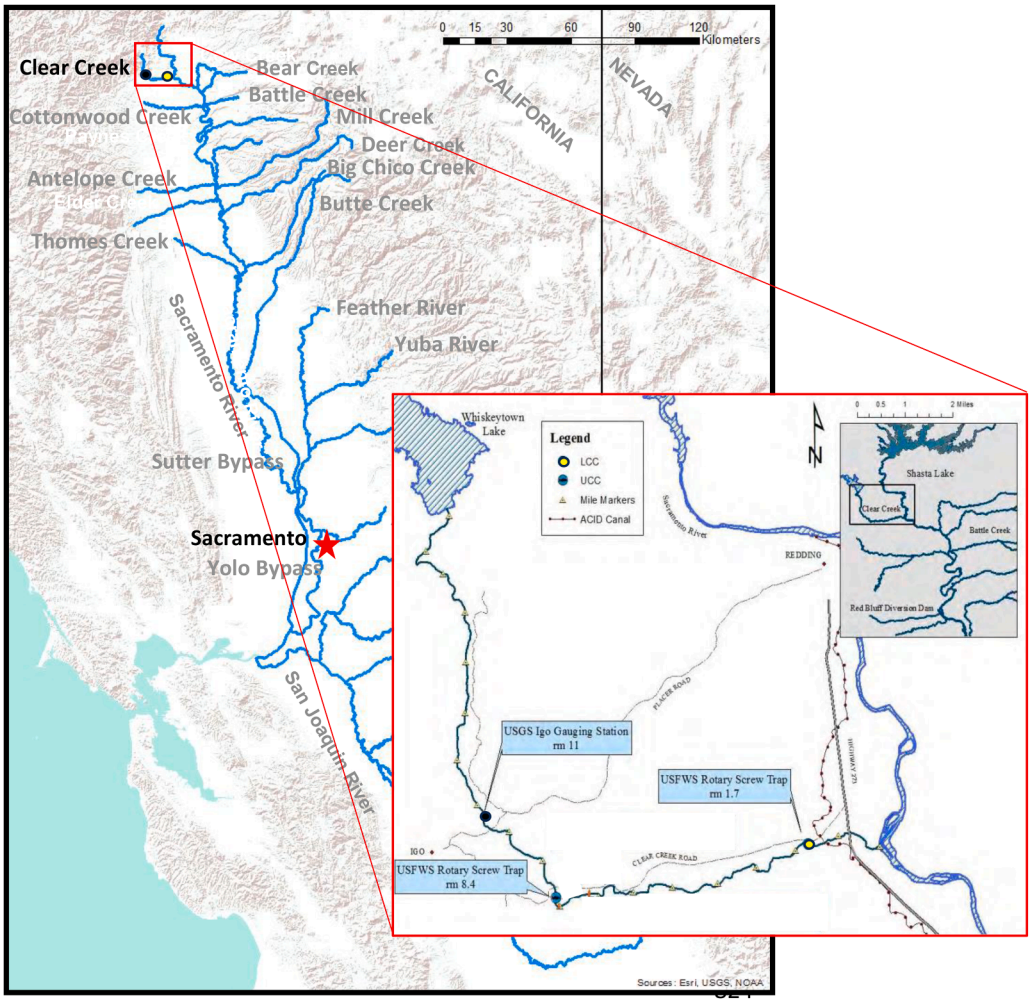

Fig. 2. Location of case study (red square) overlaid on a map of the tributaries and streams (blue lines) of the Central Valley of California. Yellow dot is the location of the lower Clear Creek, rotary screw trap and black dot is the location of the USGS Igo gauging station in Shasta County, CA, USA. Inset from Early et al. (2013).

from October through November each year was estimated using a flow-habitat model developed using field data collected on Clear Creek and hydrodynamic models developed by the USFWS and USBR (Rodriguez et al., 2023). We used the minimum amount of spawning habitat each year as our measure of available spawning habitat because eggs take approximately three months to develop into free-swimming fry.

