In Cooperation with the U.S. Fish and Wildlife Service

Assessment of Factors Limiting Klamath River Fall Chinook Salmon Production Potential Using Historical Flows and Temperatures

By John M. Bartholow and James A. Henriksen

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Conversion Factors

Inch/Pound to SI

Multiply	By	To obtain
	Length	
mile (mi)	1.609	kilometer (km)
	Area	
acre-foot (acre-ft)	1,233	cubic meter (m^3)
acre-foot (acre-ft)	0.001233	cubic hectometer (hm^3)
	Flow rate	
cubic foot per second (ft^3/s)	0.02832	cubic meter per second (m^3/s)
	Mass	
ounce, avoirdupois (oz)	28.35	gram (g)
pound, avoirdupois (lb)	0.4536	kilogram (kg)

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as follows:

°F=(1.8×°C)+32

Temperature in degrees Fahrenheit (°F) may be converted to degrees Celsius (°C) as follows:

°C=(°F-32)/1.8

SI to Inch/Pound

Multiply	By	To obtain
	Length	
centimeter (cm)	0.3937	inch (in.)
millimeter (mm)	0.03937	inch (in.)
meter (m)	3.281	foot (ft)
kilometer (km)	0.6214	mile (mi)
	Area	
square meter (m^2)	10.76	square foot (ft^2)
square kilometer (km^2)	0.3861	square mile (mi^2)
	Flow rate	
cubic meter per second (m^3/s)	70.07	acre-foot per day (acre-ft/d)
cubic meter per second (m^3/s)	22.83	million gallons per day (Mgal/d)
	Mass	
gram (g)	0.03527	ounce, avoirdupois (oz)
kilogram (kg)	2.205	pound avoirdupois (lb)

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as follows:

°F=(1.8×°C)+32

Temperature in degrees Fahrenheit (°F) may be converted to degrees Celsius (°C) as follows:

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Executive Summary

We parameterized and applied a deterministic salmon production model to infer the degree to which river flows and temperatures may limit freshwater production potential of the Klamath River in California. Specific parameter requirements, data sources, and significant assumptions are discussed in detail. Model simulations covered a wide variety of historical hydrologic and meteorologic conditions for 40+ years of environmental data.

The model was calibrated only qualitatively, appearing to perform well in predicted outmigrant timing, but overestimating growth. Egg-to-outmigrant survival was near that reported for other rivers north of the Klamath River.

Predicted production potential appeared to be determined by multiple causes involving both regularly occurring habitat-related constraints and irregularly occurring exposure to high water temperatures. Simulated production was greatest in years of intermediate water availability and was constrained in both dry and wet years, but for different reasons. Reducing mortality associated with limitations to juvenile habitat, if possible, would be expected to have the highest payoff in increasing production. Water temperature was important in determining predicted production in some years but overall was not predicted to be as important as physical microhabitat. No single mortality cause acted as a true “bottleneck” on production.

Model uncertainty is addressed through a sensitivity analysis. Predicted habitat area may be a large source of model uncertainty and sensitivity, but collectively, model parameters associated with timing of events (for example spawning, fry emergence, and emigration) or related triggers control much of the model sensitivity.

Though model uncertainty remains, one can begin to explore potential alternatives to reduce production limitations. Specific recommendations are made regarding future study and reducing uncertainty.

Introduction

Existing coho (*Oncorhynchus kisutch*) and Chinook (*O. tshawytscha*) salmon stocks from the lower Klamath River and its tributaries (Figure 1) are in continued decline or serious risk of extinction (Nehlsen and others 1991). Regional stock declines have been attributed to many factors, including habitat loss or damage, hydropower, water diversion (for example agricultural depletions and related water quality issues), logging, overfishing, and genetic alterations associated with hatchery augmentation, all of which are relevant concerns in the Klamath Basin.

The U.S. Fish and Wildlife Service, several Indian nations, State fishery agencies, and other interested natural resource groups in the area have expressed a need to more fully understand the factors that appear to limit the freshwater production of anadromous stocks now found in the lower Klamath River. It is believed that a more complete understanding and analysis of how flow and water temperature regimes downstream from the impounded reaches of the main stem likely either enhance or retard production will enable development of long- and short-term flow recommendations to the appropriate water management and control agencies, specifically the Bureau of Reclamation managing the Klamath Irrigation Project and the electric utility provider, PacifiCorp, who has responsibility for managing several hydropower facilities on the main stem Klamath River.

It is presumed by many that salmon production on the Klamath River is governed by the interaction of many physical and biological factors. Biological factors are complicated, and there is much to learn about how these factors regulate production. Physical factors, principally streamflow and physical facilities, are more subject to management control. Streamflow, in turn, affects the quantity of physical habitat in the river and, to varying degrees, Klamath River water temperatures.

Fisheries science has long recognized the role physical habitat plays in providing living space for reproduction and rearing of fish (Stalnaker and others, 1995). At the riverscape scale, quantifying habitat availability as a metric to estimate maximum salmonid productive capacity has now become a standard fisheries analysis technique (for example Beechie and others, 1994). At smaller scales, quantifying microhabitat bottlenecks through time to provide insight to a population's reproductive and rearing success has also become standard practice. However, use of microhabitat bottlenecks as metrics to evaluate a population's reproductive and rearing potential should be used with caution as stated by Stalnaker and others (1995):

> "Habitat bottlenecks are important, but sometimes poorly understood. The basic premise of the habitat bottleneck is that populations of aquatic organisms are related to the availability of habitat through time. This definition has been commonly misinterpreted to mean that … fish populations must be instantaneously correlated with habitat. Such an interpretation logically requires a belief in instantaneous mortality and spontaneous generation, or the ability of fish to move quite quickly among habitats, in order for fish populations to increase and decrease at the same rate that habitat can change in a stream. In reality, habitat limitations affecting a population usually occur prior to the time when the population size is measured. Adult populations are frequently determined by recruitment, which is highly correlated with the amount of habitat available for early life stages of the species. Such "habitat events" usually affect recruitment via habitat types directly related to the production and survival of eggs, larvae, and fry (such as spawning habitat and young-of-year rearing habitat), or indirectly related to survival by the growth rates of age-0 fish (such as temperature regime, young-of-year rearing habitat, or microhabitat for invertebrate food supplies). These habitat bottlenecks typically occur 1 to 3 years prior to maturation, when their effects are detectable in the adult population."

As habitat quantification techniques have become more sophisticated, useful generalizations have resulted (Bovee and others, 1994):

- There may be several consecutive, independent, habitat "events" that ultimately affect adult populations, and may involve spawning habitat, fry rearing habitat, thermal regime, and so forth.

- Limiting events frequently occur over variable time scales, such as short-term events that limit spawning on a single occasion, compared to events that recur every year, such as juvenile crowding.
- Habitat may be limited by both high and low flow events and by the rate of change of flow events.
- The smallest amount of habitat available during the year may not necessarily be the limiting event (such as during the winter when fish are less active).
- Habitat types not directly used by the species (such as macroinvertebrate habitat as it affects food supply for fish) may be more important than the habitat directly used by the species.

Through time, we have become more adept at conceptualizing and understanding habitat bottlenecks and other limiting factors. We have also added to our technological toolbox that helps to identify management options, evaluate trade-offs, focus on spatial and temporal effects, and recognize counterintuitive consequences resulting from changing system operations in regulated rivers such as the Klamath. In this instance, we have applied a decision support system (the System Impact Assessment Model, or SIAM) and specifically its biological component (Salmod). Both of these models have been through multiple peer review processes (see Williamson and others 1993; Bartholow and others 1993; Bartholow 1996; Campbell and others, 2001; Bartholow and others, 2004; and Bartholow, 2005). The goal of this report is to begin to understand the degree to which habitat, both microhabitat and macrohabitat (*sensu* Stalnaker and others 1995) may influence production of Chinook salmon on the Klamath River downstream from Iron Gate Dam. We do not believe we have enough high-quality data yet to do the same for other salmonids on this river.

USGS has been involved in studies on the Klamath River for several years, working to improve data quality and predictive models of water quantity, water quality, and anadromous fish production. It must be clearly understood that the U.S. Geological Survey has performed this analysis solely to assist the resource agencies with a framework for making their recommendations to water management agencies. We make no specific water management recommendations.

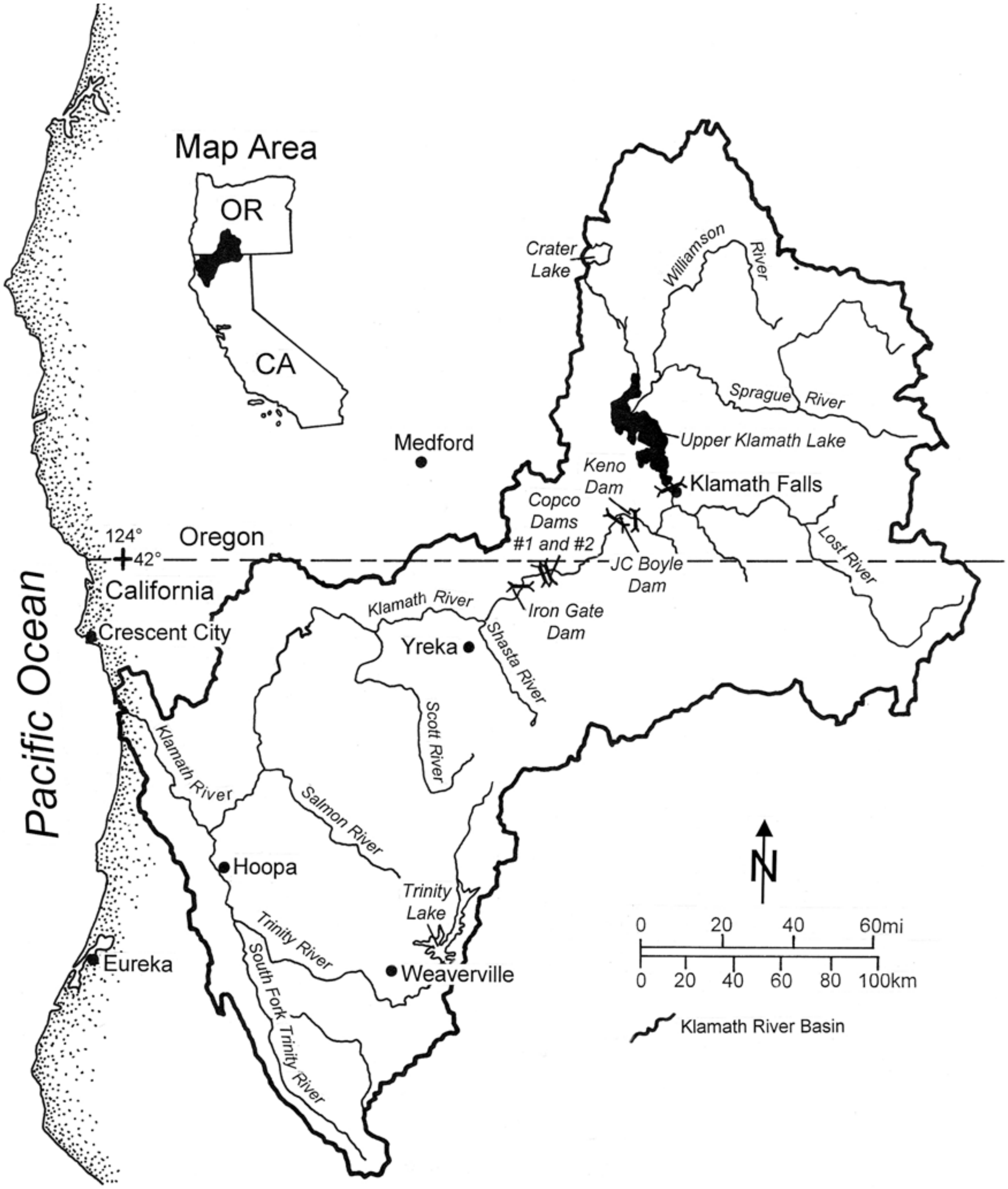

Figure 1. Klamath Basin, Oregon and California, and approximate location of power-producing facilities on the main stem. More study-area specific detail is provided in Figure 5. Map adapted with permission from the Water Education Foundation, Sacramento, California. [mi, miles; km, kilometers]

Objectives

This document addresses three relatively discrete tasks performed for this analysis in conjunction with a review committee of local Klamath River biologists:

1. Develop evidence-based model parameters and output comparison metrics for a salmon freshwater production model.
    a. Evaluate and document historical physical variables (flow and water temperature) and other biological factors relevant to parameterize a Chinook salmon production model for the lower Klamath River downstream from Iron Gate Dam.
    b. Explore alternative production metrics and choose the most relevant to quantify the Chinook salmon production in response to the variety of hydro-meteorological years from 1961 to 2003.
2. Parameterize a salmon production model with best estimate of parameter values.
    a. Conduct parameter sensitivity analysis to identify their inherent uncertainty, with attention to questioning and refining parameters demonstrating the most sensitivity.
    b. Establish a solid framework for future/continued model calibration
3. Using the parameterized model to identify (and eventually overcome) limiting factors:
    a. Compare and contrast years and seasons of dissimilar hydrology and meteorology.
    b. Identify dominant freshwater limiting factors across the historical flow and temperature record.
    c. Determine effects of river flow on microhabitat availability.

Note that rigorous calibration of this model is not yet possible. Field data techniques to enumerate the annual production of salmon on the Klamath River downstream from Iron Gate Dam are still being perfected on the main stem Klamath River. It is our hope that when several years of these data are available, the model can be more thoroughly tested and improved.

Methods

The modeling environment, including model selection and operation, and data requirements are outlined in the following sections.

Model Selection

Salmod (Version 3.74) is a component of the Instream Flow Incremental Methodology, or IFIM (Stalnaker and others 1995). Another component of the IFIM methodology, the Physical Habitat Simulation System (PHABSIM), has been criticized (for example Conder and Annear, 1987) as demonstrating no relationship between microhabitat quantification (weighted usable area, or WUA, an index to suitable microhabitat) and fish standing crop. Yet many other researchers persist in developing and using these relationships to relate WUA and standing crop (for example Capra and others 1995; Heggenes and others, 1996). Like Stalnaker and others (1995) and Bovee and others (1994), Orth (1987) argued persuasively that it is illogical to expect any instantaneous relationship between habitat availability and fish density to hold true. Orth outlined the hypothesis that microhabitat availability may limit fish populations, but episodically, not continuously. In addition, he notes that other factors, such as water temperature, must be included in an analysis. In effect, Orth (1987) said that the PHABSIM models were incomplete. In response, the Salmod model was constructed to integrate habitat limitations to a population through time and space, both microhabitat and macrohabitat. Note that when we refer to habitat limitations, this does not necessarily mean that freshwater habitat is the ultimate factor limiting populations. Habitat constraints may simply reduce production while other factors, such as ocean conditions or fishing pressure may be the ultimate "bottleneck."

Salmod was chosen for the Klamath River for three reasons. First, Salmod was initially conceived and tested on the Klamath's largest tributary, the Trinity River, specifically for that river's Chinook salmon restoration (Williamson and others 1993), building on the foundation laid by similar models. Second, the continued development and application of Salmod fits into an ongoing research program at USGS. The objectives of much of the fieldwork we have helped design and assisted with have centered on collecting data sufficient to parameterize and confirm the model's predictive ability in response to changing flow and temperature regimes. Third, Salmod has been the "third leg" of the SIAM decision support system developed for the Klamath River (Campbell and others, 2001), on a parallel with a water quantity model to predict flows and a water quality model to predict water temperatures to evaluate the efficacy of alternative water management plans that may assist resource agencies with their task of recovery of anadromous fish in the basin.

General Description of Salmod

Salmod simulates population dynamics for freshwater (for example in-river) salmonids; no population dynamics are included for ocean habitat. Though the model is applicable for both anadromous and non-anadromous salmonids, this document will only discuss the anadromous life-history implementation. The model is fully described in Bartholow and others (1993 and 2001); only an outline of the model is presented here.

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. Salmod is a spatially explicit model (*sensu* Dunning and others 1995) where habitat quality and carrying capacity are characterized by the hydraulic and thermal properties of individual mesohabitats, which serve 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 water temperature in a computation unit. Individual cohorts either remain in the computational unit in which they emerged or move, in whole or in part, to nearby units. Model processes include spawning (with redd superimposition), incubation losses (such as redd scour or dewatering), growth (including egg maturation), mortality due to water temperature and other causes, and movement (freshet-induced, habitat-induced, and seasonal).

The model is organized around events (Figure 2) occurring during a biological year (sometimes known as a production year) beginning with spawning and typically concluding with fish that are physiologically "ready" (for example presmolts) swimming downstream toward the ocean. It operates on a weekly time-step for one or more biological years. Input variables (for example streamflow, water temperature, number and distribution of adult spawners) are represented by their weekly average values. The study area is divided into individual mesohabitat types (for example pools, riffles, or runs) categorized primarily by channel structure and hydraulic geometry but modified by the distribution of features such as fish cover. (Microhabitat refers to small-scale physical features defining suitability for fish on a fish's scale, for example one meter. In contrast, mesohabitat refers to the character of the channel that defines microhabitat, for example tens of meters.) Thus, habitat quality in all computation units of a given mesohabitat type changes similarly in response to discharge variation.

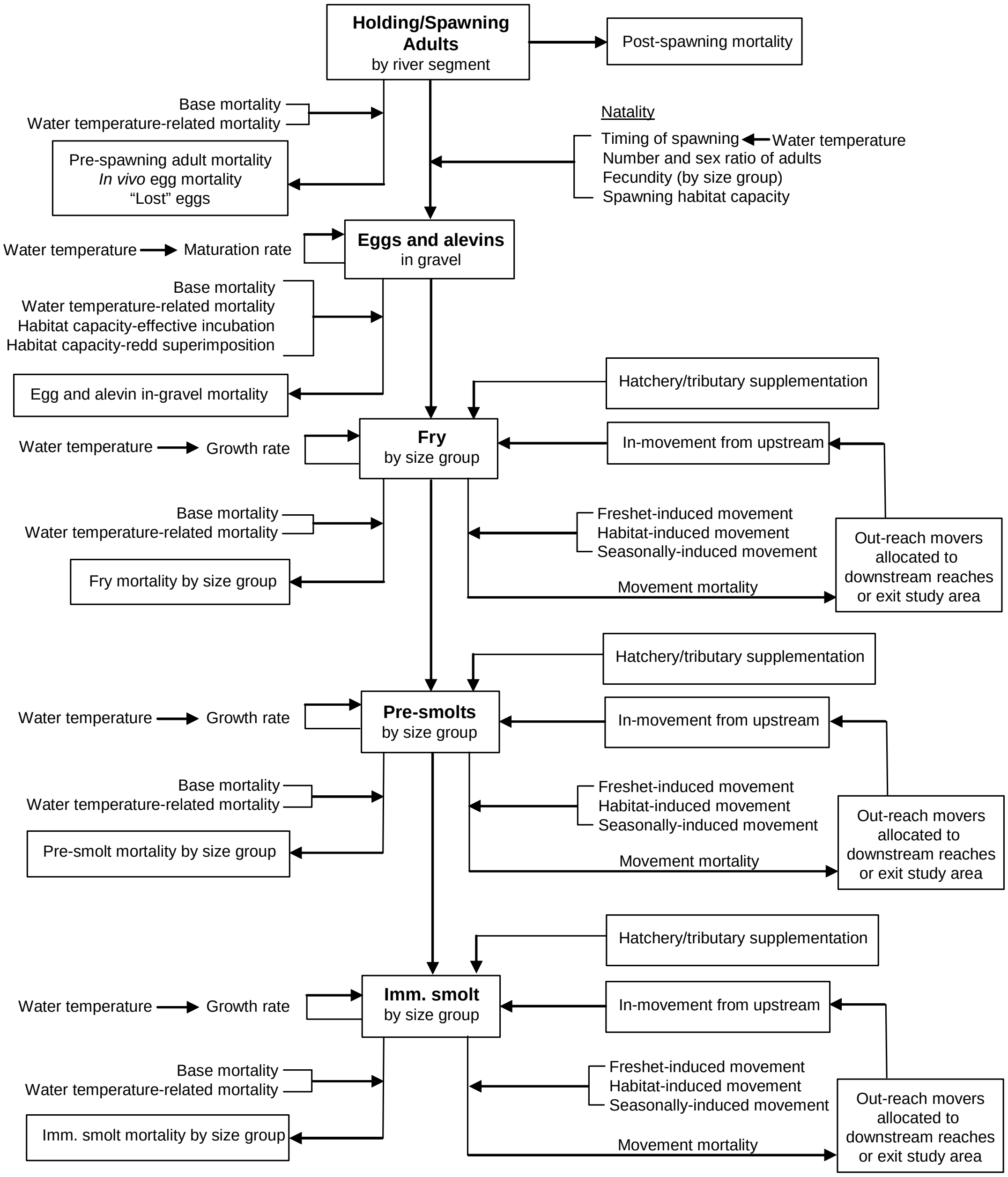

Figure 2. Conceptual illustration of the variety of factors important in controlling salmon production throughout Salmod's biological year. [Imm. Smolt, immature smolt]

Fish cohorts are tracked by life stage and size class within the spatial computation units. Streamflow and habitat type determine available habitat area for a particular life stage for each time-step and computation unit. Habitat area (quantified as weighted usable area, or WUA) is computed from flow:microhabitat area functions developed empirically or by using the Physical Habitat Simulation System (PHABSIM; Milhous and others, 1989) or similar model. Habitat capacity for each life stage is a fixed maximum number (or biomass) per unit of habitat area available estimated from literature or empirical data. Thus, the maximum number of individuals that can reside in each computation unit is calculated for each time-step based on streamflow, habitat type, and available microhabitat. Fish from outside the model domain (from stocking, hatchery production, or tributaries) may be added to the modeled stream at any point in their life cycle.

