Modeling Chinook Salmon with SALMOD on the Sacramento River, California

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Abstract. – Four races of Pacific salmon crowd the Sacramento River below a large reservoir that prevents access to historical spawning grounds. Each race is keyed to spawn at specific times through the year. A salmon population model was used to estimate: (1) the effects that unique run timing, interacting with seasonal river flows and water temperatures, have on each race; and (2) which habitats appeared to be the most limiting for each race. The model appeared to perform well without substantive calibration. Late fall, winter, and spring run Chinook do not appear to have the same production potential as fall run Chinook even though fall run production is more variable than that for the other three races. Spring fish have the lowest production on average, and production appears to be declining through time, perhaps making that race harder to recover should the population become more depressed. Rearing habitat appears to be the factor most limiting production for all races, but water temperature is responsible for most year-to-year production variation.

Key words. – Chinook salmon, Sacramento River, phenology, production potential, modeling

INTRODUCTION

Pacific salmon are ecologically important, commercially valuable and significant to the human heritage of North America, but a variety of constraints have reduced their numbers along the West Coast to disturbing levels. Conditions in the ocean, including both commercial fishing and food supply, have undoubtedly been factors in the decline of the salmon, but freshwater conditions have been the focus of much effort in trying to understand the array of factors associated with survival of these generally prolific species. Hatcheries currently supplement many salmon runs heavily, although some people would argue that that this may be accompanied by a genetic cost to the populations that is yet another factor in their decline.

The Chinook (*Oncorhynchus tshawytscha*) of the Sacramento River (Figure 1) have not been immune from these declines, due in part to the

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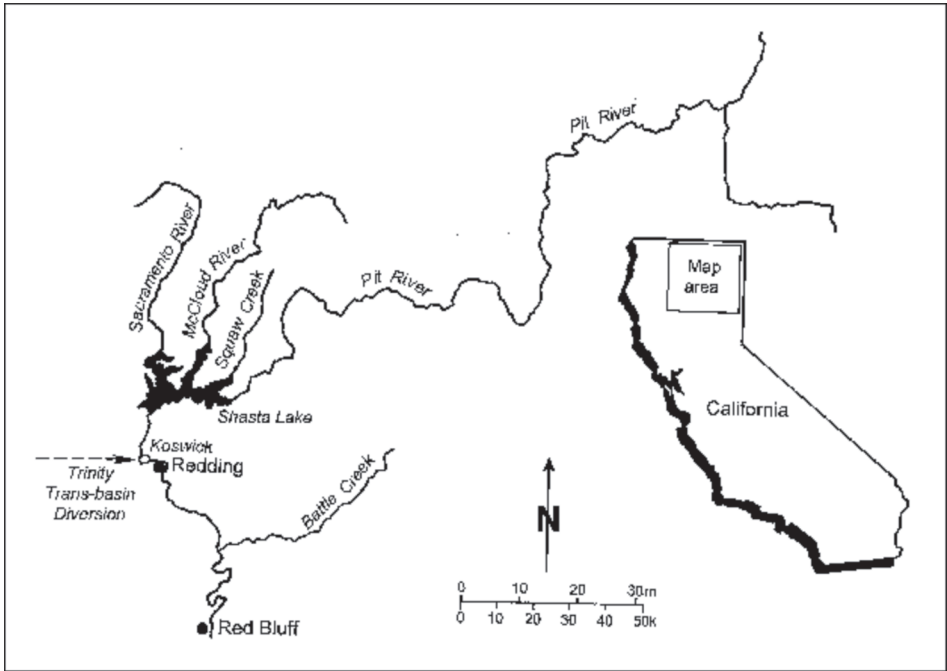
Fig. 1. – General map of the study area extending near Redding California and the upper Sacramento River watershed. The Trinity River is in a neighboring watershed to the west. Red Bluff Diversion Dam is immediately south of Red Bluff.

construction of a major impoundment on the mainstem, exploitation, and other habitat alterations (Clark 1929; Fisher *et al.* 1991; Yoshiyama *et al.* 2000). Pre-dam, the McCloud River was the premier spawning stream for all four races and the upper Sacramento a good second. The Pit River had fall and spring fish only and was considered of lesser quality (Yoshiyama *et al.* 2000). Regardless of quality, runs in all of these streams are now extirpated and what remains of their stocks crowd the mainstem and small spring-fed tributaries below the dam. Current (1991-1997) run size estimates, both natural and hatchery-reared, are on the order of 41,000 fall, 6,700 late fall, 600 winter, and 2,500 spring fish, though precise year-to-year counts are unavailable (Yoshiyama *et al.* 2000).

Adverse water temperatures in the Sacramento River below Shasta Dam are believed to be one of many factors associated with the decline of anadromous salmonids, particularly the endangered winter run Chinook salmon, the first Pacific salmon listed under the U.S. Endangered Species Act. The efficacy of the $80+ million temperature control device (TCD) recently installed at Shasta Dam was evaluated prior to the TCD's installa-

tion using a salmon mortality model developed by the Bureau of Reclamation (USBR) staff (USBR 1991) and endorsed by the National Marine Fisheries Service. The USBR model provided an estimate of salmon mortality below Shasta using monthly temperature estimates.

Three factors have stimulated the reassessment of effects of reservoir operations on salmonids covered, in part, in this paper. First, recent limnological and modeling studies (Bartholow *et al.* 2001; Hanna 1999; Saito and Bartholow 1997) have refined estimates of Shasta's daily release temperature capabilities. Modeling work has indicated the fact that the TCD appears incapable of meeting stringent downstream temperature needs in most years. Research has shown that managing water levels in the reservoir is more beneficial than using the TCD alone. Second, there is a strong likelihood of revised water allocations on the Trinity River such that less water will be available for augmenting Sacramento River flows and moderating water temperatures. Reducing transbasin water deliveries from the Trinity will directly affect the strategy for managing increasingly scarce upper Sacramento waters, even in conjunction with additional storage in Shasta Lake. It will be increasingly important to have scientifically sound estimates of the effects of water temperature on Sacramento salmon stocks. Third*,* since USBR's early salmon mortality formulation, many improvements have been

made in modeling the cumulative effect of water temperature on salmon mortality <u>and</u> growth. SALMOD, developed at the USGS Fort Collins Science Center has been shown to accurately simulate growth of fall and spring Chinook salmon on the Trinity River, California (Bartholow *et al.* 1993) and fall Chinook in New Zealand (unpublished data), as well as for rainbow and brown trout (Hickey and Bartholow, in prep.). SALMOD handles mortality and growth for adults, *in vivo* eggs, deposited eggs and immature alevins in redds (nests), and developing juveniles. An application of SALMOD was developed for the upper Sacramento (Keswick to Battle Creek) under contract with the U.S. Fish and Wildlife Service (USFWS; Kent 1999). That application has demonstrated not only effects of water temperature, but also of the flow regime.

