A Simulation Study of Factors Controlling White Sturgeon Recruitment in the Snake River

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Abstract.—Five of the nine populations of white sturgeon *Acipenser transmontanus*, located between dams on the Middle Snake River, have declined from historical levels and are now at risk of extinction. One step towards more effectively protecting and managing these nine populations is ranking factors that influence recruitment in each of these river segments. We developed a model to suggest which of seven mechanistic factors contribute most to lost recruitment in each river segment: (1) temperature-related mortality during incubation, (2) flow-related mortality during incubation, (3) downstream export of larvae, (4) limitation of juvenile and adult habitat, (5) mortality of all ages during summer episodes of poor water quality in reservoirs, (6) entrainment mortality of juveniles and adults, and (7) angling mortality. We simulated recruitment with, and without, each of the seven factors, over a typical series of hydrologic years. We found a hierarchical pattern of limitation. In the first tier, river segments with severe water quality problems grouped together. Poor water quality during summer had a strong negative effect on recruitment in the river segments between Swan Falls Dam and Hell's Canyon Dam. In the second tier, river segments with better water quality divided into short river segments and longer river segments. Populations in short river segments were limited by larval export. Populations in longer river segments tended to be less strongly limited by any one factor. We also found that downstream effects could be important, suggesting that linked populations cannot be viewed in isolation. In two cases, the effects of a factor on an upstream population had a significant influence on its downstream neighbors.

Recruitment failure is thought to be responsible for the declining status of many sturgeon populations. The Kootenai population of white sturgeon *Acipenser transmontanus*, which is federally listed in the United States, is at risk of extirpation because recruitment is not occurring. Although spawning has been documented in the Kootenai River, the offspring do not appear to survive beyond the first few years (Paragamian et al. 1996). Recruitment failure has also been observed in other North American sturgeon species, for example, Gulf sturgeon (Killgore and Chan 1996; Peterson et al. 1999), Atlantic sturgeon *A. oxyrinchus* (Secor and Waldman 1999), and pallid sturgeon *Scaphirhynchus albus* (Tews and Gardner 2001), suggesting that the period between reproduction and survival through early life stages is critical for sturgeon persistence.

Predicting recruitment has always been an important area of fisheries science. Recruitment models were originally developed to predict the sustainable harvest of abundant fish populations. Historically, "recruitment" referred to the advancement of younger, smaller fish into size classes large enough to harvest (i.e., recruiting to the fishery). Because so many fish stocks have declined, recruitment models are also used to predict the ability of small and declining fish popu-

lations to persist (e.g., Emlen 1995; Ratner et al. 1997). Restoring self-sustaining populations requires an understanding of recruitment because populations can only sustain themselves if successful reproduction, followed by survival to older age classes, occurs.

The reproductive life history of the white sturgeon is a jigsaw puzzle that has more pieces missing than not. Migration patterns have not been studied in the few remaining anadromous populations. Therefore, we know virtually nothing about environmental cues to trigger reproductive cycles or mechanism for synchronizing reproduction. Spawning activity is rarely observed because it takes place in deep, turbulent waters. Finally, offspring are rarely observed in the field until they become vulnerable to capture by fishing gear.

The few pieces of the recruitment puzzle, about which we have some information, suggest that white sturgeon likely produce infrequent, strong year-classes. Sturgeons exemplify the periodic life history strategy that serves as one extreme in the three-dimensional classification scheme for life history strategies of fishes, developed by Winemiller and Rose (1992), with high fecundity, late maturation, and high early mortality. Periodic species are typically sustained by infrequent episodes of very successful recruitment when environmental conditions are favorable. Long-term empirical studies have not yet been done to confirm that sturgeons follow this pattern.

White sturgeon recruitment is influenced by both environmental and biological factors (Anders et al. and Parsley et al., both this volume). The availability of spawning adults can be an important limitation in small populations. Angling, entrainment mortality, lack of habitat, and poor water quality are factors that can cause premature mortality of juvenile and older sturgeon and deplete the supply of spawners. The most commonly reported factor influencing year-class strength of sturgeon species is flow during the spawning and incubation period. A positive relationship between spring river flow and sturgeon recruitment has been reported for many species, including Siberian sturgeon *A. baeri* (Tsyplakov 1978; Votinov and Kas'yanov 1978), lake sturgeon *A. fulvescens* (Auer 1996), and white sturgeon (Counihan et al., in press; Kohlhorst et al. 1991; Miller and Beckman 1995).

Water temperature is another environmental factor that explains year-to-year variation in recruitment (Counihan et al., in press). Studies have documented temperature effects on the quantity and quality of spawning habitat (Parsley and Beckman 1994; Parsley et al. 1993b), egg and larval survival (Wang et al. 1985), positive and negative spawning cues (Dettlaff et al. 1993), egg quality (Dettlaff et al. 1993; Webb-Brewer et al. 1999), and feeding rate and growth (Hung et al. 1993). High spring flows, following precipitation or snowmelt events, tip the balance toward thermally extreme inflows and away from thermally moderate groundwater inputs. As a result, the effects of temperature are difficult to separate from those of flow. Recruitment failure can also occur in short, impounded river segments through the loss of an early life stage that is dispersed downstream by flow. Habitat limitation may also operate during spawning and incubation, but this, like other biotic influences, has not been studied in the field.

In this study, we used a model for the Population Viability Analysis (PVA) of white sturgeon, to rank factors in terms of their influence on simulated white sturgeon recruitment in each of nine river segments of the Snake River between Shoshone Falls and the confluence of the Salmon River (Figure 1). Our PVA is among the first attempt to heed Caughley's (1994) advice, by focusing on predictions that compare the effects of various "agents of population decline." Caughley identified two paradigms among PVAs. PVAs, following the "small-population" paradigm, concentrate on small population size as the main source of extinction risk and have the goal of forecasting the likelihood of future persistence. PVAs, following the "declining-population" paradigm, concentrate on the causes of population decline and have the goal of evaluating recovery options by assessing the increase in population viability associated with removing agents of decline. Caughley (1994) argued that understanding agents of decline is more important than understanding the consequences of smallness. Since his paper, the scientific community has come to the consensus that PVA models are, in fact, better able to predict the benefits of alternative management actions than they are to accurately forecast extinction risks. Despite this consensus, few clear examples of PVAs consistent with the declining population paradigm exist in the literature. Typically, a sensitivity analysis of demographic parameters indirectly hints at an agent of decline by suggesting a critical life stage to protect (e.g., Crouse et al. 1987). Alternatively, scenarios are compared to evaluate the influence of alternative management
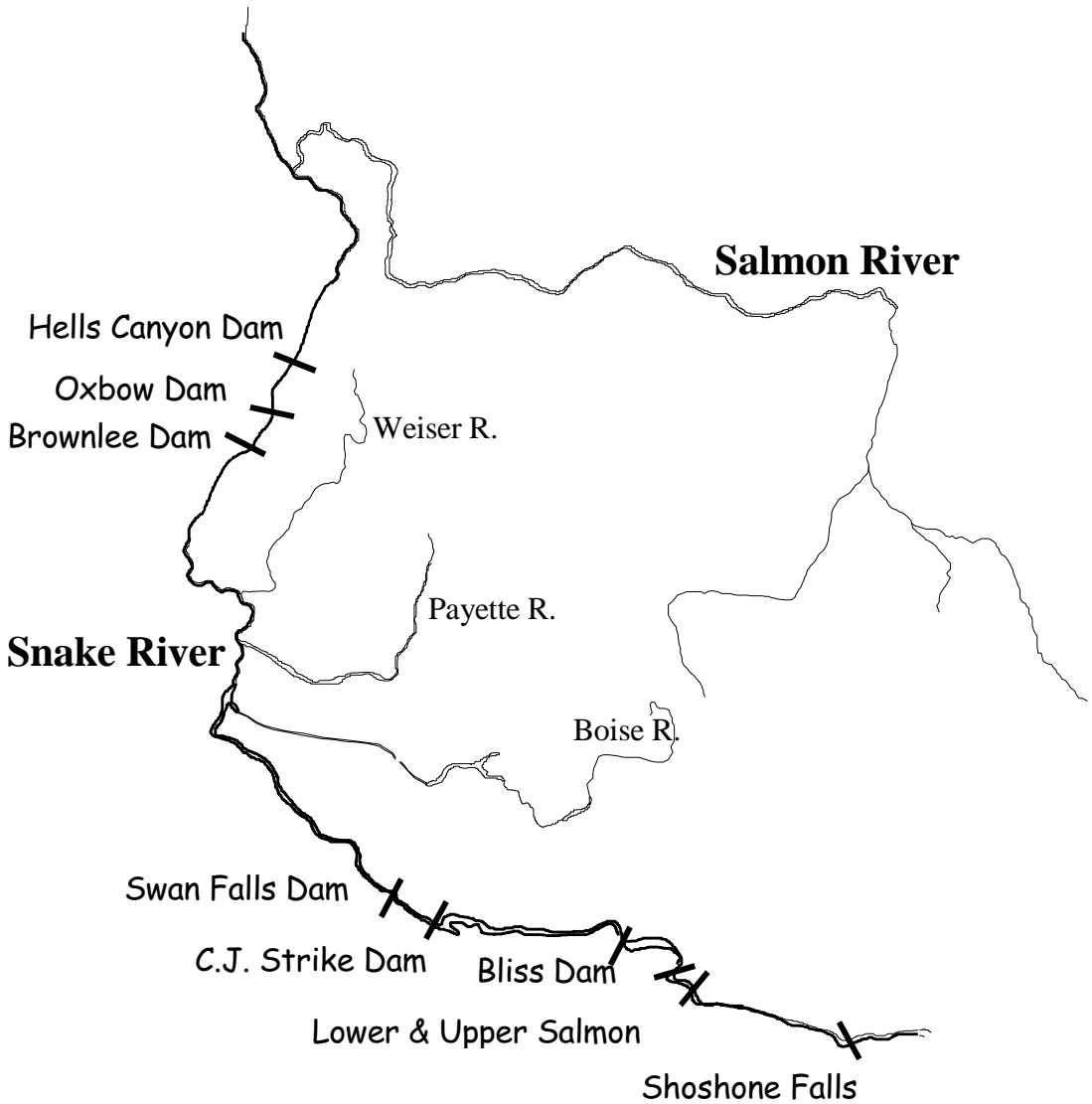
Figure 1. Nine river segments of the Middle Snake River between the confluence with the Salmon River and Shoshone Falls.

volved in predicting recruitment to age 1 include (1) mortality factors that influence recruitment by reducing the number of age-0 fish, and (2) mortality factors that reduce the number of juveniles and adults, thereby diminishing the future supply of spawning adults.