Models like Salmod are attaining confirmation in the scientific literature. For example, Capra and others (1995) has demonstrated that spawning habitat availability reductions over continuous 20-day periods correlates well with production of juvenile trout. Building on Capra's work, Sabaton and others (1997) and Gouraud (2001) have further explored the field of limiting factors, both microhabitat and macrohabitat, using population models markedly similar to Salmod, with some promising results.

Data and Parameter Sources for Salmod

In this report, we detail all the sources of data and parameter values developed or adopted for the Klamath River for fall Chinook salmon. There are three primary sources for initial parameter values for fall Chinook modeling on the Klamath River. The first is from the Trinity River flow evaluation (U.S. Fish and Wildlife Service and Hoopa Valley Tribe, 1999), which in turn was an outgrowth of the work done by Williamson and others (1993) and Bartholow and others (1993). These values were reinforced by Kent (1999) and Bartholow (2003) who applied Salmod for fall Chinook salmon (and other races) on the Sacramento River downstream from Shasta Dam. Both of these applications added credence to parameter values, strengthened confidence in the model's predictive utility, and supplemented the analysis toolbox. Somewhat less relevant, but still a useful part of the modeling foundation, is another application by Bartholow and Terrell (2001) for Atlantic salmon in the State of Maine.

Second, because there is never a full complement of values available for any site-specific model application, literature values developed for other rivers or related species are used. By necessity, data were obtained from unpublished material when this was the best source available to represent the life-history of Klamath River Chinook. Where relevant, significant assumptions are included when data are borrowed from other species, locales, or races. A summary of the important model input values and assessment of their relative certainty or uncertainty is provided.

Third, a great deal of biological information is beginning to become available for the Klamath River. Quite a bit of this information is, for the time being, found in unpublished reports and databases, but has been used extensively in developing parameters for this modeling effort.

There are two things that may enhance the readers' understanding of this report. The first is patience; there is a fundamental difficulty inherent in explaining a complex model that makes it hard to understand some portions of the model until other portions have been explained. The second is to understand that data input for many of the parameters are sets of paired values. For example, the thermal mortality values are described by a set of values for the temperature and corresponding life stage mortality rate (for example temperature_1, mortality rate_1, … temperature_n, mortality rate_n). Salmod always performs a piece-wise interpolation between user-specified values to derive intermediate results, or if outside the range of supplied values, extends, but does not extrapolate, the terminal values. The availability of Salmod's 10 input files for the Klamath River Chinook salmon is described in Appendix A.

Definition of Life-History Structure

Life Stage and Size Classes

The naming of life stages and size classes is flexible in Salmod and generally reflects the nomenclature used by the local biologists. The egg class covers both eggs and in-gravel alevins (larvae or pre-emergent fry) with a developmental index roughly dividing the two equally in time. We refer to smolts as immature solely because these fish may be of a size indicative of a smolt but are not yet tolerant to saltwater, and they are still many kilometers from the ocean. Table 1 lists the class attributes chosen for the Klamath River and is a modification of the categorization used on the Trinity and Sacramento Rivers.

Table 1. Life stage and size class naming and break points.

Salmod life stage	Sometimes known as	Development index for eggs, Length class (mm) for juveniles		
			Minimum	Maximum
Eggs/Alevins	Eggs		0.0	0.6
	Alevins		0.6	1.0
Fry	Yolk-sac fry	F1	30	35
	Fry	F2	35	55
Presmolts	Parr	P1	55	65
	Silvery parr	P2	65	80
Immature smolts	Smolts	S1	80	90
		S2	90	110
		S3	110	200

Weight:Length Data

Tom Shaw, U.S. Fish and Wildlife Service, supplied a spreadsheet containing length and weight data for the Klamath River (unpublished data). He had performed a standard regression on about 237 samples ranging from 43 to 116 mm fork length (FL). The regressions, compared to the values previously used on the Trinity, look like:

$$\text{Klamath} \quad \text{Weight(g)} = 10^{(-5.15 + 3.110 * \text{Log10(FL-mm)})} \quad (R = 0.99)$$

$$\text{Trinity} \quad \text{Weight(g)} = 10^{(-4.86 + 2.908 * \text{Log10(FL-mm)})} \quad (R = 0.74)$$

The above formulae may be contrasted with the method reported for the Sacramento River by Kent (1999) that used an alternate formula based on a cubic regression of fork length and wet weight of developed for naturally reared fall Chinook salmon with lengths between 30 and 100 mm. A cubic regression was used because the length and weight relationship for fish is approximately cubic (Busacker and others, 1990). Accordingly:

Sacramento $WW(g) = -0.67 + 0.0282FL - 0.000491FL2 + 0.0000141FL3$
(R unspecified)

where WW = wet weight (grams), and
FL = fork length (mm).

All three relations are shown in Figure 3 for the length ranges from which the data were derived. Whereas variability in the wet weight of individual fish of the same fork length may be due to true variation in weights, some variability may simply be explained by differences among individuals in fullness of the stomach or presence of water in the buccal (mouth) cavity. On the other hand, one might reasonably conclude that Klamath Chinook salmon have a better condition factor than those from the Trinity, at least for the time periods from which these fish were collected and relations developed. Klamath fish also appear to be slightly heavier than Sacramento fish of the same length. Note, however, that diseased juveniles can appear to have higher condition factors (Nick Hettrick, USFWS Arcata, written comm., 2006). Klamath River values dovetail well with "standard" values from the Piper and others (1982) hatchery handbook that were used to extend Tom Shaw's relationship above 120 mm.

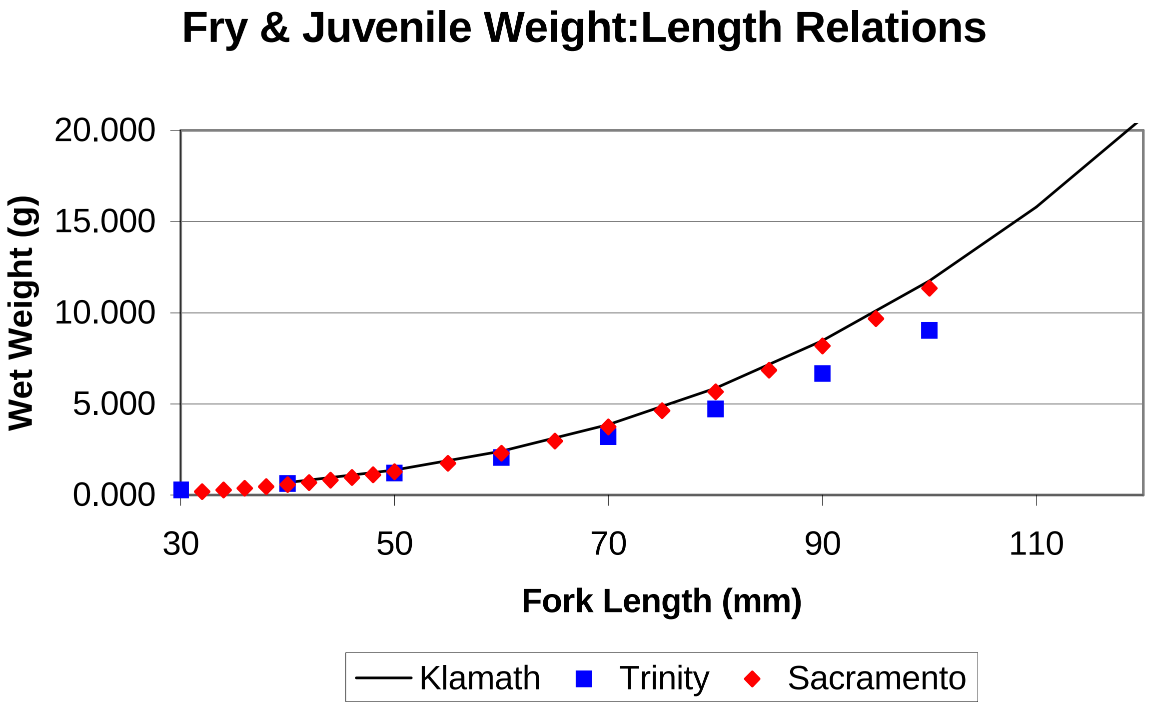

Figure 3. Weight:length relations for the Klamath River (Tom Shaw, U.S. Fish and Wildlife Service, written comm., 2005), Trinity River (Bartholow and others, 1993), and Sacramento River (Kent, 1999).

The weight:length relationship is used in Salmod to convert from one metric to the other. Fish grow in body mass (weight) and are then assigned the appropriate length. The exception to this is if fish lose weight; if so, they retain their previous length but must regain lost weight to add length. The weight:length relationship supplied to Salmod for the Klamath River is given in tTable 2.

Table 2. Weight:length relationship for Klamath River fall Chinook salmon. Values for fish less than or equal to 120 mm were derived from Tom Shaw (written comm., 2005) using the formula given in the text; values for fish > 120 mm were derived from Piper and others (1982). The number of decimal points reflects the need to convert back and forth accurately and should not be construed to imply precision.

Weight (g)	Fork length (mm)	Weight (g)	Fork length (mm)
0.278	30	92.00	200
0.680	40	179.69	250
1.361	50	310.50	300
2.399	60	736.00	400
3.875	70	1,437.50	500
5.870	80	2,484.00	600
8.466	90	3,944.50	700
11.749	100	5,888.00	800
15.803	110	7,062.44	850
20.714	120	8,383.50	900
38.81	150		

General Biological Year Timing

The fall Chinook life-history timing is illustrated in Figure 4. Adults begin entering the main stem in early August and are present near Iron Gate Dam by early September. Spawning commences in mid-October, when water temperatures cool, and is concentrated within a few weeks. Emergence is noted to begin in early February with essentially simultaneous emigration. The bulk of the ocean-type emigration from our Iron Gate to Scott study area has occurred by early June, tailing off completely by July.

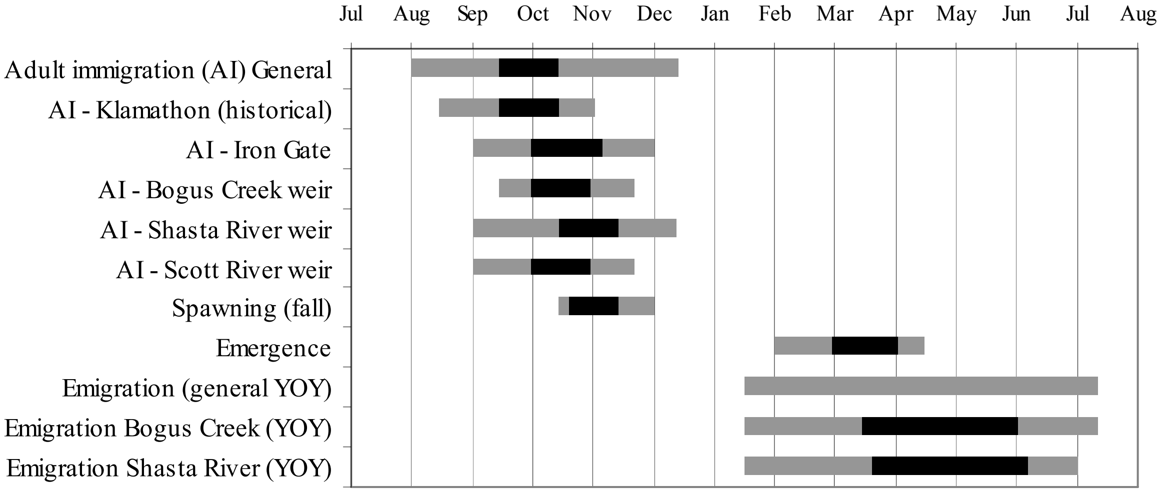

Figure 4. Approximate timing of the various ocean-type life-history phases for fall Chinook salmon, adapted from Shaw and others (1997). Other values from Shaw and others have been omitted, for example spring Chinook spawning, over-summer juvenile outmigration, and areas downstream from the Shasta River. YOY is young of year.

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. Because fall run Chinook spawning on the Klamath River begins in mid-October, we have set the biological year to begin 1 October; this is convenient because this it is also a water year boundary. The simulation time-steps needed in some of Salmod's input files are simply chronological week numbers (Table 3). Note that simulation processes are initiated on the first day of the week, but simulation results are tabulated on the last day. This can be a cause for confusion when reviewing the output.

Linda Prendergast supplied an alternative characterization of the life-history periodicity (PacifiCorp, 2003) for comparison with the Shaw and others (1997) report. Because there were notable differences, especially for outmigrant timing, we decided to rely on data collected at outmigrant trapping locations for modeling purposes. These data will be discussed in a subsequent section of this report.

Table 3. Correspondence between Salmod's weekly time-step number and the date during the biological year.

Simulation week	Beginning date	Simulation week	Beginning date
1	10/1	27	4/1
2	10/8	28	4/8
3	10/15	29	4/15
4	10/22	30	4/22
5	10/29	31	4/29
6	11/5	32	5/6
7	11/12	33	5/13
8	11/19	34	5/20
9	11/26	35	5/27
10	12/3	36	6/3
11	12/10	37	6/10
12	12/17	38	6/17
13	12/24	39	6/24
14	12/31	40	7/1
15	1/7	41	7/8
16	1/14	42	7/15
17	1/21	43	7/22
18	1/28	44	7/29
19	2/4	45	8/5
20	2/11	46	8/12
21	2/18	47	8/19
22	2/25	48	8/26
23	3/4	49	9/2
24	3/11	50	9/9
25	3/18	51	9/16
26	3/25	52	9/23

Physical Data

Study Area

The study area (Figure 5) covers a 75-km (46-mile) stretch of the Klamath River from Iron Gate Dam (RM 191.7) to just upstream from the Scott River (RM 145.3). Iron Gate forms the current upstream boundary of anadromous migration in the Klamath River, and the Scott River marks the current downstream limit of habitat that has been evaluated using PHABSIM.

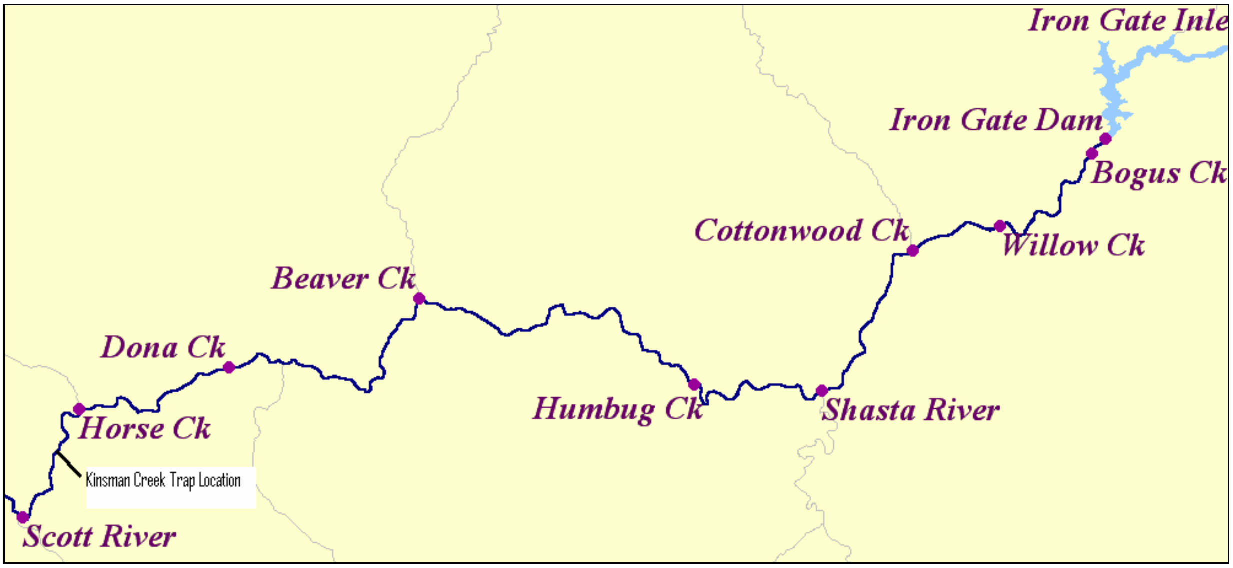

Figure 5. Salmon production model study area in northern California, ranging from Iron Gate Dam to the Scott River. This map, taken from SIAM, shows the location of several of the larger tributaries entering the Klamath River in the study area, many of which also contribute to the basin's existing salmon production. For reference, Interstate 5 crosses the Klamath River immediately upstream from the Shasta River.

Flow and Temperature Reaches

The study area was subdivided into 11 river reaches, each with its own relatively homogeneous flow and thermal regime. These reaches are described in **Table 4**.

Table 4. Defined flow and temperature reaches for Klamath River study area as used in SIAM and Salmod.

Reach	Length (km)	Reach name
1	0.32	Iron Gate Dam to Bogus Creek
2	3.70	Bogus Creek to Dry Creek
3	3.21	Dry Creek to Willow Creek
4	5.63	Willow Creek to Cottonwood Creek
5	8.69	Cottonwood Creek to Shasta River
6	6.43	Shasta River to Humbug Creek
7	10.46	Humbug Creek to Empire Creek
8	8.85	Empire Creek to Beaver Creek
9	8.85	Beaver Creek to McKinney Creek
10	11.74	McKinney Creek to Horse Creek
11	9.79	Horse Creek to Scott River

Flow and Water Temperature Data

For this analysis, mean weekly flows and water temperatures for each of the reaches listed in **Table 4** were derived from SIAM for the Klamath River.