We used rotary screw trap data for the identical years that were collected on Clear Creek above the confluence with the Sacramento River at rkm 2.7 (Schrami 2023). Trap operation was suspended in April 2020 for brood year 2019 due to Covid-19 concerns, so we omitted these data from the analysis. The trap consists of a 1.5 m diameter cone and fishes from late November through July each year. The sampling at this trap was consistent with the CVPIA's Comprehensive Assessment and Monitoring Program (CAMP) standard protocol (CAMP, 1997). Briefly, these data included counts and size measurements (i.e., fork length measured to the nearest 1.0 mm and weights to the nearest 0.01 g) of new and recaptured tagged fish, as well as trap-specific data such as date and time, creek depth, cone fishing depth, number of rotations of the trap cone, and amount of debris caught in the trap (Early et al., 2013). Trap efficiency trials were generally conducted twice weekly. For each trial, ~400 naturally produced juvenile Chinook salmon were captured, marked, and transported and released 0.32–0.64 rkm upstream of the trap (Early et al., 2013). We used the rotary screw trap data collected from December through July to match the timing of fall run juveniles in the lower Clear Creek and omitted catch data when the trap was not operational for 24 hrs (± 2 hrs) that day. Catch data were then summarized for each year by month and fish size.

We also wanted to consider environmental covariates on our demographic parameters. Flow effects on trap efficiency and fish movement are well documented (Watry et al., 2009). Similarly, water temperature is often modeled as an effect on juvenile survival (Peterson and Duarte, 2020; Wohner et al., 2022). Thus, we collated daily water temperature and stream flow data from the nearest USGS gage station (Igo, CA; Station #11372000; USGS, 2023). We calculated the average discharge for each efficiency trial period. We calculated the following flow and temperature statistics for each month of trap operation: monthly mean, minimum, and maximum daily discharge, the change in discharge (i.e., maximum – minimum) and monthly mean and maximum stream temperature. We also calculated monthly minimum rearing habitat availability using the daily discharge data and juvenile habitat availability models (Rodriguez et al. 2023). The hydrodynamic models used to estimate habitat availability were created between 2007 and 2013 after juvenile habitat restoration projects were completed in 2002 and 2007 and before completion of extensive habitat restoration in 2021. We adjusted the juvenile rearing habitat availability estimates to reflect increased habitat from restoration by subtracting the restored habitat; i.e., 7000 m^2 and 8200 m^2 for the years prior to 2002 and 2007, respectively, and adding 10,700 m^2 of rearing habitat for brood year 2021. The effects of habitat availability on juvenile salmon demographic rates are likely related to adult fish density, so we also calculated relative rearing habitat availability as the minimum habitat available divided by the total escapement. All continuous covariates were standardized to a mean of zero and standard deviation of one prior to model selection. To account for differences in trap efficiency, we created a binary (0,1) indicator variable "half cone" that was one when the rotary screw trap was partially out of the water during operation and zero otherwise. Lastly, we allowed three body sizes; medium (≥41<72) and large (≥72≤110 mm FL) with small (<41 mm FL) as the statistical baseline. Very few fish >110 mm FL were captured for the years examined, which is why this size class was omitted.

2.3.3. Model fitting

We fit logistic linear models to estimate rotary screw trap efficiency and monthly state transition probabilities—survival, growth, and outmigration. We began by fitting models with survival, growth, and outmigration modeled as constant (i.e., intercepts only) and modeling rotary screw trap efficiency as a function of rotary screw trap operation (half cone) and average discharge. We also believed that there was likely dependence with years due to changes in personnel and equipment over time. To account for this dependence, we included a random effect in the initial rotary screw trap efficiency model corresponding to year. We then evaluated the relative fit of alternative rotary screw trap efficiency that included quadratic effects for mean discharge and a half cone by mean discharge interaction. We retained each predictor when their inclusion decreased the mean deviance by two or more. The best fitting rotary screw trap efficiency was then used during model selection for the demographic parameters.

Model selection for the demographic parameters began with fitting alternative survival models holding growth and movement constant (intercepts only). We then used the best fitting survival model to conduct model selection with candidate parameters for predicting the growth size transition probabilities and finally, movement. We used the same set of candidate predictors for all demographic parameters which included body size, monthly mean and maximum daily water temperature, minimum relative habitat availability, and mean and maximum discharge. However, the fit of one additional predictor, change in discharge, was evaluated in candidate movement models because juvenile Chinook salmon migration is believed to be related to changes in discharge (Morrice et al., 2020). We also evaluated the fit of models with random effects that corresponded to year. Similar to the rotary screw trap efficiency models, we evaluated the relative fit of the candidate predictors one at a time and retained them when their inclusion decreased the mean deviance by two or more.

