

Designing Optimal Flow Patterns for Fall Chinook Salmon in a Central Valley, California, River

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Abstract.—Widespread declines in stocks of Pacific salmon in the genus *Oncorhynchus* highlight the need for research to find new and effective management strategies for recovery. Two recovery objectives are (1) to ensure that recruitment is adequate to rebuild self-sustaining populations and (2) to maintain phenotypic diversity. This study seeks to understand how seasonal flow patterns in a flow-regulated California river might be managed to attain each of these recovery objectives, specifically for the fall and late-fall runs of chinook salmon *O. tshawytscha*. We ask two questions: (1) Does the optimal pattern of seasonal flows change as the amount of water available is constrained by droughts or diversions of flows? and (2) How do optimal flow regimes designed for the two conservation objectives differ? We coupled simulated annealing with a recruitment model to find flow regimes that maximize either the number of smolt out-migrant “recruits” (MR) or the variation in spawning times among recruits (MV). Optimal flow regimes identified for both the MR and MV objectives changed as we increased the annual quantity of water available, allocating higher flows during the spring and fall seasons. Flow regimes that optimized the MR and MV objectives were different. For example, the MV flow regime with unlimited annual flow provided a pulse of high flow 2 weeks before the peak spawning date of the minority late-fall run. Simulated recruits produced by MV flow regimes were fewer in number—and had parents that spawned later and over a wider range of dates—than recruits produced by MR flow regimes. Although these results have not been verified by empirical studies, they demonstrate the potential for managing species with special conservation status by combining state-of-the-art numerical optimization methods with mechanistic ecological models.

Anadromous salmonids play a significant role as keystone species in the river ecosystems draining to the Pacific coast of North America (Willson and Halupka 1995; Cederholm et al. 1999). Historically, Pacific salmon in the genus *Oncorhynchus* permeated coastal rivers and streams from Alaska to southern California. A tendency to return to spawn in their natal river allowed salmon populations to adapt to local environmental conditions (Waples 1995) and led to an adaptive radiation in life history traits for chinook salmon *O. tshawytscha* (Healey 1994). Collectively, salmon populations diversified into an array of populations (also known as “runs,” “races,” or “stocks”) with life histories distinguished by spawning time and place. The temporal diversity and geographic distribution of salmon populations resulted in the presence of one life history type or another during

most seasons of the year in coastal rivers throughout their range. These spawning aggregations support dozens of bird, mammal, and fish predators, and decomposing salmon carcasses provide a significant nutrient subsidy to the surrounding terrestrial ecosystem (Bilby et al. 1996).

Today, the majority of Pacific salmon stocks have declined, and healthy stocks (those exceeding one-third of their historical abundances) are outnumbered by stocks that are either currently at risk or recently extirpated (Nehlsen et al. 1991; Huntington et al. 1996). Life history diversity among salmon species has also declined because habitat degradation has differentially affected some races. This loss of life history variation is of particular concern for Pacific salmon, both from a conservation biology (i.e., single species) perspective and from an ecosystem perspective. From a conservation biology perspective, salmon species are defined by an evolutionary biology that promotes diversity in life history, and by a meta-population structure that requires diversity to per-

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Received April 26, 2001; accepted April 12, 2002

sist. Homing to natal streams and infrequent straying rates promote local adaptation, and therefore phenotypic diversity. This diversity of adjacent populations in time and space increases the likelihood that straying adult spawners will recolonize locally extinct runs and thereby enhance the long-term persistence of the metapopulation (Li et al. 1995; Stanford et al. 1996). One might consider salmon as having a temporal, as well as a spatial, metapopulation structure supported by straying from populations with different spawning times. From an ecosystem perspective, Pacific salmon represented a relatively stable component of ecosystems because of the temporal and spatial partitioning of river spawning habitat among populations. Efforts to restore salmon populations typically focus on two recovery objectives: (1) rebuilding the size of salmon populations, and (2) protecting salmon populations with unique genetic and phenotypic qualities.

Flow regulation is an important policy tool available for meeting these two conservation objectives for salmon (National Research Council 1996). Salmon declines have been attributed to many factors, including the "4Hs": harvesting, hydropower, habitat, and hatcheries (Lackey 1999). The alteration of natural river flows, by diverting water for hydropower and for other social uses, has contributed to decreases in salmon spawning habitat, both in quality and quantity. River flow is viewed by Poff et al. (1997) as a master variable that regulates the ecological integrity of rivers. Flow manipulations will only be effective as a tool for restoring salmon populations if the relationship between seasonal patterns of instream flow and salmon recruitment is understood.

Flow effects differ during different life stages and seasons. For example, elevated flows during the alevin life stage has been linked with reduced survival of salmonids (Jensen and Johnsen 1999), whereas higher spring flows may increase survival of spring out-migrants (Kjelson and Brandes 1989; Kope and Botsford 1990; Cada et al. 1993; Speed 1993; but see Williams and Matthews 1995). Reduced temperature-related mortality and reduced predation are two possible factors producing a positive survival-flow relationship in spring. Because juvenile salmon have low tolerance for elevated stream temperature, high spring flows provide an indirect benefit by slowing the rise in river temperatures during late spring and early summer. Predation on migrating juveniles may be lower during higher flows for two reasons. First, predation ef-

iciency is curbed at high river flows by higher turbidity, higher water velocities, and an increased tendency for prey to form aggregations (Peterson and DeAngelis 1992). Second, faster downstream migration at high flows shortens the duration of exposure to predation risk (Berggren and Filardo 1993), but it may also hasten exposure to high predation risk in the estuary.

The effect of river flow on salmon recruitment at times of year other than spring is less clear. Higher flows in fall attract adults waiting to migrate upriver to spawn (e.g., Fleming and Gross 1994). Elevated flows may facilitate swimming past natural and artificial barriers, or they may merely serve as a cue for migration. High fall flows are correlated with lower temperatures that benefit females migrating upriver by ensuring that eggs are not damaged before spawning (Independent Scientific Group 1996). The flow level during the building of redds influences later exposure to dewatering at lower flows and to scouring during flood events, favoring stable fall and winter flows (Becker et al. 1982; Stevens and Miller 1983). Summer flows can be very critical for the juvenile life stage of spring races because they remain in the river over summer before migrating to sea.

In this paper, we use a numerical optimization technique coupled with a recruitment model to design optimal seasonal flow patterns for salmon. Our analysis builds on earlier work linking flow management to chinook salmon recruitment (Bartholow and Waddle 1995; Jager et al. 1997). We use a slightly modified version of the Oak Ridge Chinook Model (ORCM) to simulate the main linkages between salmon biology and instream flow (Jager et al. 1997). We focus on the fall and late-fall runs of chinook salmon at the southern extreme of their range in the lower Tuolumne River, a tributary of the San Joaquin River, California.

We used optimization methods to identify the optimal pattern of seasonal flow for two different management objectives: (1) maximizing overall recruitment and (2) maximizing variation in run times among recruits. Recruitment is defined here as the number of individuals that successfully reach the smolt stage and emigrate from freshwater to saltwater. The run time of a recruit is defined as the date that a recruit was spawned by its parents. For each of the two objectives, we determined how the optimal pattern of seasonal flow changes in response to changes in the annual amount of water available. Decision-makers can use this information to adjust instream flow policies to the

hydrologic conditions (e.g., wet versus dry) in a given year.

Our analysis uses chinook salmon, a well-studied species, to demonstrate how optimization methods can be coupled with a biologically detailed recruitment model to identify optimal flow conditions. We recognize that our understanding of how flow affects the growth, survival, reproduction, and movement of salmon is incomplete, and the specific recruitment model we used is one of many possible model formulations. Despite these limitations, our approach can yield insights into optimal flows for chinook salmon and illustrate the general approach of coupling optimization methods to mechanistic models. Our method should be applicable to many other species for which environmental effects on recruitment are complex and for which it is important to identify optimal environmental conditions for recruitment.

Central Valley Chinook Salmon

The Central Valley of California historically supported substantial numbers of both spring- and fall-run chinook salmon (Myers et al. 1998; Yoshiyama et al. 2000). Although spring chinook salmon were historically more abundant than fall chinook salmon, they now represent a much smaller fraction of the fishery. Fall chinook salmon still support a significant ocean fishery due, in part, to hatchery production (Moyle 1994). The spring and winter runs have been extirpated from the San Joaquin River. Dams blocking access to headwater and spring-fed streams have resulted in population declines and federal listing of the spring and winter runs in the Sacramento River as endangered under the Endangered Species Act (Fisher 1994; Healey 1994; Myers et al. 1998).

Fall chinook salmon actually include two runs: a fall run and a late-fall run. Genetic differences between these two runs indicate that they were reproductively isolated, probably by temporal and spatial segregation of spawning (Nielsen et al. 1994). Fall-run adults spawn between October and December, whereas late-fall adults spawn between January and April. Historically, both fall runs occupied the Sacramento and San Joaquin river basins (Hatton and Clark 1942; Fisher 1994). Adults of the late-fall run spawned in upper main-stem rivers, where summertime water temperatures remained low enough for juvenile growth (Fry 1961; Fisher 1994). In the Central Valley, late-fall spawners lost access to their historical spawning habitat following construction of the Friant Dam on the San Joaquin River and the Shasta Dam on

the Sacramento River. The two runs and the two river basins are regulated jointly as the Central Valley fall-run Evolutionarily Significant Unit (ESU; National Marine Fisheries Service 1999), which is not currently listed by the federal government as threatened or endangered. Three lines of evidence suggest that the late-fall run has a considerably greater risk of extinction than the fall run: (1) population sizes are smaller (Yoshiyama et al. 2000), (2) population sizes are declining faster (Yoshiyama et al. 2000), and (3) two races (spring and winter runs) that also used spawning habitat above dams are now listed or extirpated. Both fall runs are considerably more depressed in the San Joaquin River basin than in the Sacramento River basin (Myers et al. 1998). According to Huntington et al. (1996), both the fall and late-fall runs are at risk of extirpation from the San Joaquin River basin.

Fall chinook salmon spend their adult lives in the ocean. At some point between ages 2 and 5, adults migrate into rivers during the fall to spawn (Table 1). Each female digs a redd in the gravel river bottom. During courtship, she releases her eggs into her redd. After fertilization of the eggs by one or more males, the female buries the eggs. Eggs incubate through the winter, hatch as alevins (nonfeeding larvae) into intergravel spaces, and emerge from redds as fry (defined here as presmolt juveniles) in the spring. The emergent fry of fall chinook salmon feed on invertebrates along river margins for the first month or two and gradually move downstream. Fry may exit tributaries in winter or spring to rear in the lower main stem and upper estuaries before becoming smolts. The process of smoltification enables them to tolerate saltwater and migrate to the ocean.

