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Modeling composite effects of marine and freshwater processes on migratory species

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Abstract. Life histories of migratory species such as anadromous fishes make them particularly susceptible to composite effects of processes experienced across distinct habitats and life stages. Therefore, their population dynamics are difficult to quantify and manage without tools such as life-cycle models. As a model species for which life-cycle modeling is particularly useful, we provide an analysis of influential processes affecting dynamics of the Central Valley fall-run Chinook salmon (CVFC) population (*Oncorhynchus tshawytscha*). This analysis demonstrates how, through identification of covariates that affect this population at each life stage and their relationship to one another, it is possible to identify actions that best promote sustainability for this anadromous species. We developed a life-cycle model for CVFC examining primary processes influencing variability in observed patterns of escapement from 1988 to 2016. CVFC are a valuable fishery along the US West Coast; however, their natural population is a fraction of its historic size, and recent low escapements have resulted in substantial restrictions on the fishery. Our model explains 68.3% of variability in historic escapement values. The most influential processes include temperatures experienced during egg incubation, freshwater flow during juvenile outmigration, and environmentally mediated predation during early marine residence. This work demonstrates the need, and methodology, for considering the interactions between freshwater and marine dynamics when evaluating the efficacy of managerial practices in freshwater and the ocean, especially in the context of increased environmental variability, climate change, and dynamic predator populations. The methodology developed in this study can be used toward improved conservation and management of other anadromous fishes and migratory species.

Key words: anadromous fishes; California Current; climate change; composite effects; ecological interactions; ecosystem-based fisheries management; life-cycle model; migratory; salmon.

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INTRODUCTION

Worldwide, a significant number of anadromous fishes have experienced dramatic declines in abundance, including as much as 90–99% in North America (Limburg and Waldman 2009). Their complex life histories involving obligatory migrations and dependence upon freshwater, estuarine, and marine habitats make anadromous fish sensitive to human activities in these varied environments, and especially challenging to manage. To aid in recovery of anadromous species and sustain recovery gains, a life-cycle modeling approach is useful for identifying the most sensitive life stages and for developing effective management strategies. This approach is particularly useful for highly migratory species such as anadromous fishes because it accounts for additive consequences across the full life cycle, allowing for population-level assessments of the efficacy and impact of managerial practices affecting one or more stages or habitats.

We focus on California Central Valley Chinook salmon (*Oncorhynchus tshawytscha*) as a model species subject to composite effects across a wide range of habitats and life stages, and for which a life-cycle modeling approach is particularly informative (Zabel et al. 2006, Crozier et al. 2008, Hendrix et al. 2014). Pacific salmon are a forage item for predators in fresh (Michel et al. 2015) and marine waters (Wells et al. 2017), a dominant prey item in mammalian diets (Chasco et al. 2017), and provide a valuable fishery along the West Coast (Satterthwaite et al. 2015, Riddel et al. 2018). However, coincident with lost and degraded freshwater habitat (Yoshiyama et al. 1998, Williams 2006) and increased variability in the marine environment (Sydeman et al. 2013), the dominant California Chinook population (fall-run, hereafter "CVFC"; Pyper et al. 2013) has declined to a fraction of its historic size (Yoshiyama et al. 1998) and has shown enormous variability in freshwater returns over the last 30 yr (Appendix S1: Fig. S1; Satterthwaite and Carlson 2015, Pacific Fishery Management Council 2017*b*). For example, in 2008 and 2009 extremely low spawner escapement resulted in the near-complete closure of the Chinook salmon fisheries off California and much of Oregon; surprisingly, this event followed the highest recorded escapement in recent decades only six years prior (Lindley et al. 2009; Appendix S1: Fig. S1). All four Central Valley Chinook runs are managed under federal and state conservation initiatives; winter and spring runs are both protected under the Endangered Species Act (ESA), while fall- and late-fall runs have been listed as a Species of Concern by the National Marine Fisheries Service (NMFS). Describing how this population responds to different natural and anthropogenic processes informs strategic management initiatives for stock rebuilding, increased genetic portfolios (Carlson and Satterthwaite 2011), conservation of predators reliant on it (Chasco et al. 2017, Wells et al. 2017), and sustainability of the fishery (Lindley et al. 2009).

Central Valley fall-run Chinook salmon life history and pressures on the population

Central Valley fall-run Chinook salmon spawn from late September to December in the Sacramento River, its tributaries, and tributaries to the San Joaquin River (Fisher 1994, Yoshiyama et al. 1998, Fig. 1). Egg development time and survival are sensitive to water temperature (Zeug et al. 2012, Martin et al. 2017), as well as to increased or variable flows that can destroy eggs, modulate oxygen availability, or expose them to desiccation (Becker et al. 1982, Lapointe et al. 2000, Martin et al. 2017). Most locations where CVFC spawn are below reservoirs, which moderate flows and alter temperatures downstream. Egg and embryo survival can also be reduced by redd superimposition, which occurs at higher rates with increased adult abundance and decreased spawning habitat (McNeil 1964). After emergence, juveniles may rear near their place of birth or disperse downstream or onto floodplains, where growth rates are usually higher (Sommer et al. 2001). In the spring, juveniles undergo transformation to the smolt stage and migrate to the coastal ocean. Tagging studies show that survival during this period has been shown to increase with river discharge (Michel et al. 2015, Perry et al. 2018), and survival can be quite low during dry periods, most likely due to predation by other fish (Sabal et al. 2016). CVFC must migrate through the Sacramento—San Joaquin Delta, which has been heavily modified by channelization, diking, and the operations of a complex water supply infrastructure that alters the hydrodynamics and water quality of the estuary (Nichols et al. 1986). Survival rates for juvenile salmon migrating through the interior Delta are notably low (Buchanan et al. 2013). Hatchery-produced salmon may avoid or experience different mortality sources when released in different locations throughout the system (Huber and Carlson 2015). Very little is known about how

