

Thinking outside the channel: Timing pulse flows to benefit salmon via indirect pathways



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ABSTRACT

Using models to represent relationships between flow and fishes has important practical applications for managing reservoir releases. Attempts to model such relationships often neglect indirect mechanisms by which flow influences fish. For example, growth of salmon juveniles is measurably faster when flows inundate floodplain and promote higher production of invertebrate prey, but out-of-channel flows have not yet been incorporated into models. The QUANTUS model developed here represents indirect linkages between flow and freshwater survival, mediated by temperature and prey availability, for fall Chinook salmon (*Oncorhynchus tshawytscha*). Quantiles of spawning time and place were used to define cohorts of salmon in a regulated Central Valley, California river. Survival of these quantile-cohorts was simulated through incubation, juvenile growth, and eventual downstream migration. A genetic algorithm was used to optimize the seasonal timing of pulse flows. Simulated survival was highest for flow regimes that provided a modest, temperature-moderating pulse flow in early summer and, for wetter years, a second, larger pulse of over-bank flow in late winter. For many rivers of the Pacific coast that support fall Chinook salmon, the thermal window of opportunity for spawning and rearing is narrow. Optimized flows made the most of this window by providing access to accelerated juvenile growth and early survival in floodplain habitat, a result that should be verified with field experiments. Timing of optimized pulse flows differed in some respects from the region's natural hydrograph, dominated by spring runoff. This suggests that understanding the mechanisms by which flow influences fishes can be important when shaping flows in the changed context of a regulated river.

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1. Introduction

The path toward sustainable reservoir operation requires a more quantitative, science-based approach to shaping flows to benefit aquatic biota. A common approach to optimizing environmental flows uses linear goal programming to enforce downstream minimum flow targets [see review by Jager and Smith, 2008]. These targets are proscribed ahead of time and have little dependence on the state of the river ecosystem. Similarly, habitat-based approaches seek to maximize habitat for downstream species (Cardwell et al., 1996; Sale et al., 1982), but they do not represent dynamic population-level responses to flow. For example, if the entire fish population is killed on the second day, an optimization based on habitat has no way of knowing that flows on subsequent days are inconsequential. Some argue that capturing such complex flow linkages requires spatially explicit and population models (SEPMs) (Anderson et al., 2006).

Population-level responses to flow have been modeled using SEPMs linked with dynamic models of physical habitat (e.g., ORCM model, Jager et al., 1997; Perry and Bond, 2009; Van Winkle et al., 1998) and used to optimize flow regimes (Jager and Rose, 2003). This approach has three shortcomings. First, it requires significant field and modeling efforts to characterize transects and salmon habitat preferences using the In-stream Flow Incremental Methodology (IFIM). Second, IFIM habitat relationships with flow neglect the role of overbank flows and the ephemeral floodplain habitat. Third, computational resources and time required to solve for optimal flows are prohibitive because simulation of each candidate flow regime is time consuming. Model simplification is an appropriate next step, and one that is often neglected (Haefner, 2005).

Our understanding of flow-biota relationships has evolved. In the beginning, sections of streams were completely dewatered and the research question posed was “How much flow is enough?” Resource agencies acting on behalf of riverine biota, proposed minimum flows based on the In-stream Flow Incremental Methodology (IFIM; Stalnaker et al., 1995). For non-federal projects, a political licensing process set these targets. Over time, this was refined to include different minimum flows during different seasons and ramping rates to control the magnitudes of fluctuations during

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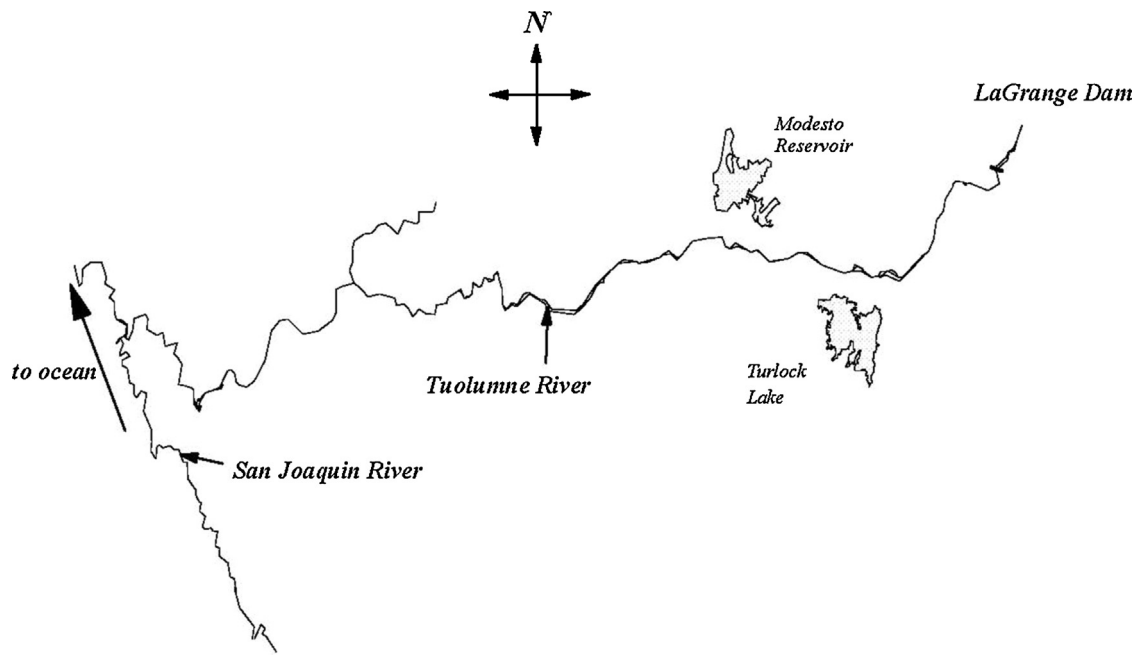


Fig. 1. Map of the Tuolumne River reach (simulated) showing the upstream barrier to migration (LaGrange Dam) and the outmigration route from the dam to the confluence with the San Joaquin River and northwest toward the ocean.

Source: Jager et al. (1997).

load-following operation (releasing flow to generate electricity during hours of peak demand). Efforts to optimize regulated flows typically use these minimum flows as constraints (Jager and Smith, 2008).

The IFIM method focuses on the extent to which suitable channel habitat increases with flow only within a restricted range of flows. The ecological values of higher flows are neglected, in part because conducting field surveys becomes dangerous at high flows and, in part, because quantifying habitat provided by rarely inundated floodplain is challenging. Teasing out complexities, including indirect pathways mediating flow's effects, population- or community-level effects, seasonal changes in flow-habitat relationships, and rare, but important, flow events, are beyond the scope of this empirical approach.

