Modelling the linkages between flow management and salmon recruitment in rivers

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Abstract

We developed a simulation model to predict instream flow effects on smolt production for fall chinook salmon (*Oncorhynchus tshawytscha*) in regulated rivers. The principal purpose of this model is to serve as a management tool to evaluate effects on salmon of instream releases from upstream reservoirs. The dramatic decline in chinook salmon in California rivers suggests a need for such a tool. We developed an individual-based and spatially explicit model to simulate the influences of riverine habitat on each lifestage leading to successful outmigration of chinook salmon. Model predictions of development, growth and survival showed good agreement with four years of field data collected on the Tuolumne River, California. Our analysis of parameter sensitivities identified flow-related redd mortality and temperature-related juvenile mortality as limitations on smolt production. © 1997 Elsevier Science B.V.

Keywords: Oncorhynchus tshawytscha; Chinook salmon; Individual-based model; Spatially explicit model; Instream flow

1. Introduction

The Oak Ridge chinook salmon model (ORCM) described here predicts instream flow effects on the number of fall chinook salmon smolts that outmigrate from a river. ORCM can simulate complex habitat effects of flow (Table 1) because it is both spatially explicit and individual-based. We can represent important spatial gradients (e.g., temperature, predator densities) between upstream spawning areas and the lower reaches inhabited by salmon during migration. ORCM simulates the influences of riverine habitat on each lifestage leading to successful outmigration of chinook salmon, including upmigration,

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Table 1
Summary of relationships between each lifestage and the dominant environmental and biological factors that influence growth and survival in the model

Factor	Growth and development				Survival			
	Egg	Alevin	Fry	Smolts	Egg	Alevin	Fry	Smolts
Temperature	X	X	X	X	X		X	X
Habitat capacity					X	X		
Juvenile density					X	X	X	X
Predator density							X	X
Physiological condition								X
Juvenile length			X				X	X
Juvenile weight			X	X				

adult spawning, and the growth, movement and survival of early lifestages (FERC, 1996).

There are three main reasons for individual-based modeling of stream fishes. First, simulating individual fish is an efficient way of modeling lifestages that move in a heterogeneous environment (Jager et al., 1993). Second, it allows us to represent individual variation (DeAngelis and Gross, 1992) in fall chinook salmon during freshwater residence, including the timing of upmigration, spawning, and return to the ocean. As a result, the model easily simulates several coexisting lifestages of the salmon, as well as hatchery strains. Individuals may have different phenotypes, in terms of environmental tolerances, habitat requirements and behavioral capabilities. Third, individual-based models are well suited for building hierarchical, mechanistic models that can be validated in parts (Murdoch et al., 1992). Such validation is not possible with 'black box' models.

ORCM adds a necessary degree of realism that is lacking in models typically used to set instream flows. The tool most frequently used, the physical habitat simulation model (PHABSIM) (Milhous et al., 1989), does not incorporate coexisting lifestages, transitions between lifestages, movement, or spatial heterogeneity. Aggregated models, such as age- or stage-based Leslie matrix population models (e.g. EA Engineering, Science, and Technology, EAEST, 1992c) are useful for adding the adult, ocean phase for chinook salmon, but they have parameters that are difficult to interpret and measure. Williamson et

al., 1992 developed a cohort model for the Trinity River that has a similar focus on spatial heterogeneity in habitat. In developing this model, we adopted some features of the two earlier models. We believe that the ecological realism of our model enhances its ability to predict the effects of reservoir operations on chinook salmon production.

The main purpose of this paper is to describe ORCM, to present comparisons of model predictions with field data collected on the Tuolumne River, California, and to present the results of a sensitivity analysis. An application of ORCM to design instream flows is presented elsewhere (FERC, 1996).

2. Model structure

The life history of fall chinook salmon is typical of many anadromous fishes. Geographic variations in life history are described in Healey, 1994. Chinook salmon spend their adult lives in the ocean. Adult fish migrate into rivers to spawn during the fall, but the age varies between 2 and 5 years. Eggs incubate through the winter, hatch as alevins (nonfeeding larvae), and emerge from their redds as fry (pre-smolt juveniles) in spring. At this point the juveniles begin to feed along river margins for the first month or two and emigrate slowly as underyearlings during their first spring.

The major components of ORCM are adult escapement, spawning, the development and mor-

tality of egg and alevin lifestages, the development, growth, movement and mortality of juveniles (fry and smolts). These occur in a spatially explicit habitat that responds to flow and temperature. Seasonal flow patterns influence the reproductive success of anadromous salmon populations in complex ways (Table 1). For example, streamflow influences the development of fry and the outmigration of smolts indirectly through changes in temperature, predator density, and habitat availability. The relationships between flow and these processes are critical to our ability to assess instream flow effects.

The values and definitions of model parameters provided as input are listed in Table 2. These parameters are referred to in the model description below.

The principle predictions of the model are estimates of the number and sizes of juvenile fall chinook salmon that leave the river. In addition to outmigrant statistics, the model generates many intermediate predictions along the way, such as the temporal and spatial distribution of redds and juveniles and the success or fate of redds and juveniles.

2.1. Spatial and temporal scale

This model focuses on the time period beginning with adult upmigration in fall and ending with smolt outmigration in spring. The model begins with upmigration of spawners. We configured the model to simulate the upstream movement of adult spawners from the mouth of the river to an upstream spawning reach. Spawning takes place in fall for the fall run and in winter for the late-fall run. For each redd, ORCM tracks the survival and development of eggs into alevins over the winter and of alevins into juvenile fish during spring. For juveniles (fry and smolts), the model tracks each individual fish (growth, location, and exposure to mortality risk) from the time that it emerges from the redd, as it moves gradually downstream, and until it leaves the river as a fry or a smolt. All of these activities are evaluated by the model on a daily basis and responds to daily average flow and temperature information.

The model divides the river system into reaches that can differ in flow. Within each reach, we partition the river into segments and keep track of the daily location of each model fish by segment. The segments differ in such physical and biotic attributes (Fig. 1) as:

- spawner preference;
- the percentage of riffle habitat versus pool and run habitat;
- the quantity of weighted usable area (WUA) suitable for each lifestage;
- water temperature;
- the number of larger conspecific competitors; and
- densities of fish predators.

2.2. Physical input data: river flow and temperature

ORCM operates on five primary data sets: (1) daily streamflow at a gauge located just downstream of the flow-regulating dam; (2) minimum flows can be specified for ranges of dates throughout the year; (3) daily water temperatures at the dam and daily air temperatures for the area; (4) WUA curves for different flows; and (5) total number of adults that return to the river for spawning. In addition, the model requires input parameter values specified by the user (Table 2).

Water temperature is an important variable driving the model, and two options are provided for simulating temperatures near the regulating dam. The user may either provide the model with daily water and air temperature data measured below the dam or allow the model to simulate seasonal changes in water temperature as a function of a constant temperature at the dam and the following sinusoidal seasonal pattern in air temperature, T_t:

$$T_t = T_{avg} + (T_{max} - T_{avg}) \sin\left((t - t_{avg}) \frac{2\pi}{365}\right), \quad (1)$$

where T_t is the average daily air temperature (°C); T_{avg} is the average annual air temperature (°C); t is the Julian day of the year (1–365); t_{avg} is the first Julian day that the air temperature reaches T_{avg}; and T_{max} is the maximum air temperature (°C).

Table 2
Parameter values used in simulations for the Tuolumne River, California (simulation value) and sensitivity analysis (nominal value).

