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Predicting the Viability of Fish Populations in a Modified Riverine Environment

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To the Graduate Council:

I am submitting herewith a dissertation written by Henriette I. Jager entitled "Predicting the Viability of Fish Populations in a Modified Riverine Environment." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

James A. Drake, Major Professor

We have read this dissertation and recommend its acceptance:

Kenneth A. Rose, Richard J. Strange, Louis J. Gross

Accepted for the Council:
Dixie L. Thompson

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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and recommend its acceptance:

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PREDICTING THE VIABILITY OF FISH POPULATIONS IN A MODIFIED RIVERINE ENVIRONMENT

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Henriette I. Jager

August, 2000

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ABSTRACT

Riverine fishes evolved to life in a highly variable, flow-driven environment. During the two past centuries, large rivers have been substantially altered by human activities. This has resulted in declines of fish populations that depend on the large river environment.

The research described here uses models to evaluate the effects of human activities on the viability of fish populations in rivers. I focused on five modifications of the river environment associated with impoundment: (1) seasonal allocation of river flow; (2) diversion of river flow; (3) fragmentation of the river habitat by dams; (4) conversion of free-flowing river to reservoir habitat; and (5) alteration of migration patterns.

To understand the role of flow regulation on chinook salmon (*Oncorhynchus tshawytscha*) recruitment, I developed an individual-based model to predict recruitment as a function of seasonal flow patterns in the Tuolumne River, California. I used simulated annealing to find flow patterns that maximize chinook recruitment under wet and dry hydrologic conditions. As water availability increased, I found that the optimal flow pattern shifted from allocating low flows uniformly across seasons to a pattern with high spring flows. When I considered a new objective: maximizing the variance of spawning times among recruits, the optimal flow regime called for a winter pulse in flow just before the peak spawning date for the minority (late-fall) run.

To evaluate the recovery options for chinook salmon in the Tuolumne River, I developed an age-based model to conduct a population viability analysis (PVA). I developed a flow-dependent spawner-recruitment relationship from the recruitment model. Its shape depended on the flow regime, suggesting that such relationships are not fixed properties of species, but depend on environmental conditions. The PVA model suggested that recovery, in the absence of straying, would be enhanced most by significantly reducing ocean harvest, followed by reduced diversion of water from the river.

For white sturgeon (*Acipenser transmontanus*) populations in the Snake River, Idaho a main concern is habitat fragmentation by dams resulting in smaller, isolated populations. Simulation experiments to evaluate the effects of fragmentation suggested that population viability was higher when dams were spaced widely enough apart to retain free-flowing habitat. A simulation experiment to evaluate the effects of altered migration patterns associated with impoundment showed that both the likelihood of persistence and the genetic diversity among white sturgeon populations were enhanced by balanced upstream and downstream migration rates.

Models that simulate the responses of fish populations to modified river habitat do not consider the potential for an evolutionary response. I designed a PVA model simulating the genetic basis of age at maturity for individual fish. Simulated individual variation in this trait lead to increased population viability only when the variation was heritable and subjected to an altered selective regime. The results support the idea that predicting population viability depends on estimating the potential for evolution in fitness-related traits for populations exposed to anthropogenic changes in the environment that impose strong, directional selective forces.

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PART 1. GENERAL INTRODUCTION

BACKGROUND

Human activities, such as damming of rivers and regulation of river flows, are responsible for declines in many native fish populations that depend on large rivers. Among fishes that depend on rivers, anadromous species have the greatest risk of extinction (Parent and Schrimi, 1995). Anadromous fish species use the freshwater environment to reproduce and develop into juveniles, and they spend the remaining time in the marine environment. Large rivers serve as the conduits for migration between the freshwater and ocean phases of life. Although marine factors play a role in the declines experienced by some anadromous species, changes to the freshwater environment associated with human development had a substantial impact. Large rivers were among the earliest and most intensively altered ecosystems (Welcomme, 1995). Because pre-industrial societies depended on large rivers for fertile floodplains, irrigation, and fishing, human developments typically spread along river corridors. Over time, rivers became more important for transportation, mechanical and, later, electrical power, industrial process water, and waste disposal. Consequently, few temperate large rivers have escaped the effects of impoundment, channelization, hydropower generation, and flow diversion (Welcomme, 1995).

The two species considered here, fall-run chinook salmon (*Oncorhynchus tshawytscha*) and white sturgeon (*Acipenser transmontanus*), share some attributes and differ in others. Both species depend on the large-river environment to reproduce and to rear offspring. The two species share an anadromous life history, growing in the marine environment and migrating long distances inland via large rivers to spawn. Both species are large: the white sturgeon is the largest freshwater fish in North America; the "king" (chinook) salmon, is the largest of the Pacific salmon. Populations of both species are found along the Pacific coast of North America, ranging from Alaska and Canada to southern California. Although each species has examples of healthy populations, many populations have declined to a sufficiently small size to raise concerns about local extinction.

The two species offer a stark contrast in other qualities, including life history attributes. Chinook salmon reach maturity between 2 to 5 years of age. They are semelparous, dying shortly after they spawn. White sturgeon females mature only after they attain at least 15 years of age, and sometimes not until they are older than 30 years. They are iteroparous, spawning at irregular intervals throughout their considerable lifespan.

More subtle differences also exist between the two species. Compared with the white sturgeon, chinook salmon have a stricter requirement for access to the ocean. White sturgeon are semi-anadromous because they can exist in landlocked populations. This species occurs in large, mainstem reaches of the Fraser, Columbia, and Sacramento River systems. When populations have access to the ocean, individuals usually remain in the estuarine environment. During ocean migration, chinook salmon stay nearer the coast and rely on estuarine rearing habitat more than other Pacific salmon. Chinook salmon are able to spawn in smaller, mainstem rivers.

OVERVIEW OF PARTS

The research presented in this dissertation uses population models to address hypotheses regarding human impacts on the long-term persistence of certain populations of these two fishes. I used population viability analysis (PVA) as a modeling framework to link fish populations to the riverine environment (Jager et al., in press). The main prediction of the two PVA models used here is the likelihood of persistence of the fish population to a specified future date.

Each part in this dissertation is self-contained, with its own abstract, introduction, results, and discussion section. A common list of references is provided at the end. Together, these parts address the following research questions:

1. What seasonal patterns of flow maximize chinook recruitment? (Part 3)
2. Does this optimal flow regime for chinook salmon change as annual flow becomes more limiting (i.e., in dry years)? (Part 3)
3. What seasonal patterns of flow maximize life history diversity in chinook salmon? (Part 3)
4. Does the optimal flow regime for chinook salmon recruitment change in response to changes in the number of adults that return to the river to spawn? (Part 4)
5. Can flow and density effects simulated by a more-complex recruitment model for chinook salmon be adequately described by a simpler equation? (Part 4)
6. What management strategies, if any, will enable chinook salmon to persist for 100 y? (Part 5)
7. How does fragmentation of large rivers by dams influence white sturgeon populations? (Part 6)
8. How is the persistence of white sturgeon populations influenced by phenotypic variation among individual fish? (Part 7)

A variety of models are used to address these eight questions (summarized in Table 1). For fall chinook salmon, I developed a detailed recruitment model that focused on the river phases of chinook salmon life history and an age-based PVA model that incorporates the ocean and adult components. The recruitment model is individual-based and operates on a finer spatial and temporal scale than the age-based PVA model. For white sturgeon, an individual-based PVA model was designed with an annual time-step. A genetic component permitted this model to examine the role of phenotypic variation in Part 7. The models used for the analysis of fall chinook salmon used input data specific to the Tuolumne River. The white sturgeon PVA model was more general, with few explicit links to Snake River habitat.

Parts 2 – 5 of this dissertation focus on factors that influence the viability of fall-run chinook salmon in a regulated California river. This run belongs to the Central Valley Fall Run Ecologically Significant Unit (ESU) (Myers et al., 1998), which is unique because it exists at the southern extreme of the species' geographic distribution. This population, along with others in the Sacramento-San-Joaquin River basin of California, has a high risk of extinction (Huntington et al., 1996). Factors thought to contribute to population declines include loss of freshwater spawning habitat, the ocean fishery, and climatic shifts (Table 2), as well as exposure to mortality caused by large-scale diversion of water from the Sacramento-San-Joaquin delta.

The relationship between seasonal changes in instream flow and salmon populations is far from clear. Although scientists understand and have quantified individual parts, models are helpful to assemble the whole picture. Over time, and with

Table 1. Simulation models used in each part of this dissertation.

Title of dissertation part	Model	Key processes
2--Modelling the Linkages between Flow Management and Salmon Recruitment in Rivers	ORCM recruitment model Daily time step; Individual based Longitudinal heterogeneity in river habitat.	ORCM simulates flow, habitat, temperature, superimposition, and predation
3--Designing Seasonal Flows to Maximize Recruitment of Fall Chinook Salmon in the Tuolumne River, California	ORCM recruitment model (see Part 2) Simulated annealing code, SIMANN 2-week decision variable in the optimizations	Varied seasonal patterns of flow by changing the daily average flows assigned to each 2-week period.
4--Model Simplification to Describe Density and Flow Effects on Recruitment of Fall Chinook Salmon	ORCM recruitment model (see Part 2) Simulated annealing code, SIMANN Fitted stock-recruitment equation	Focused on flow and density effects
5--Population Viability Analysis of Fall Chinook Salmon in the Tuolumne River, California	PVA model for chinook salmon. Annual time step; Age-based No spatial heterogeneity Includes Part 4's stock-recruitment equation	Two factors of interest are total annual flow and ocean harvesting.
6--Are White Sturgeon Populations Dammed? -- Viability of White Sturgeon Populations in a Fragmented River Habitat	PVA model for white sturgeon Annual time step; Individual-based & genetic Multiple, but identical, river segments.	Focused on the spacing of dams and the role of free-flowing habitat
7--Individual Variation in Life History Characteristics can Influence Extinction Risk	PVA model for white sturgeon (see Part 6) Simulated genetic basis for one trait. One river segment	Heritable and non-heritable variation in age at maturity.

Table 2. Factors that potentially contribute to declines in the two species and rivers of interest. X's indicate factors included in these studies.

Factor	Fall chinook salmon in the Tuolumne River	White sturgeon in the Snake River
Habitat fragmentation by dams		X
Flow regulation, changed hydroperiod	X	
Loss of suitable habitat	X	X
Fishing or hooking mortality	X	
Climatic shifts associated with El Nino	X	
Entrainment through turbines or pumps	X	

improvement, the hope is that the pictures presented by such a model will become a less distorted idealization. Part 2 describes a spatially explicit population model (ORCM) that I developed with contributions from several co-authors (Jager et al., 1997). The model was designed to quantify the relationship between recruitment of fall chinook salmon and the flow environment in the river. One feature of the model is that it can predict differences in recruitment success experienced by offspring from parents with different spawning times because of both environmental (e.g., flow and temperature) and demographic (e.g., superimposition) factors.

Regulation of instream flows below dams that are used to generate hydropower is an important and controversial means of influencing salmon recruitment in downstream reaches. Although the scientific community has provided some guidance, prevailing uncertainties have led many toward an adaptive management approach to deciding how much water to leave in the river. Part 3 attempts to find model-based solutions to the question of how flows should be managed for salmon. I used a global optimization method to seek seasonal patterns of streamflow that maximize each of two conservation objectives for chinook salmon. The first objective was to maximize the simulated recruitment of fall-run chinook salmon and the second objective was to maximize diversity in spawning times.

In Part 4, I explore the relationship between flow and density dependence during recruitment. The first question addressed is whether the optimal flow regime identified by using the recruitment model changes with spawner density. If so, this would suggest that more-complex rules for setting instream flows are required. The second question addressed is whether the number of recruits produced will ultimately decline as spawner abundance increases, or whether it will reach an upper limit. The possibility that spawning habitat is limiting recruitment is often raised as an issue. Although dams clearly block access to historical spawning habitat in upstream reaches, the importance of habitat limitation on recruitment in downstream reaches is less certain. In the past, perceived limitations have been alleviated by dumping gravel into rivers, raising barriers partway through the spawning season to prevent superimposition of upstream redds, and managing instream flows to maximize suitable spawning area.

Many anthropogenic factors likely contribute to declines in salmon populations, including fall chinook in the Tuolumne River. This can be counterproductive if it degenerates into finger pointing, rather than a search for multi-faceted solutions. Part 5 uses a PVA model to evaluate the viability of this population under several management scenarios for each of two anthropogenic factors: (1) annual diversion of flow and (2) ocean harvesting. The PVA model for this study is age-based and relies on stock-recruitment relationships derived from the ORCM recruitment model in Part 4.

Part 6 focuses on fragmentation of the Snake River habitat and its influence on the viability of white sturgeon populations. Historically, Snake River populations followed the farthest inland migration route, from estuaries near the mouth of the Columbia River. Extensive damming along this river corridor has prevented migration, leaving a number of fragmented populations, many of which are declining. In addition to the demographic effects of fragmentation, I used a PVA model for white sturgeon to simulate fragmentation effects on genetic diversity within and among populations.

Part 7 addresses the effects of individual variation on population viability. This issue has both practical and theoretical implications. The practical implication is that model developers wishing to predict population viability must decide whether it is necessary to adopt an individual-based modeling approach, and, if so, for which traits it is necessary to represent individual variation. Part 7 provides some guidance on when such variation influences model predictions. Two theoretical implications that are addressed are the capacity for evolution in life history traits in response to man-made changes in the environment, and the role of heritability in mediating the relationship between individual variation and population viability.

In Part 8, I briefly review the methods and results of Parts 2—7, answer the questions listed on page 4, and synthesize the conclusions.

PART 2. MODELLING THE LINKAGES BETWEEN FLOW MANAGEMENT AND SALMON RECRUITMENT IN RIVERS

ABSTRACT

This part of the dissertation is drawn, with some modifications, from Jager, H. I., H. E. Cardwell, M. J. Sale, M. S. Bevelhimer, C. C. Coutant, and W. Van Winkle. 1997. Modelling the Linkages between Flow Management and Salmon Recruitment in Rivers. *Ecological Modelling* 103:171-191.

Chinook salmon stocks that spawn in rivers of the California's Central Valley have declined. One important management option for recovery is the regulation of instream flows. River flow influences salmon recruitment through each phase of reproduction, from upstream migration of adults to rearing of juveniles until they develop into smolts and, finally, migrate to the ocean. In this study, we developed an individual-based and spatially explicit model to predict the effects of instream flows released from an upstream reservoir on smolt production of fall chinook salmon (*Oncorhynchus tshawytscha*) in the Tuolumne River, California. Predictions of smolt production were most sensitive to redd mortality in low-quality habitat, followed by the earliest and latest dates of upmigration, and the upper lethal temperature tolerated by juveniles. Model predictions of development, growth, and survival were compared with field data collected during four years of study in the Tuolumne River, California. This comparison verified the presence of a late-fall run and suggested that the relative importance of simulated mortality factors varied from year to year in response to changes in spawner density and environmental conditions.

INTRODUCTION

The Oak Ridge chinook salmon model (ORCM) described here predicts instream flow effects on the number of fall chinook salmon smolts produced by a specified number of adult escapes (upmigrating spawners). ORCM can simulate complex habitat effects of flow (Table 1) because it is both spatially explicit and individual based. Longitudinal gradients in water temperature, spawning habitat, and predator density are simulated for river segments as they change in character from shallower, cooler upstream segments below the dam to deeper, warmer segments inhabited by juvenile salmon during downstream migration. ORCM simulates the influences of riverine habitat on each life stage leading to successful outmigration of chinook salmon. This begins with the upstream migration, redd construction, and spawning of adults in fall or winter, and ends with the rearing and downstream migration of juveniles in spring (FERC, 1996).

There are three main reasons for individual-based modeling of stream fishes. First, simulating individual fish is an efficient way of modeling life stages 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. Consequently, the model easily simulates several coexisting life stages of salmon, as well as hatchery strains. Although not considered here, individuals with different phenotypes, in terms of environmental tolerances, habitat requirements, and behavioral capabilities, can be simultaneously included. 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) 1992b) are useful for adding the adult, ocean phase for chinook salmon. The drawback of these models is that their parameters are difficult to interpret and measure. Williamson et al. (1993) 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 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.

This study describes and documents the ORCM model. It presents a sensitivity analysis and comparisons of intermediate model predictions with field data collected in the Tuolumne River, CA.

MODEL STRUCTURE

The life history of fall chinook salmon is typical of many anadromous fishes (Healey, 1994). Chinook salmon spend their adult lives in the ocean. Adult fish migrate into rivers in fall or winter to spawn at an age of 2 to 5 years. Eggs incubate through the winter, hatch as alevins(non-feeding larvae), and emerge from their redds (nests constructed in gravel substrate) 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 under-yearlings during their first spring. During this gradual process, juveniles undergo smoltification to prepare for existence in the ocean environment.

The major components of ORCM are redd construction and spawning by adults, the development and mortality of egg and alevin life stages, 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 salmon populations in complex ways (Table 1). River flow influences temperature and habitat, each of which influences the growth, development and survival of successive life stages leading to the smolt stage. The relationships between flow and these processes are critical to our ability to assess instream flow effects. We listed the values and definitions of model parameters provided as input to the ORCM model in Table 2. These parameters are referred to in the model description below.

The principal 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, such as the temporal and spatial distribution of redds and juveniles and the success or fate of redds and juveniles.

Table 1. Summary of relationships between each life stage and the dominant environmental and biological factors that influence growth and survival in the ORCM model.

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

Table 2. Parameter values used in simulations (simulation value) and sensitivity analysis (nominal value). Nominal values 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.

Parameter name	Simula-tion value	Nominal value	Eqn. #	Parameter description
A_{fec}	-3200.2	**-3200.2**		Intercept of fecundity relationship with fish length
al	0.0005	**0.0005**	8	Intercept of fecundity relationship with fish length
A_{dd}	0.93	0.93	14	Fraction of DD_{smo} with 50% mortality risk during outmigration
a_{move}	0.25	0.16	9	Movement rate at zero flow for fry (d km^{-1})
a_{move}	0.32	0.32	9	Movement rate at zero flow for smolts (d km^{-1})
A_{rat}	250	250	9	Scaling ratio for river size
A_{redd}	216	216	4	Defended redd area (4x redd area; m^2)
A_{terr}	0.00148	0.00148	7	Coefficient in territory vs. fish length
B_{terr}	2.61	2.61	7	Exponent of fish length
B_{dd}	0.921	0.921	14	Fraction of DD_{smo} with 90% mortality risk
B_{fec}	109.4	**109.4**		Slope of female fecundity vs. length (cm)
bl	2.136	**2.136**	8	Exponent of length vs. weight relationship for fry
bq_{temp}	0.5	0.4	3	Exponent relates velocity to flow
c_{move}	$6.0 \cdot 10^{-6}$	$6.0 \cdot 10^{-6}$	9	Slope between travel time (d km^{-1}) and flow (m^3 s^{-1})
C_s	0.02	N.A.		Stomach capacity as a fraction of predator weight
DD_{eggs}	500	**500**		Degree-days from egg laying to hatch (°C)
DD_{alv}	395.8	**395.8**		Degree-days from hatch to emergence (°C)
DD_{smo}	1082	1082		Degree-days required to develop into a smolt (°C)

Table 2. continued.

Parameter name	Simulation value	Nominal value	Eqn. #	Parameter description
F_{spawn}	0.5	1.558		Min. flow required to migrate up river and spawn (m^3s^{-1})
k_{temp}	-0.001	-.00001	2	Temperature equilibration rate coefficient (s^{-1})
L_{min}	70	N.A.		Min. size required to become a smolt (mm)
L_{p_avg}	320	320		Avg. size of predators in river (black bass; mm)
L_{p_std}	25	25		S.D. of predator size (mm)
L_{a_avg}	688	688		Avg. length of adult spawners (mm)
L_{s_sd}	74	74		S.D. of spawner length (mm)
L_{s_min}	400	N.A.		Min. length of spawning adults (mm)
L_{s_max}	1400	N.A.		Max. length of spawning adults (mm)
L_{segsp}	40.5	40.5		Distance below dam used for spawning (km)
M_{egg}	0.0	0.001		Baseline daily mortality risk for redd life stages
N_{esc}	N.A.	5000		Fall run escapement (number of adults)
P_k	0.8	0.8	13	Max. probability of successful prey capture
P_{late}	0.07	N.A.		Fraction of adults in the late-fall run
P_{pock}	0.5	0.5		Avg. fraction of egg pockets superimposed
P_{int}	0.1	0.01		Perceived density of predators (fraction of actual)
P_{smo}	0.6	0.6		Fraction of max. intake obtained by smolts
P_{up}	0.4	0.1		Probability of upstream movement at low temperatures
P_{min}	0.08	0.08		Min. fraction of P_{max}
P_{max}	0.6	0.6		Max. ration at feeding stations (obtained by large fish)
R_{lag}	0	N.A.		Lag time between upmigration and spawning

Table 2. concluded.

Parameter name	Simula-tion value	Nominal value	Eqn. #	Parameter description
S_{min}	0.9995	0.9500	4	Max. daily survival rate in marginal habitat
S_{max}	1.0	1.0	4	Max. daily survival rate in excellent habitat
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}	Apr. 4	N.A.	1	First date that air temperature reaches T_{avg}
T_{avg}	16	N.A.	1	Avg. annual air temperature (°C)
T_{avoid}	22	22		Lower threshold for behavioral avoidance (°C)
T_{max}	30	N.A.	1	Max. 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}	Apr. 20	Apr. 20		Final date of upmigration/spawning, late-fall run
UP_{max}	Dec. 22	Dec. 22		Final date of upmigration/spawning, fall run
UP_{min}	Jan. 1	Jan. 1		Earliest date of upmigration/spawning, late-fall run
UP_{min}	Oct. 1	Oct. 1		Earliest date of upmigration/spawning, fall run
UP_{peak}	Oct. 27	Oct. 27		Peak date of upmigration/spawning, fall run
UP_{peak}	Mar. 1	Mar. 1		Peak date of upmigration/spawning, late-fall run
α	-10.0	-10.0	11, 12	Influences the max. probability of capture
β	200.0	200.0	11	Sets lower bound on prey length in probability of capture
η	18.0	18.0	12	Sets upper bound on prey length

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 by simulating 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 its redd, as it moves gradually downstream, and until it leaves the river or meets with a different fate. All of these activities are evaluated by the model on a daily basis and respond to daily average flow and temperature.

The model divides the river system into reaches that can differ in flow. Within each reach, the river is partitioned into 1.6-km segments and the daily location of each model fish is tracked by segment. The segments differ in a number of physical and biotic attributes (Figure 1). These include the percentage of riffle habitat vs. pool and run habitat, spawner preference, the quantity of weighted usable area (WUA) suitable for each life stage, water temperature, the number of larger conspecific competitors, and the density of fish predators.

Physical input data: river flow and temperature

ORCM operates on five primary data sets: (1) daily river flow at a gauge located just downstream of the flow-regulating dam; (2) minimum flows specified for ranges of

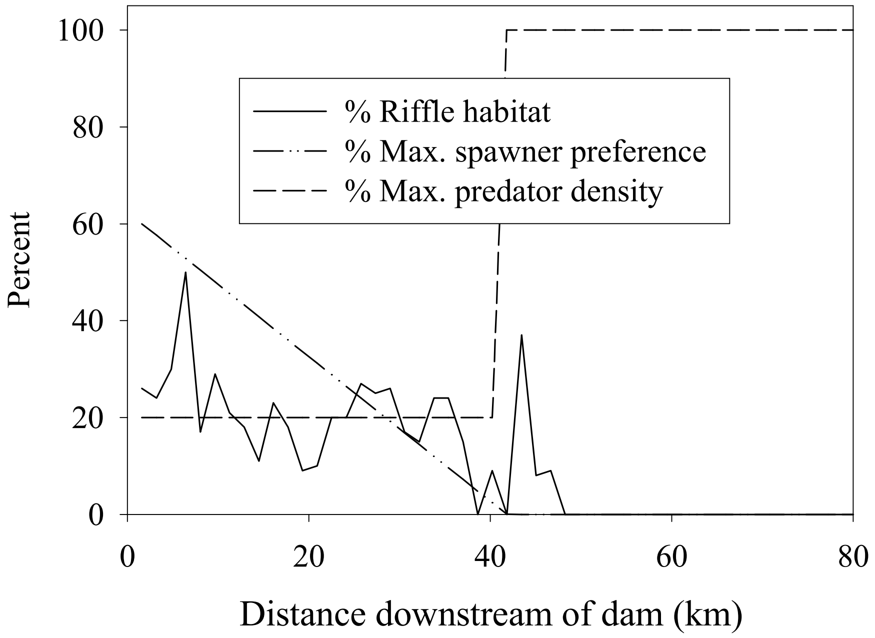

Figure 1. Longitudinal patterns in the percent riffle habitat, spawner site preference, and predator density.

dates throughout the year; (3) daily water temperatures below the dam and daily air temperatures for the area during simulated years; (4) WUA curves for different flows; and (5) the total number of adults that returned to the river to spawn during each historical year simulated. In addition, the model requires input parameter values specified by the user (Table 2).

Water temperature near the regulating dam is an important variable driving the model. In our model validation comparing four historical years, we provided the model with actual historical daily water and air temperatures measured below the dam. In other simulations, we allowed 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:

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

where T_t = average daily air temperature (°C),

T_{avg} = average annual air temperature (°C),

t = Julian day of year (1 to 365),

t_{avg} = first Julian day that air temperature reaches T_{avg}, and

T_{max} = maximum air temperature (°C).

ORCM uses a simple first-order model, equations (2) and (3), to simulate the equilibration of water temperatures downstream of the dam. We estimated parameters k_{temp} and bq_{temp} by least squares regression.

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

$$t_{dam} = x\, Q^{-bq_{temp}}, \qquad (3)$$

where T_x = average daily water temperature (°C) at segment x,

T_w = average daily water temperature below dam (°C),

T_a = average daily air temperature (°C),

k_{temp} = the temperature equilibration rate (s^{-1}),

t_{dam} = water travel time from the dam (s),

x = distance below dam (m),

Q = river flow (m^3 s^{-1}), and

bq_{temp} = relates velocity (m s^{-1}) to flow (m^3 s^{-1}).

Habitat capacity

The simulated habitat capacity (# juveniles m^{-2}) of a river segment depends on its percent of pool and run habitat vs. 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 (spawning, incubation, fry, and juveniles) and habitat type (pool and run habitat combined and riffle habitat). Because no curves were available for incubation, we adopted the spawning WUA with the assumption that spawners select redd locations according to habitat criteria that reflect future suitability for incubation. We provided an input map with the proportion of riffle habitat for each river segment, and assumed that the remaining habitat was composed of runs or pools.

Adult escapement

Simulations begin with the appearance of upmigrating fall, and then late-fall, run adults in the river. We specify 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. The total number of late-fall run spawners is specified as a fraction, P_{late}, of total spawners.

ORCM simulates the arrival of female spawners of each run over time according to a triangular distribution between two site-specific dates, UP_{min} and UP_{max}, and a peak date, UP_{peak} (Figure 2). The fall run dates (EAEST, 1992i) are earlier and distinct from those of the late-fall run (Brown and Greene, 1992).

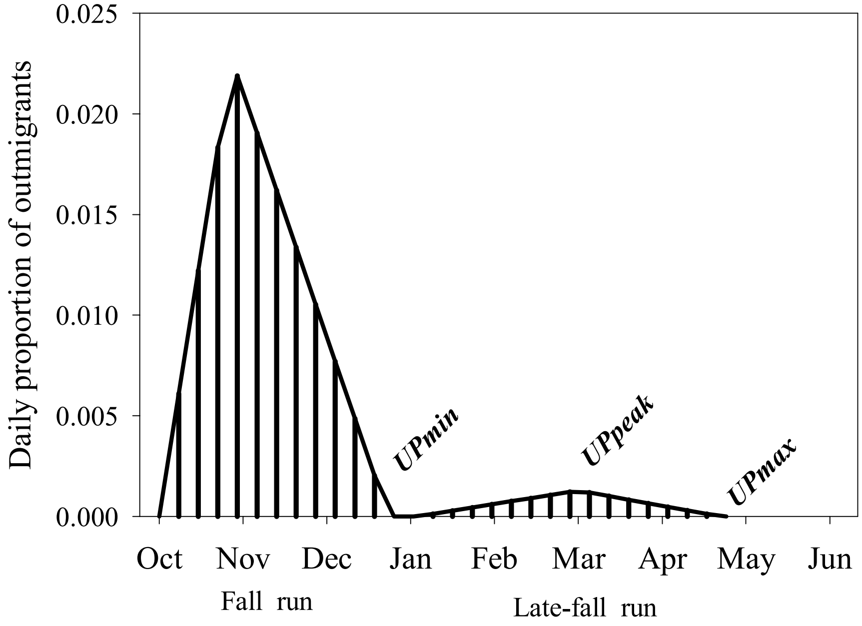

Figure 2. Simulated timing of upriver migration for fall run and late-fall run chinook salmon in the Central Valley (Up_{min}, UP_{peak}, UP_{max} in Table 2).

The number of adults seeking to migrate upstream that are 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 (Hallock et al., 1970), spawning (Chamberlain, 1907), and egg viability (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 spawner's entry to the tributary and its arrival at the spawning grounds.

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 (Figure 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. This habitat is divided into N_{opt} suitable spawning sites ranging uniformly from low quality, S_{min}, to high quality, S_{max}. We assume that neither pools nor runs are used as spawning habitat (EAEST, 1992i). N_{opt} depends on the length of the river segment, L_s; and average area per redd, A_{redd} as shown in equation (4).

$$N_{opt} = \frac{L_s \, WUA_{opt}}{A_{redd}}. \qquad (4)$$

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 equation (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 each redd a site with a given rank, it retains that site throughout incubation, but its quality will vary with flow as described below. When a later spawner selects the same site as a previous spawner, superimposition occurs.

We calculate the number of eggs deposited by a female spawner into her redd from a fecundity relationship with female size, L (cm), obtained from spawners in the Mokelumne River by the East Bay Municipal Utility District (EBMUD) (1992): number of eggs = $A_{fec} + B_{fec} L$. Female spawners are assigned lengths from a truncated normal distribution with mean L_{s_avg}, standard deviation L_{s_sd}, minimum L_{s_min}, and maximum L_{s_max}.

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%.

Egg and alevin mortality

Mortality during incubation in redds 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}, can be used to simulate other mortality factors (e.g., poor condition of spawning gravels).

Eggs and alevins are exposed to a daily temperature-related mortality risk that varies in response to daily temperature (Murray and McPhail, 1988). Temperature effects are greater on the egg than on the alevin life stage (Figure 3).

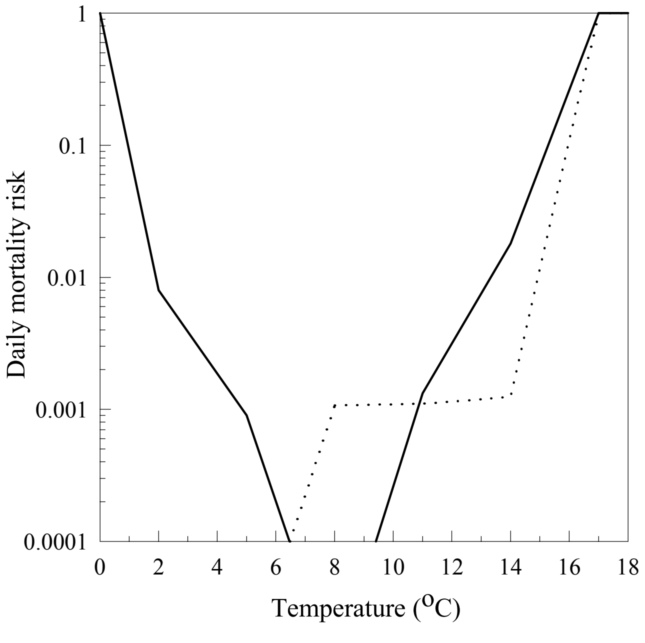

Figure 3. Temperature-related mortality for the egg (solid) and alevin (dotted) life stages.

Flow-induced habitat degradation can take the form of dewatering or scouring of redds. The effects of flow on egg and alevin survival are simulated 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 lower quality 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 (Figures 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 sub-optimal flows than those constructed when flow conditions were poor. Although ORCM does not explicitly simulate local depths and velocities, this approach increases the vulnerability of redds at extreme low and high flows when the incubation WUA is unimodal.

An additional source of mortality takes place when a new redd is constructed on the same site as an existing redd. Because the female is present to guard her redd for a short time after spawning, ORCM prohibits superimposition of each redd up to S_{wait} days after its construction. When an earlier redd is superimposed, we simulate the proportion of egg pockets destroyed as a Poisson process with mean P_{pock}. Superimposition of previously constructed model redds occurs most often when redd densities are high and spawning habitat is scarce.

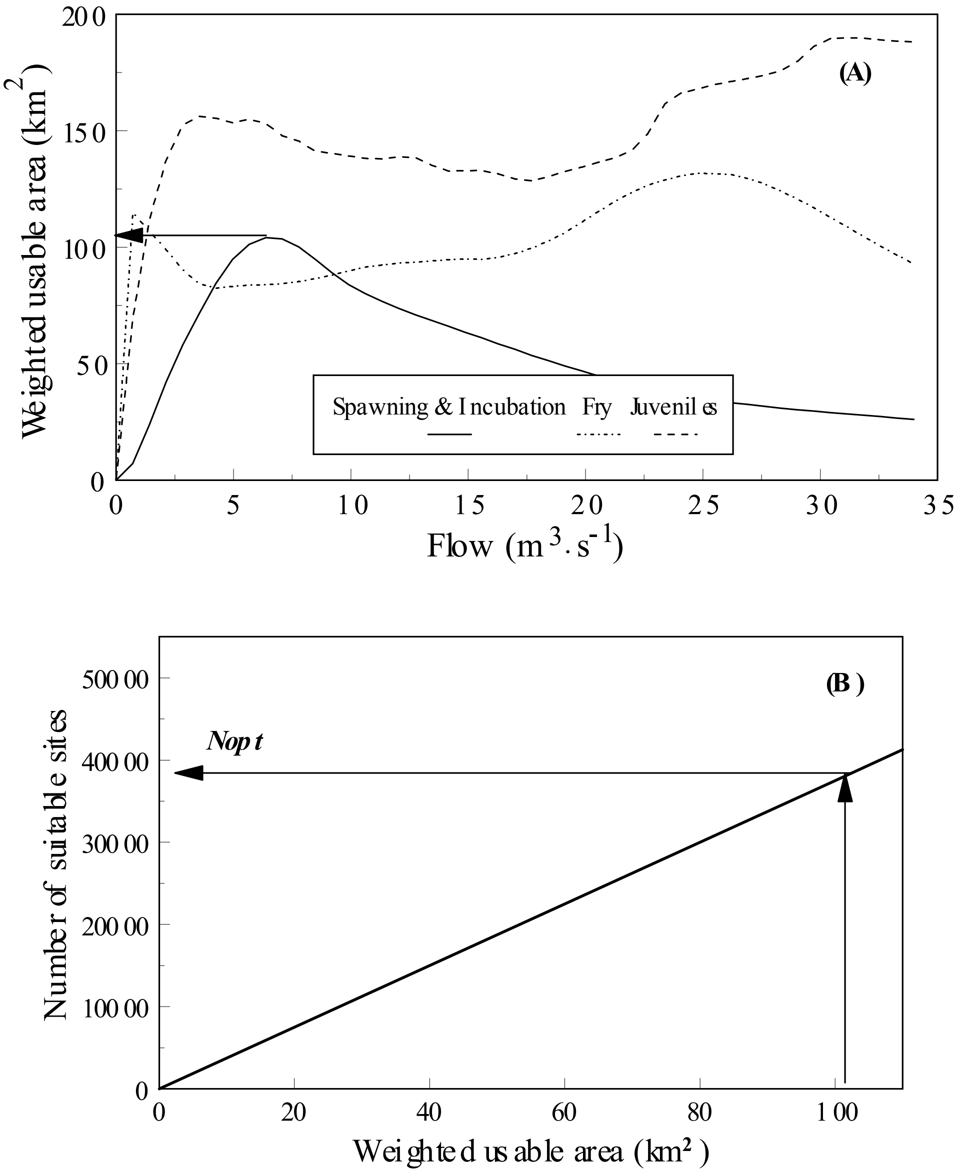

Figure 4. (A) Weighted usable area (WUA) is used as a habitat capacity for each lifestage of fall chinook salmon in the Tuolumne River (EAEST 1992b); (B) The number of suitable redd sites (or foraging stations) varies in response to flow as WUA changes. This hypothetical example is for a day with streamflow that provides 10 suitable sites (N_t = 10).

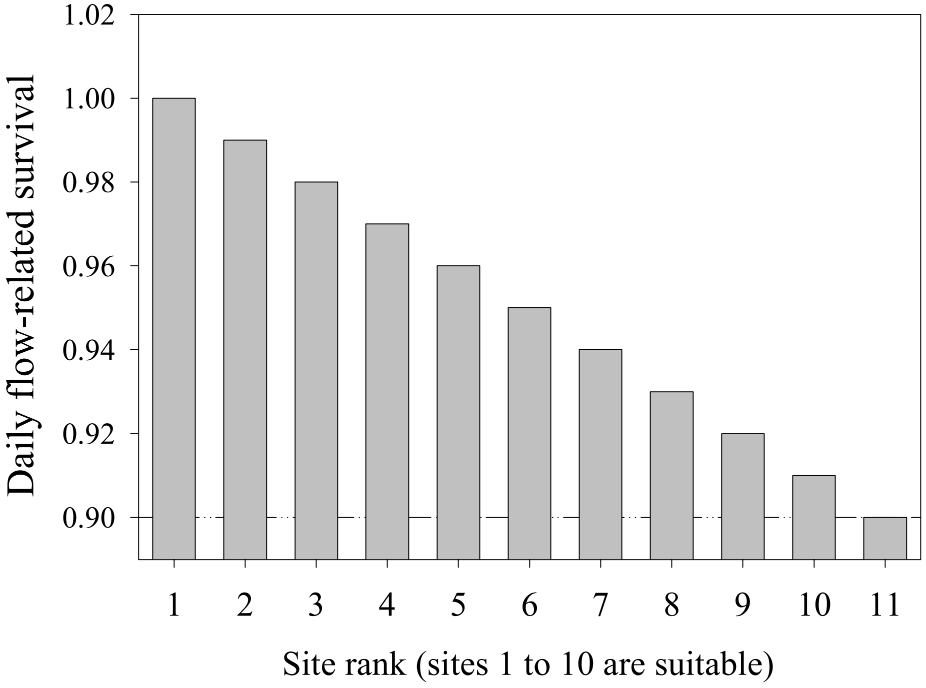

Figure 5. Simulated flow-related habitat survival rates experienced by eggs and alevins during incubation is illustrated. In this example, redds in sites ranked 11 and greater are assumed to be lost because of dewatering or scouring, depending on which end of the weighted usable area curve for incubation this day's flow is on.

Juvenile development and growth

Juveniles are between 30 and 40 mm in length when they emerge from redds as fry (EBMUD, 1992; Murray and McPhail, 1988). 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 a smolt, an individual 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 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:

$$\Delta G = C \ \ (E + F + SDA + R)\,, \quad (5)$$

where C = daily consumption, E = egestion, F = excretion, SDA = specific dynamic action, and R = 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:

$$C = p\,C_{\max}\,. \quad (6)$$

We simulate variability among growth rates of individual fry 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 territories 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 fry outnumber stations, those individuals lacking a suitable station do not grow. A resident fry may be shifted to a lower or higher ranked station as larger or smaller individuals migrate 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 ($P_{min} \leq X \leq P_{max}$) provides a fish with fraction $p = X$ of its maximum daily feeding ration. The same procedure described in the section on spawning-site quality (Figure 4) is used to decompose the quantity and quality aspects of WUA_{fry} as illustrated by Figure 6. In particular, we calculate the number of suitable feeding sites 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

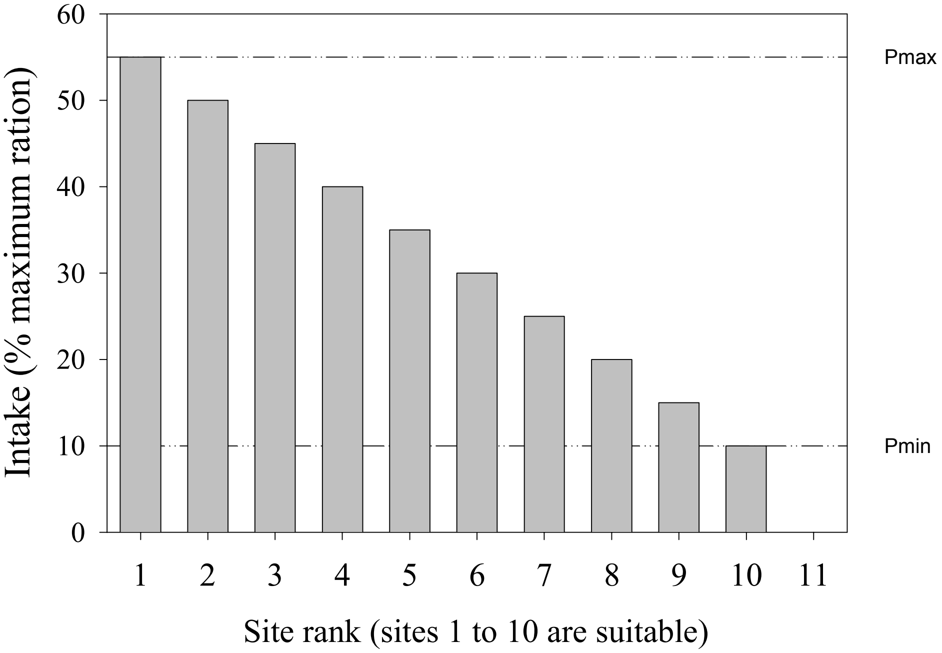

Figure 6. Simulated competition for feeding sites among fry in relation to habitat capacity is illustrated. The model allocates feeding stations to larger fish first until the total area of stations reaches the composite juvenile weighted usable area of the river segment. Foraging success (daily ration) is greater for larger fish and is zero for fish without a feeding station for this example with ten suitable sites.

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) shown in Equation **(7)**. 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 does not compete for feeding stations, focusing instead on downstream migration.

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

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).

$$W = al\, L^{bl} \qquad (8)$$

Juvenile movement

ORCM simulates the dispersal of juveniles from the spawning reach to the rearing reaches and out of the river. ORCM simulates daily movement differently for fry and smolts. Movement for simulated fry is optional and is motivated by the search for habitat that is safe (i.e., has a low risk of predation) and suitable for growth (i.e., has a high WUA and few larger competitors). We assume that fry movement depends on fry density and habitat availability as well as flow (Bilby and Bisson, 1987; Williamson et al., 1993). Each day, an individual compares the cost-benefit ratio of its current habitat (i.e., the ratio of predation risk to growth, where the density of predators provides a surrogate for predation risk) with that elsewhere (Werner and Gilliam, 1984). The quality available elsewhere is estimated as a running average based on the individual fish's previous experience in other locations (Bernstein et al., 1988). The individual moves when this comparison shows that it can probably do better elsewhere (Jager et al., 1993).

A simulated fry that departs from its current segment is more likely to move downstream than upstream. We calibrated the probability of upstream movement, P_{up}, to match the observed rate of downstream movement in juveniles captured at different locations in the river. At temperatures above T_{avoid}, we simulate the tendency for fry 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 model fry decides to move and in which direction, its rate of movement depends weakly on river flow, Q ($m^3\ s^{-1}$). We assumed that mean travel time ($d\ km^{-1}$) for downstream movement decreases with flow according to a weak linear relationship fit by us to data for sub-yearling chinook reported by Berggren and Filardo (1993):

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

The sign of c_{move} changes for upstream movement. To adapt this relationship for fry in the Tuolumne River, we adjusted the rate of movement at zero flow, a_{move}, so that no more than 30 d were required for fry to travel 122 km (Berggren and Filardo., 1993).

We also added a flow adjustment for the smaller size of the Tuolumne, A_{rat}, compared with the Columbia River.

To simulate migration out of the Tuolumne River, we adopted the hypothesis that the main factors involved operate indirectly by speeding the development of chinook fry into smolts. After reaching 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 simply assume that the necessary cues are present and that daily smolt outmigration begins when fry develop into smolts. The daily distance traveled by each smolt during outmigration depends on flow, Equation (9), and is always in a downstream direction. ORCM assumes that smolt movement is directed toward ocean migration (e.g., rather than foraging) and that individuals move every day.

Juvenile survival

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 one day of exposure. The model allows juveniles to avoid high, sub-lethal temperatures by increasing the likelihood of upstream movement.

Fish predators, including smallmouth bass (*Micropterus dolomieui*), largemouth bass (*Micropterus salmoides*), and Sacramento squawfish (*Ptychocheilus grandis*), forage on juvenile chinook (EAEST, 1992f). To simulate predation mortality we expose juveniles to an array of predators of various sizes 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 standard deviation L_{p_std} with lengths truncated at three standard deviations on either side of the mean. Length-weight relationships convert predator lengths into weights. Values for smallmouth bass were assumed for most parameters.

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, we assume that juveniles risk encountering only a fraction, P_{int}, of the predators in the same river segment.