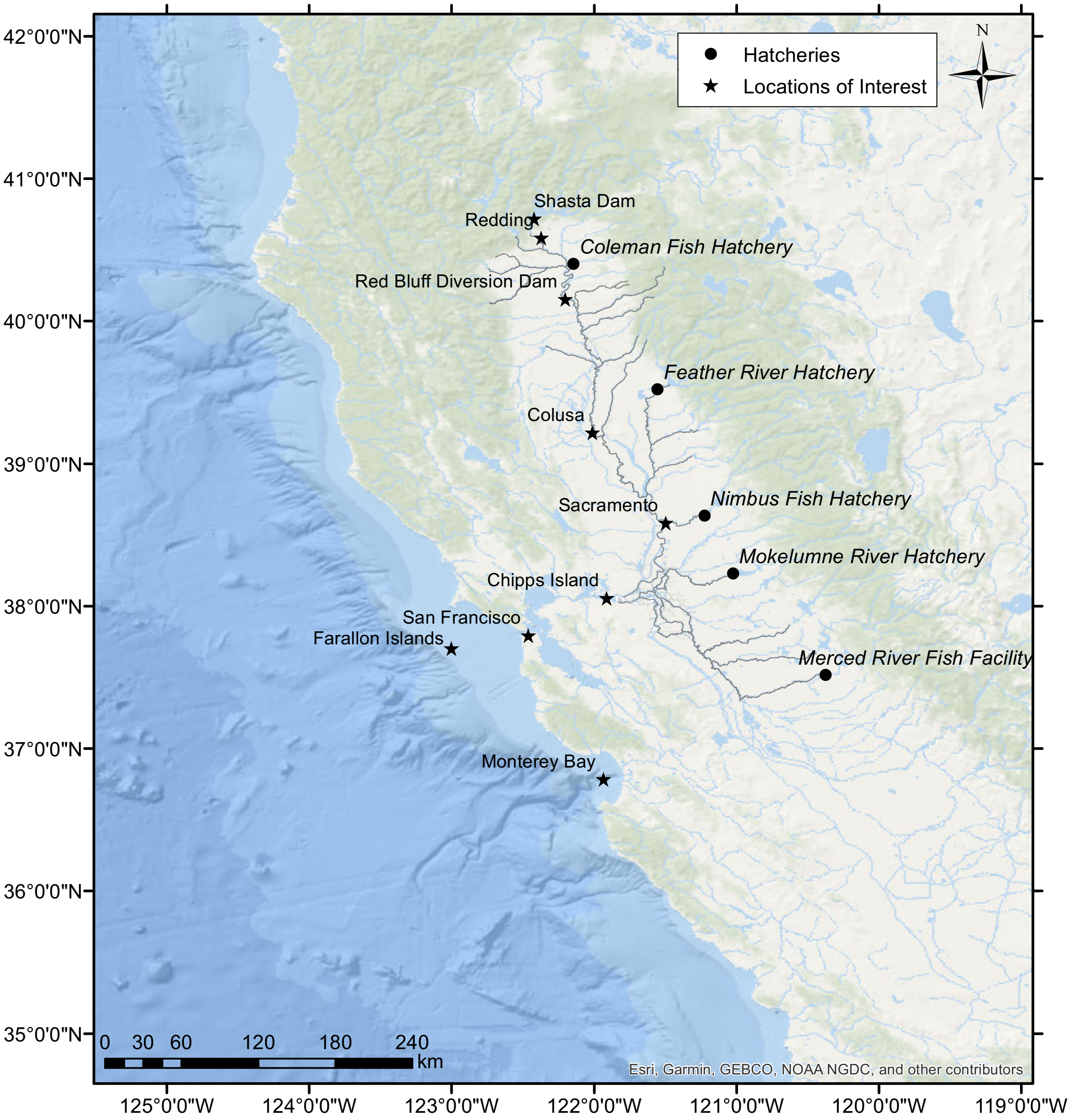

Fig. 1. Map of Central Valley fall-run Chinook habitat, hatchery locations (dots), and key locations (stars).

present conditions in the San Francisco Bay affect growth and survival of juvenile salmon. Survival of CVFC following ocean entry is dependent on predation risk and relatedly to the availability of suitable forage (Wells et al. 2012, Friedman et al. 2018), growth (Woodson et al. 2013, Fiechter et al. 2015), density dependence (Miller et al. 2013), and the occurrence of fronts enhancing trophic interactions (Woodson and Litvin 2015). These processes are affected by environmental variability modulating predator–prey relationships (Emmett and Krutzikowsky 2008, Wells et al. 2017). Factors affecting later ages, other than fishing, are less well understood, although size-at-age is variable and related to ocean conditions, and because mortality rates are often size-dependent, ocean climate variation may influence survival of later ages as well as young-of-the-year salmon (Heath et al. 1994, Wells et al. 2007).

Scope of study

Conservation and recovery efforts for this population require identification of those variables that most affect population dynamics and those that can be affected through management. In this study, we developed a model of CVFC population dynamics (FCα) to identify the processes that best explain the observed variability in CVFC population dynamics over the last three decades, as well as how additive effects among such processes relate to salmon escapement. Building from identification of key processes as well as their relationship to one another over time, we use the parameterized FCα model to illustrate potential effects of two management scenarios: changes to freshwater temperature during incubation and changes to freshwater flow during outmigration. This methodology may be applied toward conservation and management of other types of anadromous fishes and migratory species.

METHODS

Model description

FCα is an age- and stage-structured population dynamics model that produces model-based predictions of year t annual adult escapement based on observed returns $t-2$, $t-3$, and $t-4$ yr prior, together with covariates affecting the estimated survival of each brood year cohort. The model predicts the abundance of male (M'_t) and female (F'_t) returns separately; adding the two values provides a model-predicted estimate of total spawner escapement for each year (E'_t). Covariate data were assembled from 1983 to 2016, and model predictions are provided over the period of 1988–2016. A conceptual diagram of the full model is presented in Fig. 2. The model was written and tested in R (version 3.5.1; R Core Team 2018).

*Base model.—*To quantify the effect of different covariates on annual adult escapement, we first constructed a base model representing known dynamics of the CVFC life cycle. Model testing included the base model and iterative combinations of non-collinear covariates. Eq. 1 shows the base model underlying FCα. This model predicts annual spawner returns (E'_t) based on the number of reported spawners estimated to be female 2, 3, and 4 yr prior (F_{t-2}, F_{t-3}, F_{t-4}; described below); the historic average proportion of males and females that return at ages 2, 3, and 4 ($R_{m.2}$, $R_{m.3}$, $R_{f.3}$, described below); published values of survival at ages 2, 3, and 4 in the ocean (S_2, S_3, S_4) (Magnusson and Hilborn 2003); background survival terms for natural-origin fry (S_{bN}), hatchery origin releases (S_{bH}), and juvenile survival ($S_{b\phi}$) estimated by model fitting; and an annual ocean harvest survival index ($S_{V.t}$; described below). Each female was assumed to have a fecundity (Y) of 5401 (Quinn 2005), and eggs were assumed to be 50% male and female. The model-predicted estimates of male spawners (M'_t) and female spawners (F'_t) were summed to provide a model-predicted estimate of total annual escapement (E'_t). Model-predicted estimates were compared to spawner escapement values reported by the Pacific Fishery Management Council (PFMC; Pacific Fishery Management Council 2017*b*) for the Sacramento River and San Joaquin River combined, for the period of 1983–2016 (E_t). These values result from annual surveys conducted throughout the Sacramento and San Joaquin basins (Kano 2006, Killam et al. 2016); they are treated as observed values in model fitting but are themselves best estimates. Further descriptions of all variables can be found in Table 1. During this period, 93.8% of all CVFC adult escapement was comprised of spawners returning to the Sacramento Basin.

The PFMC escapement data report the total number of adult spawners and jacks returning in each year, but do not differentiate males and females. To estimate these values, we used 11 yr (2000–2010) of spawner return data from Coleman National Fish Hatchery and Feather River Fish Hatchery in the Sacramento River Basin (California Hatchery Scientific Review Group 2012) to construct a relationship between the proportion of jacks to total and proportion of adult males to total returning to the hatcheries (Appendix S1: Fig. S2). Data from these two hatcheries were used as they had the longest overlapping time series and most complete data over the time period. Total females returning each year (F_t) were estimated as $E_t - M_t$, with M_t estimated using the hatchery relationship.