Figure 2 depicts the variation in life history timing prevalent for the four races of Chinook, presumably characteristic of the ecological conditions available in the upstream tributaries. I had two objectives for this modeling exercise: (1) to determine what can be learned about how the four races respond to flow and temperature regimes in the Sacramento and (2) to determine what the apparent limiting microhabitats are for each race. In addition, I wish to point out how a model like this could be integrated into an environmental assessment process.
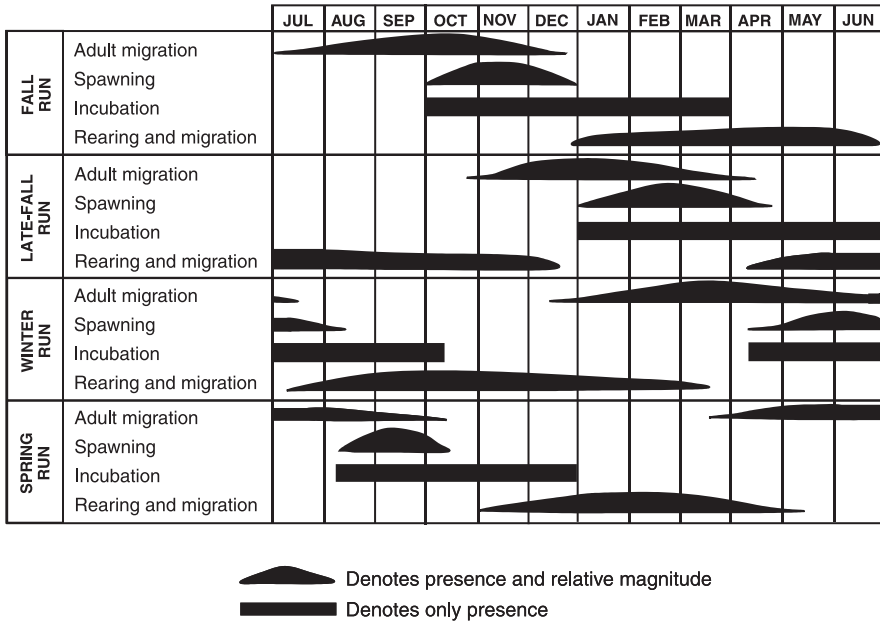
Fig. 2. – Approximate timing of the four runs of Chinook on the Sacramento River from Vogel and Marine (1991).

METHODS

Model Applied

SALMOD is a computer model that simulates the dynamics of freshwater salmonid populations. The conceptual model was developed using fish experts concerned with Trinity River Chinook restoration (Williamson *et al.* 1993). The model's premise is that egg and fish mortality are directly related to spatially and temporally variable micro- and macrohabitat limitations, which themselves are related to the timing and amount of streamflow and other meteorological variables. Habitat quality and capacity are characterized by the hydraulic and thermal properties of individual mesohabitats, which are used as spatial "computation units" in the model. The model tracks a population of spatially distinct cohorts that originate as eggs and grow from one life stage to another as a function of local water temperature. Individual cohorts either remain in the computational unit in which they emerge or move, in whole or in part, to nearby units. Model processes include spawning (with redd superimposition and incubation losses), growth (including egg maturation), mortality, and movement (freshet-induced, habitat-induced, and seasonal). The SALMOD model is more fully described by Bartholow *et al.* (1997). The remainder of the methods section describes the details in the model and data sources for rate

parameters and environmental variables. The impatient reader may skip to the results section if desired.

The foundation for this particular application is Kent (1999) who assembled the first SALMOD model for fall Chinook on the Sacramento. Kent began with the data set that had been used during the Trinity River flow evaluation (U.S. Fish and Wildlife Service and Hoopa Valley Tribe 1999), and modified it to conform with flow, water temperature, and physical habitat data available for the Sacramento. The remainder of this section details the data and parameter sources used in the model, with race-specific annotations as appropriate.

Study Area and Physical Data

The study area (Figure 1) for this project covers the upper 31.5 miles of the mainstem Sacramento from Keswick Dam (RM 303) to Battle Creek (RM 271.5), near Redding California. Keswick forms the upstream boundary of anadromous migration in the Sacramento and Battle Creek marks the boundary below which hatchery-reared salmon from the Battle Creek hatchery confound the enumeration of native salmon in the Sacramento. This study area was subdivided by Kent (1999) into four river segments from 2.3 to 12.7 km long, each with its own homogeneous flow and thermal regime.

Kent (1999) states that mean weekly flows were derived from hourly historical flow values from two websites: California Data Exchange Center (CDEC) (October 1995 to 1997) and the USGS Water Resources of the United States (water years 1970 to 1997). The hourly flow values from the two gages in the system, at Keswick Dam and upstream of Bend Bridge, were converted to weekly average flow values. The method for deriving flows at intermediate segment boundaries was prepared by Gard (1995a). Kent (1999) derived water temperature data from the California Data Exchange Center (CDEC) for three locations. Missing data were filled using common methods, but the techniques used may have underestimated some especially high temperatures during the mid-1970's drought when Lake Shasta was abnormally low (Andy Hamilton, US Fish and Wildlife Service, personal communication).

Physical Habitat Characterization

SALMOD tracks the exact sequence and length of each mesohabitat type as the computation units for the model. Kent (1999) developed six mesohabitat types for the Sacramento from data assembled by California Department of Fish and Game (CDFG). Hydraulic data for each mesohabitat was obtained from California Department of Water Resources (CDWR). The six types were flat water glide, flat water run, flat water riffle, flat water pool, bar complex run, and bar complex riffle.

Kent (1999) derived Weighted Usable Area (WUA) values for six

mesohabitat types from hydraulic modeling conducted by California Department of Water Resources (unpublished document). Habitat suitability values specific to Sacramento River fall run Chinook salmon were developed by the USFWS in 1999 (Mark Gard, USFWS personal communication). Gard (2001) refined the stream mesohabitat description and derived replacement spawning WUA estimates for each race. I have assumed that the four races do not use, *and compete for*, the same microhabitat at the same time (Chapman and Bjornn 1969; Fraser 1969). At first glance, the life history portrayed in Figure 2 belies this assumption. However, the Fisher "Race Designation" chart (more on this later) supports the contention that although the juvenile lifestages of several races may be present at the same time, they do not overlap in length. Because juvenile Chinook use progressively deeper and faster water as they grow (Chapman and Bjornn 1969), it is reasonable to assume that there is minimal competitive interaction. The same holds true with the assumption that the juveniles are not competing with those of other species (e.g., rainbow trout).

Biological Year Timing and Lifestage Categorization

SALMOD is a weekly time step model that, when used for an anadromous species with a single season in freshwater, most frequently begins with the onset of spawning and continues through the duration of outmigrating juveniles. For the Sacramento, four distinct runs of Chinook are potentially of concern, each with different life history timing.