Again, we used JAGS (Plummer, 2012) and R (R Development Core Team, 2021) via the R package *rjags* (R software, 2021) to fit our models to the Clear Creek monitoring data (see Supplemental Material for R code). We generated more posterior samples during this process due to the increased number of estimated parameters. We used four Markov chains with a 100,000-sample adaptation, a 500,000-sample burn-in and evaluated output from an additional 500,0000 MCMC updates from each chain with a thinning rate of five.

3. Results

3.1. Relative bias simulation evaluation

The model converged on stationary distributions with all parameters $\widehat{R} \leq 1.001$ and trace and density plots indicated good mixing. The median relative bias in the simulation evaluation was low-to-none for survival, movement, and growth parameters for small-, medium-, and large-sized outmigrating juveniles (Fig. 3). Mean survival for the small size class was essentially unbiased under assumptions of both high and low survival probability (Fig. 3). However, the interquartile range and outliers indicated the model underestimated survival probability for medium- and large-sized fish under assumptions of high but not low survival probability, while the opposite was true for small-sized fish. The median bias was negligible for movement parameters for all size classes under high and low assumptions of movement. The interquartile range was skewed to underestimate movement across all outmigrant sizes, albeit minimally (Fig. 3). There was relatively little bias when simulating data assuming the lower (i.e., 0.5 mm/ day) or higher (i.e., 1 mm/ day) growth rates for all size classes (Fig. 3).

3.2. Case study

Adult fall-run Chinook salmon escapement was highly variable across the study and ranged from a low of 2353 in 2017 to a high of 19,867 in 2021 (Table 2). The total number of outmigrating juvenile fall run Chinook salmon were similarly variable and were dominated by the small size class that constituted more than two thirds of outmigrating juveniles for most years (Fig. 4). A total of 316 rotary screw trap