This study focuses on the Tuolumne River, a tributary of the San Joaquin River. The LaGrange Dam, at 83.7 km above the confluence, blocks upstream migration of adult salmon returning to spawn. The average natural annual flow estimated below LaGrange Dam between 1897 and 1923 was 2,390 hm³ (1 hm³ = 10⁶ · m³; McBain and Trush 2000). The average impaired annual flow measured below LaGrange Dam between 1971 and 1999 was 952 hm³ (McBain and Trush 2000; Paterson 1987:20–23). The difference between natural and impaired flow is accounted for by upstream water diversions.

Methods

The Oak Ridge Chinook Salmon model.—The Oak Ridge Chinook Salmon model (ORCM; Jager

TABLE 1.—Timing of events leading to recruitment of fall-run and late-fall-run chinook salmon in the Central Valley, California, and the main factors influencing the growth, development, and survival of each early life stage simulated by the Oak Ridge Chinook Salmon Model (FERC 1996).

Life stage	Fall run	Late-fall run	Influences on growth and development	Influences on survival
Egg	Oct–Dec	Jan–Apr	River temperature	Temperature Weighted usable area Density of spawners
Alevin	Dec–Mar	Mar–May	River temperature	Weighted usable area Density of spawners
Fry	Jan–Apr	Apr–Jun	River temperature Fish weight Fish size (rank)	Fish size Predator density Juvenile density
Smolt	Mar–Jun	Oct–May	River temperature Fish weight	Temperature Size of smolt Predator density Juvenile density Temperature

et al. 1997) is a spatially explicit and individual-based model of fall chinook salmon recruitment in a river below a dam. The model links a spatially explicit representation of river habitat with a biotic model of chinook salmon reproduction, development, growth, and mortality. The river habitat changes seasonally and includes important spatial gradients (e.g., temperature, predator densities) between upstream spawning areas and lower reaches inhabited during out-migration. The biotic component uses a daily time-step to simulate co-existing life stages, as individuals grow, develop from one life stage to the next, move, and die (Table 1). The ORCM simulates the river phase of chinook salmon ecology, beginning with adults entering the river to spawn. For each redd, we simulate the daily development and mortality of egg and alevin life stages. After emerging from redds, the daily development, growth, mortality, and downstream movement of individual juveniles (defined here as fry and smolts) is simulated, culminating in the migration of smolts from the river (i.e., recruitment). The values and definitions of model parameters are listed in Table 2.

Habitat component.—The biotic events leading from upriver migration of spawners to the out-migration of recruits are simulated in a spatially explicit river habitat represented by a series of adjacent, 1.6-km segments differing in the proportion of riffle and pool habitat, temperature, and flow (at confluences with tributaries or diversions). Simulated average daily water temperature in each river segment is determined by allowing water released by the dam (about 12°C year-round; FERC 1996) to equilibrate to the air temperature as the water travels downstream. The simulated river temperature of each segment depends on daily air

temperature, dam release temperature, and flow rate, which controls the rate of travel downstream. Daily flow in each segment is generated as part of the optimization procedure and used to drive the ORCM.

Each river segment is assigned a habitat capacity for each life stage (numbers/m²) that depends on empirical relationships between the amount of suitable habitat (weighted usable area or WUA) and daily average flow. The WUA relationships were estimated from results of an instream-flow study conducted in the Tuolumne River for each life stage and for two mesohabitats: riffle habitat and run–pool habitats, where runs and pools are treated as one mesohabitat (EAEST 1992b). The total capacity of each segment is a weighted sum of that provided by its riffles and that provided by its runs and pools.

Upriver migration and spawning.—Simulations begin with the migration upstream of 5,000 adults (4,673 fall run and 327 late-fall run) to the tributary represented by the model. This is roughly the average annual number of spawners counted between 1971 and 1988 in the Tuolumne River (EAEST 1992a). Individual spawner sizes are drawn from a normal distribution. The initial distribution of spawning times of migrating adult spawners follows a triangular distribution with a start date, peak date, and end date for each run. However, model spawners delay upstream migration if the water temperature at the mouth of the tributary or discharge from the tributary is below a threshold. The number of migrants on each day includes the proportion calculated from this distribution, plus those unable to migrate on previous days.

On the day of spawning, each female spawner

TABLE 2.—Parameter values used in the Oak Ridge Chinook Salmon Model simulations for the Tuolumne River, California. Parameter sensitivity is measured by the standardized regression coefficient, which varies from -1 to $+1$ and reveals both the direction and magnitude of a parameter's effect. We present sensitivities to two model predictions separated by commas: the simulated number of out-migrants and the peak date of out-migration. Those parameters excluded from the Jager et al. (1997) analysis are indicated by a blank, and those with a coefficient smaller than 0.05 are shown as zeroes.

Name	Value	Sensitivity	Parameter definition
a_{fec}	3,200.2		Intercept of fecundity relationship with fish length
a_l	0.0005		Intercept of relationship between fry length and weight
a_{move}	0.25	+0.05, 0	Movement rate at zero flow for fry (d/km)
a_{move}	0.16	0, 0	Movement rate at zero flow for smolts (d/km)
A_{rat}	250	0, 0	Scaling ratio for river size against Columbia River
A_{redd}	216	0, 0	Average defended redd area ($4 \times$ actual redd area; m^{-2})
A_{terr}	0.00148	0, 0	Coefficient in relationship between territory and fish length
B_{terr}	2.61	0, -0.13	Exponent in relationship between territory and fish length
b_{fec}	109.4		Slope of fecundity versus fish length (cm)
bl	2.136		Exponent of relationship between length and weight for fry
bq_{temp}	0.5	0, 0	Power function exponent relating velocity to flow
c_{move}	-6.0×10^{-6}	0, 0	Slope between travel time (d/km) and flow (m^3/s)
DD_{alv}	395.8		Degree-days required from hatching to emergence ($^{\circ}C$)
DD_{eggs}	500		Degree-days required from egg laying to hatching ($^{\circ}C$)
DD_{smo}	1,082	0, +0.15	Degree-days required to develop into a smolt ($^{\circ}C$)
F_{spawn}	0.5	0, 0	Minimum flow needed to upmigrate and spawn (m^3/s)
K_{temp}	-0.0006	0, 0	Temperature equilibration rate coefficient (s^{-1})
L_{min}	70		Minimum size required to develop into a smolt (mm)
$L_{s,avg}$	688		Average length of adult spawners (mm)
$L_{s,sd}$	74		Standard deviation of spawner lengths (mm)
$L_{s,min}$	400		Minimum length of spawning adults (mm)
$L_{s,max}$	1,400		Maximum length of spawning adults (mm)
L_{segsp}	40.5		Stream distance below dam used for spawning (km)
N_{esc}	5,000	+0.05, 0	Fall-run escapement (number of adults)
P_{cap}	0.0001		Maximum probability of successful prey capture
P_{late}	0.07		Fraction of total chinook spawners in late-fall run
P_{pock}	0.125	0, 0	Average fraction of egg pockets superimposed
P_{smo}	0.6	0, 0	Fraction of maximum intake obtained by smolts
P_{up}	0.4	0, 0	Probability of upstream movement at low temperatures
P_{min}	0.08	0, 0	Minimum fraction of maximum ration at feeding station
P_{max}	0.6	0, 0	Maximum daily ration (obtained by largest juveniles)
S_{min}	0.9997	+0.85, -0.34	Daily survival rate in marginal habitat
S_{rat}	0.44	0, 0	Fraction of adult spawners that are female
S_{wait}	14		Period from egg laying to female departure (d)
t_{avg}	Apr 4		First date that air temperature reaches T_{avg}
T_{avg}	16		Average annual air temperature ($^{\circ}C$)
T_{avoid}	22	0, 0	Lower threshold for behavioral avoidance ($^{\circ}C$)
T_{max}	30		Maximum annual air temperature ($^{\circ}C$)
T_{spawn}	17.8	0, 0	Upper temperature threshold for chinook salmon spawning ($^{\circ}C$)
T_{ULT}	25	+0.12, -0.34	Upper lethal temperature for chinook salmon ($^{\circ}C$)
UP_{max}	Apr 20		Latest date of late-fall spawning migration
UP_{max}	Dec 22	+0.16, +0.70	Latest date of fall spawning migration
UP_{min}	Jan 1		Earliest date of late-fall spawning migration
UP_{min}	Oct 1	+0.11, +0.16	Earliest date of fall spawning migration
UP_{peak}	Mar 1		Peak date of late-fall spawning migration
UP_{peak}	Oct 27	0, 0	Peak date of fall spawning migration

is assigned to a spawning location that is identified by its river segment and its site within the segment. The river segment is chosen at random from a triangular probability distribution that imposes a preference for segments closer to the dam. Segments with a larger proportion of riffle habitat contain more habitat suitable for spawning and incubation, as measured by the weighted usable area on day t (WUA_t ; EAEST 1992a). The site within

the segment points to a randomly selected entry in a ranked list of potential redd sites, where the total number of suitable sites varies daily in response to changing flows. Each river segment has a maximum number of suitable spawning sites available under optimal flow conditions. The model assigns sequential habitat quality ranks to these sites. On a given date, the number of suitable spawning sites, N_s , may be less than the number

available under optimal flow conditions, causing sites with higher ranks to become unsuitable (Figure 1).

$$N_s = \frac{WUA_t}{\text{average quality} \times A_{\text{redd}}}, \quad (1)$$

where average quality is estimated as the midpoint of minimum and maximum suitability index assigned to suitable redd sites in the model, and A_{redd} is average redd area. This approach captures the effects of changing flow on survival of eggs and alevins at both ends of the spectrum (i.e., scouring during high flows and dewatering during low flows).

Survival and development of eggs and alevins.—The model tracks the number of eggs in each redd over time. At the time of spawning, the female deposits her eggs; the number of eggs increases linearly with female length, with intercept a_{fec} and slope b_{fec} . Daily flow-related survival of eggs and alevins is 0 at sites with rank values exceeding the number of suitable sites. Daily survival among suitable sites increases from S_{min} at the lowest quality site (site with rank N_s) to 1 at the highest quality site (the site with rank 1; Figure 1C). Two other sources of mortality of early life stages are superimposition and temperature-related mortality. When a later spawner in the model selects the same site as a previous spawner with offspring that have not yet emerged, superimposition causes a binomial fraction of older eggs to be killed. Superimposition of previous redds occurs most often when redd densities are high and spawning habitat is scarce. Temperature-related survival is highest at moderate temperatures (8°C for eggs; 5°C for alevins) and drops to zero at extremes temperatures (below 0°C or above 17.2°C; Murray and McPhail 1988).

Incubation and development of eggs takes place over the period required to accumulate a fixed number of degree-days (Murray and McPhail 1988). The duration of the alevin stage is determined by the number of posthatching degree-days required to achieve the alevin stage (Murray and McPhail 1988). For both these life stages, we discount degree-days accrued at temperatures below 5°C by 50%.

Growth and development of fry and smolts.—Alevins emerge from redds at 30–40 mm in length (Murray and McPhail 1988; EBMUD 1992). The model simulates each juvenile chinook salmon as an individual after it emerges from the redd. Each model fry develops into a smolt when it has ac-

cumulated sufficient degree-days after emergence and has reached a minimum length (Jager et al. 1997).