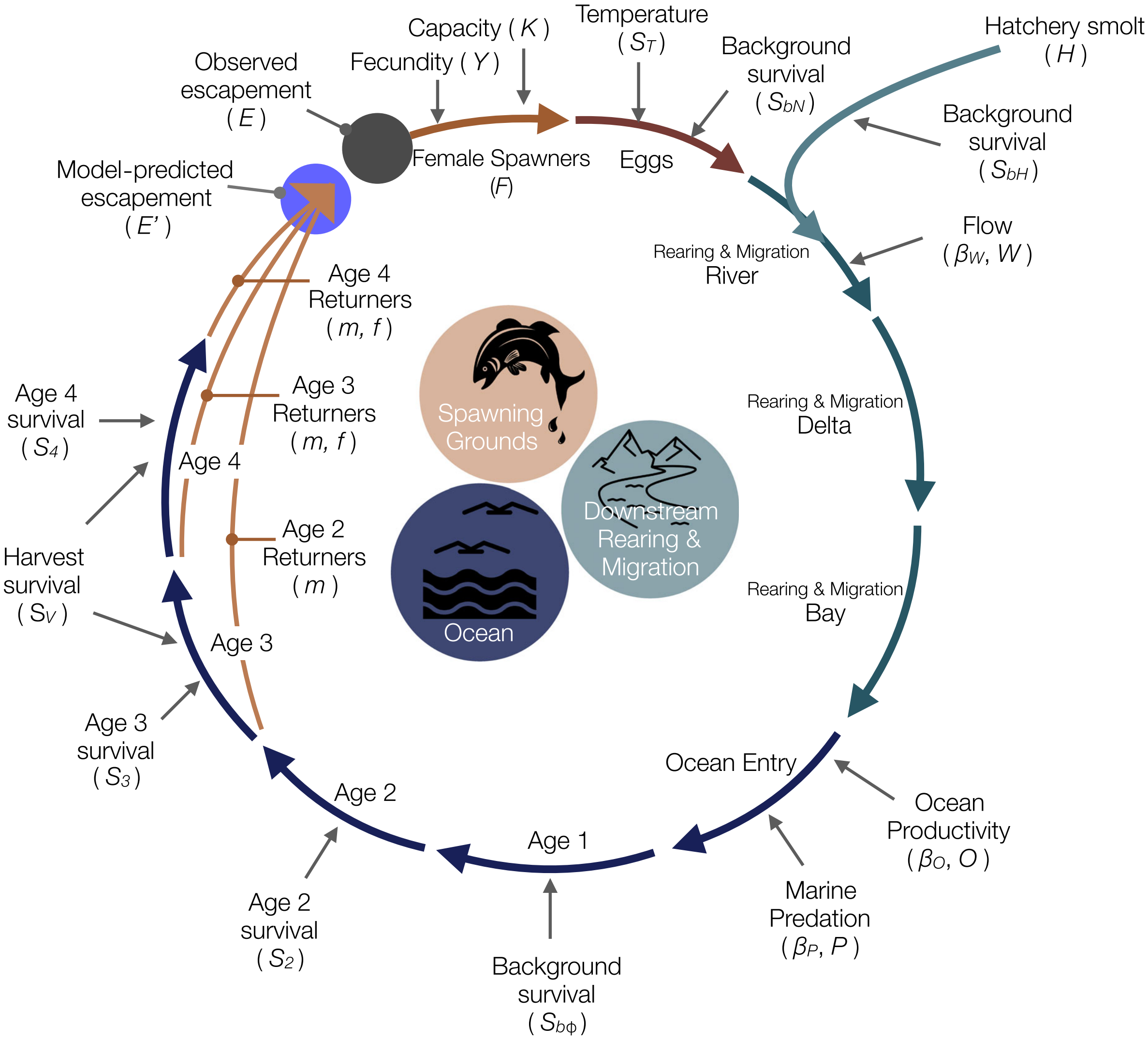

Fig. 2. Simplified diagram of the fall-run life-cycle model (FCα) showing the processes affecting a single brood year cohort. Note annual model-predicted escapement is the sum of these processes across multiple brood year cohorts (for more detail see Appendix S1: Eq. S1).

The average proportion of males and females returning by age category (corresponding to $R_{m.2}$, $R_{m.3}$, $R_{f.3}$; Table 1) were derived from the database of coded-wire-tagged fish maintained by the Regional Mark Processing Center (www.rmpc.org). We queried "Standard Reporting, All Recoveries" for all recoveries of Chinook salmon recorded over the maximum available time period (1990 to 2015) and "Standard Reporting, All Releases" for all releases of Chinook salmon recorded over the same period (1986–2014). We used only Central Valley fall-run Chinook salmon released as fry or smolts in the Sacramento River or its tributaries by Coleman National Fish Hatchery, for which there were data on release, spawner return, and the sex of recovered individuals. We estimated returning age-group percentages for each sex, based on all returns from salmon released over the 29-yr period (Appendix S1: Fig. S3). In FCα, male return estimates are the sum of estimates for age 2, 3, and 4 males (capturing 98% of the returning population; Appendix S1: Fig. S3). Female return estimates are the sum of estimates for age 3 and

Table 1. FCα model terms and descriptions. Observed data are those reported or derived from published annual escapement data.

Variable	Value	Description
t	{1983,1984,. . .,2016}	Year
E	E_t	Number of total spawners observed in year t
F	F_t	Number of female spawners observed in year t
Y	5401	Average fecundity for an adult female chinook salmon
b_T	$0.024°\mathrm{C}^{-1}\cdot\mathrm{d}^{-1}$	Slope at which mortality rate increases above T_{crit}
S_T	$S_{T.t}$	Annual temperature-dependent survival
S_2	0.6	Survival for age 2 chinook at sea
S_3	0.7	Survival for age 3 chinook at sea
S_4	0.8	Survival for age 4 chinook at sea
S_V	$S_{V.t}$	Annual ocean harvest survival index
$R_{m.2}$	0.220	Mean proportion of CWT males returning at age-2
$R_{m.3}$	0.583	Mean proportion of CWT males returning at age-3
$R_{f.3}$	0.665	Mean proportion of CWT females returning at age-3
Parameter estimates		
T_{crit}	11.56 (10.80, 12.99)	Temperature threshold at RBDD
S_{bN}	0.043 (0.003, 0.758)	Background survival for naturally spawned fry
S_{bH}	0.403 (0.060, 1.000)	Background survival for hatchery fish released in rivers
$S_{b\phi}$	0.246 (0.083, 0.658)	Background survival for natural and hatchery fish to age-2
β_W	1.448 (0.787, 2.098)	Coefficient for flow-dependent survival
β_P	−1.185 (−1.664, −0.797)	Coefficient for marine predation risk
β_O	–	Coefficient for survival based on ocean productivity
K	–	Spawner capacity
Model-based predictions		
E'	E'_t	Model-predicted number of total spawners in year t
F'	F'_t	Model-predicted number of female spawners in year t
M'	M'_t	Model-predicted number of male spawners in year t

Notes: References and further explanation of variables can be found in methods. 95% confidence intervals are reported in parentheses next to parameter estimates for covariates included in the final model (Model 1). Dashes indicate parameters that were tested but not included in the final model.

4 females (capturing 96% of the returning population; Appendix S1: Fig. S3).

During the last 30 yr, the five primary hatcheries on the Sacramento and San Joaquin rivers and tributaries (Coleman, Feather, Nimbus, Mokelumne, Merced) have released an annual average of 28.3 million hatchery-raised CVFC throughout the system (Huber and Carlson 2015) over the same period as natural fall-run juvenile outmigration. To capture the contribution of hatchery smolts to the return population, we included the total number of sub-yearling salmon released by the five major hatcheries (H). Hatchery release data for 1970–2016 were collected by Huber and Carlson (2015), Appendix B) and A. M. Sturrock et al. (*unpublished manuscript*).

We derived an annual ocean harvest survival index (S_V) from published harvest rates and population estimates defined as $S_V = 1 - (\text{ocean harvest/Sacramento Index})$ (O’Farrell et al. 2013, Pacific Fishery Management Council 2017*a*). Ocean harvest is the annual sum of ocean troll and sport harvest of SRFC south of Cape Falcon, OR, between September 1 and August 31 (Pacific Fishery Management Council 2017*a*). The Sacramento Index approximates the total population of spawners in a given year as the sum of ocean harvest, river harvest, and annual escapement (O’Farrell et al. 2013). S_V was allowed to affect only individuals greater than age 2, corresponding to those individuals typically large enough to be harvested by ocean fisheries (Pacific Fishery Management Council 2017*b*; Satterthwaite et al. 2017).

Error in our model is represented by the difference between predicted and observed data. We estimate the distribution of error as a normal distribution, with a mean equal to zero and a variance equal to the variance of our residuals.

$$\begin{aligned}
M'_t =& \left(F_{t-2} \times \frac{Y}{2} \times S_{bN} + \frac{H_{t-1}}{2} \times S_{bH}\right) \times S_{b\phi} \times S_2 \times R_{m.2} + \\
& \left(F_{t-3} \times \frac{Y}{2} \times S_{bN} + \frac{H_{t-2}}{2} \times S_{bH}\right) \times S_{b\phi} \times S_2 \times S_3 \times S_{V.t} \times R_{m.3} + \\
& \left(F_{t-4} \times \frac{Y}{2} \times S_{bN} + \frac{H_{t-3}}{2} \times S_{bH}\right) \times S_{b\phi} \times S_2 \times S_3 \times S_4 \times S_{V.t-1} \times S_{V.t} \times (1 - (R_{m.2} + R_{m.3})) \\
F'_t =& \left(F_{t-3} \times \frac{Y}{2} \times S_{bN} + \frac{H_{t-2}}{2} \times S_{bH}\right) \times S_{b\phi} \times S_2 \times S_3 \times S_{V.t} \times R_{f.3} + \\
& \left(F_{t-4} \times \frac{Y}{2} \times S_{bN} + \frac{H_{t-3}}{2} \times S_{bH}\right) \times S_{b\phi} \times S_2 \times S_3 \times S_4 \times S_{V.t-1} \times S_{V.t} \times (1 - R_{f.3}) \\
E'_t =& M'_t + F'_t
\end{aligned} \tag{1}$$