The Chinook life history timing is illustrated by Vogel and Marine (1991). The following figure was derived from this source. However, not all sources may agree with Vogel and Marine. For example, Frank Fisher created a "Race Designation Chart" (unpublished) that tends to show a much more protracted rearing period than Vogel and Marine. In addition, Healey (1994) argues that the various runs in the Sacramento have no unique phenotype, but rather characteristics that we can relate to and name. On the other hand, data summarized by Gard (1995b) is in close agreement with at least the spawn timing. For this study, I used Vogel and Marine (1991; Figure 2).

The naming of lifestages and size classes is flexible. The egg class covers both eggs and in-gravel alevins (larvae or pre-emergent fry). The classification developed by Kent (1999) was simplified and refined as shown in Table 1.

Kent (1999) fit a cubic regression to predict fish wet weight as a function of fork length for naturally reared Chinook salmon in the Sacramento River with lengths between 30 and 100 mm.: $WW = -0.67 + 0.0282FL - 0.000491FL^2 + 0.0000141FL^3$, where WW = wet weight (grams) and FL = fork length (mm).

Table 1. – Lifestage and size classification.

CDFG stage	Definition	SALMOD stage	Length class (mm)		
				Min	Max
Lifestage = 0	Yolk-sac fry	Fry	F1 =	30	40
Lifestage = 1	Fry		F2 =	40	60
Lifestage = 2	Parr	Presmolts	P1 =	60	70
			P2 =	70	80
Lifestage = 3	Silvery parr		P3 =	80	100
Lifestage = 4	Smolts	Immature Smolts	I1 =	100	150
			I2 =	150	200
			I3 =	200	269

Table 2. – Proportion of spawning by river kilometer (upstream to downstream) for upper Sacramento study area. Adapted from Gard (1995b).

Upstream (km)	Downstream (km)	Fall	Late Fall	Winter	Spring
0	5.63	0.128	0.282	0.023	0
5.63	8.85	0.206	0.259	0.489	0.570
8.85	27.35	0.238	0.224	0.306	0.290
27.35	41.51	0.190	0.165	0.114	0.097
41.51	56.80	0.238	0.070	0.068	0.043

Spawning

Kent (1999) used data derived from averages from the 1995–1998 escapements from CDFG's annual reports (CDFG 1997, 1998, 1999) to apportion spawning by river segment. In order to use comparable data for all four races, I used the table provided by Gard (1995b) that he cites from a CDFG source (Table 2).

SALMOD spreads the spawning over a several week period by specifying the portion of adult fish ready to spawn each week. As previously shown in Figure 2, Vogel and Marine (1991) provide approximate beginning and ending spawning times, with a hint of the distribution through time. This chart was used to establish a "normal" distribution for that period (Figure 3). I assumed that all adults are in the study area at the beginning of each biological year and are available for spawning, water temperature permitting (see below). SALMOD allocates adults to various portions of the river at the beginning of each simulation year. This information may be available from carcass or redd counts. The data required include the number of adults spawning in each

section of river, the proportion of male to female spawners, and their weights. In order to establish parity among the races, I have initialized each model with 24,000 spawners, 48% of which are females. This is a value very close to that used by Kent (1999) and a value recently reflective of fall run Chinook. I acknowledge that the other races have far fewer fish, but this consistency will facilitate these modeling tasks.

Spawning is postponed in SALMOD if water temperatures are outside a specified range. Values for the minimum and maximum temperatures currently in the data file supplied by Kent (1999) are 5.6°C and 13.9°C, respectively, with the latter noted as coming from a CDFG annual report.

Fecundity is a simple relationship for the number of eggs per gram of female weight. Kent (1999) states that this ratio, 5,000 eggs for a 12 kg fish, was taken from the records of the Coleman National Fish Hatchery.

SALMOD calculates the amount of spawning habitat required each week, and the probability of redd superimposition for undefended redds (McNeil 1967), by the supplied value for the size of a redd's egg pocket. A female spawner typically excavates multiple egg pockets by repeatedly digging in an upstream direction and depositing newly swept material on top of downstream pockets. The total area of disturbance may be as much as 10 m^2 (Neilson and Banford 1983), but SALMOD really requires the area of just the egg pockets, typically a much smaller value. The average size of a redd's egg pocket is given as 1.5 m^2 by Kent (1999) but after consultation with Mark Gard, USFWS, a redd size of 4.5 m^2 was used.
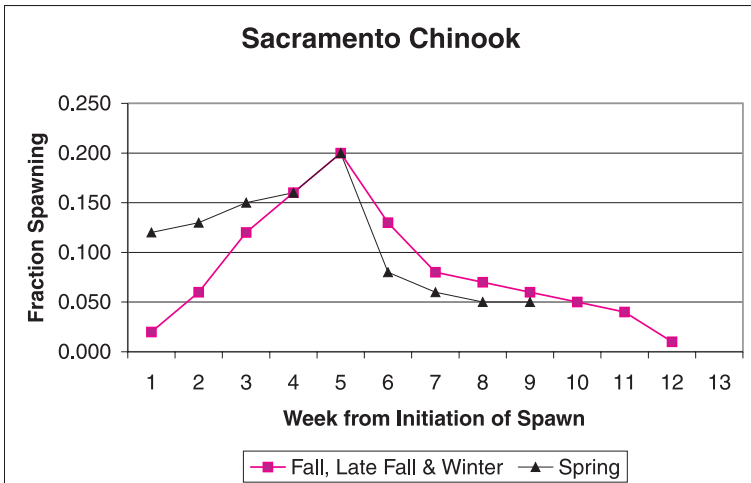

Fig. 3. – Duration and peakedness of spawning fraction for the four races. The week number is from the initiation of spawning in each biological year.

Egg Development and Growth

Crisp's (1981) quadratic equation was used to calculate each day's thermal contribution to egg development. The equation was meant to represent deposition to hatch, so the values were multiplied by 0.5 to account for the time from hatch to emergence (a slight modification of Crisp 1988). The average weight of a fry on emergence from the gravel is given by Kent (1999) as 0.275 g, equivalent to a 34 mm fish. I imposed a ±4 mm deviation from this initial value, estimated from data shown in Vogel and Marine (1991). If mean weekly water temperatures are below 8°, no emergence will occur (Jensen *et al.* 1991). Juvenile growth in SALMOD is solely a function of mean weekly water temperature. This function was obtained from Shelbourne *et al.* (1973).

Juvenile Outmigration

SALMOD moves fish that have reached a specified lifestage/size class a certain distance downstream at a specified time of year. The assumption is that these fish are physiologically ready and that external timing cues (e.g., water temperature, etc.) trigger downstream movement (McDonald 1960). Note that this does not preclude downstream movement of small fish prior to the dates listed, as those fish would be moving due to modeled habitat constraints, not from smoltification cues. Once again, using the timing given by Vogel and Marine (1991), I laid out the approximate times for outmigration for presmolts and immature smolts (not fry) of each race as shown in Table 3.