The Natural Flow Paradigm (NFP) articulates the importance of flow variability (Poff et al., 1997). This approach calls for static water allocation strategies to be replaced by strategies that protect the magnitude, frequency, duration, timing, and rate of change in flow (Arthington et al., 2006; Poff et al., 1997; Richter, 2010; Young, 1999). Under this paradigm, a pre-regulated flow regime is held up as a gold standard against which to measure regulated flow regimes. One potential flaw of the NFP is the tautological argument that aquatic biota evolved under a natural or unregulated hydrograph; therefore any deviations from this pattern are detrimental (Carlisle et al., 2011). In practice, deviations are measured by comparing univariate statistics of proposed regulated flow regimes with those of pre-impoundment flows. Any deviation is assumed to be detrimental to river biota, and all deviations are assumed to be equally bad. Is it really beneficial to mimic the unimpaired flow regime to the n th moment of its distribution? Are all statistical deviations equally harmful to aquatic biota? Is it safe to assume that relationships between flow and biota are the same in regulated tailwaters as they are in unregulated rivers?

The science of understanding flow effects requires that we move beyond both of these paradigms to quantify and understand what aspects of flow regimes are important and why (Bunn and Arthington, 2002; Jager and Smith, 2008; Poff et al., 2010). The Ecological Limits of Hydrologic Alteration framework was designed

to find univariate flow relationships (Poff et al., 2010). Although many qualitative relationships have been hypothesized (Naiman et al., 2008), few of these are sufficiently well-quantified to be used in a decision-making context. Most important influences of flow are indirect, mediated by temperature, refuge, prey availability, and other factors (Caissie, 2006), and others are context specific (McManamay et al., 2013). It is therefore important to monitor indirect pathways and to represent them in models describing flow-fish relationships. Externally derived flow targets applied without regard to context (mediating factors) are probably sub-optimal.

Extreme flows (flow pulses) play a special role, yet the indirect benefits of extreme flows have frequently been articulated, but rarely quantified. For example, Naiman et al. (2008) consider extreme floods essential for maintaining the ecological vitality of rivers. Infrequent high flows have been credited with shaping channels and inundating floodplain habitat. One empirically demonstrated example showed that juvenile fall Chinook salmon (*Oncorhynchus tshawytscha*) reared in enclosures within inundated floodplain habitat grew faster than those reared in the main channel of a California, USA river (Henery et al., 2010; Jeffres et al., 2008; Sommer et al., 2001a). The primary mechanism postulated for this growth advantage is higher production of invertebrate prey. The growth benefits of overbank flow were shown by recent field studies to be important, yet previous modeling efforts to optimize environmental flows have not considered such high out-of-channel flows.

The goal of this study was to determine whether well-timed inundation of floodplain would present a better alternative for managing flows to benefit fall Chinook salmon than those restricted to within-channel flows. I developed a model to represent bioenergetics growth benefits of floodplain inundation. The model was implemented for the lower Tuolumne River, a tributary of the San Joaquin River in California, USA, below Don Pedro Dam (Fig. 1). Jager and Rose (2003) conducted an earlier optimization for fall Chinook salmon in this tailwater using a spatially-explicit individual-based population model. For the purposes of optimization, the ideal model should be complex enough to represent important indirect, non-linear ecological responses to a wide range of flows, yet simple

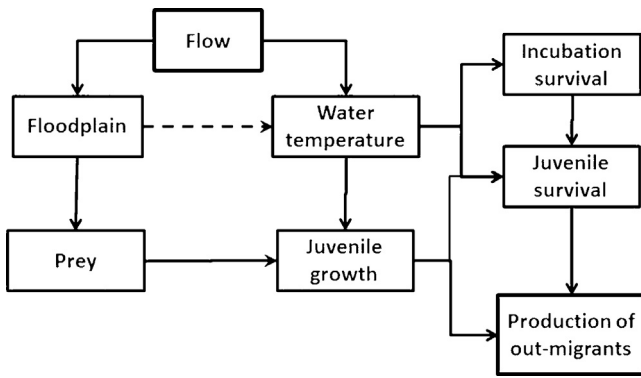


Fig. 2. Indirect pathways linking river flow and salmon production in the QUANTUS model.

enough to use in optimizations that require tens of thousands of runs. Because this study sought to understand general patterns (as opposed to real-time reservoir operation), a number of simplifications were made, including a simpler representation of physical habitat, parametric representation of pulse flows, and a space-time quantile-modeling approach. Seasonal patterns of pulse flows that maximized simulated survival from egg to outmigration were compared with the historical ‘natural’ flow pattern and with flow-optimization results using ORCM.

2. Methods

Three main parts of the approach to design flows for salmon are: (1) simulating river habitat, (2) simulating direct and indirect linkages between flow and salmon survival, and (3) optimizing the timing of pulse flows. Flow is linked to salmon survival from egg to outmigration through two indirect pathways: temperature and prey availability (Fig. 2). Parameter values used in the model are summarized in Table 1.

2.1. Model for river habitat

River habitat in this model consists of longitudinal representation of three drivers, flow, air temperature, and dam-release temperature. Flow is the decision variable in the optimization. Water temperature was derived from equilibration between dam-release temperature and air temperature as a function of flow, as described in Section 2.2 below.

2.1.1. Habitat–flow regime

The flow-regime generator allocates a total annual flow, which is expressed as the equivalent average daily flow, Q_{avg} , in $m^3 s^{-1}$. Generated flow regimes, $Q(t)$, consist of three parts: a minimum flow, Q_{smin} , and two flow pulses, Q_{pulse_1} and Q_{pulse_2} (Eqs. (1)–(3); Table 1). Each pulse was represented by a uni-modal pattern of flows and four parameters of the double Weibull distribution. Each pulse begins on day $Jday_p$ and extends for Dur_p days. Input parameters, provided as days of the year, are converted by transformation W to water-year dates that begin on day 274. Parameter k_p control how steeply each of the flow pulses increase and decrease. Eq. (1) describes the Weibull relationship for a single pulse, p . Parameter, tm_p , shifts the Weibull distribution forward or back in time. This parameter was fixed at zero (beginning of the water year) for the putative fall pulse and optimized across values less than $Jday_2$ for the second pulse. Note that this model for pulse flows is flexible; although originally envisioned as fall and spring pulses, the

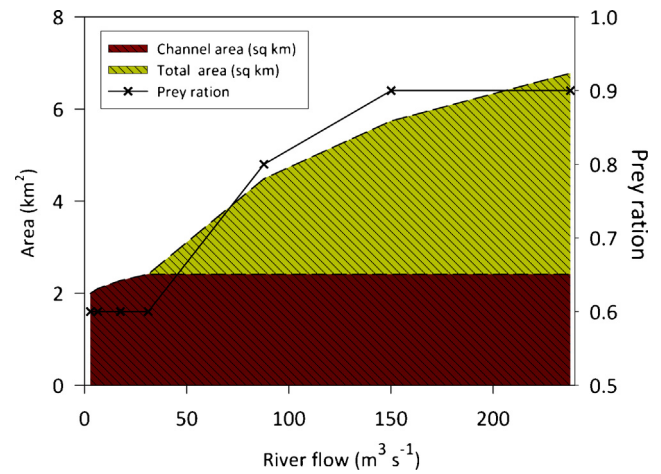


Fig. 3. Inundation of floodplain area in the Tuolumne River increases with flow once bankfull-flow is exceeded. Prey ration as shown here is simplified to be a function of a single day’s inundated floodplain area for minimum ration, $P_{min}=0.7$ and a rate of increase, $kf=0.4$.

first pulse does not necessarily have to occur before the second and they may even converge to form a single peak.