Sub-models

Temperature-dependent egg mortality.—We used a temperature-dependent mortality sub-model (Martin et al. 2017) to estimate annual survival (S_T) for eggs incubating in the Sacramento and San Joaquin and their tributaries. The model relates the temperature experienced by an embryo during the *i*th day of its development (T_i) to its instantaneous mortality rate (h_i; d^{-1}) with two parameters: T_{crit}, the temperature below which there is no mortality due to temperature, and b_T, the slope at which mortality rate increases with temperature above T_{crit} (Eq. 2)

$$h_i = b_T \times \max(T_i - T_{\text{crit}}, 0) \tag{2}$$

Central Valley fall-run Chinook salmon spawn in the Sacramento River and its tributaries, as well as tributaries of the San Joaquin River (Yoshiyama et al. 2000, Palmer-Zwahlen and Kormos 2015). To minimize complexity and data scarcity, we chose a single site, Red Bluff Diversion Dam (RBDD), to approximate patterns in temperature across the system. RBDD is located on the Sacramento River near Red Bluff CA (40°09′16″N, 122°12′07″W). We extracted daily minimum and maximum water temperature data from 1983 to 1989 from California Department of Water Resources reports (Turek 1990) and calculated the mean of these values for each day. We approximated missing data using iterative singular spectrum analysis, a nonparametric method which uses temporal and spatial correlation to fill data gaps (Kondrashov and Ghil 2006). We used daily mean water temperature at Bend Bridge, CA (USGS site 11377100) and from the RMA-11 model (Deas 2002) for this temperature reconstruction. We used temperature data for RBDD from 1990 to 2016 from the River Assessment for Forecasting Temperature (RAFT) model, which uses hydrodynamic and heat transport equations to model water temperature (Pike et al. 2013). RAFT output has a 15-min temporal resolution and 2-km spatial resolution. We averaged the sub-daily data and used linear interpolation to obtain daily mean water temperature at RBDD. To verify RBDD data were representative of the system, we compared mean daily temperatures recorded at RBDD to daily temperatures recorded at 9 other major spawning regions for CVFC and found high correlations between all sites and RBDD (Pearson's r = 0.76–0.91; Table 2). Data for each of the 9 sites were downloaded from the California Department of Water Resources California Data Exchange Center (CDEC).

Table 2. Correlations (Pearson's r) between daily temperature at Red Bluff Diversion Dam (RBDD) and temperatures recorded throughout spawning range of CVFC.

Region	Site ID	Data Coverage	Correlation to RBDD (r)
Clear Creek	IGO	1996–2017	0.80
Butte Creek	BCK	1998–2017	0.82
Feather River	FRA	2002–2017	0.85
Yuba River	YRS	2001–2017	0.83
American River	AFD	1998–2017	0.76
Mokelumne River	MOK	2008–2017	0.91
Stanislaus River	SOK	2001–2017	0.85
Tuolumne River	TTS	2004–2017	0.83
Merced River	CRS	2000–2017	0.85

Note: Site IDs are those used by CDEC.

We used published data on annual CVFC spawning periods (Vogel and Marine 1991, Williams 2006) to estimate temporal patterns in redd constructions over the spawning period (a normal distribution with peak spawning occurring on November 15, and 99.9% of redds spawned from October 1 to December 1). Incubation periods (n, days), starting at each possible fertilization day (October 1 through December 1), were determined using a temperature-dependent maturation function (Zeug et al. 2012, Martin et al. 2017), where the relative developmental state at fertilization equals 0 and increases at a rate, $0.001044(°\mathrm{C}^{-1}\cdot\mathrm{d}^{-1}) \times T_i + 0.00056(\mathrm{d}^{-1})$. Incubation periods ended when the temperature-dependent developmental state exceeded 1.

Temperature-dependent survival throughout the entire embryonic period (S_T) is the product of the daily temperature-dependent survival probabilities for each year (Eq. 3).

$$S_T = 1 - \prod_{i=1}^{n} \exp(-h_i) \qquad (3)$$

Given our temperature data do not represent the exact conditions experienced by the widespread CVFC, and to minimize model complexity, we used the published value of b_T from Martin et al. (2017) $0.024°\mathrm{C}^{-1}\cdot\mathrm{d}^{-1}$. In that study (2017), estimates for b_T were found to be similar across laboratory and field contexts, and laboratory datasets that b_T was fit to include both fall and winter-run embryos, which displayed similar thermal performance curves. T_{crit} was estimated simultaneously with all other model parameters. It is important to note that our T_{crit} estimate does not represent a physiological thermal limit, rather the temperature at one site (RBDD) above which mortality is expected to be high throughout the system.

Density-dependent superimposition of redds.—Capacity effects in spawning grounds have not been well quantified for CVFC, though are presumed to occur (Hallock 1977, Williams 2006) and are considered in the conservation objectives for the population (Pacific Fishery Management Council 2016). In particular, there may be limited optimal habitat for spawning, leading to an increased probability of redds being superimposed by later spawners when female spawner abundance (F) is high (Essington et al. 2000). We evaluated whether female spawner density affects naturally spawned egg-to-smolt survival (S_N) by testing the inclusion of a Beverton-Holt density dependence term (Beverton and Holt 1959) in our models. We note that other factors, such as competition for resources, may also contribute but are untestable at present due to limited data.

$$S_N = S_{bN}/(1 + F/K) \qquad (4)$$

In Eq. 4 S_{bN} is the expected egg-to-smolt survival probability in the absence of temperature- or density-dependent survival, and K is a capacity parameter representing the maximum number of spawners.

Environmental covariates

River conditions during outmigration (W).—Flow data used in the model were from a gauge on the Sacramento River at Colusa, CA (39°12′51″N, 121°59′57″W; USGS site 11389500). Data were downloaded from the USGS National Water Information System (https://waterdata.usgs.gov/nwis). We calculated an annual median value for flow in February, aligning with the period at which at 50% of sampled CVFC juveniles were captured by rotary screw traps at Red Bluff Diversion Dam from 2005 to 2017. These data were derived from the Juvenile Salmonid Monitoring biweekly reports provided by USFWS (Poytress et al. 2014).

Delta conditions during outmigration.—Among the possible covariates relating to conditions in the Sacramento–San Joaquin River delta during the peak outmigration period (March to May), the net delta outflow index (NDOI; http://www.water.ca.gov) provides the best approximation of the amount of water and potential habitat available to juvenile salmon. However, mean NDOI during this period was positively correlated with February flow (W, described above) (Pearson's $r = 0.62$) in the Sacramento River. All other potential variables were less descriptive of delta habitat, and those that were marginally descriptive were correlated to February flow at $r > 0.60$. In order to control for collinearity, we only included February flow in our model.

Early marine residence: ocean productivity (O) *and marine predation* (P).—The North Pacific Gyre

Oscillation (NPGO) is derived from analyses of Northeast Pacific sea-surface temperature and sea-surface height and is an indicator of upwelling strength, nutrient fluxes, and current strength in the California Current Large Marine Ecosystem (CCLME) (Di Lorenzo et al. 2008). Upwelling and nutrient availability influence the production and retention of krill and forage fish on which outmigrating juvenile salmon depend (Dorman et al. 2011, 2015, Wells et al. 2012), and the annual NPGO variability has been shown to influence synchrony of juvenile Chinook salmon survival along the CCLME (Kilduff et al. 2015). We tested the inclusion of NPGO as a covariate of juvenile salmon survival during early marine residence. Monthly NPGO indices were downloaded from a public repository (www.o3d.org/npgo) and summarized as annual means (O) (Kilduff et al. 2015). We also tested seasonal averages describing fall, winter, spring, and summer conditions, but found no significant differences in model performance over the less restrictive annual estimates used by Kilduff et al. (2015).