Parameter name	Simulation value	Nominal value[a]	Equation number	Parameter description
a_{fec}	−3200.2	**−32002**		Intercept of fecundity relationship with fish length
al	0.0005	**0.0005**	8	Intercept of relationship between fry length and weight
a_{dd}	0.93	0.93	14	Fraction of DD_{smo} with 50% outmigrant mortality risk
a_{move}	0.25	0.16	9	Movement rate at zero flow for fry (days km^{-1})
a_{move}	0.32	0.32	9	Movement rate at zero flow for smolts (days km^{-1})
A_{rat}	250	250	9	Scaling ratio for river size
A_{redd}	216	216	4	Average defended redd area (4 × actual redd area) (m^2)
A_{terr}	0.001479	0.001479	7	Coefficient in territory vs. fish length relationship
B_{terr}	2.61	2.61	7	Exponent in territory vs. fish length relationship
b_{dd}	0.921	**0.921**	14	Fraction of DD_{smo} with 90% outmigrant mortality risk.
b_{fec}	109.4	**109.4**		Slope of fecundity vs. fish length (cm)
bl	2.136	**2.136**	8	Exponent of length vs. weight relationship for fry
bq_{temp}	0.5	0.4	3	Power function exponent relates velocity to flow
c_{move}	-6.0×10^{-6}	-6.0×10^{-6}	9	Slope between travel time (days $km)^{-1}$ and flow (m^3 s^{-1})
C_s	0.02	N.A.		Stomach capacity as a fraction of predator weight
DD_{alv}	395.8	**395.8**		Degree-days required from hatching to emergence (°C)
DD_{eggs}	500	**500**		Degree-days required from egg laying to hatching (°C)
DD_{smo}	1082	1082		Degree-days required to develop into a smolt (°C)
F_{spawn}	0.5	1.558		Minimum flow needed to upmigrate and spawn (m^3 s^{-1})
k_{temp}	−0.001	-1.0×10^{-5}	2	Temperature equilibration rate coefficient (s^{-1})
L_{min}	70	N.A.		Minimum size required to develop into a smolt (mm)
$L_{p,avg}$	320	**320**		Average size of predators in river (black bass; mm)
$L_{p,std}$	25	**25**		S.D. of predator size distribution (mm)
$L_{s,avg}$	688	688		Average length of adult spawners (mm)
$L_{s,SD}$	74	74		S.D. of spawner lengths (mm)
$L_{s,min}$	400	N.A.		Minimum length of spawning adults (mm)
$L_{s,max}$	1400	N.A.		Maximum length of spawning adults (mm)
L_{segsp}	40.5	40.5		Stream distance below dam used for spawning (km)
M_{egg}	0.0	0.001		Baseline daily mortality risk in the redd
N_{esc}	N.A.	5000		Fall run escapement (number of adults)
P_k	0.8	0.8	13	Maximum probability of successful prey capture
P_{late}	0.07	N.A.		Fraction of total chinook spawners in late-fall run
P_{pock}	0.5	0.5		Average fraction of egg pockets superimposed
P_{int}	0.1	0.01		Perceived density of predators as fraction of actual
P_{smo}	0.6	0.6		Fraction of maximum intake obtained by smolts
P_{up}	0.4	0.1		Probability of upstream movement at low temperatures
P_{min}	0.08	0.08		Minimum fraction of max. daily ration at feeding station
P_{max}	0.6	0.6		Maximum ration at feeding stations (obtained by large fry)
R_{lag}	0	N.A.		Lag time between upmigration and spawning
S_{min}	0.9995	0.9500	4	Maximum daily survival rate in marginal habitat
S_{max}	1.0	1.0	4	Maximum daily survival rate in excellent habitat

Table 2 (continued)

Parameter name	Simulation value	Nominal value[a]	Equation number	Parameter description
S_{rat}	0.44	0.35		Fraction of adult spawners that are female
S_{wait}	14	N.A.		Period from egg laying to female departure (d)
t_{avg}	April 4	N.A.	1	First date that air temperature reaches T_{avg}
T_{avg}	16	N.A.	1	Average annual air temperature (°C)
T_{avoid}	22	**22**		Lower threshold for behavioral avoidance (°C)
T_{max}	30	N.A.	1	Maximum annual air temperature (°C)
T_{spawn}	17.8	**17.8**		Upper temperature threshold for chinook spawning (°C)
T_{ULT}	25	**25**		Upper lethal temperature for chinook salmon (°C)
UP_{max}	April 20	April 20		Latest date of upmigration/spawning, late-fall run
UP_{max}	December 22	December 22		Latest date of upmigration/spawning, fall run
UP_{min}	January 1	January 1		Earliest date of upmigration/spawning, late-fall run
UP_{min}	October 1	October 1		Earliest date of upmigration/spawning, fall run
UP_{peak}	October 27	October 27		Peak date of upmigration/spawning, fall run
UP_{peak}	March 1	March 1		Peak date of upmigration/spawning, late-fall run
α	-10.0	-10.0	11	Influences the maximum probability of capture
β	200.0	200.0	11	Sets the lower bound on prey length in probablility capture
η	18.0	18.0	12	Sets the upper bound on prey length in probability capture

[a] Entries for parameters that were not in the version used for sensitivity analysis or settings not selected for simulations are listed as not applicable (N.A.); bold values of parameters were held constant (not varied) in the sensitivity analysis.

ORCM uses a simple first-order temperature model to simulate the equilibration of water temperatures downstream of the dam (Eqs. (2) and (3)). Parameters k_{temp} and bq_{temp} can be estimated by least squares regression.

$$T_x = T_a + (T_w - T_a)e^{(k_{temp}t_{dam})} \tag{2}$$

$$t_{dam} = xQ^{-bq_{temp}}, \tag{3}$$

where T_x is the average daily water temperature (°C) at segment x; T_w is the average daily water temperature below the dam (°C); T_a is the average daily air temperature (°C); k_{temp} is the the temperature equilibration rate (s^{-1}); t_{dam} is the water travel time from the dam (s); x is the distance below the dam (m); Q is the river flow ($m^3 \cdot s^{-1}$); and bq_{temp} relates velocity ($m\ s^{-1}$) and flow ($m^3\ s^{-1}$).

2.3. Habitat capacity

The simulated habitat capacity (number of juveniles m^{-2}) of a river segment depends on its percent of pool and run habitat versus riffle habitat, as well as on flow. ORCM requires curves relating weighted usable area (WUA in $m^2\ km^{-1}$ of river) to flow (in $m^3\ s^{-1}$) for each lifestage and habitat type. The model requires WUA curves for chinook spawning, incubation, fry and juveniles for pool and run habitat combined and for riffle habitat. If no curves are available for incubation, one can adopt the spawning WUA with the assumption that the habitat qualities of redds were selected by the parents because they were suitable for incubation. We provide the proportion of riffle habitat for each river segment and we assume that the rest of the habitats are either runs or pools.

2.4. Adult escapement

Simulations begin with the appearance of upmigrating fall and then late-fall run adults in the river. The user specifies the total number of adults belonging to the fall run that return to the tributary for spawning migration N_{esc} from an input file for historical years and parameters of their size distribution. We assume that the total number of late-fall run spawners is a specified fraction of the fall-run spawners P_{late}.

ORCM simulates the arrival of female spawners of each run over time according to a triangular distribution between two dates UP_{min} and UP_{max} and a peak date UP_{peak} (Fig. 2). These dates may be site specific, depending on latitude, distance to spawning habitat, and other factors.

The number of spawners present at the mouth of the tributary on any day is the proportion calculated from this distribution plus those unable to migrate on previous days. On a particular day, female spawners do not migrate if the water temperature at the mouth of the tributary exceeds a threshold T_{spawn} or if discharge from the tributary is below a threshold F_{spawn}. We adopted a temperature threshold that is intermediate between the upper limits reported for upmigration (i.e. 21.1°C; Hallock et al., 1970), spawning (i.e. 15.6°C; Chamberlain, 1907) and egg viability (i.e. 15.6°C; Boles, 1988). When upmigration dates for the river come from surveys of redds or carcass counts in the spawning reach, model fish can be allowed to spawn as soon as temperature and flow conditions are adequate. For applications with upmigration data collected at the entrance to the tributary, the model provides the ability to impose an average time R_{lag} between a spawners entry to the tributary and its arrival at the spawning grounds.
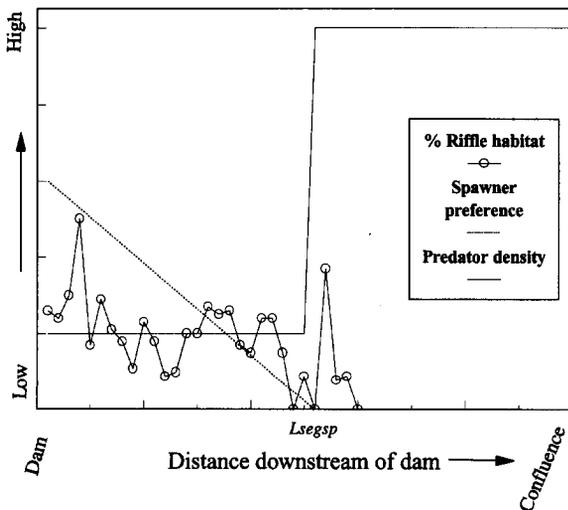
Fig. 1. Examples of longitudinal patterns in spawner preference, percentage of riffle habitat and predator density in a model river (EAEST, 1992d,h).