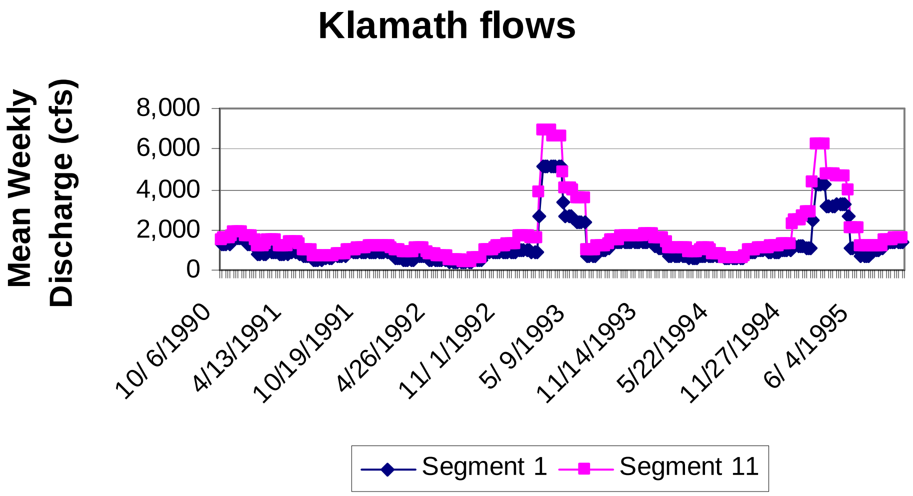

Figure **6** and Figure 7 illustrate a portion of the historical record supplied by SIAM.

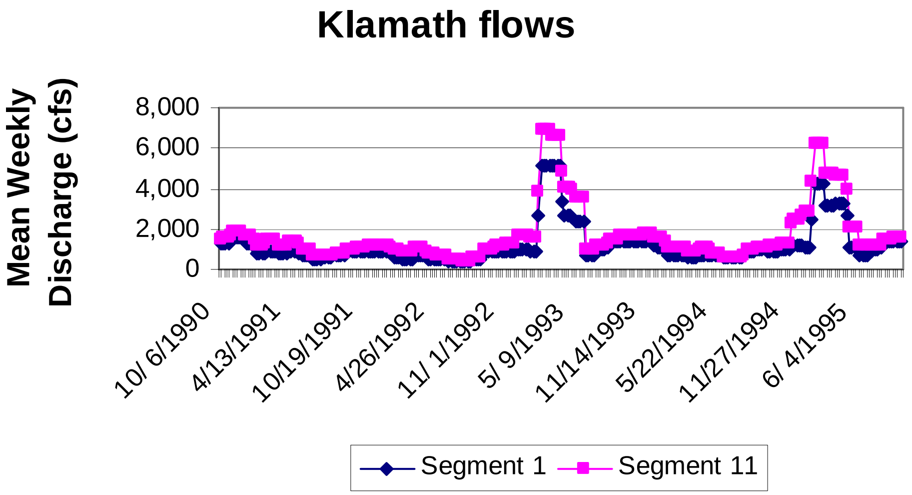

Figure 6. Mean weekly discharges in cubic feet per second (ft3/s) for two river reaches for biological years 1990–1995 from SIAM. Reach boundaries are defined in Table 4.

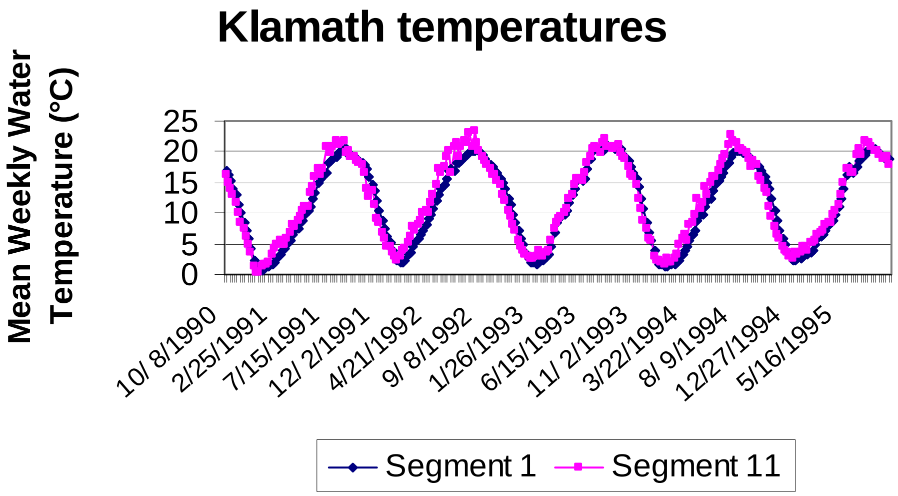

Figure 7. Mean weekly water temperatures in degrees Celsius (°C) for two reaches for water years 1990–1995 from SIAM. Reach boundaries are defined in Table 4.

Meso- and Microhabitat

Geomorphic Segments

For the physical microhabitat analysis, the study area was segmented into two geomorphic units. Segment 1 extended from Iron Gate Dam to 2.7 km downstream from Cottonwood Creek (total length 15.2 km), the approximate end of the broad valley. Segment 2 extended from 2.7 km downstream from Cottonwood Creek to the Scott River (total length 66.6 km). Channel slope and valley confinement–a broad valley in Segment 1 compared to a confined canyon in Segment 2–were the physical characteristics used to define the subsegments. An examination of the flow versus WUA relationships for the two geomorphic subsegments confirmed that meaningful differences existed for the mesohabitat types in the two geomorphic subsegments.

Mesohabitat Types

Carefully distinguishing microhabitat and mesohabitat is important. Microhabitat refers to the collection of physical characteristics (depth, velocity, substrate, cover) that determine suitability of a given river's "space" for fish of a given life stage (for example adults, juveniles), essentially on a square meter or finer scale. By contrast, mesohabitat refers to larger channel forms such as riffles, pools, or runs that tend to respond similarly to changes in flow. Morhardt and others (1983) argued that collecting data for a PHABSIM microhabitat study was best done at the mesohabitat unit (also known as a channel geomorphic unit) level where microhabitat is characterized by multiple samples of each mesohabitat type within each subsegment. Salmod carries this process further by retaining the exact sequence and length of each mesohabitat type as computation units within the model.

A complete inventory of the mesohabitat types was conducted for the study area. Mesohabitat types were classified into two primary types and several subtypes to distinguish differences in hydraulic geometry (Table 5). The two primary types were backwaters (pools with a downstream hydraulic control, sometimes referred to as pools elsewhere in this document) and slopes (not influenced by a hydraulic control and commonly referred to as runs, riffles, and so forth). Slope habitats were further classified into three subtypes: low, moderate, and steep. The terms low, moderate, and steep slope are relative to each other at a reference flow. In Segment 1, all four mesohabitat types occurred in three channel configurations: main channel, split channels (perennial vegetation, rarely inundated, island present) and side channels (no vegetation or annual vegetation, inundated annually, sand or gravel bar). In Segment 2, however, the four mesohabitat types occurred only in the main channel and side channels; there were no split channels in Segment 2. The explicit sequence of mesohabitats and their respective lengths may be found in Salmod's *Stream.Dat* input file (see Appendix A).

Table 5. Attributes of the mesohabitat types in geomorphic segments 1 and 2. Note that side channels and split channels "double count" the length of the stream. Actual length of the study area was approximately 75 kilometers. Some rounding may occur.

Mesohabitat type	Units	Mean length (meters)	Cumulative length (kilometers)	Percent length of segment
Segment 1				
Low Slope (LS)	28	193.8	5.4	36
Moderate Slope (MS)	24	127.0	3.0	20
Steep Slope (SS)	3	87.5	0.3	2
Backwater (BW)	27	182.4	4.9	32
Side Channel (SC)	8	129.3	1.0	7
Split Channel (SP)	3	182.6	0.5	4
Subtotal	93	--	15.2	100
Segment 2				
Low Slope (LS)	119	134.1	16.0	24
Moderate Slope (MS)	83	136.8	11.4	17
Steep Slope (SS)	40	104.5	8.4	13
Backwater (BW)	154	162.6	25.0	38
Side Channel (SC)	37	160.5	5.9	9
Subtotal	433	--	66.6	100
Total	526	--	81.8	--

Hydraulic and microhabitat data for PHABSIM were collected following the protocol described in Bovee (1997). Table 6 shows the number of study sites in each segment, mesohabitat types sampled, transects per mesohabitat type, and hydraulic data collected. Transect data representing individual mesohabitats were averaged to create a single description. The calibration flows at which the hydraulic data were collected were approximately 1,300 and 3,300 cubic feet per second (ft^3/s) for the full channel velocity measurements and 8,500 ft^3/s for the edge velocity measurements. Water surface elevations were measured at all three of the calibration discharges.

Table 6. Physical habitat study sites [and abbreviations], mesohabitat types sampled, (number of transects), and hydraulic data collected in Segments 1 and 2.

Attributes	Number in Segment 1	Number in Segment 2
Study sites		
Main Channel [MC]	5	5
Split Channel [SP]	2	0
Side Channel [SC]	1	0
Mesohabitat types sampled (# transects)		
Low Slope [LS]	8 (16)	3 (4)
Moderate Slope [MS]	6 (8)	3 (6)
Steep Slope [SS]	0	0
Pool/Backwater [P]	6 (28)	3 (6)
Mean column velocities (entire channel)	2	2
Edge velocities	1	1
Water surface elevations sets (all transects)	3	3

Microhabitat Suitability Criteria

Microhabitat quality in PHABSIM is defined by habitat suitability criteria for depth, velocity, and substrate or cover depending on the life stage. Table 7 shows which variables were used for spawning females, fry, and presmolts. The habitat suitability criteria for each microhabitat variable, for each life stage, may be found in Appendix B–Figures 1–3. These criteria were developed from observational data presented in Hardin-Davis, Inc. (2001; eventually published as Hardin and others, 2005), a habitat suitability criteria study conducted within the study area. We assumed rearing criteria are identical between pre- and immature smolts, an assumption supported by Hoffman and Deibel (1984), though they did note some differences. Cover was incorporated in the analysis for fry through the use of appropriate channel index codes and by restricting the available area to within ~3.5 m (12 feet) of the shoreline. The geometric mean was used as the compositing algorithm within PHABSIM. We note that the Chinook fry WUA curves for each habitat type do not reflect "irrationally" high habitat availability at low discharges experienced by some practitioners (Appendix C).

Table 7. Habitat suitability variables used for three Chinook life stages.

Life stage	Depth	Velocity	Substrate	Cover
Spawning females	X	X	X	
Fry	X	X		X
Presmolts	X	X		X

Microhabitat Quantification

Weighted Usable Area. The Physical Habitat Simulation Model (PHABSIM) was used to quantify flow:WUA relationships for each mesohabitat type for four life stages of Chinook salmon–spawning females, eggs/alevins, fry, and presmolts. WUA is expressed in ft^2/1000 ft of each mesohabitat type. Habitat relationships are provided in Appendix C, with figures 1–23 representing Segment 1 and figures 24–41 representing Segment 2.

Several noteworthy decisions were made regarding the quantification of suitable microhabitat (WUA), mesohabitat types, and the special situation of split and side channels. First, because steep slope mesohabitat types were not sampled for safety reasons (high velocities) the assumption was made that this mesohabitat type was equivalent to the minimum habitat found for all moderate slopes in each segment respectively. This assumption resulted in zero habitat for spawning. During the fall of 1999, Hardin-Davis, Inc. (2001) located 290 redds in the study area. Eighty-seven percent of the observed redds were in pools or low slope mesohabitat types. No redds were observed in steep slopes (or midchannel), appearing to substantiate the assumption that no suitable spawning habitat is available in steep-slope mesohabitats. Note also that steep slope mesohabitats account for only 2 percent of the total length of the upper segment (see Table 5).

Second, Salmod expects only a linear series of habitat types, but parallel habitat types, split and side channels, necessitated some adjustments. Split channel (SP) and side channel (SC) habitats in Segment 1 were quantitatively combined by computing their relative proportions based on total lengths (after eliminating types classified as "unknown"). Two new habitat types (named SP1 and SC1) were created by weighting the mean WUA value of each of its components (LS, P, and so forth) with the parallel main channel component proportions. This combined habitat value was doubled for these two new habitat types for fry and juveniles because a given length of river has four edges instead of two for these habitat types. This process was not necessary in Segment 2.

In a related step, the length of both split channels and side channels was summed and subtracted from the main channel habitat type. The main channel type was then followed by replacing all appropriate side channel types with the composite SP or SC for the total length of all side channel components. This keeps the river roughly the "correct" length as would be experienced by any floating particle, but with the doubling of the WUA shows that roughly twice as many fish per unit length could be found in the habitat complex represented by the split or side channels. Occasionally, two main channel types needed to be shortened to account for the total length of the SP or SC. Using this procedure, the main channel habitat type once or twice "disappeared" in the sense that this type was entirely eliminated, perhaps in conjunction with the unit downstream from the split channel. This process did not completely assimilate the main channel habitat type, but again, it is a small section of river in total. (Note that the length of river compiled from survey field notes agrees favorably with the length of river from digitized 7.5'-minute quad maps. There were individual differences of plus or minus about 7 percent, but on the average for the whole length of river, the two methods agreed within 2 percent. The mesohabitats begin at the hatchery bridge, not at the dam, so the two systems were never completely compatible, but this length difference remains insignificant for Salmod.)

We divided PHABSIM-generated WUA values by 1000 because Salmod expects ft^2/ft instead of $ft^2/1,000$ feet. This step was done for each life stage and segment and then formatted to create Salmod's *WUA.dat* input file. Note that we also inserted a zero, zero (0,0) pair for various life stage/segments to signify zero habitat at zero flow, if appropriate. These breakpoints are evident in Appendix C.

Though we did not develop egg/alevin incubation curves directly using PHABSIM, we did derive them from the simulated spawning relationship. This was accomplished by retaining the rising limb of the spawning curve with increasing discharge but then holding the maximum WUA value constant with increasing flow. This is equivalent to using a criterion of "keep the eggs wet regardless of depth." However, as is evident in Appendix C, we truncated this maximum value when flows exceed 13,000 ft^3/s, depressing the habitat value to zero at 14,000 ft^3/s, due to increasing probability of redd-destroying bed scour or entombment (Bob Milhous, U.S. Geological Survey, unpub. data). Zero habitat above 14,000 ft^3/s assumes that redd scour or entombment causes 100 percent egg mortality, an assumption for which we have little guidance. Lapointe and others (2000) estimated that scour would indeed "destroy" a redd, but they also estimated that flooding would scour a maximum of only 20 percent of a Canadian Shield stream. However, according to Bob Milhous (oral comm., 2005), their method only considered "net scour," that is, what had changed from pre- to post-flood. Such a technique risks ignoring the during-flood maximum scour extent. Montgomery and others (1996) speculated much higher mortality when scouring occurs at only modest egg burial depths, for example 80 percent at 30 cm. Note that Salmod's weekly time-step may underestimate the frequency of scour from daily peak-flow events, especially if those flows were derived from SIAM's monthly flow submodel.

As is always necessary, we had to make assumptions about how to extrapolate PHABSIM model results both above and below our measured discharges. Some of these assumptions resulted in odd-looking breakpoints seen in Appendix C but are the best we can do at present without collecting data using different methods.

Finally, we inserted a duplicate habitat unit, and halved the length of each, for units longer than 500 meters. This was because we were unsure whether Salmod would properly account for fish movement through long computation units when forced movement might be less than 500 m. This approach did not change the length of the stream, it simply added computation units.

There are two assumptions to note regarding our treatment of physical micro/ mesohabitat. First, in assessing the effects of alternative flows and water temperatures on different life stages of salmon, we are making the assumption that they do not use–and compete for–the same microhabitat at the same time, an assumption supported by Chapman and Bjornn (1969), Fraser (1969), and Mundie (1974). Although more than one juvenile life stage (for example fry and presmolts) may be present in the river at the same time, juvenile Chinook salmon use progressively deeper and faster water as they grow (Chapman and Bjornn, 1969). Therefore, it is reasonable to assume that there is minimal competitive interaction. The same holds true with the assumption that juveniles are not competing with those of other species (for example steelhead). Obviously, these are ecological niche assumptions that could be strengthened or challenged by additional research.

Second, the quantification of WUA as a function of discharge is static. That is, we assumed that none of the flows we simulate result in changes to the channel geometry, substrate composition (gravel quantity or quality), or cover availability. We know that the Klamath River does change its channel morphology during high-flow events (Ayres Associates, 1999), but the assumption we are making is that such changes are tantamount to dynamic equilibrium, in other words habitat types remain in approximately the same proportion before and after channel-changing events. The geomorphic assessment by Ayres Associates (1999) supports the assumption that although channel forming events occur every 3 years or less, there has been very little overall aggradation or degradation since 1964.

Model Processes

Spawning

Model specification of spawning involves their number, sex ratio, fecundity, habitat use characteristics, and timing.

Spawner Characteristics

Salmod requires the specification of the number and attributes of adults to “seed” the model. Magneson and others (2000) provide data showing 367 grilse and 1,978 adult spawners in the main stem Klamath River for 1999, resulting in a 45 percent spawning female to 55 percent non-spawner ratio. Mean spawner length was 694 mm (approximately 4 kg) from a historical data set reported by Healey and Heard (1984). However, recent data collected and summarized by the USFWS and USGS (Tom Shaw, U.S. Fish and Wildlife Service, and Sam Williamson, U.S. Geological Survey, written comm., 2006) indicate that the redd counts underestimate actual spawners several fold. After consultation, we increased the number of adults to 12,000 to better reflect this more recent information and used this value to seed the simulation study area for each year of all simulations unless otherwise stated.

Fecundity

Salmod uses a simple relationship for the number of eggs per gram of spawning female weight. We used average fecundity from the Lewiston Hatchery on the Trinity River of 3,732 eggs for a 4-kg fish. This is in good agreement with an older mean value from the Klamath River of 3,634 listed by Healey and Heard (1984), who also noted that Klamath stocks appeared to be only half as fecund as Sacramento River fish of the same length.

Redd Area and Superimposition

Salmod calculates the amount of spawning habitat required each week for the number of female spawners ready to spawn given the value supplied for the area of an average redd's egg pocket. The model also calculates the probability of redd superimposition for previously constructed and undefended redds (McNeil, 1967) by knowing the area already occupied by pre-existing redds. The model does not allow superimposition of redds created within one weekly time-step; in effect, this means that redds are defended for one week.

A female spawner typically excavates multiple egg pockets by repeatedly digging in an upstream direction and depositing newly swept material on top of downstream egg pockets; the total area of disturbance may be more than 10 m^2 (Neilson and Banford, 1983). However, input values to Salmod specify only the approximate area of just the egg pockets for its calculation of superimposition mortality. The egg pocket refers to that area where deep streambed disturbance is at a maximum, indicative of essentially complete destruction of any previously deposited eggs. The egg pocket area is typically a value much smaller than the total area of disturbance.

Tom Shaw (unpub. Data, 2004) supplied a spreadsheet providing Klamath River redd area measurements. We calculated values from approximately 85 individual records, each record being a unique redd followed over a maximum 4-week span. The results were as follows:

Average maximum redd disturbance area	= 15 ± 6.7 m^2
Average maximum redd mound area	= 5.9 ± 2.2 m^2
Average redd egg-pocket area	= 4.25 ± 1.4 m^2

We chose to parameterize the model with the 4.25-m^2 average value because it is close to that used by Bartholow and others (1993) for the Trinity River (4.5 m^2). Salmod can simulate superimposition using three distinct probability algorithms. For this application, we have chosen the "random" option, signifying that current spawners neither seek nor avoid previously constructed redds in agreement with Bartholow's (1996) recommendation.

Spatial and Temporal Distribution of Spawners

Salmod allocates adult spawners to designated segments of the river at the beginning of each simulation year; these segments may be defined differently from the flow and temperature division points described previously. This information is typically available from carcass or redd counts. Required data include the number of adults spawning in each section of river, the proportion of female spawners to non spawners, and their weights.