The chance of a simulated encounter between an individual predator and a juvenile salmon depends on its length, its condition, and the density of predators in the river segment. Once it encounters a predator, a juvenile's risk of being eaten depends on how full the predator's stomach is. We assume that each 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 simulate a constant rate of evacuation of stomach contents for predators that depends on predator weight, time since consumption, total weight of ingested prey, and water temperature (Rogers and Burley, 1991).

If the predator has room in its stomach, then its probability of capturing a particular juvenile, P_c, is greatest for prey with intermediate ratios of prey to predator size, L_{rat}, (Dunbrack and Dill, 1983) and for prey in poor condition:

$$P_c = R_{max} \, P_{attack} \, P_{ingest} \, . \qquad (10)$$

Relatively small prey are protected by a reduced probability of attack, P_{attack}, as shown in equation (11), whereas relatively large prey are protected by a reduced probability of successful ingestion, P_{ingest}, as shown in equation (12).

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

$$P_{ingest} = \frac{1}{1 + \exp(\alpha + \eta \, L_{rat})} \; . \qquad (12)$$

The maximum risk, R_{max}, increases linearly as the physiological condition, K, or relative weight of the juvenile deteriorates. Individuals in poor condition are more susceptible to predation, and those in good condition ($K = 1$) have a maximum capture probability of P_k.

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

Juveniles in the fry life stage may be lost because they leave the spawning tributary before developing into smolts. 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 movement, which has a downstream bias, is more frequent. For an upstream tributary, those leaving prematurely might survive and develop into smolts in a mainstem river, beyond the spatial scope of the simulation (Williams, 1994). To provide for this, ORCM offers 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 individual's risk of mortality, P_{pre}, decreases as accumulated degree-days, DD, approaches DD_{smo}.

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

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. The latter option is used in simulations reported here.

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 also identified components of the model that contributed most to the stochastic variability among replicate simulations (i.e., simulations 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 life stages to which the number of outmigrants is most sensitive.

Methods for sensitivity analysis

This sensitivity analysis was conducted on an early version of the model that did not yet include a late-fall run. We simulated fall-run chinook during a critically 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 in other regions of parameter space (i.e., different parameter values). We excluded parameters that were not of particular interest either because they are defined by data 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 (Gardner et al., 1981). The chinook model was run with 5000 different parameter combinations. Using PRISM, we drew a Latin-hypercube sample of parameter values from a jointly independent, 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-independence 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 standard deviations corresponding to one standard deviation 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 x 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%. We can use this fact to assess the influence of stochastic elements in the chinook model. Response variables with a low R^2 are 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 salmon on ration and growth and exposure to stochastic mortality risks.

Results and discussion of the sensitivity analysis

The results of the sensitivity analysis are summarized in Table 3. Parameters that do not appear in the table did not have a significant influence on any of the model responses.

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 3. 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 life stages, including the number of outmigrating smolts. Therefore, only a small number of replicate simulations are needed to obtain a good estimate of the number of outmigrants.

Key parameters that influence spawning and incubation success

We identified the parameters with the greatest influence on key model predictions (Table 3). The total number of eggs deposited was determined, not surprisingly, by the number of spawners, N_{esc}. However, a later endpoint, the number of eggs surviving to become fry, was no longer sensitive to spawner abundance. Instead the number of

Table 3. Sensitivity of model predictions (rows) to local changes in parameter values (columns). For each response variable, we present two indices, the standardized regression coefficient (SRC, plain text) and the relative partial sum-of-squares (RPSS, bold numbers). Index magnitude measures sensitivity (0 to 100) and sign indicates direction of influence. R^2's with asterisks denote response variables for which random influences call into question the sensitivity results.

Response variable		**Parameter name**									
	R^2	N_{esc}	B_{terr}	S_{min}	A_{move}	T_{ULT}	C_s	DD_{smo}	UP_{min}	UP_{max}	P_{max}
Outmigration											
Start date	0.43^{*}	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 date	0.17^{*}	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**
Fish size	0.46^{*}	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**
Number entering lifestage											
Eggs	0.82	+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	0.90	+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**	**0.0**	**0.0**	**0.14**	**0.0**
Smolts	0.79	+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**	**0.02**	**0.0**	**0.08**	**0.0**

Table 3 concluded.

Response	**R^2**	N_{esc}	B_{terr}	S_{min}	A_{move}	T_{ULT}	C_s	DD_{smo}	UP_{min}	UP_{max}	P_{max}
Outmigrants	0.81	+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	0.61	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	0.72	0.0	+0.15	+0.82	0.0	0.0	0.0	+0.10	0.0	0.0	0.0
Emigration		**0.0**	**0.02**	**0.67**	**0.0**	**0.0**	**0.0**	**0.01**	**0.0**	**0.0**	**0.0**
Predation	0.86	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	0.87	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	0.71	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	0.71	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**

emerging fry was most sensitive to the minimum quality of spawning habitat, S_{min}, which mediates the effect of flow on redd mortality. Field studies have not focused on this as an important determinant of salmon recruitment. Its importance here suggests either that it has an exaggerated importance in the model or 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 (e.g., Van Winkle et al., 1998).

Parameters related to run timing (UP_{min} and UP_{max}) had a secondary influence on incubation. Simulations that delayed the onset and end of up-migration had more survivors. 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.

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 (Table 3). Although variation in the timing of emergence was almost completely determined by variation in UP_{max}, other factors came into play by the time outmigration occurred.

Key parameters that influence successful rearing and outmigration

Flow-related mortality of eggs and alevins remained the most important factor influencing smolt production and the number of outmigrants through S_{min} (Table 3). This is probably because most mortality takes place during the early life stages that were most sensitive to this factor. We find it improbable that flow/habitat-related redd mortality is as important in the field as these sensitivity results suggest. The analysis did produce a testable prediction that years with variable flows resulting in large changes in habitat quality during incubation should produce fewer outmigrants than years with stable incubation flows.

Outmigrant numbers were also sensitive to T_{ULT}, UP_{min}, and UP_{max}. Increasing T_{ULT} decreased juvenile temperature-related mortality. Later dates of spawning migration increased recruitment in spite of an increased incidence of juvenile temperature-related mortality.

We identified parameters with a large influence on each of the three juvenile mortality risks. For the most part, the sensitivities serve as a check that the model is behaving as it should. The key parameters that influenced the number of outmigrants controlled the number surviving incubation because this represented the life stage with the lowest survival. 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 develop into smolts decreased. These results suggest that delayed development (e.g., caused by delayed spawning or low temperature) can cause many fry to exit before reaching the smolt life stage. Temperature-related deaths increased as the upper lethal 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. 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).

ITERATIVE MODEL IMPROVEMENT

Our initial model represented a preliminary collection of hypotheses concerning relationship between flow and the ecology of chinook salmon. 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 model's 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.

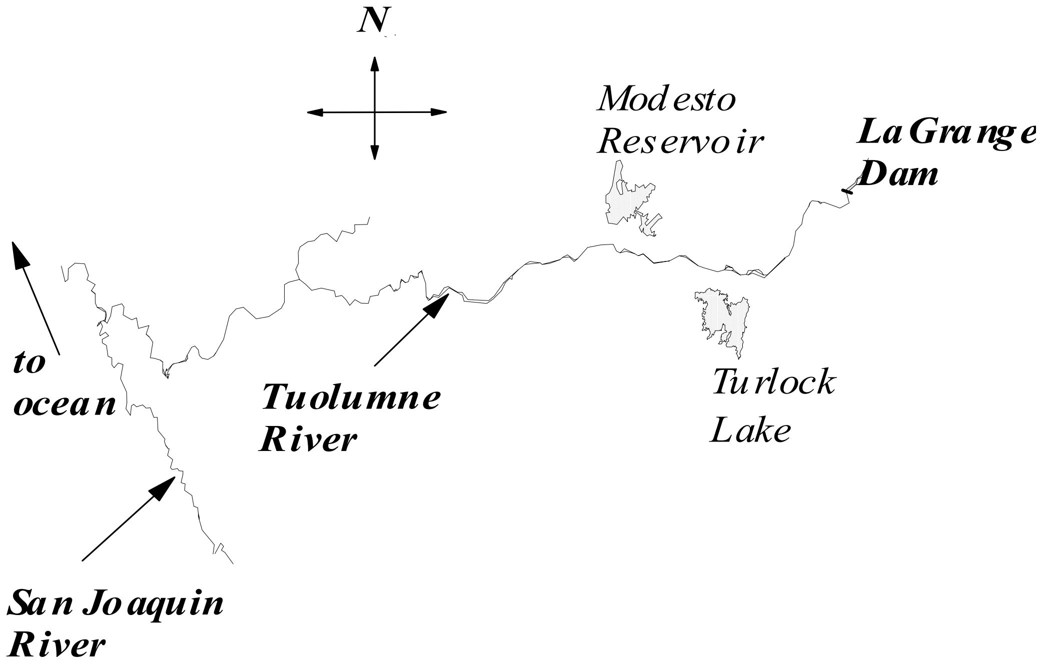

Figure 7. Map of the Tuolumne River reach simulated, showing the upstream barrier to migration (LaGrange Dam) and the outmigration route from the dam to the confluence with the San Joaquin River and northwest toward the ocean.

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 (Figure 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 4).

Life stage development

To evaluate egg and alevin development rates, we compared simulated dates of emergence from redds with dates at which 30 to 40 mm fry were observed in the

Table 4. Field studies conducted in the Tuolumne River and used to validate each component of the Oak Ridge chinook salmon model.

Model component	Field study description	Study reference
Mortality of eggs and alevin	Redd survival was studied during 1988 and 1989 by using traps. Estimates of survival to emergence were 1% and 32%, respectively. High temperature was thought to cause most redd mortality.	(EAEST, 1992h)
Juvenile development	Seining surveys at 10-d intervals from 1985 to 1989 sketch out the timing of emergence from redds and first appearance of smolts.	(EAEST, 1992c)
Juvenile growth	Seining surveys at 10-d intervals from 1985 to 1989 trace the growth and size distribution of juveniles. Sampling took place during winter and spring months.	(EAEST, 1992c)
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, 1992a)
Juvenile mortality	A predator study conducted in the Tuolumne River provided stomach contents data from May to September of 1988 during low flows.	(EAEST, 1992f)
Juvenile movement	An index of emigration was based on fyke net sampling for some years from1973 to 1986. Fyke nets were set for 24 h at three locations in the river.	(EAEST, 1992g)

Tuolumne River seining study (EAEST, 1992c). Likewise, we compared the simulated outmigration dates with those of the emigration study (EAEST, 1992g). Both studies are described in Table 4.

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 three of the four years 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, 1992c).

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 vs. 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 is believed to remain into the summer. The last smolting fish captured during the seining studies was captured on the last day sampled, June 26, 1986. Because simulated late-fall run juveniles rarely develop into smolts before summer, the model predicts that they remain in the system into summer. Survival through summer is unlikely unless thermal refuges exist to provide sub-lethal temperatures (e.g., near the dam or near groundwater upwellings). Anecdotal evidence from the American River suggests that individuals of its late-fall run remain through summer and emigrate in fall (Williams, 1994).

Egg and alevin survival

Mortality is the most sensitive and uncertain quantity in all population models, particularly during the early life stages (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 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 zero and calibrated levels of flow-related mortality (dewatering and scouring) by varying S_{min} to achieve ~30% survival to emergence. This had the effect of reducing the importance of flow-related mortality.

ORCM predicted 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 rare except for the 1985, the year with the highest escapement. 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 higher (40%) for a cold-water cohort (daily water temperature < 15°C) than for a warm-water cohort (10%) (EBMUD, 1992). Estimates of superimposition in the Mokelumne River are low (EBMUD, 1992), with only a small percentage (3 to 12%) of redds affected and, presumably, a fraction of egg pockets left undisturbed.

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. High densities of spawning adults result in a larger proportion of redds 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., the decreased quality of redd sites translated into lower flow-related survival). 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 decreases subsurface flow, diminishing irrigation of the eggs, and thereby increasing egg mortality (McNeil, 1964; Williams, 1994).

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 (Table 4) for water years (WY) 1986 to 1989 (EAEST, 1992c).

Simulated lengths of fry between 1985 and 1989 matched reasonably well with the distribution of chinook juveniles (fry and smolts) sizes in the seine catch through time, as shown for WY 1987 (Figure 8). In most years, the smallest juveniles seined remained ~30 mm in length as new fry continued to emerge. Maximum size of seined juveniles rose to between 85 and 115 mm and then declined as larger individuals migrated out. The decline in average size of model fish during May in Figure 8 results from shifting larger juveniles from the fry category to the smolt category. Smolt lengths predicted by ORCM compared well with lengths reported for smolts collected during the seining studies. For all four years, smolting juveniles were collected between April and June and ranged from 64 to 106 mm in length. In 1986, most field-captured smolts were 85 to 95 mm in length, whereas model smolts ranged from 66 to 103 mm, with an average of 83 mm (Figure 8).

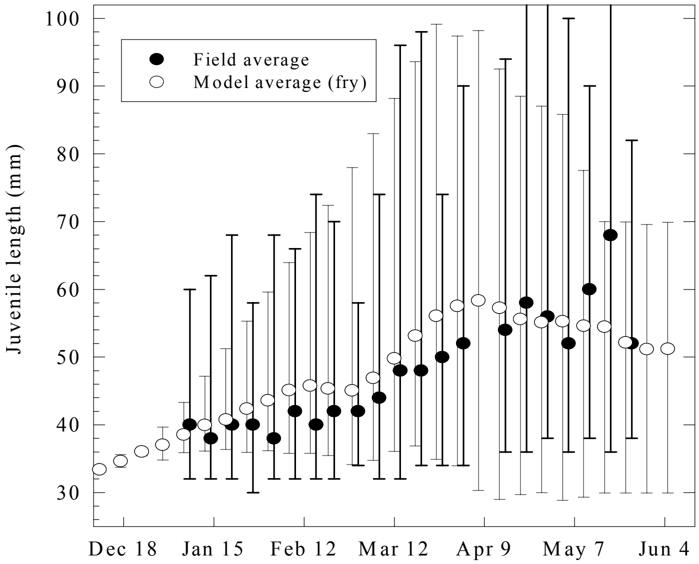

Figure 8. Comparison of the distribution of simulated fry lengths with the distribution of juvenile (fry and smolt) lengths captured by seining in 1986–1987. Error bars represent minimum and maximum lengths.

Juvenile survival

Predators in the Tuolumne River tend to congregate in sections of river with deep pools (EAEST, 1992f). Our simulated predation levels varied spatially to reflect site-specific data available for the Tuolumne River. We adopted the reported size distribution of black bass predators and set predator densities in the model to 294 predators per kilometer from the LaGrange Dam (Figure 7) to 27 km downstream (RM 25) and 59 predators per kilometer below RM 25 (EAEST, 1992f). Shuter and Post (1990) reported length-weight relationships for smallmouth bass.

We used population survey data to evaluate ORCM simulation of juvenile survival (Table 4). 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 study (EAEST, 1992a). Small numbers of recaptured fish produced Jolly-Seber estimates with large standard errors for all 4 d (Pollock et al., 1990); we adopted the estimate with the lowest standard error. The numbers surviving through each life stage and sources of mortality simulated by the model for each of the four WY are reported in Table 5.

An estimated 3,341 juveniles inhabited the 360-m stretch of river included in the mark-recapture study (standard error = 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. ORCM estimated 775,864 juveniles in the

Table 5. Summary of simulated mortality of each early lifestage of fall chinook salmon for four years.

	Simulation year (October 1 to September 31)			
Water year (WY)	WY 1986	WY 1987	WY 1988	WY 1989
Calendar year	1985–1986	1986–1987	1987–1988	1988–1989
Adult Escapement	43,959	7,798	15,783	6,741
Total annual flow (km^3)	3.685	0.808	1.013	1.620
Percent redd success	20	21	50	41
% survival to emergence	13	14	33	29
Fry per successful redd	2,795	2,772	2,822	3,077
Total eggs	83 million	15 million	30 million	13 million
Percent mortality of eggs and alevins in redds due to:				
temperature	44	65	56	50
flow	40	32	39	43
superimposition	16	3	5	7
Total fry emerged	11.2 million	2.0 million	9.9 million	3.8 million
Percent mortality of juveniles (fry and smolt) 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

system in early May 1987. ORCM predicted that 668,380 juveniles were present on May 4, 1987, and that most of these were fry (Figure 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 to 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: 6,576–23,286) juveniles, and the model predicted 15,443 juveniles.

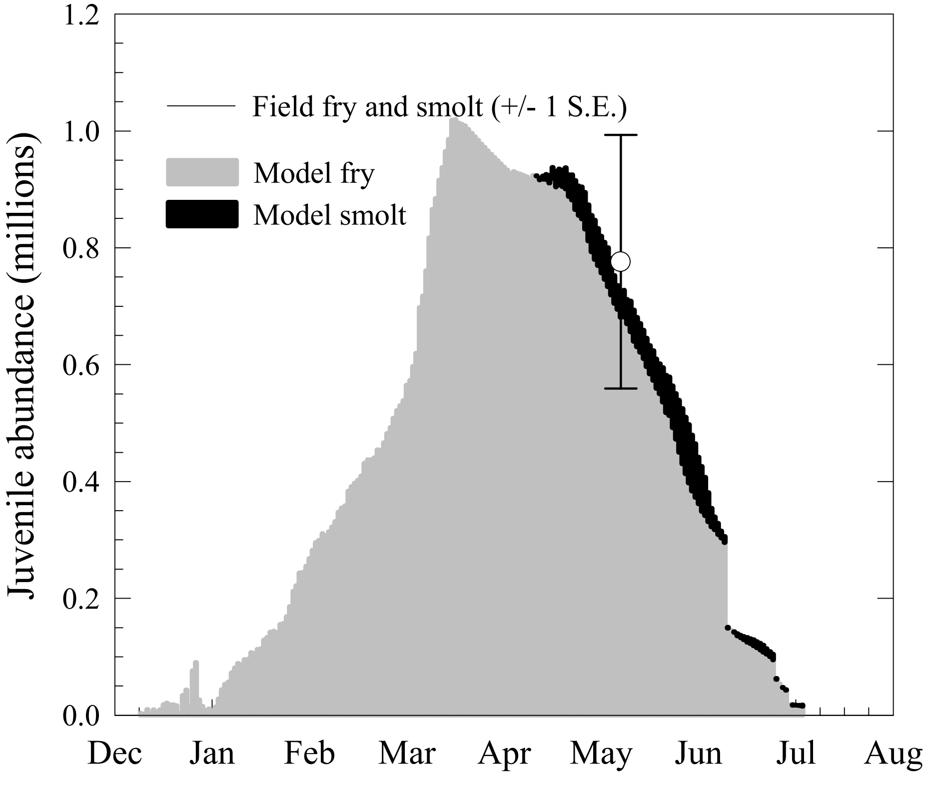

Figure 9. Comparison of model juveniles (fry=grey and smolts=black) with a field mark-recapture (Jolly-Seber) estimate of the juvenile population in early May of 1987.

The model predicted the number of juveniles within the section of river included in the mark-recapture study well. It should be noted, however, that abundances are highly variable (Figure 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, 1992a).

Although we did not have estimates of outmigrant numbers, premature 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 abundant spawners (Table 5). A small fraction of these early outmigrants may rear in the San Joaquin River or San Francisco Bay and complete the journey to sea. 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 5).

FACTORS CONTROLLING RECRUITMENT

The results here did not definitely identify factors controlling recruitment, i.e., combinations of mortality sources and life stages having the greatest negative impact on the number of outmigrants. The comparison with four years of field data and the sensitivity analysis served to corroborate some model processes and highlight problems with others. Although the sensitivity analysis highlighted egg and alevin mortality as having the largest effect on the number of outmigrants (Table 3), later calibration increased the value of S_{min} and decreased its importance. Flow-related mortality was less important than temperature-related redd mortality in magnitude in the four simulated years (Table 5). Parameters controlling mortality of juveniles exposed to high river temperatures also appeared to be important. We have higher confidence in this result because the parameter values are based on laboratory experiments of upper lethal temperature.

According to Speed (1993), the effect of flow could not be extricated from those of related factors (spawner density and temperature) in statistical evaluations of spawner returns, outmigrant survival, and average annual flow for the San Joaquin river system. This is true if only annual averages are considered, but when combined with a mechanistic model such as ORCM with intermediate predictions at different times of year, it should be possible to go farther in decomposing these factors. Further testing of intermediate predictions against field data is needed to help determine the relative importance of these component processes.

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PART 3. DESIGNING SEASONAL FLOWS TO MAXIMIZE RECRUITMENT OF FALL CHINOOK SALMON IN THE TUOLUMNE RIVER, CALIFORNIA

ABSTRACT

The goal of this study was to better understand how to design seasonal flow patterns for chinook salmon (*Oncorhynchus tshawytscha*). I addressed two objectives: maximizing (1) the number and (2) the run-time variation of chinook salmon recruits. To solve these optimization problems, I used simulated annealing with a population model, ORCM, that formalized scientific knowledge about the influences of flow-driven riverine habitat on recruitment of fall and late-fall chinook salmon. ORCM was calibrated for the Tuolumne River, California. My first objective was to find seasonal flow regimes to maximize simulated recruitment for annual hydrologic conditions ranging from wet to dry. Optimization results predicted that a minimum level of winter flow was always important. The number of simulated juvenile outmigrants produced by the optimal flow regimes increased as the amount of annual flow increased to a point. However, the benefits of additional water decreased at higher levels of total annual flow. The optimal flow regime for high annual flows produced more outmigrants by providing high flow over an extended period in spring. I addressed the second objective by identifying an optimal flow regime that maximized the variation in run times for the case of unlimited annual flow. The optimal flow regime designed to maximize run-time variation called for a pulse of high flow in early February just before the peak spawning time of the late-fall run. This seasonal flow regime produced fewer outmigrants, but increased the number of late-fall outmigrants by 30%.

INTRODUCTION

Water rights are contentious in the Central Valley of California. The high economic value of diverting water for human activities is pitted against the need to restore declining salmon populations by leaving water in the rivers (Cardwell et al., 1996; Yoshiyama, 2000). Economic pressures to divert water for municipal water supply, irrigation, and hydropower generation are high. Meanwhile, populations of fall and late-fall chinook in the lower Tuolumne River, a tributary of the San Joaquin River, have not recovered and are considered to have a high risk of extinction (Huntington et al., 1996). Thus, the stakes on both sides are high.

Reducing scientific uncertainty about the relationship between river flow (discharge) and salmon populations is important for a number of reasons. First, uncertainty creates a barrier between science and policy that prevents science from informing political decisions that affect salmon populations. Scientific uncertainty aggravates tensions and leads to gridlock in policy decisions (Policansky and Magnuson, 1998). Second, scientific uncertainty leads to conservative (i.e., more-stringent) optimal policies. Thus, economic interests (e.g., irrigators, the fishing industry, utilities, municipalities) can often benefit from improved ecological models that reduce uncertainty. For all involved, it is important to predict salmon responses to flow as accurately as possible.

Uncertainties are higher in some system components (e.g., fish population response) than in others (e.g., reservoir operations, economic costs). Modeling detail and attention tends to focus in areas that are better understood. Because reservoir operations and economic costs associated with leaving water in a river are easier to quantify than benefits to fish, models tend to focus on these aspects. Relatively simple models are typically used to predict salmon population response (e.g., Cardwell et al., 1996) instead of models that include more complex salmon biology (e.g., Bartholow and Waddle, 1995).

The National Research Council (1996) advocated change in the operation of hydropower systems on major rivers as an important option for intervention. They suggested that natural patterns of seasonal flows are best for salmon recruitment because the species have adapted to them over evolutionary time. Natural flows in the San Joaquin basin are dominated by spring snowmelt, with 60% of discharge between April and June (Johnston, 1997).

Scientific support for the Council's position comes from studies linking hydrologic flow patterns to juvenile survival (Cada et al., 1993; Kope and Botsford, 1990; Williams and Matthews, 1995). Although the mechanism behind this correlation between higher smolt survival and flow is unknown, reduced temperature-related mortality, reduced predation, and enhanced growth are three likely factors. Because chinook salmon juveniles have a low tolerance to elevated stream temperatures, high spring flows provide an indirect benefit by slowing the rise in river temperatures during late spring and early summer. Predation on outmigrating juveniles may be lower during higher flows for three reasons. First, predation efficiency may be curbed by higher turbidity, higher velocities, and aggregation of prey associated with higher river discharges (Peterson and DeAngelis, 1992). Second, faster outmigration at high flows shortens the duration of exposure to predation risk (Berggren and Filardo., 1993). Third, lower temperatures may reduce the demand by predators for food during smolt migrations. Flow may also influence juvenile growth and development. High spring flows flood riparian vegetation, creating an abundant habitat for aquatic insects on which juvenile fall chinook feed heavily during the early stages of their migration (Independent Scientific Group, 1996). Thus, higher flows yield larger and more robust smolts that survive better in the ocean.

The role of river flow at other times of year is less apparent. Higher flows in fall are called attraction flows because they are thought to attract spawners. High flows may facilitate swimming past natural barriers or they may merely serve as a cue. High flows also have indirect benefits because they lower water temperatures. In regulated rivers, water released from a dam is often drawn from cold water at the bottom of the reservoir. If flows are high, parcels of water move downstream quickly before they are able to warm through equilibration with air temperatures. Consequently, female spawners avoid exposure to temperatures above 15° C that damage eggs. The flow level during the building of redds influences later exposure to dewatering at lower flows and scouring during flood events. Thus, redd mortality could be influenced by both fall and winter flow levels.

This study uses optimization with a recruitment model to design seasonal flow patterns that are optimal for salmon. It focuses on fall chinook (including fall and late-fall runs) salmon of the lower Tuolumne River, a tributary of the San Joaquin River. Both runs have a high risk of extinction (Huntington et al., 1996). A recruitment model for fall chinook salmon, ORCM, simulates many of the linkages between salmon biology and instream flow described above (Part 2).

The optimizations conducted as part of this study evaluated two objectives. The first seeks to identify seasonal flow regimes that maximize salmon production under a range of hydrologic conditions. In the optimizations, hydrologic conditions limit or constrain the total river flow available to be allocated to instream flows and other uses on an annual basis. The second seeks to identify a seasonal flow regime to maximize diversity in the spawning dates of successful outmigrants. Such a flow regime might be used to ensure the continued survival of the late-fall run, in addition to the fall run.

FALL CHINOOK SALMON

Chinook salmon spend their adult lives in the ocean. At some point between the ages of two and five, adults migrate during fall into rivers to spawn. The females prepare nests called “redds” in the gravel river bottom. During courtship, each female releases her eggs over her redd and the eggs are fertilized by one or more males. Eggs incubate through the winter and hatch as alevins (non-feeding larvae) into inter-gravel spaces. They emerge from their redds as fry (pre-smolt juveniles) in spring. Chinook salmon fry feed on benthic insects along river margins for the first month or two and gradually move downstream. During the process of smoltification, juveniles become tolerant of saltwater conditions and emigrate to the marine environment during their first spring. Linkages between flow and recruitment simulated in the ORCM model for the riverine part of the fall-chinook life cycle are illustrated by Figure 1. Flow has both direct and indirect (through temperature) effects on survival of offspring.

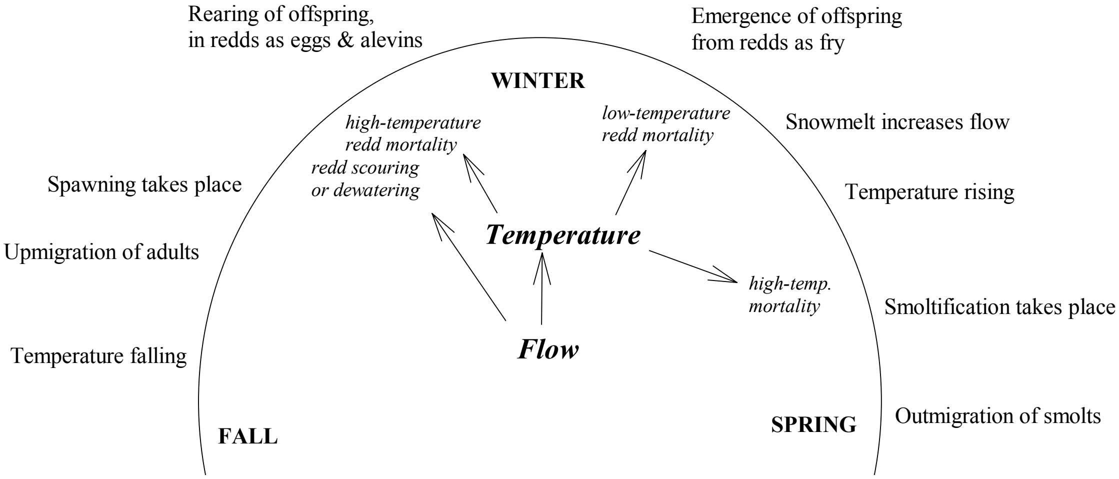

Figure 1. The river phase of the fall chinook salmon life history and simulated relationships linking flow and temperature to reproductive success.

"Fall" chinook actually include both a fall run and a late-fall run that appear to be genetically isolated to some extent (Nielsen, 1994). The late-fall run comprises an unknown, but small percentage of total "fall" chinook returns. The late-fall run constitutes approximately 7% of fall spawners in the Sacramento River. The population size of the late-fall run is believed to be declining faster than the early fall run

(Yoshiyama, 2000) and should be considered to have a considerably greater risk of extinction. Adults of the late-fall run return to spawn between January and April, after the fall run proper. Historically, late-fall adults spawned in upper mainstem rivers, where summertime water temperatures remained low enough for juvenile growth (Fisher, 1994). In the Central Valley, construction of mainstem dams (e.g., Friant and Shasta) has restricted and probably redirected late-fall spawners to alternative locations in the lower mainstem or tributary.

THE TUOLUMNE RIVER

An adult chinook salmon wishing to spawn must swim from the ocean through the San Francisco Bay and then through the Sacramento-San Joaquin Delta. At this point, the adult has "escaped" the fishery. It locates the mouth of the San Joaquin River and follows the river to its junction with the Tuolumne River. From the perspective of a salmon, the river ends 83.7 km upstream at LaGrange Dam. From 1919 to 1992, annual flows in the Tuolumne River ranged from 488 to 5,718 cubic hectameters (hm^3). On an annual basis, the regulated discharge below a dam is usually lower than the natural or "unimpaired" flow because water is diverted and evaporates during storage in upstream reservoirs. Dams and diversions have reduced the average annual flow in the Tuolumne River from 2,140 hm^3 to 920 hm^3 (McBain and Thrush, 1997).

METHODS

The Oak Ridge Chinook Model (ORCM)

The ORCM (Jager et al., 1997) is a spatially explicit and individual-based model of fall chinook salmon. The model adds ecological realism through a habitat sub-model and a biotic sub-model. This realism is lacking in other models, such as the Physical Habitat Simulation Model (PHABSIM) that are typically used to set instream flows. The habitat sub-model represents important spatial gradients (e.g., temperature, predator densities) between upstream spawning areas and lower reaches inhabited by juvenile salmon during outmigration. The biotic sub-model simulates coexisting life stages, transitions between life stages, growth, movement, and mortality.

The ORCM simulates the river phase of chinook salmon ecology, beginning with adults entering the river to spawn. For each redd, ORCM uses a daily time step to simulate mortality during the egg and alevin life stages and development from one stage to the next. After salmon emerge from redds, ORCM simulates the development, growth, mortality, and downstream movement of juveniles (fry and smolts), culminating in migration of juvenile smolts from the river. These events take place in a spatially explicit habitat that responds to flow and temperature. Seasonal flow patterns influence the reproductive success of anadromous salmon populations in the model in complex ways (Figure 1). For example, streamflow can influence the survival of egg and alevin lifestages through scouring or dewatering of redds. Streamflow affects survival and growth of fry and outmigration of smolts through changes in temperature and habitat availability.

The ORCM model, its parameter values, validation, and sensitivity results are described in Part 2. Sensitivity analysis indicated that model results were insensitive to the predation parameters and very sensitive to the parameter that controls flow-related mortality of early life stages.

For the optimization, I made two changes from the Jager et al. (1997) model. First, I increased the flow-related survival of early life stages in marginal habitat, S_{min}, from 0.9995 to 0.9999 to reduce sensitivity of results to flow-related mortality. Second, I simplified the predation model by replacing the individual encounters simulated between chinook juveniles (X) and their predators (Y) with a Holling type II functional response (Equation (1)). I calibrated the probability of capture ($Pcap$ = 0.001) to obtain the same level of predation as in the more complex version of ORCM.

$$Predation\ \ risk = \frac{Pcap\ X\ Y}{1 + Pcap\ X\ Y} \qquad (1)$$

In all other respects, the ORCM model was configured as described in Jager et al. (1997), with simulation parameter values in Table 2 of that paper.

The main prediction of the model is numbers of juvenile fall chinook salmon that migrate out of the river as smolts (recruitment). This quantity was used as the first objective maximized by simulated annealing. The variance in spawning dates of surviving smolt outmigrants was used as a second objective maximized by simulated annealing.

In addition, ORCM tracks an array of endpoints or stages, including all entries to a life stage (fry, smolt, outmigrating smolt) and all deaths by cause. The main attribute of individuals in transition to a life stage focused on in this analysis is the spawning date of smolt outmigrants. Because the ORCM model provides summaries on the fate of all eggs, it is also possible to analyze the importance of various sources of mortality. Causes of mortality include three acting on eggs and alevins in the redd (temperature-related, flow-related, and superimposition) and three acting on juveniles (temperature-related, premature outmigration, and predation).

I compared optimal flow regimes derived with different objectives and constraints with the help of these summaries. In one analysis, I compared the latest spawning date of a surviving smolt outmigrant to evaluate the variation in run times produced by different optimal flow regimes. In a second analysis, I compared the characteristics of individuals that were killed by each mortality factor to see what life stages and what factors contributed to different outcomes under different optimal flow regimes.

Seasonal Flows that Maximize Recruitment

I used simulated annealing (Metropolis et al., 1953) to identify the seasonal flow regimes that would maximize ORCM salmon production in different types of hydrologic years. My objective was to maximize the predicted annual number of outmigrating smolts. The freshwater year between upmigration in the fall and outmigration in the spring was divided into 20 two-week periods, each characterized by a fixed average daily flow. The average daily flow assigned to each period is one of 20 decision variables manipulated to optimize the simulated number of smolt outmigrants. The optimization identified daily flows, Q_i, during each time period i, that maximize $Z = F_1$ (Q_i), subject to:

$$\sum_{i=1}^{20} \mathrm{Q_i} \leq \mathrm{Q_{tot}}, \quad (2)$$

where Z is the number of outmigrating smolts produced by the ORCM model (F_1). Q_{tot} is a constraint (upper limit) on total annual flow. I assumed that summer flows (after July 7) were constant and equal to 1.416 m^3 s^{-1}. Because river flow is not available in unlimited supply in the Central Valley of California, I sought optimal flow regimes that were constrained in the total amount of water available on an annual basis. Four values of total annual flow, $Q_{tot,}$ used as limits were 122, 245, 489, and 979 hm^3 y^{-1} (50, 100, 200, and 400 kcfs-d y^{-1}).

To estimate flows that maximize salmon production, I used ORCM with the following assumptions:

1. Flow releases are only constrained by the annual total (i.e., seasonal constraints on reservoir operations are not considered).
2. Air and release temperatures follow the simulated seasonal pattern described in Part 2;
3. Daily river flows are constant within each of the twenty, two-week periods between Oct. 1 and July 7;

4. Summer flows (July 7 to Sept. 30) are not relevant for chinook salmon because of the low probability of surviving high water temperatures and the fact that most juveniles have exited the river by this time.
5. Because it was not computationally feasible to consider a range of spawner abundances (particularly high abundances), these optimizations assume that 5,000 adult salmon return to spawn. This is not a particularly low value—an average of 6,838 adults/y returned to spawn between 1970 and 1998.

Seasonal Flows that Maximize Variation in Run Time

In addition to the objective of maximizing smolt production of the combined fall and late-fall chinook salmon run, I also sought a flow regime that would maximize *variation* in run times. I calculated a variance in spawning dates (D_j, represented as an integer number of days after Oct. 1) of successful smolt outmigrants. This optimization assumed that annual flow was unlimited. The optimization program found daily flows, Q_i, during each time period i, to maximize $Y = F_2(Q_i)$, where Y is the variation of run-times of outmigrating smolts produced by the ORCM model (F_2). If N is the number of successful outmigrants (each designated by j), then Y is:

$$Y = \frac{\sum_{j=1}^{N}\left(D_j - \overline{D}\right)^2}{(N-1)} \qquad (3)$$

Simulated Annealing

I used simulated annealing (SA) as my solution method because it has a high probability of finding the optimal or a near-optimal solution for a wide range of problems. Metropolis et al. (1953) first introduced this global search technique as a direct analogue of cooling in thermodynamic systems. At high temperatures, molecules of a liquid move freely. If the liquid cools slowly, its atoms are able to line themselves up and form a pure crystal. This crystal is the state of minimum energy for the system. If the liquid is cooled quickly or quenched, then it does not reach the state of minimum energy but stops at a somewhat higher energy state. In terms of a mathematical optimization problem, the crystal is the global optimum and the quenched solution is one of many sub-optimal solutions.

Simulated annealing algorithms follow an annealing schedule that originated in the statistical mechanics of thermodynamic systems. At temperature *T*, such a system has a chance of moving from energy state E_{old} to state E_{new} with probability, *P*.

$$P = \exp\left\{ - \frac{(E_{new} - E_{old})}{k\,T} \right\} \qquad (4)$$

This probability distribution is known as the Boltzmann distribution and *k* is the Boltzmann constant. The most significant feature of this algorithm, known as the Metropolis Algorithm, is that it permits changes of state from lower to higher energy with some probability (i.e., not all transitions are to lower energy states). This feature prevents the algorithm from becoming trapped in local minima. Kirkpatrick et al. (1983) added cooling to the algorithm by reducing the temperature parameter, *T,* during the course of the search.

Among optimization methods, SA has the strongest theoretical assurance of finding a globally optimal solution (Geman and Geman, 1984). To gain statistical assurance of finding the global optima, the random walk through parameter space must begin at a sufficiently high initial "temperature" and cool at a sufficiently slow rate. As it cools, the chance of jumping out of local optima decreases. In general, optimizations do not have a physical analog for temperature, which serves as a tuning parameter that controls the rate at which the search region is restricted. One way to think of the algorithm is that it gradually transitions from a global search of the decision space to a local search.

I used the SIMANN program for simulated annealing developed by Goffe et al. (1994). I successfully tested the program on simple polynomials, SIMANN uses the following algorithm. Let *f*(*X*) be a function of parameter vector *X*; *V* is a vector of step lengths. The function is evaluated at the starting point *X*. A new *X'* is chosen by varying element *i* of *X*:

$$x_i^{'} = x_i + r \cdot v_i, \qquad (5)$$

where r is a uniformly distributed random number on [-1,1] and v_i is an element of V. The function value f' is then calculated. If f' is greater than f, X' is accepted and X is set to X′. If f' is less than f, acceptance depends on the Metropolis criterion. p' is another uniformly distributed random number on [0,1].

$$p = \exp\left\{\left[\frac{(f' - f)}{T}\right]\right\} \qquad (6)$$

If p is greater than p', the new state X' is accepted and X is set to X'. Otherwise, X' is rejected.

In the application of SA to maximize chinook salmon recruitment, the objective function is given by predictions of outmigrant numbers from ORCM. Because variation among replicate simulations was small (about 1%), and in the interest of saving time, ORCM simulated only one replicate for each combination of flows. As initial conditions for the optimization with no annual-flow constraint, I constructed a flow regime with the daily flows for each period set to 4.248 m^3s^{-1}. In optimizations of hydrologic conditions with limits on the amount of flow available, total annual flow was constrained by simply rejecting non-feasible solutions—i.e., those that sum to a total annual that exceeds the specified upper limit. The initial flow regime started with the total annual flow divided evenly among the time-periods. I followed the procedure outlined by Goffe et al. (1994) to find an initial value for the temperature parameter that would result in reasonably large initial step sizes (changes in daily average flows). An initial value for the temperature parameter of 0.02 resulted in step sizes between 2 and 21 m^3s^{-1}. SIMANN adjusted step sizes periodically (every 400 trials or 20 trials for each decision variable) to ensure that roughly half of all points (trial parameter combinations) were accepted. The algorithm reduced the temperature parameter by a factor of 0.7 after 8000 model evaluations (20 step-size adjustments). As annealing temperature decreased, the step size and the likelihood of accepting points that decrease the number of outmigrants decreased.

RESULTS

Seasonal Flows that Maximize Recruitment

The predicted optimal pattern for allocating seasonal flows changed as the total amount of annual flow available changed (Figure 2). When I simulated an unlimited supply of water, the optimal flow regime provided fall attraction flows, relatively low winter flows, and high spring flows (Figure 2E). As annual flow constraints tightened, both the magnitude and seasonal pattern of optimal flow changed. Fall attraction flows were the first to disappear (Figure 2D). Although the magnitude of flow provided in spring decreased, providing high spring flows remained optimal in all hydrologic year types (Figures 2B-E) except for the driest (Figure 2A). When the annual water became very limited (Figure 2A), an optimal flow regime allocated water more evenly across months, but provided more water in winter than in fall or spring (Figure 2A). The optimization with ORCM suggested that providing a minimum level of winter flow was very critical, but that values above this minimum level were not desirable.

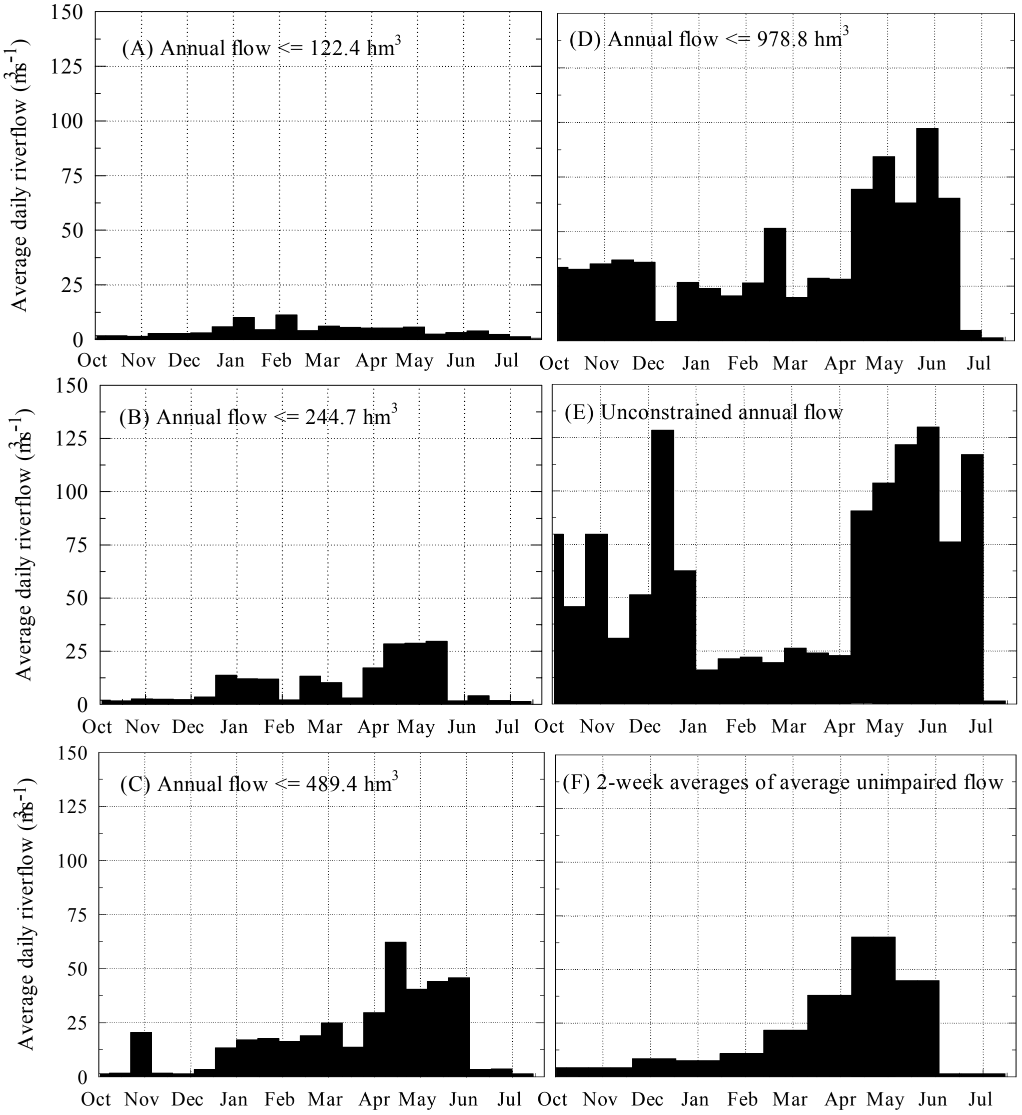

Figure 2. Optimal flow regimes that maximize simulated production of smolt outmigrants for five scenarios that represent a range of constraints on annual river flow: (A) <=122 hm^3, (B) <=245 hm^3, (C) <=489 hm^3, (D) <=979 hm^3, and (E) an unconstrained scenario. These can be compared with (F) 2-week averages of reconstructed natural flows above the Don Pedro and LaGrange dams (1919 -- 1992).