Survival of Age-0 White Sturgeon

Equation 1 describes recruitment as the number of eggs that survive each of six sources of mortality operating on white sturgeon during the first year of life:

$$\text{Recruitment} = (S_y S_1 S_2 S_3 S_4 S_5)(\text{\# eggs}). \qquad (1)$$

Total survival through the first year results from survival through the spawning and incubation period, followed by survival through the rest of the year. Total survival is the product of independent chances of surviving each factor, S_k, listed below:

- Surviving baseline mortality (S_y)
- Surviving temperature-related mortality during incubation (S_1)

- Surviving flow-related mortality during incubation (S_2)
- Surviving density-dependent and habitat-related mortality during incubation (S_3)
- Surviving larval export (S_4)
- Surviving exposure to poor water quality in reservoirs during summer (S_5)

Baseline mortality is applied first. Three factors that contribute to mortality, during spawning and incubation, are applied next (S_1–S_3). Larval export follows, and finally, we apply mortality due to poor summer water quality to offspring that survive the earlier periods of age 0.

We apportion the total number of deaths to each of the three factors that are applied simultaneously during spawning and incubation, using equation 2:

$$\#\,\text{deaths due to factor } k = \left(1 - \prod_k S_k\right)\frac{(1-S_k)}{\sum_k(1-S_k)}(\#\text{ eggs}). \qquad (2)$$

Baseline mortality of age-0 fish (S_y)–Baseline mortality sets an upper bound on survival S_y (Table 1). First-year baseline mortality includes nonviable or unfertilized eggs (50% in a hatchery setting [Doroshov1985]; 74% in the Kootenai River [Paragamian et al. 1996]), predation, and all other risks not included explicitly elsewhere in the model. Mortality during the first year can be as high as 99% (White Sturgeon Planning Committee 1992). The high fecundity of this species suggests that even higher levels of early mortality are typical (Winemiller and Rose 1992).

Incubation submodel–We developed a daily incubation submodel for the spawning and incubation period in spring and early summer, to simulate the three mechanistic factors that operate during this time. The incubation model estimates the effects of temperature, flow, and habitat during incubation, for each type of hydrologic year and each segment of the Snake River. The results are then provided to the main PVA model as input parameters (Figure 2).

The incubation model simulates a sample of 100 female spawners (or batches of eggs) with different spawning dates. These individuals are not simulated in the main PVA model; they are used here to characterize the range of environmental conditions encountered by white sturgeon during the spawning period. We first construct an empirical distribution of spawning temperatures for spawning dates estimated for eggs collected in the Snake River (mean = 14°C). Each female then draws a spawning temperature threshold from this empirical distribution to define the start of the incubation period for her eggs (Figure 3). The end of the incubation period is determined, for each batch of eggs, by simulating successive days and accumulating degree-days, as a function of average daily temperature, T_t, until a developmental threshold is reached (equation 3):

$$\text{Degree days} = 24\sum_t e^{0.071\,T_t} \qquad (3)$$

On average, white sturgeon eggs develop into free-feeding larvae after 1536 degree-days (Wang et al. 1985).

The incubation submodel was provided with historical daily average flow and temperature records over the period 1990–2000, for each river segment. The years 1990–2000 include four dry years, three normal years, and four wet years. In addition, we provided a lookup table relating weighted usable area (WUA) for spawning and flow for each river segment. The incubation model uses flow and temperature records, for each segment and year, to calculate three quantities over the incubation period for a sample of 100 females: (1) temperature-related survival, (2) average flow, and (3) minimum spawning WUA. We summarized these three quantities by calculating averages over years of the same hydrologic type and over the 100 females sampled each year. These averages are then provided to the main PVA model as site-specific input parameters (Table 2).

Temperature-related mortality (S_1)–Water temperature conditions during incubation may influence year-class strength in white sturgeon. In sturgeon species, early stages of development are the most sensitive to extreme temperatures (Nikol'skaya and Sytina 1979). Lethal temperatures and contaminants were suspected causes of high egg mortality (45%) in the Dalles Pool, compared with about 19% mortality in adjacent impoundments (Anders and Beckman 1995).

The incubation submodel (Figure 3) estimated temperature-related survival through incubation and development of larvae to the free-feeding stage for a series of years, between 1990 and 2000, in each of the segments of the Snake River. We calculate temperature-related survival through this life stage, S_1, from daily survival, as shown in equation 4:

Table 1. Parameters of the white sturgeon PVA model and values used in this analysis.

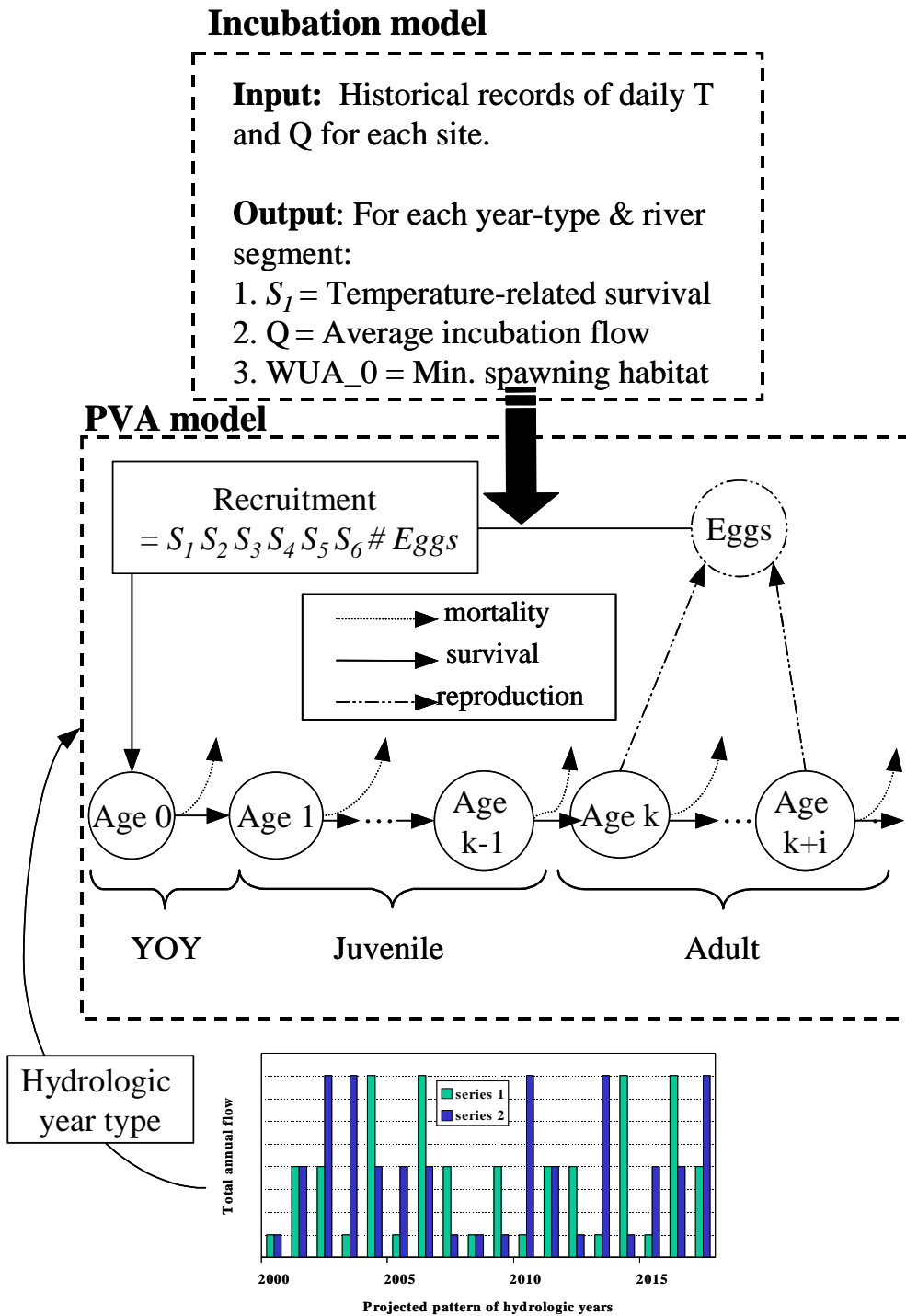| Name	Parameter description	Source and/or equation	Nominal value
S_y	Baseline first year survival rate (y^{-1})	Calibrated	0.00053
S_j	Survival rate of juveniles (y^{-1})	Calibrated	0.89
S_a	Survival rate of adults (y^{-1})	(Cochnauer 1983)	0.74
β_Q	Rate of decline in S_2 vs. average flow	Equation 5; (Counihan et al., in press)	−5.1
Qfact	Relates threshold average flow for good recruitment to 20th percentile of spring flows	Equation 5	0.60
OptEggDen	Maximum egg density with no DD (# m^{-2})	Equation 6; (Khoroshko 1970)	3,500
ResWul	Length of reservoir suitable for spawning (km)	Snake River data	1.0
LarvDur	Duration (d) of demersal larval stage	Equation 7; (Brannon et al. 1985)	1.0
L_0	Free-flowing distance with 0% chance of reaching reservoir (km)	Calibrated	45.0
L_1	Free-flowing distance with 100% chance of reaching reservoir (km)	Calibrated	12.0
Ssweep	Survival of larvae swept downstream	Calibrated	0.0001
LLT	Lower threshold temperature (°C)	Equation 8; (Wehrly 1995)	23.0
ULT	Upper threshold temperature (°C)	Equation 8	28.0
Shook	Survival of hooking	Snake River data	0.96
limit	Maximum per-capita harvest (# angler d^{-1})	Equation 14, calibrated	3.0
Dh	Density at inflection point of functional response in harvest (# km^{-1})		40.0
Mig_down	Annual downstream migration rate	Snake River data	0.02
Mig_up	Annual upstream migration rate	Fixed	0.0
Agemat_avg	Avg. age at first maturity for females, males (y)	(Cochnauer 1983)	18, 14
Shab_A	Intercept of age 1+ survival vs. juvenile and adult WUA (Table 2)	Calibrated	0.71
Shab_B	Slope of age 1+ survival vs. adult WUA (Table 2)	Calibrated	0.90
Agemat_SD	Std. dev. of age at maturity for females, males (y)	(Cochnauer 1983)	1.5, 1.5
SI_avg	Average spawning interval for females, males (y)	Snake River data	8, 2
SI_SD	Std. dev. of spawning interval for females, males (y)	Snake River data	0.8, 0.3
feca	Fecundity (# eggs) vs. fork length (cm) intercept	(DeVore et al. 1995)	0.072
fecb	Fecundity (# eggs) vs. fork length (cm) exponent	(DeVore et al. 1995)	2.94
Kvb	Rate of change in fork length (cm) with age (y)	(Lepla and Chandler 1995a)	−0.045
T_0	Initial age (y)	(Lepla and Chandler 1995a)	−0.795
L_∞	"Maximum" size of adults (cm)	(Lepla and Chandler 1995a)	275
Psweep	Maximum chance of larval export	Calibrated	0.7
LCmin	Minimum size vulnerable to capture (cm)	Snake River data	43.0
LCmax	Size fully recruited to gear (cm)	Snake River data	90.0
LHmin	Minimum legal length (cm)	Idaho state law	46.0
LHmax	Maximum legal length (cm)	Idaho state law	300.0

Incubation model

Input: Historical records of daily T and Q for each site.