2.5. Spawning

The model uses the sex ratio S_{rat} to determine how many of the N_{esc} upmigrants are female spawners. For each female spawner, the location of each redd is drawn from a triangular probability distribution that imposes a preference for segments closer to the dam and disallows spawning beyond distance L_{segsp} downstream (Fig. 1).

ORCM simulates flow-related changes in available spawning habitat without detailed spatial modeling of hydraulics and sediment transport. For each river segment, we estimate the number of spawning sites under optimal flow conditions N_{opt} by assuming that WUA_{opt} (the peak of the WUA curve for spawning) represents the maximum amount of high-quality spawning habitat present per unit stream length. We partition this habitat into N_{opt} suitable spawning sites

$$N_{opt} = \frac{L_s WUA_{opt}}{(S_{min} + S_{max}) A_{redd}} \qquad (4)$$

ranging uniformly from low quality S_{min} to high quality S_{max} and assume that neither pools nor runs are used as spawning habitat (EAEST, 1992a). N_{opt} depends on the length of the river segment, L_s, average redd quality under optimal conditions, and average area per redd A_{redd}.

On most days and at most flows fewer than N_{opt} distinct suitable spawning sites exist because flow-related WUA is less than WUA_{opt} in Eq. (1). Female spawners select a redd site within the segment at random from the suitable sites available on the date of spawning. Once the model assigns a redd a site with a given rank, it retains that site throughout incubation, but its quality will vary with flow as described in Section 2.7. When a later spawner selects the same site as a previous spawner, superimposition occurs.

The model determines the number of eggs in each redd from a fecundity relationship with female size obtained from spawners in the Mokelumne River by the East Bay Municipal Utility District (EBMUD, 1992): number of eggs $= a_{fec} + b_{fec}L$, where L is fish length in cm. Female spawners are assigned lengths from a truncated normal distribution with mean $L_{s,avg}$, S.D. $L_{s,SD}$, minimum $L_{s,min}$, and maximum $L_{s,max}$.
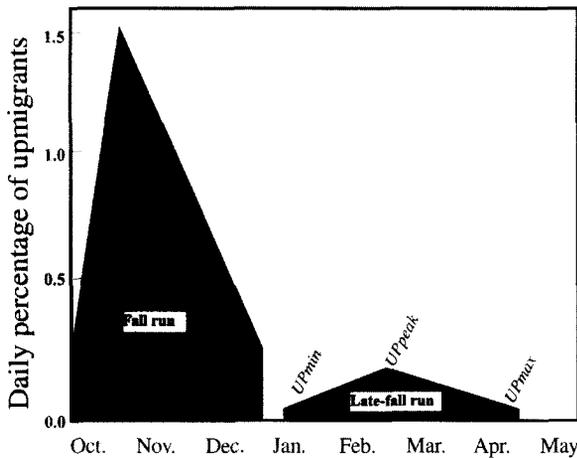
Fig. 2. Simulated timing of upriver migration for fall run (EAEST, 1992c) and late-fall run (Brown and Greene, 1992) chinook salmon in California.

2.6. Egg and alevin development

Incubation and development of eggs takes place over the period of time required to accumulate a fixed number of degree-days, DD_{eggs} (Gangmark and Bakkala, 1960; Murray and McPhail, 1988). The duration of the alevin stage is determined by the number of post-hatching days required to accumulate DD_{alv} degree-days (Murray and McPhail, 1988). For both lifestages, we discount degree-days accrued at temperatures below 5°C by 50%.

2.7. Egg and alevin mortality

Mortality during incubation in the redd is calculated daily. Eggs and alevins are exposed to several mortality risks, three of which are associated with particular events: extreme temperatures, superimposition of redds, and loss of habitat associated with extreme flows. A baseline daily risk of mortality M_{egg} is used to simulate other mortality factors (e.g. poor condition of spawning gravels).

We simulate a temperature-related mortality risk that varies in response to daily temperature for eggs and alevins (Murray and McPhail, 1988). These effects are greater for eggs than for alevins (Fig. 3).

Flow-induced habitat degradation can take the form of dewatering or scouring of the redds. We simulate the effects of flow on egg and alevin survival by varying redd site quality with the WUA for spawning. At the optimal flow for spawning, we allocate a quality ($S_{min} \leq S_{i,opt} \leq S_{max}$) to each site, i, to rank potential redd sites. S_{min} is the daily probability of survival for marginal redd locations and S_{max} is the daily flow-related probability of survival for the best redd locations. On each day, t, the number of suitable sites is a fraction of the optimal number, determined by the ratio $WUA_t : WUA_{opt}$. The quality of each of the N_t sites is simulated as a linear function between S_{min} and S_{max}, where site 1 is always higher in quality than site 2, and so forth (Figs. 4 and 5). The result is that redds constructed during optimal flow conditions are more likely to be susceptible to high flow-related mortality at suboptimal flows than those constructed when flow conditions were poor. Although ORCM does not explicitly simulate local depths and velocities, this approach has the effect of increasing the vulnerability of redds at very low and high flows. The details of this relationship can be controlled through the incubation WUA relationship provided to the model.
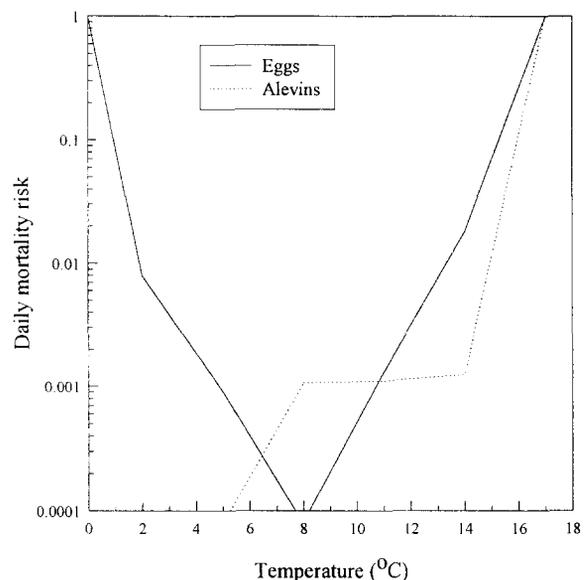
Fig. 3. Temperature-related mortality for the egg and alevin lifestages in the model.
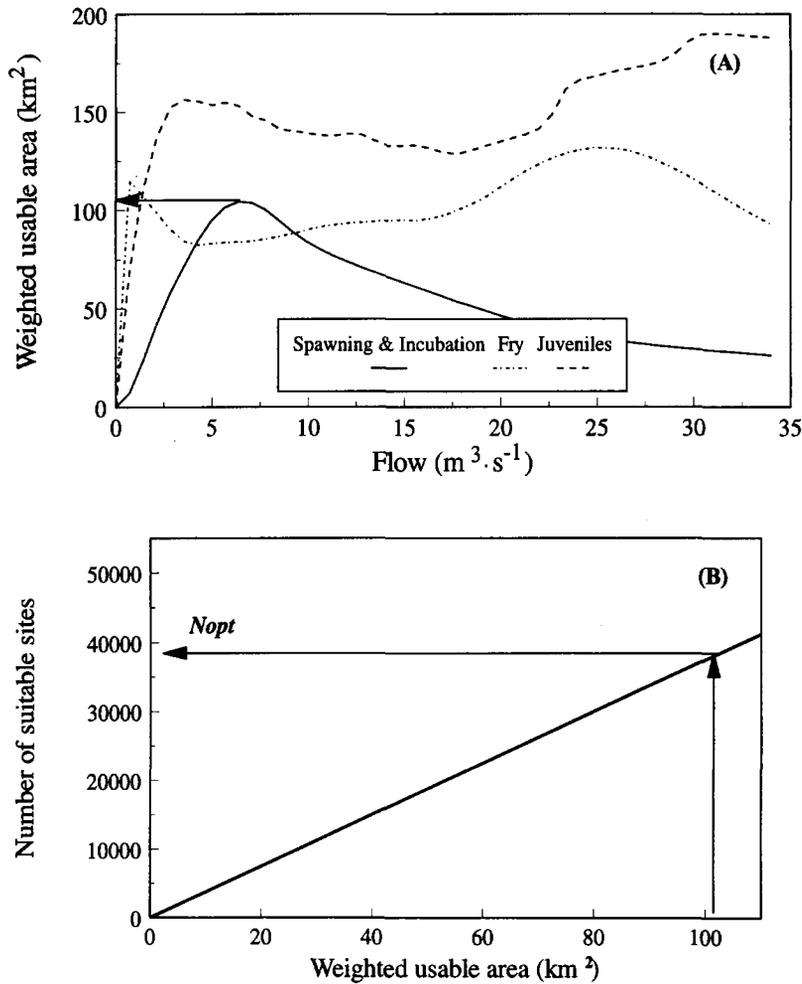
Fig. 4. (A) WUA is used as a habitat capacity for each lifestage of fall chinook salmon in the Tuolumne River (EAEST, 1992b); (B) the number of suitable redd sites (or foraging stations) varies in response to flow as WUA changes.