I compared patterns of mortality across the spectrum of annual flow constraints. Overall, egg-to-fry mortality increased and fry-to-smolt mortality decreased as annual flow became less limiting (Figure 3). Temperature was a main factor controlling this apparent trade-off between redd and juvenile mortality (Figure 4). As annual flow increased, higher redd mortality associated with extreme temperature was the leading cause of reduced survival during incubation. Decreased exposure to high spring temperatures was the leading cause of reduced mortality for juveniles.

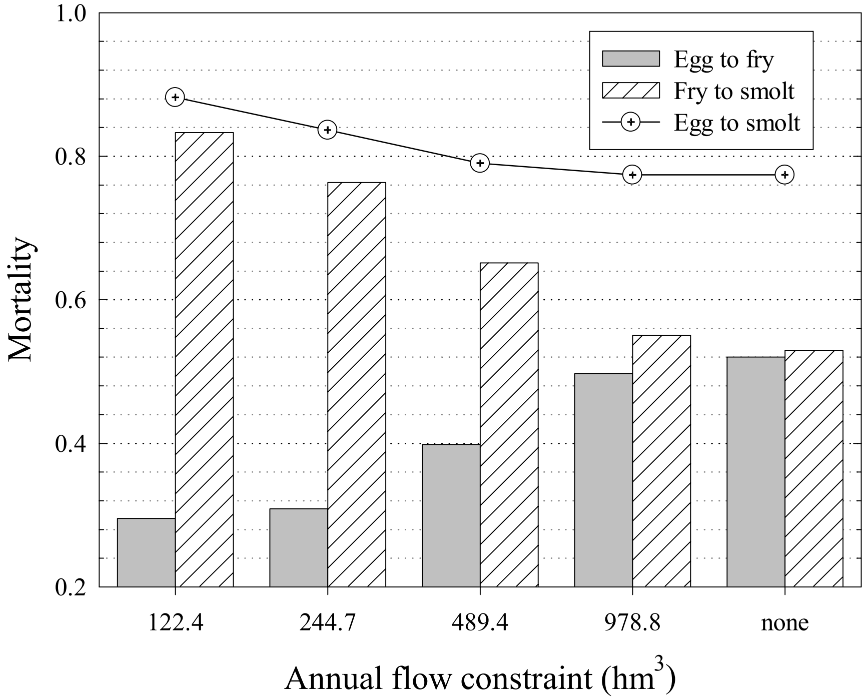

Figure 3. ORCM-simulated survival for each of two periods.

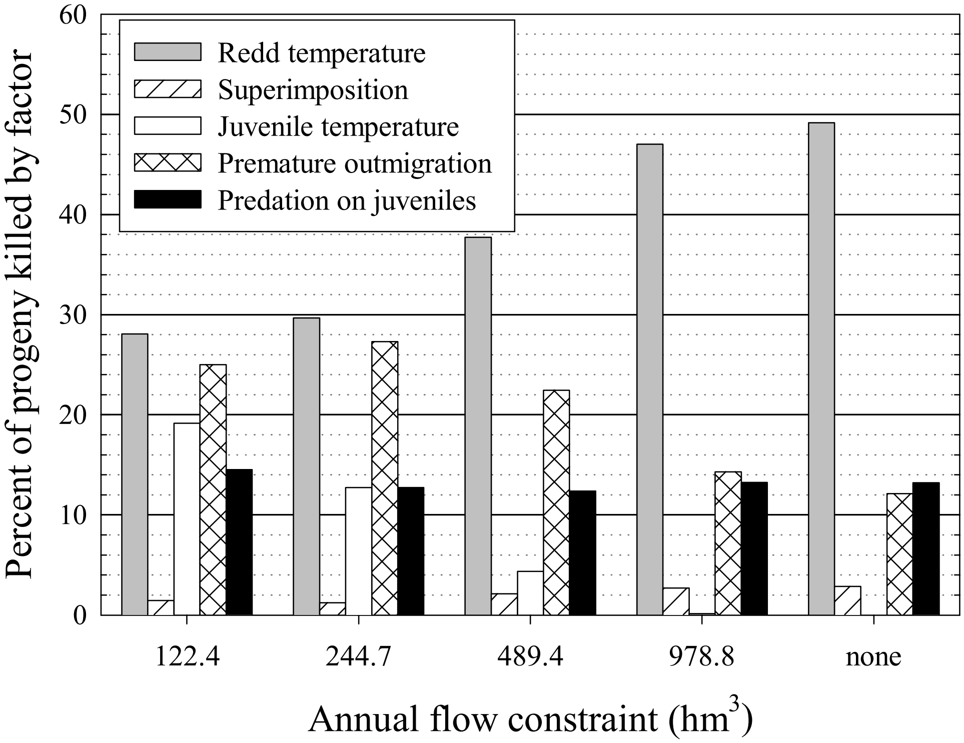

Figure 4. Five main factors caused losses between spawning of eggs in redds and outmigration of smolts in ORCM. The percentage of progeny lost to each factor is shown for the five optimal flow regimes simulated with 5,000 spawners.

As the amount of flow available on an annual basis increased, the simulated period of successful spawning became longer. The earliest successful redds were built in early October for all hydrologic years, but the last successful redds (those that produced offspring that migrated out as smolts) were constructed in mid-November in low-flow years and as late as February in high-flow years (Figure 5).

The actual annual flow requirements for optimal flow regimes obtained by SA were somewhat lower than the imposed constraints (recall that the constraints are only

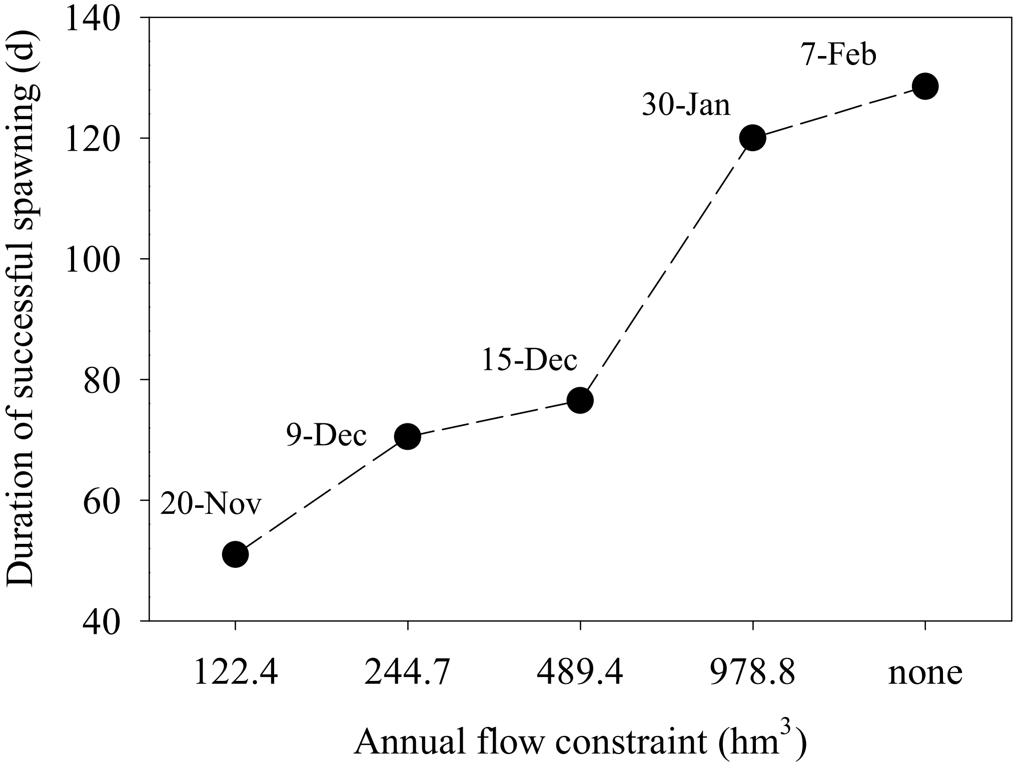

Figure 5. The temporal window of successful spawning extended farther into spring in scenarios with higher annual flows.

upper limits and do not fix the total annual flow at one value). Smolt production increased sharply for annual flows up to ~400 hm^3 (Figure 6). Beyond this point, the incremental effect of adding flow on the production of outmigrating smolts declined. Figure 6 describes the trade-off (i.e., the inverse relationship) between two competing objectives: that of increasing the number of outmigrants and that of decreasing (i.e., diverting) total annual flow.

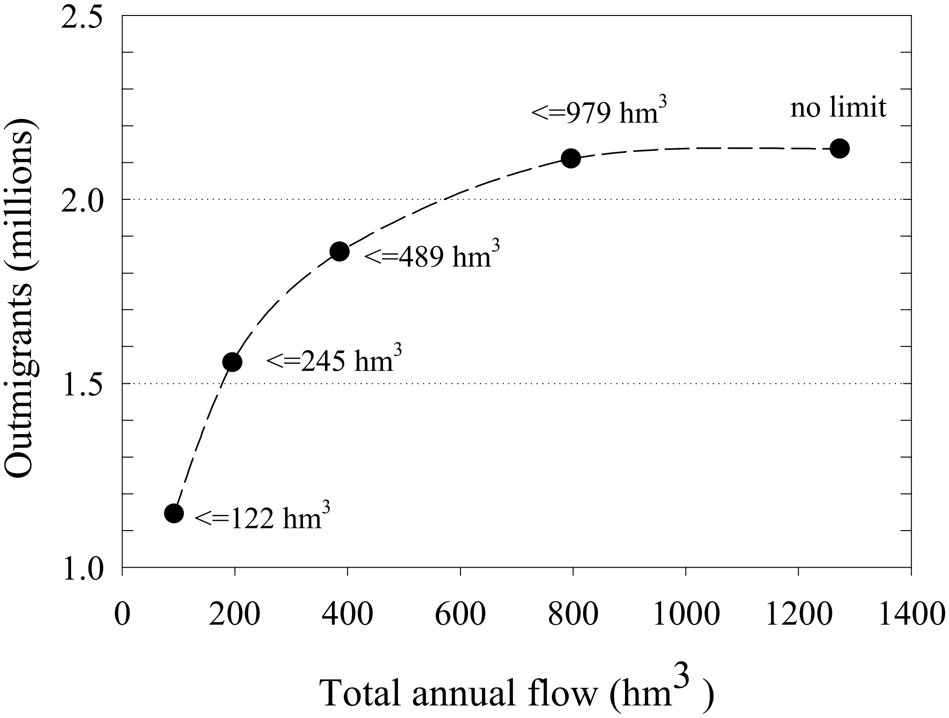

Figure 6. Trade-off between total annual flow and simulated outmigrating smolts. These values assume an optimal pattern of seasonal flows for 5,000 spawners.

Seasonal Flows that Maximize Variation in Run Timing

The solution of the "maximize variation" problem, with unlimited flow, differed somewhat from the solution of the "maximize production" problem. The most notable difference is the pulse of high flow between Feb. 4 and 17 (Figure 7). This occurs a few weeks prior to the peak of the late-fall run, as simulated in ORCM. There are smaller differences in spring and fall as well, including higher flows in early summer. These changes in the seasonal flow regime resulted in 30% more smolt outmigrants from the late-fall run, but at the cost of greatly reduced total production (Table 1).

Table 1. Predictions for an optimal flow regime that maximized variation in spawning time among smolt outmigrants and an optimal flow regime that maximized smolt production.

ORCM predictions	Maximize variation	Maximize production
Percent successful redds	75	95
Total number of outmigrants	1.565 million	2.150 million
Number of late-fall run outmigrants	402,092	298,017
Avg. julian spawn date of emerged fry	322 (S.D. = 29)	315 (S.D. = 25)
Avg. julian spawn date of smolt outmigrants	313 (S.D. = 18)	306 (S.D. = 15)

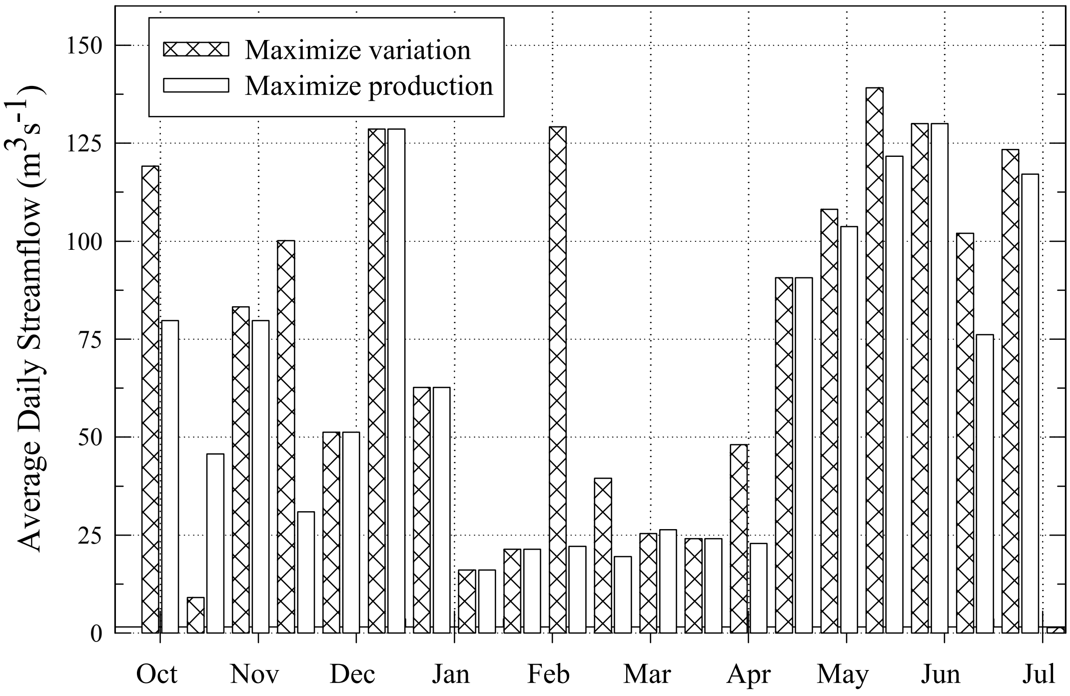

Figure 7. Flow regimes optimized with two different objectives. The "maximize variation" flow regime (hatched bars) and the "maximize production" flow regime (open bars). The optimizations assumed 5,000 initial spawners with 7% in the late-fall run, and unlimited annual flow.

Simulated Annealing

Simulated annealing turned out to be an extremely slow method of optimization. The optimizations reported here ran literally for months on dedicated DEC-Alpha workstations and Pentium II personal computers. Even so, the results can only be assumed to be nearly optimal. The slow performance of SA is well known (Goffe et al., 1994; Ingber, 1993), but it is often accepted as a trade-off because the same properties that make the algorithm slow also increase its statistical assurance of finding global solutions.

DISCUSSION

Seasonal Flows that Maximize Recruitment

Seasonal flow patterns predicted by ORCM to maximize recruitment always maintained a minimum level of winter flow. Two patterns emerged as the amount of water available annually increased. The first priority was to increase spring flow with the additional water available. A lower priority was to increase fall flows.

These results indicate that designing seasonal flows that use water only when salmon need it most can help to guide restoration efforts. The results here provide information that can be considered when weighing various management objectives for the Tuolumne River. The management objective of maximizing smolt production calls for over 1200 hm^3 (Figure 6). However, a management objective that considers competing water interests might notice that one regime with lower fall flows and moderate spring flows (e.g., Figure 2C) did almost as well as those calling for much more water. Although the two regimes with access to the most water produced the most smolt outmigrants, the benefits of higher annual flows declined as flow became less limiting (Figure 6).

From the standpoint of preserving chinook salmon stocks that differ in temporal spawning life-histories, variation-enhancing flow regimes may be important to consider. I found that an extended period of successful spawning and survival of the late-fall run contributed to higher production in wetter years. The two optimal flow regimes with the most water (Figures 2D and 2E), were the ones that successfully reared smolts from the late-fall run (Figure 5). The latest birth date of successful smolt outmigrants shifted by three months, probably because of the extended block of high spring flow provided. Because late-fall adults are not yet in the river during fall, it would be tempting to conclude that the high fall flows provided in these two wetter regimes can probably be reduced without affecting the late-fall run. However, it is possible that high fall flows reduce survival of fall-run eggs and alevin, thereby reducing competition between fall-run juveniles and later-emerging and smaller late-fall juveniles (Figure 3).

Three caveats limit the applicability of these results. First, limitations in flow storage capacity and competing demands on flow restrict the ability to manage flows according to an optimal flow regime. For example, the natural flow regime in Figure 2F suggests that water would not normally be available to provide high flows in fall. Second, part of the success of the optimal flow regimes proposed here comes from their stability. These regimes lack the day-to-day variation that is inherent in natural flow regimes. Third, the optimal flow regimes identified here depend on assumptions in the ORCM model.

According to the National Research Council (1996), salmon species are best served by conserving natural flow patterns that shaped the evolution of chinook salmon life histories (Figure 2F). Two components of a flow regime are its overall shape and its variability. The overall shape under average flow conditions of the ORCM optimal regime (Figure 2C) and the natural flow regime (Figure 2F) appear to be similar. High-elevation snowmelt in the spring and summer months raises natural flows in the Sacramento–San Joaquin River basin (Lettenmaier and Gan, 1990). According to Moyle and Yoshiyama (1997), the highest survival of San Joaquin salmon is seen when naturally high outflow events coincide with times of smolt emigration. The optimizations using ORCM support these expectations about overall shape, emphasizing the importance of high spring flow.

This study did not address the role of flow variation. Unwin (1997) found that flow variability during spring outmigration showed the strongest and most consistent positive relationship with fry-to-adult survival. Experimental pulse flows in the Stanislaus River, California stimulated juvenile migration in the short-term (2 days), with little additional benefit from prolonged high flows (Cramer, 1997). In terms of our understanding of the benefits of high flows to migrants, this makes sense. In general, the ability of high flows to speed migration is probably less important than the short-term benefits provided by pulse flows. Pulse flows serve as a behavioral cue to synchronize downstream movement, allowing migrating smolt 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 this study used two-week time periods to obtain optimal flow regimes, they are less variable than natural flow regimes. Also, ORCM does not at present include the fine distinctions above between short-term and longer-term benefits of flow. A next step would be to introduce more detailed processes in the ORCM model and to evaluate the effects of including realistic variability in flow without substantially increasing the number of decision variables.

The results presented here depend on the assumptions of the ORCM model. For example, the earliest date of upmigration in ORCM is fixed (Oct. 1), and some mechanisms (e.g., maternal egg mortality when exposed to high temperatures) are not simulated. Improved simulation of upmigration is a possible improvement of ORCM to evaluate in future. One way to evaluate the robustness of our results is to compare with results obtained from other models. There has been one previous attempt to design optimal instream flows. Bartholow and Waddle (1995) used Monte Carlo methods with the SALMOD model for chinook salmon in the Trinity River, California to find an optimal flow regime with four-week periods over a range of historical hydrologic conditions. The SALMOD flow regime is qualitatively similar to ORCM's unconstrained optimal flow regime. Both optimal solutions called for elevated flows in fall and spring.

Seasonal Flows that Maximize Variation

A comprehensive objective for salmon restoration should consider life-history variation in addition to the overall numbers of recruits. Preserving ecologically important genetic variation is usually a goal of efforts to restore populations. Smith et al. (1995) recommend that such efforts focus on genetic differences along the primary axes that permit reproductive isolation and that, 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, Neilsen (pers. comm.) 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. Although Neilsen found that only 6.6% of microsatellite allelic variation could be attributed to differences among temporal spawning runs, this low variation is likely to have high ecological relevance.

In the results presented here, pulse flows corresponding to peak spawning times of distinct runs were the most obvious feature of an optimal “maximize-variation” flow regime. This is not to imply that flow management alone is capable of solving problems that face chinook salmon for either the fall or late-fall runs. As pointed out by Healey and Prince (1995), loss of access to upstream river habitat may cause conservation efforts to fail for races, such as the late-fall run of chinook salmon, that relied on them.

Simulated Annealing

The optimization problem posed here is a very difficult one for four reasons: (1) it involves many decision variables; (2) the problem requires a black-box objective function; (3) the solution surface is rough; and (4) evaluation of the objective function (ORCM) for each flow combination is time-consuming (10-15 minutes).

The number of decision variables has a huge effect on the size and dimensionality of the decision space to be explored by the optimization. Consider that a systematic search of only 2-levels of each variable (i.e., each 2-week time period) would require evaluating $2^{20} = 1,048,576$ simulations.

Because the number of outmigrants and run-time variation must be calculated by a simulation model, the optimization cannot make use of derivatives or other prior information about the solution surface (i.e., f(X) vs. X, where f(X) is the number of outmigrants and X is the vector of 2-week flows for each of 20 time periods).

The solution surface is rough (i.e., it has many local optima) because the ORCM model is stochastic. Although only one initial random number seed was used and typical variation in outmigrant numbers is only 1%, small changes caused by a shift in flow can alter the mapping of simulated events to the sequence of random numbers.

Because so many ORCM simulations are needed, each with a different flow vector, the time required for each simulation has a large effect on the time required to reach a solution.

A number of promising modifications and hybridizations with other methods are being developed to improve performance of SA in both the global and the local phases of searching. Fox (1995) has focused on improvements gained through a smart pre-processor for the global phase of SA. This begins with random restarting to identify a good initial solution. Fox then incorporates tabu search (Glover, 1989; Glover, 1990) to penalize moves returning to previously searched regions of decision space. This requires tracking the history of previous regions searched, providing the algorithm with a memory.

Hybrid algorithms can also speed up the local phase of a stochastic search. For smooth solution spaces, SA can be combined with local optimization methods. SA conducts the earlier phase of the search, then switches to a greedy search method (one that only accepts trials that improve the objective function) to finish the search more quickly. Quenching (dropping the temperature quickly) is an alternative method to speed up the final phase of the search that does not require a smooth objective function.

Parallel algorithms for SA are another active area of research. SA is inherently sequential and is usually parallelized by running independent search paths with minimal exchange among processors. However, several other strategies for parallel computation have been developed. States can be generated in parallel prior to subjecting them to the acceptance test (Ingber, 1996). Parallel genetic simulated annealing is a hybrid method that borrows elements from genetic algorithms and SA that lend themselves to parallelization (Chen and Watson, 1998). Alternatively, the decision space can be partitioned and SA searches conducted within each partition, discarding unpromising sub-regions as the search proceeds (Demirhan, 1999).

These innovations suggest that faster methods will become available in the future. Faster optimization methods are clearly needed to explore the full range of management options relevant to this problem.

Future directions

This paper addresses two flow optimizations that are relevant to the management of instream flows for the benefit of chinook salmon, but facets of these two questions and other interesting optimization questions remain unanswered. One facet of these problems that has not been addressed here is the role of spawner density. How does spawner density influence the shape of the optimal flow regime? I begin to address this question in Part 4 by comparing optimal flow regimes at a low and a high spawner abundance when annual flow is plentiful. However, the question remains unanswered for intermediate spawner abundance and for optimal flow regimes constrained by annual flow. A second facet not addressed here is the role of variation in flow. Understanding how day-to-day variability in river flow influences smolt production can potentially improve management of pulse flows as a means of stimulating migration.

Multiple objectives can be addressed by optimization, but rely on our judgement in valuing different goals. This paper considered both the problem of maximizing smolt production of the combined fall and late-fall runs, and the problem of maximizing variation in the spawning times of successful outmigrants. A third objective that may also be of interest is to find a flow regime that maximizes the number of outmigrating smolt per unit flow. Such a flow regime would address both the benefits to fish and costs to society. Ultimately the relative importance of each objective, the feasibility of solutions, and the uncertainty in model predictions should be considered as part of the decision process.

ACKNOWLEDGEMENTS

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PART 4. DENSITY AND FLOW EFFECTS ON RECRUITMENT OF FALL CHINOOK SALMON

ABSTRACT

The determinants of salmon recruitment, once an issue for those setting harvest quotas, is now an issue for population restoration. I used a spatially-explicit, individual-based model of fall chinook salmon smolt production in the Tuolumne River, California (the Oak Ridge Chinook Model, ORCM) to explore these determinants. This simulation study focuses on two questions: (1) Does spawner abundance change the optimal flow regime? and (2) How does total annual flow influence the spawner-recruitment relationship?. To address the first question, I compared an optimal flow regime identified for 5,000 spawners and unlimited total annual flow in Part 3 with one identified for 40,000 spawning adults here. The results suggest that extended high flows in fall and spring called for in wet years when fewer adults return to spawn are no longer beneficial when many adults return.

To address the second question, I used optimal flow regimes identified in Part 3 with several different upper limits on total annual flow. I developed a simple empirical relationship to predict recruitment of fall chinook smolt outmigrants from spawner abundance and total annual flow. The relationship between recruitment and spawner abundance changed with annual flow and seasonal flow pattern. Under seasonal flow patterns optimal for drier years, the number of recruits reached an asymptote as spawners increased. Seasonal flow regimes optimal in wet years showed a unimodal response to spawner abundance. These wet-year flow regimes had extended periods of high flow in fall and spring. When spawner abundances were very high, the wet-year

optimal flow regime produced fewer smolt outmigrants than a drier-year optimal flow regime with considerably lower annual flow. For drier years, recruitment predictions by the more-complex ORCM model can be expressed as a simpler flow- and density-dependent equation.

INTRODUCTION

Predicting recruitment of fish populations is an important area of fisheries science. Spawner-recruitment (S-R) models were first developed to predict the sustainable harvest of abundant fish populations. Sadly, they are now used to predict the ability of small and declining fish populations to persist (Emlen, 1995; Ratner et al., 1997). I refer to the original purpose as the “harvest” paradigm, and the second as the “conservation” paradigm.

Under the harvest paradigm, density dependence was a central concern. Because populations at high densities suffered higher rates of mortality or reduced reproductive success, a proportion of the population could be considered “excess.” This portion would fail to contribute to the next generation, regardless of whether they were caught by the fishery or met with a different fate. This harvest paradigm gave birth to several models of density-dependence (Beverton and Holt, 1957; DeAngelis et al., 1993; Ricker, 1954). Under the conservation paradigm, depensation at low densities is a new concern and models that incorporate depensation are available (Crittenden, 1994; Emlen, 1995; Myers et al., 1995).

The relative importance of the environment and other factors external to the population, compared with internal population dynamics, is a long-standing issue (e.g., Jonsson et al., 1998; Peterman, 1987). Two aspects of internal population dynamics are important in predicting recruitment of fish populations: recruitment limitation and density-dependent reproductive success (Chesson, 1998). There is good evidence that salmon recruitment is positively related to spawner abundance (Myers and Barrowman, 1996), particularly at the reduced stock levels now occurring nearly everywhere. For many salmon stocks, spawning success for a given year hinges on the number of outmigrants several years previously, leading to periodic recurrence of strong year classes. However, in situations where habitat loss has curtailed spawning or incubation habitat, density-dependent limits to the response of salmon recruitment to spawner density may be reached. For anadromous salmonids, density-dependent limitation occurs during early lifestages (Crittenden, 1994; Jonsson et al., 1998). Delayed maturation caused by food limitation during the first year of ocean life has also been detected (Peterman, 1987).

Environmental factors also explain some portion of variation in recruitment, and they often mediate density-dependent effects. For example, the amount of suitable spawning habitat is often a function of river discharge or flow, with more water inundating a larger area of suitable spawning gravel. At low flows, the same number of spawners crowd into a smaller area, increasing the chance that newer redds are built on top of existing ones. Under the harvest paradigm, environmental effects are viewed as noise obscuring the density-dependent relationship of interest (Walters and Ludwig, 1981). Under the conservation paradigm, environmental effects, particularly those modified by human activities, are of equal or greater interest. River flow is a particularly important environmental factor controlling recruitment for Pacific salmon (e.g., Kope and Botsford, 1990).

Ideally, recruitment models should incorporate human and environmental influences on population dynamics. Some progress has been made in this direction. For example, Iles and Beverton (1998) illustrated modified S-R models that account for environmental factors of five kinds: controlling, limiting, lethal, masking, and directive. These relatively simple (one equation, 3 parameters) models can be fitted to empirical data.

In this study, I used the ORCM recruitment model for chinook salmon (Jager et al., 1997) to examine the interactions between spawner density and flow. I focused on total annual flow by assuming that patterns in the seasonal distribution of flow were managed according to optimal flow regimes--flow patterns identified in Part 3 that maximized the number of smolt produced by ORCM. I examined two questions. First, how does spawner density influence the seasonal pattern of flow distribution that maximizes recruitment? Second, how does total annual flow (i.e., the hydrologic year type) influence the relationship between spawner density and chinook salmon recruitment? As part of this question, I sought to summarize the recruitment response to spawner density and total annual flow predicted by the ORCM model by a simpler S-R relationship. According to Haefner (1997), one should never stop an analysis with the first model developed. Instead, a process of model simplification should be used to remove unneeded complexity. By summarizing the behavior of the ORCM recruitment model by one flow-dependent S-R equation, it becomes computationally practical to address larger issues.

PRELIMINARY RESULTS

Questions about the role of density were first raised by preliminary comparisons of S-R relationships produced by ORCM with optimal flow regimes derived at a density of 5,000 spawners. This comparison, shown below, revealed the existence of a better high-density optimal flow regime.

The number of adults returning to the Tuolumne River to spawn varied between 450 and 40,322 during the period from 1971 to 1988 (EAEST, 1992i). To evaluate the effects of spawner abundance, I used ORCM to simulate smolt production for a range of spawner abundances (2,000, 5,000, 8,000, 10,000, 15,000, 20,000, 30,000, and 40,000).

The flow regimes used in the ORCM simulations above were the optimal flow regimes developed for 5,000 spawning adults in Part 3. In these optimizations, simulated annealing varied 20, two-week periods of constant daily flow between the upstream migration of adults in fall and downstream migration of juveniles in spring. The objective was to find seasonal flow regimes that maximized the simulated number of smolt outmigrants. One optimal flow regime placed no limit on total annual flow (the "unconstrained" case). Four others constrained the total amount of water available on an annual basis to 122, 245, 489, and 979 $hm^3\ y^{-1}$ (10, 50, 100, 200 kcfs-d y^{-1}). These optimizations assumed 5,000 spawning adults, leaving open the question of how spawner abundance might alter the optimal flow regime for a given level of annual flow.

For the two optimal flow regimes for wetter years (Q_{tot} <= 978 $hm^3\ y^{-1}$ and no limit on Q_{tot}), I observed a change in the simulated S-R relationship from that observed with seasonal flows optimized under more-severe water restrictions. The number of outmigrants declined when the number of spawners was high and followed a hump-shaped relationship (Figure 1). This implies that a different optimal solution must exist for high spawner densities. Because of the downturn in the S-R relationship, the optimal flow regime for 5,000 spawners was no longer optimal for 40,000 spawners. The flow regime optimal for <=489 $hm^3\ y^{-1}$ in Figure 1 yielded more outmigrants for 40,000 spawners than did the two wetter regimes (<=978 hm^3 and no limit, arrows in Figure 1). This suggested that better solutions (flow regimes) must exist for higher densities.

METHODS

The Oak Ridge Chinook Model (ORCM)

The ORCM was developed to aid understanding of relationships between alternative patterns of seasonal flows and chinook salmon recruitment in the Tuolumne River, California (Part 2). Chinook salmon spend their adult lives in the ocean, returning to the river to reproduce (spawn) and die. Individual adults vary in the age at which they ascend the river to spawn. Precocial adults, including male “Jacks” and female “Jills” that spawn at age 2, are becoming more common. Historically, the typical ages of mature spawners varied between 3 and 5. Individuals also vary in the timing of

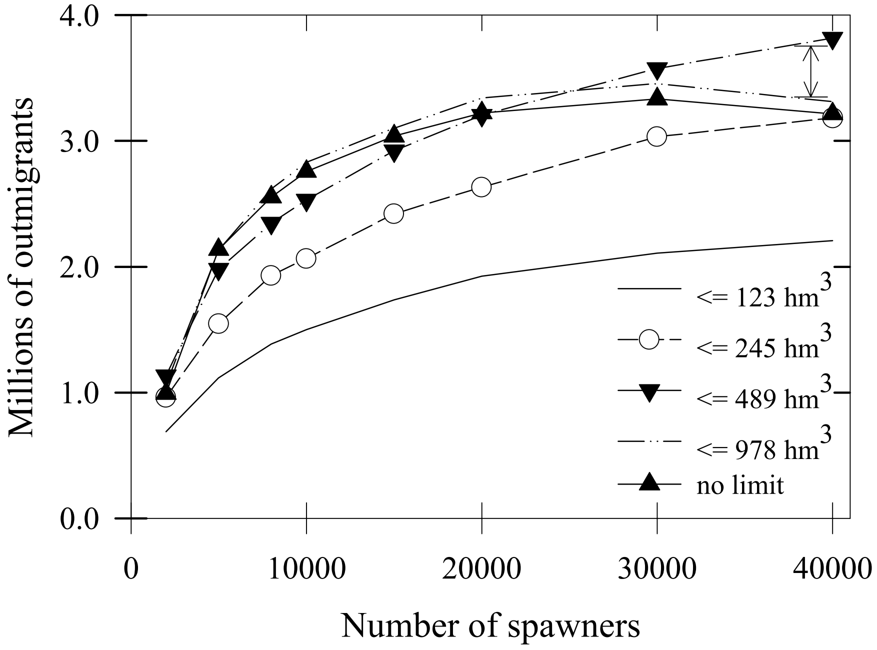

Figure 1. The shape of model-generated spawner-recruitment relationships changed in wet years under flows optimal for 5,000 spawners.

spawning. Two runs are currently present in the Tuolumne River. Adults of the fall run arrive on the spawning grounds in fall and those of the late-fall run arrive in winter and early spring. Beginning with the first arrivals in October, ORCM simulates the river phase of chinook salmon ecology juveniles migrate out of the river before mid-July of the following year. Eggs incubate through the winter and hatch as alevin (non-feeding larvae). ORCM simulates individual redds (nests) to track the development and mortality of egg and alevin life stages. These emerge from their redds as fry (pre-smolt juveniles) in spring. Chinook salmon fry live along river margins for the first month or two and emigrate during their first spring. After emergence from redds, ORCM uses a daily time step to simulate the development, growth, mortality, and movement of individual juveniles (fry and smolt), culminating in migration of juvenile smolt from the river. These events take place in a spatially explicit habitat with spatial variation in predator densities. River temperatures vary longitudinally and depend, in part, on flow. The model is provided with a specified number of adult spawners and a schedule of daily average river flows. The principal prediction of the model is the number of juvenile smolt that exit the river in spring. Jager et al. (1997) and Part 2 describe the model and present parameter values used in the simulations reported here. Linkages between environmental factors (flow and temperature), population dynamics, and recruitment are simulated in the ORCM model, which represents the riverine part of the fall-chinook life cycle (Figure 2).

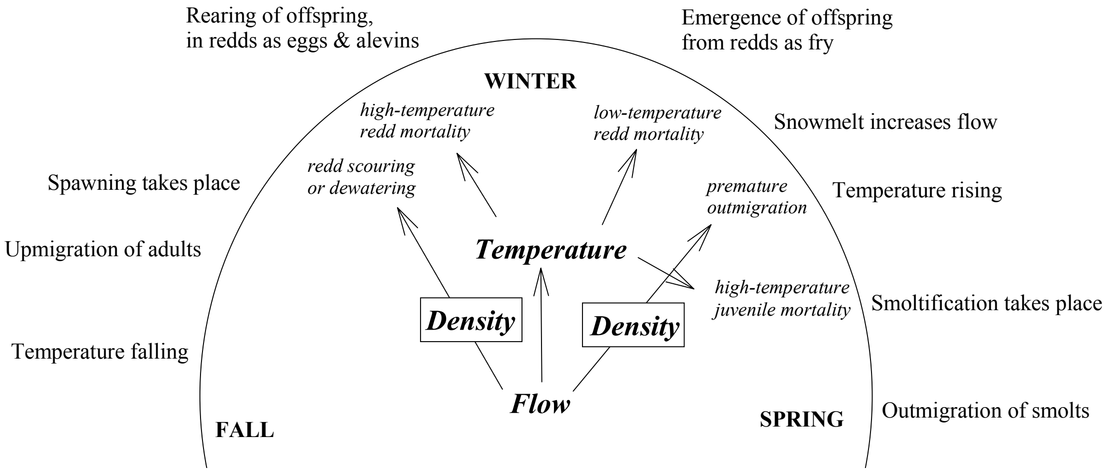

Figure 2. The riverine phase of the fall chinook salmon life history and simulated relationships linking flow, temperature, and spawner density to reproductive success.

Superimposition of redds is the best-known density-dependent factor experienced by salmonid populations. Superimposition refers to mortality of eggs dislodged by later-arriving female spawners that excavate previously constructed redds. In ORCM, the likelihood of a particular adult female re-using an existing redd site increases when the density of already-constructed redds is high and the choice of suitable sites is restricted. The availability of spawning sites is proportional to weighted usable area for incubation, which is a function of river flow.

Premature emigration is another source of density-dependent mortality. Although pulses of fry exit early in productive years, some fraction may rear successfully in the mainstem of the San Joaquin River. In ORCM, chinook salmon fry move downstream faster when feeding territories are in short supply. If the combination of flow conditions, temperatures, and juvenile densities are such that a proportion of fry salmon are unable to secure feeding stations, they continue downstream and may exit before developing into smolt.

Predation is a depensatory factor that has a smaller role in years with high juvenile densities. This is because a fixed number of predators is limited in the amount of prey it can handle. Predators can be “swamped” by dense aggregations of salmon juveniles (Peterson and DeAngelis, 1992). Simultaneous downstream movement during spring floods is believed to be a behavioral adaptation that reduces predation risk during outmigration (National Research Council, 1996). ORCM has two options for simulating predation, one simple and the other detailed. A detailed predation module simulates pairwise interactions between prey and predators, where predator densities (black bass) are higher in deeper sections of the river. Ingestion of an individual chinook juvenile prey by an individual predator depends on predator size, prey size, and stomach fullness (a function of previous meals and temperature). The simpler model uses a Type II functional response to describe the saturation of predators when prey are abundant.

How does Density Influence the Optimal Flow Pattern?

The first goal of this study was to evaluate the effect of spawner density on the optimal flow regime. Because these optimizations are time consuming, it was not feasible to do this for all levels of annual flow or all densities. In this study, I focused on the unconstrained annual flow scenario. I used simulated annealing, as before, to find seasonal flow regimes that would maximize ORCM salmon production for 40,000 adults following the procedure in Part 3. My objective was to maximize the predicted annual number of outmigrating smolt. The 20 decision variables were daily river flows for each two-week interval between upmigration in the fall and outmigration in the spring. The optimization sought daily flows, Q_i, during each time period i, to maximize $Z = F_1(Q_i)$, where Z is the number of outmigrating smolt produced by the ORCM model (F_1). I assumed that summer daily flows (after July 7) were constant and equal to 1.416 $m^3 s^{-1}$.

I compared this optimal flow regime for 40,000 spawners with the optimal flow regime for 5,000 spawners obtained in Part 3. I also compared the S-R relationships produced by both flow regimes. To clarify interactions between spawner density and optimal flow allocation in wet years, I compared mortality in simulations with 5,000 vs.

40,000 spawners, each under its optimal flow regime. The expectation is that density-dependent sources of mortality, such as superimposition and premature emigration, would be reduced by the flow regime optimized at the high spawner abundance.

How does Flow mediate the Spawner-recruitment Relationship?

To investigate how flow affects the S-R relationship, I developed an S-R model as a function of annual flow for simulated annual limits of 122, 245, and 489 hm^3 y^{-1}. I selected the Michaelis-Menton form, a modified Beverton-Holt relationship, shown in equation (1). Flow was incorporated by assuming that the carrying capacity for spawner production is an increasing function of total annual flow. ORCM generated data used to fit equation (1) to a range of simulated numbers of spawners (N_S) and outmigrant pairs. These responses were fit simultaneously to ORCM predictions obtained under seasonal flow patterns that maximized recruitment for 5,000 spawners for each of the three lower flow constraints. I used iterative non-linear regression (Marquardt, 1963), as implemented by SigmaPlot©, to estimate parameter values ($R^2 = 0.983$, S.E. = 1.14).

$$\begin{aligned} \textit{millions of outmigrants} &= \beta(Q_{tot}, N_S) = \frac{K\, N_S}{a + N_S} \\ K &= c\left(\frac{Q_{tot}}{489.4\ hm^3}\right)^b \end{aligned} \tag{1}$$

In equation (1), the asymptotic upper limit to recruitment reached when there are large numbers of spawners is K. Parameter *b* controls the shape of the relationship with relative flow. Parameter *a*, the half-saturation constant, is the spawner abundance at which recruitment attains half of its capacity.

RESULTS

How does Density Influence the Optimal Flow Pattern?

For 40,000 spawners, the unconstrained optimization obtained with 40,000 spawners reached a significantly better solution (Unc40K) than did the unconstrained optimal flow regime obtained with 5,000 spawners (Unc5K) (4,094,979 vs. 3,215,026 outmigrants). Conversely, Unc5K reached a better solution than Unc40K when both were run with 5,000 spawners (2,136,734 vs. 1,945,171 outmigrants). The Unc40K flow regime required considerably less water (1,018 vs. 1,549 hm^3y^{-1}) on an annual basis (Figure 3). High flows were concentrated in the first two weeks of October and in spring. The Unc40K optimal flow regime called for lower instream flows than did the Unc5K regime during most time periods.

The S-R relationships obtained by simulating a range of spawner abundances under each flow regime are shown in Figure 4. The Unc40K regime continues to increase with the number of spawners, whereas the Unc5K shows a slight downturn.

I compared sources of mortality with 40,000 initial spawners under the Unc5K and Unc40K flow regimes to identify factors that contribute to density-dependent mortality. Compared with the Unc5K flow regime, eggs under the Unc40K flow regime experienced higher survivorship during incubation and lower survivorship after emergence from the redd (Figure 5B). Overall, differences in survival due to mechanistic factors were slight.

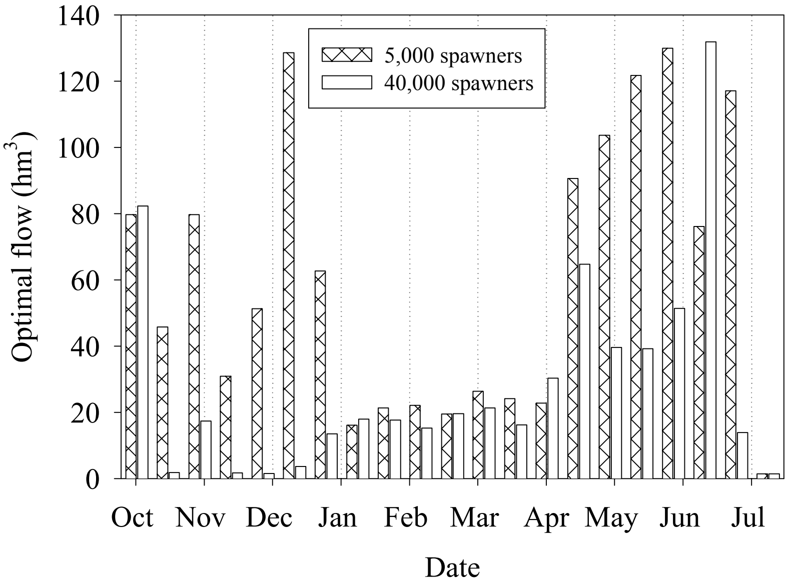

Figure 3. Optimal flow patterns in wet years (i.e., no limit on annual flow) for two spawner densities.

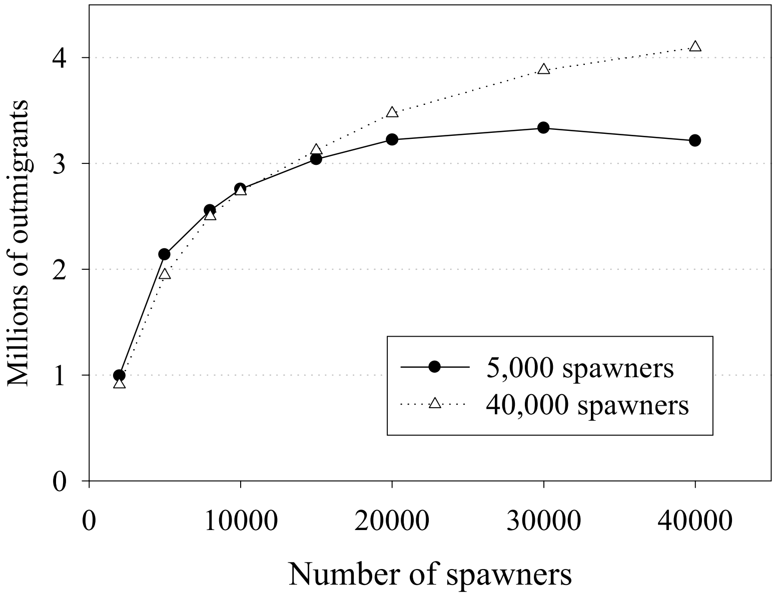

Figure 4. Simulated spawner-recruitment relationships under optimal flow regimes developed for two spawner abundances with no annual limit on flow.