Magneson and others (2000) describes the seventh annual USFWS survey from 13 October to 19 November, 1999, covering 135 river kilometers between Iron Gate Dam and the confluence of Indian Creek at Happy Camp. A total of 989 redds were observed that year, but the report also summarizes data collected back to calendar year 1993, a total of seven years. The surveys have been conducted through six standardized river reaches, each with its own specified length. The exact dates sampled and reported have not been identical each year (in terms of week one being from October X to Y) but they are similar and useful. Although the peak of the spawning run on the Klamath River is known to be slightly variable from year to year (Magneson and others, 2000), evidence from many West Coast rivers suggests that spawn time is more a function of stock genetics (Burger and others, 1985; Quinn and Adams, 1996). However some of this evidence (Quinn and Adams, 1996) comes from sockeye salmon that spawn in headwaters whose conditions may be more hydrologically and thermally stable than many near-ocean conditions.

The Magneson and others (2000) report comments on an observed trend in spawning location from year to year. For example, in 1999, 73 percent of redds lay between Iron Gate and the Shasta River, a proportion that has been increasing through time. Though it is obviously possible to develop separate spatial and temporal values for each year, we chose to aggregate them as a starting point, relying on a simple annual average. To accomplish this, we computed the relative proportions spawning through time and space from the Magneson and others (2000) data. We assumed that values in Magneson and others's (2000) table 1 represented newly constructed redds in all cases, as that seemed to be the intent, though it was not explicitly stated. It was also unclear whether the first week's measurement included redds that had been constructed more than one week in the past. Looking at the "skew" of the temporal distribution, it would appear that the spawning survey probably did not pick up the first week (or two?) of spawning. For this reason, we arbitrarily divided the first week's tally into two equal groups. In other words, we assumed spawning to have begun one week prior to the survey's start with one-half the number of redds. Though it is likely that some new redds may have been missed at the end of the reported survey period, we did not similarly divide the last week reported because the values were so low. We also forced the week boundaries into those used by SIAM/Salmod, which always begins the biological year on October 1. The average first date of spawning was October 8.

In some cases reported by Magneson and others data were missing through space for certain weeks. The average values we derived simply ignored those missing observations. In no case were the Iron Gate to Ash Creek (Reach 1) data missing however, so at least the majority of redds was counted because this is the highest density spawning area. The following table summarizes the results, which we have used to apportion spawners among simulation weeks and river segments. For example, peak spawning occurs the week of October 22. Within that week, and every week, 51+ percent of the spawning activity will be in the first 24 km downstream from Iron Gate dam.

Table 8. Average proportion of main stem Klamath River spawning by week (left hand table) and spatial spawning segment derived from Magneson and others (2000) (right hand table). Only the first three spawning segments fall within the Salmod study area; proportions of adults were recomputed for these three segments alone and supplied to Salmod.

Week beginning	Percentage of spawners		Spawning segment	Segment ending (km downstream from Iron Gate Dam)	Percentage of spawners
8-October	10.72				
15-October	10.73		1	24.41	51.43
22-October	32.32		2	48.91	5.59
29-October	30.22		3	76.01	11.72
5-November	11.69		4	94.81	6.63
12-November	3.60		5	117.51	7.42
19-November	0.72		6	136.61	17.22
Total	100.00		Total		100.00

The model does not account for “green” spawners directly, but does so indirectly by allocating spawning activity through time based on "new" redds identified in the redd counts. Thus, it does not matter if spawning occurs only in one week or is spread out over two months or more. You tell the model what proportion of the adults are "ready" to spawn each week of the designated period. These proportions will hold unless other things preclude spawning, such as temperatures being too high – they wait – or not enough spawning habitat to go around even with superimposition – the adults shed their eggs and die. Adult mortality will be discussed later, but suffice it to say that adults may suffer prespawn mortality from various causes, for example high water temperatures.

Comments on Spawn Timing

Spawn timing in Salmod is set to occur within a certain time window and is not specifically a function of streamflow or habitat availability, though it does depend on water temperature being within certain bounds. If outside the specified bounds, fish that are ready to spawn will wait for the next time-step and reevaluate the temperature.

Some biologists believe that spawn timing may be more a function of habitat availability rather than water temperature. For example, if Klamath River flows are in the 6,000 ft^3/s range there may be little spawning habitat, whereas when flows are reduced to about 1,000 ft^3/s, spawning habitat is abundant. Though spawning in Salmod does not directly respond to a habitat cue, limited spawning habitat will result in the spawners above the spawning habitat's capacity shedding their eggs or dying unspawned. Thus, Salmod does indirectly consider habitat availability.

The USGS committed to closely examine redd and carcass count records to see what water temperatures accompanied main stem spawning. We compared the measured weekly water temperatures downstream from Iron Gate Dam with carcass counts from an unpublished report supplied by Tom Shaw (USFWS). Figure 8 is the result.

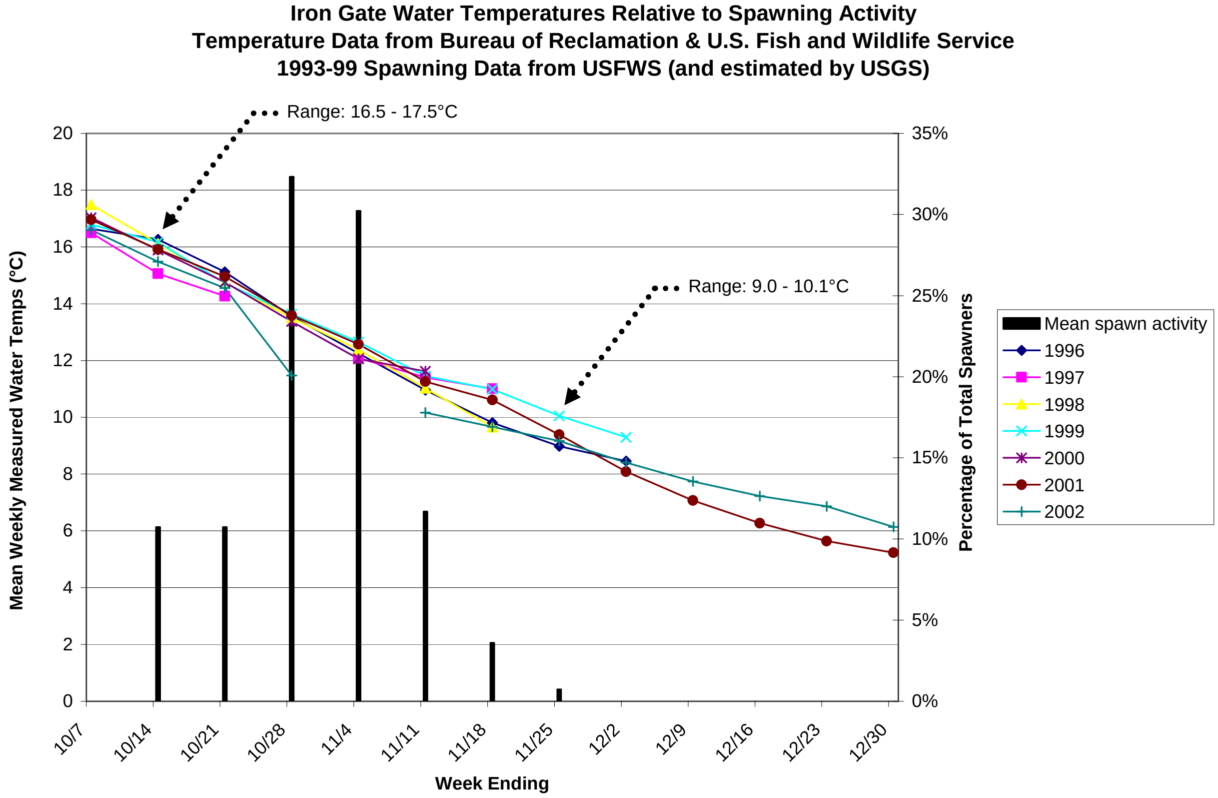

Figure 8. Comparison between measured water temperatures downstream from Iron Gate Dam and spawning activity through time. Vertical bars represent mean proportion of total spawning activity as measured by carcass counts.

It appears that main stem Klamath fall Chinook spawning occurs in a range from 9 to 17.5°C (48.2–63.5°F). Of course, this is no guarantee that temperatures outside this range limit spawning but are just associated with spawning at this location. The spawning temperature range we have been using in Salmod was 5.6 to 18.9°C (42.8–66°F) per Bell (1973) and McCullough (1999). In Salmod, if temperatures are outside these bounds, no spawning will occur that week. Because the range observed on the Klamath is within these wider bounds, we have decided to retain the broader range so that the model will be more likely to faithfully simulate the full range of historical conditions from 1961 to 2003. The broader range will likely also do a better job of simulating a variety of out-of-the-ordinary reservoir operations that might result in a wider thermal response to temperatures downstream from Iron Gate than we have seen in the historical record.

Note also that the timing of spawners arriving at the hatchery can be slightly earlier than the first week in October. Historical hatchery data supplied by Gary Curtis, Yreka Calif., FWS (written comm., 07/19/04), shows fish entering the hatchery as early as 28 September, though in small numbers.

Egg Development and Juvenile Growth

Egg Development Rate

After deposition, eggs incubate and hatch in approximately 6–12 weeks, depending on local river temperatures. Alevins remain in the gravel for an additional period, living off the still-attached yolk sac, and emerge when 100 percent of the development accumulation is reached. Crisp's (1981) quadratic equation was used to calculate each day's thermal contribution from deposition to hatch. The resulting rate values were decreased by one-half to account for the time from hatch to pre-emergence (a slight modification of Crisp, 1988), as was done for the Trinity River (Bartholow and others 1993). The resulting rate function supplied to Salmod is shown in Figure 9. This function shows that eggs will mature more rapidly at 10°C than at 2°C. Note that thermal accumulation begins with egg deposition and does not account for any ova maturation that may have occurred in vivo.

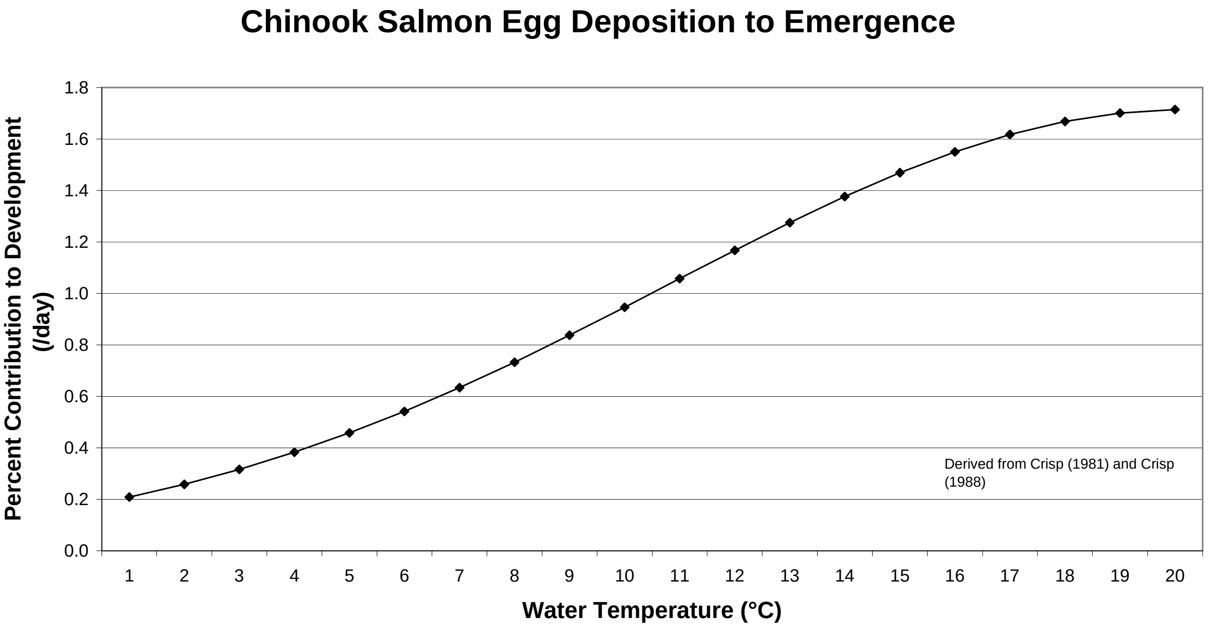

Figure 9. Egg and alevin development rate as a function of mean weekly water temperature. Each week adds to the percent development until 100 percent is reached.

Emergence Temperature

Salmod does not allow fry to emerge from the gravel until mean weekly water temperature exceeds a user-specified threshold. Previous applications have used a minimum of 8°C (46.4°F) based on studies of Atlantic salmon (Jensen and others, 1991), though it is known that in-gravel feeding for Chinook alevins may still be underway (Heming and others, 1982).

When fish are starting to be caught in rotary screw and frame net traps on the Klamath River, measured main stem water temperatures given by SIAM have averaged 6.2°C (confidence interval [CI] ±0.5°C) since 1961. However, it is always possible that warmer, spring-fed tributaries may have contributed fry to the main stem, biasing any estimate of true emergence temperature. Therefore, we looked for other sources of basin-specific data.

Jim Kilgore gave us records from an unpublished 1994 Scott River redd-monitoring study indicating that emergence was indeed highly correlated with 8°C. The Bogus Creek outmigrant study (Jong and Mills, 1993 draft) only recorded weekly maximum and minimum temperatures, but was helpful, if inconsistent. Weekly mean temperatures accompanying significant spikes in early outmigration were 10.9°C in 1986, 2°C in 1987, 5.9°C in 1988, 6°C in 1989, and 8.8°C in 1990. These values average 6.7°C if all values are used and 7.9°C if the 2°C value is considered an anomaly. We also looked at dates for Chinook fry observed emigrating from Fall Creek when that stream was still accessible to anadromous salmon. Data from an old California Department of Fish and Game report (Coots, 1957) show fry leaving that system as early as the week ending January 2, though large numbers did not typically outmigrate until the week ending January 23. Peak outmigration from Fall Creek did not typically occur until late February to early March. Temperature data from Coots (1957) are limited but do characterize water temperatures in Fall Creek in the range of 3.9 to 11.1°C (39 to 52°F) during the 1950–1951 spawning and rearing period. Finally, from charts presented in Chesney and others (2004, Chart 19), the mean weekly water temperature associated with significant early Chinook fry outmigration on the Shasta River was approximately 8.3°C (47°F).

We have consulted with others on this issue, and opinions vary. Thomas Quinn (University of Washington, written comm., 2006) believes there may indeed be a threshold emergence temperature, though it might vary from river to river or area to area. He cites anecdotal information related to ice-out conditions and to late-season temperatures being the best predictor of emergence timing. Others are not so sure. Nick Beer (also University of Washington, written comm., 2006) believes that the suite of simultaneous environmental cues is tricky to decouple, but most likely fish will synchronize spawn timing to “optimize” production and development rate is purely mechanistic. Ernie Brannon (University of Idaho, written comm., 2006) says that he knows of no situation in the field or laboratory where there was an emergence threshold below which emergence would not occur. However, he also stated that, unlike other species, Chinook can feed in the gravel and remain there after their yolk is absorbed if conditions require it.

In summary, we have “data” or observations that suggest that 7–8°C is not unreasonable. We have left the threshold value at 8°C (46.4°F) until more main stem-specific evidence may be brought to bear on the issue. Salmod has no upper temperature threshold. If temperatures are too hot, fry will die due to thermal mortality.

Emergent Length

Salmod initializes newly emerged fish with a length and weight. Because Tom Shaw's (U.S. Fish and Wildlife Service, written comm., 2005) juvenile measurements began around March 1, presumably after significant emergence had taken place, it was unclear whether his measurements could provide accurate initial estimates for newly emerged fry. For example, Shaw's early measurements (March 9–13; 98 observations) have a mean of 38 mm with a standard deviation of 1.8 mm and a total range of 7.0 mm (35.0–42.0 mm). The single smallest fish measured was 27 mm. Because Salmod initializes emerging cohorts with a uniform deviation around the specified mean, not a normal distribution, we decided to start with a mean emergence size of 35 mm ± 4.5 mm. Correspondingly, the initial mean weight of emergents was set to be 0.449 g, per the formula previously described.

Juvenile Growth Rates

Growth rates for juvenile fish are important because the size fry and presmolts achieve provides a competitive advantage to all subsequent life stages, being correlated with survival, smoltification, and reproductive success (Dill and others, 1981; Holtby and Scrivener, 1989; Quinn and Peterson, 1996). Growth rate is the most frequently reported measure of fish health (Sullivan and others, 2000), as it appears to integrate the full range of physiological responses to water temperature. In Salmod, growth is (almost) solely a function of mean weekly water temperature. Although the weekly time-step has been questioned regarding its adequacy in handling thermal mortality (but see discussion below), a mean weekly temperature approach for growth appears well justified. Several authors have investigated the effects of fluctuating temperatures on growth. Fortunately, a time-weighted mean provides essentially the same results as integration over much smaller time increments (Sullivan and others, 2000).

Growth as a function of water temperature for juvenile life stages was obtained from Shelbourne and others (1973) and is the same function used on the Trinity and Sacramento Rivers. Note that this function (Figure 10) assumes a constant food supply with juveniles fed to excess, potentially making it representative for the Klamath River, which has been preliminarily classified as mesotrophic-eutrophic (Caryn Woodhouse, California Regional Water Quality Control Board, written comm., 2005). The growth rates we use are consistent with findings from Marine and Cech (2004) who did not observe significant reductions in juvenile growth rates until daily temperatures, either means or maxima, exceeded 20°C (68°F). However, because the growth rates were derived from optimal experimental conditions, lowering them to some degree may be warranted.

The exception to the statement that growth is solely a function of water temperature is that Salmod can control whether fish that are forced to move due to a habitat/density constraint will be allowed to grow or not. There is scant literature to support one view or the other, but Titus and Mosegaard (1991) concluded the newly emerged trout fry that successfully established feeding territories grew well in contrast to those forced into downstream movement. In fact, they characterized the emigrants as “starved” based on otolith measurements. For this reason, we have set Salmod to allow growth only for juveniles not forced to move during any time-step, the assumption being that energy is preferentially expended by movers in search for new territory and is then not available for growth. In contrast, we set Salmod to allow growth during volitional seasonal downstream movement (discussed in the following section) as reported by Mikulich and Gavrenkov (1986).

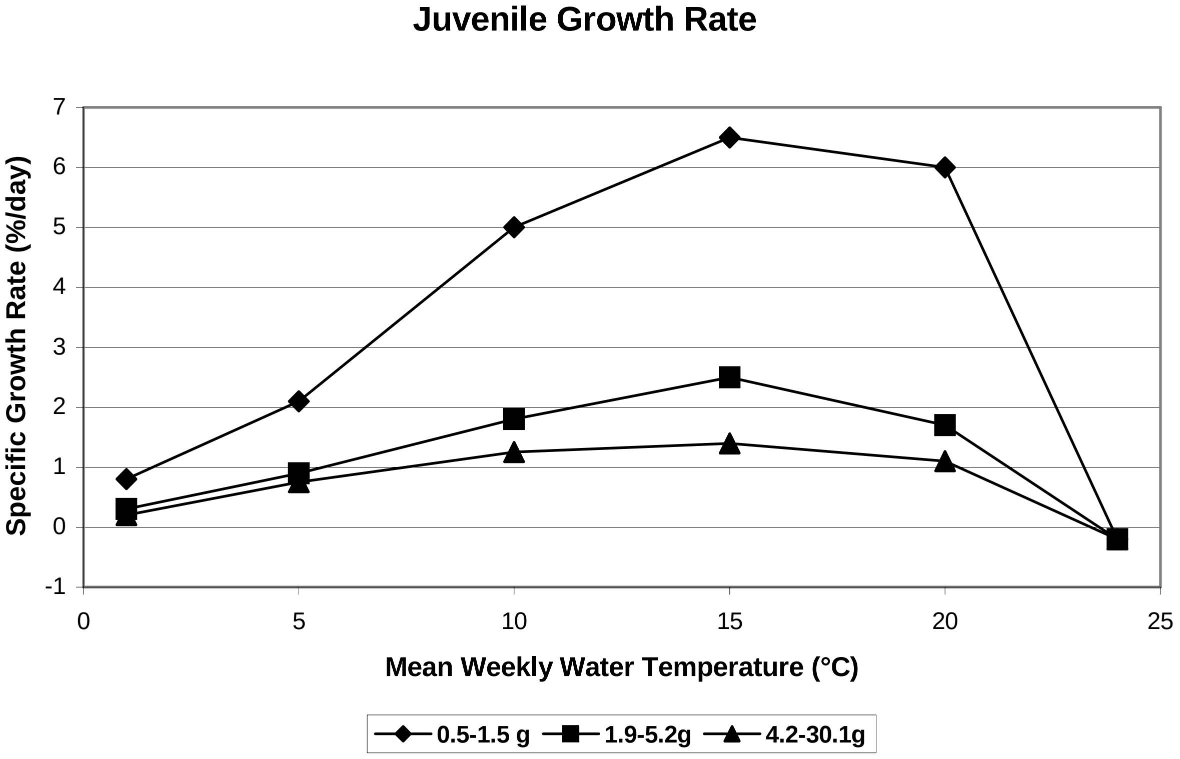

Figure 10. Juvenile growth rates for different weight fish (grams) as a function of mean weekly water temperature. Values are from Shelbourne and others (1973).