An additional source of mortality related to redds takes place when a new redd is constructed on the same site as an existing redd. ORCM prohibits superimposition of a redd up to S_{wait} days after redd construction because of the female's presence. When a model redd is superimposed by a later spawner, we simulate the proportion of egg pockets destroyed as a Poisson process with mean P_{pock}. Superimposition of previous redds occurs most often when redd densities are high and spawning habitat is scarce.

2.8. Juvenile development and growth

Alevins emerge from redds at 30–40 mm in length (Murray and McPhail, 1988; EBMUD, 1992). We assume that each model fry becomes a smolt when it accumulates a certain number of degree-days DD_{smo} after emergence (EBMUD, 1992). To become smolts, they must also reach a minimum length, L_{min}. Degree-days at temperatures below 5°C are discounted 50% on the basis of data on emergence at different temperatures (Murray and McPhail, 1988).

Emerging fry are initially located in the model river segment of their redd. ORCM tracks chinook salmon juveniles (both fry and smolt) as individuals. Information about the timing and location of releases of hatchery juveniles can be provided to the model, and stocked fish can be tracked along with other individual chinook juveniles. After emergence or stocking, the model begins to simulate individual foraging success, movement and other relevant activities.

Simulated growth rates of each individual fry depend on temperature, flow and the number of competing juveniles in its river segment. Its daily growth, ΔG (g wet weight), is

$$\Delta G = C - (E + F + \text{SDA} + R), \qquad (5)$$

where C is daily consumption; E is egestion; F is excretion; SDA is specific dynamic action; and R is standard + active respiration. We used the model and parameter values given in Stewart et al., 1983. Daily consumption C is modeled as a proportion (p) of maximum daily intake C_{max} which depends on water temperature and fish weight:

$$C = pC_{max}. \qquad (6)$$

We simulate variability among individual fry growth rates by assigning higher quality feeding stations to larger fish. This approach simulates temporal autocorrelation in growth by assuming that larger fry have a behavioral growth advantage related to the defense of a territory with high growth potential (Mason, 1969). Each day, fry residing in a segment are ranked in size. Stations are reassigned daily, with the largest fry receiving the highest quality stations. If there are more fry than stations, those fry lacking a suitable station do not grow. A resident fry may be shifted to a lower or higher ranked station as larger or smaller fry immigrate into the segment or as other resident fry die.

Resource depletion is simulated indirectly through exclusion from feeding stations at high densities or low habitat availability. We assume that a site with quality $X(P_{min} \le X \le P_{max})$ provides a fish with fraction $p = X$ of its maximum daily feeding ration. The same procedure described in the section on spawning-site quality is used to decompose the quantity and quality aspects of WUA_{fry} (Figs. 4 and 6). In particular, the number of suitable feeding sites is calculated by dividing the current WUA_{fry} by the average size of feeding territories for fish in the segment. The model allocates feeding stations to larger fish first until the total area of stations reaches the composite juvenile weighted usable area of the river segment. Territory size, T_{size} (m^2), is derived for each fry from a relationship with fish length, L (mm) from Grant and Kramer (1990):

$$T_{size} = A_{terr}L^{B_{terr}}, \qquad (7)$$

where values of A_{terr} and B_{terr} are listed in Table 2.

We assume that each smolt obtains a fixed proportion of maximum ration, P_{smo}, and do not compete for feeding stations, focusing instead on downstream migration.

The model translates weight W gains into length, L, increases by (1) assuming that juveniles in good condition meet the following relationship and (2) increasing fish length accordingly (parameters in Table 2):

$$W = al\,L^{bl} \qquad (8)$$
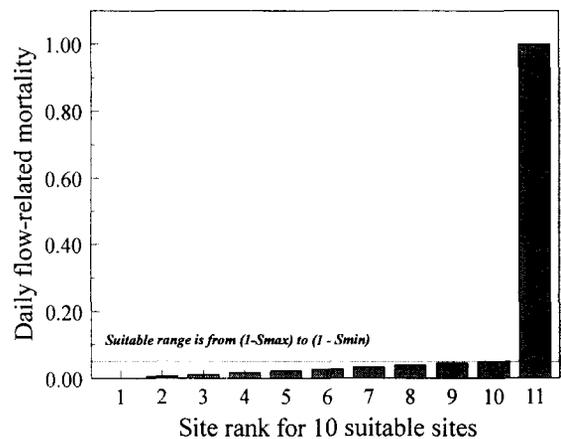
Fig. 5. Simulated flow-related habitat survival rates experienced by eggs and alevins during incubation is illustrated. In this example, redds in sites ranked 11 and greater are assumed to be lost because of dewatering and lack of irrigation or scouring depending on which end of the WUA curve for incubation flow it is on.

2.9. Juvenile movement

ORCM simulates daily movement differently for fry and smolts. Fry do not necessarily move daily, and they are motivated by the search for unoccupied habitat suitable for growth and with a low risk of predation. Smolt movement occurs every day and is directed toward outmigration.

The model allows fry to disperse from the spawning reach to the rearing reaches and out of the river. We assume that fry movement depends on fry density and habitat availability as well as flow (Bilby and Bisson, 1987; Williamson et al., 1992). Every day, each fry compares the cost–benefit ratio of its current habitat (i.e. the ratio of predation risk to growth) with an estimate of the cost–benefit in other locations (Werner and Gilliam, 1984). This estimate is based on the individual fishs experience in other locations during previous time periods. A fry moves when this analysis suggests that it can probably do better elsewhere (Jager et al., 1993).

Simulated daily movement of fry is more likely to be in a downstream direction. The probability of upstream movement P_{up} can be calibrated to match the observed rate of downstream movement in juveniles captured at different locations in the river. At temperatures above T_{avoid} model fry have a tendency to move upstream to avoid lethal temperatures (EPA et al., 1971). The probability of upstream movement increases from P_{up} at T_{avoid} to 1.0 at the upper lethal temperature for chinook salmon T_{ULT}.

Once a simulated juvenile chinook decides to move, its movement occurs at a rate that depends weakly on river flow Q (m^3 s^{-1}). We assumed that mean travel time (days km^{-1}) for downstream movement decreases with flow according to a weak linear relationship fit by us to data for subyearling chinook reported by Berggren and Filardo (1993):

$$\text{Travel time} = a_{move} + c_{move} A_{rat} Q. \qquad (9)$$

The sign of c_{move} changes for upstream movement. To adapt this relationship for fry, we adjusted the rate of movement at zero flow a_{move} so that a maximum of 30 days was required for fry to travel 122 km (Berggren and Filardo, 1993). To simulate outmigration, we adopted the hypothesis that the main factors involved operate indirectly by speeding the development of chinook salmon fry into smolts. Once chinook salmon reach the smolt stage, a variety of cues (e.g. flow, change in flow, water temperature, precipitation, turbidity, photoperiod, smolt density, the phase of the moon) can result in pulses of outmigrating fish (EBMUD, 1992). In ORCM, we assume that the necessary cues are present and that daily smolt outmigration begins when fish reach the smolt stage. The daily distance travelled by a given smolt during outmigration depends on flow (Eq. (10)) and is always in a downstream direction. There are movement studies currently underway in smaller rivers than the Columbia River (Personal communication with J. Petersen, National Biological Service, Cook, WA). We intend to revise this component once the results of these studies become available.