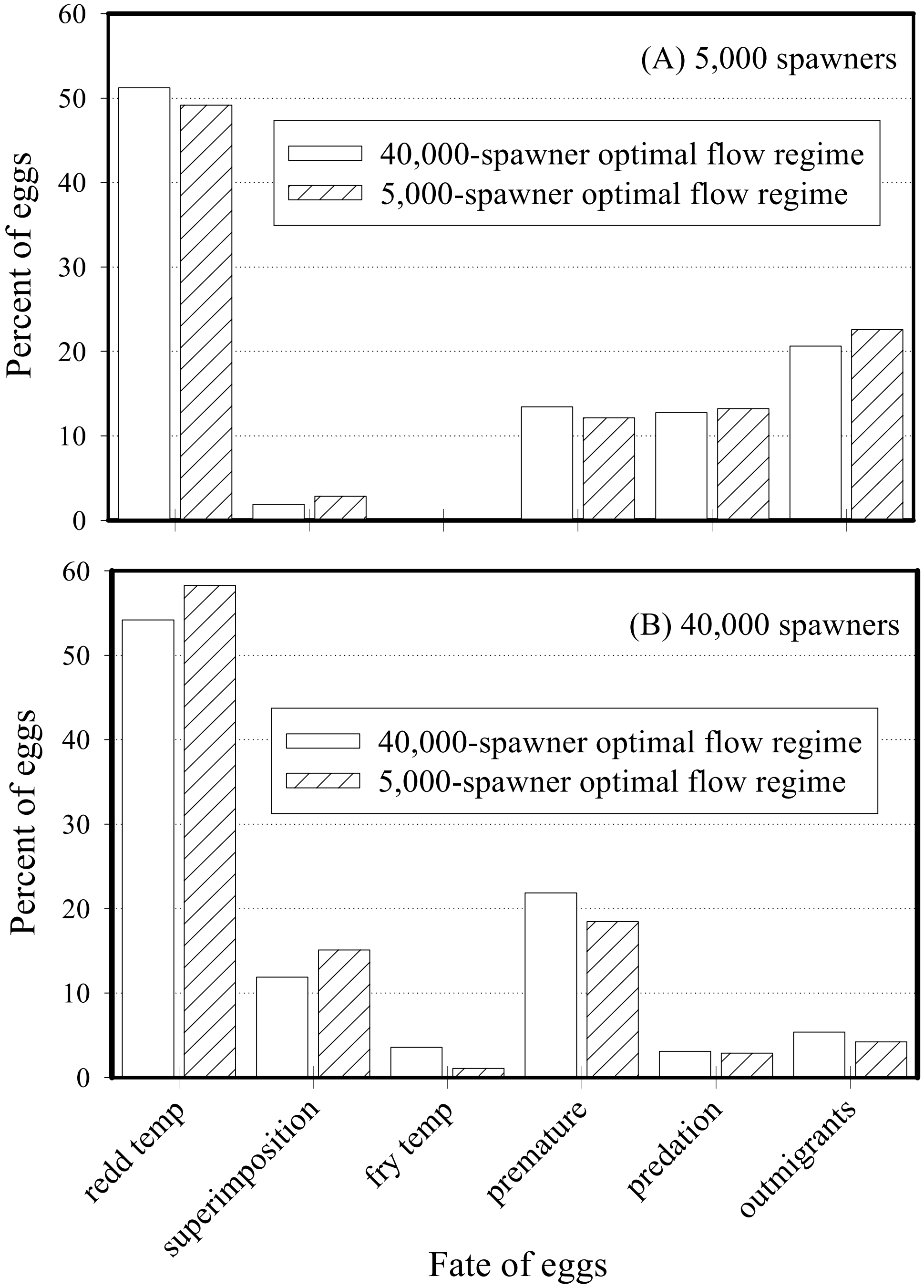

Figure 5. Simulated mortality of progeny from (A) 5,000 spawners and (B) 40,000 spawners. Each graph compares the performance of optimal flow regimes developed with no limit on annual flow under each of two spawner abundances.

Table 1. Least-squares estimates for the parameters of a flow-related spawner-recruit relationship. The T-statistic tests evaluate whether each parameter estimate is significantly different from zero. The relationship explained 98% of the variation in simulated smolt production as a function of total annual flow and the number of spawners.

Parameter	Coefficient	Standard error	T-statistic (P-value)
a	6639.23	483.88	13.72 (<0.0001)
b	0.3629	0.0189	19.19 (<0.0001)
c	44.1 million	1.08 million	40.85 (<0.0001)

How does Flow mediate the Spawner-recruitment Relationship?

For the three lowest annual flows, spawner-recruit relationships were nearly parallel with a faster rate of increase in years of higher total flow (Figure 6). All three curves were described well by equation (1) (Table 1; $R^2 = 0.983$). For these lower flows, outmigrant numbers continued to increase with spawner abundance. Outmigrant numbers were higher in wetter years regardless of the number of spawners.

DISCUSSION

Spawner-recruitment Relationships in Salmon

Studies of salmon recruitment do not clearly support one model. Even the existence of a positive relationship between recruitment and spawner abundance is not universally accepted (Peterman, 1987; Walters and Ludwig, 1981). In the most extensive survey of recruitment data reported in the literature, Myers and Barrowman (1996) found that large year classes of salmon were nearly always associated with high spawner levels.

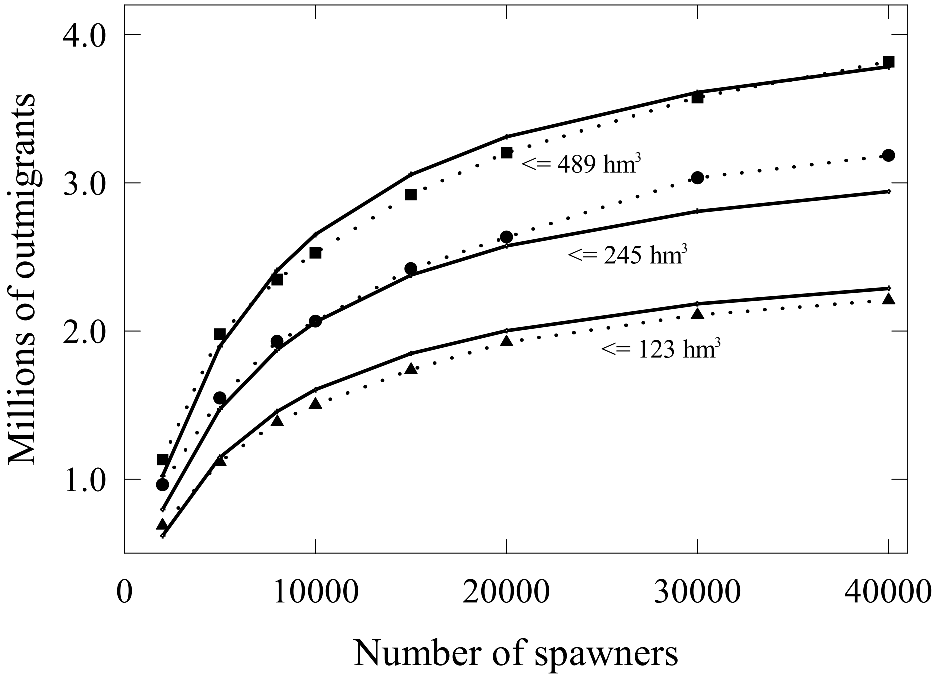

Figure 6. Relationship between recruitment and spawner abundance in the Oak Ridge chinook salmon model (ORCM) for three upper limits on annual flow. ORCM-generated predictions (dotted) are fitted by equation (1) (solid).

Considerably more disagreement exists about the density dependence acting on salmon populations, as reflected in the shape of spawner-recruitment relationships. Ratner (1997) was unable to distinguish between asymptotic and hump-shaped models based on data for spring-run chinook salmon in the Umpqua River, Oregon. Emlen (1995) included both types of density dependence for Snake River chinook salmon and he pointed out the difficulty of obtaining good estimates of parameters describing density dependence from populations at the low end of the density spectrum. Ambiguity exists even among studies of one stock. In the Central Valley, EA Engineering (1992d) suggest that the escapement data for San Joaquin chinook salmon show a clear Ricker (i.e., unimodal) S-R relationship, with an increase in recruitment to about 20,000 spawners. However, Speed (1993) was unable to discriminate between the Ricker or Beverton-Holt forms for this same stock, both fitting equally well.

The lack of statistical power associated with fitting Ricker and Beverton-Holt models and the environmental noise in the data are one likely source for these different findings (e.g., Christensen and Goodyear, 1988; Ludwig and Walters, 1981). The results presented here may also help to explain this ambivalence about the form of the stock-recruitment relationship. This modeling study found that the form of the relationship produced by ORCM depended on seasonal flow pattern. Seasonal flow patterns with extended periods of high flow in both fall and spring produced a Ricker pattern, with a slight decline in smolt production at high spawner abundances. The remaining seasonal flow patterns showed an asymptotic Beverton-Holt pattern with no decline at high spawner abundances. This suggests that different flow-release strategies should benefit recruitment in wet years with few spawners than in wet years with many spawners.

How does Density Influence Optimal Flow Pattern?

The unexpected result that lower flows were optimal in years with more spawners may not hold in years with less water available. This comparison would be interesting to repeat with a more restricted flow scenario.

When compared with Unc5k, the high-density regime, Unc40k, could be characterized as following a strategy of reducing redd mortality at the expense of juvenile mortality later in the year. Comparing the two optimal flow regimes with unconstrained annual flow, one developed with 5,000 spawners and the other with

40,000 spawners, produced another unexpected result. I expected to find that the two flow regimes differed mainly in exposure to density-dependent mortality. Instead, both density-dependent and density-independent mortality factors were important.

Comparing Figures 5A and B reveals that superimposition (redd excavation by later-arriving females) was higher at the higher spawner abundance as expected. The Unc40K flow regime experienced lower superimposition mortality during fall and winter than the Unc5K at both spawner abundances (Figure 5). Premature emigration was higher at the higher spawner abundance as expected (Figure 5). The Unc40K flow regime experienced lower premature outmigration than the Unc5K flow regime (Figure 5). The lower spring flows of this regime should retard downstream movement, suggesting that the optimization adjusted flows to minimize this density-dependent source of mortality. Predation, a depensatory mortality factor, did in fact decrease with spawner abundance in these simulations (Figure 5).

Density-independent factors, especially temperature-related mortality during incubation, were surprisingly important. The Unc5K flow regime provided extended high fall flows that may be responsible for higher temperature-related mortality in the redd when spawner numbers are high. It is interesting that a density-independent source of mortality (caused by exposure of early life stages to temperature extremes) showed the largest increase with the increased number of spawners for Unc5K. The downturn in Unc5K at the highest spawner density may therefore be caused mainly by a density-independent source of mortality. This suggests that changes in spawner abundance can produce density dependent response by shifting events associated with spawning and, thereby, exposing a larger proportion of redds to high temperatures.

A counterintuitive result suggested by this optimization is that years with fewer spawners require considerably more water on an annual basis, with extended blocks of high flow in fall and spring. If the marginal benefits gained by adding water are taken into account, different recommendations emerge for seasonal allocation of flow in wet years. Comparing the results of this study and Part 3 indicates that the optimal flow regime with 5,000 spawners and <=489 hm^3 annual flow was predicted to be nearly as good as Unc5k for years with few spawners and requires considerably less water. The Unc40k regime was predicted to be best for wet years with high spawner abundances.

How does Flow mediate the Spawner-recruitment Relationship?

Iles and Beverton (1998) derived a spawner-recruitment model equivalent to the one used here, equation (1), by treating flow as a controlling factor that influences density-independent mortality of offspring as a declining function of the environmental variable of interest. This required making some simplifications that are justified when $\{bQ/489\}$ is small, as it is here. They also derived a second, similar model by assuming that the environmental variable influenced the density-dependent term. I found that the stock-recruitment relationships derived by these two different assumptions were indistinguishable when fitted to model-generated S-R data. This is because both the density-independent and the density-dependent parameters determine the carrying capacity of this model.

The flow- and density-dependent recruitment model in equation **(1)**, with parameters estimated here (Table 1), summarizes the relationships between recruitment and two factors: annual flow and spawner density. Both total annual flow and spawner density acted similarly in that they had positive effects on recruitment, with decreasing effects at higher levels of each. At the cost of assuming optimal patterns of seasonal flow and fixed model parameters chosen for chinook salmon in the Tuolumne River, California, this simpler model can substitute for the more-complex ORCM model, as envisioned by Haefner (1997). By summarizing the behavior of the ORCM recruitment model in a single equation, it becomes practical to incorporate this equation in models that address larger issues. In particular, the simpler relationship developed here will be used to conduct a population viability analysis in Part 5.

PART 5. POPULATION VIABILITY ANALYSIS OF FALL CHINOOK SALMON IN THE TUOLUMNE RIVER, CALIFORNIA

ABSTRACT

Fall chinook salmon (*Oncorhynchus tshawytscha*) populations in the San Joaquin-Sacramento basin are considered to be at a high risk of extinction. Two anthropogenic factors thought to contribute to salmon declines are: (1) harvesting by the ocean fishery and (2) diversion of instream flows. In Part 3, I used the ORCM chinook recruitment model to identify seasonal flow regimes that maximize smolt production for different hydrologic conditions in the Tuolumne River, a tributary of the San Joaquin River. In this paper, I ask whether instream flow and harvest regulations can improve the likelihood that chinook salmon will persist for 100 years under these optimal flow regimes. I used an age-based population viability model to compare the likelihood of persistence for three levels of ocean harvesting and four levels of total annual flow. Model predictions suggest that this population has less-than-even odds of persisting to the year 2100, even if ocean harvesting is disallowed and all water is allowed to stay in the river. However, the fastest route to recovery, according to the PVA model presented here, begins by substantially reducing ocean harvesting and then reduces diversion of river flows.

INTRODUCTION

The fall chinook salmon run in the lower Tuolumne River is considered to have a high risk of extinction (Allendorf et al., 1997; Huntington et al., 1996). A high-risk stock is defined by Allendorf et al. (1997) as one with at least a 20% probability of extinction within 20 years. The Central Valley of California has the dubious distinction, among

Evolutionarily Significant Units (ESU's) along the Pacific coast, of having lost the highest percentage (40%) of its chinook salmon stocks, all attributable to construction of dams (Myers et al., 1998 pp. 7--8). The Central Valley fall chinook ESU is a candidate species for listing by the federal government. It is not considered as a stock that requires federal protection at this time (National Marine Fisheries Service, 1999)

The Central Valley Fall Chinook ESU includes geographically and temporally adjacent stocks. The ESU encompasses populations from two river basins: the Sacramento and San Joaquin. These basins owe genetic similarity, in part, to the homogenizing influence of stocking (Myers et al., 1998), although the Tuolumne River itself has had relatively little hatchery influence. Two temporally distinct runs in the Tuolumne River are encompassed by this ESU. A fall run spawns in the river between October and December; and a late-fall run spawns in the river between January and April. The late-fall run is significantly different from the fall run in the frequency of mtDNA haplotypes (Nielsen et al., 1994). A study that used ten microsatelites to evaluate genetic variation among the four remaining runs of chinook salmon in the Central Valley revealed four unique alleles in the late-fall run (J. Nielsen personal communication). Although the late-fall run is considered at greater risk of extinction than the fall run (Yoshiyama, 2000), it is not managed separately or monitored.

According to Moyle et al. (1997), the historical record of Tuolumne River fall chinook spawners shows wide year-to-year variation superimposed on an overall decline in abundance (Figure 1A). The variation shows a somewhat cyclic pattern that puts the

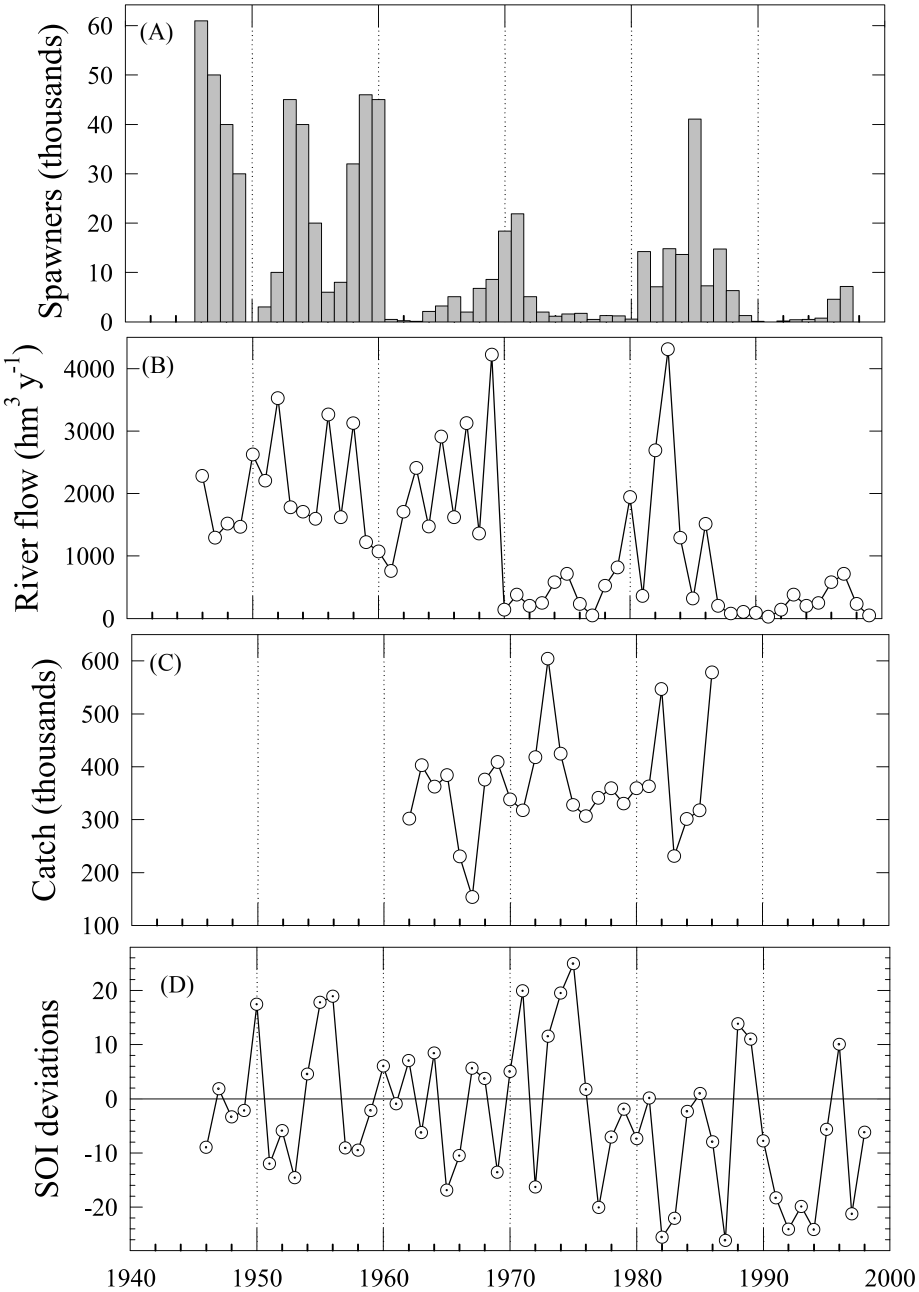

Figure 1. Four historical series: (A) spawner abundances; (B) Tuolumne River flow; (C) the ENSO index; and (D) total fishing effort.

stock at higher risk during low periods. The declining trend began more than a century ago, with near-extirpation of salmon in the 1880's caused by hydraulic gold mining and the construction of dams (Yoshiyama, 2000). Against the expectation that perhaps a new equilibrium would be established for the spawning habitat that remained below dams, the declining trend has continued. According to Yoshiyama et al. (2000), the average number of spawning adults has decreased from 23,300 in the 1950's to 1,800 in the 1990's. Myers and Barrowman (1996 p. 402) found the slope of the decline to be steeper in more recent years.

Central Valley chinook stocks bear a higher risk of extinction, in part, because they exist at the southern extreme of the species' range. Yoshiyama (1999) recounts a journal entry for February 4, 1846 by John C. Fremont: "…Salmon was first obtained on the 4th February in the To-wal-um-ne river, which, according to the Indians, is the most southerly stream in the valley in which this fish is found." Adaptations to higher temperatures are likely in these populations because higher temperatures place severe restrictions on the timing of reproduction. The window of opportunity for reproduction is brief. In fall, adults must wait until river temperatures decline to migrate upstream. The timing of the fall chinook runs in the San Joaquin basin is later, in general, than that in the Sacramento River (Myers et al., 1998). Chinook offspring must develop quickly in order to leave the river before temperatures rise again in the spring. Because marginal populations such as this one differ genetically from populations at the center of the species’ range, they make a disproportionately large contribution to the genetic diversity present in the species (Myers et al., 1998).

The degree to which various anthropogenic and natural factors are responsible for the decline of Central Valley chinook populations is controversial. Many anthropogenic factors contribute to some extent, including (1) barriers to migration posed by dam construction; (2) highly modified instream flow regimes; (3) entrainment through pumps in the Sacramento-San Joaquin delta; and (4) ocean harvesting. In addition to these factors, natural factors also contribute. For example, salmon productivity has been linked with climate cycles that decrease productivity in the California current during El Niño events (Hayward, 1997) and with drought cycles (National Research Council, 1996).

The high costs associated with reducing the impact of each anthropogenic factor, the uncertainties surrounding the effectiveness of such actions, and the potential for blaming the declines on other factors often lead to a political impasse (Lackey, 1998; Lackey, 1999). As an example of this last point, there is controversy over whether salmon declines stem mainly from changes in the river (e.g., dams, flow regulation, migration through the Delta) or changes in the ocean (e.g., harvesting, El Niño). Consumers of Tuolumne river water (e.g., for irrigation) argue that outmigrating salmon will be lost in spite of changes to instream flows as they pass the pumps in the Bay-Delta on the way to the ocean. Irrigators and utilities blame ocean harvesting, while fishermen point to water diversions and other changes in the river. Within the river part of the picture, competing water users are embroiled in political conflicts caused by the high economic value of diverting water that might otherwise be provided to salmon as instream flow (Cardwell et al., 1996; Lackey, 1999).

To address concerns about salmon declines, a federal law was enacted in 1992 requiring a management plan to double native chinook salmon populations in the San Joaquin Sacramento river basin by the year 2002 (Public Law 102-575 U.S._Congress, 1992).

> "The Secretary, in consultation with other State and Federal agencies, Indian tribes, and affected interests, is further authorized and directed to: develop within three years of enactment and implement a program which makes all reasonable efforts to ensure that, by the year 2002, natural production of anadromous fish in Central Valley rivers and streams will be sustainable, on a long-term basis, at levels not less than twice the average levels attained during the period of 1967-1991."

At this point, it seems unlikely that this goal will be met, raising the question of whether we understand what changes are needed to achieve recovery.

This study compares the relative merits of alternative recovery options. It considers the effectiveness of providing higher instream flows and reducing ocean harvest mortality as alternative paths for restoring fall chinook salmon in the Tuolumne River. A population viability analysis (PVA) model is used to predict whether some combination of river flow regulation and ocean harvesting can lead to doubling of chinook salmon production and whether it can prevent extinction within the next century.

FALL AND LATE-FALL CHINOOK SALMON LIFE HISTORY

Fall chinook salmon follow a spatial life history that encompasses three ecosystems: river, estuary, and ocean. The ocean provides habitat during late juvenile and adult life stages until they reach maturity at 2 to 5 years of age (generally younger for males than for females). Adults of the fall run migrate during fall into rivers to spawn, followed in winter by adults of the late-fall run. Fall run chinook salmon primarily use gravels of the main channel for spawning, rather than small tributaries. Eggs incubate through the winter and hatch as non-feeding larvae, known as “alevin.” Alevins develop into pre-smolt juveniles or “fry” that emerge from the river bottom in spring. Fall- and late-fall-run chinook salmon fry live along river margins for the first month or two and emigrate to the estuary and ocean during their first spring. Before entering the ocean, juveniles undergo a developmental transformation known as “smoltification” that physiologically prepares the fish to function in the marine environment.

The San Joaquin basin has been dominated by fall-run chinook for quite some time, although other runs, and even other salmon species, were historically present (Yoshiyama, 1999). Life history variation included runs or stocks that specialized on different types of habitat for spawning, as well as different spawning times. Chinook runs that historically used upstream reaches have been most affected by the construction of dams that prevent movement into cooler upstream reaches. For example, the late-fall run in the Sacramento River basin historically spawned above Friant Dam (Fisher, 1994). Because the fall run is an ocean race that minimizes its freshwater residence, it may have been less vulnerable to the high stream temperatures common during summer in the Central Valley. While the construction of dams blocking upstream movement eliminated other runs and species of salmon, the fall run, with its predisposition for getting in and out of the freshwater environment quickly, has so far been able to persist.

METHODS

The model introduced here was designed to conduct what Beissinger (1995) called an environmental-states PVA. It consists of two nested models, each linked with flow (Figure 2). A less-detailed model represents the adult ocean phase and a more-detailed recruitment model simulates the freshwater phase of chinook life history. Annual and seasonal flow regimes are also nested. A sequence of hydrologic years (e.g., wet, dry) serves as the environmental driver of the PVA model. The model generates these sequences over a 100-year time horizon. Within each year, I assumed that flow allocation among seasons followed the patterns for salmon production that I determined to be optimal for 5,000 spawners under appropriate annual flow constraint obtained in Part 3.

PVA Model

I evaluated the potential for persistence of the Tuolumne River spawning run by projecting population dynamics over 100 years for 100 replicate populations using the procedure diagrammed in Figure 2. Parameters used in the model appear in Table 1.

These projections incorporate four main sources of uncertainty:

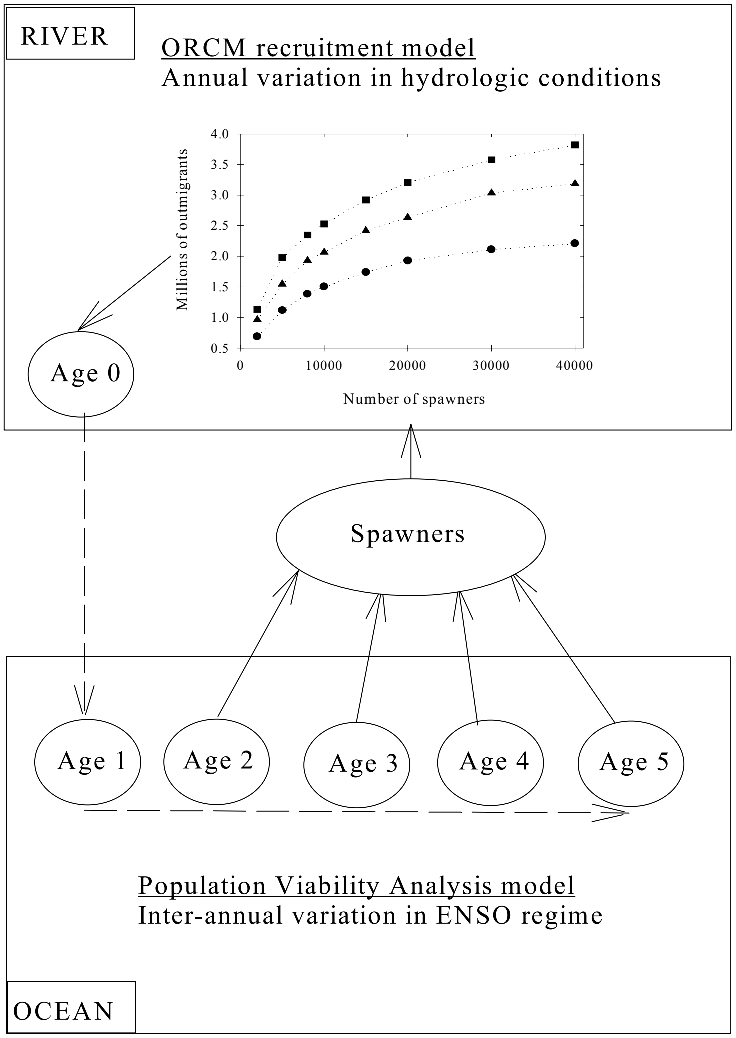

Figure 2. Flow diagram showing the approach used to forecast persistence of fall chinook salmon. The Oak Ridge chinook salmon model (ORCM) simulates production of smolt outmigrants as a function of river flow (top). The PVA model simulates population dynamics, including older life stages that reside in the ocean (bottom).

Table 1. Value, definition, source, and sensitivities for parameters of the fall chinook salmon PVA model.

Name	Parameter description	Parameter value	Std. coefficient	Source
Vs_i	Vulnerability of age i salmon to capture (sports fishing), for ages 1 to 5.	Age 1 = 0.0	0.0	(Kope and Botsford, 1990)
		Age 2 = 0.000449	-0.0137	
		Age 3 = 0.002082	-0.0481	
		Age 4 = 0.000947	0.0140	
		Age 5 = 0.001081	-0.0049	
Vc_1	Vulnerability of age i salmon to capture (commercial fishing), for ages 1 to 5.	Age 1 = 0.000030	-0.0070	(Kope and Botsford, 1990)
		Age 2 = 0.000125	-0.0091	(see text for Vc_2)
		Age 3 = 0.027676	-0.1138	
		Age 4 = 0.028027	-0.0046	
		Age 5 = 0.028739	-0.0057	
Nstock	Smolts stocked annually (calibration & sensitivity only)	50,000	-0.0297	(EAEST, 1992g)
$E[Effort_s]$	Avg. sport-fishing effort (thousand angler days)	176.176	-0.0633	(Kope and Botsford, 1990)
$SD[Effort_s]$	S.D. sport-fishing effort	46.01		(Kope and Botsford, 1990)
$E[Effort_c]$	Avg. commercial-fishing effort (thousand deliveries)	45.064	-0.1234	(Kope and Botsford, 1990)
$SD[Effort_c]$	S.D. commercial-fishing effort	10.773		(Kope and Botsford, 1990)
a	Beverton-Holt half-saturation constant	6639.23	-0.0110	Part 4
b	Beverton-Holt flow exponent	0.3629	-0.0042	Part 4
c	Beverton-Holt flow coefficient	44.10	0.0072	Part 4

Table 1 concluded.

Name	Parameter description	Parameter value	Std. coefficient	Source
β_{SD}	S.D. on recruitment, if > 0	500,000	0.0268	Part 4
Fm_i	Fraction of males reaching age i that mature at age i, i = 2 to 5.	Age 2 = 0.50	0.0712	Calibration
		Age 3 = 0.80	0.0559	
		Age 4 = 1.0	0.0	
Ff_i	Fraction of females reaching age i that mature at age i, i = 2 to 5.	Age 2 = 0.12	0.0256	Calibration
		Age 3 = 0.45	0.0703	
		Age 4 = 0.50	0.0059	
		Age 5 = 1.0	0.0	
Sout	Migration mortality in dry hydrologic years	0.1	-0.0036, -0.0268	Calibration
Sout	Migration mortality in wet hydrologic years	0.6	-0.0215, -0.2135	Calibration
E[Snat]	Average natural mortality	0.18	0.4659	(Ricker, 1976)
SD[Snat]	S.D. in natural mortality	0.14	-0.0266	Calibration
$ENSO\ R^2$	Squared correlation between age-3 natural mortality and the SOI index	0.0		Calibration

1. Variation in the numbers of outmigrants per spawner predicted by ORCM due to demographic and environmental factors;
2. Demographic variation in realized survival rates, sex ratios, and proportions of adults returning to spawn by age;
3. Environmental variation in ocean survival associated with *El Niño*—Southern Oscillation (ENSO) fluctuations in climate; and
4. Environmental variation in hydrologic conditions.

Environmental Variation

The PVA model uses two time series of autocorrelated climatic variables. One series describes temporal variation in the flow environment experienced by salmon in the river habitat and the other describes temporal variation experienced by adults in the ocean. During the river phase, I simulated year-to-year variation in hydrology as a series of hydrologic year-types generated by a Markov process. I defined four hydrologic year-types with the following ranges of annual flow: (1) 0—122 hm^3; (2) 122—245 hm^3; (3) 245—489 hm^3; and (4) >489 hm^3. These annual flow thresholds correspond to 50, 100, 200, and 400 kcfs-d y^{-1}. They were chosen to concentrate on drier conditions the ORCM model is most sensitive to (Part 3). Transition probabilities were estimated from 81 historical years of unimpaired annual flow data from the Tuolumne River (Table 2a). A U.S. Geological Survey gauge above LaGrange dam (11288000) measured riverflow for the period 1911 to 1970. For later years, (1971 to 1992) unimpaired flows were reconstructed from reservoir operations and upstream flow inputs (FERC, 1996).

Table 2. Markov transition probabilities for (a) 100%, (b) 30%, (c) 20%, and (d) 10% of unimpaired flows in the Tuolumne River.

	Range of total annual flow			
	<= 122 hm^3	122 — 245 hm^3	245 — 489 hm^3	> 489 hm^3
(a) 100% of unimpaired flows				
<= 122 hm^3	0	0	0	0
122 — 245 hm^3	0	0	0	0
245 — 489 hm^3	0	0	0	1
> 489 hm^3	0	0	0.014	0.986
Number (%) of years	0	0	1 (1.4%)	70 (99%)
(b) 30% of unimpaired flows				
<= 122 hm^3	0	0	0	0
122 — 245 hm^3	0	0	0.25	0.75
245 — 489 hm^3	0	0.087	0.348	0.565
> 489 hm^3	0	0.045	0.318	0.636
Number (%) of years	0	4 (5.6%)	23 (32.4%)	44 (62%)
(c) 20% of unimpaired flows				
<= 122 hm^3	0	0	0	1
122 — 245 hm^3	0.1	0.1	0.5	0.3
245 — 489 hm^3	0	0.194	0.387	0.419
> 489 hm^3	0	0.103	0.483	0.414
Number (%) of years	1 (1.4%)	10 (14.1%)	31 (43.7%)	29 (40.8%)
(d) 10% of unimpaired flows				
<= 122 hm^3	0.2	0.4	0.4	0
122 — 245 hm^3	0.188	0.406	0.406	0
245 — 489 hm^3	0.107	0.5	0.357	0.036
> 489 hm^3	0	0	1	0
Number (%) of years	10 (14.1%)	32 (45.1%)	28 (39.4%)	1 (1.4%)

During the ocean phase, environmental variation associated with El Niño – Southern Oscillation (ENSO) produces five to seven-year shifts in climate. I simulated these shifts by a third-order ARMA model of the Southern Oscillation Index (SOI) (Kestin et al., 1998). The white-noise error term in the ARMA model shown in equation (1) has mean zero and variance 1.505. Kestin et al. (1998) found that this simple stochastic process was able to imitate the key features of the inter-annual variability in the SOI, without any change to the background forcing.

$$\mathit{ENSO\ index}:\ X_t = 0.6885\, X_{t-1} + 0.2460\, X_{t-2} - 0.3497\, X_{t-3} + \mathit{error} \qquad (1)$$

Environmental fluctuations in ocean climate and river hydrology were simulated independently because the two series did not show much correlation between 1950 and 1990. The correlations between unimpaired riverflow and two ENSO indices, NINO3 sea-surface temperature anomalies (SST) and sea surface pressure anomalies (SOI), were -0.02 and -0.18, respectively. This is consistent with the weak relationship between California rainfall and ENSO events reported by Kope and Botsford (1990).

Model Initialization

After selecting a hydrologic year type from a probability distribution, the PVA model simulated survival of smolts as they migrate to the ocean, survival of salmon after reaching the ocean, followed by spawning and first year survival. Simulations began with an initial population consisting of 60% age-1, 30% age-2, and 5% age-3 and 5% age-4 adults. The PVA model adjusts the initial size of the ocean population to yield a specified number of initial spawners. In these simulations, the initial spawning population consisted of 18,400 adult "escapes" (individuals that successfully escaped the fishery to spawn).

The River Phase (Recruitment)

The number of adults returning to the Tuolumne River to spawn varied between 450 and 40,322 during the period from 1971 to 1988 (EAEST, 1992e). Therefore, the PVA model must be able to project the number of outmigrants produced over a range of spawner abundances. I used a flow-dependent spawner-recruitment relationship, $\beta(Q_I(t), Ns)$, to simulate outmigration over a range of spawner abundances, Ns, and hydrologic year types, Q_i. This recruitment relationship was developed in Part 4 to summarize ORCM's flow and density effects on smolt production in a simpler model. I fitted this simpler recruitment model to smolt-production "data" generated by the ORCM model with optimal flow regimes identified in Part 3 as ones that would maximize smolt production by 5,000 spawners. The overall model for annual outmigrant numbers in year t, $N_0(t)$, given $N_s(t)$ spawners is:

$$N_0(t) = \beta(Q_i(t), Ns(t)) + \beta_{SD} \qquad (2)$$

Parameter β_{SD} is the standard deviation of the average number of outmigrants predicted by ORCM. Equation (2) uses the number of outmigrants from the spawner-recruitment model given by equation (3).

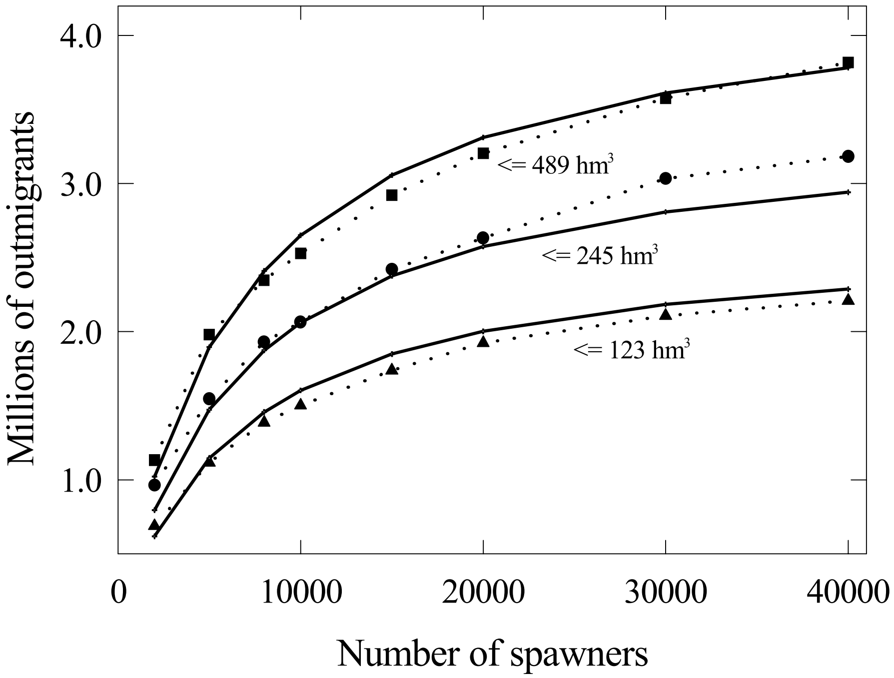

Figure 3. Relationship between recruitment and spawner abundance in the Oak Ridge chinook salmon model (ORCM) for three upper limits on annual flow. ORCM-generated predictions (dotted lines) are fitted by equation (3) (solid lines).

The fitted spawner-recruit models produced more outmigrating smolts in wetter years at all spawner densities (Figure 3). In equation (3), the number of outmigrants produced at a carrying capacity of spawners increased as the upper limit on total annual flow increased (i.e., the hydrologic year type, Q_I(t)).

$$\beta(Q_i(\mathrm{t}), N_s(t)) = \frac{c\left(\dfrac{Q_i(t)}{489\ hm^3}\right)^b N_s}{a + N_s} \tag{3}$$

The assigned value of 500,000 includes variation among replicate simulations from ORCM, error in fitting the stock-recruitment function, and other sources of uncertainty associated with our model representation of recruitment.

A recruitment model for wet years is needed because the flow-dependent spawner-recruit equation, β, did not describe the results for years with total annual flows greater than 489 hm^3. Although the spawner-recruitment relationships in wetter years did not deviate much from those under the <=489 hm^3 optimal flow regime, recruitment was somewhat higher at low spawner densities (Figure 1 in Part 4). Therefore, I fitted a separate spawner-recruit curve to ORCM predictions for the wettest hydrologic conditions that is described by equation (3) with $a = 6431.9$; $c = 45.3$; and $b = 0.0$.

Migration from the River to the Ocean

During migration from the mouth of the tributary to the ocean, smolts are exposed to many mortality risks. These risks tend to increase as river flows during outmigration decline (Morhardt and Baker, 1997). In 1987, a dry hydrologic year, the USFWS (1987) conducted a study to estimate smolt survival by releasing marked individuals in the lower Tuolumne River and in the San Joaquin River and recapturing them at Chipps Island in the Delta (Kjelson and Brandes, 1989). The results of this study suggested the following gauntlet of risks, where S is defined as survival through each stage of migration. Smolts migrate out of the San Joaquin River ($S = 0.48$), through the pumping operations in the Delta ($S = 0.36$), they are also exposed to natural mortality in the Delta ($S = 0.88$), and finally traverse San Francisco Bay ($S = 0.81$). Taken together, EA Engineering (1992b) estimates suggest that fewer than one in eight outmigrating individuals safely reached the ocean during the year of the study. In the PVA model, average survival during outmigration, *Sout*, is specified for each hydrologic year type (Table 1). The actual fraction to survive is drawn at random each year from a binomial distribution with mean *Sout*.

The Ocean Phase

The next step in the PVA model is to project the adult, ocean lifestage. This requires estimates of ocean mortality. Two main sources of ocean mortality are natural and fishing mortality. These sources of ocean survival are highly variable (Peterman, 1987).

Natural mortality

Natural sources of ocean mortality include predation by birds, fishes, and marine mammals, disease, and starvation. In addition, it has recently become evident that climatic variation plays a role in driving fluctuations in salmon abundances along the Pacific coast (Anderson, 1999; Mantua et al., 1997). The mechanisms for these correlations with climate are poorly understood, but enhanced ocean productivity associated with changes in upwelling patterns are considered an important link to the fortunes of salmon stocks. Climatic effects on California salmon show somewhat different patterns than those farther north. They show stronger correlations with five to seven year fluctuations associated the ENSO and weaker correlations with low frequency, inter-decadal scale climatic variation. Kope and Botsford (1990) found that only third-year ocean survival of Central Valley fall chinook showed a significant negative correlation (¯0.48) with ocean climatic variables that comprise the ENSO response, including an index of upwelling and sea-surface temperature.

The PVA model uses equation (4) to simulate natural survival, *Snat*(*t*) (i.e., the proportion to survive natural sources of mortality), in the ocean for each year *t*. For chinook salmon that were not age-3, the correlation with ENSO was not significantly different from zero. Therefore, substituting $R^2 = 0.0$ gave a natural mortality drawn from a normal distribution with mean E[*Snat*] and standard deviation SD[*Snat*]. For age-3 adults, natural survival of Sacramento chinook salmon was correlated (Kope and Botsford, 1990) with temporal variation in the ENSO index, X_t ($ENSO\ R^2 = 0.23$). The scaling factor, λ, is a function of year-to-year variation in natural mortality and variation in the ENSO index, Var[X_t.], which is calculated in the model. The random error, ξ, is drawn from a standard normal distribution.

$$\begin{aligned} Snat(t) &= E[Snat] + \lambda\left(ENSO\ R^2\ X_t + (1 - ENSO\ R^2)\ \varepsilon \right), \\ \lambda &= \frac{Var[Snat]}{ENSO\ R^2\ Var[X_t] + (1 - ENSO\ R^2)} \end{aligned} \tag{4}$$

Fishing mortality

Fishing mortality is the main anthropogenic factor acting on ocean survival of chinook salmon. Kope (1987) analyzed ocean mortality for chinook salmon in the Central Valley of California. He represented the fishing mortality rate for each age cohort and each type of fishing as the product of effort and vulnerability as shown in equation (5). Vulnerability to the commercial (*Vc*), and sport (*Vs*) fisheries is a function of age, *k*. The most recent estimates of vulnerabilities of adult age classes to capture and for effort are those reported in Kope and Botsford (1988).

$$Sh_k(t) = 1 - \mathrm{e}^{\{Vc_k \ Effort_c(t)\}} - \mathrm{e}^{\{Vs_k \ Effort_s(t)\}} \quad (5)$$

In the PVA model, variation in fishing effort for each of the two sources of fishing mortality is introduced for each year, *t*, by drawing effort (commercial = $Effort_c(t)$; sport = $Effort_s(t)$) from normal distributions with means and standard deviations estimated from data reported in Kope and Botsford (1988) (Table 1). Fishing mortality of age-1 salmon is treated slightly differently than that of other ages because fisheries data analyzed by Kope did not report catch of fish below the legal size threshold. Because of their relatively high abundance, age-1 fish are caught in substantial numbers and are exposed to a high (~25%) risk of mortality after release (Kimmerer and Jones & Stokes Associates, 1998). I assigned age-1 adults a vulnerability to capture in the commercial fishery that is 0.25 times the vulnerability of age-2 adults (Table 1).