To test whether inter-annual variation in predation risk was significant in the larger population dynamics of CVFC, we included an annual index of marine predation on juvenile outmigrants equal to the annual estimated abundance of common murre (*Uria aalge*) at Southeast Farallon Island multiplied by the annual proportion of murre diet consisting of salmon (Ainley et al. 1990, Roth et al. 2007, Wells et al. 2017). Common murre were chosen as a proxy for marine predation (P) during early marine residence based on the findings of Wells et al. (2017). Both population estimates and diet composition data were available for all years in the present study. Many other known and potential predators are showing increasing population trends, and may be having similar or greater impacts on juvenile salmon survival, but annual data on population and diet were not available to include in our model.

Transformations, model fitting, and model selection

We converted time series for the survival covariates (W, O, P) to standard scores and estimated coefficients for each covariate (β_W, β_O, β_P), capacity (K), and background survival (S_{bN}, S_{bH}, $S_{b\phi}$) through model optimization. We used the R package *optimx* (Nash and Varadhan 2011) to implement a box-constrained non-linear minimization routine (*nlminb*), iterating over possible beta-parameter values in concert to find a solution that minimized the sum of squared error (SSE) between log-transformed values of observed versus predicted escapement. Within the model, we multiplied standard scores of the survival covariates (W, O, P) by the corresponding coefficient, then transformed these time series using an inverse-logit function (R package *boot*) to scale the variables as survival probabilities from 0 to 1 (function *il* in Eq. 5, Appendix S1: Eq. S1). We constructed profiles of the log-likelihood surfaces for each estimated parameter to obtain 95% confidence intervals.

We used Akaike's Information Criterion (AIC; Sakamoto et al. 1986) to select the most parsimonious model among 32 candidates. All models included the base model and its associated parameters (S_{bN}, S_{bH}, $S_{b\phi}$; Eq. 1). The set of models tested included the base model with no additional parameters (Eq. 1) and all possible combinations of the base model with additional terms and associated parameters (K, S_T, β_W, β_O, β_P; e.g., all possible terms, Appendix S1: Eq. S1). Pairwise correlation coefficients (Pearson's $|r|$) among covariates ranged from 0.001 to 0.467, below established threshold values for collinearity (Dormann et al. 2013).

All models within a AIC difference (Δ) $\leq$ 4 are reported (Burnham and Anderson 2002, Deriso et al. 2008). Additional descriptive statistics reported include sum of squared error (SSE) between log-transformed values of observed versus predicted escapement, the proportion of variance predicted by the model (R^2), and goodness of fit (logL; log-likelihood ratio statistic). We used bootstrap resampling to estimate error in the model predictions.

Scenario testing

We used the parameterized FCα to evaluate the effect of two simple scenarios reflecting changes in freshwater temperatures during incubation and freshwater flow during outmigration. In the temperature scenario, the daily mean temperature matrix used to estimate egg-fry survival was varied from −3 to +3°C. These values correspond to those derived by Isaak et al. (2018) for projected increases in river temperatures in the northwestern United States. In the flow scenario, observed annual February flow values were varied from −3 to +3 standard deviations from the mean of the original time series (1 SD = 11,762 cfs).

Results

Model performance

The model with the most support included temperature-dependent egg mortality, freshwater flow, and the marine predation index (Model 1; Table 3, Eq. 5). This model explained 68.3% of the variation in spawner returns observed from 1988 to 2016 (Fig. 3). The second best model (Model 2; $R^2 = 0.715$; Table 3) was distinguished by an AIC difference of only 0.176 from the top model and included the spawner capacity submodel. However, confidence intervals for K were extremely wide, and post hoc model testing revealed a relationship between model estimates of K and background survival for natural-origin smolts (S_{bN}), with higher values of K estimated as S_{bN} were minimized. Lacking further data to constrain K, and because these two models are statistically equivalent, we conclude there is a lack of strong evidence for spawner capacity in these models and focus our results on the more parsimonious Model 1 (see *Discussion* for further detail). All additional models had ΔAIC values > 2 from the top model; those with ΔAIC values ≤4 are included in Table 3. The null model (Eq. 1) explained only 1% of the variation in spawner returns. Analysis of variable importance indicated that freshwater flow (W) and predation during the period of early ocean entry (P) were the most influential terms in our model (Fig. 4). Error in model predictions, estimated via bootstrap resampling, was minimal except in the case of a few years (Appendix S1: Fig. S5).

Final model covariates

The median daily temperature recorded from October to December each fall ranged from 10.0°C in 1983 to 14.4°C in 2014, with a positive trend over the 34-yr study period (Fig. 5A.1; see

Table 3. Best performing models found after model selection (ΔAIC ≤ 4).

Model	Terms	R^2	SSE	−logLik	AIC	ΔAIC	EP
1	$T_{\mathrm{crit}}, \beta_W, \beta_P$	0.683	6.110	22.582	−33.164	0.000	6
2	$T_{\mathrm{crit}}, K, \beta_W, \beta_P$	0.715	5.737	23.494	−32.988	0.176	7
3	$T_{\mathrm{crit}}, \beta_W, \beta_O, \beta_P$	0.680	6.114	22.573	−31.147	2.017	7
4	β_W, β_P	0.607	7.511	19.588	−29.175	3.988	5

Notes: All models include the three estimated parameters (EP) from the base model ($S_{bN}, S_{bH}, S_{b\phi}$). Model 1 is discussed in text.

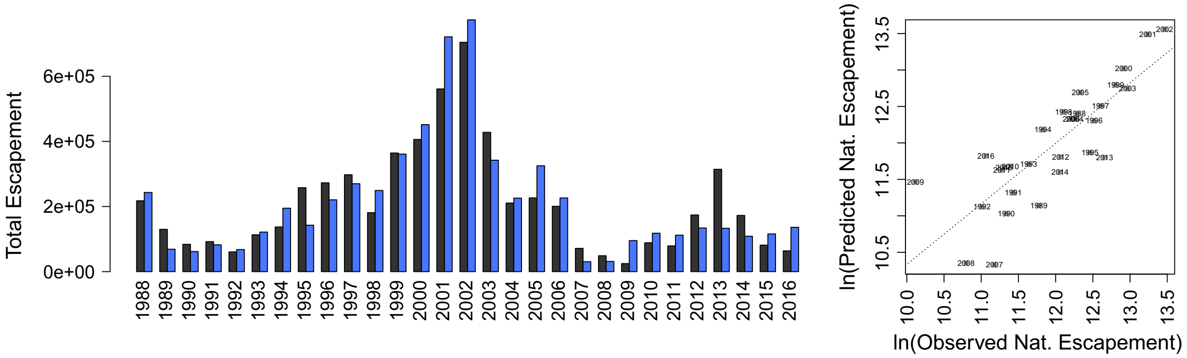

Fig. 3. Final model. Black bars indicate observed escapement; blue bars represent model-predicted escapement by FCα. 1988, 2002 peaks are captured, as are valleys in 1992 and 2008. The 2013 peak is not captured, and returns for 2001 are overestimated.

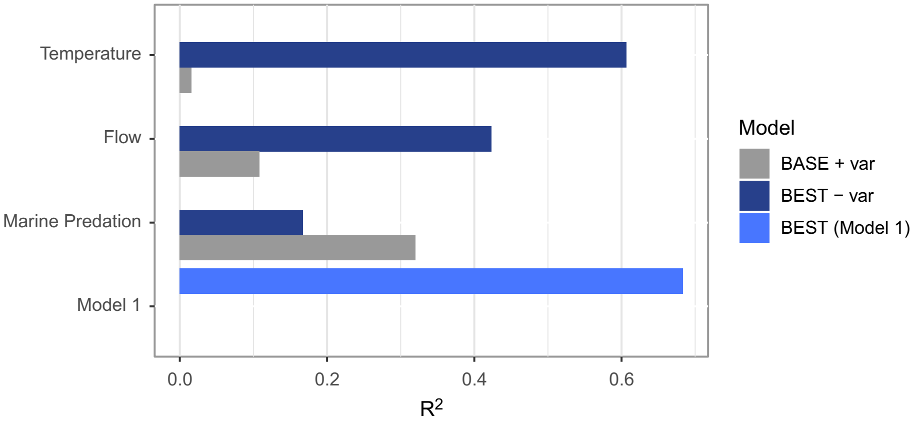

Fig. 4. Variable importance. Shown are all terms that occur in the best model (Model 1), the performance of the base model plus each term individually (gray), and the performance of the best model with that term excluded (dark blue), against the performance of the best model with all terms included (Model 1; blue).