Mortality

Background mortality rates cover all causes not otherwise considered in SALMOD, such as disease and ongoing predation. Kent (1999) developed a background mortality rate for eggs from hatchery data (Coleman National Fish Hatchery, unpublished data). Rates for the remaining lifestages came from the Trinity River study. The weekly base mortality rates were: eggs, 0.035; fry, 0.025; presmolts, 0.025; and immature smolts, 0.025. The adult rate was a guesstimate, 0.002.

Thermal effects on salmon have long been recognized as being important in the Sacramento (Boles 1988), and are the principle stimulus for managing thermal releases from

Table 3. – Time windows for outmigration for pre-smolts and immature smolts.

Race	Time period	Simulation weeks
Fall run	25-Mar to 1-Jul	30–43
Late-fall run	2-Sep to 3-Dec	40–52
Winter run	5-Nov to 4-Feb	40–52
Spring run	31-Dec to 1-Apr	35–47

Shasta Dam. Thermal concerns resulted in bypassing hypolimnetic water from Shasta in the mid-1980's and the subsequent installation of a multi-level temperature control device on the upstream side of Shasta Dam in the late 1990's to mitigate thermal mortality on eggs and juveniles. In addition to mortality, however, the water temperature regime is also known to affect egg development rate and fish growth.

Thermal mortality values for SALMOD were derived from a variety of sources and are meant to reflect exposure to weekly average water temperature. Values for juveniles and adults came from California Department of Water Resources (unpublished data). Values for eggs (including *in vivo* eggs) were derived from Richardson and Harrison (1990),

but corrected from their "crude" mortality rates to an instantaneous mortality rate and weighting the rates for eggs and sac fry (embryos) to be consistent with SALMOD's life history representation. This was done by taking the geometric mean of their respective survival rates and weighting the two survival rates by their respective durations. That is, the egg stage lasts about two-thirds of the whole egg-alevin lifestage while the sac-fry stage lasts about one-third (Table 4). Final mortality rates are shown in Figure 4. As can be seen, thermal mortality is highly sensitive to temperature above about 16°C, indicating that accurate water temperatures would be required for precise population modeling. Race-specific thermal tolerances are not available.
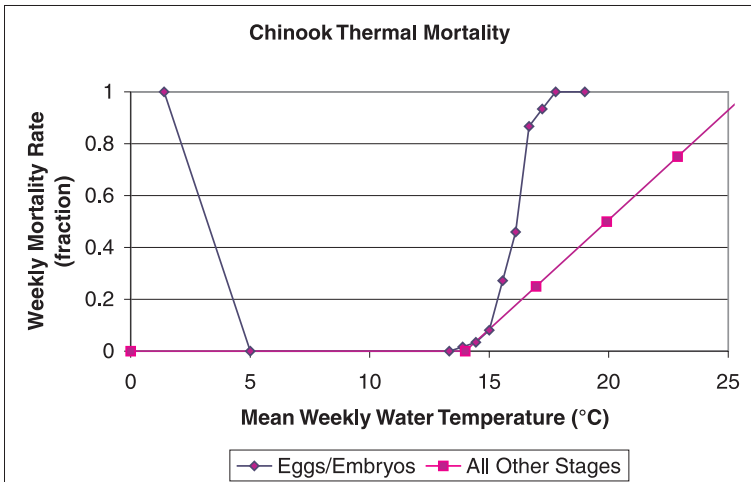

Fig. 4. – Mortality due to mean weekly water temperature.

Table 4. – Re-calculation of mean weekly mortality rate as a function of water temperature for Chinook salmon. Values on the left side of the table are from Richardson and Harrison (1990); those on the right are from my calculations.

Temp (F)	Temp (C)	Given egg mortality (%/d)	Given egg average mortality (% d^{-1})	Given sac-fry mortality (%/d)	Correct egg mortality (d^{-1})	Correct sac-fry mortality (d^{-1})	Correct egg mortality (wk^{-1})	Correct sac-fry mortality (wk^{-1})	Correct geo. mean mortality (wk^{-1})
<56	13.33	natural	0	natural	0	0	0	0	0
<57	13.89	8/24	0.4	natural	0.003	0	0.024	0	0.016
58	14.44	15/22	0.7	Natural	0.007	0	0.050	0	0.034
59	15.00	25/20	1.25	10/14	0.014	0.007	0.096	0.051	0.081
60	15.56	50/12	4.16	25/14	0.056	0.020	0.333	0.134	0.272
61	16.11	80/15	5.3	50/14	0.102	0.048	0.528	0.293	0.460
62	16.67	100/12	8.3	75/14	0.319	0.094	0.932	0.500	0.867
63	17.22	100/11	9	100/14	0.342	0.280	0.947	0.900	0.934
64	17.78	100/7	14	NA	0.482	NA	1.	NA	1.

Habitat Capacity

As mentioned, SALMOD moves fish if they are over capacity for a given mesohabitat's available area at a given flow (Chapman 1962; Mesick 1988). Kent (1999) used values from the Trinity River, but Mark Gard (USFWS, personal communication) supplied revised site-specific maximum density estimates for the Sacramento. These were based on observations (actually 90% of absolute maximum observed) of 106 fry < 60 mm and 200 juveniles > 60 mm.

Using an average weight of 0.94 gm for fry and 5.81 gm for all other juveniles resulted in the estimates in Table 5.

In the event of a habitat limitation for this application, I set SALMOD to move the most recent fry arrivals in a computation unit under the supposition that moving fish will be more likely to continue to move. Presmolts and immature smolts, in contrast, move out based on their condition factor, with the more robust fish assumed to stay with a territorial advan-

Table 5. – Maximum biomass (g/m^2) per unit WUA (m^2) used to determine habitat capacity (from Mark Gard, personal communication).

Lifestage	Max g/m^2 WUA
Fry	100
Presmolts	1162
Immature smolts	1162
Adults	--

tage. These two schemes operate only within a lifestage category, i.e., fry only compete with fry, etc. It is possible to set SALMOD to be even more size selective within a lifestage, but I have not done so for this application as it does not appear to sensitively affect the results.

In SALMOD, there is a mortality rate associated with forced movement – the further fish must go to find space, the greater the mortality. Although there are a variety of ways to enter this relationship into the model, we often simply conceptualize this as a maximum distance that can be moved in one week before 100% mortality, with a linear interpolation from zero mortality at zero distance. Kent (1999) was using 3 km regardless of life state/size class, with a note in the data file that this had come from Bill Snider (CDFG). Kent states:

No studies have been performed to find the average distance juveniles move over a specific time period while rearing. Snider (CDFG) reports that juvenile Chinook migrate long distances while rearing, such that a fry migrating 3 km downstream or more in the course of one week is not unusual. Snider also reports seeing juveniles that have physically matured faster than juveniles of similar length and age in other river systems. The process for this is unknown. Since no studies have been performed on juvenile migration, we used the expert opinion of Snider to set the upper limit of weekly juvenile movement without mortality at a conservative value of 3 km. Juveniles

which must move more than 3 km in a week due to lack of suitable rearing habitat will die. This does not apply to pre-smolts actively outmigrating.