$$Q_{pulse,p} = \begin{cases} \left(1 - e^{-\left(\frac{W(t)-W(tm_p)}{W(Jday_p)-W(tm_p)}\right)^{2k_p+1}} \right) & t > tm_p \\ e^{-\left(\frac{W(t)-W(tm_p)}{W(Jday_p)+Dur_p-W(tm_p)}\right)^{2k_p+1}} & t < tm_p \\ 0, & t \leq tm_p \end{cases}, \quad (1)$$

$$q(t) = Q_{smin} + \sum_{p=1}^2 Q_{pulse,p} \quad (2)$$

$$Q(t) = q(t) \left(\frac{T \cdot Q_{avg}}{\sum_T q(t)} \right) \quad (3)$$

2.1.2. Habitat–floodplain inundation

In the Tuolumne River, inundation of floodplain areas begins when flows exceed approximately $30 m^3 s^{-1}$ (Fig. 3), based on aerial photographs taken between 1988 through 1995 at flows ranging from 2.83 to $237.9 m^3 s^{-1}$ (Gard, 2008). However, in some rivers, floodplains can be partially inundated without overbank flow due to large influences of groundwater and/or rainfall (Reese and Batzer, 2007).

2.2. Habitat–water temperature

Water temperature is an important variable driving the model, and two options are provided for simulating temperatures in $^{\circ}C$ near the regulating dam. I simulated seasonal changes in water temperature as a function of sinusoidal seasonal patterns in air temperature, T_a and reservoir release temperature, T_r . Reservoir release temperatures below La Grange Dam (Don Pedro Lake) vary over a much narrower range than air temperatures, but follow a similar relationship to that in Eq. (4) with a different maximum and average.

$$T_{[a,r]}(t) = T_{avg} + (T_{max} - T_{avg}) \sin\left(\frac{2\pi(t - t_{avg})}{365}\right), \quad (4)$$

Table 1
Parameter values used in QUANTUS simulations for the Tuolumne River, California.

Name	Value	Parameter description
Bioenergetics parameters – prey, feeding, and growth in length		
<i>al</i>	0.0005	Intercept of relationship between fry length and weight, fitted to data from EA Engineering Science and Technology (1992) by Jager et al. (1997)
<i>bl</i>	2.136	Exponent of length vs. weight relationship for fry, fitted to data from EA Engineering Science and Technology (1992) by Jager et al. (1997)
<i>ca</i>	0.50	Maximum consumption, allometric intercept (g/g/d); increased from value of 0.35 fitted to data from Myrick (1999); Eq. (10)
<i>cb</i>	−0.275	Maximum consumption, exponent of fish weight (g) (Brett, 1971) (Stewart and Ibarra, 1991); Eq. (10)
<i>cTq10</i>	5.0	Maximum consumption, Q10 temperature parameter (Stewart, 1980); $f(T)$ in Eq. (10)
<i>cTopt</i>	18.5	Maximum consumption, optimal temperature (°C) (Stewart, 1980); $f(T)$ in Eq. (10)
<i>cTmax</i>	26.0	Maximum consumption, temperature (°C) with zero growth; (Myrick, 1999; Myrick and Cech, 2002); $f(T)$ in Eq. (10)
<i>kf</i>	0.4	Rate of increase in prey ration as overbank flow increases ($m^3 s^{-1}d$); guided by (Sommer et al., 2001b); Eq. (11), Fig. 2
<i>Pmin</i>	0.7	Minimum prey ration, calibrated to produce reasonable juvenile growth, guided by (Myrick, 1999; Sommer et al., 2001b); Eq. (11), Fig. 2
Bioenergetics parameters – energetic costs (Eq. (9))		
<i>Ep</i>	0.4	Combined fraction of consumption lost to egestion, excretion, and digestion, found to be relatively constant by Elliott (1976); Eq. (8)
<i>Ar</i>	0.00264	Respiration, allometric coefficient, g/g; fitted to (Myrick, 1999) data for Chinook salmon (Stewart and Ibarra, 1991); Eq. (9)
<i>Br</i>	−0.217	Respiration, Exponent of fish weight; Rao (1968) rainbow trout, <i>O. mykiss</i> ; Eq. (9)
<i>Cr</i>	0.06818	Respiration, temperature exponent; Rao (1968) rainbow trout; Eq. (9)
<i>Sact</i>	0.0232	Active respiration coefficient of exponential swim speed relationship (Stewart et al., 1983); Eq. (9)
<i>Aact</i>	11.7	Swim speed coefficient – intercept of weight (Stewart et al., 1983); Eq. (6)
<i>Bact</i>	0.05	Swim speed exponent of weight (Stewart et al., 1983); Eq. (6)
<i>Cact</i>	0.0405	Swim speed exponent of temperature (Stewart et al., 1983); Eq. (6)
Movement parameters calibrated to match observed timing of outmigration roughly calibrated to (EA Engineering Science and Technology, 1992)		
<i>Bmove</i>	0.15	Minimum daily rate of downstream movement ($cm s^{-1}$) when flow is near zero; Eq. (7)
<i>Fmove</i>	0.05	Effect of flow on the rate of downstream migration ($s m^{-3}$); Eq. (7)
<i>Fmove</i>	0.5	Fraction of minimum smolt size, L_{smolt} required to begin migration, dimensionless; Eq. (7)
Parameters describing river habitat (Eqs. (1)–(5))		
<i>Lsegsp</i>	40.5	Redd distribution – maximum distance below dam (km), see Jager et al. (1997)
<i>DamRkm</i>	84	Location of dam (from San Joaquin confluence), tributary length (km), see Jager et al. (1997)
<i>UPmin, UPmid, UPmax</i>	274, 307, 357	Julian dates characterizing a triangular distribution that describes the timing of spawner upmigration and produces temporal quantile-cohorts of offspring, see Jager et al. (1997)
<i>tavg</i>	94	Julian day that air temperature first reaches T_{avg} in spring; fitted to local air temperatures by Jager et al. (1997); Eq. (4)
<i>Tavg</i>	16.0	Average annual air temperature (°C; sinusoidal function); fitted to local air temperatures by Jager et al. (1997); Eq. (4)
<i>Tmax</i>	30.0	Maximum annual air temperature (°C; sinusoidal function) fitted to local air temperatures by Jager et al. (1997); Eq. (4)
<i>ktemp</i>	0.0002	Temperature equilibration rate coefficient (s^{-1}) fitted to local air and water temperatures by Jager et al. (1997); Eq. (5)
<i>TdelFlood</i>	1.5	Temperature increment during floodplain inundation (due to a higher proportion of shallow water); (Sommer et al., 2001b)
Parameters describing biological development		
<i>DDeggs</i>	500	Degree-days required from egg laying to hatching (°C) (Murray and McPhail, 1988)
<i>DDalv</i>	395.8	Degree-days required from hatching to emergence (°C) (Murray and McPhail, 1988)
<i>Lsmolt</i>	75	Minimum size required to develop into a smolt (mm) (EA Engineering Science and Technology, 1992)
Survival parameters		
<i>Kstarve</i>	0.5	Condition factor leading to starvation of juveniles, see Jager et al. (1997)
<i>STkL</i>	2, 12	Incubation temperature survival – steepness parameter (eggs, alevin) (Jager, 2011b); Eq. (13)
<i>STkU</i>	12, 12	Incubation temperature survival – steepness parameter (eggs, alevin) (Jager, 2011b); Eq. (13)
<i>Tlo</i>	3.5, 0.5	Lower temperature tolerance (°C–egg, alevin) (Jager, 2011b); Eq. (13)
<i>Thi</i>	16.5, 16.0	Upper temperature tolerance (°C–egg, alevin) (Jager, 2011b); Eq. (13)
<i>SLmin</i>	0.98	Minimum daily length-dependent survival fitted by Perkins and Jager (2011) to data in Connor et al. (2004); Eq. (14)
<i>SL50</i>	0.9642	Length-dependent juvenile survival fitted by Perkins and Jager (2011) to data in Connor et al. (2004); Eq. (14)
<i>SL90</i>	0.9917	Length-dependent juvenile survival fitted by Perkins and Jager (2011) to data in Connor et al. (2004); Eq. (14)
<i>STLC50</i>	25.4	Temperature-dependent survival – LC50 – full day exposure (Blahm and McConnell, 1970); Eq. (15)
<i>STLC90</i>	29.0	Temperature-dependent survival – LC90 – full day exposure (Geist et al., 2006; Hanson, 1997; Myrick and Cech, 2004); Eq. (15)