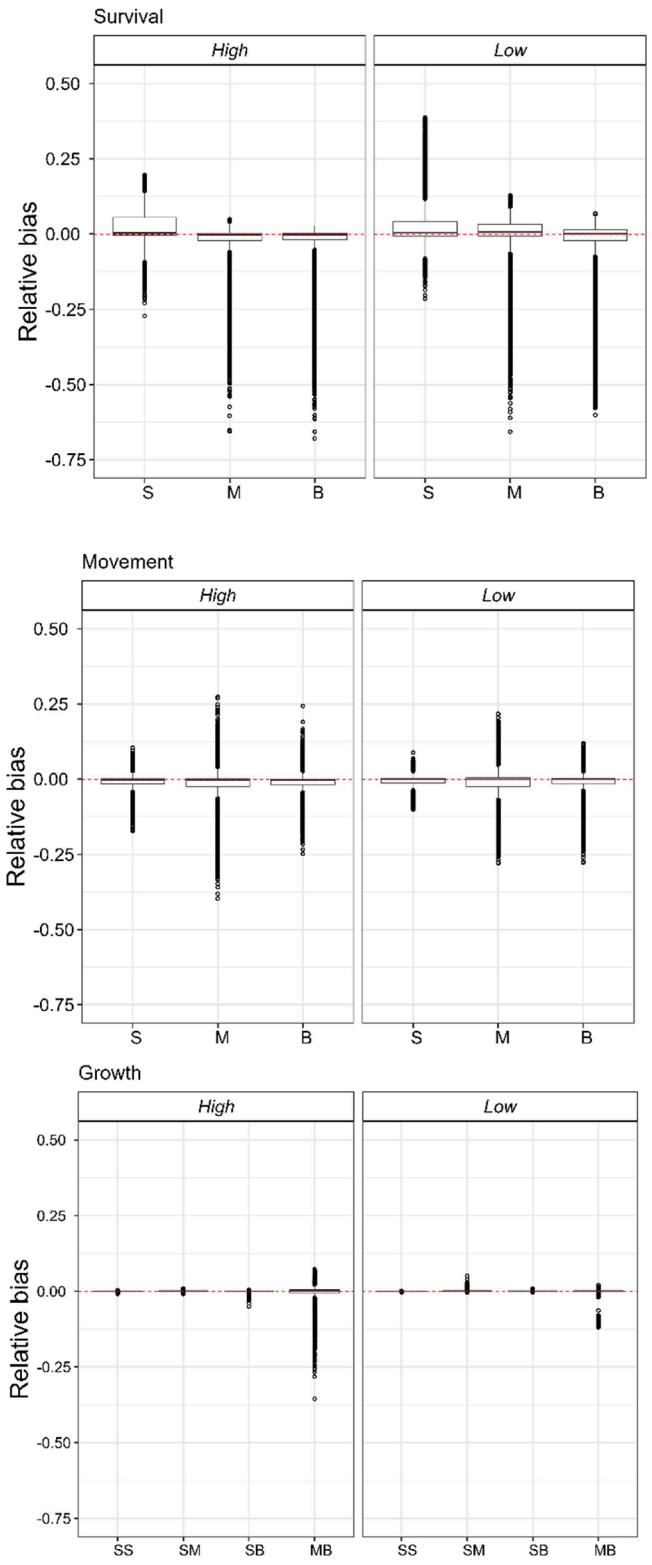

Fig. 3. Evaluation of relative bias (estimate–truth) for high and low values of survival and movement for small (S), medium (M), and large (B) outmigrating juveniles, and growth parameters (bottom) for small to small (SS), small to medium (SM), small to large (SL), and medium to large (ML) juveniles used to build the simulated data (truth) versus estimates from the model (estimate).

Table 2
Mean, standard deviation, minimum, and maximum values for measurements evaluated in the integrated model for fall run juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in Clear Creek, CA, USA.

Parameter	Mean	SD	Range
Number marked fish during efficiency trials	359.7	125.65	14–832
Discharge during efficiency trials (m^3/s)	8.4	2.46	6–18
Number efficiency trials per year	16.6	12.89	3–49
Proportion of time half cone operating during efficiency trials	0.8	0.38	0–1
Adult fall Chinook salmon escapement	8587.7	4653.27	2353–19,867
Spawning habitat availability (m^2)	39,822.1	7119.05	27,689–51,450
Relative rearing habitat availability (m^2/spawner)	4.3	2.72	1–12
Mean maximum daily temperature (°C)	13.5	2.91	8–19
Mean daily temperature (°C)	10.6	2.41	6–16
Mean discharge (m^3/s)	8.1	3.88	2–28
Maximum discharge (m^3/s)	18.4	17.73	2–102
Change in discharge (m^3/s)	12.7	17.00	0–95
Proportion of time half cone operating during surveys	0.6	0.37	0–1
Proportion month monitored during surveys	0.7	0.11	0–1

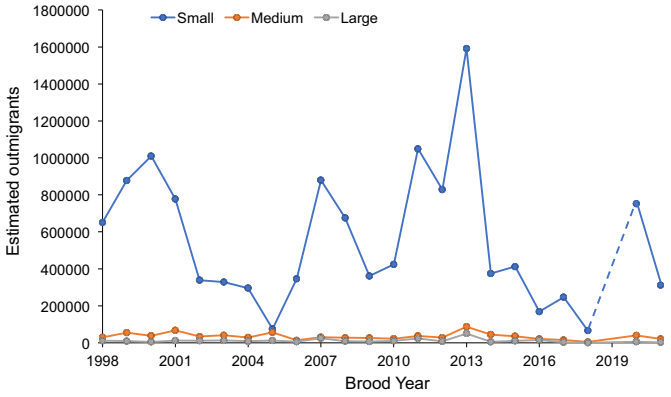

Fig. 4. Estimated number of outmigrating fall run juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in Clear Creek, CA, USA, by brood year and size class. Estimates were made using the best fitting integrated model.

efficiency trials were conducted over the study period with an average of more than16 trials per year (Table 2). The average daily discharge and cone operation were also similar for the efficiency trials and survey periods.

The best fitting models converged on stationary distributions with all parameters $\widehat{R} \leq 1.001$ (Table 3) and trace and density plots indicated good mixing when fitting the model to empirical fall run Chinook salmon monitoring data collected on Clear Creek. Model selection based on lowest deviance revealed support for two candidate models that were identical except for different growth transition submodels with one containing mean temperature and the other containing the relative habitat availability (Table 3). The best fitting survival submodels contained mean daily discharge and mean daily maximum temperature with survival positively and negatively related to each, respectively. The growth transition was positively related to mean daily temperature and relative habitat availability with temperature having a greater effect on growth (Table 3). In contrast, the monthly outmigration probability was negatively related to mean maximum daily temperature in both best fitting models. The best fitting rotary screw trap efficiency models contained mean discharge, half cone operation, and a year random effect (Table 3). Rotary screw trap efficiency was positively related to discharge and negatively to half cone operation. However, the relatively large year random effect suggested that efficiency varied strongly among

Table 3
Parameter estimates with mean, standard deviation (SD), and 95 % credible intervals, for top two integrated models of fall run juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in Clear Creek, CA, USA.