Beer and Anderson 2013, Isaak et al. 2018, for more detailed analyses of temperature trends in this region).

The temperature-dependent mortality model estimated an annual survival based on estimated spawning date, temperature-dependent incubation period, and temperatures experienced during incubation. Therefore, while the median temperature from October to December describes some of the pattern of estimated mortality, it is not a complete depiction of experienced temperatures. Estimated survival based on temperature (Fig. 5A.2, A.3) ranged from <0.01 in 1991, 1996, and 2014 to 0.88 in 2011. The estimate for T_{crit} was 11.56°C (95% CI 10.80, 12.99).

Freshwater flow significantly affected model performance. With flow excluded, the model explained only 42.3% of the variation in CVFC escapement (Fig. 4). The estimate for the flow coefficient (β_W) was 1.448 (95% CI 0.787, 2.098). Significantly, above-average annual flows were uncommon during the period of our analysis, but corresponded to high survival estimates for the years when they occurred (1983, 1986, 1998–2000) (Fig. 5B.1, B.2).

The marine predation index contributed significantly to model performance. Without the inclusion of marine predation, the model explained only 16.7% of the variation in CVFC escapement (Fig. 4). The estimate for the marine predation coefficient (β_P) was −1.185 (95% CI −1.664, −0.797). Marine predation was especially high in the early 2000s and was above average for 11 yr between 2002 and 2016 (Fig. 5C.1, C.2).

Scenarios

We used FCα to evaluate the effect of two simple scenarios reflecting plausible changes in freshwater temperatures during incubation and freshwater flow during outmigration. Results should be interpreted as annual one-year-ahead predictions rather than multi-year patterns.

In years when observed escapement was mid to high (1996–2006), decreases in temperature during the incubation period predicted appreciably higher values of escapement than what was observed. However, in years when observed escapement was low, changes to temperature during the incubation period showed marginal effects. Overall, even a +1°C or −1°C degree shift in incubation temperatures showed substantial effects across years (Fig. 6A).

Increases in flow showed broad effects across years, with higher escapement predicted by increases in flow during the outmigration period in all years except for 2007–2008, when escapement has been shown to have been largely modulated by variability in ocean processes and related predation events (Lindley et al. 2009, Wells et al. 2017). Across all years, the −2 SD and −3 SD flow scenarios were associated with substantially lower escapement. (Fig. 6B).

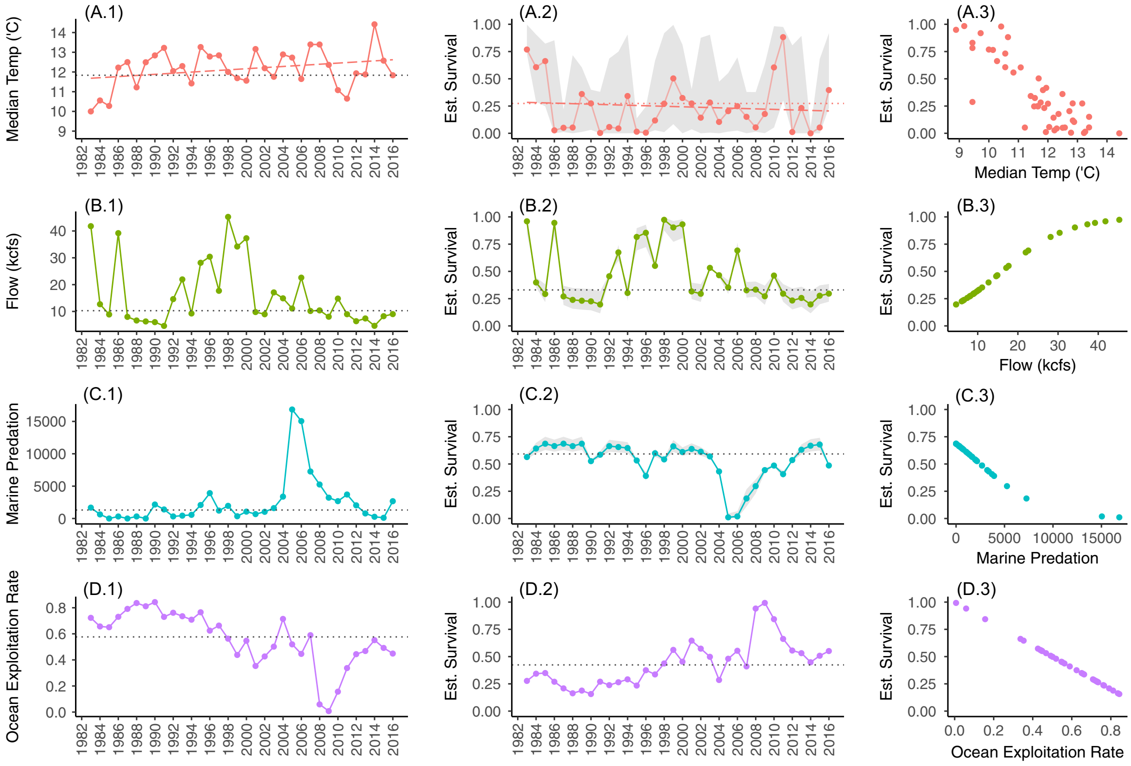

Fig. 5. Annual observed values for final environmental covariates (Temp, Flow, Marine Predation) and annual ocean harvest rate (A.1–D.1). Covariate relationships to model-predicted survival each year based on final parameter values (Table 1) are shown in A.2–D.2. Gray ribbons around model-predicted survival reflect 95% confidence intervals around parameter estimates for T_{crit}, β_W, and β_P (A.2., B.2, C.2, respectively). The median values for each covariate across the study period are shown as gray dotted lines. A trend line for median incubation temperatures (A.1) and temperature-dependent survival (A.2) is shown in red (dashed). A.3–D.3 shows covariate relationships to survival. Note, presented here are median temperature values during the spawning period from October to December to summarize the range of conditions included in the temperature-mortality model.

$$\begin{aligned}
M'_t =& \left(F_{t-2} \times \frac{Y}{2} \times S_{T.t-2} \times S_{bN} + \frac{H_{t-1}}{2} \times S_{bH}\right) \times il(\beta_W W_{t-1}) \times il(\beta_P P_{t-1}) \times S_{b\phi} \times S_2 \times R_{m.2}+ \\
&\left(F_{t-3} \times \frac{Y}{2} \times S_{T.t-3} \times S_{bN} + \frac{H_{t-2}}{2} \times S_{bH}\right) \times il(\beta_W W_{t-2}) \times il(\beta_P P_{t-2}) \times S_{b\phi} \times S_2 \times S_3 \times S_{V.t} \times R_{m.3}+ \\
&\left(F_{t-4} \times \frac{Y}{2} \times S_{T.t-4} \times S_{bN} + \frac{H_{t-3}}{2} \times S_{bH}\right) \times il(\beta_W W_{t-3}) \times il(\beta_P P_{t-3}) \times S_{b\phi} \times S_2 \times S_3 \times S_4 \times S_{V.t-1} \\
&\times S_{V.t} \times (1-(R_{m.2}+R_{m.3})) \\
F'_t =& \left(F_{t-3} \times \frac{Y}{2} \times S_{T.t-3} \times S_{bN} + \frac{H_{t-2}}{2} \times S_{bH}\right) \times il(\beta_W W_{t-2}) \times il(\beta_P P_{t-2}) \times S_{b\phi} \times S_2 \times S_3 \times S_{V.t} \times R_{f.3}+ \\
&\left(F_{t-4} \times \frac{Y}{2} \times S_{T.t-4} \times S_{bN} + \frac{H_{t-3}}{2} \times S_{bH}\right) \times il(\beta_W W_{t-3}) \times il(\beta_P P_{t-3}) \times S_{b\phi} \times S_2 \times S_3 \times S_4 \times S_{V.t-1} \\
&\times S_{V.t} \times (1-R_{f.3}) \\
E'_t =& M'_t + F'_t
\end{aligned} \tag{5}$$