2.10. Juvenile mortality

ORCM simulates mortality resulting from exposure to extreme water temperatures and predation for all juveniles. Model juveniles remaining in a segment with water temperatures above T_{ULT} (Brett, 1952) die after 1 day of exposure. The model allows juveniles to avoid high, sublethal temperatures by increasing the likelihood of upstream movement.

Fish predators, including smallmouth bass (Micropterus dolomieui), largemouth bass (M. salmoides) and Sacramento squawfish (Ptychocheilus grandis) forage on chinook juveniles. To simulate predation mortality we expose juveniles to an array of predators of various size classes that are distributed spatially along the river reaches of interest. We simulate the sizes of predators from a normal distribution with a specified mean $L_{p,avg}$ and S.D. $L_{p,std}$ with lengths truncated at 3 S.D. on either side of the mean. Length–weight relationships convert predator lengths into weights.

Spatial variation in predator densities can be specified for each of the smaller longitudinal segments of the model river reach. In addition, we assume predators inhabit pool and run habitats

but not riffles. Because predators and prey are not 'well-mixed' in rivers (i.e. prey have access to refuges), juvenile chinook salmon risk encountering only a fraction P_{int} of the predators in the same river segment.

Simulated encounters between individual predators and prey—the chinook juveniles—depend on the characteristics of an individual prey and its location in the river. The predation risk of each juvenile depends on its length, its condition, and the stomach fullness of predators that it encounters. Each individual predator feeds during daylight hours unless its stomach contents reaches its capacity, C_s (Peterson and DeAngelis, 1992), which we represent as a fraction of predator weight. We simulated a constant rate of evacuation of stomach contents for smallmouth bass (*M. dolomieu*) that depends on predator weight, time since consumption, total weight of ingested prey and water temperature (Rogers and Burley, 1991).

The probability of capture, P_c, is greatest at intermediate ratios of prey to predator size, L_{rat}, (Dunbrack and Dill, 1983) and for prey in poor condition:

$$P_c = R_{max} P_{attack} P_{ingest}. \tag{10}$$

Relatively small prey (juveniles) are protected by a reduced probability of attack P_{attack}

$$P_{attack} = \frac{\exp(\alpha + \beta L_{rat})}{1 + \exp(\alpha + \beta L_{rat})}, \tag{11}$$

whereas relatively large prey are protected by a reduced probability of successful ingestion P_{ingest}.

$$P_{ingest} = \frac{1}{1 + \exp(\alpha + \beta L_{rat})}. \tag{12}$$

The maximum risk, R_{max}, increases linearly as the physiological condition K or relative weight of the juvenile deteriorates:

$$R_{max} = 1 + (P_k - 1)K. \tag{13}$$

Thus, chinook in poor condition are more susceptible to predation, and chinook in good condition ($K = 1$) have a maximum capture risk of P_k.

In addition, juveniles in the fry lifestage may be lost because they leave the spawning tributary before reaching the smolt lifestage. This premature outmigration is most likely to occur when fry densities exceed the number of feeding stations. Under these conditions, growth for smaller chinook fry is inadequate and downstream movement is more frequent. For an upstream tributary, 'premature' outmigrants may survive and smolt in a mainstem river outside the spatial scope of the simulation (Williams, 1994). To provide for this, we offer two ways to estimate the proportion of these fry that die. One option is to assume that all fry exiting the tributary die because of premature exposure to salt water or predation. The other option is to assume each individuals risk of mortality P_{pre} decreases as accumulated degree-days, DD, approaches DD_{smo}:

$$P_{pre} = \frac{1}{1 + \exp\left(A_{dd}\dfrac{DD}{DD_{smo}} + B_{dd}\right)}. \tag{14}$$

Parameters A_{dd} and B_{dd} are derived by assuming that a_{dd} is the fraction of DD_{smo} associated with 50% outmigrant mortality risk and that b_{dd} is the fraction associated with 90% mortality risk (Table 2).

3. Iterative model improvement

Our initial model represented a preliminary collection of hypotheses concerning relationship between flow and chinook ecology. We followed an iterative process of model improvement that parallels the scientific process (Overton, 1977). In this section, we describe comparisons between intermediate ORCM predictions and field observations in the Tuolumne River in California. This ability to validate intermediate model predictions is an important advantage of mechanistic models (Murdoch et al., 1992). As discrepancies appeared, we identified likely mechanisms causing the problem and changed our hypotheses (i.e. the model). Sometimes we changed the models structure and sometimes we only calibrated a parameter of the model. After several iterations we reached a point where we had done as much to improve the model as was clearly indicated by the field data. At this point further improvements must await new field information for important, but poorly understood, influences on smolt production.
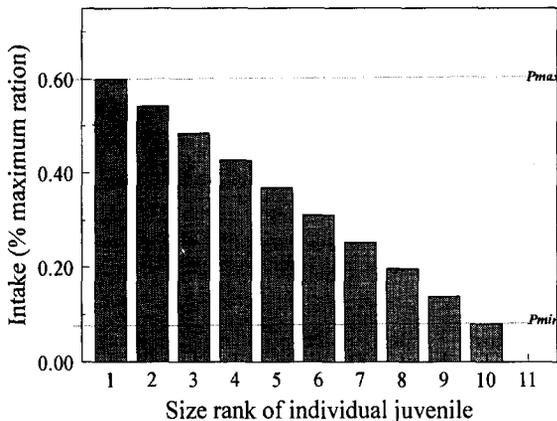
Fig. 6. Simulated competition for feeding sites among fry in relation to habitat capacity is illustrated. The model allocates feeding stations to larger fish first until the total area of stations reaches the composite juvenile WUA of the river segment. Foraging success (daily ration) is greater for larger fish and is 0 for fish without a feeding station for this example with 10 suitable sites.

3.1. Simulation input and initial conditions

We calibrated and tested ORCM against available field data in the Tuolumne River, a tributary of the San Joaquin River that empties into the Sacramento–San Joaquin Delta in California (Fig. 7). We compared model predictions with field data for each year from the fall of 1985 to the spring of 1989. Our calibration focused on three lifestages and processes (egg and alevin survival, juvenile survival and juvenile growth) and relied upon three field studies for comparative data (Table 3).

3.2. Life stage development

To evaluate egg and alevin development rates we compared simulated dates of emergence from redds with dates at which 30–40 mm fry were observed in the Tuolumne River seining study (EAEST, 1992e; Table 3). Likewise, we compared the simulated outmigration dates with those of the emigration study (EAEST, 1992g; Table 3).

ORCM predictions of timing of egg and alevin development compared well with field data for the four years. In general the model predicted the onset of fry emergence in mid-December and the

end of emergence extending into May or June. Juveniles that emerged from model redds after mid- to late-March were the progeny of late-fall run spawners. The seining data for 3 of the 4 year suggest that incubation extended into May and June and confirmed the presence of a late-fall run and a 'prolonged emergence, and possibly spawning, period' (EAEST, 1992e).

One of the mysteries highlighted by these simulations is the question of how important offspring of the late-fall run are in rivers with managed versus natural flows. The late-fall run in the Tuolumne River has not been studied. Consequently, we were unable to determine how long the juvenile chinook remained in the tributary, although a small fraction of the chinook are believed to remain into the summer. The last smolting fish observed in the seining studies was captured on the last day sampled, June 26, 1986. Our simulations suggest that late-fall run individuals may be those that remain in the system through summer if they can find locations with sublethal temperatures (e.g. near the dam or near groundwater upwellings). Anecdotal evidence suggests that the late-fall chinook salmon oversummer in the American River and emigrate in fall (Williams, 1994).

3.3. Egg and alevin survival

Mortality is the most sensitive and uncertain quantity in all population models, particularly in the earliest lifestages (Bart, 1995; Bartholow, 1996) and field studies quantifying early causes of mortality are scarce. Dill (1969) believes that the period of the life-history from deposition of the eggs in the redds to emergence of the fry from the gravel accounts for most of the gaps in our knowledge.