On each day, t , the model simulates juvenile growth (weight gain is ΔW in g wet weight) using the bioenergetic model developed by Stewart et al. (1983):

$$W_{t+1} = W_t + \Delta W, \quad (2)$$

where wet weight gain, ΔW , equals consumption minus energetic costs (egestion, excretion, specific dynamic action, and respiration).

The length, L_{t+1} , of a juvenile chinook salmon increases only when it is in good physiological condition and experiences a positive weight gain:

$$L_{t+1} = \max \left[L_t, \left(\frac{W_t}{al} \right)^{1/bl} \right]. \quad (3)$$

Daily consumption is modeled by calculating ration as a proportion of maximum daily intake, which depends on water temperature and fish weight. The ration obtained by an individual depends on its rank (i.e., the number of larger, competing juveniles in its river segment). Energetic costs depend on temperature and fish weight.

Growth rates vary among individuals because of differences in their locations and sizes. We simulate variability among individual fry growth rates by assigning higher quality feeding stations to larger fish. Each day, fry living in a segment are ranked by size. Feeding stations are reassigned daily, such that the larger fry receive the higher quality stations that provide a higher rate of prey intake (Figure 1C). If there are more fry than stations, those fry lacking a suitable feeding station do not grow. A resident fry may be shifted to a lower- or higher-ranked feeding station as larger or smaller fry immigrate into the segment, as new fry emerge, or as resident fry die or leave.

We assume that a site with quality X ($P_{\text{min}} \leq X \leq P_{\text{max}}$) provides a fish with fraction $P = X$ of its maximum daily feeding ration. The same procedure used to define the number of spawning sites from spawning habitat capacity, WUA_s , is used to define the number of feeding sites based on juvenile habitat capacity, WUA_{juv} . The number of suitable feeding sites is the current WUA_{juv} divided by the average size of feeding “territories” for individuals in the segment (Figure 1A). Feeding stations are allocated to individual fry in inverse order of size (larger individuals first) until the total area of stations reaches WUA_{fry} for the river seg-

ment. Territory size, T_{size} (m^2), is derived for each fry from a relationship with fish length, L (mm) from Grant and Kramer (1990):

$$T_{\text{size}} = A_{\text{terr}} L^{B_{\text{terr}}}, \quad (4)$$

We assume that each smolt obtains a fixed proportion of maximum ration and does not compete for a feeding station, focusing instead on downstream migration.

Juvenile movement.—The ORCM allows each juvenile to disperse from the river segment of birth to other river segments and, eventually, out of the river. We assume different motivations for movements by fry and smolts. Smolt movements are directed toward migration out of the river, which progresses each day. Fry are motivated by the search for unoccupied rearing habitat with low predation risk and good conditions for growth, which can result in continued occupation of a single site. Simulated fry movement depends on fry density, habitat availability, and river flow and has a tendency to progress downstream. The probability of upstream movement was calibrated so that predicted rate of downstream movement matched the observed rate of downstream movement at different locations in the Tuolumne River. At temperatures above T_{avoid} , model fry tend to move upstream to avoid lethal temperatures (EPA 1971). The probability of upstream movement increases from P_{up} at temperature T_{avoid} to 1.0 at T_{ULT} .

Once a simulated juvenile decides to move, its movement occurs at a rate that depends weakly on river flow in the segment, Q (m^3/s). The model uses a linear relationship between mean travel time (d/km) during downstream movement and Q :

$$\text{travel time} = a_{\text{move}} + c_{\text{move}} \cdot A_{\text{rat}} \cdot Q, \quad (5)$$

where c_{move} is the flow coefficient fitted to data reported by Berggren and Filardo (1993) for sub-yearling chinook in the Columbia River and A_{rat} accounts for differences in river size between the Columbia and the Tuolumne rivers. To adapt this relationship for fry in the Tuolumne River, a_{move} was adjusted so that a maximum of 30 d was required for fry to travel 122 km (Berggren and Filardo 1993). For upstream movement of fry, the sign of c_{move} is reversed.

To simulate out-migration, the ORCM assumes that environmental influences indirectly act on migration times by hastening or delaying development into smolts. For smolts, a variety of cues (e.g., flow, change in flow, water temperature, precipitation, turbidity, photoperiod, smolt density,

the phase of the moon) can produce pulses of emigration (EBMUD 1992). The ORCM assumes that the necessary cues are present and that out-migration begins when fry become smolts. The daily distance traveled by a given smolt depends on flow (equation 5) and is always in a downstream direction.

Juvenile mortality.—The ORCM simulates mortality resulting from exposure to extreme water temperatures, premature emigration, and predation. Juveniles that remain in a segment with water temperatures above T_{ULT} (Brett 1952) die after 1 d of exposure. The model allows juveniles to avoid high, sublethal temperatures by increasing the likelihood of upstream movement.

Mortality may occur when fry leave the spawning tributary before smolting. Premature emigration is a more significant source of mortality when fry densities exceed the number of feeding stations because slower growth causes individuals to move downstream more frequently.

Fish predators, including smallmouth bass *Micropterus dolomieu*, largemouth bass *M. salmoides*, and Sacramento pikeminnow *Ptychocheilus grandis*, forage on chinook juveniles. Predator densities are specified for each of three river reaches defined by tributary confluences. Within each reach, predator densities are lower in segments with a high proportion of riffle habitat.

The original version of the ORCM simulated individual predator–prey encounters (Jager et al. 1997). This approach was computationally intensive, and sensitivity analysis indicated that ORCM model results were insensitive to the predation-related parameters (Jager et al. 1997). In the analyses here, we used a computationally more efficient option to simulate predation by replacing the individual encounters simulated between juvenile salmon (X = number of prey) and their predators (Y = number of predators) with the type II functional response (Holling 1959) shown in equation (6). We calibrated the probability of capture to obtain the same average level of predation as in the simulations that used individual encounters:

$$\text{Predation risk} = \frac{P_{\text{cap}} \cdot XY}{1 + P_{\text{cap}} \cdot XY}, \quad (6)$$

Testing and sensitivity analysis of the ORCM.—Jager et al. (1997) reported on the results of corroboration and sensitivity analysis of the ORCM. We summarize the results here. Corroboration consisted of comparing model predictions of juvenile growth and population size to field data collected

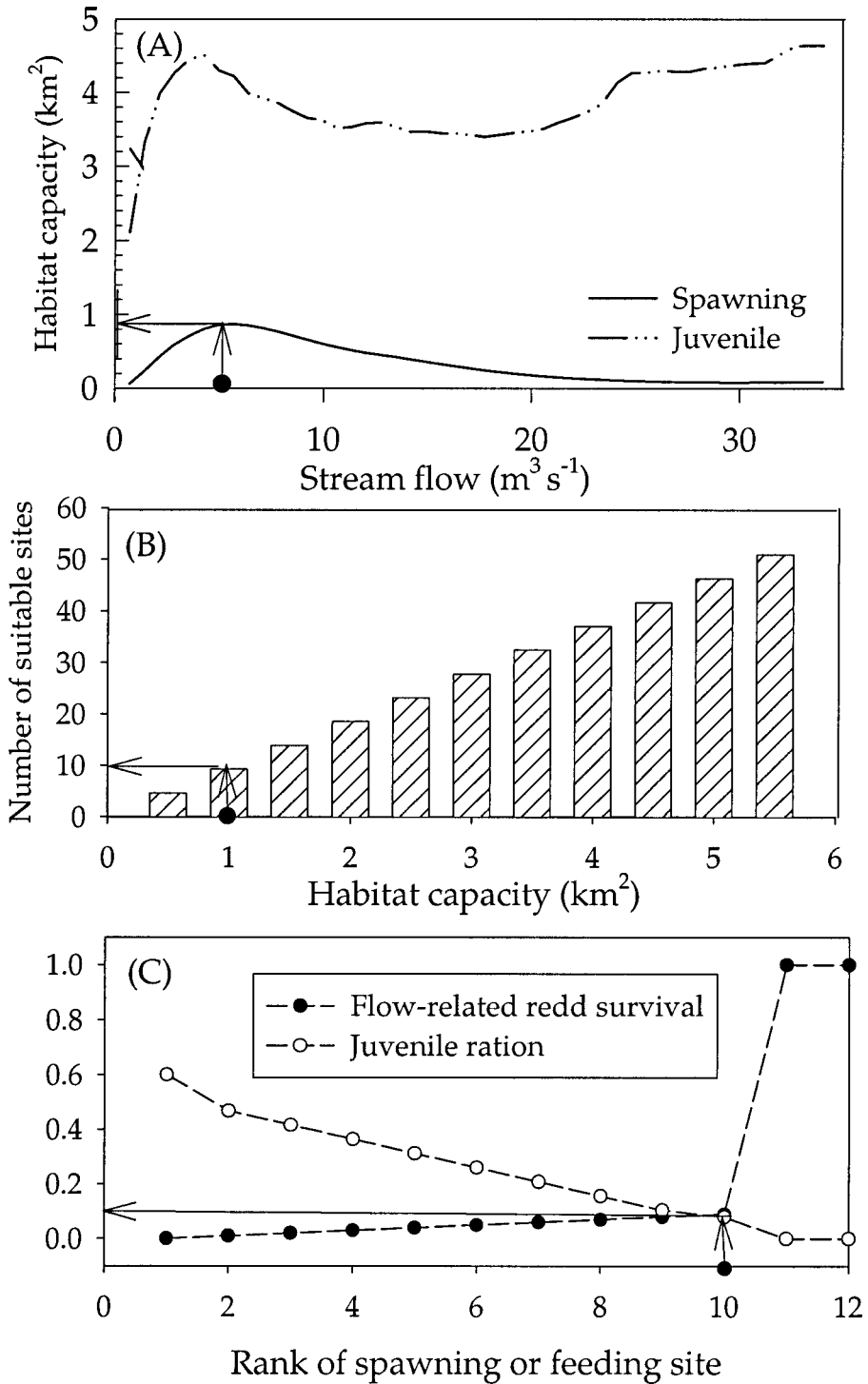


FIGURE 1.—Model representation of habitat effects on survival in redds and juvenile foraging. The model (A) represents habitat capacity as a function of river flow; (B) specifies a proportional relationship between the number of suitable sites and habitat capacity; and (C) specifies an inverse relationship between daily habitat-related survival in redds (ration) and the rank of the redd site (feeding station). To determine survival (ration) at a flow of 5 m^3/s , follow the arrows in panel A to calculate habitat capacity from stream flow, then calculate the number of suitable sites

in the Tuolumne River. Jager et al. (1997) compared the length distribution of simulated fry to the observed average, minimum, and maximum sizes from weekly seining catches in the Tuolumne River from January to May 1987. The average predicted and measured juvenile lengths had a maximum difference of 6 mm. Both the model predictions and the field data showed a great deal of variation among individuals. Although the maximum length increased as spring progressed, the minimum length remained constant at around 30 mm, suggesting the continual appearance of newly emerged fry. A second comparison was made between simulated population size at one date and a temporal and spatial snapshot of population size obtained using mark–recapture in early May 1987. An estimated $3,341 \pm 935$ (95% confidence limits) juvenile chinook salmon inhabited the 360-m stretch of river included in this study. We extrapolated that estimate to $14,920 \pm 4,174$ for our 1,609-m-long river segment. This extrapolated field estimate was similar to ORCM's prediction of 15,443 juveniles in segment 3 on May 4, 1987. Although model predictions were deemed sufficiently similar to observed values, there is extremely high variability in population size during this period when juveniles are leaving the system. Direct corroboration of the predicted number of out-migrants was not possible because emigrating smolts were not counted.