Movement and Associated Mortality

Freshet Movement

Freshets (sudden increases in discharge) have been associated with displacement of fry in some rivers (Godin, 1981; Irvine, 1986; Saltveit and others, 1995). It is not clear whether such displacement is due to volitional movement, or is entirely involuntary, or some combination of the two. Nor is it clear whether the stimulus is discharge, turbidity, temperature, or some combination (and note that a water temperature "signal" may not occur in regulated rivers immediately downstream from sizable impoundments). Salmod can displace stages/classes according to user-specified parameters governing proportion of fish moved per weekly time period, the distance they are displaced downstream, and any associated mortality. There are currently three options in Salmod for defining a freshet: (1) when the current time-step's flow is greater than or equal to twice the previous time-step's flow or is greater than or equal to twice the average of the previous three flows; (2) when the current time-step's flow is greater than or equal to twice the previous time-step's flow and is greater than or equal to twice the average of the three previous time-step's flows; or (3) user specified in the *Flow.Dat* input file.

Freshet movement was used initially in the model for the Trinity River but was discontinued due to lack of direct evidence for movement stimulus. The freshet option is currently disabled for the Klamath River because contemporary trapping data have shown no indication of freshet-induced movement in our study area (Sam Williamson, oral comm., 2005). However, because flow fluctuations downstream from Iron Gate are minimal, especially in dry years, there may be little opportunity to witness a "freshet." Trapping data downstream from the Scott River did appear to stimulate a large number of juveniles to emigrate in 1994, but only late in the season well after June 15, after hatchery-released fish were present, and after fish had achieved a mean size of 75–80 mm (Craig, 1994). Field personnel continue to monitor the situation.

Note that a corollary to the previous discussion is that a lack of freshet stimulations may "encourage" juveniles to remain longer in freshwater than they might otherwise do (Irvine, 1986).

Seasonal Movement Timing and Attributes

Salmod moves juveniles a specified distance downstream through a specified time period. The assumption is that these fish are physiologically "ready" and that some combination of external timing cues (water temperature, moon phase, discharge, and so forth) trigger downstream volitional movement of (pre)smolts (McDonald, 1960; Bjornn, 1971).

Though the entire period for seasonal outmigration was shown in Figure 4, recent trapping data reveal a more concentrated timing (Figure 11) extending from the weeks beginning March 11 and ending May 12 (weeks 24–32), though some outmigration at the lowest site (Kinsman) persists longer. Trapping data were of two forms, rotary screw trap and frame netting. The two data sets have been combined in figure 11 by simple averaging because, per Tom Shaw (written comm., 2005), they both have their unique biases. Frame nets likely have problems under turbid conditions and in catching larger Chinook (>55 mm); screw traps likely have problems catching smaller fish. Screw traps must be set in deep water with high velocity, and frame nets must be set in fairly shallow water with moderate velocity. Debris load and variable flows are constant problems with both kinds of traps. Screw traps can ride out most events (but have mechanical breakdowns for other reasons), whereas frame nets wash out more often.

Note that these data have not yet been "expanded" to account for trapping method efficiencies, so they cannot be used for quantitative validation of Salmod. Any outmigration occurring earlier in the biological year may be explained by habitat-constrained movement (or freshets) and not physiological readiness. It should also be remembered that these data may reflect recent evidence of juvenile disease that may "abnormally" abbreviate the outmigration season. Please refer to the section on disease herein.

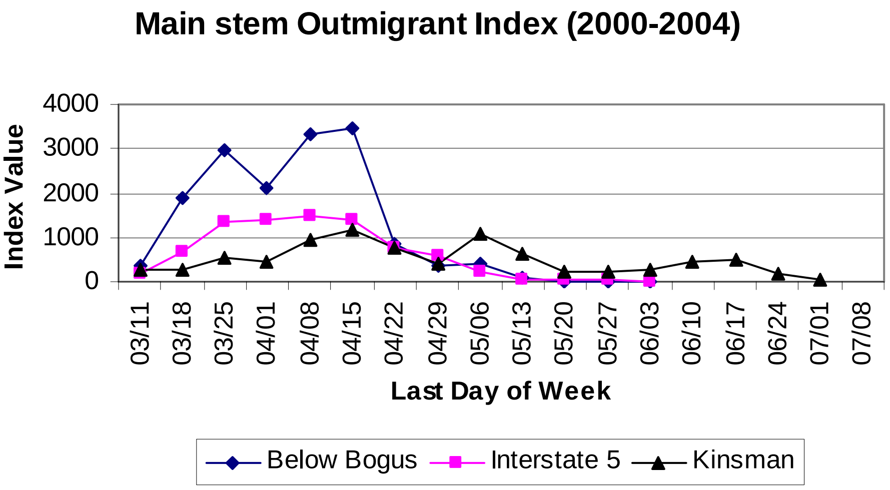

Figure 11. Index to the average number of juvenile Chinook trapped at each of three locations along the Klamath River, 2000 to 2004. This is an index only and should not be construed as absolute numbers. The Kinsman trap is immediately upstream from the Scott River. Data courtesy of the Arcata Fish and Wildlife Office.

To achieve the approximate shape of the outmigrant temporal distribution shown in figure 11, Salmod also requires a description of the proportions of each size class moving per week. This is used to roughly produce the number and length distribution in outmigrants as noted in the field trapping data. Parameter values describing this movement as currently implemented are given in Table 9, indicating that larger fish move farther than smaller fish. This fact was verified by California Department of Fish and Game (2003) who found that the average travel times for Iron Gate hatchery-reared Chinook to the estuary ranged from 26 to 40 days, depending on size. This translates into approximately 82 to 53 km per week, respectively; but of course there is no guarantee that the movement rates are constant either through time or space. We assumed that 10 percent of all emigrating juveniles died each week as they navigated the main stem Klamath River, and we believe this mortality may be largely associated with predation, but offer no proof. This value (10 percent) is questionable and sensitive (see Appendix D) and should be scrutinized closely.

Table 9. Attributes for seasonal outmigration for pre- and immature Chinook smolts for March 11 to May 12 of each year. Parameter values are preliminary calibration values.

Size class	Distance moved (kilometers/week)	Proportion moving (graded from first week to last, respectively)	Mortality (%)
F1	60	2–10%	10
F2	60	2–10%	10
P1	70	2–10%	10
P2	70	2–10%	10
S1	80	2–10%	10
S2	80	2–10%	10
S3	80	2–10%	10

Note that Salmod does not adjust movement distance based on the river's discharge, as has been documented for the Columbia and Snake Rivers (Berggren and Filardo, 1993). This is an area of potential improvement in the model, though we would need reasonable estimates of travel time relative to discharge for the mobile life stages. Movement rates found by Berggren and Filardo (1993) would not be applicable because in that study, movement rates were computed for fish moving through impoundments as well as riverine reaches and were on rivers substantially larger than the Klamath.

Base Mortality Rates

Base, or background, rates of mortality cover all causes of death not otherwise modeled by Salmod. For example, "normal" or “background level” predation fall into this category, as would mortality due to chronically low dissolved oxygen and egg survival. The fractional rates we used came from the calibrated Trinity River model. The weekly base mortality rates were: eggs 0.035, fry 0.025, presmolts 0.025, and immature smolts 0.025. The adult rate was 0.002 based on judgment. Note that “catastrophic” thermally induced disease has been handled differently in Salmod and is discussed in the following section.

Thermal Mortality Rates

Thermal effects on salmon have long been recognized as important on the Klamath River (CH2M Hill, 1985). Thermal concerns span the range from (1) physiological changes, including direct or indirect mortality, growth rate, embryonic development, and susceptibility to parasites and disease; (2) changes to behavior, including seeking special habitat such as thermal refugia, altering feeding activity, shifting fish spatial distributions, and altered species interaction; (3) changes to periodicity, including duration of incubation, onset of spawning, onset of migration, and gonad maturation; and (4) interaction with other water quality constituents, including dissolved oxygen. Most of the temperature focus on West Coast rivers has been high temperatures, with both the Central Valley of California and the Columbia River getting the largest share of attention. However, there is growing concern on East Coast rivers as well as selected interior habitats, for example Ozark and Appalachian Mountains.

Thermal mortality values for Salmod are meant to reflect 7-day exposure-related effects of water temperature. Acute mortality is generally defined as anything up to 96 hours, but Salmod’s 7-day (168-hour) time-step encompasses both acute and longer term (chronic) mortality. The reason that Salmod uses mean weekly water temperatures instead of maximum daily temperatures is that there is a growing consensus that chronic, sublethal temperatures are often more significant than acute lethal temperatures, with the effects being both cumulative and positively correlated with the duration and severity of exposure (Ligon and others, 1999). Brett (1956) concludes that sublethal thermal stress is as decisive as lethal temperatures to survival. Sublethal effects are also associated with suboptimal growth rates, reduced swimming performance and associated predation, increased disease risk, and impaired smoltification (U.S. Environmental Protection Agancy, 2003, Marine and Cech, 2004).

Salmod deals with thermal mortality for each life stage: egg and alevin, fry, juvenile, and adult. There is also a special in vivo category for eggs inside female spawners. Literature suggests that exposure of eggs to high temperatures in vivo may not directly kill the eggs, but rather result in unviable fry that have high mortality. Salmod, however, calculates in vivo mortality as if it occurred prespawn. (Note that in vivo egg mortality is calculated independently of other adult mortality; if an adult female dies for any reason, her eggs also die.) Thermal mortality tends to be sensitive for fall Chinook salmon during the early fall (October) for eggs and late spring/early summer for presmolts (National Biological Service, 1995). Obviously, any residual (stream type) presmolts that over-summer in the main stem Klamath River would also be exposed to high temperatures.

Egg Thermal Mortality Rates

The basis for egg and embryo (including in vivo egg) mortality rates used in Salmod was work done by the U.S. Fish and Wildlife Service and the Bureau of Reclamation to evaluate the effectiveness of adding temperature control to Shasta Dam on the Sacramento River. For that project, Bureau of Reclamation (1991) built a salmon mortality model parameterized with values supplied by the USFWS (Richardson and Harrison, 1990) in collaboration with the California Department of Fish and Game. The exact origin of the rate values supplied by Richardson and Harrison is somewhat obscure, but they cite Hinze and others (1956) and Boles (1988), among others.

Unfortunately, the USFWS calculated what is called "crude" mortality rates because for most, but not all, of the rates they presented (Table 10), they took the percent mortality and divided it by the number of days in the reference period to get the average daily mortality. Crude mortality rates would not be correct for Salmod or similar models because the model's mortality rates operate sequentially. For example, the egg mortality rate given by Richardson and Harrison (1990) for a temperature of 61°F is 80 percent at 15 days. Using their "crude" averaging method resulted in an average daily rate of 5.33 percent (they report 5.3 percent). But if one applied such a crude rate for 15 consecutive days, the resulting mortality rate would be:

$$15 \text{ day mortality } (M_{15}) = 1 - (1 - 0.0533)^{15} = 1 - 0.44 = 0.56$$

far different from the 80 percent they expected and that Salmod requires.

We have corrected the values reported by Richardson and Harrison (1990) using a formula to calculate what is called an "absolute" or "instantaneous" mortality rate and then converting those rates to the reference time period, namely one week for Salmod. Continuing with the same example for illustration, we use:

$$M_1 = 1 - (1 - M_n)^{1/n}$$

where n is the number of days in the reference period. Thus we have:

$$M_1 = 1 - (1 - M_{15})^{1/15} = 1 - (1 - 0.8)^{1/15} = 1 - 0.898 = 0.102$$

Then a seven-day mortality rate would be calculated as:

$$M_7 = 1 - (1 - 0.102)^7 = 1 - 0.472 = 0.528$$

Regrettably, the 100 percent mortalities for temperatures over 62°F given in Richardson and Harrison (1990) present a challenge for this technique. The best we can do is to assume a 1 percent survival for mathematical convenience. Thus a single-day mortality rate that would result in 99 percent mortality at 12 days could be calculated as:

$1 - (1 - M_1)^{12} = 0.99$
$1 - M_1 = 0.01^{1/12}$
$M_1 = 1 - 0.6812 = 0.3187$

We also averaged the mortality rates Richardson and Harrison (1990) used for eggs and sac fry (embryos) to be consistent with the combined life-history simulated in Salmod for the Klamath River. This was done by first calculating the absolute weekly mortality rate for both egg and sac fry. We then averaged these two rates by taking the geometric mean of their respective survival rates (analogous to what we were doing above). We have complicated this somewhat by weighting the two survival rates by their respective durations. That is, the egg stage lasts about 2/3 of the whole egg-alevin life stage whereas the sac-fry stage lasts about 1/3. Thus, these two survival rates were weighted accordingly. This method assumes independence, which is probably not true, but we do not know a better alternative.

With one exception, the last column of Table 10 then records the in-gravel egg mortality rates used in the model. Richardson and Harrison (1990) did not evaluate temperatures below 13°C (55.4°F), but Combs and Burrows (1957) supply relevant data for egg mortality under low constant water temperatures (Figure 12). Data from their study indicate substantial mortality below about 4.5°C (41°F). However, because SIAM tends to underestimate the coldest winter-time water temperatures by about 1.5–1.7°C (unpublished model results), we adjusted the low temperature egg mortality rates to keep from overestimating total mortality.

Table 10. Calculation of mean weekly mortality rate as a function of mean daily water temperature (diel fluctuations of 3°F) for Chinook salmon. Values on the left side of the table were given by Richardson and Harrison (1990); those shaded on the right are our replacement calculations. [Temp, temperature; °F. degrees Fahrenheit; °C, degrees Celsius; %, percent; frct, fraction, <, less than; NA, not applicable]

Temp (°F)	Temp (°C)	Given egg mortality (%/days)[1]	Given egg avg. mortality (%/day)	Given sac-fry mortality (%/days)	Egg mortality (frct/day)[3]	Sac-fry mortality (frct/day)	Egg mortality (frct/week)	Sac-fry mortality (frct/week)	Geometric mean mortality (frct/week)
<56	13.33	Natural[2]	0.00	Natural	0.000	0.000	0.000	0.000	0.000
57	13.89	8 / 24	0.40	Natural	0.003	0.000	0.024	0.000	0.016
58	14.44	15 / 22	0.70	Natural	0.007	0.000	0.050	0.000	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	5.30	50 / 14	0.102	0.048	0.528	0.293	0.460
62	16.67	100 / 12	8.30	75 / 14	0.319	0.094	0.932	0.500	0.867
63	17.22	100 / 11	9.00	100 / 14	0.342	0.280	0.947	0.900	0.934
64	17.78	100 / 7	14.00	NA	0.482	NA	1.000	NA	1.000

[1]. Percent mortality for the number of days indicated.

[2]. Natural implies not elevated above normal background levels.

[3]. Mortality expressed as a fraction.

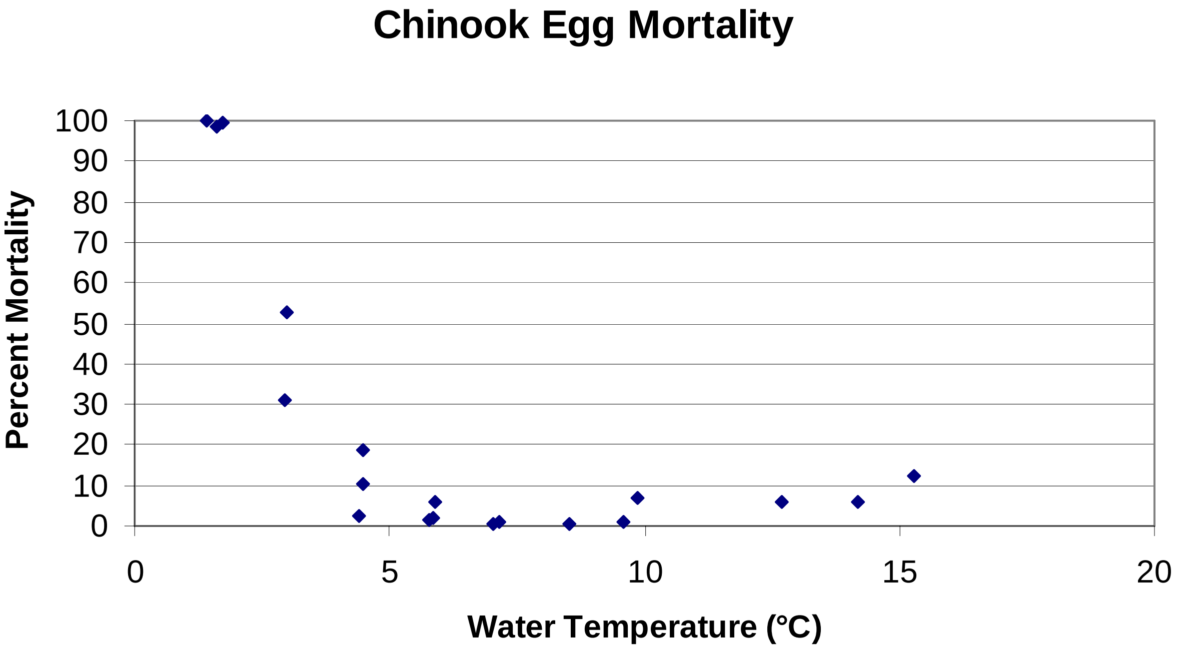

Figure 12. Egg mortality from low constant water temperatures, from Combs and Burrows (1957).

In Vivo Egg Mortality

Donaldson (1990) compiled an extensive list of likely potential effects of stressors (not just water temperature) on sexually maturing adults, including changes in gonad development, changes in the endocrine control system, and changes in gametes, all of which may reduce reproductive success or ultimate recruitment. In Salmod, these effects due to temperature have been lumped into the in vivo egg mortality category. In previous model applications, Salmod has been parameterized using an in vivo mortality rate as a function of water temperature identical to the rate used for in-gravel eggs.

Though not cited by the USFWS, probably the strongest evidence for in vivo gamete mortality has been presented by Billard (1985, his Figure 7) citing his own published work (but in French), Berman (1990), Berman and Quinn (1991) and Leitritz and Lewis (1980). Berman held adult spring Chinook salmon at 14°C and 19°C. The group held at 19°C produced a greater number of pre-hatch mortalities and developmental abnormalities as well as smaller eggs and alevins. As with Berman and Quinn (1991), sample size was too small to permit statistical analysis, and disease was an issue. Leitritz and Lewis (1980, p. 33) dealt primarily with hatchery methods, stating that young rainbow trout should be reared at around 15.5°C (60°F) for good growth, but then maturing rainbows (including Chinook) should be held at water temperatures not exceeding 13.3°C (56°F), and preferably not above 12.2°C (54°F), for a period of at least 6 months before spawning. Flett and others (1996) speculated that low egg survival of coho swimming through warm lake surface water to spawn in tributaries was due to "overripening" in females exposed to high, but not lethal, temperatures. Unfortunately, exact thermal exposure was unknown. Smith and others (1983) showed that cutthroat trout (*Salmo clarki lewisi*) whose holding temperatures ranged from 2 to10°C produced better quality eggs than those fish held at a constant 10°C, but the water sources were different.