The age-based model estimates the number of spawner returns annually. A realized number of female (male) spawners is drawn from a binomial distribution, $b(p, N_s(t))$ with mean proportion $p = Ff_k$ (Fm_k.). $P_{k,f}(t)$, the realized proportion of age-k salmon that are female and that return to spawn in year t, is obtained by dividing the realized number of females by the total. Finally, $P_k(t)$ is defined as the realized fraction at age k that return to spawn in year t (both male and female). The number of spawners returning in subsequent years, t, is then given by $N_s(t)$ in equation (6).

$$N_s(t) = \sum_{k=2}^{5} P_{k,f}(t)\, N_k(t) + P_{k,m}(t)\, N_k(t). \qquad (6)$$

Salmon surviving to age class t from $t-1$, equation (7), are those that did not return to spawn the previous year and that also survived both natural mortality, $Snat(t)$, and harvesting by the ocean fishery, $Sh_k(t)$.

$$N_k(t) = Snat(t)\, Sh_k(t)\, (1 - P_k(t-1))\, N_k(t-1) \qquad (7)$$

The initial average sex ratio (fraction of females) is set based on ratios reported by EAEST (1992d). In subsequent years of the simulation, the model adjusts the sex ratio of adults in the ocean, $R_k(t)$, to reflect changes caused by differences in the age at maturity. Because male and female salmon differ in the age at maturity, the average fraction spawning at each adult age *k* (parameters Fm_k and Ff_k in Table 1) differs for males and females. The ratio of females in the ocean of age *k* next year is:

$$R_{k+1}(t+1) = \frac{R_k(t) - P_{k,f}(t)}{1 - P_k(t)} \qquad (8)$$

Chinook stocks from the San Joaquin River and its tributaries mature earlier than other Californian stocks, possibly due to warmer water temperatures (Myers et al., 1998). This leads to a high fraction of precocious spawners in the Tuolumne River. Speed (1993) estimated the likelihood of spawning for each age (Table 1). He found that nearly 20% of spawners were 2-year-olds. The proportion of 2-year-old females is not well documented, although it is well-known that these so-called “Jills” are found among returning spawners in the San Joaquin River (Myers et al., 1998). Tim Heyne (Tuolumne River Restoration Project, California Department of Fish and Game, personal communication) estimated that Jills represent up to 10% of returning female spawners.

Variation in the sex ratio and the age at maturity are two main sources of demographic variability in the PVA model. The sex ratio and age composition of spawning adults in the Tuolumne River varies considerably from year to year. Between 1971 and 1988, the percentage of spawners that were female ranged from 25% to 67%. Low values occurred in years dominated by 2-y-old spawners (EAEST, 1992e). In the PVA model, both the realized sex ratio of adults in the ocean and the realized fraction returning to spawn from each age class and sex are drawn from binomial distributions with mean values listed in Table 1.

Model Calibration

I calibrated the PVA model against a historical record of spawner counts between 1946 and 1998. Functional contrasts between models and field data can be used to ensure that the model reproduces key relationships observed in nature (Jager et al., accepted). Similarly, functional calibration targets specific functional relationships in the model by adjusting the appropriate parameters. Calibration focused on four main links between free (i.e., unspecified by literature or data) parameters and correlations between model predictions and field data.

For each comparison, I simulated five replicate populations with one set of parameter values. If the fit for a particular comparison was poor, I adjusted the appropriate parameter and repeated the five simulations. In these simulations, historical records of environmental drivers replaced the previously described methods for generating future sequences of values. These drivers (Figures 1B, C, and D) included (1) the actual hydrologic year type; (2) the ENSO index, and (3) reported commercial and sport fishing effort between 1952 and 1986 (gaps were filled by the usual simulation). Another realistic feature of these simulations was a low level of stocking (*Nstock* = 50,000) after 1973. Stocking prevents simulated populations from remaining extinct if they reach zero.

First, I calibrated the parameters controlling age at maturity for each sex so that the model would produce a similar distribution of spawner ages and sex ratios to those observed in the field. During this calibration, I inflated natural survival to ensure adequate numbers of all ages. I compared the average of five age and sex distributions of spawners, at a date midway through the historical simulations, to a target distribution (EAEST, 1992b). We do not have reliable targets for 4 or 5-y-old spawners because they represent a small fraction of returning adults. Focusing on younger ages, I adjusted the fraction of ocean adults of each sex returning to spawn (Fm_k and Ff_k, age $k = 2$, 3, and 4) to obtain reasonable agreement with data.

Second, I calibrated the variation in the record of spawner returns. To do this, I first decreased average natural mortality, E[*Snat*], to obtain average numbers of spawners similar to those in the historical record. (Note that the fully calibrated PVA model will yield higher numbers, on average, because it assumes optimal seasonal flows.) I then adjusted Var[*Snat*] to obtain roughly the same variance in spawners over the historical period as was found in the historical record.

Finally, I conducted a functional calibration of two parameters against environmental drivers. I calculated the correlation between the average number of spawners among five replicate simulations and the historical record for each environmental variable from 1946-1998. I compared these model-generated correlations with the corresponding correlation between field estimates of spawners and the environmental variables of interest. Comparing correlations with the ENSO index calibrated the value of $ENSO\ R^2$. Correlations with riverflow were used to calibrate survival during outmigration, S_{out} for each hydrologic year type.

Sensitivity Analysis

Sensitivity analysis identifies parameters that have a large influence on model predictions. These parameters can then be the focus of improved measurements in the field. PRISM is a tool that has been successfully applied to a variety of population models (e.g., Jager et al., 1997; Jager et al., 1993). Parameter sets are drawn by Latin-hypercube sampling from a multivariate normal distribution with mean values in Table 1, and a 20% coefficient of variation. Transformation produces nearly independent parameters. I simulated each of 500 parameter combinations over the historical period from 1946-1998. I simulated the environmental drivers, rather than taking them from the historical record, to make use of parameters involved in projecting future environment. The standardized regression coefficient between the final number of returning spawners predicted by the PVA model and each parameter is an index of how sensitive model predictions are to changes in that parameter.

POPULATION VIABILITY ANALYSIS

The PVA experiment was designed mainly to answer the question "Will the Tuolumne River fall chinook run persist for 100 y under this management scenario?" I conducted a simulation experiment that varied management regulations controlling instream flow and ocean fishing.

The first factor considered was instream flow. I simulated four levels of flow regulation. The natural, unconstrained inflow to the Tuolumne River at the Don Pedro dam represents an upper limit to annual flow. Actual river flows are currently lower because of diversions to competing uses of water, such as irrigation and municipal water supply. The Tennant method provides simple guidelines for determining miminum in-stream flow regulations to protect riverine fishes (Tennant, 1976). According to the Tennant method, 30% of natural river flows is required to maintain a healthy fish community. A lower limit of 10% natural river flows represents an absolute minimum. In the PVA analysis, I compared unimpaired, natural flows to 10%, 20% and 30% of unimpaired flow.

The second factor varied was the intensity of ocean fishing in an attempt to address the relative importance of ocean and freshwater risks. Kope (1987) reported that the annual probability of surviving ocean fishing was 0.37 for the most vulnerable age class. I compared this level of fishing mortality with a scenario that decreased harvesting effort by 50% and a scenario with no harvesting at all.

Interest in the goals set forward by the Central Valley Improvement Act (CVIA) suggested a second question: “What is the likelihood that Tuolumne River fall chinook run will double in size by the year 2100?” The actual CVIA goal is much shorter-term: to double the natural production of anadromous fish observed between 1967 and 1991 by the year 2002. This time frame is too short for model predictions because the results would still be influenced by initial conditions. I also focused on the number of returning spawners instead of smolt production because historical records of smolt production are not available. The average number of adults returning to the Tuolumne River during this period was 15,478 (S.E. = 1891.2). In summary, I recorded the fraction of replicate simulations that predicted at least double the historical average number of returning adults by 2100, for each scenario.

The PVA simulations involved the following steps:

1. Choose a minimum flow scenario (i.e., 10%, 20%, 30%, or 100% of unimpaired, natural flows) and an ocean fishing scenario (100%, 50%, and 0% of current harvest).
2. Project future hydrology using the Markov model, with the selected percentage of flow diverted, for 100 years into the future.
3. Estimate the number of spawner returns by projecting the survival of outmigrating smolts through the adult, ocean phase of chinook-salmon life history.
4. Identify recruitment in response to seasonal flow patterns that are optimal under each year's hydrologic type.
5. Assume the seasonal flow pattern identified in Part 2 as one that maximizes the number of recruits produced by 5,000 spawners for the threshold in annual flow that serves as the upper bound on the range of annual flows that includes this year.
6. Estimate outmigrant production as a function of the number of adult spawners using the spawner-recruitment relationship obtained from ORCM in Part 3.

RESULTS

Model Calibration

The first step of calibration sought to vary parameters controlling age at maturity for each sex to match the reported distribution of spawner ages and sex ratios. Both age distribution and sex ratios match better for younger than older age classes--field data for older spawners is less reliable because they are rare. The spawner returns produced by calibrated parameter values (Table 1) followed temporal patterns more similar to those of the historical data (Figure 4) than those produced by other parameter values tested.

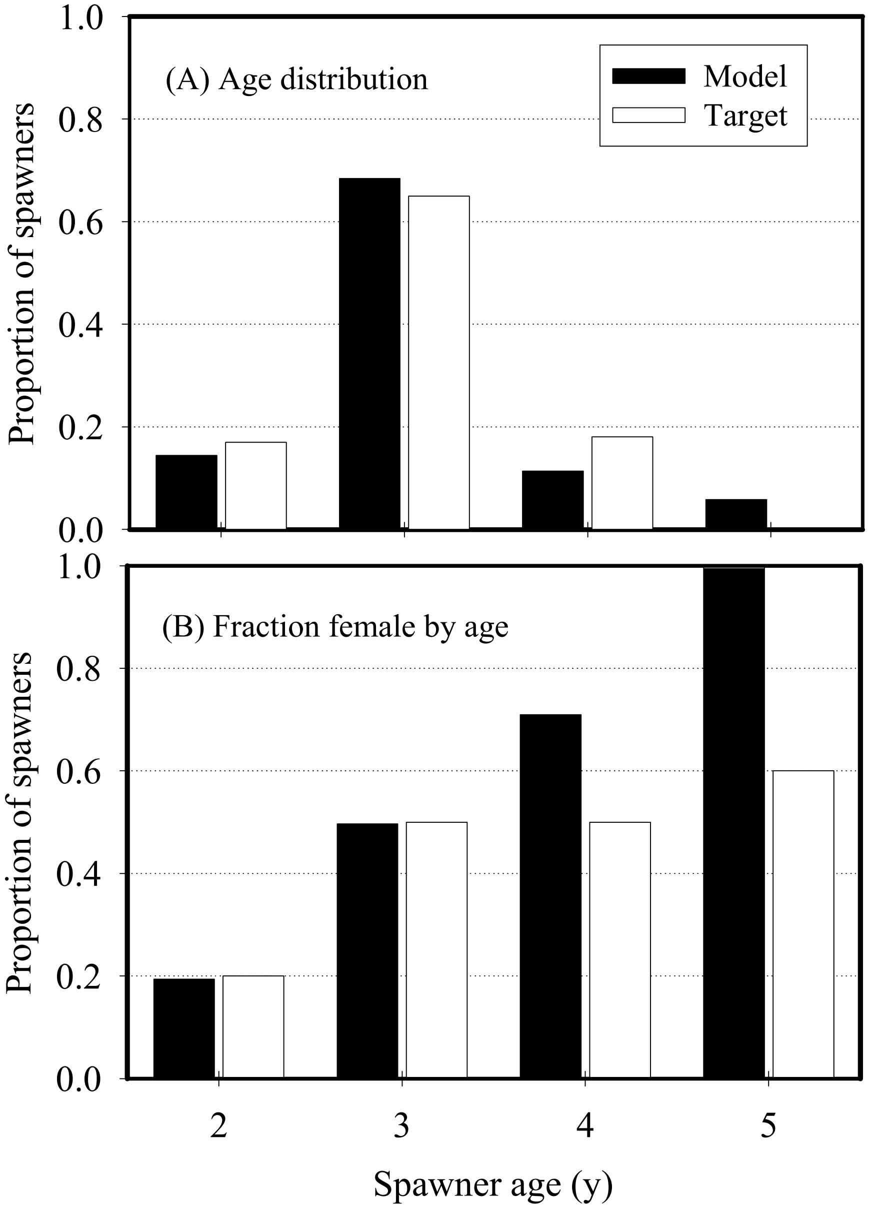

Figure 4. Simulated and target values for spawner characteristics, including (A) age distribution and (B) sex ratio (proportion female) by age.

Table 3. Functional calibration for a particular environmental variable compares its correlation with average model-simulated spawner abundance to its correlation with field-estimated spawer abundance. Comparisons reported here with no parameter name were not used to tune model parameters.

Parameter	Environmental variable	Model correlation	Field correlation
ENSO R^2	ENSO index	0.121	0.042
Sout, by hydrologic year	Annual flow	0.288	0.142
	Annual flow, lagged by 2 y	0.558	0.627
	Annual flow, lagged by 3 y	0.458	0.473
	Commercial effort	-0.549	-0.402
	Sport effort	-0.017	0.160
	Combined effort, lagged by 1 y	-0.567	-0.277

Trial-and-error changes in Var[*Snat*], *Sout*, and *ENSO* R^2 produced simulated spawner records with the model correlations with field data shown in Table 3. Because the observed correlation between field estimates of spawner abundance and the ENSO index was near zero, I turned off the influence of ENSO on ocean mortality in the PVA analysis by setting *ENSO* $R^2 = 0$. Even so, the model produced a larger correlation than observed (Table 3). The final values for *Sout* ranged from 0.1 in the two lower-flow hydrologic conditions to 0.6 under the two higher-flow conditions, values that are consistent with reported estimates.

Simulated spawning adults were usually more abundant than indicated by the historical data (Figure 5). I did not attempt to match average spawner abundance because these simulations assume optimal seasonal flow patterns that might be expected to

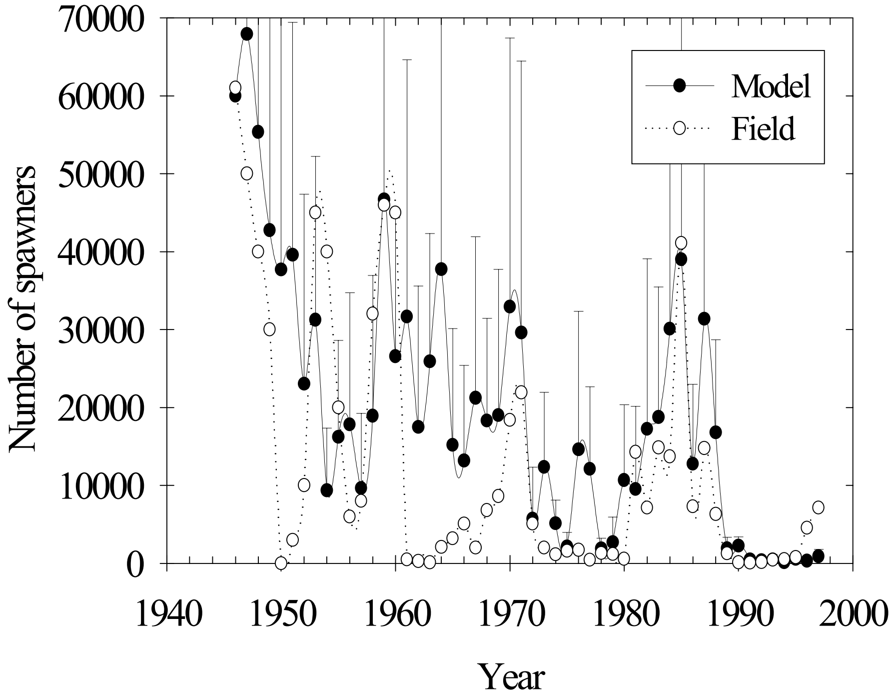

Figure 5. Comparison of historical field data with the average of five simulated records of spawner abundances. Error bars on model-simulated values indicate the variation among the five replicate simulations (+1 standard error).

produce optimistic predictions. The overall correlation between model-predicted and field estimated spawner abundance was 0.687. Predictions after 1970 (building of Don Pedro Dam) showed a stronger correlation with historical abundance (0.825) than predictions before 1970 did (0.546).

Sensitivity Analysis

Simulated final run size was most sensitive to natural mortality, followed by survival during downstream migration in wet years, average commercial fishing effort, and vulnerability of age-3 salmon to fishing mortality (Table 1). These results are typical for population models – survival or mortality rates are often the most uncertain.

Unfortunately, these parameters are often also the most important to model projections of future population size.

Population Viability Analysis

PVA results appear in Figure 6, which shows the likelihood of population persistence to 100 years with each combination of management scenarios. The projected maximum chance of persistence was just less than 50%. Under the nearest scenario to current management (30% water remaining and 100% current harvesting), the simulated chance of extinction, in the absence of stocking, over the next 20 years was 30%, suggesting that fall-run chinook salmon in the Tuolumne River meet the definition of a high-risk stock. However, these simulations do not include straying.

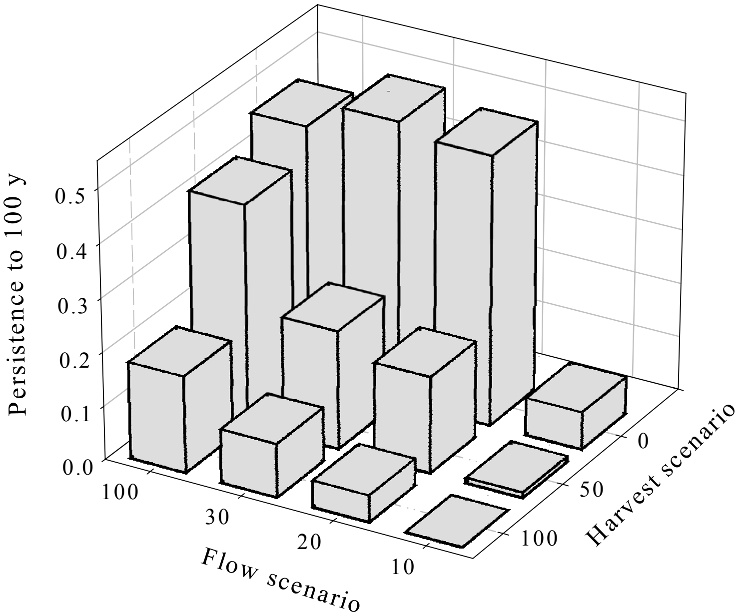

Figure 6. Simulated persistence to 100 years of fall-chinook salmon in Tuolumne River under 12 management scenarios: 10%, 20%, 30%, and 100% of natural, unimpaired flows, and 100%, 50%, and 0% of current ocean harvest. These simulations assume seasonal patterns of flow that maximized the number of recruits produced by 5,000 simulated spawners in ORCM.

There appear to be trade-offs between the two regulatory knobs, where, for example, a decrease in diversion and increase in harvest can lead to the same outcome. Because current management is near the point of 30% water remaining and 100% current harvest, moving in the direction of reduced harvest is the more profitable option. After this, either reduced diversion of flow or elimination of harvest bring the likelihood of persistence to the highest values attainable using these two factors.

Because short-term predictions for 2002 are not very reliable, I used 2100 as a longer-term, and perhaps more realistic, target. The proportion of simulations reaching this goal suggests which management scenarios (Figure 7) would most likely to lead toward recovery of spawner abundances to Central Valley Improvement Act (CVIA)

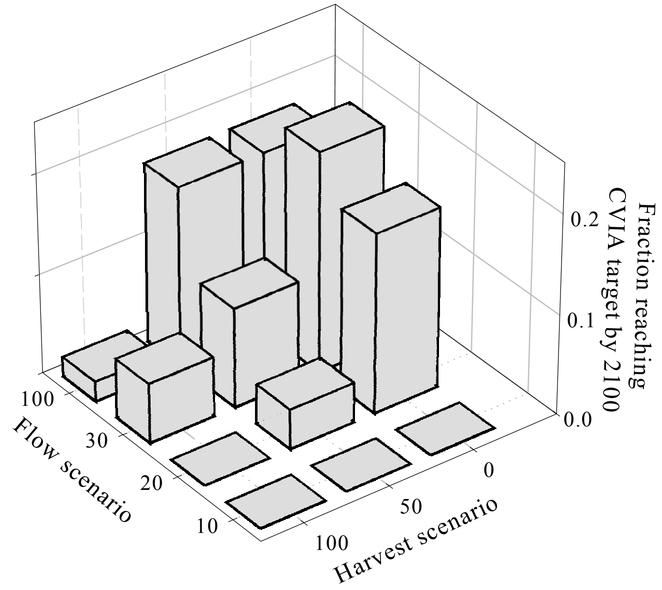

Figure 7. Proportion of simulations reaching the goal of doubling the number of adult spawners by the year 2100 under each of 12 management scenarios: 10%, 20%, 30%, and 100% of natural, unimpaired flows, and 100%, 50%, and 0% of current ocean harvest.

targets. The zero-harvesting scenarios achieved the fastest recovery and largest fraction of simulations with more than 15,478 adults that returned to spawn in 2100.

DISCUSSION

To assess the viability of Tuolumne River fall chinook salmon hardly requires a sophisticated PVA model. It is evident from Figure 1A that this population has repeatedly experienced years with very low reproduction. The duration of these events has increased to exceed the generation time of this species, which would result in local extirpation in the absence of stocking or straying of adults from nearby rivers.

A statistical approach to estimating population viability would predict extinction solely because of the negative 40-y trend in spawner abundance (Figure 1A). According to this approach (Dennis, 1989),

"It is not possible for chinook salmon populations to persist very long into the future unless the population is stable or increasing. To meet the minimal requirement for persistence, then, each female spawner must replace herself. Even if this condition is met, stochastic fluctuations in density can lead to extinction." However, even with a record over 40-years long, a statistical viability analysis focusing on population trends and variation does not seem very useful in *explaining* the patterns observed in Figure 1. First, population abundance is highly variable and cyclic. Second, the mechanisms causing the observed temporal patterns are unknown. For example, the long-term historical trend could be negative because of a lowered carrying capacity of the river environment following flow modifications after the construction of the Don Pedro dam in

1970, even though a somewhat lower, sustainable population remained. This would argue for focusing on a shorter time series by removing pre-1970 data. For other types of mechanisms, the longer the time series, the better. For example, natural shifts in climate caused by alternate series of wet and dry years can mask an overall decline (or increase) in salmon populations driven by anthropogenic trends. Such a mechanism would produce a rachet-like pattern (Lawson, 1993) with misleading short-term trends, but accurate long-term trends.

When the goal is to restore populations, a PVA model that attempts to explain the mechanisms behind observed patterns in population abundance is needed. Caughley (1994) urged conservation biologists to focus on the causes of population decline and attempts to generalize from the seemingly disparate forces acting on different populations. The functional calibration reported here was an effort to tease out the correlations between historical records of spawning salmon and environmental conditions that regulate their numbers. In this PVA analysis, I included two main anthropogenic factors (instream flow and ocean harvesting), as well as natural factors, that influence chinook salmon in the Tuolumne River. However, the uncertainty associated with predictions from this PVA model, as in others, is likely to be high (Beissinger and Westphal, 1998). Therefore, it is better to use this PVA to compare factors that influence persistence than to make absolute projections of extinction risk.

In comparing the effects of the amount of flow left in the river and ocean harvesting, both appeared to exert a strong influence on the likelihood of persistence (Figure 6). When only 10% of the flow remained in the river, the PVA model predicted certain extinction, regardless of ocean harvesting levels. To put these numbers in a realistic context, over 60% of average unimpaired flows below the Don Pedro Dam are typically diverted for irrigation and municipal water supply (FERC, 1996). At this flow level (40% remaining), the PVA analysis suggests that the fastest route to recovery would be large reductions in ocean harvest (Figure 7). Reductions in both ocean harvest and diversion of water in the river can improve the future outlook for the Tuolumne River stock, but would not ensure its survival.

These results should be taken with a grain of salt. The PVA analysis assumed no straying, which increases chances for extinction. It also assumes that instream flows are managed optimally, which decreases chances for extinction.

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PART 6. ARE WHITE STURGEON POPULATIONS DAMMED? -- VIABILITY OF WHITE STURGEON POPULATIONS IN A FRAGMENTED RIVER HABITAT

ABSTRACT

This part of the dissertation is drawn, with minor changes, from Jager, H. I., W. Van Winkle, Kenneth B. Lepla, and James A. Chandler. accepted. Are White Sturgeon Populations Dammed? -- Viability of White Sturgeon Populations in a Fragmented River Habitat, *Environmental Biology of Fishes*.

Dams fragment most of the world's large rivers. Fragmentation of the river ecosystem isolates fish populations and converts free-flowing river to reservoir habitat that is unsuitable for species that require flowing-water. In this study, an individual-based model was used to study the effects of fragmentation on the viability and genetic diversity of white sturgeon populations (*Acipenser transmontanus*). First, I simulated the fragmentation of a 200-km river reach by building one to twenty virtual dams to evaluate the effects of population isolation alone and combined with habitat loss. Increasing isolation alone produced an exponential decline in the likelihood of persistence with no clear extinction threshold to suggest a minimum viable length of river. Adding habitat loss had no additional influence on persistence until almost no free-flowing habitat remained, at which point extinction was certain. I also simulated the effects of river fragmentation on genetic diversity. As the first several dams were "built," genetic diversity shifted from within subpopulations to among subpopulations. Adding more dams caused the number of persisting subpopulations to decline, and led to erosion of genetic diversity both within and among subpopulations. In another simulation experiment, I evaluated the effects of different levels of upstream and downstream migration between river segments on population viability and genetic diversity. Higher

downstream, than upstream, rates are typical in impounded rivers. These migration experiments suggested that complete isolation poses a lower extinction risk than high rates of unbalanced migration. Both the demographic and genetic results of this study supported the view that metapopulation dynamics play a significant role in determining the long-term viability of riverine populations.

INTRODUCTION

The term "metapopulation" is used here to refer to population dynamics influenced by both within sub-population dynamics and by migration among sub-populations. The importance of metapopulation dynamics is better appreciated in terrestrial than in aquatic ecosystems. Even the term "landscape ecology" suggests that the theoretical study of organisms and their movement in a spatially heterogeneous environment is more appropriate in terrestrial, than in aquatic, ecosystems. One process that has been extensively studied with models of 2-dimensional, terrestrial landscapes is habitat fragmentation. The process of fragmentation leads to two types of landscape changes that I address here: (1) increasing the distance among patches (i.e., isolation) and (2) loss of habitat (Andren, 1994).

Demographic effects of the two types of landscape changes associated with habitat fragmentation differ. Two-dimensional landscape models suggest that extreme levels of migration (very high or none) lead to the highest risk of extinction. This suggests isolating subpopulations is detrimental. One demographic prediction from landscape models is the existence of a threshold size – a critical minimum area of habitat needed to sustain a population (Gilpin and Soule, 1986; Soule, 1980). This seductive idea stimulated both enthusiasm and controversy: enthusiasm over the important management implications for the design of reserves and controversy over whether such sharp threshold sizes actually occur in nature (e.g., Kareiva, 1990; Quinn et al., 1989). Theory suggests that the second change associated with fragmentation, loss of habitat, reduces the size of population supported and increases exposure to extinction risks associated with small populations.

In addition to these direct demographic consequences, models suggest that habitat fragmentation has adverse genetic consequences that elevate the risk of extinction (McCauley, 1993). According to theory, genetic diversity declines when alleles are lost from each population due to random genetic drift. Inbreeding among surviving adults then redistributes the remaining alleles, increasing the proportion of homozygous loci and reducing fitness. This loss of fitness further reduces population size, hastening the spiral toward extinction. Gilpin and Soulé (1986) warned that small, isolated populations risk falling into an "extinction vortex" after a catastrophe or fragmentation event. However, the dire predictions made at the scale of a single population contrast with those obtained by genetic models at the scale of the metapopulation. At a metapopulation scale, genetic models predict that the isolation of populations can increase the genetic diversity among subpopulations, in spite of the lower diversity within subpopulations (Wright, 1978). This occurs because the particular alleles lost through genetic drift differ among subpopulations.

Habitat fragmentation of large rivers is unique for two reasons. The fragmentation process is different in rivers than in other ecosystems, and it has reached a more advanced stage. Because of their important role in human society, large rivers are among the most intensively fragmented ecosystems that exist. Most large rivers in the temperate zone had already been modified by the early 1900s, leaving only tropical rivers to be studied under natural conditions (Welcomme, 1995). Dams that restrict movements of river fishes now fragment nearly every large river in the world (Welcomme, 1995).

Despite the prevalence of fragmentation in rivers, few theoretical studies have considered river fragmentation and its effect on collections of linked fish populations. This is not because spatial processes, including metapopulation dynamics, are less important in rivers. The role of straying among runs (subpopulations) of salmon that otherwise show high fidelity in the timing and location of spawning is a well-known example of a metapopulation (Li et al., 1995; Quinn and Dittman, 1990; Waples, 1995) in the strict sense of a demographic entity maintained by migration. Metapopulations of bull trout have been studied and seem to show a similar pattern, with infrequent recolonization of headwater reaches (Dunham and Rieman, 1999; Rieman and McIntyre, 1995). Although little is known about either the stock structure and among-population dynamics of most other riverine fishes, new genetic tools are beginning to reveal patterns of spatial and temporal fidelity that were previously unsuspected (e.g., Gross et al., 1994).

Regardless of whether a particular riverine fish species forms distinct local stocks or satisfies Hanski's (1991) strict definition of a metapopulation, among-population dynamics are likely to have important effects on persistence. Many fish species rely on migration to respond to predictable, seasonal changes. Different habitats are often required during different seasons and by different life stages (Poddubny and Galat, 1995; Schlosser, 1991). The size-based structure of fish communities described by Werner (1984) carries over into both longitudinal and latitudinal patterns of habitat use. In addition to the dominant longitudinal patterns of migration, many species make lateral seasonal migrations between the main channel and slackwater habitats (Junk et al., 1989; Langhurst and Schoenike, 1990; Welcomme, 1995).

The process of habitat fragmentation in rivers differs from that in other ecosystems. Man-made disturbances are often linear features (i.e. roads) or patches. In landscapes, isolation of patches is often a chance by-product of many disturbances that are independent random events. In rivers, isolation is not a chance by-product of random changes. Rather, complete fragmentation of river systems is a purposeful goal that must be achieved to realize the benefits of hydropower and flood control. In contrast to 2- and 3-dimensional landscapes, a single damming event is sufficient to complete the isolation of adjacent river segments. An analogous single-stroke fragmentation event in 2-dimensions would be the building of a racetrack dividing one population into an interior and an exterior population. Another important distinction is the directional nature of river flow. Dams are designed to control downstream flow and, by their construction, hinder upstream movement of fish more than they do downstream movement. Thus, fragmentation of rivers tends to produce asymmetric patterns of migration.

This study addresses the effects of habitat fragmentation in a large river on land-locked populations of white sturgeon, historically a wide-ranging anadromous species adapted to the large-river environment. An individual-based PVA model is used to examine the effects of river fragmentation on a series of adjacent white sturgeon populations. Table 1 lists the questions addressed by this study regarding the effects of population isolation and habitat loss on population persistence and genetic diversity. Two simulation experiments address (1) the effects of river fragmentation alone and (2) the effect of river fragmentation accompanied by habitat loss. In addition to the general theoretical questions in Table 1, the final question that I address is the relevance of these experiments to white sturgeon populations in the Snake River.

CASE STUDY -- WHITE STURGEON IN THE SNAKE RIVER

This study focuses on the white sturgeon (*Acipenser transmontanus*) in the Snake River, Idaho. Concerns about the white sturgeon stem, in part, from the declines that have been observed in other species of sturgeon and paddlefishes (Birstein et al., 1997a; Rochard et al., 1990). When rivers are impounded, migratory species, such as sturgeon, are the first to disappear (Poddubny and Galat, 1995; Welcomme, 1995). Declines in many of the 18 land-locked populations of white sturgeon in North America also raise concern (Beamesderfer and Farr, 1997; Cochnauer et al., 1985). One of these, the Kootenai population, has been listed under the Endangered Species Act (USFWS, 1994).

White sturgeon populations in the Columbia River basin historically migrated from the Columbia River estuary up into the Columbia River and farther inland into the Snake River to spawn (Brown et al., 1992b; Schaffter, 1997; Warren and Beckman, 1993). Access from the Snake River to the estuary was blocked by the construction of the first dam on the Columbia River in 1938 (Beamesderfer et al., 1995). Since that time, construction of additional dams has sequentially divided the river habitat into smaller

Table 1. This study addresses the following questions about the effects of habitat fragmentation in rivers. These questions address two categories of effects: the role of population isolation and the role of habitat loss.

POPULATION ISOLATION

1a) How does isolation of populations in different river segments influence the likelihood of population persistence?

1b) Is there a critical length of river habitat below which the likelihood of persistence suddenly declines?

2) How does isolation of populations in different river segments influence genetic diversity within and among subpopulations?

3) How do upstream and downstream migration rates influence the likelihood of population persistence?

4) How do upstream and downstream migration rates influence genetic diversity within and among subpopulations?

HABITAT LOSS

5a) How does conversion of free flowing to reservoir habitat influence the likelihood of persistence?

5b) Is there a critical length of river habitat below which the likelihood of persistence suddenly declines?

6) How does conversion of free flowing to reservoir habitat influence genetic diversity within and among subpopulations?

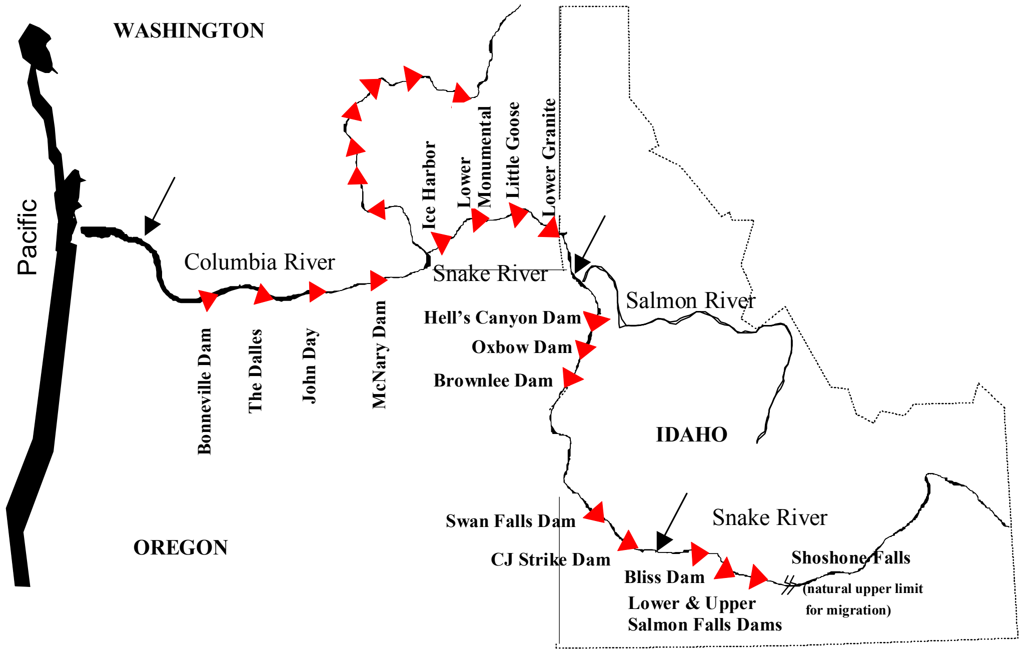


Figure 1. Fragmentation of the Columbia and Snake River system by dams. Arrows indicate three river sections with the highest levels of recruitment. (Map by Ken Lepla).

segments, many of which lack free-flowing river habitat for spawning (Figure 1). The Snake River supports at least 2 populations that appear to be doing quite well, but also 5 small populations that lack significant recruitment.

A number of factors probably contributed to the decline of some of the smaller white sturgeon populations in the Snake River. Several of these factors involve fragmentation, including population isolation and habitat loss. The next sections describe the processes of population isolation and habitat loss that are relevant to the case of white sturgeon in the Columbia River basin. In particular, I will address two habitat loss scenarios, one involving reduced reservoir survival and the other involving reduced spawning habitat.

Population Isolation

In large, impounded rivers such as the Columbia and Snake Rivers, breeding populations of sturgeon are isolated to some extent from those in other river segments by dams. Sturgeon tend to stay near the bottom of deep pools and are too large to use fish ladders as effectively as salmon do, although some ladder designs appear to work (Warren and Beckman, 1993). There is no evidence that white sturgeon in the Snake River move upstream (Cochnauer, 1983), but downstream movements by juvenile sturgeon are not uncommon (Lepla and Chandler, 1995). Compared with adult fish, juveniles are more likely to move downstream and they are more likely to escape turbine mortality.

Once populations are isolated, loss of genetic variation and inbreeding may contribute to population declines. Genetic studies of white sturgeon indicate that land- or dam-locked populations have lower genetic diversity than populations with ocean access (Bartley et al., 1995; Brown et al., 1992b).

Habitat Loss

Construction of dams on the Snake River has converted 37% of free-flowing habitat to reservoir (Cochnauer, 1983). Because white sturgeon prefer free-flowing habitat, fragmentation might reduce the viability of white sturgeon populations indirectly by removing free-flowing river habitat. Reservoir habitat provides some benefits to white sturgeon. For example, Lepla and Chandler (1995) found that individuals caught in reservoirs with good water quality were in better physiological condition than those caught in free-flowing sections of river. However, two commonly cited drawbacks of reservoir habitat for sturgeon are poor water quality and lack of turbulent flow conditions for spawning. Each of these factors is discussed below.

Reduced reservoir survival

Seasonal deterioration of water quality can be severe enough to kill fish in deep storage reservoirs that receive high nutrient loadings from the surrounding watershed (Cochnauer, 1983). This is a particular concern for sturgeon because they reside on river bottoms in deep pools or reservoirs. Episodes of anoxic conditions occur during periods of high summer temperatures, when high water temperatures limit access to shallower, but better-oxygenated, habitat. When this occurs, the reservoir habitat becomes intolerable during summer for white sturgeon and other species (White Sturgeon Planning Committee, 1992).

Reduced spawning habitat

Like most sturgeon species, white sturgeon depend on free-flowing rivers and seasonal floods for spawning (Beamesderfer and Farr, 1997; Parsley et al., 1993). Typically, spawning takes place during high spring runoff, and positive correlations between spring river flows and sturgeon recruitment have been reported in the literature (Auer, 1996b; Kohlhorst et al., 1989; Tsyplakov, 1978; Votinov and Kas'yanov, 1978). Adults form mating aggregations in fast, turbulent waters with backwaters used for staging nearby. Specific flow-related habitat requirements for spawning may serve as a mechanism that allows spawners to find each other. Reservoirs have less fast, turbulent habitat than free-flowing sections of river, potentially reducing reproductive success in reservoirs.

Several hypotheses about the adaptive role of fast, turbulent waters during spawning remain untested. High river flows may be needed to clear spawning areas (Votinov and Kas'yanov, 1978). Broadcasting demersal, adhesive eggs in fast, turbulent water might enhance egg viability by dispersing eggs and preventing clumping. Clumping, in turn, reduces the proportion of eggs fertilized, prevents aeration and waste removal, increases the incidence of fungal infection, and attracts the attention of egg predators. Turbulence associated with high water velocity might exclude visual egg predators. Finally, dispersal by flow may reduce competition among post-larval fish and provide access to a wider array of feeding areas (McCabe and Tracy, 1994).

METHODS

Model Description

I used both demographic and genetic currencies to describe simulated white sturgeon population responses to habitat fragmentation. The likelihood of persistence simulated over 1000 years measured the demographic effects of population subdivision. Genetic currencies used to measure the effects of population subdivision were (1) average heterozygosity within populations and (2) genetic diversity within and among populations.

Simulated River Habitat

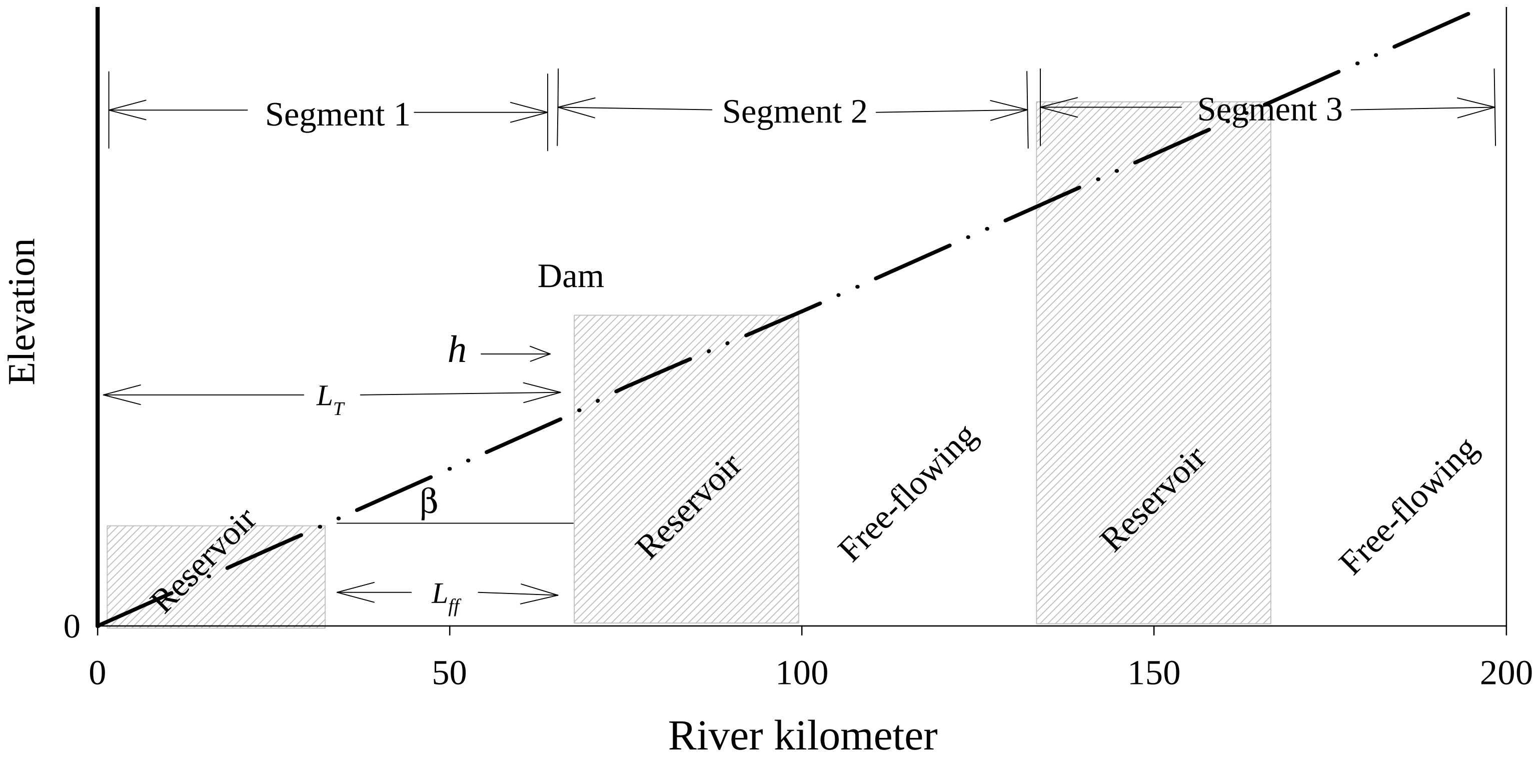
The white sturgeon PVA model represents serially linked river segments separated by dams. Spatially, the model falls in the category of a one-dimensional “stepping-stone” model (e.g., Kimura and Weiss, 1964). Each segment is divided into a reservoir portion downstream and a free-flowing portion upstream. After specifying the number of segments, the river's length is divided evenly into segments. Reservoir length is calculated as one leg of the triangle defined by dam height (h), converted to km, and river slope (β) (Figure 2). The length of each river segment that remains free flowing (L_{ff}) is the difference between the total length of the segment in km (L_T), and reservoir length, as shown in equation (1).

$$L_{ff} = L_T - \frac{h}{b}\sqrt{1-b^2} \qquad (1)$$

Founder Population

The model generates a historical founder population with ages drawn from an exponential distribution with the mean age as its parameter. Individuals entering the population draw two life history attributes from normal distributions with parameter values listed in Table 2: age at first maturity and the interval between subsequent spawning events. Other attributes (e.g., fecundity and mortality risk) vary among

Figure 2. Diagram of a typical 200-km segment of river fragmented by two dams. The length of free-flowing habitat (L_{ff}) is calculated from total segment length (L_T), dam height (h), and river slope (b).



Segment 1
Segment 2
Segment 3
Dam
h
L_T
β
L_{ff}
Reservoir
Reservoir
Free-flowing
Reservoir
Free-flowing
Elevation
0
0
50
100
150
200
River kilometer

Table 2. Information about model parameters, including name, description, value used in simulation experiments, and sensitivities. Two sensitivity indices, the standardized regression coefficient (SRC) and the relative partial sum of squares (RPSS), are given for parameters included in the sensitivity analysis.

Name	Parameter description	Baseline	SRC	RPSS
N_0	Initial population density (# km^{-1})	1.0		
A_0	Initial population average age (y)	8	0.0343	0.0004
h	Average dam height (m)	30		
β	Average slope of riverbed	0.001		
S_y	First year survival rate (y^{-1})	0.0005	0.0432	0.0006
S	Survival rate of juveniles and adults (y^{-1})	0.70	0.1239	0.0046
K	Carrying capacity of refuge from anoxic conditions (# km^{-1})	210		
lek_size	Maximum number of female spawners per km	0.5	-0.0046	0.0000
agemat_avg	Average age at first maturity for females, males (y)	18, 14	-0.1394, -0.0156	0.0062, 0.0002
agemat_SD	Std. dev. of age at maturity for females, males (y)	1.5, 1.5	0.0484, 0.0714	0.0007, 0.0016
SI_avg	Average spawning interval for females, males (y)	5, 2	-0.0462, -0.0180	0.0006, 0.0001
SI_SD	Std. dev. of spawning interval for females, males (y)	0.8, 0.3	-0.0035, 0.0479	0.0000, 0.0008
feca	Fecundity (# eggs) vs. fork length (cm) intercept	0.072	0.0347	0.0004
fecb	Fecundity (# eggs) vs. fork length (cm) exponent	2.94	0.5841	0.1297
sp_ratio	Maximum number of males per female spawner	5	0.0095	0.0001
Kvb	Change in fork length (cm) with age (y)	-0.045	-0.0687	0.0015
T_0	Initial age in Von Bertallanfy growth curve (y)	-0.795	-0.0333	0.0003
L_∞	"Maximum" size of adults (cm)	275	0.1513	0.0069
μ	Mutation rate (per generation)	10^{-5}		

individuals as a function of age or size. Populations are initialized with 8 of 32 possible alleles per locus and 10 loci. The genotype of each individual in the founder population is generated from a uniform distribution of initial allele frequencies for each locus under the assumption that loci are independent.