Output: For each year-type & river segment:
1. S_1 = Temperature-related survival
2. Q = Average incubation flow
3. WUA_0 = Min. spawning habitat

PVA model

Recruitment
$= S_1 S_2 S_3 S_4 S_5 S_6 \# Eggs$

Eggs

⋯⋯⋯► mortality
───────► survival
─·─·─·─►reproduction

Age 0 → Age 1 → ⋯ → Age k-1 → Age k → ⋯ → Age k+i →

YOY   Juvenile   Adult

Hydrologic year type

series 1
series 2

Total annual flow

2000   2005   2010   2015

Projected pattern of hydrologic years

Figure 2. Overview of the PVA model. The incubation sub-model calculates input parameters used by the PVA model to simulate three mechanistic influences on white sturgeon recruitment. The environmental submodel simulates year-to-year variations in hydrologic year type as a first-order Markov process.
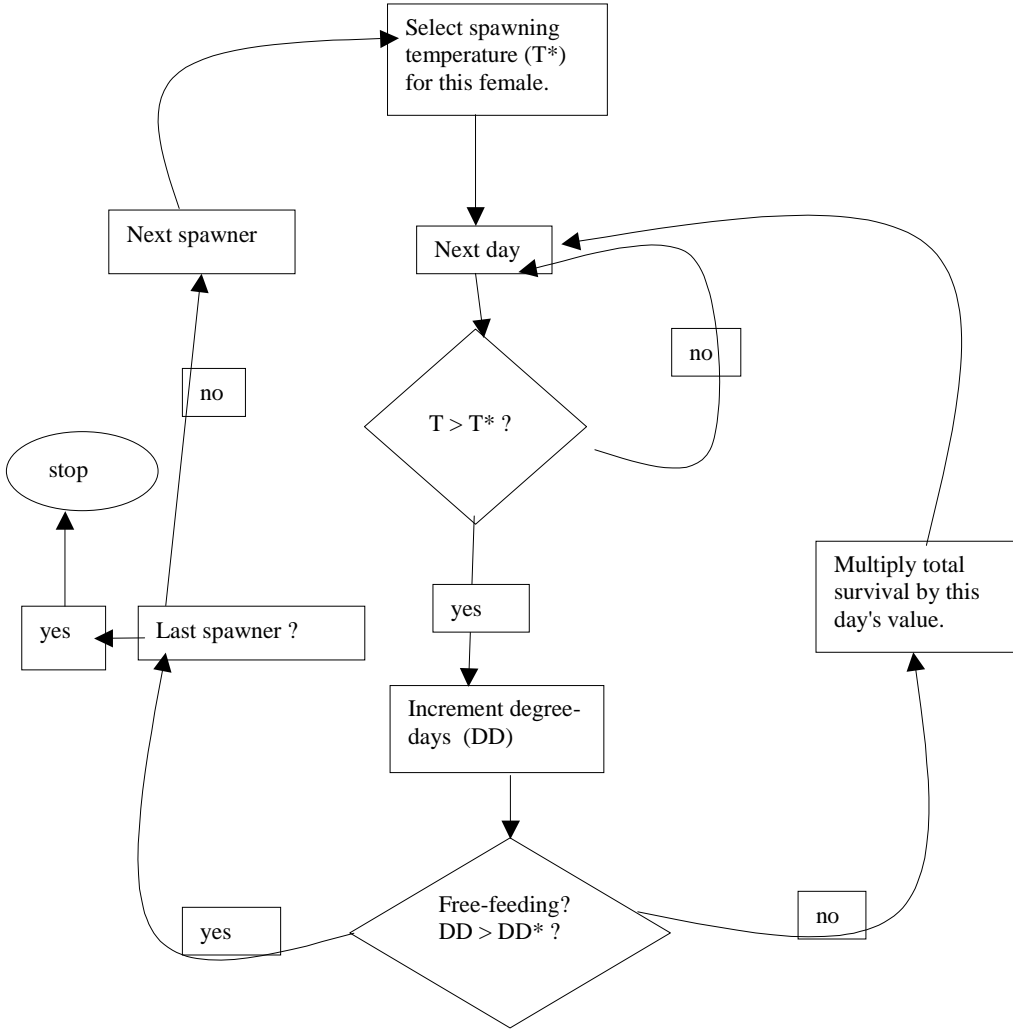
Figure 3. Flow chart of the incubation submodel depicting the estimation of temperature-related survival (S_1) during incubation for one female's eggs. The temperature threshold for spawning for a given female is T^*, and the degree-day threshold for development into a free-feeding larva is DD*.

$$S_1 = \prod_{t=1}^{tfeed} S(T_t), \qquad (4)$$

where *tfeed* is the number of days for the eggs spawned by a given female to develop to the free-feeding stage. On a given day, *t*, we calculate daily survival, $S(T_t)$, as a function of the average daily temperature, T_t (Figure 4). Wang et al.'s (1985) temperature-related survival data from laboratory experiments with California stocks are used, requiring us to assume that Snake River stocks have similar tolerances. We assume that temperatures

below 6ºC and above 21.5ºC are lethal and that temperatures between 6ºC and 17.5ºC do not pose any significant mortality.

The PVA model uses the average temperature-related survival through incubation for each river segment and hydrologic year type (S_1 in Table 2). We estimated S_1 by averaging results over the simulated egg batches and over years with similar (dry, normal, or wet) hydrology.

Flow-related mortality (S_2)–Sturgeons are believed to benefit from spawning in high velocity, turbulent waters. Various explanations have been pro-

Table 2. Segment-specific parameters of the white sturgeon PVA model.

Parameter description	Name	Hydro. year	River segment above dam listed								
			Upper Salmon	Lower Salmon	Bliss	C.J. Strike	Swan Falls	Brown-lee	Oxbow	Hells Canyon	Salmon River
Dam location	*dam_km*	All	989	933	922	902	795	737	459	439	398
Segment length (km)	*seg_km*	All	56.51	10.62	20.44	106.7	58.41	277.93	19.31	40.88	95.91
Free-flowing (km)	L_{ff}	All	46.02	0.17	11.58	60.83	38.62	185.68	0.00	0.00	95.91
Average width (km)	*width*	All	0.14	0.21	0.13	0.22	0.28	0.30	0.22	0.25	0.12
Initial density (# km^{-1})	*N0*	All	25	25	25	25	25	25	25	25	25
Initial % <95 cm	*Plen[0]*	All	73	73	73	73	73	73	73	73	73
% 95 to170.5 cm	*Plen[1]*	All	21.56	21.56	21.56	21.56	21.56	21.56	21.56	21.56	21.56
% > 170.5 cm	*Plen[2]*	All	5.44	5.44	5.44	5.44	5.44	5.44	5.44	5.44	5.44
Harvest effort (d./km)	E_i	All	8	8	8	8	8	8	8	8	8
Prob. of release	*Prel*	All	1.0	1.0	1.0	1.0	0.99	1.0	1.0	1.0	0.98
Flow threshold (Kcms)	*Q20%*	All	0.357	0.357	0.459	0.532	0.581	0.581	1.144	1.144	1.249
Slope of strike vs. size	*strike*	All	0.011	0.005	0.010	0.011	0.005	0.011	0.012	0.011	0.006
Trash rack spacing (cm)	*trash*	All	23.0	23.0	23.0	22.2	13.3	15.2	12.7	14.0	0.0
Avoidance threshold	*R**	All	0.78	0.78	0.78	0.78	0.67	0.78	0.78	0.78	0.78
Prob. entrainment	*entrain*	Dry	0.96	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.0
Prob. entrainment	*entrain*	Normal	0.78	0.99	0.97	0.98	0.99	1.00	0.96	0.97	0.0
Prob. entrainment	*entrain*	Wet	0.52	0.95	0.86	0.87	0.94	1.00	0.76	0.79	0.0
Retention time (d)	*Retain*	Dry	0.07	1.04	0.57	18.78	0.52	62.5	2.91	8.21	0.0
Retention time (d)	*Retain*	Normal	0.05	0.76	0.47	15.57	0.41	44.95	1.95	5.16	0.0
Retention time (d)	*Retain*	Wet	0.05	0.41	0.28	10.46	0.23	24.71	1.46	3.03	0.0
Temp. survival	S_1	Dry	0.948	0.951	0.957	0.943	0.801	0.807	0.827	0.826	0.894
Temp. survival	S_1	Normal	0.834	0.929	0.890	0.871	0.787	0.782	0.872	0.873	0.879
Temp. survival	S_1	Wet	0.845	0.919	0.892	0.884	0.742	0.795	0.787	0.627	0.781
DO-T fraction risk-free	*DOfree*	Dry	1.000	1.000	1.000	0.516	0.000	0.041	0.060	0.045	1.000
DO-T fraction risk-free	*DOfree*	Normal	1.000	1.000	1.000	0.745	1.000	0.301	0.001	0.084	1.000
DO-T fraction risk-free	*DOfree*	Wet	1.000	1.000	1.000	1.000	1.000	1.000	0.709	0.752	1.000
DO-T avg. risk	*DOrisk*	Dry	0.000	0.000	0.000	0.950	0.300	0.878	0.883	0.764	0.000
DO-T avg. risk	*DOrisk*	Normal	0.000	0.000	0.000	0.941	0.000	0.799	0.711	0.611	0.000
DO-T avg. risk	*DOrisk*	Wet	0.000	0.000	0.000	0.000	0.000	0.718	0.206	0.725	0.000
YOY WUA[1]	*WUA_0*	Dry	0.008	0.008	0.019	0.015	0.009	0.014	U[2]	U[2]	U[2]
YOY WUA[1]	*WUA_0*	Normal	0.008	0.008	0.019	0.016	0.032	0.023	U[2]	U[2]	U[2]
YOY WUA[1]	*WUA_0*	Wet	0.008	0.008	0.029	0.021	0.066	0.025	U[2]	U[2]	U[2]
Adult WUA[1]	*WUA_1*	Dry	0.005	0.057	0.026	0.120	0.006	0.179	0.163	0.172	0.2
Adult WUA[1]	*WUA_1*	Normal	0.005	0.057	0.026	0.120	0.006	0.179	0.163	0.172	0.2
Adult WUA[1]	*WUA_1*	Wet	0.005	0.057	0.026	0.120	0.006	0.179	0.163	0.172	0.2
Average flow (Kcms)	*Qspawn*	Dry	0.019	0.154	0.155	0.208	0.194	0.199	0.358	0.327	0.312
Average flow (Kcms)	*Qspawn*	Normal	0.151	0.187	0.186	0.241	0.344	0.344	0.998	1.000	1.011
Average flow (Kcms)	*Qspawn*	Wet	0.237	0.385	0.372	0.426	0.494	0.459	0.916	1.013	1.011