Gary Curtis, USFWS Yreka (07/19/04), supplied historical Iron Gate hatchery egg fertility rate data summarized by temporal lot number over the years 1970 to 2001. These data showed a depression in fertility rate in the early portion of the run compared with the later arrivals that could be related to water temperature or some other factors. The linear trend was not high ($r^2 = 0.5$), but the pattern was pervasive and collectively represented many eggs, and therefore smolts. Curtis commented that the early lots are composed of few fish and that the Klamath stock may be more thermally tolerant than other stocks. Though data were not definitive, they were consistent with the earlier portion of the run generally being exposed to higher temperatures. On the other hand, we generally seed the Salmod study area with the full complement of adults in early October, resulting in a potential overestimate of in vivo mortality if all adults have not actually been exposed to the same water temperatures.

We looked more closely at the Iron Gate hatchery fertility data by examining temperatures that each individual lot was exposed to rather than across all lots combined. Plotting the lot fertility rate as a function of hatchery-entry water temperature resulted in the two charts shown in figures 13 and 14. There are two charts because we have a complete record of simulated temperatures but only a spotty record of measured temperatures. Data are sparse on both graphs above 17°C, presumably because hatchery personnel do not start letting Chinook into the hatchery until about October 1, which means that the data set has been abnormally truncated.

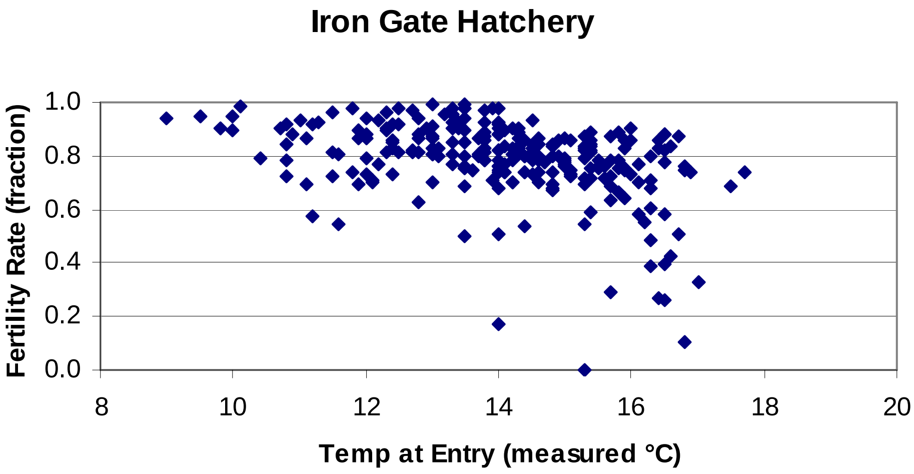

Figure 13. Fertility rate of lots of Iron Gate eggs plotted against measured main stem water temperature at the time of entry.

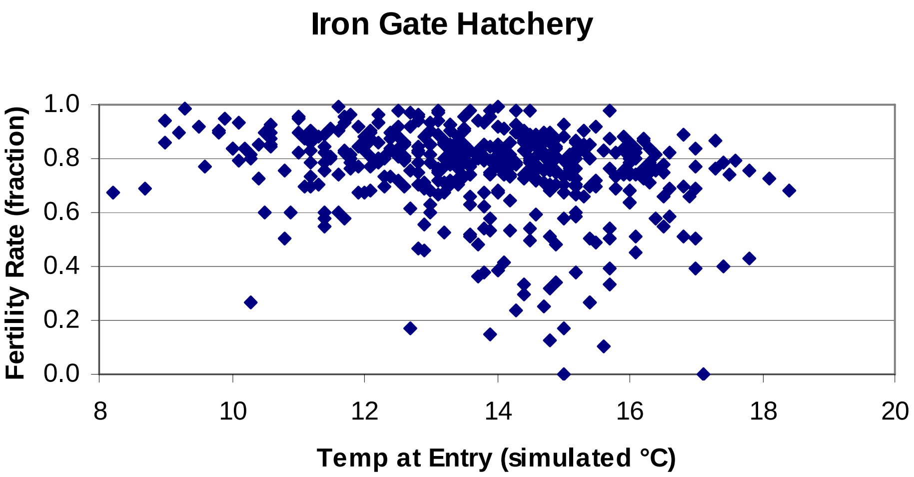

Figure 14. Fertility rate of lots of Iron Gate eggs plotted against simulated main stem water temperature at the time of entry. We have a complete record of simulated temperatures compared with measured temperatures.

At entry temperatures up to about 14°C, most but not all fertility rates are quite high. At entry temperatures above 14°C, the maximum fertility rate begins to decline steadily and low fertility rates become much more common. It looks like the maximum fertility rate could have a "ceiling" at about 75–80 percent when temperatures exceed 18°C.

We consulted with Keith Marine (North State Resources, Redding, California) on this subject. Dr. Marine noted that the principal shortcoming of this data set is that we cannot decompose the effect of temperature on egg fertility into its component effects on the gametes (pre-spawning), sperm motility/ovum membrane function/fertilization/nuclear fusion (spawning), and the initial stages of embryogenesis (incubation), or its effects on the egg at least until eye-up or the customary stage when hatcheries addle eggs to determine fertility. The fertility pattern exhibited in figures 13 and 14 could be affected by temperature during one or all of these stages.

The important thing as far Salmod is concerned is that the model captures the cumulative effect of thermal exposure regardless of the exact sequence of events or causes. However, our preference is certainly to mimic "reality" to the degree possible and not postulate a relationship that we cannot stand behind. Because there is a considerable body of published literature that suggests that there is a real in vivo thermal effect, we have chosen a compromise. We will assume that the in-gravel egg thermal mortality rates apply for in vivo eggs, but we will also assume that adults are behaviorally capable of buffering themselves (and their eggs) from the warmest in-river temperatures. For lack of any other value, we will use the 2.5°C difference found by Berman and Quinn (1991) in the Yakima River. We recognize that this compromise is not supported by McIntosh and Li (1998) for the Klamath (see next section), but it is bolstered by Mike Belchik’s (Yurok Tribe) associate, Josh Strange, who has unpublished data showing that at least some adults use water (refugia) that is 2–4°C cooler than the ambient main stem temperature in the lower Klamath River. Because we have not been able to track down the data from Josh Strange, and because of continued uncertainty, this topic could be a priority for future research.

Juvenile and Adult Thermal Mortality Rates

Thermal mortality rates for juvenile and adult life stages were derived from Baker and others (1995) who used coded-wire tag data to conclude that hatchery-raised fall run Chinook salmon migrating through the Sacramento-San Joaquin Delta had an upper incipient lethal temperature (LT50) of 23.01±1.08°C (73.4±1.9°F). This value is slightly lower than well-recognized laboratory data with established acclimation temperatures, but was pragmatically estimated in the field from trawl runs 2 to 5 days after hatchery releases. One can use the Baker and others (1995) data to estimate a survival curve from a quasi-likelihood function the authors fitted:

$$\text{Survival rate} = \frac{1}{1 + e^{-a-bT}}$$

where a = 15.56
b = -0.6765, and
T = mean daily water temperature for the sampling period

This method is appealing because it avoids problems associated with applying laboratory results to field situations and has an exposure period roughly equal to Salmod's. We assumed that mortality rates for juveniles derived from Baker at al. (1995) also represent adult thermal mortality.

Though there are other data sets in the literature for adults, we wanted to retain the best estimate from field methodology. However, as has been discussed for in vivo eggs, adults may also be buffered from ambient thermal mortality. The study by Berman and Quinn (1991) demonstrated that adult spring Chinook salmon could maintain an average internal body temperature 2.5°C (4.5°F) below ambient river temperatures through a combination of specific cool-water habitat selection and behavioral timing. Though their study was for the Yakima River in Washington, some areas of cool-water refuges generally associated with tributary mouths are known to exist in the Klamath River (Belchik, 1997). Though limited monitoring of adults by McIntosh and Li (1998) found no evidence that upstream-migrating adult fall Chinook salmon were behaviorally thermoregulating, other researchers (Josh Strange) have now found evidence for a 2–4°C buffer in the lower Klamath (unpub. Data, 2005). For this reason, and to be consistent with our in vivo mortality compromise, we have chosen to buffer adults by using the same 2.5°C value. In other words, the model would treat an ambient water temperature of 17.5°C as if it were only 15°C for adults in calculating thermal mortality. The mortality curves we used are shown in Figure 15.

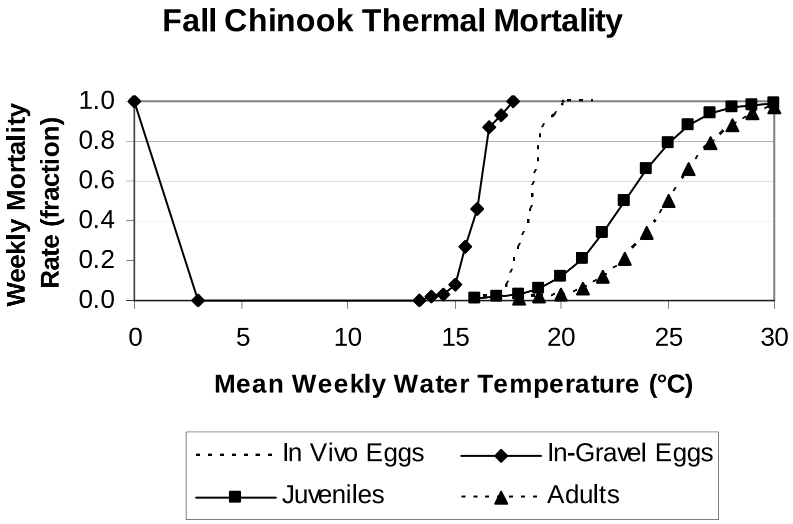

Figure 15. Mortality as a function of mean weekly water temperature used in Salmod simulations. See text for a description of data sources and assumptions. Mortality values used for in vivo eggs and adults have been shifted to the right by 2.5°C to reflect assumed adult behavioral "thermoregulation."

Verification of Thermal Mortality Rates

Because Salmod was sensitive to thermal mortality rates for all life stages, it was appropriate to seek independent verification. Representative values from the literature follow. In general, the authors are referring to constant temperature experiments, but occasionally their metrics are not specific:

Healey (1977) examined egg-to-fingerling mortality at the Coleman National Fish Hatchery and concluded that main stem Sacramento River temperatures should not exceed 14.2°C (57.6°F) to prevent abnormally high (~80 percent) mortality.

Boles (1988) reviewed thermal requirements for each Chinook life stage. Though not quantified in a manner suitable for direct comparison, his findings include: (1) adults held at temperatures in excess of 15.5°C (60°F) exhibited "poor" survival and "reduced" egg viability; (2) eggs incubated at temperatures in excess of 15.5°C (60°F) suffer "high" mortality; (3) eggs incubated in the range of 12.8–14.2 (55–57.5°F) experienced sac-fry mortality in excess of 50 percent; (4) fingerlings appear to have an upper lethal temperature of approximately 25.8°C (78.5°F) for long-term exposure.

Marine (1992) explored a wide variety of thermal effects with an emphasis on adults and their progeny. His findings are summarized in Table 11.

Table 11. A compilation of published information and summary of the observed relationships between water temperature and various attributes of spawning performance in Chinook salmon, with inferences on the sublethal elevated temperature range, derived from the scientific literature, agency reports, and interviews with fishery biologists and hatchery workers. Reproduced from Marine (1992). [°F. degrees Fahrenheit; °C, degrees Celsius; <, less than; >, greater than]

Temperature range	Effect on adult salmon and reproduction	Sources cited by Marine
< 6°C (< 42.8°F)	Increased adult mortality, retarded gonad development and maturation, infertility.	Leitritz and Lewis (1976); Piper and others (1982).
10°C–18°C (50–64.4°F)	Physiological and behavioral optimum temperature range for non-gravid adult salmon.	Coutant (1977); Piper and others (1982); Raleigh and others (1986).
6°C–14°C (42.8–57.2°F)	Optimal pre-spawning broodstock survival, maturation, and spawning temperature range.	Leitritz and Lewis (1976); Piper and others (1982).
15°C–17°C (59–62.6°F)	For chronic exposure, inferred range of incipient sublethal elevated water temperature for broodstock, increased infertility, and embryonic developmental abnormalities.	See text for derivation of this temperature range.
17°C–20°C (62.6–68°F)	For chronic exposure, incipient range of upper lethal water temperature for pre-spawning adult Chinook salmon (primarily derived from observations of captive broodstock).	Hinze and others (1956); Rice (1960); Bouck and others (1977); Berman (1990); and personal communications (see text).
13°C–27°C (55.4–80.6°F)	Increased pathogenesis of many of the important salmonid disease organisms with potential for impairing reproduction in Chinook salmon.	Fryer and Pilcher (1974); Becker and Fujihara (1978); Post (1987).
25°C–27°C (77–80.6°F)	Range of highest elevated temperatures observed to be transiently passed through during migrations or tolerated for short-term by adult Chinook salmon.	Moyle (1976); Piper and others (1982); Department of Water Resources (1988).

Myrick and Cech (2001) provide a recent comprehensive review for Central Valley salmon. They conclude that eggs can survive between 1.7 and 16.6°C (35.1–61.9°F), but with increased mortality below 4°C (39.2°F) or above 12°C (53.6°F). The chronic upper lethal level is approximately 25°C (77°F) with higher temperatures, up to 29°C (84.2°F), tolerated for short periods. Marine and Cech (2004) provide the latest information for juveniles. They conclude that juvenile fall Chinook salmon can withstand chronic (> 60 day) exposure to temperatures in the range 21–24°C (69.8–75.2°F) (with diel fluctuations) and even grow when fed ad lib, albeit at reduced rates. At these temperatures, smoltification was impaired and the smaller fish were at increased vulnerability to predation. Fish reared at 17–20°C (62.6–68°F) grew well, but experienced variable smoltification impairment and higher predation rates than fish reared at 13–16°C (55.4–60.8°F). Although Marine and Cech (2004) conclude that the Baker and others (1995) results likely represented indirect thermal effects as opposed to direct upper incipient lethal thermal effects, for Salmod's purposes, the distinction is unimportant because thermal mortality covers both direct and indirect effects.

Olson and Foster (1955) showed that Columbia River Chinook eggs suffered a total of 79 percent mortality through the fingerling stage if initial incubation temperatures were 18.4°C (65.2°F), but only 10.4 percent mortality if the temperature was 16°C (60.9°F). The latest compilation of information appears in information assembled in support of thermal criteria developed by USEPA primarily for use in Total Maximum Daily Load (TMDL) analyses (Poole and others, 2001). This compilation drew heavily from the work of McCullough (1999) and is summarized in Table 12.

Table 12. Estimates of thermal conditions known to support various life stages and biological functions of anadromous salmon. These numbers do not represent rigid thresholds, but rather represent temperatures above which adverse effects are more likely to occur. In the interest of simplicity, important differences between various species of anadromous salmon are not reflected in this table. Likewise, important differences in how temperatures are expressed are not included (for example instantaneous maximums, daily averages, and so forth). Adapted from Poole and others (2001). [°C, degrees Celsius; <, less than; >, greater than]

Consideration	Anadromous salmon	
Temperature of common summer habitat use	10–17°C	50–62.6°F
Lethal temperatures (one week exposure)	Adults: >21–22°C	>69.8–71.6°F
	Juveniles: >23–24°C	>73.4–75.2°F
Adult migration	Blocked: >21–22°C	>69.8–71.6°F
Swimming speed	Reduced: >20°C	>68°F
	Optimal: 15–19°C	59–66.2°F
Gamete viability during holding	Reduced: >13–16°C	>55.4–60.8°F
Disease rates	Severe: >18–20°C	>64.4–68°F
	Elevated: 14–17°C	57.2–62.6°F
	Minimized: <12–13°C	<53.6–55.4°F
Spawning	Initiated: 7–14°C	44.6–57.2°F
Egg incubation	Optimal: 6–10°C	42.8–50°F
Optimal growth	Unlimited food: 13–19°C	55.4–66.2°F
	Limited food: 10–16°C	50–60.8°F
Smoltification	Suppressed: >11–15°C	>51.8–59°F

Finally, a relatively new report (Richter and Kolmes, 2005) synthesizes numeric water temperature criteria on a mean weekly basis as follows: spawning and incubation, 10°C (50°F);

juvenile rearing, 15°C (59°F); adult migration, 16°C (61°F); smoltification, 15°C (59°F). So, in short, there does not appear to be any information that provides more temperature dose-response quantification than that developed from Richardson and Harrison (1990), Combs and Burrows (1957), and Baker and others (1995) with the modifications we have applied. However, it is apparent that much of the emphasis has been on developing thermal standards (thresholds), not examining exposure-related mortality. To corroborate the estimates we derived from Baker and others (1995) we examined the more “classic” approach to calculate mortality given exposure time and acclimation temperature. Armour (1991) summarizes parameters for an equation that, if evaluated to be greater than 1.0, mortality is expected to occur:

$$1 \geq \frac{\text{minutes}}{10^{[a + b\,(\text{temperature}^\circ\text{C} + 2^\circ\text{C})]}}$$

where a = 22.9065 and b = -0.7611 for an acclimation temperature of 20°C (68°F).

Using this equation and a weekly exposure (10,080 minutes), a temperature of 23°C (73.4°F) is expected to result in 50 percent mortality, in remarkably exact agreement with the Baker and others (1995) formula (see Figure 15**)**. Thus, using multiple lines of evidence, relevant data and accepted methods point to the conclusion that the relationships given in Figure 15 are acceptable for modeling, if not universally subscribed to.

Uncertainty in Thermal Mortality Rates

Having said that we are comfortable with our initial compilation of mortality rates, we also acknowledge room for evaluation and adjustment. Let us briefly revisit both the egg and juvenile/adult criteria.

Eggs

It well could be that the egg mortality rates derived from hatchery studies are too high at moderate temperatures because eggs, and presumably embryos, remain buried in approximately 10–30 cm of gravel and may be buffered from in-channel water temperatures that would otherwise be too hot, or too cold, for optimum survival. Shepherd and others (1986) showed that intragravel temperatures approximately 10 cm into the streambed causes parallel but lagged and buffered heating and cooling trends in infiltration-source intragravel water compared with surface water. Such waters were generally 0.5–1.0°C warmer in winter and 0.5–1.5°C cooler in summer, with crossovers around March and October. Hannah and others (2004) showed that in-gravel incubation temperatures were, on average, 1.97°C warmer than water-column temperatures in a coastal Scottish salmon stream. However, Geist and others (2002) found that Chinook, unlike chum salmon (*Oncorhynchus keta*), in the Columbia River tended to spawn in zones of downwelling water where, presumably, a redd’s thermal environment would be more like that of the main river.

Linda Prendergast (PacifiCorp) said that she could make data for intragravel temperatures downstream from Iron Gate Dam available. USGS was contacted by a PacifiCorp consultant (Richard Raymond, ES Environmental Services) who had attempted to conduct a study of intragravel dissolved oxygen in October 2004. He used methods similar to those used previously on the Deschutes River and supplied a report of his work. At one site downstream from Iron

Gate dam approximately 100 m upstream from the hatchery bridge, they simultaneously deployed two multi-parameter probes. One was in a standpipe in an artificially created gravel redd and the other was in the river at about mid-depth. Unfortunately, the effort was “sabotaged” by salmon attempting to spawn on top of their artificially created redd. The salmon repeatedly rearranged the redd’s gravel, knocking down and mostly burying the standpipe. A spreadsheet of data capture was supplied and examined. Despite the apparent problem with the data, they appeared somewhat useful. There was a characteristic lag between ambient river temperatures and what occurred in the gravel, but no significant difference between the two on a daily average basis, at least at this site.