Individual-based Simulation

The individual-based population model operates on an annual time step. The model tracks individual attributes of white sturgeon, including age, size, sex, genetic composition, age at maturity, spawning interval, and location (river segment). During each time step, simulated sturgeon are exposed to three events: reproduction, migration, and death. I describe the simulation of these events in three sections below. All parameters referred to in the text below are listed in Table 2.

Reproduction

Simulated reproduction has four components that occur each year. First, a pool of eligible spawners is identified. Second, simulated spawning aggregations are formed. Third, the fecundity is determined for each female that successfully spawns. Finally, the model simulates the inheritance of genetic material by offspring.

The pool of eligible spawners includes all mature adults that reach reproductive readiness in a given year. The timing of reproduction is determined by the age at first maturity and the interval between spawning events. In the model, I assign these two reproductive parameters to individual fish from specified normal distributions at birth or at the start of the simulation.

White sturgeon form mating aggregations during spring. The model simulates just one aggregation in each river segment. Density-dependent limits restrict the number of female spawners allowed to join the mating aggregation, where the maximum number of spawning females is the product of the maximum density per km of river (*lek_size*) and the length of spawning habitat. When the ratio of males to females is high it is unlikely that excess males will fertilize eggs. Therefore, the sex ratio of spawning aggregations is restricted to *sp_ratio* by randomly excluding excess adult males.

The fecundity of adult sturgeon increases with size (Chapman et al., 1996; Cochnauer, 1983; Van Eenennaam et al., 1996). The model calculates the fecundity of each female in two steps. First, I estimate female length from a Von Bertallanfy relationship with parameters values (maximum length, L_{∞}, and initial age, T_0) estimated from fish in the Snake River (Lepla and Chandler, 1995). Next, fecundity is predicted from female length with parameter estimates for *feca* and *fecb* from DeVore (1995). Parameter values used in Equations (2) and (3) are listed in Table 2.

$$\{Female\ length\} = L_{\infty} \left(1 - e^{Kvb\{Female\ age\}+T_0} \right) \tag{2}$$

$$\{Number\ of\ eggs\} = feca\ \{Female\ length\}^{fecb} \tag{3}$$

After simulating egg production by females in the spawning aggregation, I simulate the inheritance of alleles by offspring. This assumes that all males in the spawning aggregation are equally likely to fertilize a given egg. At each locus, one allele is drawn from each parent at random. I assume that the white sturgeon genome is functionally diploid, i.e., that all but two alleles per locus have been silenced (Van

Eenennaam et al., 1998b). After offspring inherit alleles from each parent, mutation from the inherited allele to an adjacent one occurs randomly and infrequently (Kimura and Ohta, 1978).

Migration

To simulate migration, each individual in subpopulation *k* is assigned an annual probability, $M(k,j)$, of moving from its current river segment to each alternative segment *j* in the river. Thus, the number of sturgeon emigrating increases in proportion to population size.

Mortality

The risk of natural mortality assigned to age-0 individuals (S_y) is higher than that assigned to older individuals (S) (Table 2). In addition to natural mortality, one of the two habitat-loss scenarios that I considered represents mortality associated with poor water quality in reservoir habitat. The model assumes that free flowing river habitat serves as a refuge from this mortality and individuals able to remain in the refuge are not exposed to mortality risks associated with anoxic conditions during these episodes. The average fraction of individuals killed due to exposure to anoxic reservoir conditions, S_x, is the fraction in excess of the carrying capacity of free-flowing habitat. This fraction depends on the number of individuals in the subpopulation, N, the carrying capacity per km of river, K, and the length of free-flowing river habitat, L_{ff} as shown in equation (4).

$$S_x = min\left(1, \frac{K\,L_{ff}}{N}\right) \quad (4)$$

Sensitivity Analysis

Because there is uncertainty associated with the parameter values used in these simulations, I conducted a sensitivity analysis to evaluate the sensitivity of a model's predictions to its parameters. The analysis was conducted with the basic model (i.e., not the version set up specifically for these simulation experiments), and includes the main demographic parameters. This analysis allowed me to rank model parameters by their impact on final population size.

PRISM, a program for sensitivity analysis, has successfully evaluated parameter sensitivities of other individual-based models of fish populations (Jager et al., 1997; Van Winkle et al., 1998). The white sturgeon model was run with 5000 different parameter combinations drawn as a Latin-hypercube sample from a truncated multivariate Gaussian distribution with specified mean (baseline) values (Table 2) and a coefficient of variation of 1%. This variation is not intended to represent uncertainty in the parameters, but only to estimate the influence of varying the parameters near one point in parameter space. The algorithm ensured near-independence among parameters. Two sensitivity indices reported below are the standardized regression coefficient (SRC) and the relative partial sum of squares (RPSS). 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 standard deviations corresponding to one standard deviation 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, 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%.

DEMOGRAPHIC AND GENETIC MEASURES OF POPULATION VIABILITY

In all simulation experiments, I report one demographic and two genetic measures of viability. Model response variables represent averages from 25 replicate populations, each simulated over a period of 1000 years with the parameter values listed in Table 2. The demographic response is the likelihood of persistence to year 1000, P_{1000}. Persistence is defined in this study as the ability of white sturgeon populations to recover from a catastrophe. I simulate a catastrophe by starting with a population density low enough that demographic uncertainty may prevent recovery. Demographic uncertainty in these simulations can result from variation in the age structure and reproductive life history parameters of individuals in the initial populations and from random deaths.

As my genetic response variables, I report two indices describing change in the genetic diversity of neutral markers within and among subpopulations. The first index is average heterozygosity, a commonly measured index of genetic diversity within subpopulations. An individual's heterozygosity measures the fraction of gene loci that have two distinguishable alleles. For each subpopulation, H is the average heterozygosity over individuals as well as loci. H_I, the average H over subpopulations, is the probability of heterozygosity of any one gene drawn from the combined subpopulations. Because the simulated subpopulations are random mating, $H_I \approx H_S$, the probability of heterozygosity of a gene drawn from an equivalent random-mating subpopulation.

The second index, G_{ST}, quantifies the effects of population subdivision on inbreeding and reflects the genetic differentiation among subpopulations (Nei, 1973). This is an extension of the hierarchical F-statistics to the case of multiple alleles.

$$G_{ST} = \frac{H_T - H_S}{H_T} \qquad (5)$$

H_T is the probability of heterozygosity of a gene drawn from an equivalent random-mating *total* population. Because mating is random in these simulations, population subdivision is the only factor contributing to inbreeding -- G_{IS} is always near zero and $G_{IT} \approx G_{ST}$. In my simulations, both genetic drift and the chance occurrence of different mutations in subpopulations can increase diversity among subpopulations. I report the percent change in the two indices above from the start to finish of the simulation, with a standard error reflecting variation among replicates.

SIMULATION EXPERIMENTS

Fragmentation Experiment without Habitat Loss

I designed the first simulation experiment to address the first three questions about the effects of population isolation on demographic and genetic attributes of populations (questions 1a-, 1b, and 2 in Table 1). I simulated fragmentation of a 200-km river habitat into segments created by building 1 to 20 virtual dams. The length of the river segments, L_T, ranged from 200 to 5 km as I added dams.

Fragmentation Experiment with Habitat Loss

The second experiment addressed the three questions (5a, 5b, and 6 in Table 1) associated with habitat loss. In the habitat-loss scenarios, I introduced the effects of reduced habitat quality following impoundment on white sturgeon persistence. The first scenario evaluated the effect of reduced spawning habitat, and the second scenario evaluated the effect of reduced water quality. These two scenarios contrasted habitat losses that influence demography through reproductive parameters with habitat losses that act through survival parameters.

The methods for the two habitat loss scenarios mirrored those of my simulations of fragmentation alone described above. I varied the number of dams placed within a river having a total distance of 200 km. Unlike the simulations without habitat loss, these simulations distinguished between free-flowing and reservoir habitat. In simulations that did not consider loss of spawning habitat resulting from fragmentation, the length of spawning habitat was the total length of the river segment (L_T in Figure 2). To simulate the changes in the quantity of spawning habitat with fragmentation, I replaced L_T with L_{ff}, the length of free-flowing habitat. I simulated the mortality due to anoxic reservoir conditions, with free-flowing habitat serving as a refuge, equation 4.

Migration Experiment

The third simulation experiment addressed questions about isolation effects on demographic and genetic population attributes (questions 3 and 4 in Table 1). In the migration experiment, I simulated different rates of downstream and upstream migration (10^{-1}, 5×10^{-2}, 4×10^{-2}, 3×10^{-2}, 2×10^{-2}, 10^{-2}, 10^{-3}, 10^{-4}, 10^{-5}, 10^{-6}, and 0 yr^{-1}). I simulated all combinations with upstream migration rate less-than-or-equal-to the downstream rate.

RELEVANCE TO SNAKE RIVER POPULATIONS

I am interested in the potential role of fragmentation in explaining observed densities of white sturgeon populations among segments of the Snake River. Although eight river segments was too small a sample size for a rigorous quantitative analysis, I plotted a comparison between observed population estimates and length of free-flowing habitat.

RESULTS

Sensitivity Analysis

Sensitivity analysis results showed that the model was most sensitive to the exponential rate of increase in fecundity, *fecb*, with fish size (Table 2). Fortunately, this is a parameter that has been well-estimated for Columbia River populations (DeVore et al., 1995). The model was also sensitive to values of the Von Bertallanfy parameter for maximum adult size, L_∞, juvenile and adult survival, S, and the average female age at maturity, *agemat_avg*. Among these, survival is the most uncertain.

Fragmentation Experiment without Habitat Loss

Demographic Effects

In simulations with no migration or habitat loss, the average likelihood of subpopulation persistence to 1000 y (P_{1000}) decreased from near 1 to near 0 with progressive fragmentation of the river (open circles in Figure 3). The exponential pattern of decline did not suggest a particular minimum length of river habitat as a threshold. A small fraction of replicate subpopulations persisted even in very short segments of river.

Genetic Effects

Average heterozygosity within isolated, fragmented subpopulations decreased with fragmentation as expected (open circles in Figure 4A). However, the genetic diversity among subpopulations (G_{ST}) increased initially as expected (open circles in Figure 4B), but then decreased in an erratic fashion.

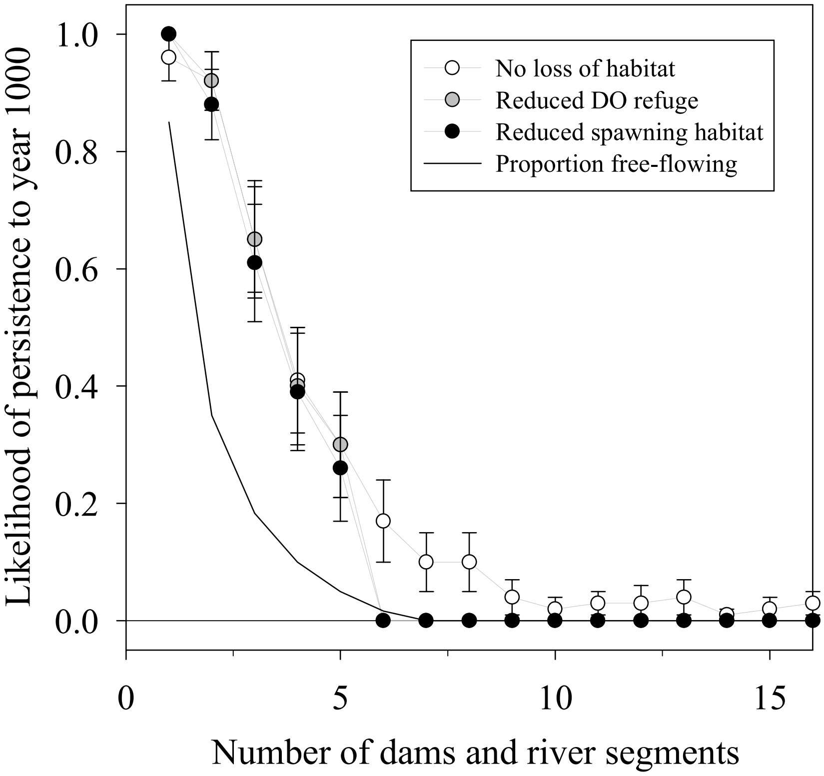


Figure 3. Increased fragmentation of the river habitat caused a decrease in the average likelihood of subpopulation persistence 1000 years into the future, P_{1000}. Results are shown for simulations with no loss of habitat and for two habitat-loss scenarios. Circles indicate the average of P_{1000} over subpopulations and error bars show the standard error in P_{1000} among replicate simulations, averaged over subpopulations.

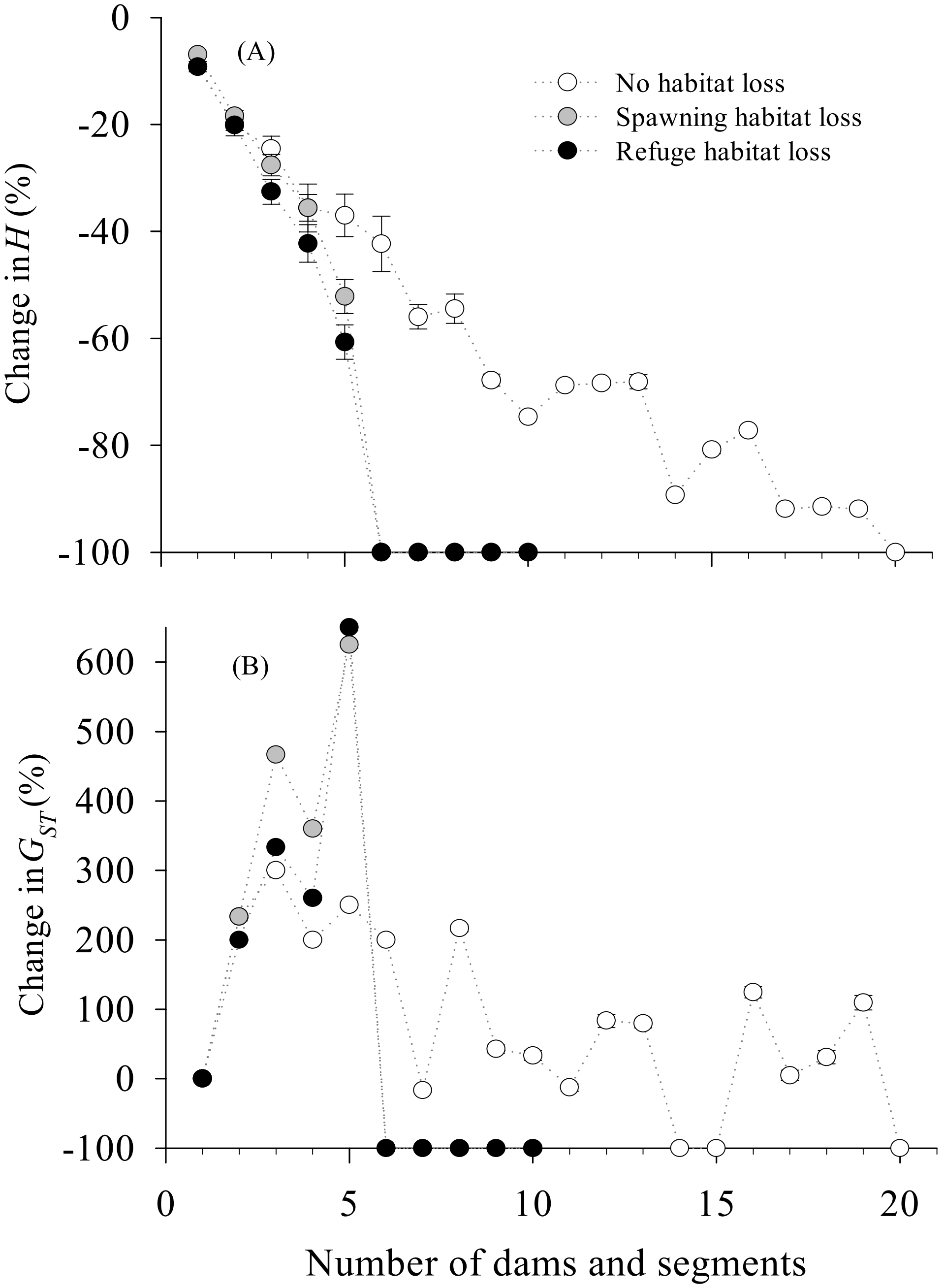


Figure 4. Simulated effects of river fragmentation on genetic diversity: A) change in average heterozygosity (H) within subpopulations from an initial value of 0.87 and B) change in Nei's index for genetic diversity among subpopulations (G_{ST}). Error bars show 1 S.E..

Fragmentation Experiment with Habitat Loss

Demographic Effects

The two habitat-loss scenarios gave similar predictions. Both reached certain extinction when 6 or more dams fragmented the river (Figure 3). This level of fragmentation nearly eliminated free-flowing river between dams. Up to this point, neither habitat-loss scenario showed significantly different behavior from the fragmentation scenario without habitat loss (Figure 3).

Genetic Effects

I can only compare the two genetic response variables for up to 6 dams or segments because the populations reached extinction at this point in each of the two habitat-loss scenarios. Habitat loss amplified the genetic effects of population subdivision. Within subpopulations, heterozygosity declined faster as fragmentation increased in the two habitat-loss scenarios (Figure 4A). Among subpopulations, genetic diversity, G_{ST}, increased faster with fragmentation in the habitat-loss scenarios than it did in the scenario with no habitat loss (Figure 4B).

Migration Experiment

Demographic Effects

I observed two general results. First, migration increased the likelihood of persistence of the recipient subpopulation at the expense of the donor subpopulation (Figure 5A). In the absence of upstream migration, adding downstream migration lowered the likelihood of persistence (P_{1000}) for the upstream river segment and raised

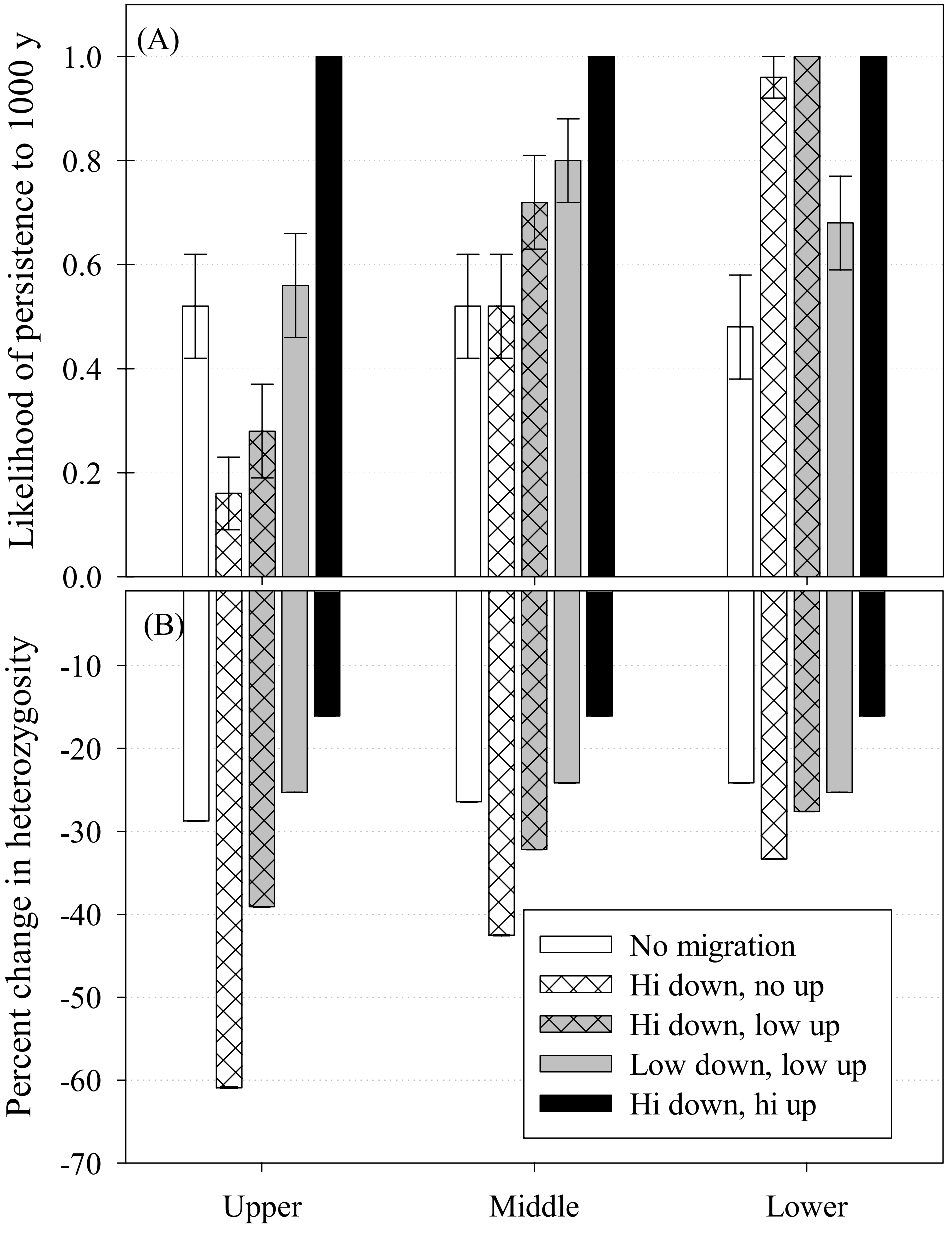


Figure 5. Subpopulations in three connected river segments with various combinations of upstream and downstream migration rates are compared with respect to (A) the likelihood of persistence and (B) percent change in average heterozygosity. Error bars are 1 S.E.. The low rate is 1 x 10^{-5} y^{-1} and the high rate is 0.03 y^{-1}.

P_{1000} for the segment farthest downstream (open vs. open, cross-hatched bars in Figure 5A).

The second result is that asymmetry between upstream and downstream migration rates lead to high extinction risk in the source subpopulation. Under high rates of downstream migration (striped bars in Figure 6A), chances for persistence in the middle subpopulation improved as the rate of upstream migration increased to match the downstream rate. When upstream migration was blocked, downstream migration rates greater than 0.001 y^{-1} decreased both the likelihood of persistence and the average heterozygosity in upstream river segments (grey bars).

In the middle subpopulation, P_{1000}, was highest when up and downstream rates of migration were nearly equal (the plateau along the diagonal in Figure 7A). Only when upstream and downstream migration rates were similar is a rescue effect observed -- an increased chance of subpopulation persistence resulting from moderate levels of migration -- in a centrally located river segment (Figure 7A). Extremely low or high rates of migration diminished the likelihood of persistence – in the absence of migration $P_{1000} = 0.53 \pm 0.10$.

Genetic Effects

Increasing migration rates produced three changes in genetic diversity. First, when comparing migration scenarios for a series of three river segments, upstream subpopulations simulated with downstream migration lost more genetic diversity than downstream subpopulations over the 1000-year simulation (Figure 5B). In contrast, isolated subpopulations, and those at the downstream end of the river system retained more genetic diversity.

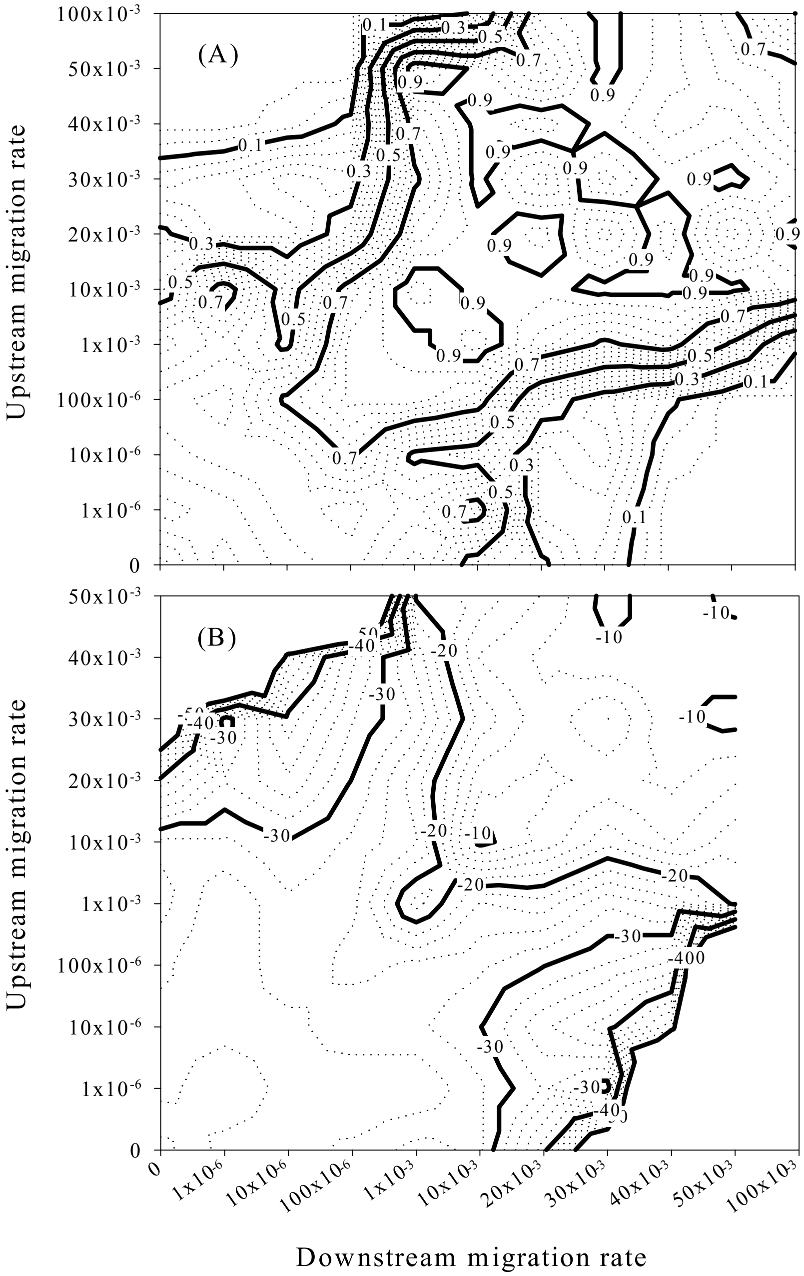


Figure 6. Downstream and upstream migration rates are fixed in turn to examine the effect of the other rate on (A) the likelihood of persistence and (B) loss of heterozygosity in the middle subpopulation of three connected river segments, each with 1 S.E. error bars.

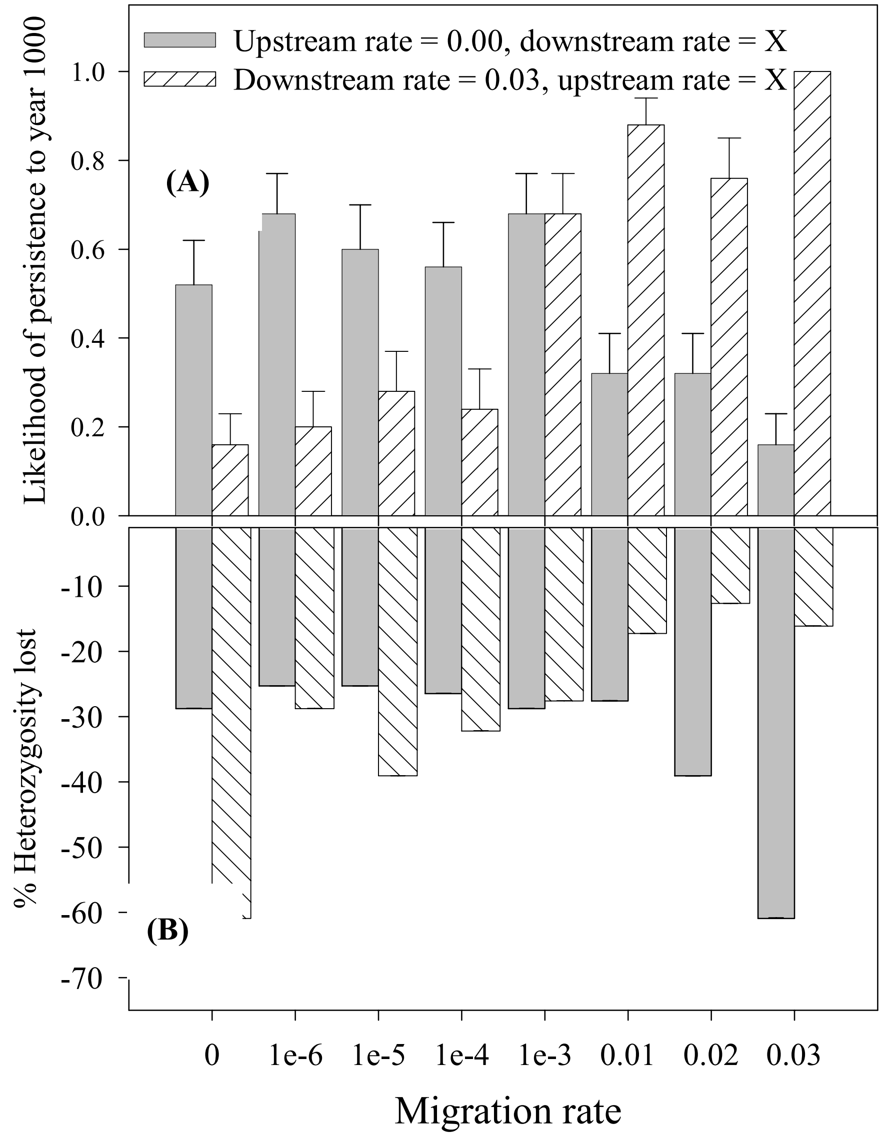


Figure 7. Contours of (A) the likelihood of persistence, P_{1000}, and (B) change in average heterozygosity, *H*, simulated for the middle section of river are shown for various downstream and upstream migration rates.

Second, asymmetry between up and downstream migration rates caused high loss of heterozygosity within subpopulations (bottom, right and top, left corners of Figure 7B). Simulations with no upstream migration illustrate the effects of unopposed downstream migration (solid bars in Figure 6B). I found that erosion of *H* increased as the rate of downstream migration increased. Those simulations with moderately high downstream migration rates illustrated the effects of upstream migration (striped bars in Figure 6B). Even a low annual rate of upstream migration (e.g., 10^{-6} y^{-1} in Figure 6B) helped to retain within-population genetic diversity in upstream subpopulations.

Third, for simulations with symmetric upstream and downstream rates of movement between populations, those with high rates showed the least erosion of heterozygosity (top, right corner of Figure 7B).

Relevance to Snake River Populations

The amount of free-flowing habitat appears to influence the ability of these river segments to support remnant white sturgeon populations in that no very short segments support measurable populations (open circles in Figure 8). However, two river segments support smaller populations than expected from the amount of free-flowing habitat, possibly because other factors limit population size.

DISCUSSION

Here, I discuss how the results of the simulation experiments addressed each of the study's questions listed in Table 1. The first set of questions pertains to the effects of fragmentation operating through population isolation and the second set pertains to the effects of fragmentation that operate through habitat loss.

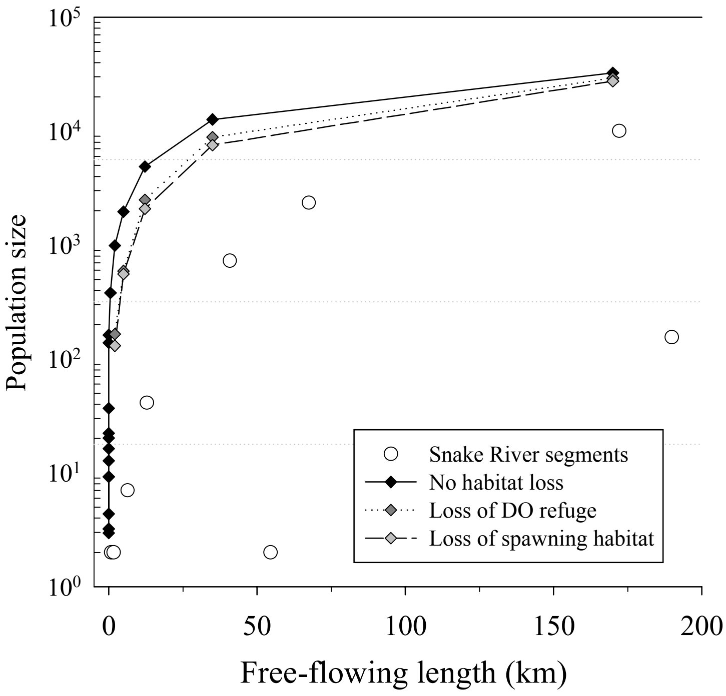


Figure 8. Population estimates for each of eight Snake River segments generally seem to increase with the length of free-flowing habitat. To allow inclusion of segments with such small population that no reliable estimates are possible, I assigned a value of two fish. Three curves describe the average, final population size of simulations in each of three fragmentation experiments as a function of free-flowing river length.

Population Isolation

How does isolation of populations in different river segments influence the likelihood of population persistence?

Two of the simulation experiments address this question. First, my fragmentation experiment without habitat loss suggests that one large segment has a better chance for persistence than many small segments do. This result is similar to those of 2-dimensional landscape models (e.g., Burkey, 1988). Second, the migration experiment showed an increase in the likelihood of persistence for an interior river segment at intermediate levels of migration, but only if the rates of upstream and downstream migration were roughly equal.

How does isolation of populations in different river segments influence genetic diversity within and among subpopulations?

In simulations of isolated populations that experienced habitat loss, fragmentation produced the expected response, shifting genetic diversity from within to among subpopulations according to Wright's (1978 and earlier) shifting balance theory. In simulations without habitat loss, among-population diversity, G_{ST}, did not increase as expected. G_{ST} was influenced by the number of subpopulations remaining at the end of the simulations, which initially increased with fragmentation, but then decreased as more subpopulations reached extinction. This result highlights a potentially important interaction between demography and genetics that is neglected by purely genetic models (Whitlock, 1992) and by purely demographic models.

How do upstream and downstream migration rates influence the likelihood of population persistence?

Two-dimensional metapopulation models suggest that moderate levels of migration can substantially increase metapopulation persistence through "rescue effects" (Burkey, 1988; Darwen and Green, 1996; Hanski and Gilpin, 1991). The migration experiment in the riverine model gave similar results for subpopulations in which rates of immigration exceeded rates of emigration.

I identified an additional concern associated with fragmentation in rivers. The potential risks imposed by asymmetry between downstream and upstream migration may be more important than the effects of isolation. Such an imbalance can quickly lead to problems in the reaches serving as sources, usually those upstream. When migration rates in both directions are low, this is less of a danger.

Practical ways of achieving balanced two-way migration are not obvious in the situation faced by river sturgeons because of the difficulties in providing upstream passage. The Russians have experimented with fish elevators as one solution (Rochard et al., 1990). Assisted movements are another possible short-term solution.

How do upstream and downstream migration rates influence genetic diversity within and among subpopulations?

As in 2-dimensional landscapes (Gaggiotti and Smouse, 1996), I found that even low levels of migration were effective in preventing erosion of genetic diversity within segments in the river setting. I also observed a pattern of decreasing genetic diversity upstream when rates of downstream migration exceeded upstream rates. These results suggest that a pattern of decreasing genetic diversity upstream may indicate an imbalance between upstream and downstream migration. Heterozygosities determined from protein allozyme electrophoresis in three upstream populations were lower than those of downstream populations of white sturgeon (H = 1.4% vs. 5.9% Kootenai R.; H = 0.30% above vs. 0.49% below Bonneville Dam, Columbia River; H = 0.22% above vs. 0.70% below Hell's Gate Rapids, Fraser River)(Bartley et al., 1995; Brown et al., 1992b). This pattern is supported by preliminary results from an ongoing mtDNA analysis (P. Anders, personal communication). Depending on the circumstances, longitudinal patterns of increasing heterozygosity in rivers may have several alternative explanations. Three alternatives are (1) cumulative genetic contributions from headwater populations (Setter and Brannon, 1992), (2) selective pressures associated with impoundment in upstream reaches (Brown et al., 1992a; Brown et al., 1992b), and (3) straying among anadromous populations of diverse origins in downstream reaches.

Habitat Loss

Is there a critical minimum river length?

Past experience suggests that threshold values identified by models do not necessarily provide a sound basis for policy because of model uncertainty (Ludwig et al., 1993). Maybe it is fortunate, then, that these results did not suggest a particular threshold value. My simulations suggest that the fate of isolated (sub)populations of fish is determined by both the length of the river segment and the presence of limiting habitat. It also suggests that it may be possible to identify a reach length and a supply of limiting habitat that is sufficient to maintain a given population with a specified low risk of extinction before 1000 y.

It is interesting to consider the implications of this study for the management of large rivers. If rivers are managed to ensure persistence of a larger metapopulation (i.e., some subpopulations in a linked series are always present), then costs involve facilitating movement among river segments. If we consider the river a series of distinct subpopulations, then costs involve providing adequate habitat for all life stages in each segment and under a broad range of environmental conditions. These alternatives present different ecological and economic costs and benefits. Understanding how river habitat (size, quality, and diversity) and movement between impounded reaches influence riverine fish fauna at the scale of the metapopulation is an important part of this equation.

Auer (1996a) proposed an alternative method for defining a minimum river length that relies on historical migration distances prior to dam construction. The minimum migration distance available to historical white sturgeon populations that forms the basis for Auer's minimum was 715 km in the Fraser River (Lane, 1991). However, there is also a population upstream of a natural barrier in the Fraser River, suggesting that this distance is not a strict requirement for population persistence.

How does conversion of free-flowing to reservoir habitat influence the likelihood of persistence?

Neither habitat-loss scenario had an appreciable effect on persistence beyond that produced by isolation until free-flowing habitat became scarce. In contrast, the effects of habitat loss exceeded those of population isolation in randomly fragmented landscapes simulated by Bascompte and Sole (1996) until a large proportion of habitat was lost. In these simulations, the presence of a small amount of critical habitat serving as a refuge or a site for spawning was sufficient to prevent habitat loss from aggravating the effects of fragmentation alone. This result is reminiscent of the well-known benefits conferred by refuge in models of host-parasite or predator-prey interactions. In a sense, a guaranteed refuge or source (i.e., habitat where survival and reproduction of some portion of the population was ensured) provided a self-contained rescue effect for isolated populations.

ACKNOWLEDGEMENTS

Ken Lepla, Jim Chandler, and Phil Bates shared their considerable knowledge about Snake River white sturgeon. The three of them, Webb Van Winkle, and the white sturgeon research community in the Columbia River basin, including Paul Anders, Mike Parsley, Ray Beamesderfer, Tom Rien, Vaughn Paragamian, Tim Cochnauer, and Matt

Powell, helped me to develop a *gestalt* for the species and river used in the case study by sharing information and participating in workshops. This research was sponsored through a tailored collaboration between the Electric Power Research Institute and Idaho Power Co. under contract with Oak Ridge National Laboratory. I appreciate reviews of draft manuscripts by Kenny Rose, Tony King, and Paul Anders.

PART 7. INDIVIDUAL VARIATION IN LIFE HISTORY CHARACTERISTICS CAN INFLUENCE EXTINCTION RISK

ABSTRACT

The white sturgeon (*Acipenser transmontanus*) shows great individual variation in the age at maturation. This study examines the consequences of model assumptions about individual variation in this trait on predicted population viability. I considered (1) the influence of variation in age at maturation alone; (2) the effects of heritability; and (3) the influence of a stable and an altered selective regimes. Two selective regimes represented conditions before and after the impoundment of a river, blocking access of anadromous white sturgeon populations to the ocean. In contrast to previous simulation studies (with different traits), I found that increased individual variation in the age at maturity did not necessarily lead to a higher likelihood of persistence. Individual variation in this trait only increased the simulated likelihood of persistence when: (1) the variation was heritable, and (2) the selective regime had changed. The results of this study support the idea that quantifying the potential for a selective response may be necessary to understand how populations will fare in an environment greatly altered by human activities.

INTRODUCTION

The relationship between individual variation and population viability remains an unresolved question in ecology (Uchmanski, 1999). As a practical matter, we need to understand this relationship to decide when it is necessary to represent individual variation in models used to assess population viability (e.g., Pfister, 1999). As a theoretical matter, this relationship is at the interface between ecology and evolution.

Different sub-disciplines of ecology and evolutionary biology offer different perspectives on the question of how individual variation influences persistence. Most studies coming from an ecological perspective conclude that individual variation improves the odds for population persistence (Conner and White, 1999; Rice et al., 1993). Yet conservation biologists claim that a related phenomenon, demographic stochasticity, increases extinction risk in very small populations (Fox, 1993; Lande, 1993). Those coming from an evolutionary perspective suggest that heritable variation can have either positive or negative population-level consequences, depending on the selective context (Lande and Shannon, 1996). There are many examples of traits in which variation should be selected against: for example, canalized early development and frequency dependent behaviors that favor conformity, such as synchronized spawning times.

This study addresses three questions. First, how does individual variation influence persistence when the variation is not heritable? Second, how does heritability influence the relationship between individual variation and persistence? Third, what is the role of selection in mediating the relationship between individual variation and population persistence? These three questions are evaluated in the context of a Snake River white sturgeon population before and after impoundment of their river habitat using the individual-based model described in Part 6. Each question is introduced in a separate section below.

The Role of Individual Variation

Most theoretical studies coming from an ecological perspective conclude that populations made up of uniform individuals are more extinction-prone than populations made up of variable individuals (Conner and White, 1999; Rice et al., 1993; Uchmanski, 1999). In the simplest case, an extreme phenotype has the highest fitness. The distribution of fitness among individuals is such that the initial presence of at least some individuals with high fitness is enough to make the difference between population growth and decline. For example, Conner and White (1999) found that increasing the simulated individual heterogeneity in birth and death rates increased the probability of persistence of small populations.

The population-level benefits of initial individual variation can be greatly amplified if a phenotype with an initial advantage is able to develop into a phenotype that is even more dominant in terms of its fitness. This phenomenon has been demonstrated in the growth of individuals belonging to species that are able to capitalize on an early growth advantage. At least two mechanisms, allometric growth (DeAngelis et al., 1993; Pfister, 1999; Rice et al., 1993) and social dominance hierarchies (Lomnicki, 1988), can produce this type of an autocorrelation in individual ranks. When individuals differ in their abilities to acquire resources, populations are able to persist at much smaller population sizes because dominant individuals are able to monopolize resources (van Noordwijk, 1994). In populations lacking social hierarchies that create variation among individuals, all individuals starve as equals (van Noordwijk, 1994). The specific example of growth is unusual because of this positive feedback between size and growth that amplifies the population’s variability in individual sizes. When combined with selection for large size, it is easy to see how higher population persistence can result.

The first question addressed by this study is “How does individual variation influence persistence?” I focused on a fish with an extreme and variable life history. The white sturgeon (Figure 1), the largest freshwater fish in North America, is a long-lived, late-maturing species. Because individuals vary greatly in the age at maturation, this study focused on the role of individual variation in this trait and its influence on the

Figure 1. The white sturgeon (*Acipenser transmontanus*). Drawing by Kelly Lepla.

likelihood of persistence. The individual-based PVA model described in Part 6 was used to simulate individual variation for this species.

The Role of Genetic Inheritance

Evolutionary theory suggests that the ability to respond to selection should increase a population's ability to persist. This implies that we need to understand the genetic underpinnings of traits to predict population persistence in population viability analysis (PVA). The second question addressed by this study is, "How does heritability influence the relationship between individual variation and population persistence?"

I simulated heritable variation in the age at maturation for a range of heritabilities. This required a modeling approach that could represent the genetic underpinnings of the simulated trait. Chambers (1993) suggested that an individual based modeling approach would provide a natural starting point for a merger between demography and genetics. For a previous study (Part 6), I developed an individual-based model to represent neutral genetic variation among individuals, not unlike the genetic component in the VORTEX model (Lacy, 1993). The next step was to link the individual's genetic identity to its expression as a specific phenotypic trait. Therefore, I added a generic representation for the genetic underpinnings for age at maturation. This model bridges the gap between simple, analytically tractable 1-locus, 2-allele models and statistical quantitative genetic models.

The Role of Selection

Evolutionary theory suggests that the effect of individual variation on persistence can be either positive or negative, depending on the selective regime. For example, Lande and Shannon (1996) found that genetic variation had different effects on population persistence under different selective regimes. This has important implications for PVA, because it suggests that the genetic underpinnings of traits exposed to selection can influence predictions. Although PVA models sometimes include a genetic component to address genetic risks, they typically focus on random genetic drift or mutation, and not selection (Lacy, 1993; van Noordwijk, 1994).