We calibrated ORCM to produce survival rates similar to those observed in field studies and evaluated the simulated levels of temperature-related mortality, superimposition and flow-related mortality. We adopted parameters from the literature for temperature-related mortality and superimposition. We set baseline mortality to 0 and calibrated levels of flow-related mortality (dewatering and scouring) by varying S_{min} to achieve $\sim 30\%$ survival to emergence.
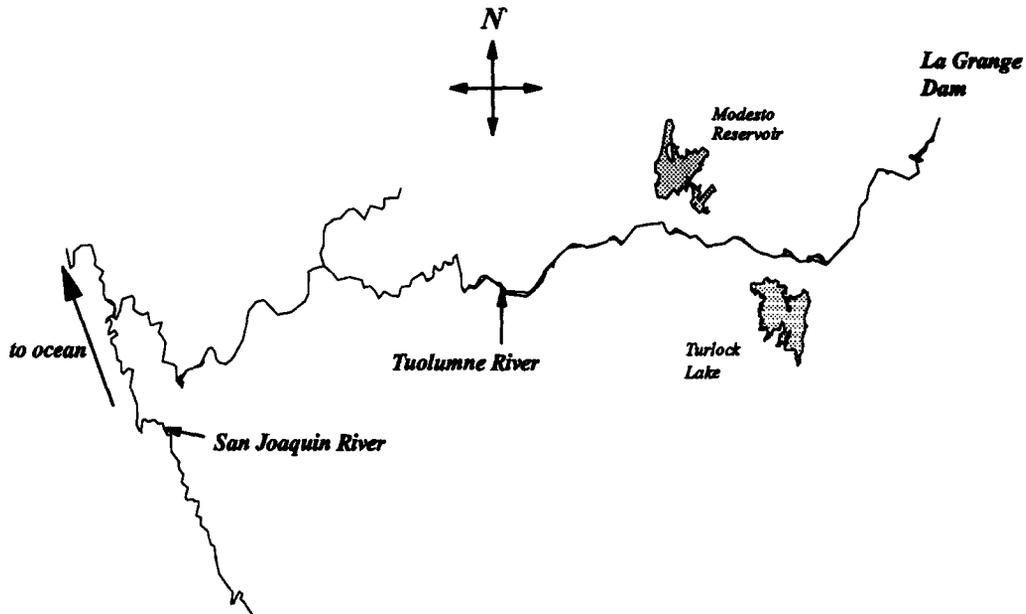
Fig. 7. Map of the Tuolumne River reach (simulated) showing the upstream barrier to migration (LaGrange Dam) and the outmigration route from the dam to the confluence with the San Joaquin River and northwest toward the ocean.

ORCM predicts reasonable levels of overall mortality and the causes appear reasonable. Temperature was the most important factor in all years simulated closely followed by flow or habitat-related mortality (e.g. dewatering, scouring). Superimposition was low except for the year with the highest escapement, 1985. Studies in the Mokelumne River (EBMUD, 1992) support model results concerning the relative importance of temperature-related mortality and relative lack of importance of superimposition. Egg-to-fry survival in the Mokelumne River was at 40% for a cold-water cohort (daily water temperature < 15°C) and 10% for a warm-water cohort (EBMUD, 1992). A small percentage (3–12%) of redds were superimposed and, presumably, some egg pockets would not be disturbed (EBMUD, 1992).

The importance of flow-related redd mortality in these rivers is unknown. Model results suggest that flow-related mortality acts as a density-dependent limitation because at high densities more redds are constructed in marginal locations. Changes in flow during incubation caused model redds initially constructed at near-optimal flows

to be dewatered or scoured (i.e. redd site quality decreased along with the flow-related survival rate). High fall flows followed by winter reductions in flow contributed to this mortality. Laboratory evidence suggests that streamflow reductions through dewatering (Reiser and White, 1990) can cause significant mortality, particularly on the alevin lifestage (Becker et al., 1982). In some rivers lowering flow during incubation may decrease subsurface flow diminish irrigation of the eggs and thereby increase egg mortality (McNeil, 1969; Williams, 1994).

3.4. Juvenile growth

We compared simulated growth rates (juvenile lengths) with the reported average and ranges of lengths calculated from weekly seining catches in the Tuolumne River for water years (WY) 1986 to 1989 (EAEST, 1992e; Table 3).

Simulated lengths of fry for the 4 years from 1985–1989 matched reasonably well with the distribution of chinook juveniles (fry and smolt) sizes in the seine catch through time, as shown for WY 1987 (Fig. 8). In most years, the smallest juveniles

Table 3
Field studies conducted in the Tuolumne River and used to validate each component of the Oak Ridge Chinook salmon model

Model compo-nent	Field study description	Study reference
Mortality of eggs and alevins	Redd survival was studied during 1988 and 1989 by using traps. Survival to emergence estimates were 1 and 32%, respectively. High temperature was thought to cause most redd mortality.	EAEST, 1992d
Juvenile development	Seining surveys at 10 day intervals from 1985 to 1989 sketch out the timing of emergence from redds and first appearance of smolts.	EAEST, 1992e
Juvenile growth	Seining surveys at 10 day intervals from 1985 to 1989 trace the growth and size distribution of juveniles. Sampling was conducted during winter and spring months.	EAEST, 1992e
Juvenile mortality	A mark-recapture study produced a Jolly-Seber estimate of population size in a section of the Tuolumne River during May 4–7, 1987.	EAEST, 1992f
	A predator study conducted in the Tuolumne River provided stomach contents data from May to September of 1988 during low flows.	EAEST, 1992h
Juvenile movement	An index of emigration was based on fyke net sampling for some years from 1973 to 1986. Fyke nets were set for 24 h at three locations in the river.	EAEST, 1992g

seined remained ~ 30 mm in length as new fry continued to emerge. Maximum size of seined juveniles rose to between 85–115 mm and then declined, presumably because larger individuals migrated out. The decline in average model fish size during May is an artifact caused by shifting larger juveniles from the fry category to the smolt category (Fig. 8).
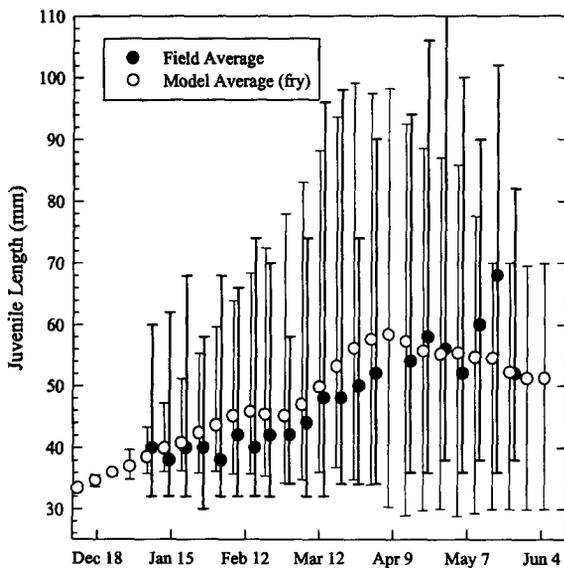
Fig. 8. Comparison of the distribution of simulated fry lengths with the distribution of juvenile (fry and smolt) lengths captured by seining in 1986–1987. Error bars represent minimum and maximum lengths.

The smolt sizes predicted by ORCM compare well with lengths reported for smolts collected during the seining studies. For all years smolting juveniles were collected between April and June and ranged from 64 to 106 mm in length. In 1986, the majority of captured smolts were between 85 and 95 mm in length. Our 1986 model results predicted a range of 66 to 103 mm and an average length of 83 mm.

3.5. Juvenile survival

Simulated predation levels varied spatially to reflect site-specific data available for the Tuolumne River (EAEST, 1992h; Table 3). We adopted the reported size distribution of black bass predators and set predator densities in the model to 294 predators per km from the La-Grange Dam to 27 km downstream (RM 25) and 59 predators per km below RM 25 (see Fig. 7; EAEST, 1992h). Shuter and Post (1990) provided length–weight relationships for smallmouth bass (M. dolomieiu).

We used population survey data to evaluate ORCM simulation of juvenile survival (Table 3). A juvenile chinook mark-recapture study provided a snapshot of population size in one section of the river. We evaluated overall mortality rates by comparing the number of juvenile fish (fry and smolt) predicted by the model against a Jolly-Seber population estimate from a mark-recapture

Table 4
Summary of simulated mortality of each early lifestage of fall chinook salmon for four years

	Simulation year (October 1 to September 31)			
Water year	1986	1987	1988	1989
Calender year	1985-1986	1986-1987	1987-1988	1988-19897
Egg and alevin lifestages				
Escapement	43959	7798	15783	6741
Total annual flow (km³)	3.685	0.808	1.013	1.620
Percent redd success	20	21	50	41
Percent survival to emergence	13	14	33	29
Fry per successful redd	2795	2772	2822	3077
Total eggs (millon)	83	15	30	13
Percent mortality due to:				
Temperature	44	65	56	50
Flow	40	32	39	43
Superimposition	16	3	5	7
Juvenile lifestage				
Total fry emerged (millon)	11.2	2.0	9.9	3.8
Percent mortality due to:				
Temperature	19.1	15.0	22.8	58.5
Premature emigration	67.5	0.9	36.3	6.0
Predation	12.6	56.5	17.3	27.4
Percent outmigrants	0.79	27.6	23.6	8.2

study (EAEST, 1992f). Small numbers of recaptured fish produced Jolly-Seber estimates with large standard errors for all 4 days (Pollock et al., 1990); we adopted the estimate with the lowest standard error.