During the Yreka workshop, it was also suggested that we need to revisit egg mortality at cold water temperatures (< 5°C) per the Combs and Burrows (1957) data. Scant data exist on this because these temperatures are so rarely encountered under hatchery conditions, but a recent published review (Myrick and Cech, 2004) confirms that temperatures below 5.6°C are associated with increasingly high egg mortality, so we have retained the Combs and Burrows (1957) portion of the mortality curve.

In summary, Klamath-specific data did not appear to justify any adjustment to egg thermal mortality rates in either cold or hot conditions. We have chosen to assume (per Geist and others, 2002) that intragravel egg temperatures are likely to be little different from main-channel water temperatures. This may be an appropriate area for research in the future.

Juveniles and Adults

There may be problems using the Baker at al. (1995) technique applied previously. The data were collected from fall-run hatchery fish traversing the sometimes-brackish waters of the Sacramento bay-delta system. Fish recoveries were made from mid-water trawls that may bias the interpretation for fish not actively (or passively) outmigrating. There are a variety of mathematical assumptions implicit in the curve fitting that Baker and others (1995) did. Exposure times were not uniform and may or may not conform to Salmod's weekly time-step. Finally, the data represent only smolts, yet we have applied the results to all juvenile and adult life stages. In spite of these limitations, we feel that this approach is a step forward from the more simplistic habitat suitability index (HIS)-type method used in previous Salmod applications and helps avoid using unmodified laboratory-derived data in real-world applications (Ligon and others, 1999).

There has always been speculation that the Klamath River stocks may exhibit higher thermal thresholds than other West Coast stocks. However, during the course of our literature review, we found no conclusive evidence that this is true. McCullough (1999) investigated the issue of stock-specific thermal adaptation as part of his comprehensive review and found that, although there are well recognized genetic adaptations to temperature that appear to tailor the fitness of stocks to their environment, absolute differences are small, generally attributable to morphological distinctions, and never result in a conclusion that thermal standards should be stock specific. Myrick and Cech (2001) comment that Central Valley Chinook salmon, despite their southerly distribution, do not appear to have any greater thermal tolerance than more northerly races. Further, thermal tolerance is a function of acclimation history that is, of course, an implicit consequence of each unique physical setting and time series of thermal exposure.

It is reasonable to speculate that fish survive thermal extremes best with abundant food availability. Brett and others (1982) and others have shown that both optimum growth temperatures and the point of zero net growth shift toward lower temperatures as ration declines and sublethal growth stress increases. The Klamath River may be classified as an enriched river (Caryn Woodhouse, California Regional Water Quality Control Board, written comm., 2005) and therefore Klamath fish may be expected to exhibit some of the highest levels of growth in response to otherwise non-lethal high temperatures. Speculation about the uniqueness of Klamath stocks relative to thermal mortality, however, will remain an issue.

In sum, we feel comfortable that we have identified suitable sets of thermal mortality rates for each of the Chinook life stages, at least initially. Remaining uncertainty leaves some room for adjusting those rates, up or down, as we learn and adapt during model calibration. Further research would always be advisable.

Effect of disease on juvenile thermal mortality

Disease is emerging as a potentially significant issue for juvenile Chinook on the Klamath River, and we treat it here as a unique concern. At a review workshop held in Yreka in January 2005, participants reached no consensus about river reaches involved in high-incidence disease outbreaks, likely triggers of the three juvenile diseases, or related issues except that the incidence of disease appears low when water temperatures are below 10°C.

To better capture information from others not present at the workshop, a conference call was convened on March 17, 2005, with several individuals, notably researchers Jerry Bartholomew (Center for Fish Disease Research, Oregon State University) and Scott Foott (USFWS CA-NV Fish Health Center, Anderson, California). The stage was set by generally describing the Salmod model (including that thermal exposure was handled on a mean weekly basis) and outlining several options for how one might account for what is known about juvenile Chinook disease-induced mortality into the Salmod model. Options ranged from (1) just incorporating disease as a “background” mortality rate, (2) considering a disease “window” though time and space where disease prevalence or virulence were especially high, (3) considering that disease-induced mortality was a function of water temperature or discharge, or both, and (4) any of the above with a fish density component.

Though the conversation ranged widely, it was clear from the beginning that the immediate focus was *Ceratomyxa Shasta.* The researchers were confident that the entire stretch of river between Iron Gate Dam and the Scott River was problematic for this disease infecting juvenile Chinook salmon. High mortalities to relatively short exposures were commonly observed, depending on water temperatures, particularly those over 10°C.

There was also speculation that there may be a higher incidence of disease during years of lower flow, on the Klamath and on other rivers in Oregon. Low flows may act by (A) not adequately flushing substrates, (B) concentrating actinospores released by polychaete populations, or (C) stimulating an overgrowth of Cladophora and related species thought to provide quality habitat for polychaete rearing. In addition, although *C. Shasta* itself is not a contagious disease, other co-occurring diseases are, and when they act synergistically, there may be a reason to believe that disease-induced mortality from the complex of hosts is density dependent. It was speculated that low river flows may simultaneously restrict fish habitat, thus concentrating fish. Low flows may also render some microhabitats unavailable that could have provided some protection (refuge) from water-borne diseases. Thus, in low water years, both fish and intermediate hosts may be in closer proximity simply because habitat is limited.

A report by the Oregon Department of Fish and Wildlife (2000) demonstrated a clear relationship between Willamette River discharge and downstream water temperatures. However, the relationship between flow and water temperature downstream from Iron Gate Dam is neither as clear cut nor as intuitive as on the Willamette River. We (USGS) have carefully examined the relationship between discharge and water temperature in all months (unpublished data) and can confidently state that varying Iron Gate discharge in April between 500 and 2,500 ft^3/s has virtually no effect on mean daily water temperature because temperatures throughout the river are essentially uniform and the reservoirs have little or no hypolimnetic storage. Varying the discharge in May from 500 to 2,500 ft^3/s actually increases water temperatures, but by less than 2°C, because you are simply bringing more ambient ("hot") water down from Upper Klamath Lake. Increasing the flows during the summer months results in similar temperature increases. Annual variation in meteorology over the 40+ year period we have looked at is far more influential in controlling water temperatures, accounting for about 4–6°C in year-to-year (and month-to-month) water temperature variation. This does not mean that flow is unimportant in disease-induced salmon mortality given the hypothesis that spore concentration is increased at low flow. It does mean, however, that until we have a more definitive (and defensible) base of evidence on the Klamath, it would be unwise to make the juvenile Chinook temperature:mortality function in Salmod flow dependent – except to further explore this as a hypothesis.

Dealing for the moment with water temperature alone, it is clear that the parasites replicate as a function of water temperature and that the infection process is therefore temperature-dependent. Though infection has been observed as low as 4°C, 10°C is the commonly cited threshold above which the infection rate and degree of mortality both increase rapidly regardless of life stage, size class, or whether the fish were of "wild" or hatchery origin. Several references were cited by participants that pointed to 10°C as the approximate threshold (Ratliff, 1981; Ratliff, 1983; Hendrikson and others, 1989; Bartholomew, 1998; and Udey and others, 1975) with an increasing incidence of infection, ultimate mortality rate and reduction in time to death above that temperature. [For an excellent discussion of diseases affecting West Coast streams, see Washington State Department of Ecology (2002).]

Spatially, it was noted that Iron Gate Reservoir, or at least the hatchery withdrawal below Iron Gate's surface, did not appear to contain *C. Shasta* because both hatchery and sentinel fish placed immediately downstream from the dam had a low rate of infection relative to downstream locations. For example, only a few river kilometers downstream near the I-5 Bridge, infection rates were high. This also seems to be true in the Upper Klamath area near Keno Dam, Oregon. There was some speculation that adult Chinook salmon in the main stem transport the spores upstream to spawning areas and that high density spawning areas might themselves be "hot spots" for infection. It was also noted that there must be some degree of disease resistance in Klamath stocks because at least a small proportion of hatchery fish return each year to spawn and these fish are clearly exposed but have not succumbed to the disease.

Given this information, we discussed several possibilities to describe the functional relationship between water temperature and mortality in Salmod. The following table compares current Salmod values, proposed values from the phone conversation, and values being used in the Ecosystems Diagnostics and Treatment (EDT) model. As discussed elsewhere, current weekly values were derived from the Sacramento River (Baker and others, 1995) with no major mortality attributable to *C. Shasta* in that river. Note that proposed mortality estimates are given as a range (uncertainty arising from other as yet unquantified factors) derived from expert opinion and comparable to the relationship being used in the EDT model. Mortalities represent not just those due to *C. Shasta* alone, but also other synergistic diseases. It seems clear that the mortality rates currently being used in Salmod are too low to account for the recently observed disease prevalence. (It would also appear that the EDT values may be too low, especially considering the monthly time-step.)

Table 13. Comparison of juvenile Chinook mortality rates as a function of mean water temperature. Shown are the values used in Salmod with and without disease mediation and current EDT model values. The disease-mediated values were proposed by Jerri Bartholomew (Oregon State University) and Scott Foott (USFWS), whose opinions were supplemented by experimental results and field data collections (Bartholomew, 1998; Foott and others, 1999; Foott and others, 2002; Foott and others, 2003; Foott and others, 2004) and are the values applied in this analysis. [Temp, temperature; 5, percent; °C, degrees Celsius; <, less than; >, greater than; EDT, Ecosystems Diagnostics and Treatment]

Salmod No Disease		Salmod with Disease		EDT	
Temp (°C)	Weekly Mortality (%)	Temp (°C)	Weekly Mortality Range (%)	Temp (°C)	Monthly Mortality (%)
		10	0–20	<10	0
		12	20–40		
		15	>50		
		…	…	10–16	20–60
<16	0.0	…	…		
16	0.9	Interpolated	Interpolated	16	20–60
17	1.7	…	…	17	50->90
18	3.3	…	…	18	50->90
19	6.3	…	…	19	50->90
20	11.6	20	80–100	20	50->90
21	20.5	…	…	21	50->90
22	33.7	…	…	22	50->90
23	50.0	23	~100	23	>90
24	66.3	>23	100	24	>90
25	79.5			25	>90
26	88.4			26	>90
27	93.7			27	>90
28	96.7			28	>90
29	98.3			29	100
30	99.1			30	100

After much consideration, we decided that for the historical analysis we will apply only the post-1994 mortality values because these values reflect the current and foreseeable management environment. In other words, the historical analysis relies on the historical flow and temperature time series but estimated current biological phenomena. Any model calibration meant to reflect true historical conditions should apply the pre-1994 values as appropriate because it appears likely that high *C. Shasta* mortality rates might not have been associated with Klamath stocks before that time (Foott and others, 1999).

Habitat Capacity

Salmod assumes a relatively fixed "capacity" per unit of available physical habitat for adult and juvenile fish (Chapman, 1962; Mesick, 1988; Beechie and others, 1994). Capacity is computed by knowing the flow in each computation unit, translating that into square meters of available habitat for each life stage, and knowing the maximum biomass or number of individuals for that life stage that can occupy a square meter of optimum habitat. The model moves juvenile and adult fish that exceed capacity to a downstream computation unit.

In previous Salmod applications, we have used either the maximum number of fish or maximum biomass per unit area. On the Trinity River, for example, the biologists preferred the maximum number because it best matched the data they had collected from systematic snorkel observations. Kent (1999) subsequently applied the Trinity River derived values to the initial Sacramento River model but did not calibrate the model. Burns (1971) preferred to quantify habitat capacity in terms of the average weight of fish per unit of surface area or, in our case, habitat area (and as a note, Salmod is to a degree based on Burns' early work). Bartholow (2005) used the maximum biomass approach rather than numbers of individuals because he believed that (1) it is more consistent with what we understand in terms of bioenergetic requirements, (2) measuring density with numbers per unit area has the problem that two individuals of different body size should not count equally, and (3) because biomass increases as fish grow in length and weight, such growth would result in a somewhat constant "pressure" for some individuals to move (Grant and Kramer, 1990; Bohlin and others, 1994; though see Grant and others, 1998, for a critique). Another approach used in France is to choose the median biomass per unit area.

Regardless of the technique used, it is apparent that one can obtain vastly different density estimates in different riverine settings, and great care must be used if one transfers site-specific density values from another river to the Klamath unless verified. Density estimates described by Grant and Kramer (1990) were largely from small "natural" streams; the Klamath River with several in-line reservoirs is anything but natural and small. Further, Salmod assumes that maximum habitat capacity is per unit of ideal habitat (WUA), and the quality of ideal habitat may not be transferable from small streams to large rivers (Grant and others, 1998). The factor most likely to influence the currency, and therefore lack of transferability from one stream to another, is food availability because food productivity is thought to directly affect minimum territory size (Grant and others, 1998). For example, Allen (1969) cites an average salmonid density of 1.7 g/m^2 for New Zealand rivers, an order of magnitude lower than the values from Grant and Kramer (1990). Hume and Parkinson (1987) cite stocking densities as low as 0.3–0.7 fry/m^2 in low-productivity British Columbia streams.

In consultation with field biologists, it was agreed that we would use numbers of fish, rather than biomass, as the best way to express this value on the Klamath River. Tom Shaw (USFWS) sent spreadsheets compiled from their 1998–2004 database of juvenile density estimates derived from a Moran-Zippin multi-pass calculation method and summarized as fish/m^2. The 90-percentile density was calculated after eliminating data records inappropriate for this method, under the assumption that values in excess of the 90-percentile are aberrations above carrying capacity. Although the data base did include some fish above 55 mm, the vast majority (>97 percent), especially early in the year when high densities are expected, were for fish below 55 mm. The 90-percentile value was 15.3 fry/m^2, remarkably close to the literature value we have used previously of 15.48 fry/m^2 (Grant and Kramer, 1990).

There was no clear evidence that the average density has varied through time (across years), but there was a clear gradient along the river from the high-density spawning areas to low densities farther downstream, as would be expected. There was variation in density by habitat type (for example low slope, mod slope, and so forth), but not extreme. In the future, we may wish to consider trying to correct for any assumed differences in habitat "quality" between habitat types. For this report we have assumed 15.3 fry/m^2. Because this value is so close to Grant and Kramer (1990), and there were not enough samples in the Arcata FWS database for fish > 55 mm, we have used Grant and Kramer's estimates of 3.23 presmolts/m^2 and 0.93 immature smolts/m^2 as well. As with thermal mortality rates, we must acknowledge considerable uncertainty in these estimates of maximum density per unit usable area. The values will be sensitive in controlling relative Chinook salmon production. However, the good news is that these values have generally been found to only shift (scale) the relative magnitude of production rather than alter the absolute ranking of one flow scenario over another (unpublished modeling results).

Table 14 compares fish density values used in some previous Salmod applications. As mentioned, the Kent (1999) density values were used on the Trinity and initial Sacramento River models. The Grant and Kramer (1990) values have been used for the Atlantic salmon model because we had nothing better to apply. Differences between rivers remain unexplained but likely represent differences in methodologies.

Table 14. Comparison of maximum number of individuals per unit weighted usable area (WUA; m^2) used in different applications. The values for Grant and Kramer (1990) were calculated by using the mean weight for each respective life stage.

Life stage	Maximum number/m^2 WUA (Kent, 1999)	Maximum number/m^2 WUA (Grant and Kramer, 1990)	Maximum number/m^2 WUA For the Klamath River (fry value from Arcata Fish and Wildlife Service)
Fry	86.0	15.48	15.3
Presmolts	11.8	3.23	3.23
Immature smolts	11.8	0.93	0.93
Adults	0.01	0.01	0.01

Habitat-Induced Movement Rules

In the event that fry in a computation unit exceed the computed habitat capacity, we set Salmod to first move the most recent arrivals out of that computation unit under the supposition that moving, non-territorial fry are more likely to continue to move. In contrast, the model moves the more territorial presmolts and immature smolts with the lowest condition factor first, assuming that more robust fish have a territorial advantage. These two methods operate only within in a life stage category, in other words fry only compete with fry, and so forth. It is possible to set Salmod to be even more size selective within a life stage. In other words, one could move the smallest, most recently arrived fry first, but we have not done so for this Klamath application as it does not appear to significantly affect the results. On the Klamath River, all habitat-induced movement is set to be downstream only.

Distance Moved Mortality Rate

There is a mortality rate associated with habitat-induced movement–the farther fish must travel to encounter unoccupied habitat, the greater their mortality. Though there are a variety of ways to quantify this mortality in Salmod, we find it conceptually easiest to specify the maximum distance that can be moved in one week before 100 percent mortality, linearly interpolating back to zero mortality at zero distance, though it is possible to describe any curvilinear function one can support or hypothesize.

Kent (1999) used 3 km as the maximum distance regardless of life state/size class on the Sacramento River, stating:

> No studies have been performed to find the average distance juveniles move over a specific time period while rearing. Bill Snider of the California Department of Fish and Game reports that juvenile Chinook salmon migrate long distances while rearing, such that a fry migrating 3 kilometers 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.
>
> Because 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 kilometers. Juveniles which must move more than 3 kilometers in a week due to lack of suitable rearing habitat will die.

In contrast, values applied for the Trinity River are shown in Table 15, illustrating the assumption that smaller fish may be more vulnerable to mortality during a forced movement. These are the values currently used in the Klamath River Salmod model. Note that these values only apply during a forced movement. Mortality associated with seasonal emigration are specified independently.

Table 15. Maximum distance moved per week associated with 100 percent mortality during habitat-induced movement (from Bartholow and others, 1993). [m, meters]

Stage	Size class	Maximum distance (m) moved before 100% mortality
Fry	F1	800
	F2	1,000
Presmolts	P1	1,500
	P2	2,500
Immature smolts	S1	3,000
	S2	3,500
	S3	4,000

Exogenous Production

Chinook salmon production in the Klamath River downstream from Iron Gate is not isolated to the main stem. Several tributaries and the Iron Gate hatchery also produce fish that supplement main stem production, entering the main stem at specific locations and specific times. It was agreed at the Yreka workshop that we needed to get an idea of the magnitude, timing, and length classes for juveniles emerging from the monitored Shasta River and Bogus

Creek and other tributaries in the Iron Gate to Scott River modeling area. These additional contributions then become part of the standard Salmod input file (*Suplement.Dat*) for use in model simulations to shed light on the effects that these tributary fish may have on other main stem-spawned juveniles. However, it should be understood that these tributaries are not modeled; rather the tributary production was simulated as a constant for each year.

Several steps were involved in doing this and we lay these steps out below, including important assumptions that accompany the process. (We also note that there was some discussion at the workshop that historical tributary production might have been considerably larger than at present.)

Tributary Contributions

Bill Chesney supplied copies of the CDFG Shasta River Chinook fry outmigrant studies for 2001–2004, the later year being draft only, with accompanying spreadsheets (Chesney, 2002; Chesney and others, 2003; Chesney and others, 2004). The summary data Chesney supplied had already been corrected for trap efficiency and river volume sampled. We took a simple average of the 2001–2004 data by week, converted these weekly averages from 6-day per week estimates to 7-day per week estimates, and summarized the data as shown in Figure 16. Because part of the objective is to "test" the main stem model with a substantial number of tributary juveniles, we elected to use the higher average rather than the median number of juveniles per week, recognizing that the average, or even the 2001 number, may be small relative to historical estimates of production.