	Mean	SD	2.5 %	97.5 %
Best approximating model deviance = 6740,614.2 ± 42.77				
Monthly survival				
Intercept	2.0148	0.0056	2.0038	2.0259
Mean discharge	1.7062	0.0042	1.6980	1.7144
Maximum daily temperature	−3.1389	0.0060	−3.1507	−3.1272
Monthly growth transition				
Intercept	−1.7504	0.0063	−1.7631	−1.7384
Mean daily temperature	3.4702	0.0077	3.4551	3.4854
Monthly outmigration				
Intercept	−5.3081	0.0015	−5.3109	−5.3052
Maximum daily temperature	−1.4586	0.0010	−1.4606	−1.4567
Rotary screw trap efficiency				
Intercept	0.5884	0.0039	0.5808	0.5960
Half Cone	−0.1206	0.0025	−0.1254	−0.1157
Discharge	0.7277	0.0025	0.7229	0.7325
Year random effect*	4.1665	0.7425	3.0151	5.9003
Second best approximating model deviance = 6740,616.1 ± 43.568				
Monthly survival				
Intercept	1.8492	0.0046	1.8402	1.8583
Mean discharge	1.5044	0.0062	1.4922	1.5166
Maximum daily temperature	−2.8992	0.0063	−2.9115	−2.8869
Monthly growth transition				
Intercept	−5.7902	0.0151	−5.8305	−5.7697
Relative habitat availability	1.3861	0.0080	1.3714	1.4034
Monthly outmigration				
Intercept	−5.3535	0.0016	−5.3568	−5.3503
Maximum daily temperature	−1.4991	0.0011	−1.5012	−1.4970
Rotary screw trap efficiency				
Intercept	0.5979	0.0039	0.5902	0.6055
Half Cone	−0.1179	0.0025	−0.1228	−0.1130
Discharge	0.7352	0.0024	0.7304	0.7399
Year random effect*	4.1810	0.7425	3.0282	5.9206

* Random effect is expressed as a standard deviation.

years.

4. Discussion

Integrated models are becoming increasingly common in fisheries and wildlife to leverage different, albeit related, datasets to better understand ecosystem processes (reviewed in Schaub and Kéry, 2021). Indeed, the integration of data/information has been used to merge historical and contemporary monitoring programs to understand dynamic species distributions (Weldy et al., 2023), increase precision in the estimated parameters (Schaub and Abadi, 2011), formally link monitoring and decision-support modeling (Duarte et al., 2017; Wohner et al., 2022), and estimate parameters of interest with little-to-no direct information (Abadi et al., 2010; Duarte et al., 2016), among other objectives (Williams et al., 2018; Ly et al., 2024). By simulating data under a range of conditions, we demonstrated that our new parameterization for integrated population models allows for the accurate estimation of transition probabilities (i.e., survival, growth, and movement) for naturally produced juvenile anadromous fishes without the marked fish that are typically required to estimate these parameters. Thus, our model adds to the growing literature on the use of data fusion techniques to overcome data limitations for estimating demographic parameters that are useful for informing natural resource management.

Within a subset of tributaries across the Central Valley, juvenile monitoring via rotary screw traps and adult monitoring via spawning ground surveys occur as part of a larger anadromous fish monitoring program. These data have been used to track the timing of juvenile outmigration, the distribution of body sizes of juvenile outmigrants, the number of juvenile outmigrants and returning adults, the sex ratio of returning adults, prespawn mortality, and female fecundity. These types of information are undoubtedly useful with respect to understanding the general state of the system and to evaluate trends related to management actions. However, on their own these data do not provide a direct path towards the estimation of demographic parameters that are needed to gauge what the optimal management strategy is within a tributary based on our understanding of system dynamics (i.e., the DSMs; Peterson and Duarte, 2020). With our integrated approach, managers can directly use monitoring data to estimate the demographic parameters needed to effectively implement state-dependent decision-making as in Peterson and Duarte (2020).