where $T_{[a,r]}$ = average daily air or release temperature, T_{avg} = average annual air or release temperature, t = day of year (1 to 365), t_{avg} = first day of the calendar year that average air and release temperature reach T_{avg} , and T_{max} = maximum air or release temperature. As parcels of water released from the dam travel downstream, they equilibrate to air temperatures at a rate controlled by water velocity (Eq. (5)), with a specified minimum of 3 °C.

$$T_{w,x} = T_a + (T_r - T_a)e^{(k_{temp} \cdot x/v)}, \quad (5)$$

where $T_{w,x}$ = average daily water temperature (°C) at segment x , T_r = average daily water temperature below dam (°C), T_a = average daily air temperature (°C), k_{temp} = the temperature equilibration rate (s^{-1}), v = water velocity ($m s^{-1}$), and x = distance below dam (m). Water velocities were obtained from relationships with flow measured by dye studies (Stillwater Sciences, 2011). Details on the approach used to fit this temperature model are given in Jager et al.

(1997). Finally, when floodplain was inundated, water temperature was incremented by $TdelFlood$ (Table 1).

2.3. QUANTUS, a quantile-based model of salmon production

QUANTUS tracks the development, growth, and survival of fall Chinook salmon by representing quantiles of the temporal and spatial distribution of redds (nests). Although the model can accommodate arbitrary number of quantiles, here, 5th, 25th, 50th, 75th, and 95th quantiles were used to characterize the distribution of redds in time and space. Temporal variation in spawning dates was described by quantiles from a triangular distribution beginning October 1st (day $UPmin$), peaking on October 27th (day $UPmid$) and ending on December 22nd (day $UPmax$) (Table 1). The spatial distribution of initial redds was also represented by quantiles of a triangular distribution over the upper portion of the river from the dam to the lower point below the dam where spawning takes place, $Lsegsp$ (Table 1). Five state variables tracked (i.e., attributes

of space-time quantiles) included: (1) day, (2) location in river km, (3) accumulated degree days, (4) life stage, (5) juvenile size, and (6) the number of surviving individuals.

Quantile-cohorts encountered seasonal changes in flow and water temperature at different developmental stages and sizes. For each quantile-cohort, progressive development through the egg and alevin life stages were defined by the number of degree days accumulated, DD_{egg} and DD_{alv} (Table 1). Incubation survival was modeled as a function of temperature for each stage. Fry were assumed to emerge from the gravel with a length of 35-mm after accumulating $DD_{egg} + DD_{alv}$ degree days. From this point forward, QUANTUS tracked growth and survival of cohorts until individuals in the cohort attained a length, L_{smolt} , required to become saltwater-tolerant smolts ready to migrate to the estuary and ocean.

After growing to fraction, F_{move} , of L_{smolt} , each cohort began to move downstream from their initial redd locations. Optimal swim speed was assumed to increase with cohort (fish) weight, W , and water temperature, T (Eq. (6), Table 1).

$$S_{opt} = A_{act} W^{B_{act}} e^{C_{act} T(t)} \quad (6)$$

Maximum distance (km) depended on S_{opt} and B_{move} , which controls the rate of increase in daily movement as a function of flow (Table 1). Locations, $x(t)$ for each day, t , were estimated by Eq. (7), in units of km below the dam.

$$x(t+1) = \begin{cases} x(t) + A_{move} S_{opt} [1 - e^{-B_{move} Q(t)}], \\ \frac{L(t)}{L_{smolt}} > F_{move} \\ x(t), \text{ otherwise} \end{cases} \quad (7)$$

2.3.1. Salmon bioenergetics

The juvenile growth model simulates the growth of each quantile cohort from emergence until fry became smolt and leave the tributary. The simulated growth rate of juveniles belonging to a quantile cohort depends on temperature, fish size, and the amount of inundated floodplain (a function of flow). Daily growth, ΔW (g wet weight), is

$$\begin{aligned} W(t) &= W(t+1) + \Delta W, \\ \Delta W &= C - Ep \cdot C - R, \end{aligned} \quad (8)$$

where C = daily consumption and R = standard + active respiration. Elliott (1976) observed that three energetic costs: egestion, excretion, and specific dynamic action (cost associated with digestion) varied widely as individual components, but tended to sum to a constant proportion Ep of consumption (Table 1). This simplified model for energetic costs achieved better success in matching empirical data than a fuller model (Jager, 2011a).

$$R = A_r W^{B_r} e^{C_r T} e^{S_{act} S_{opt}} \quad (9)$$

Consumption was modeled as a unimodal function (Eq. (10)) of fish weight, W in g and daily temperature, $f(T)$. A model for prey ration, P , is described by Eq. (11). Three parameters in Table 1, cT_{max} , cT_{opt} , cT_{q10} are used to model temperature dependence via function $f(T)$, as described by Mitchell et al. (1977).

$$C = PC_{max}; \quad C_{max} = caW^{cb}f(T) \quad (10)$$

To estimate growth in length from growth in weight, expected length, L (mm), was estimated from an allometric relationship with weight, with parameters al and bl (Table 1). In days when the length of juvenile salmon in a quantile-cohort fell below that expected based on their weight, length was increased to that expected (see Jager et al., 1997).

2.3.2. Flow effects on growth

The influence of flow and floodplain inundation on growth is mediated by productivity and prey availability. Ration (P) was increased from a minimum of P_{min} to one as the antecedent area of floodplain inundated, Fd , increased (Eq. (11)). Parameter kf controls the rate at which ration increases in response to floodplain area. The antecedent area of inundated floodplain, Fd , is a running average of floodplain area using a memory factor of 0.5. Antecedent area is measured in $\text{km}^2\text{-d}$, and resets to zero whenever flows fall below bank-full flow. The relationship between prey ration and river flow is illustrated by Fig. 3.

$$P(Fd) = P_{min} + [1 - P_{min}] [1 - e^{-kf \cdot Fd(t)}] \quad (11)$$

2.3.3. Salmon survival

Survival. Survival is simulated through each life stage, as defined by thresholds in fish size and position. Overall quantile-weighted survival from egg to smolt serves as the objective function to be maximized (Eq. (12)).