1. Fraction of segment length
2. U indicates that the value is unknown and that we did not feel comfortable extrapolating from a similar segment.
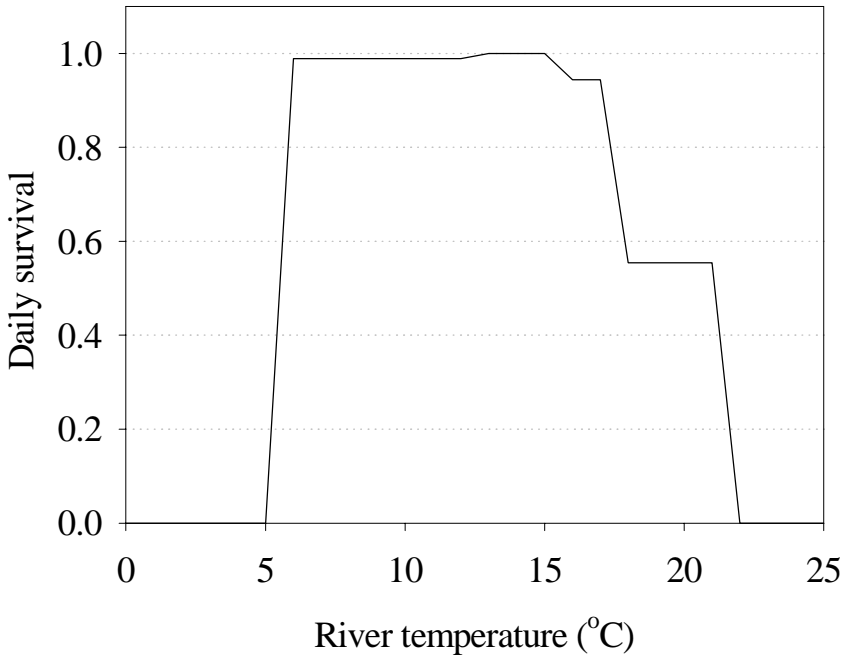
Figure 4. Flow chart of the incubation submodel depicting the estimation of temperature-related survival (S_1) during incubation for one female's eggs. The temperature threshold for spawning for a given female is T^*, and the degree-day threshold for development into a free-feeding larva is DD*.

posed. High river flows may be needed to remove fine sediments from spawning areas (Votinov and Kas'yanov 1978). Broadcasting eggs in fast, turbulent water may enhance egg viability, by dispersing adhesive eggs and preventing clumping. The tendency for egg predators to use slower water suggests that spawning in fast, turbulent water reduces predation on eggs. Dispersal by flow may also distribute eggs and, thereby, reduce competition (McCabe and Tracy 1994).

We hypothesized that flow-related survival, S_2, follows a truncated linear model, increasing with average flow during incubation, , until the average flow reaches a threshold, Q^*, above which flow-related survival is assumed to be 1.0. Empirical relationships involving flow are difficult to generalize to other sites because flow is usually a surrogate for other, less-easily measured variables, such as velocity or turbulence. We therefore defined Q^* as a segment-specific reference value set to a proportion (*Qfact*, Table 1) of the flow exceeded on 20% of the days between April, May, and June, $Q20\%$. The value of $Q20\%$ was calculated for each segment based on historical flow data (Table 2).

Counihan et al. (in press) evaluated the relationship between annual year-class strength of age-0 and age-1 white sturgeon in Bonneville Reservoir, below Dulles Dam, between 1989 and 1999. They found a positive partial correlation of 0.42 between recruitment and average flow, after removing the effect of temperature. We found that equation 5 described the relationship between the fraction of the maximum catch per unit effort of age-0 white sturgeon (used as a surrogate for survival, S_2) and average flow between May and July ($\overline{Q}$) with $\beta_Q = -5.1$ (Table 1):

$$S_2 = \begin{cases} e^{\beta_Q \frac{Q^* - \overline{Q}}{Q^*}}, & \overline{Q} \le Q^* \\ 1, & \text{otherwise.} \end{cases} \quad (5)$$

Density-dependent habitat mortality (S_3)–Lack of suitable habitat for the number of white sturgeon eggs spawned can lead to density-dependent early mortality. Khoroshko and Vlasenko (1970) reported poor survival of sturgeon eggs on artificial spawning grounds with egg densities in excess of 3,500 eggs m^{-2}. In our model, density-

dependent survival does not decrease from one until the fraction of eggs, at egg density, D, exceeds an upper density threshold, $OptEggDen$. At such high densities, density-dependent survival (factor S_3) equals the proportion of the eggs in excess of the threshold (equation 6):

$$S_3 = \begin{cases} 1, & D \leq OptEggDen \\ \dfrac{OptEggDen}{D}, & D > OptEggDen \end{cases} \quad (6)$$

This source of mortality will not be imposed in these simulation experiments, but we describe it here for use when the data needed as input become available.

Egg density, D, is calculated as the number of eggs divided by the length of habitat suitable for spawning and incubation, which changes with flow. Ideal spawning conditions for white sturgeon occur in free-flowing rivers during seasonal floods that normally occur during high spring runoff (Anders and Beckman 1995; Beamesderfer and Farr 1997; Marcuson et al. 1995; Parsley et al. 1993a). Although white sturgeon spawning behavior has not been formally studied, the behavior of white sturgeon is similar to that of other sturgeon species. These observations typically describe aggregation of adult spawners in deep pools that serve as staging areas for rolling and leaping displays. Spawning takes place in fast, turbulent waters located nearby (Parsley et al. 1993).

The availability of habitat suitable for the incubation period is estimated by weighted usable area (WUA) per km of river. Studies relating WUA to flow have not yet been completed in all nine segments in the Middle Snake River. Values of WUA_0 are listed in Table 2. We used the relationship between WUA and flow developed by Chandler and Lepla (1997) for free-flowing sections of the Snake River. These site-specific WUA-flow relationships relied on habitat suitability data for newly spawned eggs reported by Parsley and Beckman (1994) and a hydraulic characterization of the Snake River by Anglin et al. (1992).

For each batch of eggs, the incubation model computes a minimum WUA over the incubation period for free-flowing sections of river (Figure 2). An average minimum WUA, computed for each hydrologic year type, is provided to the main PVA model. The minimum WUA was lower in dry years than in normal years and lower in normal than in wet years, for all segments of the Snake River with free-flowing habitat.

The value of reservoir habitat for spawning and incubation is uncertain. Successful spawning takes place during wet years in tailraces of dams on the Columbia River, where dam spacing is close enough to eliminate free-flowing habitat (Parsley and Beckman 1994). We assume that river segments with no free-flowing habitat contain a relatively short distance of suitable habitat in the tailrace (*ResWul*; Table 1) that is only used when no free-flowing habitat is available for spawning.

In river segments that also have free-flowing habitat, reservoir habitat may contribute to or detract from WUA. Reservoir habitat may detract from recruitment by acting as a sink (Pulliam 1988), attracting spawners to areas that deteriorate in quality when changes in discharge or reservoir operations shift the locations of suitable habitat. Alternatively, reservoir habitat may be sufficiently riverine to contribute a small amount of habitat suitable for spawning and incubation. Our simulations assume that reservoirs had no effect on WUA in segments with free-flowing habitat.

Larval export (S_4)–One theory to explain low recruitment in short reservoir segments of river is that early life stages are lost to downstream populations (Seyler 1997). Like many riverine fishes, the white sturgeon has an early life stage that is buoyant and disperses downstream. In reservoirs with high turnover rates, larvae may be unable to settle to the bottom before being swept downstream to the next river segment.

White sturgeon are particularly likely to move downstream during the first year of life. In the Lower Columbia River, larvae were found downstream of sites where eggs had previously been observed (Parsley et al. 1993a). Brannon et al. (1985) observed that larvae entered the water column immediately after egg-hatch and remained in the water column 1 to 5 days. After this, they observed that larvae seek cover during the vulnerable stage of yolk-absorption. Larvae exposed to higher velocities initiated hiding behavior earlier. Larvae came out of hiding again at the larval-fry transition, which is marked by the initiation of feeding (Brannon et al. 1985). White sturgeon fry rose up into the water column, possibly as a way of dispersing from areas with insufficient food. In Brannon et al.'s experiments, the proportion of individuals in the water column increased to around 50%, during this stage. Young-of-the-year fish have also been observed moving downstream later in the year, possibly following a natural pattern of out-migration

(Coon et al. 1977). Lepla and Chandler (1995b) estimated that 6% of hatchery fry, released above Bliss Dam in 1991, moved downstream and survived entrainment at some time before summer sampling two years later.

The PVA model simulates only the first mechanism, larval migration of age-0 fish. The proportion of larvae that migrate is estimated by the product of the probability that a larva will reach the reservoir, P(reservoir), and the probability that a larva that has reached the reservoir will be swept downstream, P(swept|reservoir). We assume that spawning adults prefer free-flowing areas, when they are available. The simulated probability that a larva enters the reservoir decreases exponentially as the length of free flowing river, L_{ff}, increases. The probability of being swept downstream, once in the reservoir, decreases as its retention time, $Retain$, increases and as the duration of the demersal stage, $LarvDur$, increases. The retention time of each reservoir differs for the three hydrologic year types (Table 2). We estimate the proportion of larvae moving downstream according to equation 7:

$$S_4 = 1 - P(\text{swept}|\text{reservoir})P(\text{reservoir})$$

$$P(\text{reservoir}) = \begin{cases} 0, L_{ff} \geq L_0 \\ \dfrac{(L_{ff} - L_0)}{(L_1 - L_0)}, L_1 \leq L_{ff} \leq L_0 \\ P_{sweep}, L_{ff} \leq L_1 \end{cases}$$

$$P(\text{swept}|\text{reservoir}) = \begin{cases} \dfrac{LarvDur}{Retain}, LarvDur \leq Retain \\ 1, \text{otherwise} \end{cases} \quad (7)$$

Survival of larval export, S_4, is simply the fraction not swept downstream.