To evaluate parameter sensitivities of the ORCM, model parameters were varied and used to simulate recruitment under flow and temperature conditions for the 1986–1987 year. Jager et al. (1997) identified a subset of important parameters by excluding those with a strong basis in field data, and therefore low uncertainty, and those redundant in their effects with other parameters. Jager et al. generated 5,000 parameter combinations drawn by Latin-hypercube sampling from truncated Gaussian distributions with specified mean values, a coefficient of variation of 1%, and no correlations among parameters. For each set of parameter values, ORCM predicted a number of responses, from which we have selected the two most relevant to this optimization: number of recruits and the peak date of emigration. The standardized regression coefficient obtained by regression between 5,000 model predictions and the

parameter values that produced them provided an index of sensitivity. The same parameters tended to influence both predictions (Table 2); redd mortality in marginal habitat had the largest effect on the number of recruits, and the final date of upstream migration had the largest effect on the peak date of out-migration. The earliest date of upstream migration by spawners and the upper lethal temperature for juveniles also had important effects on both the number of recruits and the peak date of out-migration.

Seasonal flows that maximize recruitment.—We used simulated annealing (Metropolis et al. 1953) to find a seasonal flow regime that maximized model-predicted salmon recruitment in hydrologic years ranging from wet to dry. Our first objective was to maximize the predicted number of out-migrating smolts (i.e., recruitment). The freshwater portion of the chinook salmon life cycle between upstream migration in the fall and out-migration in the spring was divided into 20 periods, each 2 weeks, characterized by a fixed average daily river flow. The flow assigned to each period is one value in a vector, \mathbf{Q} , of 20 decision variables manipulated to maximize the simulated number of emigrating smolts. The optimization program found the flow vector that maximized $Z = F(\mathbf{Q})$, where Z is the number of predicted recruits and F denotes ORCM's prediction of the objective function (i.e., recruitment).

This optimization problem is of limited practical interest because it assumes that the annual quantity of river flow is unlimited. Therefore, we also sought optimal flow regimes that maximized Z , subject to a constraint on the total amount of water available annually, Q_{tot} . We repeated the optimization for Q_{tot} values that increased geometrically: 122, 245, 489, and 979 hm^3 . The threshold values above correspond to the 20th, 45th, 60th, and 78th percentiles of distribution of historical annual flows (e.g., 20% of years had annual flows of 122 hm^3 or less and 60% of years had annual flows of 489 hm^3 or less). In addition, we assumed that flows within each 2-week period were only constrained by the annual total and not by short-term constraints, such as daily demands by irrigators, that might restrict daily flows. Summer flows between July 8 and September 30 were not considered relevant for fall chinook salmon because most

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from habitat capacity in panel B, and finally calculate the survival (ration) at the site from its rank in panel C. Sites with a rank exceeding the number of suitable sites (e.g., 10) have zero survival (ration).

juveniles emigrate by then and water temperatures are too high for survival of those remaining. Therefore, we set daily average flows for July 8 through September 30 to be 1.42 m³/s for the purpose of calculating an annual total flow.

All optimizations assumed 5,000 adult spawnners, which is roughly the average historical number of returning adults in the Tuolumne River. This assumption is more likely to be a concern in extrapolating to higher abundances that are influenced by density-dependent effects, than for lower abundances (Jager 2000).

Seasonal flows that maximize spawning-time variation.—In addition to the objective of maximizing smolt recruitment for the combined fall and late-fall chinook salmon runs, we also used simulated annealing to find flow regimes that maximized variation in spawning times. We calculated the standard deviation (SD) in the parental spawning dates of recruits for each simulation. The parental spawning time is the integer number of days after October 1 that a given smolt emigrant was spawned by its parents. For the optimization of variation in spawning-run times, we considered two cases: unlimited annual flow and annual flows of 489 hm³ or less. The optimization program found the vector \mathbf{Q} of daily flows, during the 20 2-week time periods, that maximized the objective function, $Z_v = F_v(\mathbf{Q})$. For a given flow regime \mathbf{Q} , Z_v is the standard deviation in spawning run times of out-migrating smolts predicted by the ORCM model, F_v .

Simulated annealing.—We used simulated annealing (SA) as our solution method because it is flexible and has a high probability of finding the optimal or a near-optimal solution for a wide range of optimization problems (Kirkpatrick et al. 1983). Simulated annealing has theoretical assurance of finding a globally optimal solution for problems with finite solution spaces (Geman and Geman 1984). Simulated annealing performed better than other methods in at least one comparison of heuristic algorithms for an optimal reserve design problem (Pressey et al. 1997). However, the solution method that works best for one problem is not guaranteed to work best for another.

Simulated annealing is an ad hoc search procedure that gives good results although we lack a mathematical understanding of its success in finding optimal solutions. Such heuristic algorithms do not guarantee finding a globally optimal solution and have no way of measuring the distance of individual solutions from the global optimum. However, these algorithms have at least two ad-

vantages over optimization methods that have mathematical guarantees: (1) they are feasible for large problems, and (2) they are completely general and can be used with any (ecological) simulation model. This frees the ecological model to describe relationships between organisms, their environment, and potential management policies with whatever degree of complexity is needed. Because the ecological model is separate from the optimization, the model does not have to be simplified or otherwise tailored to meet the assumptions of a particular optimization method.

Simulated annealing has three possible disadvantages. First, SA is not the best choice for optimization problems with a structure that is suitable for nonheuristic methods, such as linear programming. Simulated annealing would not take full advantage of such a problem's structure and would therefore be slower to reach a solution. Second, SA is inherently a sequential algorithm that does not lend itself to parallelization, although finding hybrid parallel algorithms is an active area of research. Third, SA is very slow compared with other heuristic methods.

Metropolis et al. (1953) first introduced SA after observing an optimizing process in physical systems whereby thermodynamic systems minimize free energy during cooling (e.g., annealing of metals). At high temperatures, molecules of a liquid move freely. If the liquid cools slowly, its atoms are able to line themselves up to form a pure crystal. If the liquid is cooled too quickly (quenched), it solidifies in a higher energy state and does not reach the crystal state that has the lowest free energy. In terms of a mathematical optimization problem, the crystal is the global optimum, and the quenched solution is one of many locally optimal solutions. The ability of SA to find global optima derives from its ability to avoid becoming trapped in local minima by permitting "uphill" movements.

We used the SIMANN program developed by Goffe et al. (1994) to optimize each of our two objectives under the ORCM model. As initial conditions, we constructed a flow regime, \mathbf{Q} , by setting the daily flows for each period to 4.248 m³/s. We ensured reasonably large initial step sizes. During the SA search, SIMANN used ORCM to evaluate its objective function (i.e., calculate the number of recruits or the variation in spawning times for each new trial flow regime). As the search progressed, changes in flow depended on \mathbf{V} , a vector of step sizes having a value for each of the 20 periods. Step sizes were adjusted as the search

progressed to ensure acceptance of roughly half the trial flow vectors evaluated. In each subsequent step of the search, a new vector of seasonal flows \mathbf{Q}' was chosen by varying the average daily flow during one 2-week period, i . If we let q_i represent the i th element of vector \mathbf{Q} , then the updated flow at the next step was

$$q_i' = q_i + (U \cdot v_i), \quad (7)$$

where U represents a uniformly distributed random number between -1 and 1 , and v_i is the i th element of \mathbf{V} . The updated flow vector was provided to the ORCM model, which then calculated the new value of the objective function, Z' . If Z' was greater than Z , flow regime \mathbf{Q}' was always accepted as a new starting point for the search. If Z' was less than Z , acceptance became less likely as the size of the difference and the duration of the search increased.

In optimizations constrained by the amount of flow available, we constructed an initial flow regime by dividing total annual flow evenly across the 20 periods. We imposed constraints by rejecting solutions if the sum of the 2-week flows and summer flows exceeded the specified upper limit on annual flow.

Model predictions.—We first present the optimal flow regimes for the maximize-recruitment objective for five total annual flow scenarios (four scenarios with different constraints on total annual flow and one scenario with no limit on annual flow). We also compare these SA-derived optimal flow regimes with historical flows. Next, we present the number of ORCM-simulated recruits produced by each of the annual flow scenarios. To understand how increasing the limit on annual flow influenced differences in recruitment among scenarios, we then present average egg-to-fry and fry-to-smolt mortality rates and the duration of successful spawning for each scenario. To explain the differences in mortality rates among annual-flow scenarios, we show river temperatures at two locations in the river for the scenario with no limit and the scenario with annual flows of 122 hm^3 or less.

We present the optimization results designed to maximize variation in spawning times and compare these with results from optimizations designed to maximize recruitment for two annual flow scenarios (no limit and $\leq 489 \text{ hm}^3$). We compare predictions for the two objectives, including the optimal flow regimes, the predicted number of recruits, the mean and standard deviation of

spawning times of successful recruits, and the contribution of the late-fall run.

Finally, we present average results for historical flow regimes for water years 1980–1989. These values were predicted by ORCM by assuming 5,000 spawners for each year and historical daily flows and temperatures. Comparisons of results under optimal flow regimes with results under historical flows and temperatures measure how much improvement would have been realized by following an optimal flow regime.

Results

Seasonal Flows that Maximize Recruitment

The SA search reached our stopping criteria after very long periods of computation (on the order of months). Progress for several of the maximize recruitment optimizations was marked by long periods with no improvement, punctuated by intermittent bursts of improvement (Figure 2).

The predicted optimal pattern for allocating seasonal flows among the 20 periods changed as the total amount of annual flow increased (Figure 3A–E). When we simulated dry hydrologic conditions (i.e., a low limit on total annual flow), the optimal flow regime allocated water more evenly across months, but it allocated more water in winter than in fall or spring (Figure 3A). This was the only scenario that did not provide elevated spring flows. As total annual flow increased (Figure 3B–E), the amount of flow allocated during spring months increased dramatically. We observed that high spring flows remained optimal in all hydrologic-year types, except for the very driest. As total annual flow increased, flows provided during winter months did not increase very much (Figure 3A–E). When we simulated an unlimited supply of water, the optimal flow regime allocated high flows during fall months, in addition to the high flows during spring (Figure 3E). As annual flow constraints tightened, we found that elevated fall flows were the first to disappear (Figure 3D) and elevated spring flows were the last to disappear (Figure 3D, A). These results suggest that providing a minimum level of winter flow is critical but that values above this minimum level are not particularly beneficial for maximizing fall chinook salmon recruitment.