Summary of Model Parameters

In summary, my intent has been to construct models for each race using parameters (and variables) consistent between them unless there was good race-specific information available. This was done to facilitate comparison among the models and reveal how each race individually reacts with its physical environment. Table 6 summarizes what is the same and what is different across races.

RESULTS

Model Verification

The SALMOD model was not calibrated per se. Although the original intent of Kent's work was to set the model up for calibration, several main factors have hindered that task. First, only in recent years has the California Department of Fish and Game (2000) begun to calculate efficiency factors for their downstream smolt traps meaning that there is insufficient data to quantitatively calibrate the outmigrant numbers for each race. Second, as mentioned, historic water temperature data are limited for this study area, although that may be rectified soon. Third, the PHABSIM data for juvenile rearing are being re-done for each race using newly gathered habitat preference data and the latest

Table 6. – Summary of similarities and differences between models for each race.

Factors that are identical	Factors that differ
Number of spawning adults and their sex ratio	Mesohabitat descriptors differ slightly to reflect spawning and other minor features
Flows and temperature values	
WUA data for juveniles	WUA data for spawning
Lifestage and size class attributes	Biological year timing
Weight versus length	Spawning spatial and temporal distribution
Fecundity and redd area	
Spawning and emergence thermal criteria	
Egg development and juvenile growth rates as functions of water temperature	
Seasonal movement characteristics	Seasonal movement timing
Base and thermal mortality rates	
Habitat capacity	
Distance moved mortality rates	

hydraulic modeling techniques. Finally, data collection has likely concentrated on fall Chinook because of their relative abundance in the mainstem.

Nonetheless, the model's behavior was scrutinized to make sure there were no gross errors and to assure that its results were reasonably close. Most of the initial model runs were done by simulating a single biological year for each race where that year's flow and temperature values were created from the weekly medians for the entire 27-year data set. The following items were looked at carefully for those median year simulations.

The first runs of the model showed initial fry emergence exactly when expected, but emergence extended for too long a period. This, in part, resulted in too many juveniles not emigrating during the migration period and remaining instream at the end of the biological year. I shifted the spawn timing to the left (as mentioned previously), making the skewed shape much more like that originally used by Kent (1999). This change resulted in the end of the emergence period exactly like that given by Vogel and Marine (1991), and it reduced the number of residual fish remaining instream at the end of the biological year to less than 1% of the total fry emergents, a number I felt was acceptable. This is perhaps too low given Clark's (1929) estimate that 10–20% of zero+ fish remain in the stream past one year, and may be especially true for late-fall and spring runs (Andy Hamilton, US Fish and Wildlife Service, personal communication).

Frank Fisher, CDFG, assembled a "Race Designation Chart" showing expected length (mm) class of each

race of Chinook by calendar date (un-published, although nominally repre-senting calendar year 1994). For example, if one found a 65 mm fish on January 1, one would determine that the proper bin was 55–100 mm and that bin would represent a winter run Chinook. It is my understanding that this chart is widely used in the ab-sence of strict genetic confirmation of race, even though everyone recog-nizes that it is simply a guide.

Note that the Fisher chart could also be an independent check on the race phenology in that it shows when each race would be expected to be present or absent. However, the phenology depicted is very much at odds with the timing reported by Vogel and Marine (1991) in that rear-ing fish are present in the river for much longer. As previously men-tioned, because this study area is small and the farthest upstream, I would not expect rearing to be so pro-longed, nor fish to get as big as the values reported by Fisher. Emer-gence times, however, are in agree-ment within about two weeks between the two sources.

This chart was used for partial veri-fication that the model was simulating growth with reasonable accuracy. Since there are few observations of fish greater than 80 mm in this study area (Mark Gard, personal communi-cation), the maximum lengths in the Fisher chart may be too great. Even with all the caveats, the "chart" is still a useful growth guide. A simplified version of essentially the same infor-mation has been developed by Gard (1995b).

Spot checks of length classes of fall outmigrants agreed favorably with results from screw trap catches by California Department of Fish and Game (2000). For example, trap re-sults from the week of June 6–12 showed a minimum length of 60 mm up to a maximum of about 100 mm, with a peak in the 70–80 mm range. Simulation results were quite compa-rable. A more exhaustive comparison is certainly possible, but beyond the scope of this analysis. Data from fall Chinook are shown in Figure 5 and show SALMOD to be simulating gen-erally in the middle of two estimates for instream fish.

Table 7 summarizes the simulated response of each race to the median flow and temperature regime. It is useful in getting a general idea of the production bottlenecks for each race.

Accurate annual estimates of the number of surviving fall Chinook juve-niles passing Red Bluff Diversion Dam are difficult to obtain. A compli-cating factor is the fact that I am using a constant number of adult spawners (24,000) so that I must be quite liberal in determining whether the model is generating approximately the right number of outmigrants. As can be seen in Table 7, the simulation model produced between 2 and 4 million outmigrants for median conditions, with fry to outmigrant survival on the order of 20%. This survival rate is well within the 3% to 34% range men-tioned by Kjelson *et al*. (1982) re-ported for the years 1980–1982,
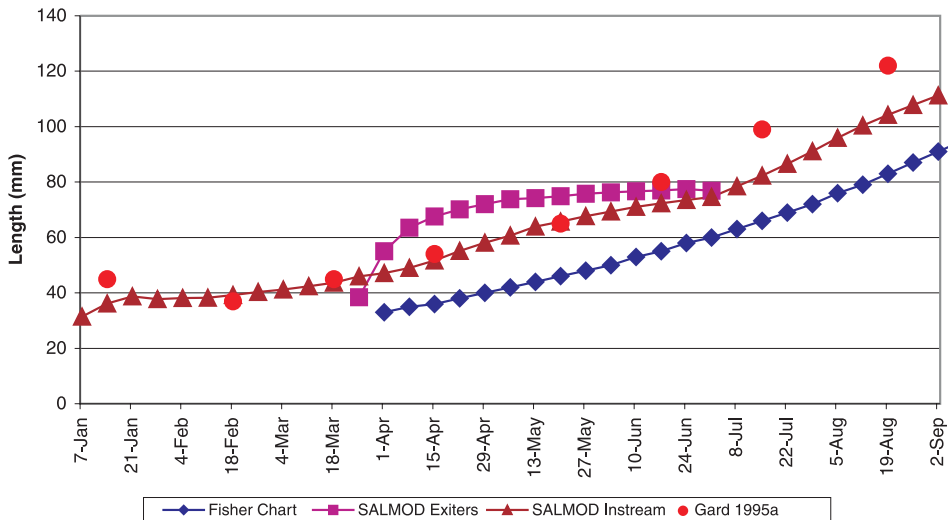
Sacramento Fall Chinook

Fig. 5. – Comparison between simulated and measured fall run juvenile (0+) lengths using the median flow and median water temperature scenario. Fisher chart data is from Frank Fisher's daily growth chart. Gard (1995b) reports monthly values that are here plotted mid-month. SALMOD exiters is all the juvenile fish exiting below Battle Creek, and SALMOD Instream are those fish still rearing in the study area.

although Kjelson may have meant survival all the way through the Delta.