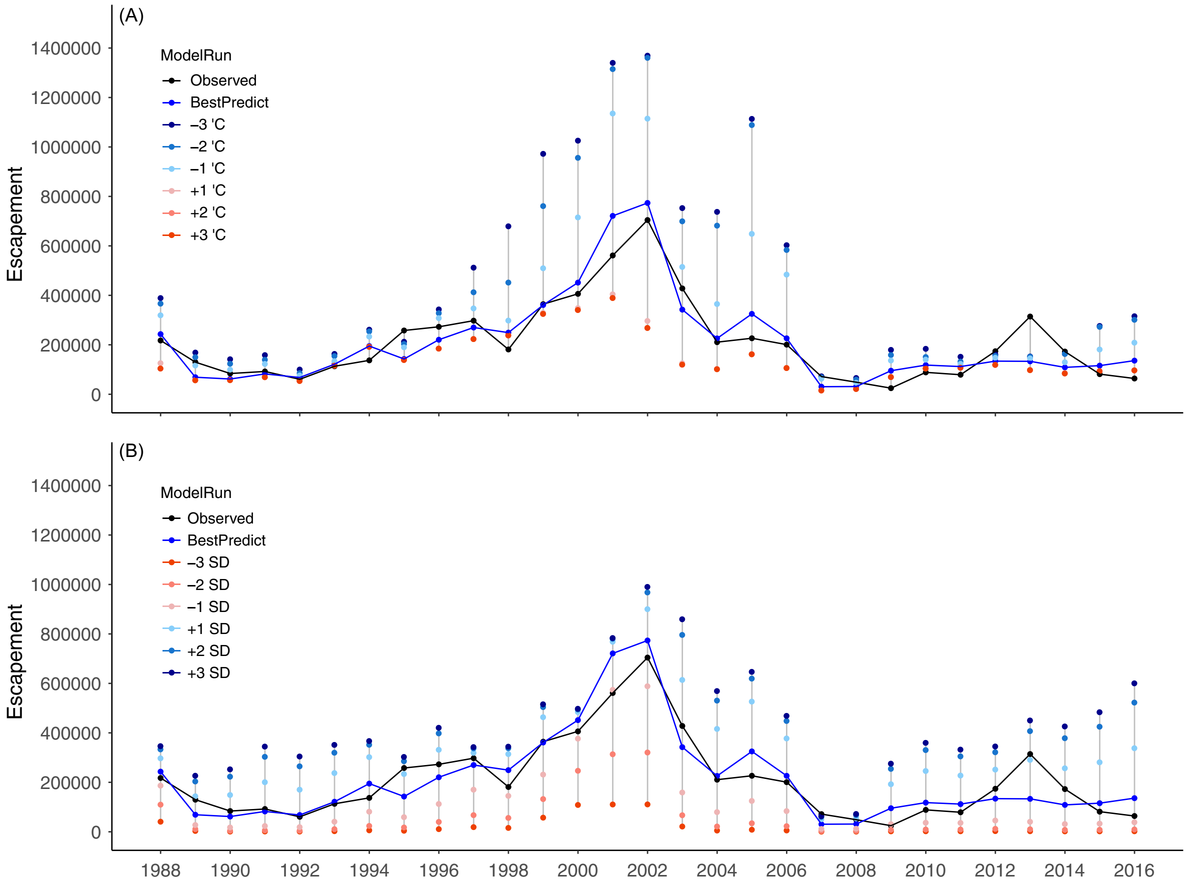

Fig. 6. Annual point estimates of escapement in response to scenarios of increased or decreased freshwater temperatures during incubation (A), and flow during outmigration (B). 1 SD pertains to a fixed variation of 11762 cfs applied to the observed flow each year. Results should be interpreted as annual point estimates rather than multi-year or cumulative patterns.

DISCUSSION

Our results show that population dynamics of CVFC result from composite effects of processes in the freshwater and marine environment. For example, during the limited years of high flow observed in this time series our model predicted high survival when other processes were more typical (1998–2000; Fig. 5). In 2006, above-average flows corresponded to a higher survival estimate for juvenile outmigrants, but marine predation during the early marine residence period was particularly high. Notably, 2006 was the year of outmigration for much of the adult cohort that contributed to the low returns observed in 2008. In a different phase of the system, the fall of 1995 was estimated to have extremely low egg-fry survival corresponding to high incubation temperatures. However, flow in the spring of 1996 was particularly high, which may have compensated for the temperature effect and contributed to relatively high returns in 1999 (Figs 3, 5).

We observed a positive trend in fall incubation temperatures throughout the study period (Fig. 5A.1), and the temperature-dependent mortality model was included in three of the four top models. Temperature-dependent mortality has also been shown to affect Central Valley winter-run Chinook salmon (Martin et al. 2017). Given the increasing trend toward warmer temperatures and known egg-fry mortality, it is likely this covariate will become increasingly important as we focus on the current period and near future.

This may be especially so for CVFC as they spawn in lower-foothill reaches of the Sacramento and San Joaquin rivers (Fisher 1994, Yoshiyama et al. 1998), likely making them more susceptible to intra-annual temperature fluctuations as well as increasing temperature trends. This situation may be exacerbated by the effects of reservoirs, which typically elevate water temperatures in the fall and winter in downstream river reaches (Caissie 2006, Olden and Naiman 2010).

Flow has direct and indirect effects on juvenile salmon outmigration dynamics. Freshwater flow, moderated by snowmelt, rain, and water operations, affects outmigration timing, size, and survival of juvenile Chinook salmon. Timing of juvenile salmon outmigration coincides with peak flows (Kjelson et al. 1982, Healey 1991, Williams 2006). Michel et al. (2015) and Wells et al. (2017) demonstrated higher survival for juvenile Central Valley Chinook salmon outmigrating during higher flows. Sturrock et al. (2015) found significant differences in the phenology of outmigrating CVFC between a wet and dry year, with fry contributing to a higher proportion of returning spawners from the same broodyear, and evidence suggesting higher in-river mortality in the drier year. High flows in the Sacramento and San Joaquin rivers are positively correlated with turbidity, which has been associated with higher survival, likely due to increased ability to avoid predation (Gregory and Levings 1998). Higher flows likely create improved rearing and migration habitat (e.g., increased woody debris, primary productivity, and access to flooded sloughs and wetlands; Quinn 2005). From the standpoint of management, high flows are related to pumping operations and routing probabilities in the Sacramento–San Joaquin Delta, and higher survival among outmigrants in this region has been observed during higher flows (Brandes and McLain 2001). Water management and habitat modifications (e.g., dams, diversions) have altered freshwater flow and temperatures experienced by outmigrating CVFC (Yoshiyama et al. 2001). These changes coupled with reduced genetic and phenotypic diversity in the population (see Satterthwaite and Carlson 2015, Herbold et al. 2018) mean the population is likely more susceptible to inter-annual variations in temperature and flow resulting from natural processes, climate change, and management practices (Lindley et al. 2009, Herbold et al. 2018). Thus, the effects of freshwater flow and temperature described here may be increased over what we expect with a more diverse population.