The numbers surviving through each lifestage and sources of mortality simulated by the model for each of the four WY are given in Table 4.

An estimated 3341 chinook juveniles inhabited the 360.26 m stretch of river included in the mark-recapture study (S.E. = 935). We extrapolated these estimates to the stretch of river below the LaGrange Dam by multiplying the ratio of total river length (83.7 km) to the distance of river surveyed. We estimated 775 864 juveniles in the system in early May 1987. ORCM predicted that 668 380 juveniles were present on May 4, 1987, and that most of these were fry (Fig. 9).

To avoid introducing the additional uncertainty from extrapolating to the whole river, we also compared the number of juvenile in the section of stream 3–4 river miles below LaGrange Dam with the mark-recapture estimate for the same river section. The mark-recapture population estimate for the river section where the study was conducted was 14 920 (range: 6576–23 286) juveniles, and the model predicted 15 443 juveniles.

The model did well in predicting the number of juveniles within the section of river included in the mark-recapture study. It should be noted, however, that abundances are highly variable (Fig. 9). Population estimates for a single point in time when the number of juveniles is changing rapidly are very difficult to make with any certainty because of the many immigrants, emigrants and deaths—from 17 to 48% of marked fish were lost daily (EAEST, 1992f).

Although we did not have estimates of outmigrant numbers, premature outmigration was observed in WY 1986 and other years and large catches of small fry were associated with high and/or fluctuating flows early in the season (EAEST, 1992g). In the model premature emigration was strongly density-dependent and played a large role in the years with high numbers of spawners (Table 4). A small fraction of these early outmigrants may rear in the San Joaquin River or San Francisco Bay and complete the journey to

sea in spite of high susceptibility to size-selective predators. The other two factors, predation and high temperature, were responsible for a significant fraction of simulated mortality in all years. Predation dominated mortality in WY 1987 and temperature dominated in WY 1989 (Table 4).

4. Sensitivity analysis

Because it is important to understand which model components are most critical it is advisable to conduct a sensitivity analysis of individual-based models before using them to make management decisions (Bart, 1995). A sensitivity analysis of ORCM ranked model parameters by their impact on key model predictions. We identified four key types of model predictions: (1) the number of fall chinook salmon entering each lifestage, (2) the number succumbing to each of three mortality risks, (3) the average size of out-migrating smolts, and (4) the timing of development for each lifestage. As a result of the sensitivity analysis, we fine-tuned several key parameters in the next iteration of model development. We were also able to identify components of the model that contributed most to the stochastic variability in repli-

Fig. 9. Comparison of model estimates (sum of grey and black shaded areas) with a field mark-recapture (Jolly-Seber) estimate of the juvenile population in early May, 1987.

cate simulations (i.e. with the same parameter values but with different random number seeds).

Sensitivity analysis also identified factors that limit simulated fall chinook salmon recruitment by highlighting parameters of processes and lifestages to which the number of outmigrants is most sensitive.

4.1. Methods

This sensitivity analysis was conducted on a version of the model that did not include a late-fall run. We simulated fall-run chinook during a critical dry year (1986–1987) with an average of 5000 spawners. Parameters that we included in the analysis varied around a mean or nominal value (Table 2). Sensitivity analysis is a local estimate of the partial derivative of the response variable with respect to each parameter at a given point in parameter space defined by the nominal values. Sensitivities may be different at other points in parameter space. We excluded parameters that were not of particular interest because data defining them are generally of high quality (e.g. fecundity parameters a_{fec} and b_{fec}) or because they are redundant with other parameters in the way they influence model results (e.g. L_{segsp} and A_{redd}).

We conducted the sensitivity analysis with PRISM, a software for sensitivity analysis developed at Oak Ridge National Laboratory (Gardner et al., 1981). The chinook model was run with 5000 different parameter combinations. PRISM draws a latin-hypercube sample of parameter values from a truncated multivariate Gaussian distribution with specified mean (nominal) values (Table 2) and a coefficient of variation of 1%. This variation is not intended to represent our uncertainty in the parameters, but only to estimate the influence of varying the parameters near one point in parameter space. The algorithm ensured near-independance among parameters.

We present two sensitivity indices here. The standardized regression coefficient (SRC) is estimated from a least-squares regression analysis in which the model parameters are independent variables and the response variable is the dependent variable. This index gives the change in the model prediction in S.D. corresponding to 1 S.D. change in the model parameter, given that all other
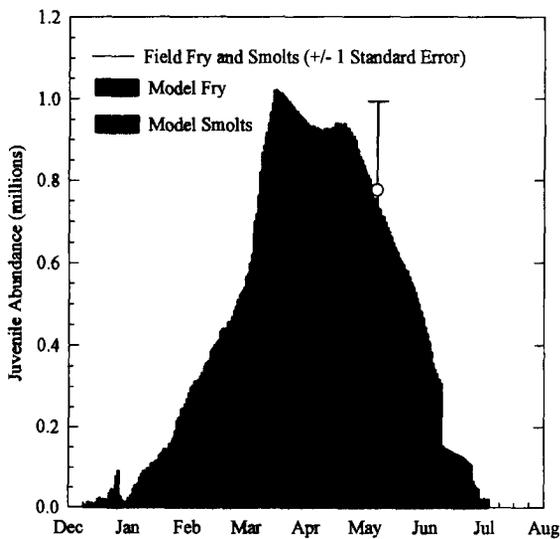
parameters are constant. The sign of the index indicates the direction of the response. The second index, the relative partial sum of squares (RPSS), indicates the additional percentage of variance explained by each parameter given that all other parameters are in the model. RPSS values range from 0 to 100%.

We report the overall percentage of variation ($R^2 \equiv r^2 \times 100\%$) in the response variable explained by all of the parameters together. In a sensitivity analysis of a deterministic model, the R^2 should be close to 100%. Because we allowed the model to remain stochastic (the random number seed was not controlled as a parameter in the sensitivity analysis), we can also assess the influence of stochastic elements in the chinook model. A low R^2 suggests that the response variable is strongly influenced by stochastic elements (e.g. simulated events that depend on the specific locations occupied by model fish at each time step). Model fish location influences competitive effects of other chinook on ration and growth and exposure to stochastic mortality risks.

4.2. Results and discussion

The results of the sensitivity analysis are summarized in Table 5. Parameters that do not appear in Table 5 did not have a significant influence on any of the model responses.

4.2.1. Stochastic variability

Because the ORNL chinook model is stochastic, not all of the variability in model results was accounted for by the variation in parameter values, as shown by low R^2 values in Table 5. The model predictions most influenced by chance events were (1) the start and end dates of outmigration; (2) the average size of outmigrants, and (3) the number of model fish killed by exposure to extreme water temperatures. For these response variables, it is best not to place much confidence in sensitivity results. Model results that were robust to chance events were (1) the peak (i.e. average) date of outmigration and (2) the number of model chinook in each of the lifestages (including the number of outmigrating smolts). Therefore, it is only necessary to run a small number of replicate simulations

to obtain a good estimate of the number of outmigrants.

4.2.2. Key parameters that influence spawning and incubation success

We identified the parameters with the greatest influence on key model predictions (Table 5). The total number of eggs laid was determined mainly by the number of spawners, N_{esc}. The number of eggs surviving to become fry was no longer sensitive to spawner densities. Instead the number of emerging fry was most sensitive to the minimum quality of spawning habitat, S_{min} which mediates the effect of flow on redd mortality. The importance of this relationship suggests that field studies to quantify flow-related redd mortality (caused by dewatering and scouring) are needed. On the modeling front, a more mechanistic simulation of scouring and dewatering is possible in rivers for which both habitat mapping of the entire river and hydraulic relationships to simulate local velocities and depths for representative transects are available (i.e. Van Winkle et al., 1996).