California Department of Fish and Game (2000) reported a catch of 66,101 fall Chinook in screw traps with an average efficiency of 0.007. Although they reported no totals in that report, using these two numbers it is possible to estimate 9.4 million fish produced. Similar data from their 1999 publication (29,292; 0.0145) yields 2 million fish. Thus, SALMOD appears to be at the low end of a reasonable range. Although it would be possible to calibrate the model further using more accurate escapement and water temperature data, I felt that this uncalibrated model would suffice to illustrate the population responses. Additional information on actual winter run outmigrant numbers, size, and timing may be found in Martin *et al*. (2000).

In summary, the only things that were changed from Kent's (1999) parameter set were the length and shape of the spawn-timing curve. In fact, I actually went back to almost the same curve Kent had used for fall Chinook spawn timing from my first estimates. I also had to change the temporal distribution for seasonal movement somewhat for each race simply to match Vogel and Marine's

Table 7. – Comparison of initial model runs for four races of Chinook, each initialized with the same number of adults (24,000) and run with median hydrology and water temperatures. Total outmigrants, residual fish, and biomass all include fry. Smolt outmigrants exclude fry.

Attribute	Fall run	Late Fall run	Spring run	Winter run
Escapement (k)	24	24	24	24
Adult female base mortality (%)	1.21	1.41	2.41	2.23
Adult female thermal mortality (%)	1.66	0	1.84	0
In vivo egg mortality (k)	1,123	0	1,647	0
Eggs deposited (m)	54.8	56.8	53.4	56.3
Superimposition (%)	37.3	44.6	52.1	52.3
Emerged fry (m)	18.0	16.7	10.9	14.6
Incubation thermal mortality (%)	0	0	0.21	1.04
Fry thermal mortality (%)	0	0.19	0	2.22
Fry habitat mortality (%)	59.3	58.42	57.35	55.14
Presmolt thermal mortality (%)	0.24	4.89	0	0.33
Presmolt habitat mortality (%)	0.01	0.03	0	0.06
Immature smolt thermal mortality (%)	5.11	1.57	0	0
Immature smolt habitat mortality (%)	0	0.04	0	~0
Total outmigrants (k)	3,729	3,429	2,171	3,225
Outmigrant biomass (kg)	16,566	38,001	10,351	23,139
Outmigrant length (mm)	72.5	95.3	75.0	83.5
Smolt outmigrants (k)	3,466	3,163	2,146	3,023
Smolt biomass (kg)	16,330	37,835	10,324	23,003
Smolt length (mm)	74.7	100.0	75.3	86.3
Residual fish instream (k)	169	0	191	1
Fry to outmigrant survival (%)	20.7	20.5	19.9	22.1
Fry to smolt survival (%)	19.2	18.9	19.7	20.7

(1991) phenology. Once these changes were made, everything else (growth, survival) seemed to fall nicely into place. Additional calibration is certainly possible, but beyond the scope of this initial analysis.

The SALMOD model was next exercised in a variety of ways to address the objectives. I used different metrics depending on the situation to answer these wide-ranging questions.

What Can Be Learned From the Productivity of Each Race?

The initial questions were: What can be learned about how the four races respond to flow and temperature regimes in the Sacramento? Why has there been such a dramatic recent decline in winter run Chinook? Is it explainable?

Many things can be inferred from Table 7 even though 24,000 adults of each race do not return to this study area each year (Yoshiyama *et al*. 2000). The relative response of each race to the median flow and temperature regimes still can shed some light on their adaptability. Fall fish are the most productive regardless of whether you count total outmigrants or smolts (i.e., exclude fry). This is true even though they do not succeed in depositing the most live eggs. The rate of superimposition is relatively smaller for fall fish than for the other races, presumably due to the habitat-mediated flow regime, although fry habitat limitations are devastating to all races. Similarly, other thermal and habitat-related losses are *in toto* smaller for the falls. There is a cost to the productivity, however. Their mean length is small (74 mm for the pre and immature smolts).

In contrast, the late fall run succeeds in generating the largest imma-

ture smolts, but at the expense of numbers. Not only are they limited by fry habitat, but smolt habitat too takes a somewhat large toll. The spring run produces the smallest total number of outmigrants because of a hefty superimposition loss on top of the highest combined adult and *in vivo* egg loss. The winter run appears to be sort of "in the middle", outstanding only in the high superimposition, incubation and fry thermal mortality.

Running the simulation for the full historical run (1970–1996) provides a different picture. These simulations reveal other angles if displayed graphically as in Figure 6 and Figure 7. Fish production for all races is highly variable through time, somewhat more so for the fall run. Spring Chinook are the weakest producers; good conditions during the juvenile stage are more than offset by poor adult, *in vivo*, and superimposition mortality. The rare exceptionally "good years" are apparent for fall Chinook, but appear clipped for the other races. Remember, too, that each year of these simulations begins with 24,000 adults and therefore displays the relative productivity without considering actual numbers for all races. If actual contemporary numbers were used, the picture told by these graphs would presumably be far bleaker for all but the fall run.

Clearly, the four runs of Chinook have had their periods of ups and downs through the more distant past (Heizer 1973), with much speculation as to why. If one were to superimpose a trend line on top of each trace in Fig-
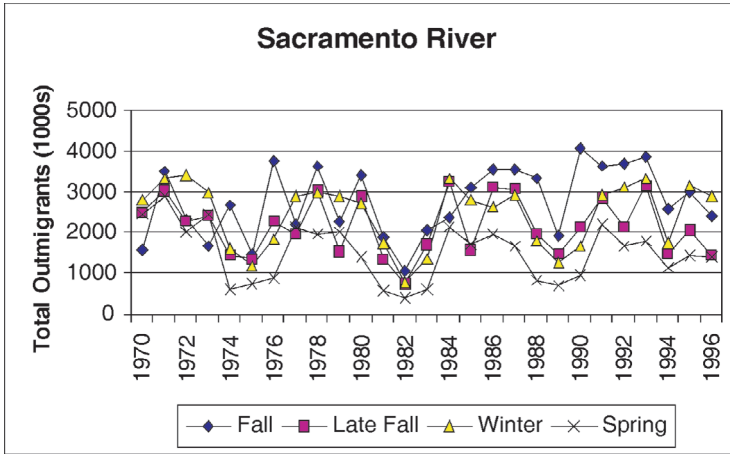
Fig. 6. – Variability in total outmigration through time for each race. Simulations each began with an escapement of 24,000 adults of each race.
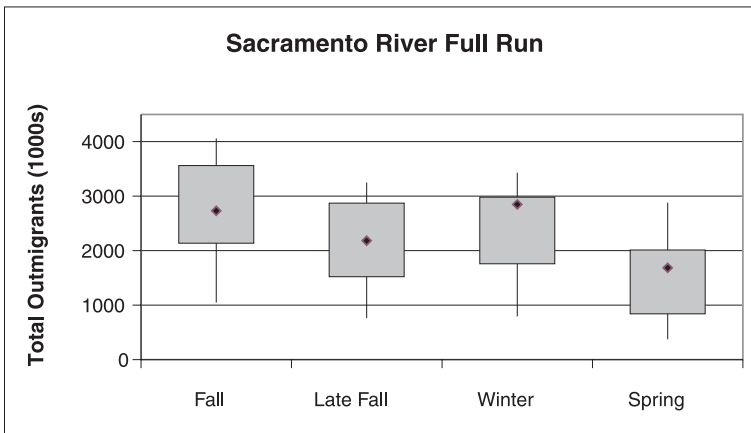