Our model structure also allows for the direct linkage between changes in environmental conditions (i.e., water flow and temperature) brought on by management actions (i.e., flow regulation) and demographic parameters typically included in animal population DSMs. Demographic parameters that lack empirical estimates are typically included in the conceptual models used to develop DSMs that model animal responses to potential effects of management. In such cases, model developers often obtain demographic parameter estimates using less rigorous methods such as expert elicitation, borrowing parameter estimates from studies in other basins or systems, and/or estimating parameters during DSM calibrations. Otherwise, they are forced to omit these potential effects from models altogether. Although these other approaches for estimating demographic parameters are certainly useful and valid, our integrated model allows for the estimation of system-specific, data-driven demographic estimates to ensure DSM predictions are using the most relevant and robust information when more involved monitoring strategies are not implemented. Although the demographic parameter estimates from our integrated model may still have some inaccuracies under some cases, our model provides baseline estimates that are well within plausible ranges based on system-specific monitoring data. For example, our two top Clear Creek models had similar estimates in the expected direction for survival which decreased with temperature and increased with flow (Peterson and Duarte, 2020; Wohner et al., 2022). As with any DSM parameter, parameter uncertainties can (and should) be subsequently evaluated using sensitivity analyses to understand their effect (if any) on the decision-making process.

Using Clear Creek as an example, we demonstrated how to analyze real-world monitoring data using the integrated model to match the spatial and temporal dimensions of DSMs that are used to evaluate candidate salmon restoration actions in California Central Valley streams (Peterson and Duarte, 2020). This provides the direct feedback loop between monitoring and DSMs, which is a process that is often lacking when implementing an adaptive management program. Our analysis could certainly be extended to include other tributaries in the Central Valley (and beyond) that collect similar datatypes to better inform the decision-making process. During preliminary modeling efforts, we found that many of the current salmon monitoring efforts in the Central Valley had inconsistent and/or unstandardized methodology which prevented their use in a single integrated analysis. Standardized data from multiple systems would have facilitated the sharing of information and provided greater insights into the factors related to juvenile demographic parameters across the Central Valley. This highlights the importance of coordinating monitoring efforts across systems to increase consistency in standard operating procedures to ensure transferability of information learned and increase our ability to formally integrate data to support the management programs that are directing the monitoring efforts. Solutions for future modeling efforts will likely require increased coordination among monitoring programs and while difficult to achieve, is possible, as evidenced by progress currently being made by the monitoring subgroup within the CVPIA SIT.

Our simulation evaluation demonstrated that our model estimates juvenile transition probabilities with no-to-little bias across a range of low and high values of parameters for juvenile outmigrants. However, it is important to note that our simulation assumed all heterogeneity in the monitoring data was appropriately accounted for by the model structure and covariates considered. Although this may seem limiting, it is worth

noting that this is a typical assumption required for estimators used to calculate population abundance and demography. Indeed, others have shown this is a limitation for multiple widely used estimators in the field of ecology (e.g., occupancy models; MacKenzie et al., 2017, N-mixture models; Duarte et al., 2018, other parameterizations of integrated population models; Riecke et al., 2019). Nevertheless, we did detect bias in some cases, and we suspect that bias could also occur in the estimated parameters when combinations of processes result in transition probabilities that approach a boundary (i.e., one or zero). Thus, we still consider marking and tracking naturally produced individuals within a large-scale targeted monitoring framework to be the gold standard to estimate movement and survival of fish. Importantly, collecting such targeted data would allow for the direct estimation of a subset of the parameters of interest, which could be integrated with our model structure to reduce the number of demographic parameters, e.g., growth, survival, movement, estimated through pure data integration and/or help inform the estimation of transition probabilities using informative priors.

5. Conclusions

We developed and evaluated a new parameterization for integrated population models that allows for the accurate estimation of growth, movement, and survival probabilities of unmarked juvenile anadromous fish. Although these demographic parameters are often found to be important for informing management decision making for anadromous fishes, they are typically inestimable for naturally produced, unmarked juvenile fish when using traditional statistical approaches to analyze typical fish monitoring program data. Thus, our model structure serves as a useful approach within decision-making processes for anadromous fishes that rely on DSMs within adaptive management programs for evaluating direct responses to alternative management actions. Our integrated approach represents the first of its kind and can readily be applied to multiple sites and other anadromous fish species with quality and consistent monitoring data. Our model will allow fisheries managers to directly link management actions to survival, growth, and movement probabilities of unmarked, naturally produced fish stocks using relatively inexpensive monitoring data and facilitate learning by doing, i.e., adaptive management.

CRediT authorship contribution statement

Patti J. Wohner: Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Formal analysis. **Adam Duarte:** Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **James T. Peterson:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data are freely available on public domain as mentioned in the MS.

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Supplementary materials

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