QUANTUS simulates survival from egg to outmigration. Survival is estimated for two periods, incubation and the juvenile rearing period. Values are calculated for cohorts each space-time quantile and depend on the unique temperatures and growth opportunities that they experience. Calculation of survival ends once the cohort reaches the smolt life stage and migrates out of the tributary. At the end of the simulation, survival through these periods is used to reweight quantiles when calculating the number of juveniles that survive to migrate to sea. Thus, the final proportion of eggs, E_{fr} , surviving to migrate as smolts is a convolution of the probability covered by each space-time quantile, $f_{qs,qt}$ and its egg-smolt survival, $S_{qs,qt}$ (Eq. (12)). Maximizing E_{fr} , is the optimization problem's objective.

$$E_{fr} = \sum_{qs} \sum_{qt} f_{qs,qt} S_{qs,qt} \quad (12)$$

Components of survival that affect different life stages are described in the subsections below.

Incubation. During the incubation period, a uni-modal function described the response of survival to temperature (Eq. (13)). Parameters were fitted by Jager (2011b) as part of a meta-analysis of available studies and represent tolerances of eggs and alevins (larvae) weighted by sample sizes of these studies.

$$S(T_t) = \left[1 - e^{-(T_t/T_{lo})^{2ndkl+1}} \right] \left(e^{-(T_t/Thi)^{2ndkl+1}} \right) \quad (13)$$

For each quantile, overall survival through the life stage is the product of daily survival values.

Rearing. Juvenile survival for a given quantile cohort continues to decline until that day in spring when the cohort attains length L_{smolt} and reaches the confluence with the mainstem San Joaquin River. L_{smolt} is a minimum size required to begin the smoltification process needed to achieve saltwater tolerance, a prerequisite for entering the estuary environment. Because rearing can occur downstream in the San Joaquin River, cohorts that reach the confluence and that have not grown large enough are permitted to continue growing in the last downstream cell.

Survival of juveniles through each day is a product of length-based survival of predation and temperature-related survival. In addition, quantile cohorts for which relative weight, W_t/all_t^{bl} fell below a critical value, $Kstarve$, at any point between emergence and out-migration starve (Table 1).

Fish length is known to affect predation risk, and a logistic model (Eq. (14)) was used to describe length-based survival based on

tagged releases. The equation below was fitted to data by Connor et al. (2004) by (Perkins and Jager, 2011).

$$S_L = SL_{min} + \frac{1 - SL_{min}}{1 + e^{a+b \cdot L_t}};$$

$$b = \frac{\log(1 - 0.9) - \log(0.9)}{SL90 - SL50};$$

$$a = \log(1 - 0.9) - \log(0.9) - b \cdot SL90$$
(14)

High temperatures retard the process of becoming saltwater-tolerant and can cause mortality by elevating respiration costs (Marine and Cech, 2004; Myrick and Cech, 2002). Temperature-related survival was represented in Eq. (15) by a decreasing logistic function of daily average water temperature, T in °C, with a minimum of zero, as described in Jager (2011b).

$$S_T = 1 - \frac{1}{1 + e^{a+b \cdot T_t}};$$

$$b = \frac{\log(1 - 0.9) - \log(0.9)}{STLC90 - STLC50};$$

$$a = \log(1 - 0.9) - \log(0.9) - b \cdot STLC90$$
(15)

2.4. Scenarios

Because optimal flow allocation could differ in years with different amounts of water, I sought optimal flow regimes for three hydrologic scenarios with total annual flows of 0.315 km³ (256 thousand acre-feet; TAF), 0.631 km³ (511 TAF) and 0.946 km³ (767 TAF). Allocated uniformly throughout a year, these would correspond to constant flows of 10, 20, and 30 m³ s⁻¹, respectively. For reference, the quartiles of regulated flows in the Tuolumne River between 1971 and 1997 were 25% ≤ 6.4 m³ s⁻¹, 50% ≤ 12.0 m³ s⁻¹, and 75% ≤ 36.5 m³ s⁻¹ (Brown and Ford, 2002). Unimpaired flows were historically much higher, with a median daily average flow of 33.6 m³ s⁻¹ (Brown and Ford, 2002).

2.5. Pulse-flow optimization

This study posed an optimization problem that shapes seasonal flows to maximize salmon survival to outmigration as simulated by the QUANTUS model based on relationships between seasonal flow patterns and salmon production. The problem involved eight decision variables (model parameters) describing flow regime, including scaled minimum flow, Q_{smin} , and seven parameters that control the seasonal timing and duration of two pulses in flow. An evolutionary search algorithm implemented in R [“Rgenoud” package (Mebane and Sekhon, 2004)] solved for the values of this vector of eight parameters. An absolute minimum flow, $Q_{smin} = 1.91$ m³ s⁻¹, the summer minimum flow in the Tuolumne River (Jager et al., 1997), was imposed as a hard constraint. No constraints were imposed on pulse magnitudes, but the resulting pulses were all lower than the legally mandated maximum of 2500 m³ s⁻¹ below Don Pedro Dam (Federal Register 2682, April 25, 1956, §208.82).

Evolutionary or genetic algorithms borrow concepts from evolution. A sequence of generations is simulated for a virtual population, where each ‘genotype’ corresponds with a set of parameter values that describe the flow regime (see text before Eq. (1)). These parameters [Q_{smin} , $FallJday$, $FallJdel$, $SprJday$, $SprJdel$, $Falltmin$, $FallK$, and $SprK$] were treated as integer decision variables (Q_{smin} scaled by 1000). The ‘fitness’ of each genotype is the optimization’s objective value (i.e., salmon production). As with other heuristic global search methods, genetic algorithms have both a deterministic and a random component. In genetic algorithms, mutation and sexual recombination are random features that provide the capability to generate new combinations that permit the search to escape from local optima.

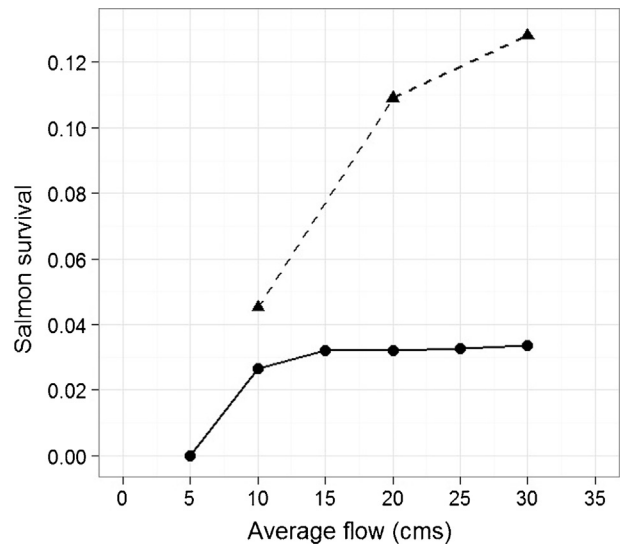


Fig. 4. Simulated juvenile survival increases as a function of flow for constant flow regimes (solid line) and optimal flow regimes (dashed line).