Fig. 7. – Box-and-whisker plot of the variability in total number of simulated outmigrants (including fry) through the full 1970–1996 simulation. Simulations each began with an escapement of 24,000 adults. The top of each line is the maximum outmigrants produced; the bottom is the minimum. Each white bar represents the first and third quartiles of production variation. The diamond represents the median production.

ure 6, the fall run would show a mild positive trend (slope = 38k fish/year), winter Chinook would show no trend (slopes = ~0 fish/year), late-fall would be just slightly negative (slope = –4k fish/year), and spring fish would exhibit a moderately negative (–22k fish/year). This certainly does not explain the decline in winter Chinook, but looks suspicious for the spring fish.

Which Habitats are Limiting?

To address the question of whether spawning or rearing habitats appear to be the most limiting, I systematically doubled and halved both types of habitat in the simulation model as a crude form of sensitivity analysis. As with most other analyses, I began each simulation with an escapement of 24,000. Adjustments to the spawning habitat were made to the WUA file multiplier; adjustments to the fry and juvenile habitat were made using the maximum habitat capacity values in the Relation file. Like the situation on the Trinity River (USFWS and Hoopa Valley Tribe 1999) simulations proved to be quite sensitive to these changes in rearing habitat, but were relatively insensitive to changes in spawning habitat, consistent to what we saw in Table 7, above. These results are shown in Table 8. The races were quite consistent in their sensitivity to these

Table 8. – Sensitivity of each race to changes in rearing habitat. Values are: (1) number of outmigrants including fry, (2) number of outmigrants excluding fry, and (3) biomass of outmigrants, excluding fry. Baseline indicates median water conditions.

Measure	Baseline	Halve spawning habitat	Double spawning habitat	Halve rearing habitat	Double rearing habitat
Fall					
Exiters (m)	3.73	2.96	4.35	2.40	5.06
% Change	100%	79%	117%	64%	136%
Smolts (k)	3,469	2,891	3,767	2,049	4,934
% Change	100%	83%	109%	59%	142%
Smolt Wt. (kg)	16,367	13,489	18,007	9,521	23,768
% Change	100%	82%	110%	58%	145%
Late Fall					
Exiters (m)	3.43	2.74	3.72	2.26	4.52
% Change	100%	80%	108%	66%	132%
Smolts (k)	3,163	2,597	3,407	1,860	4,466
% Change	100%	82%	108%	59%	141%
Smolt Wt. (kg)	37,836	29,637	41,732	22,362	54,682
% Change	100%	78%	110%	59%	145%
Winter					
Exiters (m)	3.23	2.55	3.63	2.18	4.14
% Change	100%	79%	112%	67%	128%
Smolts (k)	3,023	2,398	3,393	1,829	4,097
% Change	100%	79%	112%	60%	135%
Smolt Wt. (kg)	23,003	17,157	26,797	13,856	32,338
% Change	100%	75%	116%	60%	141%
Spring					
Exiters (m)	2.17	1.69	2.64	1.43	2.84
% Change	100%	78%	122%	66%	131%
Smolts (k)	2,147	1,678	2,632	1,335	2,840
% Change	100%	78%	123%	62%	132%
Smolt Wt. (kg)	10,324	7,771	13,101	6,376	13,873
% Change	100%	75%	127%	62%	134%

changes. The fall race was slightly more sensitive to an increase in rearing habitat and the spring race the most sensitive to an increase in spawning habitat.

As an aside, what sensitivity there was to changes in the amount of spawning habitat was due solely to redd placement and not any adult density restrictions. That is, there was never a need for an adult spawner to move to seek spawning habitat based on the maximum biomass per unit WUA. Rather, the dynamics were controlled by how many redds could occupy the available habitat.

I do not want anyone, however, to come away with the idea that just because rearing habitat is more sensitive that spawning habitat is not important. Restoration activities that improve *both* obviously have merit. As an example, if one doubled both spawning and rearing habitat, the modeled improvement in production would be approximately 178%.

Another way to ask the question about which habitats are the most limiting is to frame the question as microhabitat versus macrohabitat, i.e., what kills more eggs or fish, habitat limitations or water temperature? Both elements impact the populations through several channels. The habitat-related mortality includes not only juvenile rearing area, but also redd superimposition, incubation losses, and any spawners unable to locate suitable spawning habitat in the time allotted. Temperature-related mortality includes all adult, egg, and juvenile direct mortality, including *in vivo* egg mortality.

To explore this issue, I ran the simulation model for the full 1970–1996 data set and examined the mortality totals. When tallied in this manner (Table 9), it is clear that the preponderance of mortality can be attributed to habitat rather than temperature in most years. These data are shown collectively in Figure 8.

Table 9. – Comparison of ratio of habitat-related mortality to water temperature-related mortality for the four races of Chinook for the period 1970–1996.

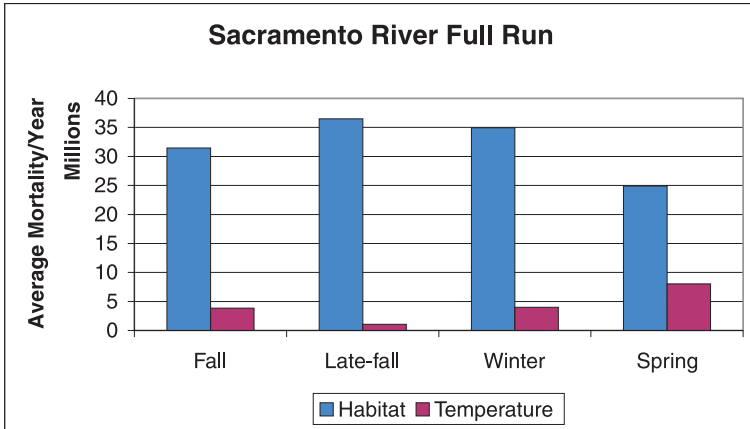| Race	Habitat-related mortality/ temperature-related mortality	Comments
Fall	8 times	Temperature was a larger component of mortality in only three years of the series
Late-fall	34 times	Water temperature essentially not a problem for late fall fish
Winter	9 times	Temperature was a greater cause or roughly equal to habitat mortality in 8 years of the series
Spring	3 times	Like the fall race, temperature was a larger component of mortality in only three years of the series