If free-flowing habitat is present, we assume that spawning occurs there. Without know-ing hydraulic details of a river segment, it is reasonable to suppose that larvae are less likely to be swept into the downstream reservoir in segments with longer free-flowing stretches of river. If we assume spawning aggregations are equally likely to occur anywhere in the free-flowing stretch, the average upstream distance of spawning sites increases with the length of the free-flowing habitat. As the upstream distance increases, so does the distance that must be traveled to reach the reservoir and the opportunities for settling out of the water column. We defined two parameters, L_0 and L_1, the free-flowing river lengths associated with a minimum (= 0) and maximum (= P_{sweep})

probability of reaching the reservoir, respectively (Table 1).

Water quality mortality of age-0 fish (S_5)–After the spawning and incubation period in spring, age-0 white sturgeon are vulnerable to episodes of poor water quality that occur in some reservoirs during summer. This factor is discussed in the next subsection with mortality factors that operate on older life stages.

Survival of Age-1 and Older White Sturgeon
Successful recruitment depends on the availability of adults to spawn and the number of eggs initially produced (equation 1 and Figure 2). Therefore, mortality factors acting on adults also influence recruitment. Natural survival rates of juvenile and adult white sturgeon are thought to be high because fast early growth makes them relatively invulnerable to predators (other than humans). Disease and starvation were likely the dominant components of natural mortality. Our simulations exposed juvenile and adult sturgeon to a baseline survival of S_j and S_a, respectively (Table 1). White sturgeon are exposed to additional mortality related to human activities, including (1) mortality during episodes of poor water quality in summer, (2) turbine mortality during entrainment, (3) lack of habitat for older life stages, and (4) angling (hooking mortality and tribal harvest). We considered mortality caused by these four mechanistic factors in our simulation experiments.

Water quality mortality of older fish–A combination of high water temperatures and low levels of dissolved oxygen (DO) in reservoirs, during summer months, can be lethal to white sturgeon. Twenty-eight white sturgeon were found dead in Brownlee reservoir in July of 1990, presumably because of anoxic conditions (DO < 1 mg/L). Episodes of anoxic conditions in these reservoirs typically coincide with high summer temperatures. Thus, high water temperatures limit access to shallower, but better oxygenated, habitat, while anoxic conditions limit access to deeper habitat. Coutant (1987) referred to this situation as a "DO-temperature squeeze."

In the PVA model, we use temperature and DO data for the day with the worst water quality, to estimate the probability of surviving each factor. These formulations are described in the two following paragraphs for a given location i. Once the two survival factors are calculated, we adopt the parsimonious assumption that the two risks

upper temperature tolerance limit for this species. We also observed that juvenile white sturgeon appeared stressed upon exposure to temperatures exceeding 23°C. In the PVA model, survival, as described by equation 8, decreases with temperature between a lower threshold, LT, and an upper threshold, UT, temperature.

$$
S_{T_i} = \begin{cases} 0, T_i > UT \\ \left(\dfrac{T_i - LT}{UT - LT} \right), LT \le T_i \le UT \\ 1, T_i < LT \end{cases} \tag{8}
$$

Low levels of dissolved oxygen (DO) can also contribute to white sturgeon mortality in reservoirs. Klyashtorin (1974) found that four species of Russian sturgeon shared DO thresholds over a range of temperatures. We fitted linear relationships, equation 9, between dissolved oxygen thresholds (mg/L) and temperature T (°C), to Klyashtorin's data:

$$
\begin{aligned} UDO &= 2.557 + 0.071 T, \text{stressful} \\ LDO &= 1.052 + 0.027 T, \text{lethal} \end{aligned} \tag{9}
$$

The upper threshold, UDO, is the concentration below which respiration is depressed, and the lower threshold, LDO, is the concentration below which sturgeon are killed during short-term laboratory experiments. As shown in equation 10, we assume that survival increases from zero to one, as DO increases from LDO to UDO:

$$
S_{DO_i} = \begin{cases} 0, DO_i < LDO \\ \left(\dfrac{DO_i - LDO}{UDO - LDO} \right), LDO \le DO_i \le UDO \\ 1, DO_i > UDO \end{cases} \tag{10}
$$

The equations above apply to any single location i. We estimate population-level exposure to poor water quality spatially over the reservoir, by assuming that the proportion of the sturgeon population exposed to poor water quality depends on the amount of refuge and the average risk in nonrefuge areas for the current hydrologic year type. We assume that individuals are distributed evenly throughout the river segment, prior to the worst summer episode. Each individual's annual chance of surviving this episode, shown in equation 11,

$$
\text{Survival} (= S_4 \text{ for age-0 individuals}) = [DOfree \times 1.0] \\ + \left[(1.0 - DOfree) \times S_{WQ} \right], \tag{11}
$$

depends on the fraction of river length that is risk free (DOfree in Table 2) and the average survival in the remainder of the river length, S_{WQ}. We estimated DOfree and S_{WQ} for the summer date, with the poorest water quality conditions for a representative year of each type: dry (1992), normal (1995), and wet (1997).

The CE-QUAL-W2 reservoir water quality model predicted the spatial distribution of water quality conditions for two reservoirs, Brownlee and C. J. Strike. The remaining reservoirs have uniform spatial patterns in water quality that could be deduced from sparse field measurements. In each reservoir, we summarized water quality in a matrix of all combinations of temperature and DO, in intervals of 1°C and 1 mg/L, respectively. For each cell i, in this matrix, we determined the volume within two meters of the reservoir bottom V_i, falling within this cell's range of water quality conditions (Figure 5A), and the probability of survival S_i (Figure 5B), for a white sturgeon exposed to those conditions.

Because we assume that individuals are evenly distributed throughout the river segment, risk-free is also the proportion of individuals with zero risk (survival = 1.0). For the remaining individuals, the chance of surviving temperature and DO conditions in the reservoir, during the episode, is S_{WQ}:

$$
S_{WQ} = \begin{cases} \dfrac{\left[\dfrac{\sum_i V_i S_{DO_i} S_{T_i}}{\sum_i V_i} - DOfree \right]}{1 - DOfree}, DOfree < R^* \\ 1, \text{otherwise} \end{cases} \tag{12}
$$

The assumption that individuals are uniformly distributed probably overestimates mortality because sturgeon can avoid poor water quality to some extent. We therefore added a threshold risk-free proportion, R^*, that accounts for the ability of individuals to avoid poor water quality (Table 2). This is needed because mortality estimates can be sensitive to movement assumptions, as demonstrated by a spatially explicit model by A. Sullivan (Oak Ridge National Labo-
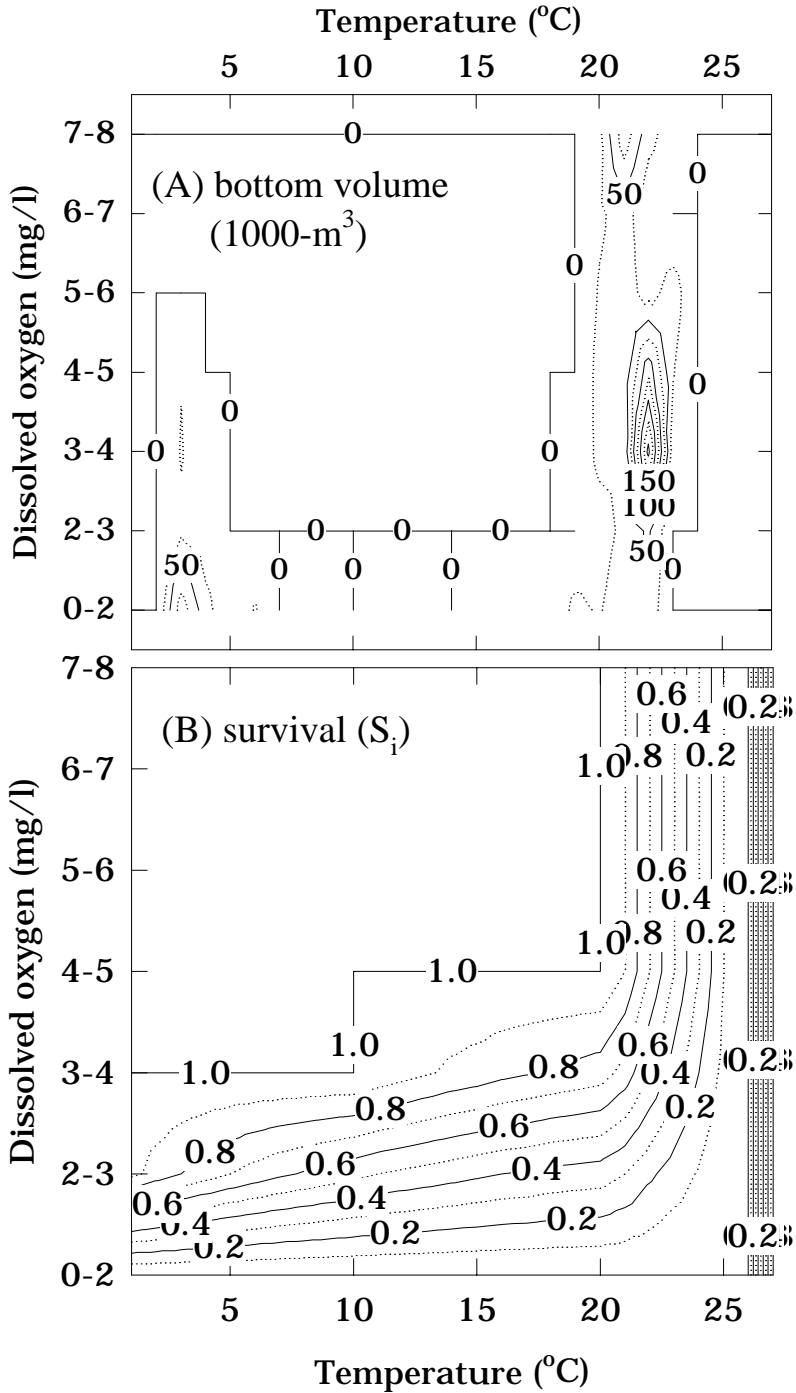
Figure 5. An example of two distributions used to simulate summer mortality caused by poor water quality in reservoirs. We summarize total risk-free bottom volume and average mortality risk for the remaining bottom volume from distributions of (A) reservoir bottom volume (1000 m³) and (B) survival over the ranges of dissolved oxygen and temperature shown.

ratory, personal communication), for Brownlee Reservoir. Sullivan's spatial model uses a daily time-step to simulate the movement of individual white sturgeon. An advective component represents movement in response to spatial gradients in water quality, and a diffusive component represents random exploratory movement. For sturgeon in the model that fail to escape risky habitat, this model applies a location-specific survival (S_{DO} and S_T). Simulating daily movement, in this manner, nearly doubles the predicted survival of white sturgeon through summer, in Brownlee Reservoir.