The assumption of selective neutrality is not appropriate for ecological applications that involve anthropogenic changes in the environment that are likely to impose a strong and directional selective force (Lynch and Lande, 1993). To understand how natural populations will fare in the face of anthropogenic shifts in the environment, it may be important to know the potential for a selective response, if not to predict the response. The evolution of life history traits in a changing environment has practical implications in pest control, fisheries, climate change, and other areas of ecological research (Kareiva et al., 1993). For example, size-selective mortality imposed on fisheries has resulted in the evolution of an earlier ages at maturation (Harris and McGovern, 1997; Martinez-Garmendia, 1998; McAllister and Gillis, 1996; Miller and Kapuscinski, 1994; Miller and Kapuscinski, 1996; Reisenbichler, 1997; Reznick et al., 1990; Rodd and Reznick, 1991; Rowell et al., 1989; Sheridan, 1996).

The third question addressed by this study is “What is the role of selection in mediating the relationship between individual variation and population persistence?” To explore the role of selection, this study compares two hypothesized selective regimes for white sturgeon in the Columbia River basin. Historically, white sturgeon followed an anadromous life history, periodically moving into large rivers to spawn and returning to estuaries along the Pacific coast. The selective regime of this species has been altered by dam-building activities that blocked most populations from the ocean. This last question was addressed by comparing the relationships between individual variation and persistence for a pre-impoundment and a post-impoundment selection regime.

CASE STUDY: WHITE STURGEON IN THE SNAKE RIVER

White Sturgeon Demography

In this study, I use a model to evaluate the effect of individual variation, both inherited and not, on the likelihood of persistence of land-locked white sturgeon populations. The white sturgeon is perfectly suited as a model for exploring this relationship for three reasons. First, this species shows extremely high variation in demographic traits such as age at maturation. Second, the selective regime experience by white sturgeon in the Columbia and Snake rivers has been changed by dam-building activity. Third, this species represents a class of fishes following a life history that is highly vulnerable to extinction.

The white sturgeon, like other sturgeons and paddlefishes, shows great variation in demographic traits. Females reach maturity between the ages of 13 and 34 years. Males reach maturity a few years earlier. The number of years between spawning attempts is also highly variable. The spawning interval is plastic: in the hatchery environment, males can reproduce annually and females can reproduce every other year. This high frequency is not observed in natural populations, where intervals can range up to 11 years between spawning events (Cochnauer, 1983; Semakula and Larkin, 1968). This study focuses on age at maturity as the trait of interest.

The selective regime has changed for white sturgeon and similar species. Historically, adults migrated long distances from estuaries on the Pacific coast of North America into large river systems to spawn, returning afterward to the estuarine environment (Chapman et al., 1996; Kohlhorst et al., 1989; Warren and Beckman, 1993). The Columbia River system is the only river on the American continent long enough to have supported a two-stage migration pattern such as those observed in long rivers on the Asian and European continents (Bemis and Kynard, 1997).

Sequential development of hydroelectric projects along the Columbia and Snake Rivers progressively created white sturgeon populations isolated between dams. This transition from an anadromous to a land-locked existence has changed the selective regime in a numerous ways. Most changes involve reduced access to a variety of habitats, in part by converting free-flowing habitat to reservoir. Poor water quality in storage reservoirs can be a problem. In addition, regulated flows can adversely affect reproduction by reducing spring flows associated with larger year classes (Artyukhin, 1978; Auer, 1996b; Kriksunov and Mamina, 1995).

Sturgeons and paddlefishes are presently depleted, threatened, or extinct almost everywhere they occur (Beamesderfer and Farr, 1997). In the Pacific Northwest, fish ecologists are concerned about land-locked populations of white sturgeon for two reasons. First, this species' life history matches the profile of other threatened and endangered species (Boreman, 1997; Parent and Schrimi, 1995). Sturgeons and paddlefishes exemplify the periodic life history of Winemiller and Rose (1992), with a large size at maturity, low early survival, and high fecundity. This group includes many anadromous species that periodically return to spawn in the freshwater environment. Second, large rivers have been highly altered by dredging, impoundment, and waste disposal over the past few centuries. Anadromy, dependence on large rivers, large body size, and delayed maturation all contribute to the white sturgeon's vulnerability (Parent and Schrimi, 1995).

White Sturgeon Genetics

The white sturgeon is an ancient species that belongs to the order Acipenseriformes that is thought to have resulted from one tetraploidization event 300 Myr ago (Birstein and Vasiliev, 1987). This order is autopolyploid in origin and contains two groups, presumably formed by several more independent polyploid events (May et al., 1997). One group includes species generally considered to be tetraploid (Dingerkus and Howell, 1976) and a second group of species (including the white sturgeon) that are generally considered to be octoploid in origin (Birstein and Vasiliev, 1987). However, Fontana (1994) has raised a dissenting opinion, claiming that the first two groups are diploid and tetraploid, respectively, based on an analysis of nuclear organizing regions.

The white sturgeon genome is now believed to be functionally diploid. According to Van Eenennaam (1997), long-established and naturally occurring autopolyploids that show bivalent pairing at metaphase I have essentially become diploidized. Birstein and Vasiliev (1987) suggested that Acipenseriformes have a mechanism to compensate for the unusual number of active nucleoli, which controls the functional diploidization of the genome. The number of chromosomes in the karyotype of this fish has been estimated between 2n = 240 and 276 (Van Eenennaam et al., 1998a).

Sturgeons exhibit relatively low genetic diversity (Birstein and Vasiliev, 1987). It has been observed that impounded populations of white sturgeon tend to have lower genetic diversity than populations with access to the ocean (Bartley et al., 1995; Brown et al., 1992b). Brown et al. (1992a) suggested that selective pressures associated with impoundment may be responsible for reducing genetic variation in landlocked populations.

Little is known about the genetic basis for age at maturity in white sturgeon. Because adults spawn at a considerably younger age when raised in aquaculture environments that speed growth (Doroshov et al., 1997), the trait is known to be under partial environmental control. Genetic studies of other fishes have quantified heritability in this trait. For example, Gjerde and Schaeffer (1989) reported a heritability of 0.42 for age at maturity for the semelparous Atlantic salmon and 0.14 for rainbow trout. These values fall within the range reported for life history traits of 0.1 to 0.5 (Roff, 1997 p. 65).

THE WHITE STURGEON PVA MODEL

Demographic Model

The demographic white sturgeon PVA model simulates the growth, reproduction, and mortality of individuals (Figure 2A). The individual-based PVA model operates on an annual time step. During each time step, simulated sturgeon are exposed to two events: reproduction and death. Each of these events is simulated as described below.

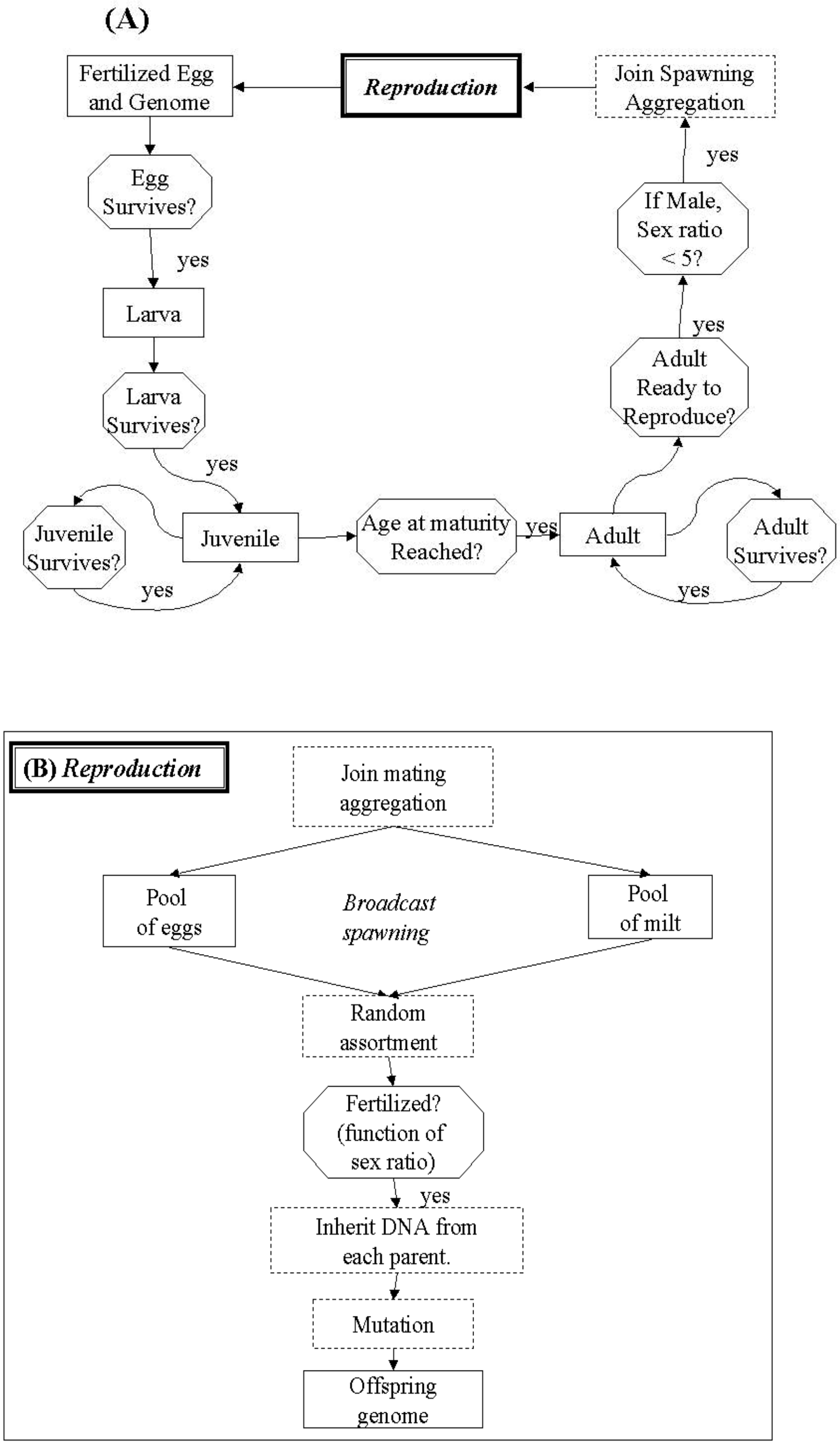


Figure 2. Flow-chart diagram of (A) the demographic individual-based model of white sturgeon and (B) the genetic sub-model.

Reproduction

Simulated reproduction has four components. First, the model identifies a pool of eligible spawners each year. Second, aggregations of spawners form. Third, the fecundity of each female that successfully spawns is determined. Finally, the model simulates the inheritance of parental genetic material by offspring.

The pool of eligible spawners includes all mature adults that reach reproductive readiness in a given year. The timing of reproduction is determined by the age at first maturity and the interval between spawning events. The model assigns these two reproductive parameters to individual fish from specified normal distributions. For females (males), the mean age at maturity is 18 y (14 y). In simulations with individual variation, the standard deviation in age at maturity was 1.5 y. Similarly, the average interval between spawning attempts was 5 y (2 y) for females (males), with a standard deviation of 0.8 y (0.3 y), respectively.

White sturgeon are broadcast spawners that form mating aggregations during spring. The model simulates one aggregation in each river segment. Density-dependent limits regulate the number of female spawners allowed to join the mating aggregation. I calculate the maximum number of spawning females as the product of the maximum density per km of river (100 km^{-1}) multiplied by the length of spawning habitat (50 km). When the ratio of males to females is high it is unlikely that excess males will fertilize eggs (Domeier and Colin, 1997). Therefore, the model limits the sex ratio of spawning aggregations (<5 males per female) by randomly excluding excess males.

The fecundity of adult sturgeon increases with size (Chapman et al., 1996; Cochnauer, 1983; Van Eenennaam et al., 1996). The model estimates the fecundity of each female in two steps. First, female length is simulated according to a Von Bertallanfy relationship with parameters values estimated for the Snake River. Next, the model predicts fecundity from female length with parameter estimates from DeVore (1995).

After simulating egg production by females in the spawning aggregation, the model simulates the inheritance of alleles by offspring. All males in the spawning aggregation are equally likely to fertilize a given egg. At each locus, one allele is drawn from each parent at random. After offspring inherit alleles from each parent, mutation can occur.

Death

Simulated mortality is relatively simple. Annual survival is lowest during the first year, increasing from zero at high egg densities ($10^{5.5}$ eggs) to a maximum of 0.05% at low egg densities. Annual survival is substantially higher for juveniles and adults (81%). The model simulates random catastrophes that reduce the population by 90%. Catastrophes occur at an average frequency of one every 100 years. In addition, the experiment to address the role of selective regime simulates mortality associated with spawning migration as described in section "Simulation Experiments."

Genetic Model

Here, I describe the genetic components of the model (Figure 2*b*). The true mechanistic pathways linking genes that contribute to determining the age of maturity of a particular individual are not known. To make progress, this genetic model required a number of simplifying assumptions (Table 1).

Table 1. Simplifying assumptions made in the genetic individual-based model.

1. The white sturgeon has a functionally diploid genome.
2. Evolution in the trait age at maturation is unopposed by environmental correlations (e.g., reduced growth leading to increased mortality) or genetic correlations (pleiotropy with other traits).
3. The number of loci and alleles contributing to this trait is similar to the arbitrary intermediate values selected here.
4. Genetic variation is additive and contributions from dominance and epistasis are not important.
5. Mutations are not inherently different from wild alleles in effects, their effects are unrelated to prior state, and there is no asymmetry in the rates of forward vs. backward mutation.
6. Allelic effects are symmetric normal with zero mean and no kurtosis.
7. There are no genotype-by-environmental interactions.

I represented the deviation from mean age at maturation (Z-μ) as the combination of a genetic (Z_G) and an environmental (Z_E) component:

$$Z = \mu + Z_G + Z_E. \quad (2)$$

At the start of the simulation, I specify a gender-specific mean, μ, and standard deviation, σ in the trait (e.g., age at maturation) that applies to the initial population. Heritability of each trait, h^2, is also specified. I assume that the environmental component is random normal with mean zero and variance $\sigma^2 (1\text{-}h^2)$. The genetic component represents additive effects, x, from alleles at $M = 10$ loci. The mapping function $A(k)$ points to the index of the allele occurring on copy k. Because white sturgeon are considered functionally diploid ($N = 1$), each parent contributes one allele and accounts for one term in equation (2). The identity of the contributed allele, $A(k)$, is chosen at random from the two grandparental alleles of the parent. For each individual, $Z_G = \sigma\, g$, where

$$g = \frac{1}{\sqrt{PM}} \sum_{i=1}^{M} \left(\sum_{k=1}^{N} x_{A(k)} \right) + \frac{1}{\sqrt{PM}} \sum_{j=1}^{M} \left(\sum_{k=1}^{N} x_{A(k)} \right) \quad (2)$$

Because the effects, x, are standard normal, Z_G has variance $\sigma^2 h^2$ at the start of the simulation. This model makes the simplifying assumptions that genetic and environmental contributions to the trait are independent, and that genetic variation contributing to the trait is additive.

Initialization

At the start of the simulation, I draw the effects of each allele on each trait from a standard normal distribution truncated at ±3 standard deviations. I assume that a specified number of alleles are initially represented at each locus in the white sturgeon population with equal probability. Each individual in the initial population draws a vector of alleles for each locus from a multinomial distribution of the 32 alleles by individuals. In the simulation experiments reported here, I initialized the populations with 8 alleles, each with a frequency of 0.125. The remaining 24 alleles may enter the population later through the process of mutation.

I verified that the scenarios produced initial populations with the same, specified, phenotypic means and variances for heritabilities ranging from 0 to 1. I found that simulations could produce initial populations with average trait values that deviated significantly from the specified mean, particularly when the number of alleles and loci was small. Differences in extinction occurred because favorable initial trait values happened to be present in some, but not other populations. To correct this, the model now calculates the realized trait mean in the initial population and subtracts the mean to remove bias from all allelic effects.

Mutation

Mutation is the source of new genetic information for simulated populations. Mutation rates for white sturgeon have been reported to be low (Birstein et al., 1997b). I adopted a stepwise mutation model (Kimura and Ohta, 1978) with a mutation frequency $\mu = 10^{-5}$ per locus and generation. Each mutation results in a 1-unit increase or decrease in the allele index. Because allele indices are not ordered by effects on a trait, the allelic effect resulting from mutation is unrelated to the effect of its wild precursor.

SIMULATION EXPERIMENTS

I used the white sturgeon model described above to address the following questions in three simulation experiments:

1. How does individual variation in age at maturation influence the likelihood of persistence?
2. Does heritability change the relationship between individual variation and the likelihood of persistence?
3. How do shifts in the selective regime influence the relationship between individual variability and persistence?

My design varied each of these three factors (individual variation, heritability, and selective regime) as shown in Figure 3. Question #1 compared predictions of population persistence for “None” and “Not heritable”; question #2 compared predictions of “Not heritable” and “Heritable”; and question #3 compared predictions for the pre- and post-

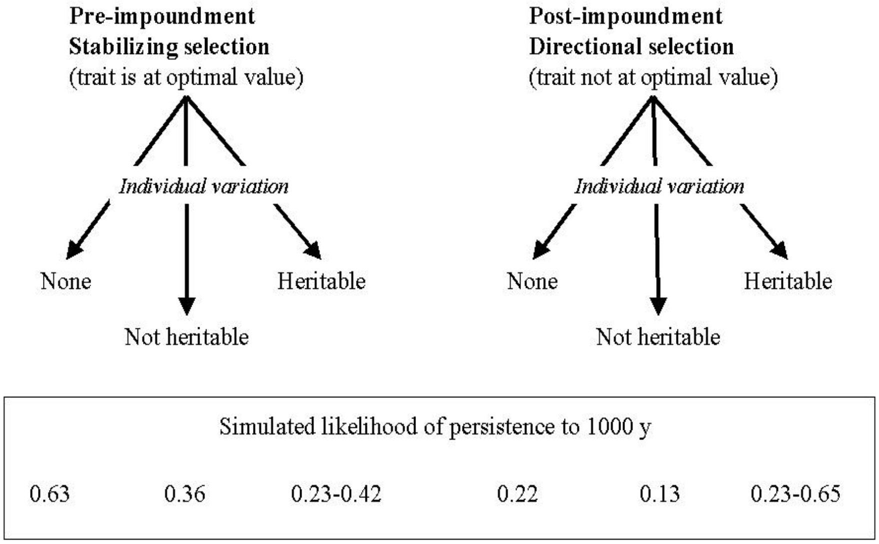


Figure 3. Simulation experiments are designed to examine the effects of: (1) individual variation in age at maturity, (2) heritability, and (3) selective regime on population persistence. Results are summarized in the box.

impoundment scenarios. Two selective regimes are described below, each with a no-variation scenario and a range of scenarios with realistic individual variation that differ in heritability. For each scenario, I simulated 100 replicate populations for 1000 y. The likelihood of persistence to 1000 y is defined as the fraction of replicate populations that had at least one male and one female after 1000 y.

Initial Conditions

The initial populations had densities of 50 individuals km^{-1} in a 50-km reach, distributed according to an exponential age distribution with a mean age of 8 y. I assigned each individual an age at maturity, with the specified combination of genetically determined and random environmental variation as described above. Scenarios with variation in age at maturity produced ages at maturity ranging between 14 and 23 y for females. Likewise, each fish was assigned a spawning interval drawn from a normal distribution, with the assumption that variation in this trait was not heritable. I assumed that the last year of spawning for a given fish was equally likely to have occurred at any time between the previous year and a full spawning interval prior to the start of the simulation.

Two Selective Regimes

One of the questions addressed here is how the shift in selective regime influences persistence and the role of individual variation in life history. This leads to the question, "What adaptive value would delayed maturation have?" According to life history theory, several mechanisms may lead to the evolution of delayed maturation (Roff, 1984; Stearns and Crandall, 1981). In the case of the white sturgeon, I hypothesized that three factors may have favored delayed maturation (Figure 4). First, precocious individuals suffered

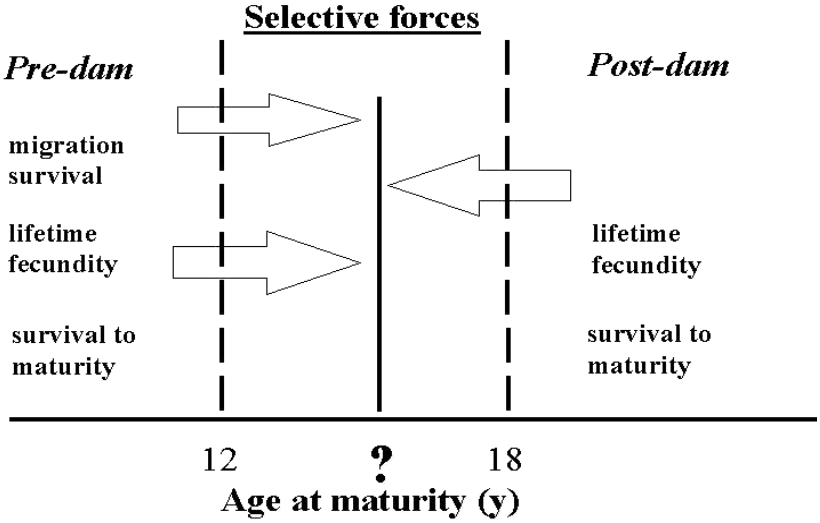


Figure 4. Diagram of hypothetical forces acting on the evolution of age at maturity of white sturgeon. Life history theory suggests that increased (decreased) age at maturity evolves when survival to maturity is high (low). Delayed maturation, when accompanied by an increased mature body size, enhances both the likelihood of surviving spawning migrations and lifetime fecundity of females. The main difference between the pre- and post-dam selective regime is the removal of migration survival as a selective force tending to increase the age at maturity.

increased mortality resulting from the energetic costs of a long upstream spawning migration. Second, mortality risk while waiting in the marine or estuarine environment would be relatively low. Third, fecundity increases as a power function of body size (Chapman et al., 1996). These factors may have favored waiting to attain a substantial size before migrating. Sturgeon grow quickly and develop an outer covering of scutes, both of which protect them from predators and reduces juvenile mortality.

I simulated two hypothetical selective regimes (Figure 3). For the pre-dam situation with a stable selective regime, I calibrated the model to produce an equilibrium age at maturity (that resulting after 1000 y of selection) close to that observed recently among populations in the Snake River. I calibrated a linear relationship, equation (3), between survival through a spawning migration, $S(t)$, and the age of the migrating adult, t, until it resulted in no shift from the initial average values after 1000 years. Final calibrated parameter values were $S_0 = 0.75$ and $S_A = 0.10$. Variable t_A is the average age at maturity.

$$S(t) = \min\left\{S_0 + S_A\,(t - t_A), 1\right\} \tag{3}$$

For the post-dam situation, I simulated a shift in the optimal age at maturity corresponding with a land-locked selective regime by removing mortality associated with spawning migration ($S_0 = 1$). This represents the current situation with land-locked populations that no longer commute between freshwater and the sea. To compensate for this, I increased survival during the first year of life so that both the pre- and post-dam simulations with heritability = 0.25 produced the same likelihood of persistence.

RESULTS

Simulation results for each of the three questions are described in three sections that follow. They are also summarized at the bottom of Figure 3.

How Does Individual Variation in Age at Maturation Influence the Likelihood of Persistence?

Individual variation in age at maturity had a large effect on the likelihood of simulated persistence to 1000 y (Figure 5). Simulations with no variation had a higher simulated likelihood of persistence (0.63 vs. 0.36 pre-impoundment and 0.22 vs. 0.13 post-impoundment) as shown in Figure 5 for $h = 0$. In the pre-impoundment scenario, the initial average age at maturity is near the selected optimum. The absence of individual variation implies that all fish have the optimal value of the trait. Higher individual fitnesses translated into a larger final population size (Figure 6; $h = 0$) and enhanced likelihood of persistence (Figure 5; $h = 0$) at the population level. Individual variation did not have as large an effect in the post-impoundment scenario, but it did not improve the likelihood of persistence. Final population sizes did not differ significantly (Figure 6; $h = 0$), but the likelihood of persistence was higher in the simulations with no individual variation (Figure 5; $h = 0$).

Does Heritability Change the Relationship between Individual Variation and the Likelihood of Persistence?

The first experiment addressed the role of individual variation in the life history trait, age at maturity, for white sturgeon. In this second simulation experiment, I ask whether it makes a difference if there is a genetic basis to that variation. Here, the realistic individual variability in age at maturity is provided with both an environmental and a genetic basis.

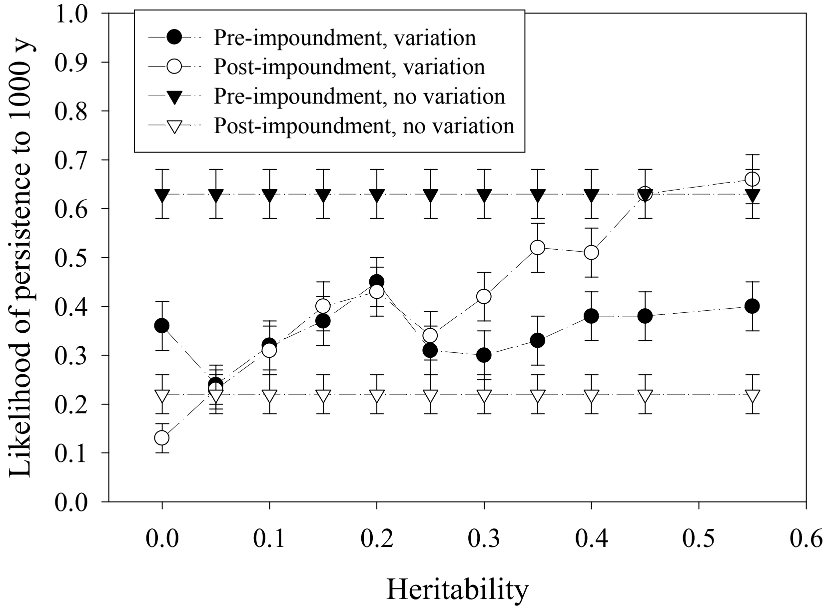


Figure 5. Changes in the likelihood of persistence to 1000 y simulated with no phenotypic variation and with variation ranging in heritability from completely environmental to a heritability of 0.55 for a pre-and a post-impoundment scenario.

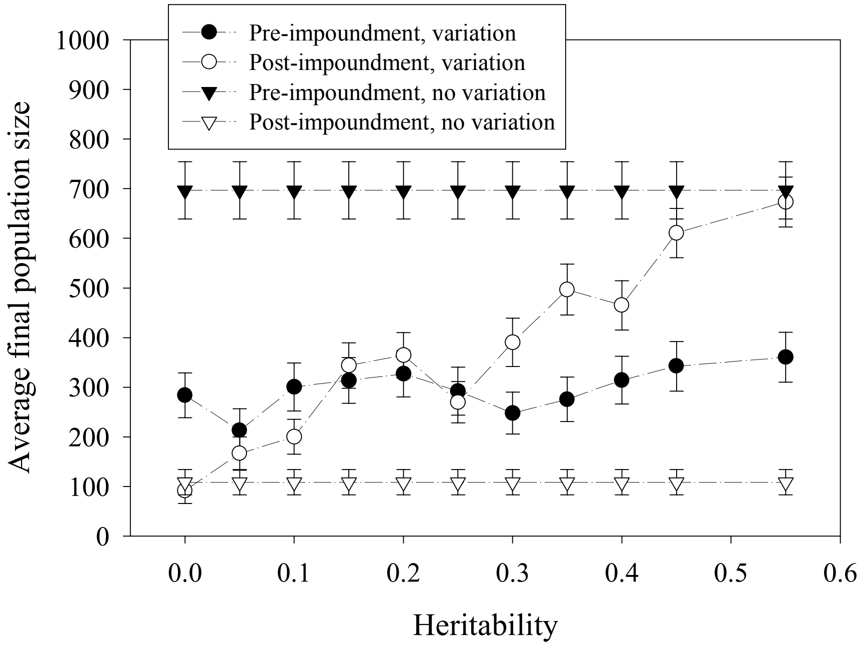


Figure 6. Changes in final average population sizes simulated with no phenotypic variation and with variation ranging in heritability from completely environmental to a heritability of 0.55 for a pre-and a post-impoundment scenario.

The two situations (pre- and post-impoundment) gave different results. The pre-impoundment simulations showed no trend in population viability as heritability changed. In contrast, the post-impoundment simulations showed an increase in population viability with increased heritability (Figures 5 and 6). Because the two scenarios are calibrated to produce the same likelihood of persistence at $h^2 = 0.25$, it is not possible to compare absolute values between scenarios, but it is legitimate to compare patterns.

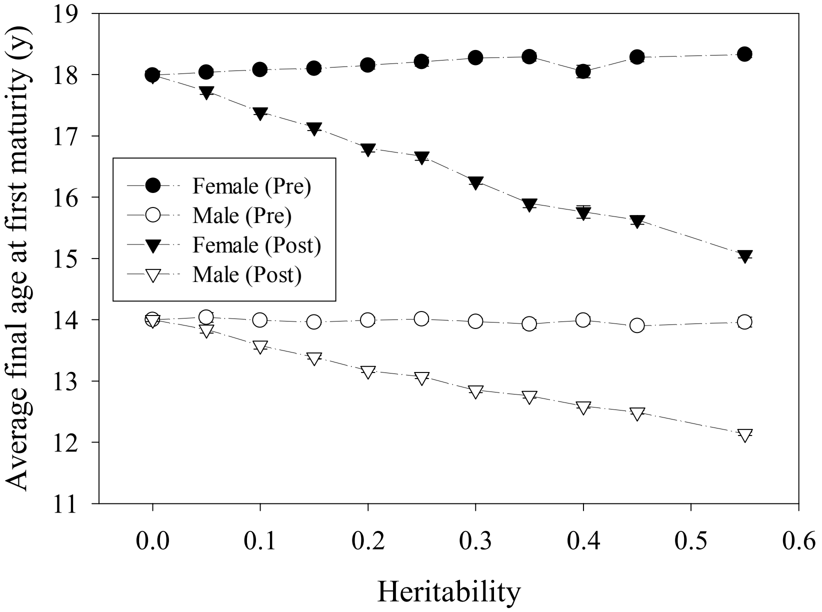


Figure 7. Changes in mean age at maturation simulated with no phenotypic variation and with variation ranging in heritability from completely environmental to a heritability of 0.55 for a pre-and a post-impoundment scenario.

The final age at maturity in the pre-impoundment simulations did not respond to heritability, consistent with a trait under stabilizing selection (circles in Figure 7). In contrast, the mean final age of maturity in the post-impoundment scenario decreased with heritability in a way that is consistent with directional selection (triangles in Figure 7).

In these simulations, the mean trait value decreased over the 1000-y period for those populations that persisted. The variation in the population around the mean value decreased in both the pre-and post-impoundment scenarios (Figure 8). Under the pre-impoundment regime (circles in Figure 8), stabilizing selection reduced phenotypic variation as expected. Under the post-impoundment regime (triangles in Figure 8), directional selection decreased the variation among males more than it did variation among females.

How Does the Selective Regime Influence the Relationship between Individual Variability and Persistence?

The answer to each of the previous two questions reported above differed completely under the two selective regimes considered. When the mean age at maturity was optimal under the selective regime (i.e., the pre-dam regime), individual variation was detrimental to the population and heritability had no effect. In contrast, a mean age

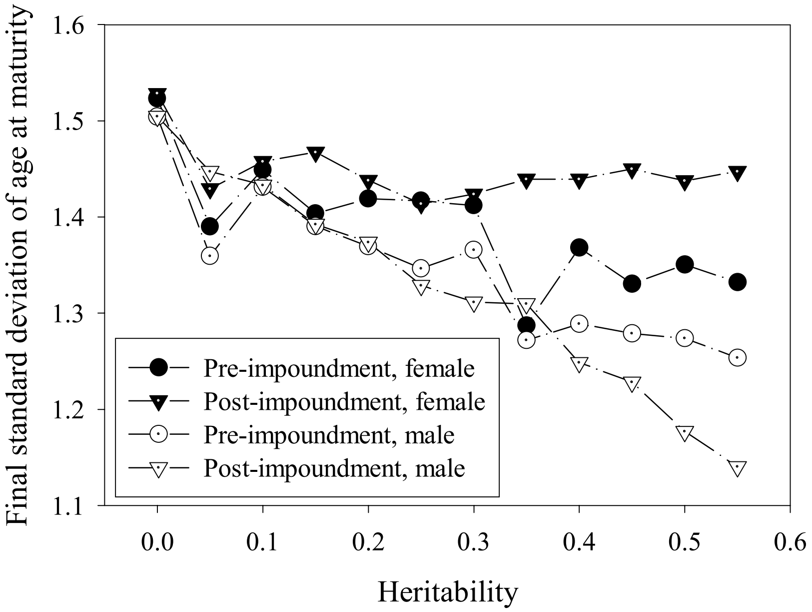


Figure 8. The standard deviation in male and female ages at maturity among individuals remaining in the simulated populations in year 1000 is shown as a function of heritability for the pre- and post-impoundment selective regimes.

at maturity away from the optimum (i.e., the post-dam regime) led to the conclusion that non-heritable individual variation had no significant effect, but that heritable variation was beneficial.

DISCUSSION

The three questions addressed here evaluated the effects of (1) individual variation; (2) heritability; and (3) selective regime on population persistence. These are discussed below.

How Does Individual Variation in Age at Maturation Influence the Likelihood of Persistence?

The first simulation experiment showed that population viability results can be sensitive to whether variation observed among individuals in life history traits is portrayed. The answer suggested by this study is that individual variation in age at maturation had different effects on simulated persistence depending on whether the trait was heritable and whether it was under selection (Figure 3). For non-heritable variation, uniform populations lacking individual variation enjoyed a higher likelihood of persistence than those harboring a range of individual phenotypes.

For heritable variation, the effect of individual variation on population extinction risk depended on the juxtaposition of trait values with respect to an optimal trait value. An "optimal" age at maturity under a given selective regime is defined as a value yielding the highest fitness within a specified region of possible trait values. In the situation addressed here, the fitness surface is smooth enough to neglect the issue of multiple local optima. Operationally, an optimal trait value can be estimated as the stable average reached in genetic simulations after a long period of time from a particular initial state.

One implication of this is that a population model can be checked to see whether its demographic parameters evolve. If they do not, then the parameters are in equilibrium with the selective regime simulated. The results give some indication of how individual variation in fitness-related traits will influence simulated population persistence.

To put these results in the context of previous studies, these results are unusual in that I did not find an increased chance of persistence associated with adding (non-heritable) individual variation. In the pre-impoundment selective regime, the constant age at maturity of individuals is at the optimal value. Therefore, in the absence of over-compensating density dependence, higher fitness of equivalent individuals translates directly into higher population sizes and persistence. When variation is added, causing some individuals to deviate from the optimal age at maturity, lower fitnesses are reflected at the population level.

It is unclear why variation in age at maturity did not lead to a higher chance of persistence under the post-impoundment selective regime. One would expect that the presence of some individuals with extreme phenotypes having higher fitness (i.e., those with shorter generation times) would reduce extinction risk at the population level. That is, one would expect that maximum fitness of the population (i.e., the minimum age at maturity present) would be the best predictor of persistence. Instead, these results show that non-heritable variation in age at maturity among individuals did not greatly influence persistence at the population level. This contrasts with the results from similar studies, especially that of Conner and White (1999). Conner and White studied populations with average birth and death rates leading to zero population growth. The results of this study may differ because random effects dominate fitnesses simulated by the model. Two examples of random effects are catastrophes and density-dependent exclusion from spawning. The fact that the simulated population has a positive growth rate in the absence of these two factors may also be a cause. If demographic parameters placed the populations nearer to an equilibrium, zero-growth, condition, slight fitness differences among individuals might translate into larger differences in persistence at the population level. To the best of my knowledge, the life history parameters used here reflect a "real" feature of sturgeon populations – spawning females have very high fecundities that should provide high potential for population growth when conditions are right (Beamesderfer and Farr, 1997; Winemiller and Rose, 1992).

Does Heritability Change the Relationship between Individual Variation and the Likelihood of Persistence?

To address the second question, I compared the effect of simulating variation in age at maturation with a genetic basis, as well as an environmental basis. To explore the effect of heritability, I compared results over a range of simulated heritabilities (narrow-sense = broad-sense), h^2 between 0.0 and 0.55.

Heritability changed the effect of individual variation on persistence under the post-dam selection regime, but not under the pre-dam selection regime. Under the pre-impoundment selective regime with individual variation, persistence did not show a significant trend in persistence as heritability increased. Under the post-impoundment selective regime with individual variation, persistence did show an increasing trend with increased heritability. Extinction risk was lower when the variation was heritable because the trait (age at maturity) distribution evolved downward in response to selection.

In reality, the evolutionary response in age at maturity that I simulated might be prevented by pleiotropic responses in other traits that were not given a genetic basis in my model. The extent to which life history traits, such as age at maturity, are able to evolve is controversial. It has long been held that the constant exposure of life history traits to strong selection will erode their genetic variability (thus heritability). Houle (1992) challenged this view in a survey of over 200 quantitative genetic studies of animal populations. Houle found that traits closely related to fitness had higher additive genetic and non-genetic variability.

Theory suggests at least three possible explanations for this variation. One explanation is that inheritance of life history traits is polygenic (Istock, 1982). In a hierarchical view, one might rank traits according to the degree of aggregation. As one moves down the pyramid, traits are defined to mirror the parameters needed for population models of increasing complexity. In this view, fitness is the single trait at the top of the pyramid; birth and death rates are in the second tier; the three life history traits, survival, age at maturity, and fecundity, form the third tier; and so on. Individual differences in life history traits arise as the integrated result of many specific, lower-level traits that develop during the lifetime of the organism (e.g., de Jong and Noordwijk, 1992). Thus, even a small amount of genetic variation at one locus can add up to a significant overall amount. A different explanation is that selection that appears to be stabilizing is actually a result of short-term fluctuations in directional selection, and, therefore, does not erode genetic variation. For example, the fitness associated with one genotype may fluctuate in response to either population density or environmental cycles. A third argument is that protected polymorphisms, maintained by antagonistic pleiotropy, tend to evolve among life history traits (Hartt and Haefner, 1998).

There is empirical evidence that age at maturity can evolve in response to selection. For example, several studies have measured selective differentials in the ages and sizes at maturity in fish populations exposed to size-selective predation (Reznick et al., 1990; Rowell et al., 1989).

How Does the Selective Regime Influence the Relationship between Individual Variability and Persistence?

The importance of the selective regime is a main result. The implication is that it is not possible to predict the effect of individual variation, heritable or not, on persistence without understanding the selective regime. Genetic variation in this study had the greatest effect on population persistence in a changed environment, as Lande and Shannon (1996) observed. Correspondence between the mean value of demographic parameters and the parameter value(s) leading to an optimal simulated fitness seemed to determine how individual variation influenced population persistence in these simulation experiments. This suggests that it is difficult to interpret comparisons between results produced with and without individual variation without first understanding the fitness surface produced by the model. Note that this result applies equally to genetic and non-genetic population models.

This study only looked at constant selection regimes and a single time horizon of 1000 y. Wright (1978) first articulated a wrinkle in the relationship between heritable genetic variation and the population persistence. He recognized that stabilizing selection would have the effect of reducing individual variation in the short term, while longer-term persistence of the population might depend on the presence of genetic variation. Therefore, the long- and short-term effects of heritability may differ under a changing selective regime.

FUTURE DIRECTIONS

Does Individual Variation Evolve?

This paper addressed the effect of individual variation on persistence, but leaves open the question of whether individual variation tends to be promoted by selection when it has positive effects and vice versa. In situations when individual variation does increase the chances of population persistence, positive feedback mechanisms may exist that promote individual variation within populations. Population-level, individual-level, and soft selection provide three potential mechanisms.

Population-level selection provides one mechanism for altering individual variation, with higher variation in changing environments. The "risk-spreading" argument states that heterogeneous populations are more likely to persist because they spread the risk of extinction over a variety of phenotypes (den Boer, 1982; Uchmanski, 1999; van Dijk, 1982). This argument is the mirror image of the idea that rugged, fast-changing fitness surfaces promote genetic variation by dodging selection. In the long term, this argument requires a lack of predictability in the environment to prevent plasticity from evolving. Because individual variation enhances persistence under selective regimes that maintain variation, a positive feedback mechanism adjusts variation.

A similar argument, supported by individual-level selection, involves "bet-hedging." Parents that employ a bet-hedging strategy produce offspring with a variety of plastic phenotypes (Seger and Brockmann, 1987). By adopting this strategy, they are able to hedge against unpredictable environments and the risk of complete reproductive failure. This strategy raises the possibility that genetic mechanisms exist for passing along variation itself as a trait (Via, 1993).

Positive feedback between soft selection and individual variation provide a third class of mechanisms for regulating variation in traits. For example, individual variation in resource acquisition can promote persistence through density-dependent population regulation, where regulation is viewed in the sense of bounding populations away from very small and very large sizes (Conner and White, 1999; Pfister, 1999; Uchmanski, 1999). Conversely, density-dependence, because it is usually a temporary or intermittent condition, can promote individual variation by creating opportunities for alternative phenotypic solutions. Frequency dependence is a second soft-selection mechanism that can promote individual variation. This occurs when rare phenotypes have higher fitness than common phenotypes. If variation in such a trait improves persistence at the population level (e.g., individuals that specialize on different prey, and thereby experience reduced competition), the feedback cycle is complete.

Phenotypic Plasticity

A final topic of discussion is the role of phenotypic plasticity. In the simulations reported here, environmental variation among individuals was random. I did not consider the potential role of environmental factors such as temperature or food availability or population density on the age at maturation. The ability to hasten time to maturation in a hatchery setting shows that such influences do contribute to this trait in white sturgeon. In contrast to the previous studies (Parts 2—6), this study did not focus on the role of environmental factors. A next step would be to consider more realistic reaction norms between age at maturity and these environmental factors. A practical consideration is that this removes the ability to control simulated heritability.

CONCLUSIONS

This study, in contrast to previous simulation studies, found that increased individual variation in the age at maturity did not necessarily lead to a higher likelihood of persistence. Individual variation in this trait only increased the simulated likelihood of persistence under an altered selective regime when the individual variation was heritable.

These simulation experiments demonstrated the potential need for PVA models to represent heritable variation in fitness-related traits that are subject to strong anthropogenic selection. They showed that it is possible to represent heritable variation in traits in an individual-based population model without a great deal of specific information about genetic architecture. The challenge ahead is to consider how we can predict the future viability of populations with a limited understanding of the relationships between the genetic composition of the population and its potential response to a changing environment.

ACKNOWLEDGEMENTS

Ken Lepla, Phil Bates, and Jim Chandler deserve credit for providing me with information on Snake River populations. Along with Webb Van Winkle, they participated in providing data and insights used in the development of the white sturgeon PVA model. Thanks go to Paul Anders and Matt Powell for conversations about white sturgeon genetics. I appreciate reviews of this manuscript by Webb Van Winkle, Jerry Tuskan, and Kenny Rose.

PART 8. CONCLUSIONS

Fishes that use large rivers, and anadromous species in particular, coexist with many human alterations of the river environment. This study used PVA modeling to evaluate linkages between fish populations and three of the infamous 4H's (Harvest, Habitat, and Hydropower, but not Hatcheries). This research produced answers to each of the original questions listed in the introduction and repeated (in bold) below.

TUOLUMNE RIVER FALL AND LATE-FALL CHINOOK SALMON

According to the age-based PVA model for fall-chinook salmon (Part 1; Table 1), harvesting during the ocean phase of life has a significant impact on the future viability of the run. Likewise, model results suggest that hydropower operation, diversion of water, and sub-optimal flow regimes contribute to observed run declines. Without the 4th H (hatchery stocking) and straying of adult spawners to the Tuolumne River from nearby natal rivers, it is unlikely that this population would have survived the remaining 3H's to the present. Five-year sequences of poor returns would be sufficient to cause local extinction. In Part 3, I used the ORCM recruitment model to aid in designing seasonal flow regimes to maximize the production of fall chinook salmon smolts (Part 1; Table 1). I determined that the optimal solutions derived from ORCM differed for different hydrologic years and spawner densities. In Part 4, the relationship between recruitment and spawner density was also found to change depending on the flow regime. In Part 5, I compared PVA predictions of population persistence for different flow regulations and different levels of ocean harvesting on fall chinook salmon.

The questions posed in Part 1 related to chinook salmon are answered below using the results of Parts 2--5.

1. **What patterns of seasonal flow maximize chinook recruitment**?

This question was addressed for a moderate abundance of 5,000 spawning adults in Part 3. Simulated annealing varied flow levels for each of 20 2-week periods between the migration of adults into the river in fall and migration of their offspring out of the river in the spring. The ORCM recruitment model simulated the number of smolts outmigrants produced (Table 1 in Part 1).

In years with little or no limitation on flow, the optimal flow pattern included pulses of higher flow in fall, lower flow in winter (Jan. -- April), and very high flow in spring. An unanticipated result was that such wet-year optimal flow regimes were the only ones that successfully permitted individuals of the late-fall run to develop into smolts and migrate to the ocean.

2. **Does the optimal pattern change as annual flow becomes more limited (i.e, in dry hydrologic years)?**

Using the same general approach described in Question 1, I placed a limit or constraint on the total annual flow available. Those combinations of 2-week flows exceeding this limit were not considered by the simulated annealing algorithm and were not evaluated by the ORCM recruitment model.

As availability of water was restricted, the elevated fall flows in the optimal flow pattern were reduced first, followed by reductions in the spring flows. One feature of optimal flow regimes did not change with the total flow available was that a minimum winter flow level was always included in the optimal flow regimes.