Once winter needs are met, additional flows during spring are more beneficial to recruitment. Recruitment increased sharply for total annual flows up to 489 hm^3 (Figure 4). Increasing annual flow beyond 489 hm^3 led to progressively smaller in-

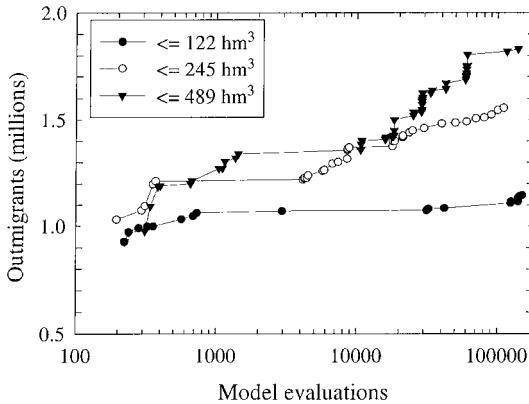


FIGURE 2.—Progress during the course of a simulated annealing search. The maximum value of the objective (i.e., the number of out-migrants) increases with the number of model evaluations of trial flow regimes. Results are shown for three optimizations with different constraints on total annual flow (≤ 122 , ≤ 245 , and ≤ 489 hm^3 , where $1 \text{ hm}^3 = 10^6 \cdot \text{m}^3/\text{year}$).

creases in the numbers of recruits. This relationship suggests that, even when water is released in an optimal manner for salmon, a trade-off exists in drier years between allocating water to instream flow or diverting water for other purposes.

Overall, as the annual flow increased, egg-to-fry mortality increased and fry-to-smolt mortality decreased (Figure 5A). Temperature was a main factor controlling this apparent tradeoff between egg-to-fry and fry-to-smolt mortality (Figure 5B). The decrease in fry-to-smolt mortality with increasing annual flow was caused by elevated flow during the spring. The flow regimes optimized with higher annual flows provided higher flow during spring. These elevated spring flows carried the cooler water released from the dam farther downstream before it reached equilibrium with the air temperature. As a result, juveniles in simulations with optimal flow regimes with higher annual flows were not exposed to lethal (high) spring temperatures. Forty km below the dam, water temperatures were higher under optimal flow regimes with lower annual flow (e.g., the 40-km, ≤ 122 - hm^3 line in Figure 5B) than under optimal flow regimes with higher annual flow (e.g., the 40-km, no-limit line in Figure 5B). Consequently, juvenile mortality was lower in simulations with higher annual flow.

The pattern of increasing egg-to-fry mortality with increasing annual flow was due to elevated flow effects on temperature during the fall. Simulations of optimal flow regimes with higher an-

nual flows were characterized by higher egg-to-fry mortality because higher fall flows produced more extreme downstream temperatures. Egg survival during incubation is optimal at 8°C (Figure 5B); warmer and colder temperatures are stressful (Murray and McPhail 1988). In fall, water released from upstream storage reservoirs is typically warmer than the air (Petts 1984), which exposes redds concentrated below the dam to higher temperatures (e.g., the 16-km, no-limit line in Figure 5B) than those farther downstream (e.g., the 40-km, no-limit line in Figure 5B). In years having elevated fall flows, redds farther downstream experience elevated temperatures because faster-moving water travels farther before reaching equilibrium with colder air temperatures.

Successful spawning occurred over a longer period under flow regimes with higher annual flow (Figure 6). The earliest successful redds were built in early October for all hydrologic years, but the last successful redds (those that produced offspring that survived to emigrate as smolts) were constructed in mid-November in simulations with low annual flow and as late as mid-February in simulations with high annual flow.

Seasonal Flows That Maximize Spawning Time Variation

The flow regime that maximized the variation in run times (MV) differed from the flow regime that maximized recruitment (MR) for both the unlimited annual flow and the flow of 489 hm^3 or less. Under unlimited annual flow, the MV flow regime was characterized by higher flows than the MR flow regime during first 2-week period in October and then for an extended period in spring between February 4 and May 26 (Figure 7A). One interesting feature of the MV flow regime is the large pulse of high flow between February 4 and 17, just before the March 1 peak in spawning for the late-fall run (Figure 7A). The two management objectives also produced different optimal flow regimes when annual flows were constrained to 489 hm^3 or less. Between October 1 and the end of December, except for 2 weeks between October 29 and November 11, the MV flow regime provided higher flows than the MR flow regime. The MV flow regime provided higher flows than the MR flow regime in April, but lower flows in the surrounding months of March and May.

The parents of recruits spawned later and over a longer period when incubated and reared under MV flow regimes than they did under MR flow regimes (Table 3). For annual flows of 489 hm^3 or

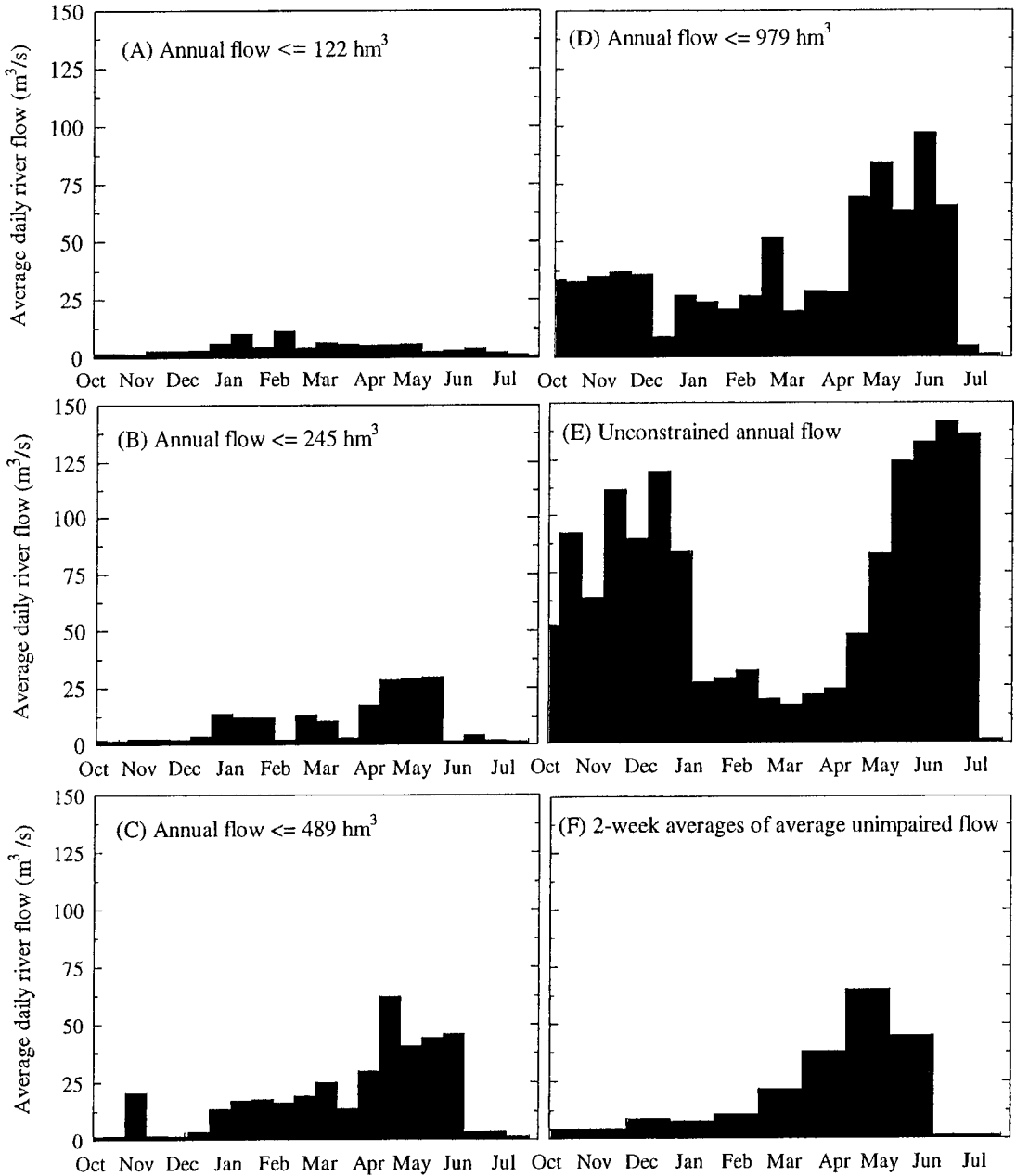


FIGURE 3.—Optimal flow regimes that maximize the simulated recruitment of chinook salmon smolt out-migrants for five scenarios representing a range of constraints on annual river flow: (A) $\leq 122 \text{ hm}^3$ ($1 \text{ hm}^3 = 10^6 \cdot \text{m}^3/\text{year}$), (B) $\leq 245 \text{ hm}^3$, (C) $\leq 489 \text{ hm}^3$, (D) $\leq 979 \text{ hm}^3$, and (E) an unconstrained scenario. These can be compared with (F) the 2-week averages of natural flows above the Don Pedro and LaGrange dams between 1919 and 1992.

less, the mean spawning date for the parents of recruits shifted from October 27 under the MR flow regime to November 8 under the MV flow regime. No progeny of the late-fall run were predicted to survive to recruitment. For unlimited an-

nual flows, the mean spawning date shifted from October 31 under MR flow regime to November 7 under the MV flow regime. For unlimited annual flows, this shift toward later spawning under the MV flow regime corresponded to increased sur-

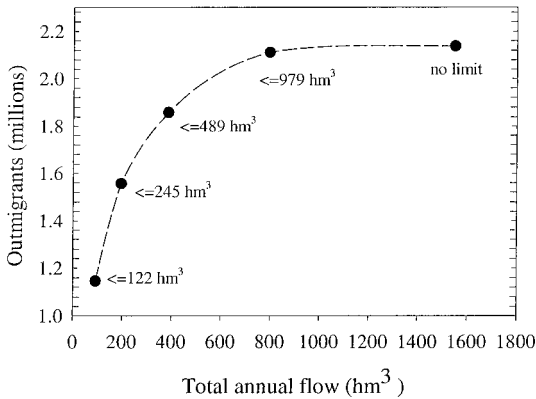


FIGURE 4.—Simulated recruitment of chinook salmon smolt out-migrants under flows designed to maximize recruitment of smolt out-migrants for each of five annual limits on flow.

vival of late-fall progeny (Table 3). Not surprisingly, variation in successful spawning time, as measured by the standard deviation of spawning dates, was greater under the MV flow regimes than under the MR flow regimes for both annual flow scenarios. For annual flows of 489 hm³ or less, the SD of spawning times of offspring surviving to the recruit stage increased from 11 d under the MR flow regime to 21 d under the MV flow regime. Under unlimited annual flow, the SD of spawning dates increased from 15 d under the MR flow regime to 19 d under the MV flow regime. The same pattern of later mean spawning time and higher standard deviations under MV flow regime was also observed when survival to the fry stage was considered (Table 3).