Parameters related to the timing of up-migration (UP_{min} and UP_{max}) had a secondary influence. Simulations that delayed the onset and end of up-migration had more survivors. Apparently, the start date of upmigration influenced the number of eggs produced, whereas the final date of upmigration influenced survival to the fry lifestage. These results suggest that the representation of upmigration and spawning times in the model should be a secondary focus for future model improvements. One change already made in the model as result of both this analysis and the model comparisons with field data was the addition of a late-fall run. Future efforts to characterize the timing of upmigration as a function of flow and temperature from early fall to winter should improve our ability to predict redd success.

4.2.3. Key parameters that influence timing and development

The peak dates of emergence, smoltification, and outmigration were all strongly linked to UP_{max}, the final date for upmigration of spawners. Although the timing of emergence was almost completely tied to UP_{max}, other factors came into play by the time outmigration occurred.

Table 5
Sensitivity indices for the response of key model predictions (rows) to local changes in parameter values (columns)

Response variable	R^2 (%)	Parameter name									
		N_{esc}	B_{terr}	S_{min}	A_{move}	T_{ULT}	C_s	DD_{smo}	UP_{min}	UP_{max}	P_{max}
Number entering lifestage											
Eggs	82	+0.89	0.0	0.0	0.0	0.0	0.0	0.0	+0.15	0.0	0.0
		0.79	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.02**	**0.0**	**0.0**
Fry	90	+0.05	0.0	+0.86	0.0	0.0	0.0	0.0	+0.11	+0.37	0.0
		0.0	**0.0**	**0.75**	**0.0**	**0.0**	**0.0**	**0.00**	**0.0**	**0.14**	**0.0**
Smolts	79	+0.05	-0.13	+0.81	0.0	0.0	0.0	-0.13	+0.07	+0.29	0.0
		0.0	**0.01**	**0.66**	**0.0**	**0.0**	**0.0**	**0.20**	**0.0**	**0.08**	**0.0**
Outmigrants	81	+0.05	0.0	+0.85	0.0	+0.12	0.0	0.0	+0.11	+0.16	0.0
		0.0	**0.0**	**0.72**	**0.0**	**0.02**	**0.0**	**0.0**	**0.01**	**0.03**	**0.0**
Number killed by factor											
Temperature	61	0.0	-0.05	+0.37	+0.08	-0.21	0.0	0.0	0.0	+0.64	0.0
		0.0	**0.0**	**0.14**	**0.0**	**0.05**	**0.0**	**0.0**	**0.0**	**0.40**	**0.0**
Premature emigration	72	0.0	+0.15	+0.82	0.0	0.0	0.0	+0.10	0.0	0.0	0.0
		0.0	**0.02**	**0.67**	**0.0**	**0.0**	**0.0**	**0.01**	**0.0**	**0.0**	**0.0**
Predation	86	0.0	0.0	+0.30	0.0	0.0	+0.46	0.0	0.0	+0.71	-0.11
		0.0	**0.0**	**0.09**	**0.0**	**0.0**	**0.21**	**0.0**	**0.0**	**0.50**	**0.01**
Peak simulation dates											
Emergence	87	0.0	0.0	0.0	0.0	0.0	0.0	0.0	+0.21	+0.90	0.0
		0.0	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.04**	**0.81**	**0.0**
Smoltification	71	0.0	-0.11	-0.26	0.0	0.0	0.0	+0.17	+0.17	+0.75	0.0
		0.0	**0.01**	**0.07**	**0.0**	**0.0**	**0.0**	**0.03**	**0.03**	**0.57**	**0.0**
Outmigration	71	0.0	-0.13	-0.34	0.0	0.0	0.0	+0.15	+0.16	+0.70	0.0
		0.0	**0.02**	**0.12**	**0.0**	**0.0**	**0.0**	**0.02**	**0.02**	**0.49**	**0.0**
Outmigration dates											
Start	43[c]	0.0	0.0	-0.12	0.0	0.0	0.0	+0.26	+0.58	0.0	0.0
		0.0	**0.0**	**0.01**	**0.0**	**0.0**	**0.0**	**0.07**	**0.34**	**0.0**	**0.0**
End	17[c]	0.0	0.0	0.0	0.0	0.0	0.0	+0.10	0.0	+0.38	0.0
		0.0	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.01**	**0.0**	**0.15**	**0.0**
Outmigrant size	46[c]	0.0	0.0	-0.24	0.0	0.0	0.0	0.0	-0.11	-0.61	0.0
		0.0	**0.0**	**0.06**	**0.0**	**0.0**	**0.0**	**0.0**	**0.01**	**0.37**	**0.0**

For each response variable the first row shows values of the standardized regression coefficient (SRC) index[a] and the second row (bold) shows values of the relative partial sum-of-squares (RPSS) index[b].

[a] Index magnitude indicates the sensitivity and the sign indicates direction of influence; SRC values smaller than 0.05 in magnitude and RPSS values smaller than 0.01 in magnitude are shown as zeros.

[b] Index values range from 0 (not sensitive) to 100 (sensitive).

[c] The random influences on this response variable call into question the sensitivity results for specific parameters.

4.2.4. Key parameters that influence successful rearing and outmigration

Flow-related mortality of eggs and alevins remains by far the most important factor influencing smolt production and the number of outmigrants (through S_{min}). This is probably because mortality is highest in the early lifestages.

Density-dependence in juvenile feeding, acting through parameter B_{terr}, has a weak negative effect on the number of fry that survive to the smolt lifestage and a weak positive effect on the number exiting prematurely. However, the average size of outmigrants did not decrease with feeding station size. These results suggest that although high juvenile densities lead to increased mortality through premature outmigration the average size of outmigrants is not affected.

Our results identified parameters with a large influence on each of the three mortality risks. In general, the key parameters that influenced the number of juveniles (S_{min} and UP_{max} also influenced mortality by controlling the number surviving incubation to die later. A large fraction of the incremental fry production is compensated for by juvenile mortality.

Premature outmigration increased as the number of degree-days required to reach the smolt lifestage DD_{smo} increased, although the number of fry surviving to smolt decreased. These results suggest that delayed development (e.g. caused by delayed spawning or low temperatures) can cause many fry to exit before reaching the smolt lifestage. Temperature-related deaths increased as the critical upper temperature T_{ULT} decreased. The greatest influence on predation risk was the ending date of upmigration UP_{max} which when delayed, contributed to consumption by predators. This does not augur well for a late-fall run. Predation pressure increased with increased predator stomach capacity C_s and with reduced fry condition (S_{max} links the ration of individual fish to its size rank and habitat quality).

4.3. Results and discussion: recruitment bottlenecks

We define a recruitment bottleneck as the mortality source and lifestage that has the greatest negative impact on the number of outmigrants. This definition does not require density dependence. In Table 5, note that the parameters that most influence the number of fish reaching the fry lifestage also retain a strong influence on the number of outmigrants (primarily S_{min} but also UP_{min} and UP_{max}). In this configuration of the model, redd mortality caused by habitat loss appears to be the most important bottleneck. A secondary bottleneck is caused by mortality of juveniles as a result of high river temperatures.

These results suggest that greater effort is needed to calibrate the relationship between survival rates during incubation and either flow or the availability of incubation habitat. While these sensitivity results are supported by reproduction studies that show high mortality during incubation (e.g. Dill, 1969) others believe that incubation is a relatively stable phase of salmonid life compared with the post-emergence period (Latta, 1969).

Bartholow (1996) conducted a selective sensitivity of the SALMOD model, developed for fall chinook salmon in the Trinity River, California. He considered structural sensitivity to model options and noted that the model was sensitive to assumptions about superimposition. He did not specifically evaluate the importance of habitat-related redd mortality—the most sensitive process in ORCM. In our model spawner densities were generally not high enough to limit the population although superimposition mortality was higher in years with more spawners.

The importance of flow-related factors on smolt production has been observed in statistical evaluations of spawner returns, outmigrant survival and average annual flow for the San Joaquin river system (Speed, 1993). Speed concluded that the effect of flow could not be extricated from those of related factors (spawner densities and temperatures), which is true if only annual averages are considered. Together these models suggest that (1) the signal from smolt production is not overwhelmed by later events in the ocean; (2) smolt production is related to annual average flow; and (3) survival in the egg and alevin lifestages controls fall chinook salmon production.

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