Turbine mortality–The risk of turbine mortality depended on the size of an individual fish, the hydrologic year type, and the type of turbine. This mortality acted on age-1 and older sturgeon that migrate downstream. We assumed that 2% of the population migrated downstream annually, based on two estimates in the Snake River by K. Lepla. In other words, migration is considered a voluntary behavior of juveniles and adults. To move from above to below a dam, a sturgeon must either be spilled over the dam or entrained through the turbines. Given that an individual is migrating, its risk of entrainment through the turbines is estimated by the ratio of the volume of flow entrained by turbines to the total volume of flow (Figure 6A; *entrain* in Table 2). As a result, survival is enhanced during wet years, when a higher proportion of flow is spilled rather than routed through turbines.

The size-dependence of turbine mortality is hydropower project-specific. We calculated turbine mortality from project-specific parameters, using formulas developed for the appropriate turbine style: one for Kaplan turbines (Von Raben 1957, cited in Cada 1990) and another for Francis turbines (Nece 1991). For both styles, the probability that an entrained sturgeon would be struck by a turbine increased linearly with sturgeon length (Figure 6B; *strike* in Table 2). This model assumes that any blade strike is lethal.

Habitat-related mortality–Because sturgeons use a variety of large-river habitat types, as well as coastal estuaries and ocean habitat, a much broader definition of habitat would ideally be used for this group than is typically applied to fishes (Beamesderfer and Farr 1997). Unfortunately, no such measure of habitat quality has been developed for sturgeon, and we are left with using the usual weighted usable area (WUA) for juvenile and adult life stages. Our approach focuses on quantifying WUA, in free-flowing habi-

tat, but supplements this estimate with a simple estimate of suitable habitat contributed by each reservoir. In reservoir habitat, we applied the depth suitability criteria to bathymetric data at a fixed time, to estimate suitability for juveniles and adults. In free-flowing river habitat, we used habitat suitability criteria, involving both depth and velocity, to obtain a relationship between WUA and flow. Developing a relationship between WUA and flow requires (1) suitability criteria, and (2) hydraulic data as a function of river flow. We used historical daily flow data to estimate the average WUA for each hydrologic year type and river segment. Finally, the free-flowing and reservoir values were summed.

Habitat suitability criteria for free-flowing habitat were quantified for juvenile (≤120 cm) and adult (>120 cm) white sturgeon in the free-flowing segment below Bliss Dam (Lepla and Chandler 1995a). They developed suitability criteria for each life stage, by fitting a piecewise linear relationship between catch per unit effort (CPUE) and depth and another between CPUE and velocity. Since the Bliss study, suitability criteria have been updated, with habitat use data from other riverine sections of the Middle Snake River for use in the model. In general, juveniles and adults were more frequently found in deep habitat than in shallow habitat and in low-velocity habitat than in high-velocity habitat.

Hydraulic data were available for free-flowing sections of river below Lower Salmon Falls, Bliss, C. J. Strike, and Swan Falls dams. Field measurements of depth and velocity, at several flows, were taken at representative cross-sections in a variety of free-flowing habitat types (e.g., pools, riffles, runs). A hydraulic model was used to predict the depth and velocity distribution available in each of the segments at different flows. The suitability criteria were combined with these depth and velocity distributions to produce a relationship between weighted usable area and flow.

In two river segments with free-flowing sections (below Shoshone Falls and below Hell's Canyon Dam), hydraulic data have not yet been quantified. We inferred WUA below Shoshone Falls as follows: (1) we estimated the proportion of habitat in each habitat type (run-pool-riffle-rapid) from aerial photos; (2) we then applied the estimates of WUA per unit length for low, median, and high flows below Lower Salmon Falls Dam for these four habitat types, to the corresponding habitat types below Shoshone Falls. Hydraulic data are now being collected below Hells Canyon
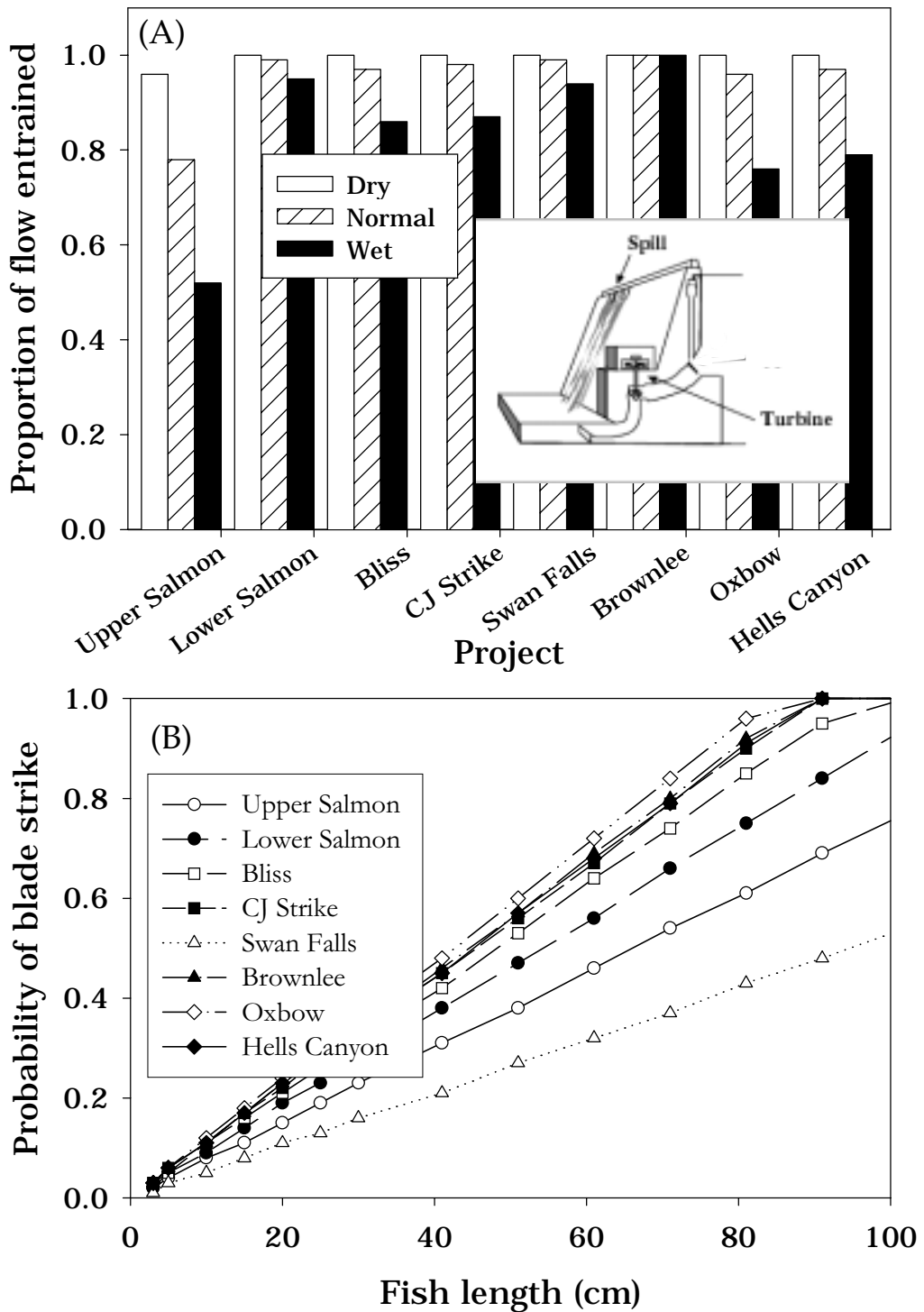
Figure 6. Entrainment mortality of juvenile and adult white sturgeon that are migrating downstream results from two events: (A) entrainment of the fish through turbines (more-likely in dry years), and (B) the turbine blade striking the fish (more likely for larger fish).

Dam. For the present, we assumed that the amount of suitable habitat below Hells Canyon Dam per unit river length slightly exceeds that in the segment with the highest quantity because this segment is considered to have the best spawning habitat.

The influence of habitat quantity on survival of age-1 and older white sturgeon has not been quantified in the field. Therefore, we assumed that the effect of suitable habitat availability on survival follows a simple linear function of WUA for juveniles and adults, *WUA_1*. Two parameters of this relationship are the intercept, *Shab_A* and *Shab_B* (Table 1).

Angling mortality–After 1970, the Idaho Fishery permitted only catch-and-release fishing, except for Native American tribes (Cochnauer 1983; Cochnauer et al. 1985). Although this policy has led to partial recovery of the populations affected (Cochnauer et al. 1985), populations are still exposed to hooking mortality, poaching, and legal harvest by native tribes.