The number of late-fall-run recruits was highest for the optimal flow regime designed for the MV objective under unlimited annual flows. However, the total number of recruits was substantially smaller in MV flow regimes than in MR flow regimes. For annual flows of 489 hm³ or less, total recruitment decreased from 1,780,889 under the MR flow regime to 664,300 under the MV flow regime and neither the MR or MV flow regime produced any late-fall-run emigrants. For unlimited annual flow, total recruitment decreased from 1,960,200 under the MR flow regime to 1,369,200 under the MV flow regime. For unlimited annual flow, the MR flow regime produced 3,900 late-fall-run recruits, but the MV flow regime produced 12,500 late-fall-run recruits.

Optimal versus Historical Flow Regimes

According to ORCM predictions, fewer recruits were produced under historical flows (av-

erage = 647,800, SD = 218,095) than under the MR flow regime for annual flows of 489 hm³ or less (1,780,889) or for unlimited annual flows (1,960,200). The variation in spawning times produced under historical flows (average = 15.0 d, SD = 5.0 d) was also less than the variation in spawning times produced under the MV flow regime for annual flows of 489 hm³ or less (21.2 d) and the MV flow regime for unlimited annual flow (18.9 d).

Discussion

Seasonal Flows That Maximize Recruitment

The seasonal flow patterns that maximized predicted recruitment changed with the total amount of water available annually. This suggests that management of flows to recover salmon stocks requires different regimes in dry hydrologic years than in wet hydrologic years. Fall flows increased in scenarios exceeding 900 hm³; a relatively low minimum winter flow was always optimal, and spring flows increased as the availability of water increased. These patterns suggest the following priorities for flow management aimed at increasing recruitment of fall chinook salmon: (1) provide a winter minimum flow in all hydrologic years, (2) obtain additional flows to provide high spring flows in all but the driest years, and (3) provide fall attraction flows in very wet years.

The importance of the high fall and spring flows that characterized optimal seasonal flow regimes developed with unlimited annual flow depends on the management objectives for the river. A flow regime with lower fall flows and more moderate spring flows (e.g., Figure 3C) did almost as well in maximizing overall recruitment as the unlimited optimal flow, which maximized recruitment by supplying much more water (Figure 3E). Although the flow regimes using more water produced more recruits, the incremental benefits of higher annual flows decreased as annual flow increased. The importance of the extra water should be evaluated in terms of whether the increment in recruitment is needed to sustain the population.

An extended period of successful spawning and survival of the late-fall run contributed to higher recruitment in wetter years. Only the two optimal flow regimes designed for the wettest conditions (Figures 3D and 3E) successfully reared late-fall-run smolts (Figure 6). The latest date that an individual out-migrant was spawned shifted by 3 months as constraints on annual flow were relaxed, probably because of the extended block of high

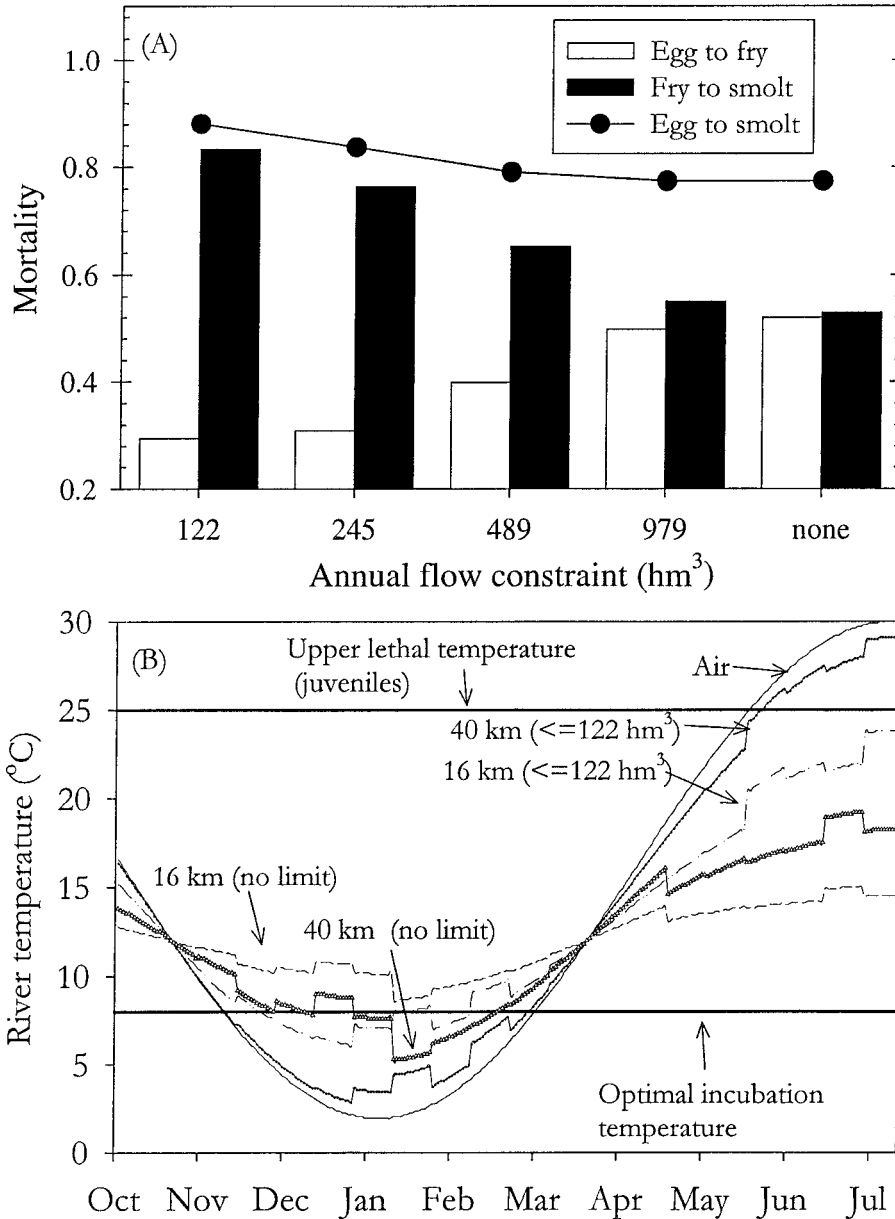


FIGURE 5.—(A) Simulated proportion of chinook salmon eggs killed before reaching the fry stage (egg-to-fry mortality) and the proportion of simulated fry killed before migrating as smolts (fry-to-smolt mortality); the line summarizes the total fraction of eggs killed (egg-to-smolt mortality). (B) Seasonal changes in river temperatures at two distances below the dam and under two optimal flow regimes: annual flow constrained to be $\leq 122 \text{ hm}^3$ ($1 \text{ hm}^3 = 10^6 \cdot \text{m}^3/\text{year}$) and no limit on annual flow. Simulated air temperature, upper lethal temperature for juvenile chinook salmon, and optimal temperature for eggs are shown for reference.

spring flow. Because late-fall adults are not in the system during fall, one might be tempted to conclude that the high fall flows provided in these two wetter regimes could be reduced without affecting

the late-fall run. However, it is possible that high fall flows reduce fall-run survival of eggs and alevins in redds and thus reduce competition with later-emerging and smaller offspring of late-fall

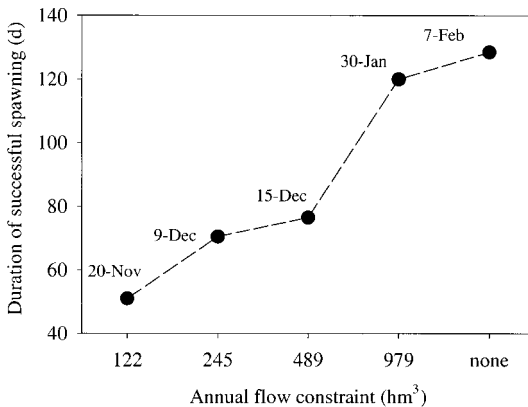


FIGURE 6.—The duration of simulated chinook salmon spawning dates used by parents of successful smolt out-migrants under optimal flow regimes designed to maximize recruitment under different limits on annual flow ($1 \text{ hm}^3 = 10^6 \cdot \text{m}^3/\text{year}$). Data labels indicate the final dates of successful spawning.

spawners. The two flow regimes that require the most water may be important to consider if restoring the late-fall run is a management priority.

One approach to designing flow patterns is to assume that we cannot understand all of the complex influences of flow on salmon and that the best policy is, therefore, to mimic the natural flow patterns under which salmon life histories evolved (National Research Council 1996). Our model-based results, like those of Bartholow and Waddle (1995), support the notion that seasonal flows shaped with a peak during spring are best for chinook salmon. The shape of the optimal regime for annual flows of 489 hm^3 or less (Figure 3C) is similar to the shape of the 2-week average natural flow regime (Figure 3F). Natural flows in the San Joaquin basin are dominated by spring snowmelt, with 60% of discharge occurring between April and June (Lettenmaier and Gan 1990). According to Moyle and Yoshiyama (1997), the highest survival of chinook salmon in the San Joaquin River occurs when naturally high flow events coincide with times of smolt emigration.

Seasonal Flows That Maximize Spawning Time Variation

Smith et al. (1995) recommend that conservation efforts focus on genetic differences along the primary axes that permit reproductive isolation and thereby define species and races. In salmon, distinct races are defined by temporal partitioning of spawning times as well as by geographic partitioning (e.g., Utter et al. 1995). In the specific

case of the Central Valley, J. L. Nielsen (U.S. Forest Service, personal communication) determined that the two late-fall populations of chinook salmon (Sacramento and San Joaquin) are more similar to each other than to any other spawning run in the basin. However, some stakeholders in the Central Valley question the historical importance of the late-fall run in the San Joaquin and Tuolumne rivers and argue that restoration is not warranted. The results of this study suggest that regulating flows in a manner that would conserve a wider range of run times would produce fewer total recruits than would regulating flows in a manner that maximizes total recruitment.

Optimal versus Historical Flow Regimes

Optimal flow regimes produced considerably more recruits and greater variation in spawning times than did average values during the historical period, especially for the MR objective. The significance of these increases, like all differences predicted here, depends on both the uncertainty of ORCM predictions and the sensitivity of the chinook stocks to flow-related differences in recruitment or variation in spawning time.

Caveats and Future Directions

Designing seasonal flow patterns that provide higher flows when salmon need it most can help to guide conservation and restoration efforts. Three caveats limit the applicability of the results presented here. First, some salmon stocks may be limited by factors other than flow regime. Second, the optimal flow regimes identified here depend on the assumptions about the effects of flow on survival, growth, reproduction, and movement in the ORCM model. There are many possible flow effects that are not explicitly simulated in the model, and predictions about the effects of changes in flow regime should always be verified in the field. Third, the water required by an optimal flow regime might not be available when it is needed.