3. What patterns of seasonal flow maximize life history diversity in chinook salmon?

A different response variable simulated by ORCM, the variance in spawning times of outmigrating smolts, was used in an optimization similar to that described to answer Question 1 above. In this optimization, which is reported in Part 2, flows were varied to maximize diversity of spawning times.

According to the ORCM, a flow regime with a pulse flow in early February and extended high spring flows produced higher diversity in run times, with 30% more outmigrants belonging to the late-fall run accompanied by a similar reduction in overall numbers.

4. Does the optimal pattern change in response to changes in the number of adults that return to the river to spawn?

In Part 4, the optimization reviewed in Question 1 was repeated with 40,000 rather than 5,000 spawners for the case with unlimited total annual flow.

The optimal pattern changed when the number of adults returning to spawn increased. Annual flow was lower in the high-abundance optimal regime than in the low-abundance optimal regime, especially during fall and spring.

5. Can a simpler recruitment model summarize flow and density effects in ORCM?

In Part 4, I fitted a flow-dependent stock-recruitment equation to predictions of outmigrant numbers generated by ORCM with different initial spawner abundances and assuming the appropriate optimal flow regime obtained in Part 3.

Except for the two highest annual flow limits, the optimal flow regimes showed similar, parallel responses to spawner density. A generalized Beverton-Holt relationship summarized the stock-recruit relationship simulated by the ORCM model for fall chinook salmon. In this relationship, density-dependent mortality was represented as a function of total annual flow. For simulations with unlimited or nearly unlimited total annual flow, the optimal flow regimes derived for 5,000 spawners were no longer optimal for higher spawner abundances.

The optimal flow regime with the highest annual flow limit and the flow regime with no limit on annual flow produced a hump-shaped spawner-recruitment curve in response to increasing spawner density. This has two implications. First, the shape of the density-dependent response of recruitment to spawner density can change in response to the environment (in this case, river flow). Second, the flow regime that is optimal for one level of spawner densities was not optimal at a higher density, suggesting that optimal flow regimes would be needed for a range of spawner densities.

6. What management strategies, if any, will enable chinook salmon to persist for 100 y?

In Part 5, I developed a PVA model for the Tuolumne River (Table 1 in Part 1). I compared the simulated likelihood of persistence for four flow scenarios (percent of natural flows not diverted for other uses) and for three harvesting scenarios (percent of current harvest levels). I used a Markov model to simulate year-to-year variation in hydrology (total annual flow), with different transition probabilities associated with different flow scenarios. The flow scenario influenced recruitment through the S-R equation developed in Part 4. The harvesting scenario influenced mortality of ocean lifestages.

The PVA for Tuolumne River fall chinook salmon suggested that the prognosis is not good, but that both harvest and instream flow regulations could be used to facilitate recovery. Simulations suggest that large reductions in ocean harvesting would expedite recovery the most. Once harvesting has been reduced, decreases in the amount of freshwater diverted would also lead to substantial improvement.

SNAKE RIVER WHITE STURGEON

As with chinook salmon, the 4H's are the management knobs currently available to help maintain white sturgeon populations in the Snake River. My analysis in Part 6 addressed two significant concerns in the Snake River: Habitat and Hydropower. The fragmentation study presented in Part 6 demonstrated the importance to white sturgeon populations of providing longer stretches of free-flowing river habitat between hydroelectric dams. Ensuring a balance between upstream and downstream migration was also identified as an important need. I did not evaluate hatchery or harvesting influences here. Fishing regulations set by the state of Idaho in 1970 prohibited harvesting of white sturgeon and hatchery supplementation is not practiced, although it is likely that the Nez Perce tribe is seeking funding to establish a put-and-take fishery in one or more reservoirs. The specific questions from Part 1 are repeated below, along with answers suggested by studies reported in Parts 6 and 7.

7. How does fragmentation of large rivers by dams influence white sturgeon populations?

I developed an individual-based PVA model for white sturgeon. Three important features of the model were: (1) the ability to simulate changes in the length of free-flowing vs. reservoir habitat as a function of distance between dams; (2) the ability to simulate the effects of river habitat on white sturgeon spawning and mortality; (3) the ability to control downstream and upstream migration rates; and (4) the ability to simulate changes in genetic diversity.

Simulated river fragmentation indicated that impoundment was less likely to lead to extinction of dam-locked populations of white sturgeon (and probably other species that require free-flowing habitat) if the intervals between dams were sufficiently long to provide free-flowing habitat. Unbalanced migration (i.e., downstream without upstream) also contributed to a high risk of extinction and reduced genetic diversity in upstream river segments. These simulations showed that partitioning of genetic diversity did not continue to shift from within to among populations as fragmentation proceeded. Rather, as the spacing of dams became sufficiently close, genetic diversity among sub-populations eroded because of the high likelihood of extinction—an interaction between demographic and genetic effects that a strictly genetic model would not predict.

8. How is population persistence influenced by phenotypic variation among individual fish?

The PVA model used to address Question 7 was also used to address Question 8. This version included a hypothetical genetic model for the trait age at first maturity. I adjusted parameters to equilibrate to a pre-impoundment situation. I then compared the effect of individual variation (heritable and non-heritable) in age at maturity under two selective regimes (pre- and post-impoundment) on the likelihood of persistence for 1000 y.

This study demonstrated that individual variation does not necessarily enhance population viability. Increased variation in the age at maturity of white sturgeon increased the simulated likelihood of persistence only when (1) the variation was heritable and (2) the selective regime had changed.

CONCLUDING REMARKS

In conclusion, the research described in this dissertation focused on a collection of questions that are related by a common theme. The principal theme of these questions is to understand how anthropogenic changes to the riverine environment influence fish populations, in particular those associated with hydropower. Parts 2—4 focused on the relationship between chinook salmon recruitment and instream flows on a seasonal scale. Parts 3 and 5 broadened this perspective to consider the relationship between flow and population response on an annual basis. Part 6 focused on different aspect of hydropower: the fragmentation effects of dam construction, the conversion of free flowing to impounded habitat, and alterations to natural migration patterns. These questions have a broader interest because of the many other rivers and fish species that face similar anthropogenic changes to the river environment.

Density dependence is one of two secondary themes. In particular, the role of environmental factors, such as flow, in mediating density dependent control of populations. In Part 4, I described the interactions between density and flow in determining chinook salmon recruitment, as simulated by the ORCM model. At high densities of chinook salmon, individuals spawned too early are more likely to be superimposed, while those spawned too late are more likely to suffer from competition with other juveniles and emigrate before becoming smolts. I found that different flow regimes lead to different relationships between recruitment and spawner density. Some regimes produced an increase in recruitment with density to a carrying capacity set by flow. This relationship is typical when habitat or territoriality limits access to resources to a subset of the population. Other regimes produced a unimodal recruitment response to density. In Part 7, density dependence is described as one mechanism that can link individual variation to enhanced population persistence.

Finally, the theme of individual variation in life history. Parts 2 and 3 use the spatially explicit and individual-based recruitment model ORCM to understand how individuals that vary in spawning time meet with different fates under different flow regimes. Part 6 evaluates the influence of fragmentation and migration on neutral genetic diversity. Part 7 focuses on individual variation in the age at maturity and its influence on persistence.

The research questions described here ranged from very applied (designing instream flows) to very theoretical (understanding the effect of individual variation). A suite of different models and quantitative tools were developed and applied to address these questions. Although I focused on two specific case studies, chinook salmon in the Tuolumne River and white sturgeon in the Snake River, the results are likely to generalize to similar situations elsewhere.

REFERENCES

Allendorf, F. W., D. Bayles, D. L. Bottom, K. P. Currens, C. A. Frissell, D. Hankin, J. A. Lichatowich, W. Nehlsen, P. C. Trotter, and T. H. Williams. 1997. Prioritizing Pacific salmon stocks for conservation. Conservation Biology 11(1): 140-152.

Anderson, J. J. Decadal climate cycles and declining Columbia River salmon. Proceedings of the Sustainable Fisheries Conference, Victoria B.C.

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71: 355-366.

Artyukhin, Y. N. 1978. The gonads of the sturgeon, *Acipenser guldenstadti*, in the zone below the dam of the Volgograd water engineering system. Journal of Ichthyology 18(6): 912-923.

Auer, N. A. 1996a. Importance of habitat and migration to sturgeons with emphasis on lake sturgeon. Canadian Journal of Fisheries and Aquatic Sciences 53(Suppl. 1): 152-160.

Auer, N. A. 1996b. Response of spawning lake sturgeons to change in hydroelectric facility operation. Transactions of the American Fisheries Society 125: 66-77.

Bart, J. 1995. Acceptance criteria for using individual-based models to make management decisions. Ecological Applications 5(2): 411-420.

Bartholow, J. M. 1996. Sensitivity of a salmon population model to alternative formulations and initial conditions. Ecological Modelling 88: 215-226.

Bartholow, J. M., and T. J. Waddle. The search for an optimum flow regime using a salmon population model. Waterpower '95 331-339.

Bartley, D. M., G. A. E. Gall, and B. Bentley. 1995. Preliminary description of the genetic structure of white sturgeon, *Acipenser transmontanus*, in the Pacific Northwest. Environmental Biology of Fishes 14(1): 105-109.

Bascompte, J., and R. V. Sole. 1996. Habitat fragmentation and extinction thresholds in spatially explicit models. Journal of Animal Ecology 65: 465-473.

Beamesderfer, R. C. P., and R. A. Farr. 1997. Alternatives for the protection and restoration of sturgeons and their habitat. Environmental Biology of Fishes 48(1-4): 407-417.

Beamesderfer, R. C. P., T. A. Rien, and A. A. Nigro. 1995. Differences in the dynamics and potential production of impounded and unimpounded white sturgeon populations in the lower Columbia River. Transactions of the American Fisheries Society 124: 857-872.

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.

Beissinger, S. R. 1995. Modeling extinction in periodic environments: everglades water levels and snail kite population viability. Ecological Applications 5(3): 618-631.

Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62(3): 821-841.

Bemis, W. E., and B. Kynard. 1997. Sturgeon rivers: an introduction to acipenseriform biogeography and life history. Environmental Biology of Fishes 48: 167-183.

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.

Bernstein, C., A. Kacelnik, and J. R. Krebs. 1988. Individual decisions and the distribution of predators in a patchy environment. J. Animal Ecology 57: 1007-1026.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Fisheries Investigations London Serial 2: 533.

Bilby, R. E., and P. A. Bisson. 1987. Emigration and production of hatchery coho salmon (Oncorhynchus kisutch) stocked in streams draining an old-growth and a clear-cut watershed. Canadian Journal of Fisheries and Aquatic Sciences 45: 1397-1407.

Birstein, V. J., W. E. Bemis, and J. R. Waldman. 1997a. The threatened status of acipenseriform species: a summary. Environmental Biology of Fishes 48(1-4): 427-435.

Birstein, V. J., R. Hanner, and R. DeSalle. 1997b. Phylogeny of the Acipenseriformes: cytogenetic and molecular approaches. Environmental Biology of Fishes 48(1-4): 127-155.

Birstein, V. J., and V. P. Vasiliev. 1987. Tetraploid-octoploid relationships and karyological evolution in the order Acipenseriformes (Pisces). Karyotypes, nucleoli, and nucleolus-organizer regions in four acipenserid species. Genetics 72: 3-12.

Boles, G. L., 1988. Water temperature effects on chinook salmon (*Oncorhynchus tshawytscha*) with emphasis on the Sacramento River: a literature review. , California Department of Water Resources, Northern District.

Boreman, J. 1997. Sensitivity of North American sturgeons and paddlefish to fishing mortality. Environmental Biology of Fishes 48(1-4): 399-405.

Brett, J. R. 1952. Temperature tolerance in young pacific salmon, genus Oncorhynchus. Journal of the Fisheries Research Board of Canada 9(6): 265-309.

Brown, J. R., A.T. Beckenbach, and M. J. Smith. 1992a. Mitochondrial DNA length variation and heteroplasmy in populations of white sturgeon (*Acipenser transmontanus*). Genetics 132: 221-228.

Brown, J. R., A. T. Beckenbach, and M. J. Smith. 1992b. Influence of Pleistocene glaciations and human intervention upon mitochondrial DNA diversity in white sturgeon (*Acipenser transmontanus*) populations. Canadian Journal of Fisheries and Aquatic Sciences 49: 358-367.

Brown, R. L., and S. Greene, 1992. Effects of Central Valley Project and State Water Project Delta Operations on Winter-run Chinook Salmon. , California Department of Water Resources.

Burkey, T. V. 1988. Extinction in nature reserves: the effect of fragmentation and the importance of migration between reserve fragments. Oikos 55(1): 75-81.

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.

Cardwell, H., H. I. Jager, and M. J. Sale. 1996. Designing instream flows to satisfy fish and human water needs. Journal of Water Resources Planning and Management 122: 356-363.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63: 215-244.

Chamberlain, F. J., 1907. Some observations on salmon and trout in Alaska. 627, U.S. Bureau of Fisheries.

Chambers, R. C. 1993. Phenotypic variability in fish populations and its representation in individual-based models. Transactions of the American Fisheries Society 122: 404-414.

Chapman, F. A., J. P. V. Eenennaam, and S. I. Doroshov. 1996. The reproductive condition of white sturgeon, Acipenser transmontanus, in San Francisco Bay, California. Fishery Bulletin 94: 628-634.

Chen, H., and D. W. Watson. 1998. Parallel genetic simulated annealing: a massively parallel SIMD algorithm. IEEE Transactions on Parallel and Distributed Systems 9(2): 126-136.

Chesson, P. 1998. Recruitment limitation: A theoretical perspective. Australian Journal of Ecology 23: 234-240.

Christensen, S. W., and C. P. Goodyear. 1988. Testing the validity of stock-recruitment curve fits. American Fisheries Society Monograph 4: 219-231.

Cochnauer, T. G., 1983. Abundance, distribution, growth and management of white sturgeon (*Acipenser transmontanus*) in the Middle Snake River, Idaho. , Idaho Power Company, Boise.

Cochnauer, T. G., J. R. Lukens, and F. E. Partridge, 1985. Status of white sturgeon, *Acipenser transmontanus*, in Idaho. North American Sturgeons, F. P. Binkowski and S. I. Doroshov, eds., Dr W. Junk, publishers, Dordrecht, The Netherlands.

Conner, M., and G. White. 1999. Effects of individual heterogeneity in estimating the persistence of small populations. Natural Resources Modeling 12(1): 109-127.

Cramer, S. P. Use of managed pulses in flow to stimulate outmigration of juvenile salmon. Water for a changing global community, San Francisco, CA.

Crittenden, R. N. 1994. A model for the processes regulating recruitment for a sockeye salmon stock. Ecological Modelling 71: 85-106.

Darwen, P. J., and D. G. Green. 1996. Viability of populations in a landscape. Ecological Modelling 85: 165-171.

de Jong, G., and A. J. V. Noordwijk. 1992. Acquisition and Allocation of Resources: Genetic (Co)Variances, Selection, and Life Histories. American Naturalist 139(4): 749-770.

DeAngelis, D. L., and L. J. Gross, 1992. Individual-based Models and Approaches in Ecology. , Chapman and Hall, New York 525 pp.

DeAngelis, D. L., K. A. Rose, L. B. Crowder, E. A. Marschall, and D. Lika. 1993. Fish cohort dynamics: application of complementary modeling approaches. American Naturalist 142(4): 604-622.

Demirhan, M. 1999. FRACTOP: A geometric partitioning metaheuristic for global optimization. Journal of Global Optimization 14(4): 415-436.

den Boer, P. J. 1982. On the stability of animal populations, or how to survive in a heterogeneous and changeable world. Pages 211-232 *In* D. Mossakowski and G. Roth, (eds.), Environmental Adaptation and Evolution, Gustav Fisher, New York.

Dennis, B. 1989. Allee effects: population growth, critical density, and the chance of extinction. Natural Resource Modeling 3(4): 481-538.

DeVore, J. D., B. W. James, C. A. Tracy, and D. A. Hale. 1995. Dynamics and potential production of white sturgeon in the unimpounded Lower Columbia River. Transactions of the American Fisheries Society 124: 845-856.

Dill, L. M. 1969. The sub-gravel behavious of Pacific salmon larvae. Pages 89-99 *In* T. G. Northcote, ed. Symposium on Salmon and Trout in Streams, University of British Columbia, Vancouver.

Dingerkus, G., and W. M. Howell. 1976. Karyotypic analysis and evidence of tetraploidy in the North American paddlefish, *Polyodon spathula*. Science 194: 842-844.

Domeier, M. L., and P. L. Colin. 1997. Tropical reef fish spawning aggregations: defined and reviewed. Bulletin of Marine Science 60(3): 698-726.

Doroshov, S. I., G. P. Moberg, and J. P. V. Eenennaam. 1997. Observations on the reproductive cycle of cultured white sturgeon, Acipenser transmontanus. Environmental Biology of Fishes 48: 265-278.

Dunbrack, R. L., and L. M. Dill. 1983. A model of size dependent surface feeding in a stream dwelling salmonid. Environmental Biology of Fishes 8(3/4): 203-216.

Dunham, J. B., and B. E. Rieman. 1999. Metapopulation structure of bull trout: Influences of physical, biotic, and geometrical landscape characteristics. Ecological Applications 9(2): 642-655.

EAEST, 1992a. Don Pedro Project, 1987 Juvenile Chinook Salmon Mark-Recapture Study, Volume IV, Appendix 10. , EA Engineering, Science, and Technology, Lafayette, California.

EAEST, 1992b. Don Pedro Project, Chinook Salmon Population Model Documentation and Validation, Volume III, Appendix 1. , EA Engineering, Science, and Technology, Lafayette, California.

EAEST, 1992c. Don Pedro Project, Data Reports: Seining of Juvenile Chinook Salmon in the Tuolumne, San Joaquin, and Stanislaus Rivers, 1986-1989, Volume V, Appendix 12. , EA Engineering, Science, and Technology, Lafayette, California.

EAEST, 1992d. Don Pedro Project, Fisheries Study Report, Volume III, Appendix 2. , EA Engineering, Science, and Technology, Lafayette, California.

EAEST, 1992e. Don Pedro Project, Fisheries Study Report, Volume III, Appendix 3. , EA Engineering, Science, and Technology, Lafayette, California.

EAEST, 1992f. Don Pedro Project, Lower Tuolumne River Predation Study, Volume VII, Appendix 22. , EA Engineering, Science, and Technology, Lafayette, California.

EAEST, 1992g. Don Pedro Project, Preliminary Juvenile Salmon Study, Volume IV, Appendix 13. , EA Engineering, Science, and Technology, Lafayette, California.

EAEST, 1992h. Don Pedro Project, Spawning Gravel Studies Report, Volume IV, Appendix 8. , EA Engineering, Science, and Technology, Lafayette, California.

EAEST, 1992i. Don Pedro Project, Tuolumne River Salmon Spawning Surveys 1971-1988, Volume II, Appendix 3. , EA Engineering, Science, and Technology, Lafayette, California.

EBMUD, 1992. 1992 EBMUD Lower Mokelumne River Management Plan.

Emlen, J. M. 1995. Population viability of the Snake River chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 52: 1442-1448.

EPA, AEC, and NMFS, 1971. Columbia River Thermal Effects Study. Volume I: Biological Effects Studies.

FERC, 1996. Final Environmental Impact Statement. Reservoir release requirements for fish at the New Don Pedro Project, California. FERC-EIS-0081-F, Federal Energy Regulatory Commission (FERC), 88 First Street, N.E., Washington D.C. 20426.

Fisher, F. 1994. Past and present status of Central Valley chinook salmon. Conservation Biology 8: 870-873.

Fontana, F. 1994. Chromosomal nucleolar organizer regions in four sturgeon species as markers of karyotype evolution in Acipenseriformes (Pisces). Genome 37: 888-892.

Fox, B. L. 1995. Simulated Annealing: folklore, facts, and directions. *In* H. Niederreiter and P. J.-S. Shiue, (eds.), Monte Carlo and Quasi-Monte Carlo Methods in Scientific Computing, Springer-Verlag

Fox, G. A. 1993. Life history evolution and demographic stochasticity. Evolutionary Ecology 7: 1-14.

Gaggiotti, O. E., and P. E. Smouse. 1996. Stochastic migration and maintenance of genetic variation in sink populations. American Naturalist 147(6): 919-945.

Gangmark, H. A., and R. G. Bakkala. 1960. A comparative study of unstable and stable (artificial channel) spawning streams for incubating king salmon at Mill Creek. California Fish and Game 46: 151-164.

Gardner, R. H., R. V. O'Neill, J. B. Mankin, and J. H. Carney. 1981. Comparison of sensitivity analysis and error analysis based on a stream ecosystem model. Ecological Modelling 12: 173-190.

Geman, S., and D. Geman. 1984. Stochastic relaxation, Gibbs distribution and the Bayesian restoration in images. IEEE Transactions in Pattern Analysis and Machine Intelligence 6(6): 721-741.

Gilpin, M. E., and M. E. Soule. 1986. Minimum viable populations: processes of species extinction. *In* M. E. Soule, ed. Conservation biology: the science of scarcity and diversity, Sinauer Associates, Sutherland, MA.

Gjerde, B., and L. R. Schaeffer. 1989. Body traits in rainbow trout II. estimates of heritabilities and of phenotypic and genetic correlations. Aquaculture 80: 25-44.

Glover, F. 1989. Tabu search - part I. ORSA Journal on Computing 1(3): 190-260.

Glover, F. 1990. Tabu search - part II. ORSA Journal on Computing 2(1): 4-32.

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.

Gross, M. L., A. R. Kapuscinski, and A. J. Faras. 1994. Nest-specific DNA fingerprints of smallmouth bass in Lake Opeongo, Ontario. Transactions of the American Fisheries Society 123(4): 449-459.

Haefner, J. W. 1997. Modeling Biological Systems Principles and Applications, Chapman and Hall, New York, 473 pp.

Hallock, R. J., R. T. Elwell, and D. H. Fry, 1970. Migrations of adult king salmon (*Oncorhynchus tshawytscha*) in the San Joaquin Delta, as demonstrated by the use of sonic tags. 15, California Department of Fish and Game.

Hanski, I., and M. E. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. Pages 3-16 *In* I. Hanski and M. E. Gilpin, (eds.), Metapopulation Dynamics, Academic Press, London.

Harris, P. J., and J. C. McGovern. 1997. Changes in the life history of red porgy, *Pagrus pagrus*, from the southeastern United States. Fishery Bulletin 95: 732-747.

Hartt, L., and J. W. Haefner. 1998. How phenotypic variation and life history trait correlation enhance mean fitness in prey populations. Theoretical Population Biology 54: 50-61.

Hayward, T. L. 1997. Pacific ocean climate change: atmospheric forcing, ocean circulation and ecosystem response. Trends in Ecology and Evolution 12(4): 150-153.

Healey, M. C. 1994. Life history of chinook salmon (*Oncorhynchus tshawytscha*). Pages 312-393 *In* C. Groot and L. Margolis, (eds.), Pacific Salmon Life Histories, U.B.C. Press, Vancouver.

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* J. L. Nielsen, ed. Evolution and the Aquatic Ecosystem: Defining Unique Units in Population Conservation, American Fisheries Society Symposium 17, Bethesda, Maryland.

Houle, D. 1992. Comparing evolvability and variability of quantitative traits. Genetics 130: 195-204.

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.

Iles, T. C., and R. J. H. Beverton. 1998. Stock, recruitment and moderating processes in flatfish. Journal of Sea Research 39: 41-55.

Independent Scientific Group, 1996. Return to the river: restoration of salmonid fishes in the Columbia River ecosystem. , Northwest Power Planning Council, Portland, OR.

Ingber, A. L. 1996. Adaptive simulated annealing (ASA): Lessons learned. Control and Cybernetics 25(1): 33-54.

Ingber, L. 1993. Simulated annealing: Practice versus theory. Mathl. Comput. Modelling 18(11): 29-57.

Istock, C. A. 1982. Some Theoretical Considerations Concerning Life History Evolution. *In* H. Dingle and J. P. Hegmann, (eds.), Evolution and Genetics of Life Histories, Springer-Verlag, New York.

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.

Jager, H. I., D. L. DeAngelis, M. J. Sale, W. VanWinkle, D. D. Schmoyer, M. J. Sabo, D. J. Orth, and J. A. Lukas. 1993. An individual-based model for smallmouth bass reproduction and young-of-year dynamics in streams. Rivers 4(2): 91-113.

Jager, H. I., W. H. Hargrove, C. C. Brandt, A. W. King, R. J. Olsen, J. M. O. Scurlock, and K. A. Rose. accepted. Constructive contrasts between modeled and measured climate responses over a regional scale. Ecosystems.

Jager, H. I., W. V. Winkle, K. Lepla, J. Chandler, and P. Bates. in press. Population viability analysis of white sturgeon and other riverine fishes. Environmental Science and Policy.

Johnston, W. R. The Tuolumne River, California, USA: A managed system. Water for a changing global community, San Francisco, CA.

Jonsson, N., B. Jonsson, and L. P. Hansen. 1998. The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. Journal of Animal Ecology 67(5): 751-762.

Junk, W. J., P. Bailey, and R. E. Sparks. 1989. The flood pulse concept in river floodplain systems. Canadian Special Publications of the Fisheries and Aquatic Sciences 106: 110-127.

Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. Philosophical Transactions of the Royal Society of London **B** 330: 175-190.

Kareiva, P. M., J.G. Kingsolver, and R. G. Huey, 1993. Biotic Interactions and Global Change. , Sinauer Associates Inc., Sunderland, MA.

Kestin, T. S., D. J. Karoly, J.-I. Yano, and N. A. Rayner. 1998. Time-frequency variability of ENSO and stochastic simulations. Journal of Climate 11: 2258-2272.

Kimmerer, W., and I. Jones & Stokes Associates, 1998. Conceptual framework for the Sacramento River chinook salmon individual-based model. JSA 96-170, Tiburon, Sacramento, California.

Kimura, M., and T. Ohta. 1978. Stepwise mutation model and distribution of allelic frequencies in a finite population. Proceedings of the National Academy of Sciences 75(6): 2868-2872.

Kimura, M., and G. H. Weiss. 1964. The stepping stone model of population structure and the decrease of genetic correlation with distance. Genetics 49: 561-576.

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 on Fisheries and Aquatic Sciences 105: 100-115.

Kohlhorst, D. W., L. W. Botsford, J. S. Brennan, and G. M. Cailliet. Aspects of the structure and dynamics of an exploited central California population of white sturgeon (*Acipenser transmontanus*). Acipenser, Actes du Premier Coloque International sur l'esturgeon, Bordeaux, France 277-293.

Kope, R. G. 1987. Separable virtual population analysis of pacific salmon with application to marked chinook salmon (*Oncorhynchus tshawytscha*) , from California's Central Valley. Canadian Journal of Fisheries and Aquatic Sciences 44: 1213-1220.

Kope, R. G., and L. W. Botsford. 1988. Detection of environmental influence on recruitment using abundance data. Canadian Journal of Fisheries and Aquatic Sciences 45: 1448-1458.

Kope, R. G., and L. W. Botsford. 1990. Determination of factors affecting recruitment of chinook salmon *Oncorhynchus tshawytscha* in Central California. Fishery Bulletin 88: 257-269.

Kriksunov, Y. A., and K. M. Mamina. 1995. Effect of flows in the Ural River on recruitment of stellate sturgeon, *Acipenser stellatus*. Journal of Ichthyology 35(1): 52-58.

Lackey, R. T. 1998. Fisheries management: integrating societal preference, decision analysis, and ecological risk assessment. Environmental Science and Policy 1: 329-335.

Lackey, R. T. 1999. Salmon policy: science, society, restoration, and reality. Environmental Science and Policy 2: 369-379.

Lacy, R. C. 1993. VORTEX: A computer simulation model for population viability analysis. Wildlife Research 20: 45-65.

Lande, R. 1993. Risks of Population Extinction From Demographic and Environmental Stochasticity and Random Catastrophes. American Naturalist 142(6): 911-927.

Lande, R., and S. Shannon. 1996. The role of genetic variation in adaptation and population persistence in a changing environment. Evolution 50(1): 434-437.

Lane, D. E. 1991. Status of the white sturgeon, *Acipenser transmontanus,*in Canada. Canadian Field Naturalist 105(2): 161-168.

Langhurst, R. W., and D. L. Schoenike. 1990. Seasonal migration of smallmouth bass in the Embarass and Wolf Rivers, Wisconsin. North American Journal of Fisheries Management 10: 224-227.

Lawson, P. W. 1993. Cycles in ocean productivity, trends in habitat quality, and the restoration of salmon runs in Oregon. Fisheries 18(8): 6-10.

Lepla, K. B., and J. A. Chandler, 1995. A Survey of White Sturgeon in the Bliss Reach of the Middle Snake River, Idaho. Technical Report Appendix E.3.1-E, Idaho Power Company, Boise, Idaho.

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., et al. 1995. Safe havens: refuges and evolutionarily significant units. Pages 371-380 *In* J. L. Nielsen, ed. Evolution and the Aquatic Ecosystem: Defining Unique Units in Population Conservation, American Fisheries Society, Bethesda, MD.

Lomnicki, A. 1988. Population Ecology of Individuals, Princeton University Press, Princeton, NJ.

Ludwig, D., R. Hilborn, and C. J. Walters. 1993. Uncertainty, resource exploitation, and conservation: Lessons from history. Science 260: 17-36.

Ludwig, D., and C. J. Walters. 1981. Canadian Journal of Fisheries and Aquatic Sciences 38.

Lynch, M., and R. Lande. 1993. Evolution and extinction in response to environmental change. Pages 234-250 *In* P. M. Kareiva, J. G. Kingsolver, and R. G. Huey, (eds.), Biotic Interactions and Global Change

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78: 1069-1079.

Marquardt, D. W. 1963. An Algorithm for Least Squares Estimation of Parameters. Journal of the Society of Industrial and Applied Mathematics 11: 431-441.

Martinez-Garmendia, J. 1998. Simulation analysis of evolutionary response of fish populations to size-selective harvesting with the use of an individual-based model. Ecological Modelling 111: 37-60.

Mason, J. C. 1969. Hypoxial stress prior to emergence and competition among coho salmon fry. Journal of the Fisheries Research Board of Canada 26: 63-91.

May, B., C. C. Krueger, and H. L. Kincaid. 1997. Genetic variation at microsatellite loci in sturgeon: primer sequence homology in Acipenser and Scaphirhynchus. Canadian Journal of Fisheries and Aquatic Sciences 54: 1542-1547.

McAllister, M. K., and D. M. Gillis. 1996. Comment -- Estimation of selection differentials from fish scales: A step towards evaluating genetic alteration of fish size in exploited populations. Canadian Journal of Fisheries and Aquatic Sciences 53: 936-939.

McBain, S., and W. Thrush. The fluvial geomorphology of the Tuolumne River: Implications for the riverine ecosystem and salmonid restoration. Water for a changing global community, San Francisco, CA.

McCabe, G. T., Jr., and C. A. Tracy. 1994. Spawning and early life history of white sturgeon, *Acipenser transmontanus*, in the lower Columbia River. Fishery Bulletin 92: 760-772.

McCauley, D. E. 1993. Genetic consequences of extinction and recolonization in fragmented habitats. Pages 217-233 *In* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, (eds.), Biotic Interactions and Global Change

McNeil, W. J. 1964. Redd superimposition and egg capacity of pink salmon spawning beds. Journal of the Fisheries Research Board of Canada 21(6): 1385-1395.

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.

Milhous, R. T., M. A. Updike, and D. M. Schneider, 1989. Physical Habitat Simulation System Reference Manual-Version II. 26, U.S. Fish and Wildlife Service.

Miller, L. M., and A. R. Kapuscinski. 1994. Estimation of selection differentials from fish scales: a step toward evaluating genetic alteration of fish size in exploited populations. Canadian Journal of Fisheries and Aquatic Sciences 51: 774-783.

Miller, L. M., and A. R. Kapuscinski. 1996. Reply -- Estimation of selection differentials from fish scales: a step towards evaluating genetic alteration of fish size in exploited populations. Canadian Journal of Fisheries and Aquatic Sciences 53: 934-935.

Morhardt, J. E., and P. F. Baker. Downstream challenges to salmon restoration on the Tuolumne River--Salmon survival in the Sacramento-San Joaquin basin. Water for a changing global community, IAHR Proceedings, San Francisco, California.

Moyle, P., and R. Yoshiyama. The role of adaptive management in restoring chinook salmon to the Tuolumne river. Water for a changing global community, San Francisco, CA.

Murdoch, W. W., E. McCauley, R. M. Nisbet, W. S. C. Gurney, and A. M. deRoos. 1992. Individual-based models: combining testability and generality. Pages 18-35 *In* D. L. DeAngelis and L. J. Gross, (eds.), Individual-based Models and Approaches in Ecology, Chapman and Hall, 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. Can. J. Zool. 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. NMFS-NWFSC-35, U.S. Dept. Commerce.

Myers, R. A., and N. J. Barrowman. 1996. Is fish recruitment related to spawner abundance. Fishery Bulletin 94: 707-724.

Myers, R. A., N.J. Barrowman, J.A. Hutchings, and A. A. Rosenberg. 1995. Population dynamics of exploited fish stocks at low population levels. Science 269: 1106-1108.

National Marine Fisheries Service. 1999. Endangered and threatened species; threatened status for two chinook salmon evolutionarily significant units (ESUs) in California. Federal Register 64(179): 50394-50415.

National Research Council. 1996. Upstream: Salmon and Society in the Pacific Northwest., National Academy Press, Washington D.C..

Nei, M. 1973. Analysis of gene diversity in subdivided populations. Proceedings of the National Academy of Sciences 70(12): 3321-3323.

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(3): 882-884.

Overton, W. S. 1977. A strategy of model construction. *In* C.A.S. Hall and J. W. Day_Jr., (eds.), Ecosystem Modeling in Theory and Practice: An introduction with case histories, University Press of Colorado, Niwot, CO.

Parent, S., and L. M. Schrimi. 1995. A model for the determination of fish species at risk based upon life-history traits and ecological data. Canadian Journal of Fisheries and Aquatic Sciences 52: 1768-1781.

Parsley, M. J., L.G. Beckman, and G. T. McCabe_Jr. 1993. Spawning and rearing habitat use by white sturgeons in the Columbia River downstream from McNary Dam. Transactions of the American Fisheries Society 122: 217-227.

Peterman, R. M. 1987. Review of the components of recruitment of pacific salmon. American Fisheries Society Symposium 1: 417-429.

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 Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 49: 2551-2565.

Pfister, C. A. Model choice in population viability analysis. Population Viability Analysis: Assessing models for recovering endangered species, San Diego, CA.

Poddubny, A. G., and D. L. Galat. 1995. Habitat associations of upper Volga River fishes: Effects of reservoirs. Regulated Rivers: Research and Management 11: 67-84.

Policansky, D., and J. J. Magnuson. 1998. Genetics, metapopulations, and ecosystem management of fisheries. Ecological Applications 8(1 (Supplement)): S119-S123.

Pollock, K. H., J. D. Nichols, D. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107: 1-97.

Quinn, J. F., C. L. Wolin, and M. L. Judge. 1989. An experimental analysis of patch size, habitat subdivision, and extinction in a marine intertidal snail. Conservation Biology 3(3): 242-251.

Quinn, T. P., and A. H. Dittman. 1990. Pacific Salmon Migrations and Homing: Mechanisms and Adaptive Significance. Trends in Ecology & Evolution 5: 174-177.

Ratner, S., R. Lande, and B. B. Roper. 1997. Population viability analysis of spring chinook salmon in the South Umpqua River, Oregon. Conservation Biology 11(4): 879-889.

Reisenbichler, R. R. 1997. Genetic factors contributing to declines of anadromous salmonids in the Pacific Northwest. *In* D. J. Strouder, ed. Pacific Salmon and Their Ecosystems: Status and Future Options, Chapman and Hall, NY.

Reiser, D. W., and R. G. White. 1990. Effects of streamflow reduction on chinook salmon egg incubation and fry quality. Rivers 1(2): 110-118.

Reznick, D. A., H. Bryga, and J. A. Endler. 1990. Experimentally induced life-history evolution in a natural population. Nature 346: 357-359.

Rice, J. A., J. T. Miller, K. A. Rose, L. B. Crowder, E. A. Marschall, A. S. Trebitz, and D. L. DeAngelis. 1993. Growth rate variation and larval survival: inferences from an individual-based size-dependent predation model. Canadian Journal of Fisheries and Aquatic Sciences 50(1): 133-142.

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada 11: 559-623.

Ricker, W. E. 1976. Review of the rate of growth and mortality of Pacific salmon in salt water, and non-catch mortality caused by fishing. Journal of the Fisheries Research Board of Canada 33: 1483-1524.

Rieman, B. E., and J. D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. Transactions of the American Fisheries Society 124(3): 285-296.

Rochard, E., G. Castelnaud, and M. LePage. 1990. Sturgeons (Pisces: Acipenseridae); threats and prospects. Journal of Fish Biology 37 (Supplement A): 123-132.

Rodd, F. H., and D. N. Reznick. 1991. Life history evolution in guppies: III. the impact of prawn predation on guppy life histories. Oikos 62: 13-19.

Roff, D. A. 1984. The evolution of life history parameters in teleosts. Canadian Journal of Fisheries and Aquatic Sciences 41: 989-1000.

Roff, D. A. 1997. Evolutionary Quantitative Genetics, Chapman and Hall, New York.

Rogers, J. B., and C. C. Burley. 1991. A sigmoid model to predict gastric evacuation rates of smallmouth bass (*Micropterus dolomieui*) fed juvenile salmon. Canadian Journal of Fisheries and Aquatic Sciences 48(5): 933-937.

Rowell, C., K. Stokes, and R. Law. 1989. Does fishing generate selection differentials? Journal of Fish Biology 35(Suppl. A): 335-337.

Schaffter, R. G. 1997. White sturgeon spawning migrations and location of spawning habitat in the Sacramento River, California. California Fish and Game 83(1): 1-20.

Schlosser, I. J. 1991. Stream fish ecology: A landscape perspective. Bioscience 41: 704-712.

Seger, J., and H. J. Brockmann. 1987. What is bet-hedging? Oxford Survey of Evolutionary Biology 4: 182-211.

Semakula, S. N., and P. A. Larkin. 1968. Age, growth, food, and yield of the white sturgeon (*Acipenser transmontanus*) of the Fraser River, British Columbia. Fish. Res. Bd. Canada 25(12): 2589-2602.

Setter, A., and E. Brannon, 1992. A summary of stock identification research on white sturgeon of the Columbia River. DOE/BP-97298-1, Bonneville Power Administration, Portland, OR.

Sheridan, A. K. 1996. Comment -- Estimation of selection differentials from fish scales: A step towards evaluating genetic alteration of fish size in exploited populations. Canadian Journal of Fisheries and Aquatic Sciences 53: 933-933.

Shuter, B. J., and J. R. Post. 1990. Climate, population viability and the zoography of temperate fishes. Transactions of the American Fisheries Society 119: 314-336.

Smith, G., J. Rosenfield, and J. Porterfield. 1995. Processes of origin and criteria for preservation of fish species. Pages 44-57 *In* J. L. Nielsen, ed. Evolution and the Aquatic Ecosystem: Defining Unique Units in Population Conservation, American Fisheries Society Symposium 17, Bethesda, Maryland.

Soule, M. E. 1980. Thresholds for survival: maintaining fitness and evolutionary potential. *In* M. E. Soule and B. A. Wilcox, (eds.), Conservation biology: an evolutionary-ecological perspective, Sinauer, Sunderland, Mass.

Speed, T. 1993. Modelling and managing a salmon population. Pages 267-292 *In* V. Barnett and K. F. Turkman, (eds.), Statistics for the Environment, Wiley, New York.

Stearns, S. C., and R. E. Crandall. 1981. Quantitative Predictions of Delayed Maturity. Evolution 35(3): 455-463.

Tennant, D. L. 1976. Instream flow regimens for fish, wildlife, recreation and related environmental resources. Fisheries 1(4): 6-10.

Tsyplakov, E. P. 1978. Migrations and distribution of the sterlet *Acipenser ruthenus,* in Kuybyshev reservoir. Journal of Ichthyology 18(6): 905-912.

U.S._Congress. 1992. Reclamation Projects Authorization and Adjustment Act of 1992. H.R. 429, Washington D.C.

Uchmanski, J. 1999. What promotes persistence of a single population: an individual-based model. Ecological Modelling 115(2-3): 227-241.

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. Fishery Bulletin 95: 812-825.

USFWS, 1987. The needs of chinook salmon, *Oncorhynchus tshawytscha*, in the Sacramento-San Joaquin Estuary. San Francisco Bay/Sacramento-San Joaquin Delta Estuary Water Quality/Water Rights Hearing Phase I, USGWS Exhibit 31, Fisheries Assistance Office, USFWS, Stockton, California.

USFWS. 1994. Final Rule. Endangered and threatened wildlife and plants: determination of endangered status for the Kootenai River population of the white sturgeon. Federal Register 94549: 23.

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* J. L. Nielsen, ed. Evolution and the Aquatic Ecosystem: Defining Unique Units in Population Conservation, American Fisheries Society Symposium 17, Bethesda, Maryland.

van Dijk, T. S. 1982. Individual variability and its significance for the survival of animal populations. Pages 233-251 *In* D. Mossakowski and G. Roth, (eds.), Environmental Adaptation and Evolution, Gustav Fisher, New York.

Van Eenennaam, A. L., 1997. Genetic analysis of the sex determination mechanism of white sturgeon (*Acipenser transmontanus* Richardson), PhD Dissertation, University of California, Davis, Davis, CA.

Van Eenennaam, A. L., J. D. Murray, and J. F. Medrano. 1998a. Mitotic analysis of the North American white sturgeon, *Acipenser transmontanus* Richardson (Pisces, Acipenseridae), a fish with a very high chromosome number. Genome 41: 266-271.

Van Eenennaam, A. L., J. D. Murray, and J. F. Medrano. 1998b. Synaptonemal complex analysis in spermatocytes of white sturgeon, *Acipenser transmontanus* Richardson (Pisces, Acipenseridae), a fish with a very high chromosome number. Genome 41: 51-61.

Van Eenennaam, J. P., J. G. Watson, S. I. Doroshev, D. S. Moore, G. P. Moberg, and J. Linares. 1996. Reproductive conditions of the Atlantic sturgeon (*Acipenser oxyrinchus*) in the Hudson River. Estuaries 19(4): 769-777.

van Noordwijk, A. J. 1994. The interaction of inbreeding depression and environmental stochasticity in the risk of extinction of small populations. Pages 131-147 *In* V. Loeschcke, J. Tomiuk, and S. K. Jain, (eds.), Conservation Genetics, Birkhauser Verlag, Basel, Switzerland.

Van Winkle, W., H. I. Jager, S. F. Railsback, B. D. Holcomb, T. K. Studley, and J. E. Baldrige. 1998. Individual-based model of sympatric populations of brown and rainbow trout for instream flow assessment: model description and calibration. Ecological Modelling 110: 175-207.

Via, S. 1993. Adaptive phenotypic plasticity: target or by-product of selection in a variable environment? American Naturalist 142(2): 352-365.

Votinov, N. P., and V. P. Kas'yanov. 1978. The ecology and reproductive efficiency of the siberian sturgeon, *Acipenser baeri*, in the Ob as affected by hydraulic engineering works. Journal of Ichthyology 18(1): 20-29.

Walters, C. J., and D. Ludwig. 1981. Effects of measurement errors on the assessment of stock-recruitment relationships. Canadian Journal of Fisheries and Aquatic Sciences 38: 704-710.

Waples, R. S. 1995. Evolutionarily significant units and the conservation of biological diversity under the Endangered Species Act. Pages 8-27 *In* J. L. Nielsen, ed. Evolution and the Aquatic Ecosystem, American Fisheries Society, Monterey, CA.

Warren, J. J., and L. G. Beckman, 1993. Fishway Use by White Sturgeon on the Columbia River. WSG-AS 93-02, Washington Sea Grant Program, Seattle.

Welcomme, R. L. 1995. Relationships between fisheries and the integrity of river systems. Regulated Rivers: Research and Management 11: 121-136.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15: 393-425.

White Sturgeon Planning Committee, 1992. White Sturgeon Management Framework Plan. , Pacific States Marine Fisheries Commission, Portland, OR.

Whitlock, M. C. 1992. Temporal fluctuations in demographic parameters and the genetic variance among populations. Evolution 46(3): 608-615.

Williams, J. G., 1994. Report of the Special Master John G. Williams. 425955, Environmental Defense Fund, Inc. (plaintiff) vs. EBMUD et al. (defendants).

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. Fishery Bulletin 93(4): 732-740.

Williamson, S. C., J. M. Bartholow, and C. B. Stalnaker. 1993. Conceptual model for quantifying pre-smolt production from flow-dependent physical habitat and water temperature. Regulated Rivers: Research and Management 8: 15-28.

Winemiller, K. O., and K. A. Rose. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences 49(10): 2196-2218.

Wright, S. 1978. Variability within and among natural populations, University of Chicago Press, Chicago.

Yoshiyama, R. 2000. Chinook salmon in the California Central Valley: an assessment. Fisheries 25(2): 6-20.

Yoshiyama, R. M. 1999. A history of salmon and people in the Central Valley region of California. Reviews in Fisheries Science 7(3&4): 197-239.

VITA

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