Fig. 8. – Mortalities partitioned between habitat-related and temperature-related deaths for the four races of Chinook averaged across all years, 1970–1996.
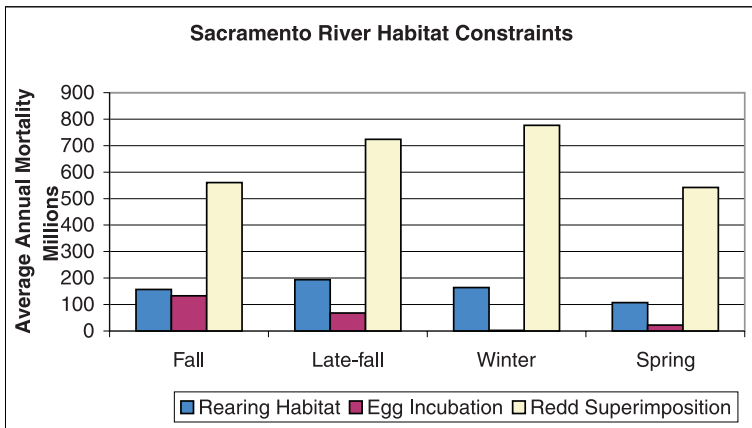

Fig. 9. – Relative microhabitat limitations on the four races.

One can step this analysis down further by partitioning the habitat-related mortalities into categories. We can deduce from Table 7 that both superimposition and fry habitat limitations are important determinants of overall survival. But how do the components of habitat mortality compare with one another? See Figure 9.

DISCUSSION

The interesting thing about this model application was seeing how the life history timing of the four races led to different levels of predicted salmon production. (I assumed that the timing was relatively fixed and ac-

curate, a matter which may be disputed within the multitude of those who work on the Sacramento.) In effect, the timing overlaid on the flow and temperature signature of the river led to the results. In general, given the same number of returning adult spawners, the fall run was predicted to have the highest average number of outmigrating fish; it also exhibited the greatest frequency of high production years. Production for the other races is depressed relative to fall fish with some indication that their production potential has been declining through time, which may be true, especially for the spring and winter races. It is interesting that even though fall fish are predicted to be more numerous, they also have a smaller average length than the other races. In contrast, the late-fall run produces the largest immature smolts at the expense of numbers of fish, but this could simply be due to the protracted rearing period used in the model from Figure 2. In both cases, the model's prediction is without food being directly simulated and serves to raise the question of whether numbers or biomass is the best measure of run success. The spring run seems to be the weakest stock, both in median production and the absolute minimum number produced.

The winter run results were rather unremarkable, with no hint of a "smoking gun" for why that stock is so low. Conditions outside of this model and study area may play a larger factor in their depressed state. Slater (1963) compiled a variety of anecdotal and other evidence related to the apparent initial boom in winter run Chinook experienced after Shasta Dam was closed, precluding return of the winter run to their historic breeding habitat in the spring-fed and largely inaccessible McCloud River system. After an initial population crash, Slater reports that the winter run rebounded, "reaching an abundance comparable to the fall run." (Slater also points out that the spring run was marginal to "speculative" in the mainstem Sacramento at the time of his writing, speculating that hybridization with the fall run was responsible.) But since their peak, the winter run seems to have declined substantially to the point where its survival is in serious doubt (Botsford and Brittnacher 1998).

Habitat constraints to production were similar across the four races. Fry rearing habitat was consistently a bottleneck to production, whereas macrohabitat (due to water temperature) was not predicted to be much of a problem in this upstream study area, especially for the late-fall run. Spawning habitat was shown to be a limiting factor in all races, with each race exhibiting a high level of superimposition (with the same number of spawners for each race). It is surprising that fry habitat seems to be the ultimate bottleneck given that predicted egg mortality is so high, but in this case, the later-operating fry habitat constraint appears to govern the ultimate level of simulated production. The explanation may be that superimposition mortality is a density depend-

ent function of adults whereas rearing habitat mortality is a density dependent function of juveniles. Fry habitat capacity seems to operate more as a ceiling to production, and that ceiling operates almost regardless of the absolute mortality related to spawning habitat restrictions. However, relaxing either constraint would result in more simulated production across all races.

Overall, these findings are consistent with those of Holtby and Scrivener (1989) who found that most of the variability in adult returns of coho and chum salmon resulted from climatic variability (hydrology and water temperature) in both the stream environment and ocean. The variation in life history timing was an important determinant in adult return variability, tracing back to temperature-induced timing changes in fry emergence and smolt outmigration, something much akin to what's going on in this modeling application. However, as we have seen, SALMOD predicts that habitat constraints were more dominant than water temperature.

No true calibration was possible for this model application; therefore the reader is reminded that simulated outmigration numbers are best used not as absolute values, but rather as an index in comparing to a specified baseline condition. Even if the model were calibrated, the measurements for outmigrating salmon are imprecise and subject to poorly understood biases. Further, since this is not a full life cycle model including complex estuarine and ocean dynamics, noth-

ing is suggested here about what happens to salmon successfully migrating below Battle Creek, where other density dependent phenomenon may constrain the populations. Also, SALMOD is clearly not an ecosystem model. It is basically a single species model only and predictions are limited to that target. Parameter values have come from a variety of literature describing studies in different locations and river settings, have been extrapolated across runs, and in some cases, even been borrowed across species. One must be forever critical of what has been published. I am rather fond of a statement from Healey and Heard (1984), to wit: "Much of the work that has been done ... is tantalizing rather than conclusive. Most of the studies were undertaken to describe consequences rather than to test specific hypotheses. Unfortunately, sampling and analysis methods were sometimes inadequate and replication was usually insufficient."

Models similar to SALMOD have recently been used to explore issues surrounding microhabitat and macrohabitat limitations. For example, Sabaton *et al.* (1997) and Gouraud *et al.* (2001) have looked at how the monthly time series of WUA and water temperature affect trout simulated with an age-structured model. Their model is similar in that habitat fluctuations stimulate trout displacement and associated mortality, and water temperatures control growth but can result in reduced survival. However, their model is somewhat different in

that it is calibrated based on a presumption of population equilibrium except when negatively perturbed as is evidenced by their inclusion of density-dependent mortality. Their manuscripts in the current compilation of papers illustrate an evolution toward finer time steps and shed more light on how habitat 'carrying capacity' may limit populations. Importantly, they take excellent steps toward validating their model with field data collected over several years with multiple populations. Their work, as with other SALMOD applications, indicates that population limits may be very different from study area to study area, particularly in the relative balance between micro- and macro-habitat constraints.

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