The genetic algorithm simulated 1600 ‘genotypes’ (parameter combinations) (Gibbs et al., 2011), for up to 1000 generations or until no changes in the solution were observed for twelve generations, within a specified solution tolerance of 10⁻⁵ for the fraction of surviving eggs. Numerical derivatives were checked before stopping. Solutions were reached within 24–80 h. For each scenario, optimal flow regimes were compared using different initial starting points in to evaluate whether they converged to the same solution. Results for the two solutions with highest objective values are presented for each scenario.

2.6. Sensitivity analysis

Sensitivity analysis can be used to identify which parameters influence model-simulated survival for fall Chinook salmon. I implemented broadband sensitivity for 55 input parameters for the scenario with an average annual 20-m³ s⁻¹ flow and parameters for the optimal flow regime. For each parameter, a sample of size 10,000 was drawn independently from a beta distribution with a mode set to a selected value (Table 1), shape parameter equaling 2, and limits specified as the mode ±10% (Gramacy and Taddy, 2010). Draws resulting in values beyond the parameter’s domain (survival, $SL_{min} > 1$ or crossing over of limits, e.g., $Up_{mid} > Up_{max}$) were rejected, leaving 9727 valid parameter combinations. Sensitivity was assessed by comparing semi-partial Pearson correlations between egg-outmigration survival and each parameter. Semi-partial correlations assess the influence of one parameter, holding others constant. Positive values indicate a positive influence on survival and vice versa.

3. Results

Simulated salmon production increased with total annual flow for both optimal and constant flow regimes, but optimal flow regimes showed much higher survival than corresponding constant flow regimes (Fig. 4 and Table 2). Differences in survival were larger for years with more water, as indicated by the average flow (Fig. 4).

3.1. Pulse-flow optimization

Hydrographs produced from different initial starting values converged, as illustrated by the difficulty in distinguishing their

Table 2

Optimization results for scenarios representing a range of hydrologic conditions, as indicated by total annual flow in km³ and thousand acre feet (TAF). Parameters are scaled minimum flow index (*Q_{min}*), begin dates (*Jday*), and duration (*Jdel*) of each of two flow pulses, location parameter for the second pulse (*tmin*), and steepness parameters (*k*) for each of the two simulated pulses.

Total annual flow	Average flow (cms)	<i>Q_{min}</i>	<i>Jday</i> ₁	<i>Jdel</i> ₁	<i>Jday</i> ₂	<i>SprJdel</i> ₂	<i>tmin</i>	<i>k</i> ₁	<i>k</i> ₂	Optimal-flow salmon survival	Constant-flow salmon survival
0.316 km ³ (255.6TAF)	10	0.057	340	88	160	39	59	17	15	0.0451	0.0273
0.632 km ³ (511.2TAF)	20	0.056	176	7	57	53	56	9	25	0.1090	0.0331
0.946 km ³ (766.8TAF)	30	0.167	179	1	46	70	45	7	10	0.1280	0.0347

solutions in Fig. 5. A late-spring pulse flow around day 180 coincided with extremes in temperature during all hydrologic years (Fig. 5). An early-spring pulse (~day 90) inundated floodplain during the period of juvenile growth for the two wetter years (Fig. 5). No pulses exceeding bank-full flow were included in the optimal regime for driest year, and the second pulse was extended throughout winter (10 m³ s⁻¹ in Fig. 5), with low minimum flows during the remainder of the year.

Survival for quantiles differed in space and time. Patterns in incubation survival were similar for the three flow regimes; it was generally poorer for eggs and alevins in the latest cohort of redds (Time quantile 5 of “Egg-Hatch” and “Hatch-Emerge” cubes in Fig. 6a–c). Post-hatch survival was lower for redds located just below the dam (Space quantile 1 “Hatch-Emerge” in Fig. 6a–c). Low temperatures below the dam slowed development and delayed simulated emergence of upstream redds. However, the latest redds built survived better in moderated temperatures just below the dam than they did farther downstream (Time quantile 5 in Fig. 6a–c).

Juvenile survival showed a pattern of highest survival in progeny from redds constructed early and farther downstream (lower right corner “Emerge-Smolt” in Fig. 6a–c). In the bottom row of Fig. 6a–c, the plot labeled “Emerge-Smolt” summarizes survival of three contributing sources of mortality shown in the middle row of the plots. Predation survival was highest for juveniles originating in early, downstream redds (“Juv-Pred” in Fig. 6a–c). Because it is length-based, survival is higher for faster-growing cohorts and those with less far to travel. This pattern was consistent across hydrologic years. Temperature-related mortality had a much larger impact on simulated juvenile survival in the driest year, especially for progeny of earlier redds located farther upstream (“Juv-Temp” in Fig. 6a–c).

Simulated starvation occurred only in the driest year (“Juv-Starve” in Fig. 6a vs. b and c), with a large impact on juveniles from later redds.

To summarize overall patterns of survival, early redds always produced more outmigrants than later redds. Survival of redds located upstream was higher in dry years, whereas downstream redds experienced higher survival in wet years. Despite delayed emergence, juveniles from earlier redds below the dam experienced faster growth than their counterparts farther downstream. Consequently, they reached the requisite size to migrate out earlier. They thereby avoided elevated temperatures in late spring (Fig. 6c). In the driest year, juveniles farther downstream succumbed to temperature-related mortality and starvation (Fig. 6a). Temporal quantile-cohorts from redds just below the dam experienced similar temperatures just after emergence. After emergence, these quantile-cohorts traveled through lower temperatures as they moved downstream. Unlike the growth patterns produced by the wet-year optimal flow regime, early and late quantile-cohorts spawned near the dam in the driest year followed parallel growth trajectories. Growth trajectories converged for cohorts originating farther downstream.

3.2. Sensitivity analysis

Survival from egg to outmigrant, as simulated by QUANTUS, was most sensitive to variation in a parameter that controls predation on juveniles (length-dependent survival), *SLmin* (Fig. 7). Other parameters with influence were those influencing temperature itself (*TAIRmax* and *TAIRopt*) or temperature-related survival, *STLC50*, *STLC90*, *CTopt* (Fig. 7). Sensitivity to the growth exponent, *bl*,

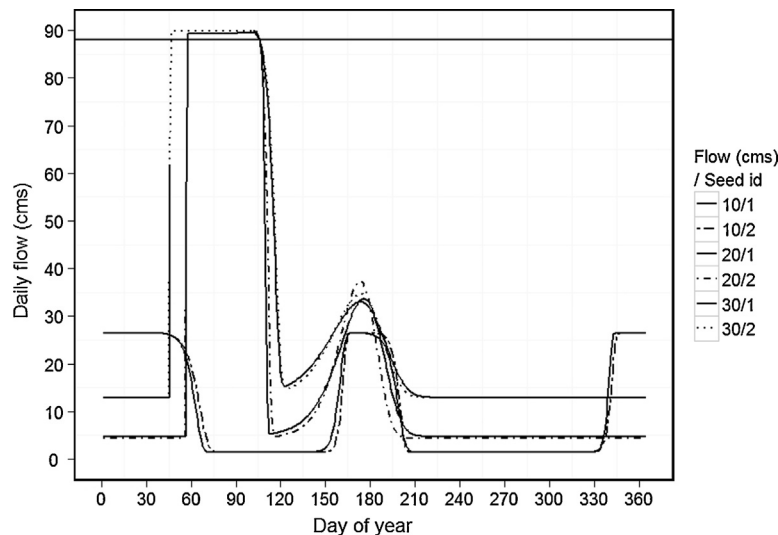


Fig. 5. Optimal flow regimes with two pulses over a range of hydrologic years with different average flows in cubic meters per second (cms) corresponding to total annual flows of 0.316, 0.632, and 0.946 km³, respectively. Degree of overlap between solid and dashed or dotted lines demonstrates the convergence of solutions obtained from two different initial seeds for each flow scenario. Floodplain is fully inundated at flows above the horizontal line.