We represent the likelihood of catching a given sturgeon as a function of its size, the size-selectivity of gear, and the fishing effort expended. We simulate the annual risk of angling mortality, for a particular individual, as a chance of being captured and suffering mortality. The probability of capture for a given river segment j, P_{cap}, is the product of two risk factors that each increase from zero to one, scaled by fishing effort E_j (Table 2). Factor F_1 depends on the density of the population in segment j, D_j, and risk factor F_2 depends on the size of the individual fish, L.

$$P_{cap} = E_j F_1(D_j) F_2(L) \qquad (13)$$

Fishing pressure typically increases with fish population density. We define a density factor that follows a Type-3 functional response to population density, D, where we specify the density at which the inflection point occurs (D_h) and the limit on hourly catch per person (*limit*).

$$F_1(D_j) = \frac{limit\, D_j^2}{D_h^2 + D_j^2} \qquad (14)$$

Larger individuals are more vulnerable to capture and harvesting. To reflect this reality, we adjust harvest risk for individual size L, which we calculate from age. Sturgeon that are smaller than LC_{min} are not vulnerable to capture (i.e., $F_2(L) = 0$),

and those larger than LC_{max} are completely vulnerable (i.e., $F_2(L) = 1.0$).

$$F_2(L) = \frac{L - LC_{min}}{LC_{max} - LC_{min}} \qquad (15)$$

We assume that the risk of harvest is zero for sturgeon smaller than a minimum legal length, LH_{min}, and for sturgeon larger than a maximum legal length, LH_{max}, as set by fishing regulations. To simulate hooking mortality of fish that are captured but then released, we specify the probability of release (*Prel* in Table 2) and the probability of surviving hooking (*Shook* in Table 1). The overall probability of surviving harvest and hooking mortality, $S_{H\&H}$ for a fish of size L is

$$S_{H\&H} = \begin{cases} (1-P_{cap}) + P_{cap} P_{rel} S_{hook}, \\ LH_{min} \le L \le LH_{max} \\ \qquad (1-P_{cap}) + P_{cap} S_{hook}, \text{ otherwise} \end{cases} \qquad (16)$$

Model Calibration

We calibrated the model by comparing current population sizes with those predicted by the model after simulating a 200-year period. The model was initialized with densities of 25 sturgeon/km in each river segment. We assumed an initial age distribution of age-1 and older fish that would result in the current size distribution below Hells Canyon reservoir: 73% less than 95 cm, 22% between 95 and 170.5 cm, and 5% greater than 170.5 cm. We compared model predicted population densities in the final year with current field estimates of population densities for each segment. The three baseline mortalities (Table 1; S_y, S_j, S_a) were calibrated in an automated fashion. Following this step, we adjusted mortality-related model parameters, within the range of reported values, until the predicted population densities matched field-estimates reasonably well. Comparisons of age distributions and catch data were also used to guide decisions about which parameters to change.

Simulation Experiment

To estimate the importance of the mechanistic mortality factors, we used the PVA model to simulate the final number of age-1 recruits for each of the river segments. Parameter values were ob-

tained by calibration as described above (Tables 1 and 2). Mortality factors that were not of specific interest, such as baseline mortality, were included but did not vary among treatments in the simulation experiment presented here. We conducted the simulation experiment by simulating 100 replicates of the Middle Snake River populations for 200 y. The main prediction from the model was the recruitment to age 1 in the last year of the simulation. We compared a baseline scenario that included all mechanistic mortality factors operating on model fish with scenarios in which we removed various factors, one at a time. The seven factors that we considered were

1. temperature-related mortality during incubation,
2. flow-related mortality during incubation,
3. downstream export of larvae,
4. episodes of poor water quality in reservoirs during summer (all ages),
5. habitat-related mortality of juveniles and adults,
6. turbine strike following entrainment, and
7. angling mortality (harvesting or hooking).

Sensitivity Analysis

We conducted a sensitivity analysis using the PRISM software developed at ORNL (Gardner et al. 1981). We included both nonsegment-specific input parameters (i.e., those in Table 1) and segment-specific parameters (i.e., those in Table 2), particularly those associated with modeling the effects of mechanistic factors. For the segment-specific variables, we defined new parameters that served as multipliers of the values in Table 2, so that only one value was needed for all segments. The PRISM program drew a Latin hypercube sample of parameters of size 5,000 from a multivariate normal distribution, with a 10% coefficient of variation surrounding the nominal value and no correlations among parameters (Table 1).

We conducted Monte Carlo simulation of the 5,000 parameter sets to predict recruitment. In Table 3, we report the relative partial sum of squares between model-predicted recruitment for each river segment and each parameter.

Results

The following three sections will present three types of results. The first section will describe the results of model calibration. The second section will describe the results of our simulation experi-

ment to evaluate limiting factors. The third section will describe the results of our sensitivity analysis.

Model Calibration

The results of model calibration are shown in Figure 7. The inset figure shows the relationship between model-predicted and field estimates of population size. For those river segments with populations too small to estimate, we used the actual number of white sturgeon captured.

Simulation Experiments

We compared recruitment predicted by simulations with all mortality factors and with each of the mechanistic factors of interest removed (Figure 8). Removal of each factor usually led to either no significant change or to an increase in recruitment, compared with the simulations with all factors (Figure 8A). In some cases, decreases can result from stochastic variation among simulations or from density-dependent effects.

Between Shoshone Falls and Upper Salmon Falls Dam[1], habitat-related mortality, acting on age-1 and older fish, was the factor that, when removed, led to the greatest increase in simulated recruitment (Figure 8B). Although this segment is otherwise well suited for habitation by age-1 and older white sturgeon, much of the flow is diverted above Shoshone Falls for irrigation purposes.

In the two short reservoirs below Upper Salmon Falls Dam and below Lower Salmon Falls Dam, eliminating larval export had the greatest potential to increase simulated recruitment (Figure 8B). The river segment between Bliss and C. J. Strike dams is relatively long, with one of the two largest populations in the Middle Snake River. Our simulations suggest that small benefits resulted from removing each factor, but removing angling mortality resulted in the greatest increase (Figure 8B).

Between C. J. Strike and Swan Falls dams, angling mortality and larval export were the two factors that, upon removal, resulted in the largest increases in recruitment. Turbine strike played a secondary role. The segment below C. J. Strike Dam is known to be a popular fishing site for stur-

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[1]A 2001 survey found a much larger population consisting mainly of stocked white sturgeon in this segment. The results reported here were produced by a model calibrated to a much lower estimate of population size.

Table 3. Sensitivity of predicted final recruitment in the river segment above the dam listed (columns) to selected parameters (rows). The relative partial sum of squares in the body of the table include a sign to indicate the direction of influence. Values can range in magnitude from –1.0 to +1.0; those smaller than 0.01 are shown as zeroes. We omitted the segment between Oxbow and Hells Canyon Dams because variations in parameters did not lead to sufficient variation in recruitment (= 0.0).

Parameter Name	Upper Salmon	Lower Salmon	Bliss	C.J. Strike	Swan Falls	Brownlee	Oxbow	Salmon River
Agemat_avg	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–0.0337
Dh	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
R*[1]	0.0	0.0	0.0	–0.1074	–0.0657	–0.0903	0.0	0.0
DOfree[1]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
DOrisk[1]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
dtrash	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Effort[1]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Entrain[1]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
limit	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
L_0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
L_1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MaxFshDen	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mig_down	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Psweep	0.0	–0.0146	–0.0168	0.0	0.0	0.0	0.0	0.0
β_Q	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Qfact	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Retain[1]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
ShabA	0.1015	0.0465	0.0	0.0	0.0410	0.0	0.0	0.0
ShabB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Shook	0.0333	0.0217	0.0	0.0501	0.0410	0.0	0.0	0.1422
SI_avg	–0.0868	–0.0598	–0.0283	–0.1651	–0.1332	–0.0288	0.0	–0.3296
Ssweep	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S_1[1]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Strike[1]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WUA_1[1]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
R^2 (%)[2]	0.2617	0.1668	0.0715	0.3603	0.3237	0.1367	0.0125	0.5242

1. Sensitivity to segment-specific parameters was determined by varying a multiplier of these parameters around a value of 1.00.
2. Low R^2 values suggest that random influences are important and call into question the sensitivity results for this response variable.

geon catch-and-release angling.

In the three river segments between Swan Falls Dam and Hell's Canyon Dam, the model predicted no recruitment after 200 y, with all factors present. Only by removing poor water quality as a factor, did the model predict recruitment. In the river segment below Hell's Canyon Dam, small increases in recruitment resulted from removing angling and poor water quality. The effect of water quality occurs because the upstream segments provide a supply of downstream migrants only when this factor is mitigated.

Sensitivity Analysis

We found that the most sensitive parameter was often one that controlled the most important mechanistic factor operating in a segment (Table 3). Parameters *Shab_A* and *WUA_1* were impor-

tant in the segment between Shoshone Falls and Upper Salmon Falls Dam, where juvenile and adult habitat was predicted by the model to be the most limiting habitat. Parameter *Psweep* was important between Upper Salmon and Bliss dams, where larval export was predicted to be the dominant factor. Parameter *R**, which controls the ability of sturgeon to avoid poor water quality, was important between C. J. Strike and Oxbow dams. Poor water quality was identified by the model as a dominant factor in two of the three segments in this range (between Swan Falls and Oxbow dams). The segment between Oxbow and Hells Canyon dams was excluded because small variations in parameters did not alter recruitment predictions, which were always zero. Below Hells Canyon Dam, *Shook*, which is associated with angling mortality, was identified as important.
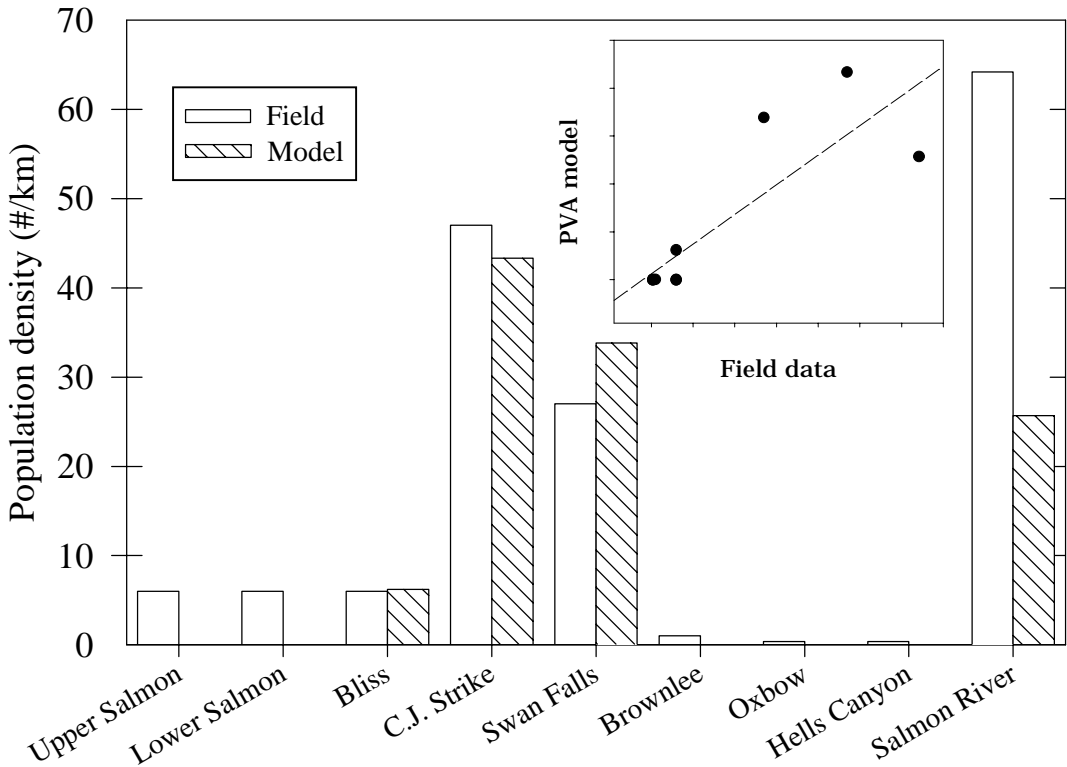
Figure 7. Comparison of calibrated final population density simulated by the PVA model, including all mortality factors, with those observed in the field.