The inclusion of the marine predation index had the most significant effect on model performance. Common murre, among several predator populations, have been recovering in the Gulf of the Farallones region and have shown a sharply increasing abundance since 2001 (Wells et al. 2017). Predation was exceptionally high during 2005–2006 when there were very low abundances of krill and juvenile rockfish (Schroeder et al. 2014). Predation pressure remained higher than the median for the majority of years following Common murre increases in the early 2000s (Fig. 5). In the absence of preferred prey (juvenile rockfish), common murre shift to a diet dominated by northern anchovy, which overlap spatially and temporally with outmigrating juvenile salmon, resulting in significant incidental impacts on salmon (Wells et al. 2017, Warzybok et al. 2018). It is likely that under similar circumstances additional predators switch to forage inshore on anchovy, further increasing predation risk on juvenile salmon (e.g., rhinoceros auklet (*Cerorhinca monocerata*), Warzybok et al. 2018). For example, Fleming et al. (2016) reported a similar phenomenon for humpback whales in the central California Current ecosystem whose isotopic ratios indicated a switch to diets consistent with sardine and anchovy during years of low krill abundance. With increasing environmental variability in the CCLME (Sydeman et al. 2013), and increasing predator populations (e.g., California sea lions (*Zalophus californianus*), Laake et al. 2018; harbor seals (*Phoca vitulina*), Carretta et al. 2016; common murre, Wells et al. 2017; Brandt's cormorants (*Phalacrocorax penicillatus*), Capitolo et al. 2014), it is likely there will be increasingly higher and more variable predation risk for outmigrating juvenile salmon, especially in years in which primary forage are less abundant. This is likely to cause greater variability in adult population dynamics and increased likelihood of reductions in the fishery and escapement.

Recruitment to the fishery and ultimately escapement variability may be more dependent on ocean conditions for CVFC than other Central Valley Chinook runs. For example, the ocean condition during winter, when late-fall and winter-run salmon outmigrate (Fisher 1994), is less variable temporally and spatially than the spring when CVFC outmigrate (Checkley and Barth 2009). In winter, upwelling intensity is lower (Checkley and Barth 2009), the associated mesoscale features (e.g., fronts, upwelling shadows, eddies) are less common (Graham and Largier 1997, Wing et al. 1998), and the salmon preyscape is less rich (Ainley et al. 1996). However, when upwelling begins in late winter, it promotes a more abundant forage base in the spring (Schroeder et al. 2013, Fiechter et al. 2015, Friedman et al. 2018). Optimal upwelling in spring and summer creates heterogeneous retentive areas in which forage is available to outmigrating salmon (Graham and Largier 1997, Wing et al. 1998); however, if upwelling is too intense forage can be advected offshore (Cury and Roy 1989). Such physical and biological dynamics are largely responsible for variability in forage and, ultimately, survival of CVFC salmon during their first spring and summer at sea (Fiechter et al. 2015, Wells et al. 2016, Henderson et al. 2019). Reduced prey availability leads to reduced growth (Fiechter et al. 2015, Henderson et al. 2019) and increased predation on smaller fish (Woodson et al. 2013), including from predators seeking alternative prey (Wells et al. 2017). This process, emergent from a series of regional conditions, is likely the reason basin-scale covariates such as annual NPGO were uninformative when predation was included in the model (note, post hoc analyses using seasonal averages of NPGO also did not improve model performance); that is, while NPGO describes some of the underlying processes mediating forage availability and predation pressure, predation pressure is the more proximate covariate of outmigration survival. Importantly, our results indicate that a life cycle model parameterized with demonstrated processes will improve fit above the inclusion of coarse ecosystem indicators alone.

Our analysis was inconclusive on whether female spawner densities (K) affect egg-to-fry survival in CVFC. A comparison of Model 1 and Model 2 (which included K) showed the main effect of including K was to substantially decrease the starting number of natural-origin fry the model, while increasing the estimate of background survival (S_{bN}) for those natural fry remaining. The low capacity (K) estimated in Model 2 effectively decoupled the relationship between the number of spawners and the number of emergent fry, leading to similar estimates of natural-origin fry abundance regardless of spawner densities. Unfortunately, we cannot differentiate between these two models without additional data on the number of natural-origin fry in the system, or their proportion relative to hatchery-origin fry. Importantly, all other final parameters (T_{crit}, S_{bH}, $S_{b\phi}$, β_W, β_P) were similar between the two models, with marine predation, flow, and temperature showing the strongest relationship to variability in annual escapement. Improved estimates of spawning habitat availability over time would be particularly useful for future models.

Our model examines the effects of environmental factors on the productivity of CVFC. However, as discussed by Lindley et al. (2009), there has likely been a reduction in the underlying productivity of this stock related to physiological changes in individuals (e.g., reduced egg size, age at maturation, reduced genetic diversity; Heath et al. 2003, Satterthwaite and Carlson 2015), brought on by large-scale habitat modification (Yoshiyama et al. 2001) and hatchery introgression (Willmes et al. 2018). Due to a lack of physiological time series and knowledge of confounding effects with environmental covariates (Heath et al. 1994), we were unable to include these physiological effects in the model presented here. However, we separately tested the inclusion of a survival term that decreased over time (corresponding to the hypothesis of decreased productivity) and found that it increased model performance in terms of AIC, log-likelihood, and variance explained. The top model including this term was otherwise identical to our final model. As these physiological time series become available, it will be prudent to include such terms in future models.

Finally, we used the parameterized FCα model to estimate the effect of changes in temperature during incubation, as well as flow during outmigration, on model-predicted escapement. As flow was the stronger covariate in the model, it is no surprise that variations in flow showed a greater effect, with increases in flow during outmigration relating positively to increased adult escapement. Interestingly, for the recent years characterized by low freshwater flow and high incubation temperatures, the models representing increased temperature and decreased flow beyond what was observed provided a more accurate prediction than our final parameterized model (Fig. 6). This indicates compounding effects beyond what is presently captured in our model. Freshwater conditions have carryover effects on the survival of salmon at sea as they relate to the size, condition, timing, and abundance of outmigrants. Each of these dynamics can affect survival at sea through size-selective mortality (Woodson et al. 2013), match–mismatch of salmon with their preferred prey (Satterthwaite et al. 2014), and competition (Miller et al. 2013). This points to a need to consider the interactions between freshwater and marine dynamics when considering the tradeoffs associated with different managerial scenarios. As well, this makes clear the need to consider a full life-cycle model to accommodate the implications of environmental variability and managerial action at any given life stage on the fisheries and spawning populations.

Life-cycle models such as the one presented here provide a tool that enables integration of data series and mechanistic models across life stages and habitats to describe the composite effects of processes contributing to population dynamics and can be used for strategic ecosystem-based management of migratory species such as anadromous fish. Our results support the hypothesis that escapement variability in CVFC is largely described by composite effects of freshwater and marine processes during the smolt to juvenile period. These results align with and reconcile previous research demonstrating the importance of these phases for recruitment to the population (Beamish and Mahnken 2001, Kilduff et al. 2014, Woodson and Litvin 2015, Wells et al. 2016, Michel 2018). Our results also point to key management levers related to the most influential processes found to affect the CVFC population (freshwater temperature, flow, and marine predation). In particular for CVFC, freshwater temperatures may be managed, as is presently done for Central Valley winter-run Chinook, through modification of dam operations to optimize the temperature of spawning areas. Similarly, pulse flow releases during juvenile outmigration will likely increase survival rates through the freshwater system. However, this operation will be most effective if considered relative to the potential for survival at sea, which relates both to predation risk (Wells et al. 2017) and the development of suitable forage (Friedman et al. 2018) upon which outmigrating juvenile Chinook rely. With increasingly variable marine conditions (Sydeman et al. 2013), in addition to increasing and dynamic predator populations (Chasco et al. 2017, Wells et al. 2017), the impact of prey-switching in years of low productivity will likely increase. Continued study of marine ecosystem dynamics can be pursued simultaneously with, and complement efforts to increase survival in the freshwater phase. Overall, management actions that promote diversity in the natural population will increase resilience in the population through strengthened portfolio effects (Mantua and Francis 2004, Carlson and Satterthwaite 2011, Satterthwaite and Carlson 2015, Herbold et al. 2018). The results of our work can be used to develop long-term strategies to sustain populations such as CVFC and thereby reduce variability in harvest and escapement. Finally, the methodology developed in this study can be used to improve conservation and management of other anadromous fishes and migratory species.

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SUPPORTING INFORMATION

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