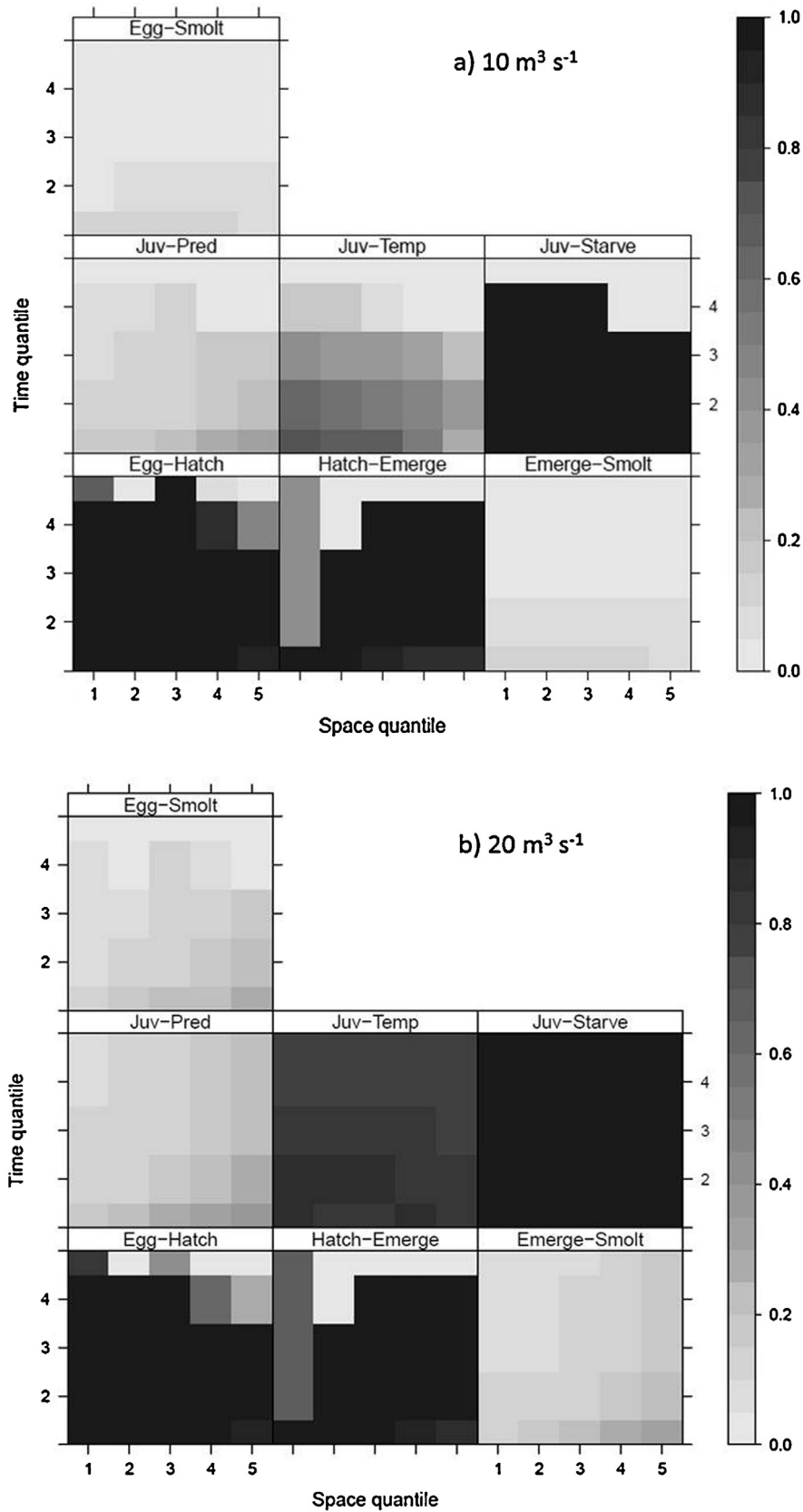


Fig. 6. Patterns of survival among space-time quantiles for a hydrologic year with (a) 0.316 km^3 , (b) 0.632 km^3 , and (c) 0.946 km^3 . Within each cube, the top plot labeled “Egg-Smolt” summarizes overall survival. Below this, survival through each of three early lifestages (bottom row), and three causes of juvenile mortality (middle row) are depicted.

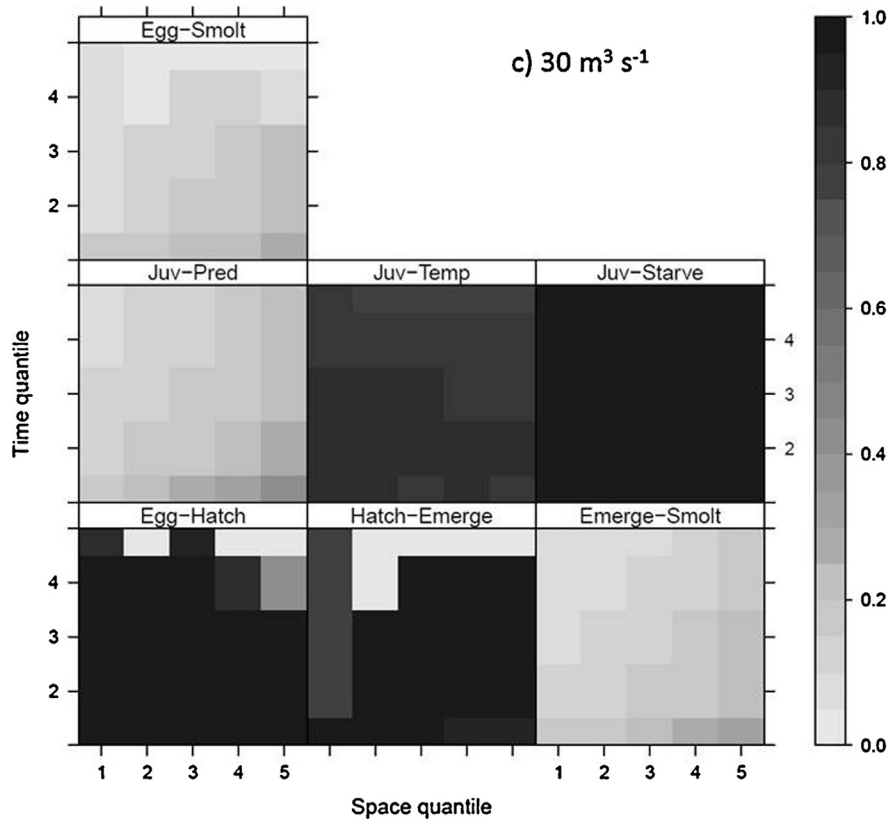


Fig. 6. (Continued).