An important caveat to our results is that flow management alone may not be capable of solving the problems that salmon face. Any conservation effort that fails to focus on restoring access to upstream river habitat will probably fail for certain races, such as spring and winter chinook salmon, that historically relied on these areas for spawning (Healey and Prince 1995). For these stocks, flow management should be seen as a second-tier solution following the first-tier solution of providing passage around dams and removal of other barriers to migration. In general, the first step should be

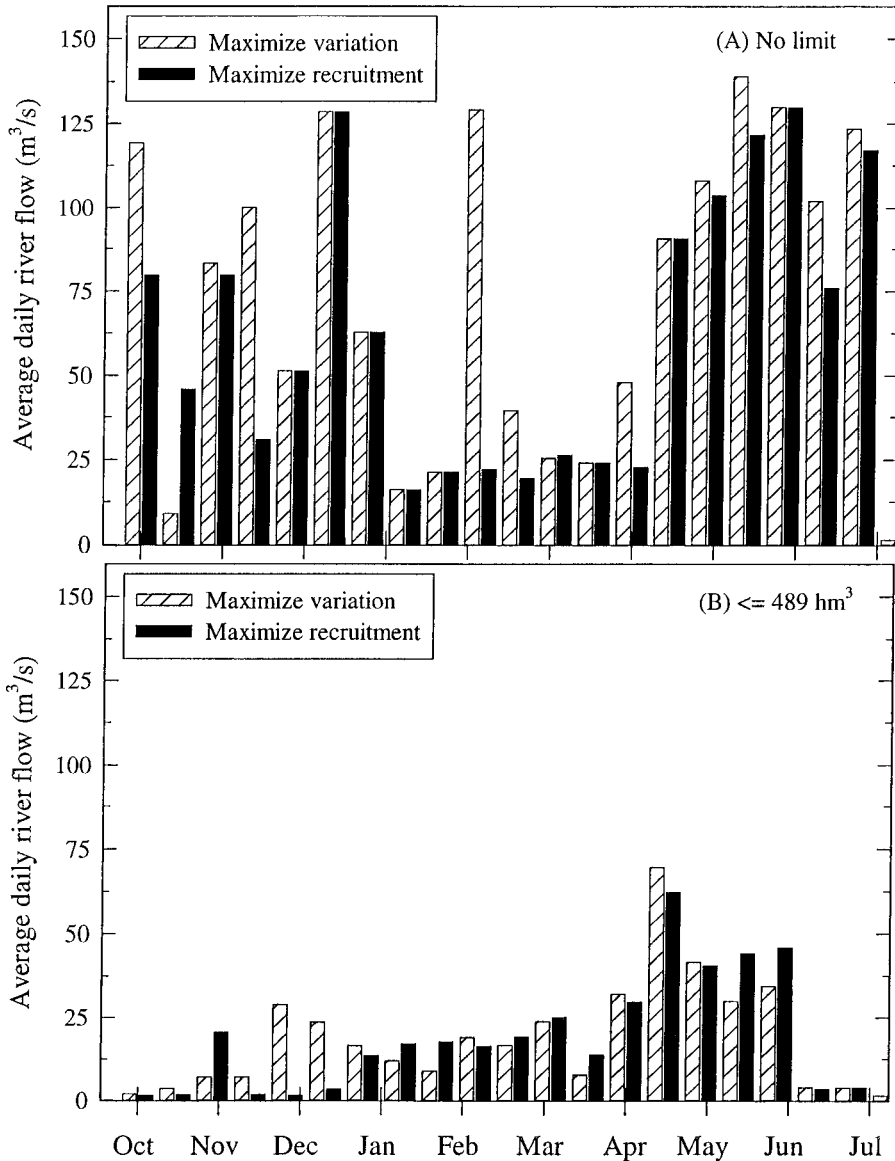


FIGURE 7.—A comparison of optimal flow regimes designed to maximize recruitment (solid bars) and variation in spawning times (hatched bars). Results are shown for (A) unlimited annual flow and (B) annual flow $\leq 489 \text{ hm}^3$ ($1 \text{ hm}^3 = 10^6 \cdot \text{m}^3/\text{year}$).

to identify improvements that are most likely to effect recovery, which might not always emphasize providing a flow regime that is beneficial for salmon.

Although the ORCM goes farther than other population models for salmon in its attempt to represent mechanistic linkages between salmon biology and flow, it has its limitations. Despite its complexity, ORCM selectively articulates key ecological relationships affected by flow. There are

many numerous indirect effects of flow that ORCM does not represent (e.g., benthic invertebrate production, effects of predation risk on foraging time, debris flow, gravel redistribution).

The ORCM focuses on the scale of daily changes in flow and does not represent the effects of longer- or shorter-term variations in flow. At one extreme, long-term drought cycles require a full life-stage model that incorporates the ocean phase and simulations spanning decades. At the other

TABLE 3.—Model predictions for flow regimes designed to maximize the variation in chinook salmon spawning times and for flow regimes designed to maximize recruitment in the Tuolumne River, California. We report total recruitment, late-fall-run recruitment, and spawning-date statistics (average and SD) for parents of offspring that survived to the fry stage and for those whose offspring survived to leave the river as smolts. The results for optimal flow regimes restricted to an annual flow of $\leq 489 \text{ km}^3$ ($1 \text{ hm}^3 = 10^6 \text{ m}^3/\text{year}$) and optimal flow regimes with unlimited annual flow are compared.

Model predictions	Annual flow $\leq 489 \text{ hm}^3$		Unlimited annual flow	
	Maximize recruitment	Maximize variation	Maximize recruitment	Maximize variation
Total number of emigrants	1,780,889	664,300	1,960,200	1,369,600
Late-fall-run emigrants	0	0	3,900	12,500
Average parental spawning date for fry	Nov 9	Nov 18	Nov 11	Nov 17
SD of spawning dates (d) for survivors to fry stage	21.0	30.5	25.6	29.3
Average parental spawn date for emigrants	Oct 27	Nov 8	Oct 31	Nov 7
SD of spawning dates (d) for survivors to emigration	11.1	21.2	15.4	18.9

extreme, with its daily time-step and 2-week optimization intervals, ORCM did not represent the effects of within-day variation in flow. Natural variation in flow regimes shape the disturbance regime in rivers in much the same way that fire shapes grassland ecosystems (Reeves et al. 1995; Poff et al. 1997). Unwin (1997) found that flow variability during spring out-migration showed the strongest and most consistent positive relationship with fry-to-adult survival of chinook salmon. Experimental pulse flows in the Stanislaus River, California, stimulated out-migrations in the short-term (2 d) but little additional benefit resulted from prolonged high flows (Cramer 1997). These results suggest that the ability of high flows to speed emigration may be less important than the short-term benefits provided by pulse flows. Pulse flows may serve as a behavioral cue to synchronize downstream movement, allowing smolts to overwhelm potential predators. Increased turbidity associated with pulse flows is also a short-term event (one that may not occur in regulated rivers). Because our study used 2-week periods, our optimal flow regimes are less variable than natural flow regimes. Also, the ORCM does not at present include the fine distinctions between short-term and longer-term benefits of flow. A next step in our analysis would be to introduce processes that operate at different time scales in the ORCM model and to evaluate the effects of including realistic short- and long-term variability in flow without substantially increasing the number of decision variables.

Limitations in flow availability can restrict the ability to manage flows according to an optimal flow regime. Droughts, combined with limits on storage capacity and competing demands for water, can make it difficult to follow a specified regime. Such competing water needs could be incorporated

as constraints into an optimization analysis like ours. Likewise, economic considerations could be added in future to address both the benefits to fish and costs to society.

The optimization approach described here could be used to design instream flows for conservation objectives involving different rivers and salmon runs as well as for other species. Applications to chinook salmon that spawn in different rivers would merely require changing values for site-specific model parameters. Applications to different salmon species might require structural changes to ORCM to reflect a more complex life history. For example, chinook salmon show a much wider variation in life history patterns in rivers farther north than in the California river used in our study, including runs that remain in the river much longer and exit as yearlings. Although the specific quantitative results presented here are specific to a particular stock, the qualitative recommendations presented for designing flows that benefit salmon in different hydrologic years and in situations with multiple runs should have wider application.

In this study, we compared the optimal flow regimes designed to independently address two different conservation objectives. It is also possible for optimization to address multiple objectives. With many more optimizations, one could construct a Pareto frontier of flow regimes that assign weights to the two objectives that we considered (maximizing the recruitment and maximizing variation in the spawning times). In our analysis, managing flows to conserve a variety of runs required compromising overall recruitment. This implies that the relative weight assigned to the two objectives should depend on the conservation status of the runs. If the larger runs are stable or increasing, then diversity-enhancing flows may be favored,

whereas a dominant run that is declining may require sacrificing smaller runs. If the temporal metapopulation structure of the runs resembles a core satellite structure, with one dominant run that recolonizes the others by temporal straying, then there is a danger that managing flows for run-time diversity would create temporal sinks, analogous to the spatial sinks described by Pulliam (1988). In contrast, managing for run-time diversity would be important for classic metapopulations that depend on recolonization by temporal strays for persistence.

Acknowledgments

We appreciate discussions with Hal Cardwell and Steve Bao for sharing their expertise in optimization theory. Mac Post provided helpful suggestions on efficiency, and Forrest Hoffman helped to transport the optimizations to various UNIX and LINUX platforms. Reviews were provided by Webb Van Winkle, Chuck Coutant, Lou Gross, Barry Smith, and Paul Higgins.