The sensitivity analysis identified demographic parameters for females, *Agemat_avg* and *SI_avg*, as important in river segments with relatively large simulated recruitment. The direction of effect of the parameter variations was as expected (i.e., increased age at maturity leads to decreased recruitment), which is encouraging.

Discussion

The ranking of factors, predicted by the model to influence recruitment, differed among river segments, but the following hierarchical pattern emerged: first, we observed a clear distinction between river segments limited by episodic poor water quality and those with adequate water quality. Second, among river segments with better water quality, short river segments were regulated by different factors than longer segments. These patterns are discussed below, in three separate sections.

River Segments with Poor Water Quality

In those segments with poor summer water qual-

ity, this factor dominated all others. Poor summer water quality was important between Swan Falls Dam and Hells Canyon Dam and even had indirect consequences downstream of Hells Canyon Dam. The model predicts that removal of other factors would not be sufficient to reestablish recruitment in these populations, unless water quality also improved. One interesting result was that simulated mortality, due to poor water quality in Brownlee, reduced migration input to the long segment of river below Hell's Canyon Dam.

Brownlee reservoir experiences severe water quality degradation in dry and normal hydrologic years because of nutrient influxes from agricultural activity and municipal wastes from the surrounding watersheds. In wet years, summer flows are high enough to prevent development of large populations of algae that produce anoxic conditions in the reservoir.

Short Reservoir Segments with Adequate Water Quality

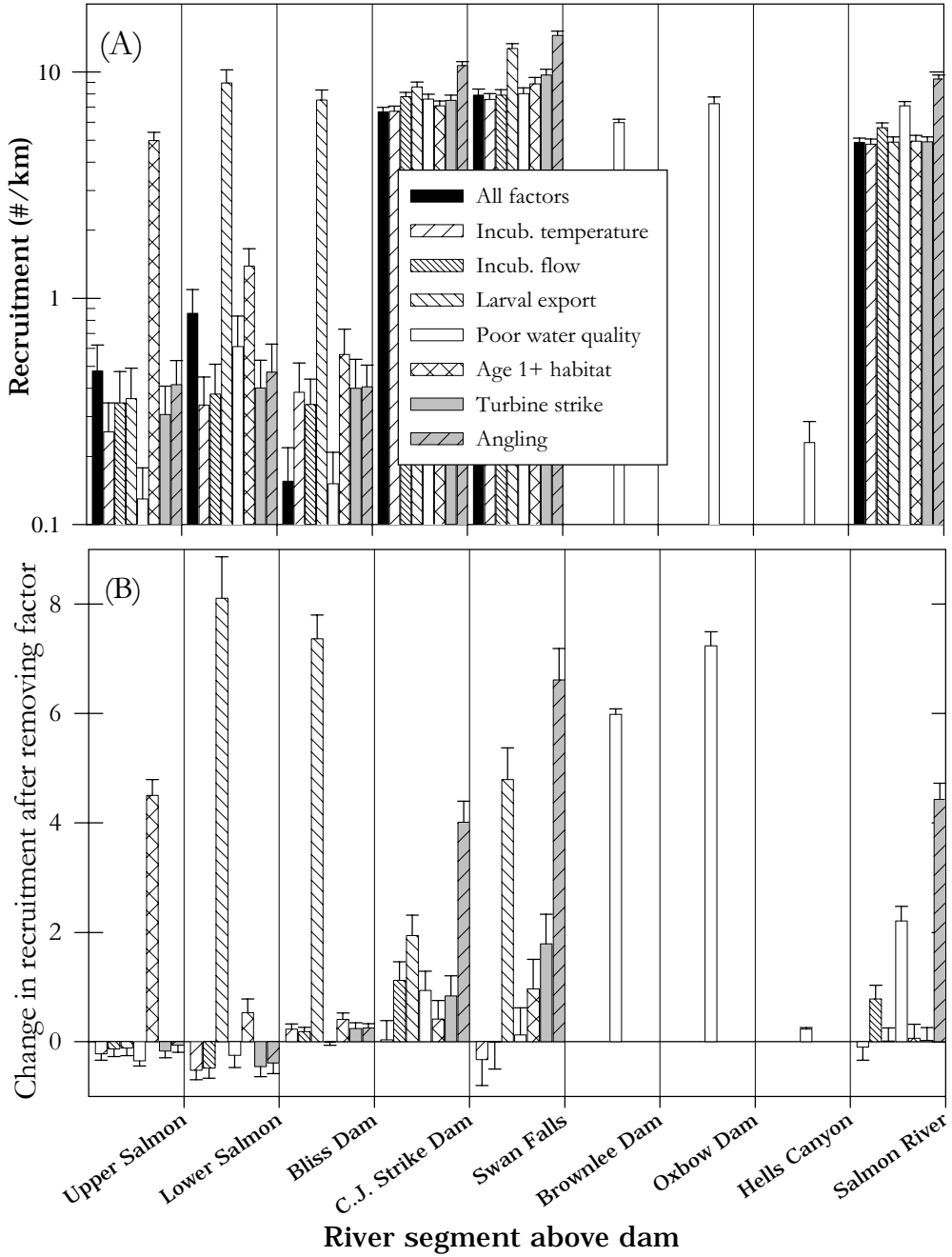Four short river segments (i.e., above Lower Salmon, Bliss, Oxbow, and Hells Canyon dams;

Figure 8. The effect of removing each mechanistic factor (Incub. = during incubation) on recruitment in each river segment is indicated by (A) the simulated final average recruitment and (B) the difference between simulated final average recruitment with all factors included and with one factor removed.

11, 21, 19, and 42 km in length, respectively) consist primarily of impounded reservoir habitat. Field studies indicate that these reservoirs support very small white sturgeon populations (Figure 7) and produce no detectable numbers of young fish. These segments have little or no free-flowing habitat because of the close spacing of adjacent dams. The two segments between Upper Salmon Falls Dam and Bliss Dam do not have severe water quality problems. Larval export was predicted to be a limiting factor in these reservoirs. Export losses have been implicated as a cause for the extirpations of broadcast spawning cyprinid species with semibuoyant eggs, in short, impounded segments of the Rio Grande and Pecos rivers of New Mexico (Plantania and Altenbach 1998). In the case of white sturgeon, the eggs are adhesive and dispersal occurs later, during the larval and early juvenile life stages. Additional studies of the dispersal strategies and spatial ecology of this species are needed to evaluate minimum river length requirements.

We note that spawner limitation might also be important as a cause of lost recruitment in short river segments. Because fewer adults are available to reproduce in these short segments, simulated opportunities for reproduction and recruitment are less frequent. As a result, small populations are typically more vulnerable to extinction than larger populations. These simulation experiments were not designed to quantify spawner limitation in these reservoirs, but these effects of fragmentation are discussed more generally in Jager et al. (2001).

Longer River Segments with Adequate Water Quality

Four longer river segments with adequate water quality are the segments below Shoshone Falls, Bliss, C. J. Strike, and Hells Canyon dams. We will not include the segment below Shoshone Falls in this discussion (see footnote on page 17). The idea of identifying a single limiting factor was not as useful for these segments because recruitment showed a relatively weak response to several factors. Angling, larval export (or rather larval import from upstream), flow during incubation, turbine strike, and poor water quality had an impact in one or more of these longer river segments.

Two mortality factors that increase in proportion to population size tended to be important in the longer segments with larger populations between Bliss and C. J. Strike dams and below Hells Canyon Dam. For example, angling reduced simulated recruitment between Bliss and Brown-lee dams and below Hells Canyon Dam because angling pressure increased in these segments with higher sturgeon densities. Likewise, the importance of entrainment and turbine strike increases with the size of the upstream population.

Downstream Effects

In two instances, we observed a factor that was important to recruitment in a river segment, not because it had a direct influence within the segment but because of its influence on the upstream population. This explains the influence of poor water quality on the population below Hells Canyon Dam, which experiences good water quality but receives fewer immigrants from upstream populations, when the effects of poor water quality are simulated. A second example is the influence of larval export on the river segment between C. J. Strike and Bliss dams and the river segment between Bliss and Swan Falls. These two longer segments experience lower immigration when the two short upstream segments dwindle in size.

Caveats and Future Directions

The relative importance of the seven factors for the nine river segments depends on assumptions and parameter values used by the PVA model. As new information becomes available, these results will require revision. Several factors that are often mentioned as negatively affecting sturgeon recruitment were less important than expected in our model results, for example, flow conditions during spawning and incubation. This may indicate that the current model formulation may improve as we learn more about these processes.

Because the relative ranking of the factors depends on parameter values that are, in some cases, best guesses, it will be important to supplement this analysis with an uncertainty analysis. In contrast to sensitivity analysis, which identifies parameters with the greatest local influence, uncertainty analysis quantifies changes in model predictions (i.e., factor rankings) over a much broader range of possible parameter values (Drechsler 2000).

Because mortality attributed to the mechanistic factors simulated here has not been quantified, field studies to improve confidence in the choices of equations and parameter values are needed. For example, poor water quality and larval export were two dominant factors predicted by our model to limit recruitment. Although the effect of low dissolved oxygen on early life stages has been

studied in the lab (Klyashtorin 1974), the tolerances of juvenile and adult white sturgeon and the ability of all ages to avoid poor habitat are less well known and could benefit from further study. The interactions among factors, such as temperature and dissolved oxygen, are poorly understood and are not now represented in the model. Brief exposure to one factor may cause enough stress to increase susceptibility to another factor, resulting in a greater cumulative impact. Larval export was also highlighted by our results as an important process that reduces recruitment in shorter river segments. Studies to quantify travel distances for larvae at different flows, and studies to quantify the effect of density on survival of early life stages, would provide valuable insights into this process.

Clearly, there is no lack of opportunity for learning more about factors that influence white sturgeon recruitment in this highly modified large-river ecosystem.

Acknowledgements

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