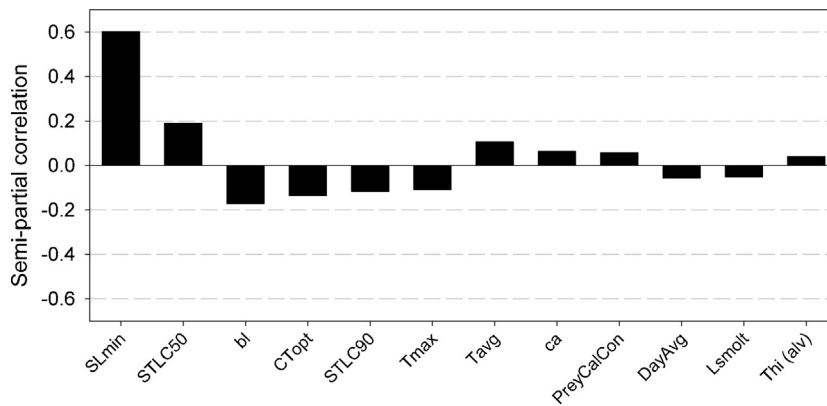


Fig. 7. Sensitivity index (semi-partial correlation) between simulated Chinook salmon survival and QUANTUS model parameters, excluding those with magnitudes < 0.04.

was also high, possibly because this parameter influences length-based predation risk.

4. Discussion

It is commonly believed that natural flow patterns will produce the best outcomes for riverine biota. The spring snowmelt recession is an important feature that shapes the hydrograph in the Central Valley (Yarnell et al., 2010), and salmon and other river biota are likely to have some adaptations that perform better in response to a historical hydrograph (Carlisle et al., 2011). The optimal patterns produced here differed in two respects from the seasonal pattern of natural, unimpaired flows. One pulse flow was allocated late spring/early summer for all three hydrologic scenarios. This pulse occurred about several weeks to one month later than that of historical, unimpaired flows [late June vs. mid-May; Lettenmaier and

Gan (1990)]. QUANTUS results for this pulse were consistent with the results from a more complex individual-based model, which provided the highest flows in spring for all but the driest hydrologic year (Jager and Rose, 2003).

QUANTUS optimization allocated a second, much larger pulse flow during late-winter in wetter years. This is a time that would not typically experience such events in a Central Valley hydrograph, except during rain-on-snow events (Lettenmaier and Gan, 1990). In fact, Cain et al. (2003) presented the 1985 hydrograph with high winter flows as an example of how unnatural patterns of flow in the Tuolumne River have become. Young et al. (2009) suggested that the timing of runoff in the Tuolumne River watershed will shift four weeks earlier if air temperatures increase by 4 °C. The favorable performance of a late-winter pulse suggests that a novel seasonal pattern might in some cases do more to enhance salmon production than the historical natural hydrograph when temperatures and

flows are regulated. Given the short generation time of salmon and the apparent plasticity in salmon life histories, the question becomes whether adaptation to new conditions is a feasible option. In southern rivers, such as the Tuolumne, the temporal window during which temperatures are tolerable is short, therefore requiring faster growth. Habitat-mediated limitations on growth can have a significant role in determining survival (Kennedy et al., 2008), and for salmon, the size at the time of ocean (and possibly estuary) entry is known to have a strong influence on smolt-to-adult survival. Thus, it is not surprising that the strategy of early emigration and estuary rearing is important in the San Joaquin basin (Miller et al., 2010).

4.1. Quantile modeling

The quantile approach introduced here can be extended to other species and rivers, but not all. It is most suitable when life history timing (e.g., early vs. late breeding) has a strong influence on how populations experience of flow-influenced habitat and situations where cohorts stay together over time and space for the period of interest (here, freshwater residence). When it is suitable, quantile modeling reveals patterns among space-time quantiles. Such patterns might help to understand trade-offs between traits that control the timing and location of breeding. For optimal flow regimes, earlier redds experienced an advantage over later ones. Compared with those under drier-year optimal flow regimes, the spatial location of redds with a better survival shifted downstream under wetter-year optimal flow regimes. However, this approach did not represent superimposition of earlier redds by later ones, which might be expected reduce the advantage of early spawning that was observed here. Such density-dependent phenomena are easier to represent in a spatially explicit population model [e.g., Jager et al., 1997].

4.2. Future directions

This study codified one of three mechanisms whereby elevated flow leading to floodplain inundation can promote juvenile growth and survival. Not only salmon, but many other fishes rely on the main-channels of larger rivers not as primary habitat, but as ‘highways’ that provide access to productive floodplain and off-channel habitat (Galat and Zweimuller, 2001). Two other mechanisms (lower velocities and elevated water temperatures) that promote growth were not modeled here, but could be explored in future. Flow effects may also be mediated by predation (e.g., Cavallo et al., 2013), but such effects are poorly documented. On the other side of the ledger, QUANTUS did not represent stranding risk associated with floodplain rearing, which has been raised as a potential concern (Grand et al., 2006). However, Sommer et al. (2005) concluded that the majority of juvenile salmon in Yolo Bypass emigrated successfully as the floodplain drained and did not remain in isolated ponds. Representing stranding might result in a less-steep descending limb for high pulse flows.

Ideally, the benefits of pulse flows presented here will be confirmed using large-scale flow experiments varying the timing and magnitude of pulse flows as recommended by Korman et al. (2012). Such experiments would require monitoring juvenile survival associated with lower, floodplain-inundating pulse flows. In addition, measuring covariates that mediate flow effects is likely to be important.

The model used for this study was not designed to proscribe real-time reservoir releases, but rather to understand qualitative patterns. The optimization problem posed here can be generalized to allow more pulses. To be used as a management tool, other competing objectives must realistically be included to provide practical guidance for reservoir operators. For the Don Pedro Dam, irrigation

is an important use of water. Future research should compare trade-offs and complementarities between flows shaped for ecological, energy, and those designed for other objectives.

4.3. Conclusions

This study demonstrated a relatively simple approach for determining key times when flow pulses are likely to benefit fishes. The space-time quantile-modeling approach captured what are likely to be the most essential features of the freshwater life history influenced indirectly by flow for this anadromous species. Simulated effects of flow were mediated by temperature and prey availability. A key result suggests that the strategy of allocating more water to late-winter pulse flows that inundate floodplain will benefit salmon production by speeding growth and expediting out-migration from rivers that become inhospitable in summer. However, under the natural hydrograph for the Central Valley, peak runoff typically occurs later, in spring. More generally, the natural hydrograph may not always be the best solution for fishes in regulated rivers because relationships with mediating factors have changed. In theory, better schedules for fish in tailwaters may be found by considering the mechanisms by which flow influences fish populations. The challenge remains to develop a better understanding and models of these relationships.

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