References

- Allen, M. A., and T. J. Hassler. 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Southwest): chinook salmon. Report to the U.S. Fish and Wildlife Service and the U.S. Army Corps of Engineers, Biological Report 82 (11.49) and TR EL-82-4, Washington, D.C., and Vicksburg, Mississippi.
- Bartholow, J. M., and T. J. Waddle. 1995. The search for an optimum flow regime using a salmon population model. Pages 331–339 in J. J. Cassidy, editor. Waterpower '95: proceedings of the international conference on hydropower. American Society of Civil Engineers, New York.
- Becker, C. D., D. A. Neitzel, and D. H. Fickeisen. 1982. Effects of dewatering on chinook salmon redds: tolerance of four developmental phases to daily dewaterings. *Transactions of the American Fisheries Society* 111:624–637.
- Berggren, T. J., and M. J. Filardo. 1993. An analysis of variables influencing the migration of juvenile salmonids in the Columbia River basin. *North American Journal of Fisheries Management* 13:48–63.
- Bilby, R. E., B. R. Fransen, and P. A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. *Canadian Journal of Fisheries and Aquatic Sciences* 53:164–173.
- Brett, J. R. 1952. Temperature tolerance in young pacific salmon, genus *Oncorhynchus*. *Journal of the Fisheries Research Board of Canada* 9:265–309.
- Cada, G. F., M. D. Deacon, S. V. Mitz, and M. S. Bevelhimer. 1993. Review of information pertaining to the effect of water velocity on the survival of juvenile salmon and steelhead in the Columbia River basin. Northwest Power Planning Council, Portland, Oregon.
- Cederholm, C. J., M. D. Kunze, T. Murota, and A. Sibatani. 1999. Pacific salmon carcasses. *Fisheries* 24(10):6–15.
- Cramer, S. P. 1997. Use of managed pulses in flow to stimulate outmigration of juvenile salmon. Pages 563–568 in S. Y. Wang and T. Carstens, editors. Environmental and coastal hydraulics: protecting the aquatic habitat. Proceedings of theme B, water for a changing global community, 27th Congress of the International Association for Hydraulic Research. American Society of Civil Engineers, New York.
- EAEST (EA Engineering, Science, and Technology). 1992a. Tuolumne River salmon spawning surveys, 1971–1988. Report of Turlock irrigation district and Modesto irrigation district pursuant to Article 39 of the license for the Don Pedro Project, volume 2, appendix 3. Prepared for Turlock irrigation district, Turlock, California, and Modesto irrigation district, Modesto, California.
- EAEST (EA Engineering, Science, and Technology). 1992b. Analysis of 1981 Lower Tuolumne River IFIM data. Report of Turlock irrigation district and Modesto irrigation district pursuant to Article 39 of the license for the Don Pedro Project, volume 3, appendix 5. Prepared for Turlock irrigation district, Turlock, California, and Modesto irrigation district, Modesto, California.
- EPA (U.S. Environmental Protection Agency). 1971. Columbia River thermal effects study, volume 1, biological effects studies. Cooperative Report with the Atomic Energy Commission and the National Marine Fisheries Service, Portland, Oregon.
- FERC (Federal Energy Regulatory Commission). 1996. Final environmental impact statement. Reservoir release requirements for fish at the New Don Pedro Project, California. FERC, FERC-EIS-0081-F, Washington, D. C.
- Fisher, F. 1994. Past and present status of Central Valley chinook salmon. *Conservation Biology* 8:870–873.
- Fleming, I. A., and M. R. Gross. 1994. Breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. *Evolution* 48:637–657.
- Fry, D. H. 1961. King salmon spawning stocks of the California Central Valley, 1940–1959. *California Fish and Game* 47:55–71.
- Geman, S., and D. Geman. 1984. Stochastic relaxation, Gibbs distribution and the Bayesian restoration in images. *IEEE (Institute of Electrical and Electronics Engineers) Transactions in Pattern Analysis and Machine Intelligence* 6:721–741.
- Goffe, W. L., G. D. Ferrier, and J. Rogers. 1994. Global optimization of statistical functions with simulated annealing. *Journal of Econometrics* 60:65–99.
- Grant, J. W. A., and D. L. Kramer. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. *Canadian*

- Journal of Fisheries and Aquatic Sciences 47:1724–1737.
- Hatton, R. S., and G. H. Clark. 1942. A second progress report on the Central Valley fishery investigations. California Fish and Game 28:116–123.
- Healey, M. C. 1994. Variation in the life history characteristics of chinook salmon and its relevance to conservation of the Sacramento winter run of chinook salmon. Conservation Biology 8:876–877.
- Healey, M. C., and A. Prince. 1995. Scales of variation in life history tactics of Pacific salmon and the conservation of phenotype and genotype. Pages 176–184 in Nielsen and Powers (1995).
- Holling, C. S. 1959. Some simple types of predation and parasitism. Canadian Entomologist 91:385–398.
- Huntington, C., W. Nehlsen, and J. Bowers. 1996. A survey of healthy native stocks of anadromous salmonids in the Pacific Northwest and California. Fisheries 21(3):6–14.
- Independent Scientific Group. 1996. Return to the river: restoration of salmonid fishes in the Columbia River ecosystem. Northwest Power Planning Council, Portland, Oregon.
- Jager, H. I. 2000. Predicting the viability of fish populations in a modified riverine environment. Doctoral dissertation. University of Tennessee, Knoxville.
- Jager, H. I., H. E. Cardwell, M. J. Sale, M. S. Bevelhimer, C. C. Coutant, and W. VanWinkle. 1997. Modelling the linkages between flow management and salmon recruitment in streams. Ecological Modelling 103: 171–191.
- Jensen, A. J., and B. O. Johnsen. 1999. The functional relationship between peak spring floods and survival and growth of juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). Functional Ecology 13:778–785.
- Kirkpatrick, S., J. C. D. Gelatt, and M. P. Vecchi. 1983. Optimization by simulated annealing. Science 220: 671–680.
- Kjelson, M. A., and P. L. Brandes. 1989. The use of smolt survival estimates to quantify the effects of habitat changes on salmonid stocks in the Sacramento–San Joaquin Rivers, California. Canadian Special Publication of Fisheries and Aquatic Sciences 105:100–115.
- Kope, R. G., and L. W. Botsford. 1990. Determination of factors affecting recruitment of chinook salmon *Oncorhynchus tshawytscha* in central California. U.S. National Marine Fisheries Service Fishery Bulletin 88:257–269.
- Lackey, R. T. 1999. Salmon policy: science, society, restoration, and reality. Environmental Science and Policy 2:369–379.
- Lettenmaier, D. P., and T. Y. Gan. 1990. Hydrologic sensitivities of the Sacramento–San Joaquin River basin, California, to global warming. Water Resources Research 26:69–86.
- Li, H. W., K. Currans, D. Bottom, S. Clarke, J. Dambacher, C. Frissell, P. Harris, R. M. Hughes, D. McCullough, A. McGie, K. Moore, R. Nawa, and S. Thiele. 1995. Safe havens: refuges and evolutionarily significant units. Pages 371–380 in Nielsen and Powers (1995).
- McBain, S., and W. Trush. 2000. Habitat restoration plan for the lower Tuolumne River corridor. Prepared for the Tuolumne River Technical Advisory Committee, Turlock, California.
- Metropolis, N., A. Rosenbluth, M. Rosenbluth, A. Teller, and E. Teller. 1953. Equations of state calculations by fast computing machines. Journal of Chemical Physics 21:1087–1092.
- Moyle, P. 1994. The decline of anadromous fishes in California. Conservation Biology 8:869–870.
- Moyle, P. B., and R. M. Yoshiyama. 1997. The role of adaptive management in restoring chinook salmon to the Tuolumne River. Pages 557–562 in S. Y. Wang and T. Carstens, editors. Environmental and coastal hydraulics: protecting the aquatic habitat. Proceedings of theme B, water for a changing global community, 27th Congress of the International Association for Hydraulic Research. American Society of Civil Engineers, New York.
- Murray, C. B., and J. D. McPhail. 1988. Effect of incubation temperature on the development of five species of Pacific salmon (*Oncorhynchus*) embryos and alevins. Canadian Journal of Zoology 66:266–273.
- Myers, J. M., R. G. Kope, G. J. Bryant, D. Teel, L. J. Lierheimer, T. C. Wainwright, W. S. Grant, F. W. Waknitz, K. Neely, S. T. Lindley, and R. S. Waples. 1998. Status review of chinook salmon from Washington, Idaho, Oregon, and California. U.S. Department of Commerce, NMFS-NWFSC-35, Washington, D.C.
- National Marine Fisheries Service. 1999. Endangered and threatened species; threatened status for two chinook salmon evolutionarily significant units (ESUs) in California. Federal Register 64:156 (17 August 1999):50394–50415.
- National Research Council. 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington D. C.
- Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4–21.
- Nielsen, J. L., and D. A. Powers, editors. 1995. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.
- Nielsen, J. L., D. Tupper, and W. K. Thomas. 1994. Mitochondrial DNA polymorphisms in unique runs of chinook salmon (*Oncorhynchus tshawytscha*) from the Sacramento–San Joaquin River basin. Conservation Biology 8:882–884.
- Paterson, A. M. 1987. Land, water, and power: a history of the Turlock Irrigation District, 1887–1987. Arthur H. Clark Company, Glendale, California.
- Peterson, J. H., and D. L. DeAngelis. 1992. Functional response and capture timing in an individual-based model: predation by northern squawfish (*Ptychocheilus oregonensis*) on juvenile salmonids in the Co-

- lumbia River. *Canadian Journal of Fisheries and Aquatic Sciences* 49:2551–2565.
- Petts, G. E. 1984. Page 196 in *Impounded rivers*. John Wiley and Sons, Chichester, UK.
- Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. *BioScience* 47:769–784.
- Pressey, R. L., H. P. Possingham, and J. R. Day. 1997. Effectiveness of alternative heuristic algorithms for identifying indicative minimum requirements for conservation reserves. *Biological Conservation* 80: 207–219.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- Reeves, G. H., L. E. Benda, K. M. Burnett, P. A. Bisson, and J. R. Sedell. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. Pages 334–349 in Nielsen and D. A. Powers(1995).
- Smith, G., J. Rosenfield, and J. Porterfield. 1995. Processes of origin and criteria for preservation of fish species. Pages 44–57 in Nielsen and D. A. Powers(1995).
- Speed, T. 1993. Modeling and managing a salmon population. Pages 267–292 in V. Barnett and K. F. Turkman, editors. *Statistics for the environment*. Wiley, New York.
- Stanford, J. A., J. V. Ward, W. J. Liss, C. A. Frissell, R. N. Williams, J. A. Lichatowich, and C. C. Coutant. 1996. A general protocol for restoration of regulated rivers. *Regulated Rivers: Research and Management* 12:391–413.
- Stevens, D. E., and L. W. Miller. 1983. Effects of river flow on abundance of young chinook salmon, American shad, longfin smelt, and delta smelt in the Sacramento–San Joaquin River system. *North American Journal of Fisheries Management* 3:425–437.
- Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsal. 1983. An energetics model for lake trout, *Salvelinus namaycush*: application to the Lake Michigan population. *Canadian Journal of Fisheries and Aquatic Sciences* 40:681–698.
- Unwin, M. J. 1997. Survival of chinook salmon, *Oncorhynchus tshawytscha*, from a spawning tributary of the Rakaia River, New Zealand, in relation to spring and summer mainstem flows. *U.S. National Marine Fisheries Service Fishery Bulletin* 95:812–825.
- Utter, F. M., D. W. Chapman, and A. R. Marshall. 1995. Genetic population structure and history of chinook salmon of the Upper Columbia River. Pages 149–168 in Nielsen (1995).
- Waples, R. S. 1995. Evolutionarily significant units and the conservation of biological diversity under the Endangered Species Act. Pages 8–27 in Nielsen and Powers(1995).
- Williams, J. G., and G. M. Matthews. 1995. A review of flow and survival relationships for spring and summer chinook salmon, *Oncorhynchus tshawytscha*, from the Snake River basin. *U.S. National Marine Fisheries Service Fishery Bulletin* 93:732–740.
- Willson, M. F., and K. C. Halupka. 1995. Anadromous fish as keystone species in vertebrate communities. *Conservation Biology* 9:489–497.
- Yoshiyama, R., E. R. Gerstung, F. W. Fisher, and P. B. Moyle. 2000. Chinook salmon in the California Central Valley: an assessment. *Fisheries* 25(2):6–20.