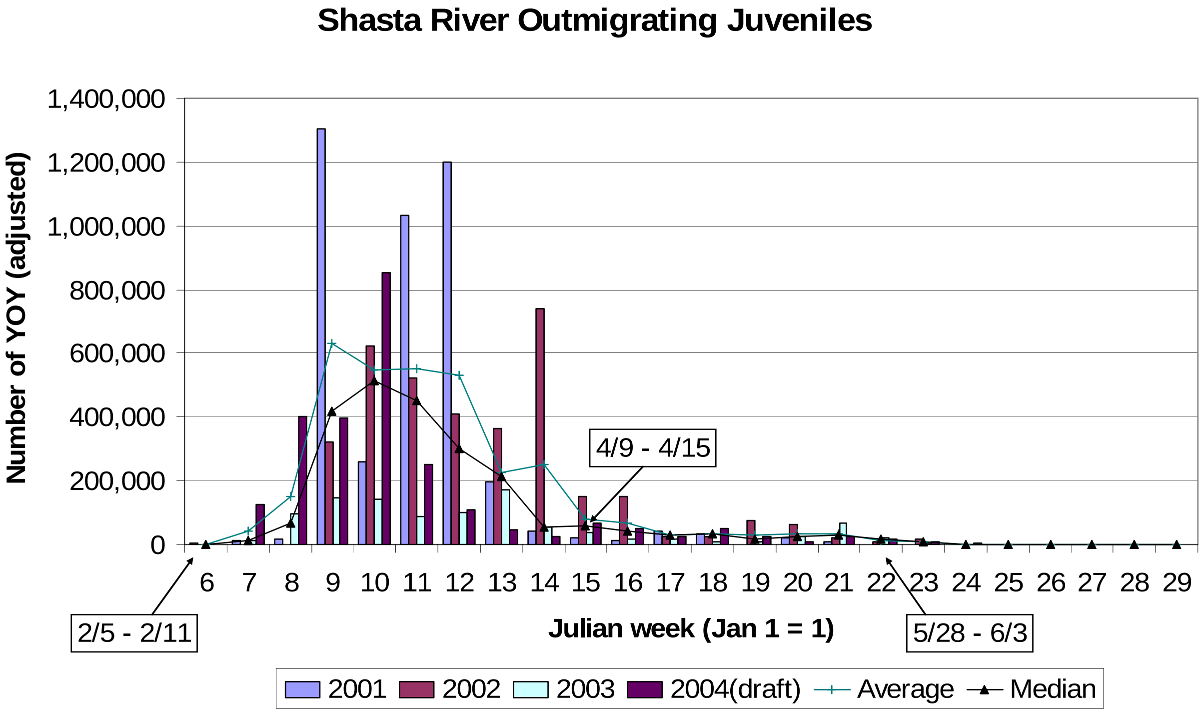

Figure 16. Data supplied by Bill Chesney (California Department of Fish and Game) for young-of-year (YOY) Chinook outmigrants on the Shasta River.

“Raw” trap data supplied by Chesney were used to compute the relative proportion of juveniles in each of several size classes for each sampling week. These data were “raw” in that they had not been corrected for sampling efficiency, but they were suitable for computing size class proportions to be applied to the average weekly corrected estimates. No data were available to suggest that one size class was more or less susceptible to trapping, so no further adjustments were made. The raw trap data Chesney supplied recorded a few juveniles in weeks not represented in his outmigrant summaries; because these represented only trivial tails of each annual distribution, we ignored these small numbers.

Chinook salmon production data for Bogus Creek were also compiled from California Department of Fish and Game reports (Jong and Mills, 1993, unpublished data). Unlike data available for the Shasta River, the Bogus Creek data were not true production estimates, instead representing an unexpanded index. Thus we had no computed estimate of total Bogus Creek production. Bill Jong and Mark Pisano (California Department of Fish and Game, written comm., 2005) offered their speculation that the Shasta River produces more total juveniles than Bogus Creek. They stated that Bogus Creek likely has more adult escapement given its proximity to the hatchery (and that many, if not most, adults ascending Bogus Creek are likely of hatchery origin). Redd superimposition probably occurs more often in Bogus Creek than in the Shasta River, but abundance of spawning substrate is greater in Bogus Creek than at least the canyon portion of the Shasta River, which argues for higher hatching success in Bogus Creek. However, the Shasta River is longer (64 km compared to 24 km), has a generally lower gradient (1.6 compared to 7.2 percent), and has a higher flow during the spawning season (35 to 208 ft^3/s compared to 14 to 21) (Jong and Mills, 1993, unpublished data). The Shasta River also has a greater abundance of suitable spawning gravels and higher water quality (temperature) in its upper reaches. For these reasons, we (USGS) have assumed that Bogus Creek produces one-half the YOY juveniles that the Shasta River produces, on average.

The draft report on Bogus Creek production (Jong and Mills, 1993, unpublished data) recorded the total weekly catch for 1986–1990 from which we could once again compute an overall weekly average production index. These weekly index values were then totaled and adjusted as discussed above to equal ½ of the Shasta production. Though the Bogus Creek report did not contain length:frequency data, it did contain a weekly mean length and standard deviation. Therefore, we divided the weekly juvenile production computed into two length/weight categories, mean ± standard deviation to reflect the variance to the degree supported by the data. Both the average weekly production and length classes are shown in Figure 17.

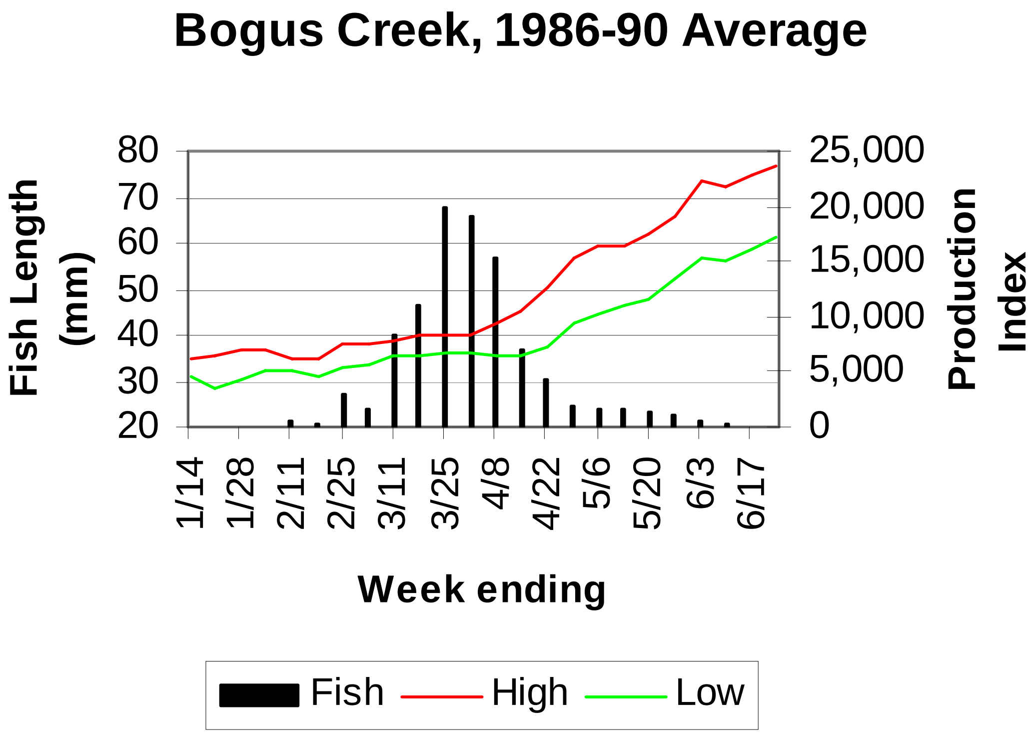

Figure 17. Juvenile production index for Bogus Creek calculated from unpublished data (Jong and Mills, 1993 draft). Fish refers to numbers of juvenile Chinook, whereas High and Low refer to the mean plus and minus one standard deviation for length classes.

We assumed that the total juvenile contribution from the Shasta River and Bogus Creek combined represented 80–90 percent of the total tributary juvenile contribution between Iron Gate Dam and the Scott River, on average. Though it would have been possible to allocate this remaining percentage among the other minor tributaries according to their location along the modeling reach, for simplicity we added 15 percent to the total Bogus and Shasta contributions, respectively, (by dividing each by 0.85) because we believed that such few juveniles distributed elsewhere would not result in a noticeably different effect in Salmod.

Conceptually, tributaries enter the simulation model’s virtual river at one computation unit. Adding one week’s tributary contribution to a single computation unit would potentially permit disproportionate crowding in that unit. An alternative would be to distribute these fish for a distance equal to one week’s travel time downstream, but this would essentially permit distribution throughout the entire study area. We chose a compromise by assuming that tributary fish, like hatchery fish discussed in the next section, would be distributed throughout a 5-km “mixing zone” downstream from each tributary. Juveniles entering the main stem are treated just like main stem cohorts; if they are moving seasonally, they will continue to do so.

Hatchery Contributions

Mark Hampton supplied a spreadsheet of Iron Gate hatchery data so that we could develop estimates of juvenile releases into the main stem (Table 16). Unlike the values we computed for the Shasta River and Bogus Creek, these releases are so “late” and generally homogeneous in length and weight, we chose not to divide them into length classes, which would have been difficult from the available data anyway.

Table 16. Date of release, number and weight of juveniles released from Iron Gate Hatchery into the Klamath River since the beginning of the "early release" strategy. All values were computed from spreadsheet supplied by Mark Hampton (CDFG, written comm., 2005). Averages at the bottom of the table are meant to be representative and are the values used in Salmod. Values for yearlings released in November were ignored.

Year	Release date	Salmod week	Number of fry	Weight (grams)
2001	5/21	34	868,165	5.04
2001	5/26	34	869,265	4.93
2001	5/26	34	1,738,503	3.94
2001	5/26	34	1,464,064	2.77
2002	5/10	32	862,908	4.98
2002	5/21	34	854,456	5.04
2002	5/28	35	1,699,858	5.34
2002	6/5	36	1,549,867	4.32
2003	5/13	33	896,871	4.93
2003	5/23	34	896,410	4.98
2003	5/29	35	1,775,835	5.15
2003	6/4	36	1,547,049	3.84
2004	5/13	33	1,021,023	4.77
2004	5/20	34	1,037,860	4.77
2004	5/24	34	1,012,623	4.77
2004	5/28	35	1,008,388	4.54
2004	6/3	36	1,102,198	3.78
Average	5/14	33	912,242	4.93
Average	5/22	34	914,498	4.93
Average	5/26	34	1,556,705	4.80
Average	5/31	35	1,334,313	3.85

Summary of Model Parameters and Variables

Obviously Salmod has many input requirements. To the degree possible, we have endeavored to derive evidence-based inputs from Klamath-specific sources. However, some values were derived from literature sources, previous model applications, and assumptions. Table 17 summarizes these values. In addition, please refer to the Sensitivity Analysis provided in Appendix D. Both the initial parameters and the initial sensitivity analysis were reviewed by an interagency team at a workshop held in Yreka, California, January 11–12, 2005. Consensus suggestions have been incorporated into this document.

Table 17. Summary of important model structural elements, parameters, variables, and potential calibration data, with notes on their origin, status, and inherent uncertainty. [NA, not applicable; WUA, weighted usable area]

Element, parameter or variable	Klamath- specific	Status	Uncertainty
Study area	Yes	Fixed at present	NA
Flow and temperature reaches	Yes	Eleven reaches, well matched to hydrology and thermal characteristics of the river	Minor
Flow and water temperature data	Yes	Coming from SIAM	Masks peaks; need measured data if calibrating
Mesohabitat typing data and sequence	Yes	Good	Unknown
PHABSIM WUA quantification	Yes	Available, with assumptions	Hydraulics validated, remainder untested
Biological year timing	Yes	Good	Minor
Life stage nomenclature and size class breakpoints	Yes	Good	Unknown
Weight:length relationship	Yes	Well defined	Agrees well with Sacramento River
Spawning spatial and temporal distribution	Yes	Well defined, but using multi-year average	Minor
Spawning initiation temperature	Yes	Reasonably well defined	Unknown
Spawner density and characteristics	Yes	Have some data	May not all be specific for main stem study area
Fecundity	Partially	From Lewiston Hatchery	Could perhaps improve with values from Iron Gate Hatchery
Redd area and superimposition	Yes	Well defined	Some room for variation around 4.25 ± 1.4 m^2
Egg development rate	No	From reliable literature	Some uncertainty in hatch to pre-emergent timing; may need to adjust during calibration
Emergent length	Yes	From field measurements, but not explicitly for this measure	Contains some uncertainty
Emergence temperature	Yes	Reasonable estimate	Some uncertainty
Juvenile growth rates	No	Well defined literature values that have worked well on other rivers	Some uncertainty because values derived from ad lib feeding
Freshet movement attributes	Not used on Klamath	Monitor	Largely stable flows in dry years have precluded measurement
Seasonal movement timing and attributes	Yes for timing and distance	Other values derived from other applications	Values may have been influenced by recent disease

Base mortality rates	No	Values derived from Trinity River	Uncertainty due to endemic disease
Thermal mortality rates	No	Values composite from multiple literature sources	Uncertainty due to many causes, and will be sensitive to model behavior
Habitat capacity	Partial	Based on extensive sampling	Uncertainty from multiple causes
Habitat capacity movement rules	No	Literature and previous model based	Unknown
Distance moved mortality rate	No	Derived from Trinity and Sacramento River models	Much uncertainty
Exogenous production	Yes	Derived from hatchery, Bogus Creek, and the Shasta River data	Bogus Creek is an estimate with considerable uncertainty
Calibration metrics			
Juvenile growth	Yes	Review possibilities	Uncertainty due to tributary contribution and sampling gear
Overall survival/production	Review	Need best information	Potential gear biases; may be influenced by recent diseases

Calibration Targets

As mentioned, it is not yet possible to rigorously calibrate this model. We have few years of estimated outmigrants, the estimates have not yet been expanded for trap efficiency, and when expanded, confidence intervals–and uncertainty–will likely be high. However, we can make some judgments about whether the model is behaving properly and producing reasonable, or at least not irrational, results.

General Model Timing

Generally, the first thing to do in approaching Salmod model calibration is to verify that the model timing is approximately correct. Some timing elements are fixed as inputs, such as spawn initiation and duration, and general seasonal outmigration timing. But others, such as time of first and peak emergence, depend on other model processes operating (computing) correctly. Figure 11 (previously presented) serves as the best reference for outmigration timing. The length of instream and outmigrant fish is presented below.

Juvenile Growth

There are at least two different ways to characterize measured juvenile growth data. Tom Shaw (USFWS) supplied a spreadsheet recording length measurements from 3,217 young-of-year fish. [The spreadsheet also contained data for a few yearling fish (8), not enough to yield reliable estimates.] Three different sampling techniques–electrofishing, fyke net, and seine–were used to gather the data. The data appear to show (Figure 18) that (1) there may be considerable sampling differences among the techniques, (2) the length of the smallest fish changes little through time, probably due to entrants from tributaries with timings that differ from the main stem, and (3) the variance in length expands considerably through time, another potential indicator of tributary or hatchery influence. We will refer to these fish as "instream" fish, though some of them may be emigrating.

Figure 19, in contrast, shows the average length of emigrating Chinook trapped at the same locations previously illustrated in Figure 11. As expected, the average length generally increases the farther downstream you sample. Initial "calibration" will rely on these data to see if, or how well, the model reflects the relative trend and magnitude in outmigrant length.

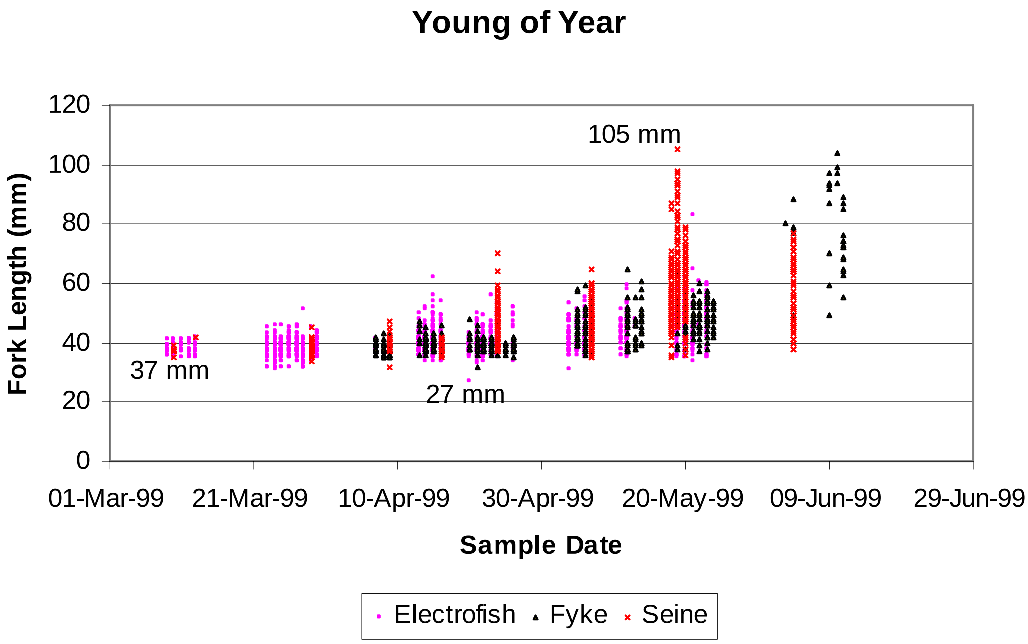

Figure 18. Young of year (YOY) length measurements from Tom Shaw (USFWS, written comm., 2005) labeled to highlight initial, maximum, and minimum values. [mm, millimeters]

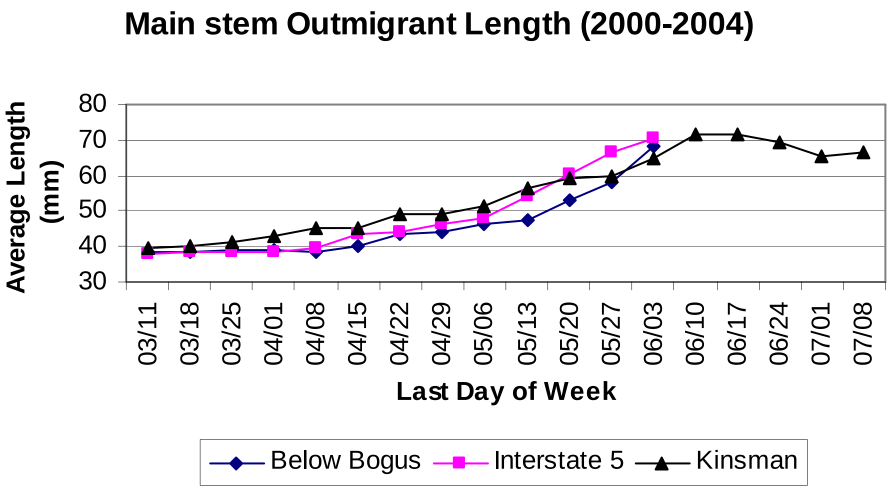

Figure 19. Average length of emigrating juvenile Chinook salmon trapped at each of three locations along the Klamath River, 2000 to 2004. Data courtesy of the Arcata Fish and Wildlife Office.

Note that Salmod produces variability in the predicted length of rearing and outmigrating fish for several reasons. First, recall that the model introduces an initial random deviation to the length of emergent fry. Second, emergence is spread through time, introducing an inherent, temporally-induced length variance. Third, juveniles forced to move due to habitat limitations do not grow, fueling a gap with cohorts of similar age and thermal history that do grow. It should also be noted that fish moving out of the system often result in a bimodal length distribution because outmigration arises from two processes, (A) the often severe habitat limitations immediately after the peak of emergence forcing newly emerged fish out of the study area (Unwin, 1997), and (B) subsequent seasonally-induced movement (due to assumed physiological readiness) later in the biological year. These factors, along with tributary and hatchery contributions, collectively account for variance and bimodality, not some more elaborate bioenergetics explanation dealing with food availability and individual competition (Elliott, 1990).

Index of Abundance

On the Trinity River, we had bi-weekly indices of abundance at several reference sites along the study area. These were quite helpful in “monitoring” the abundance (as well as length/weight) of juveniles through time, both in terms of time of emergence and in the longitudinal progression of slowly outmigrating juveniles. We have not yet pursued using this or similar type of monitoring on the Klamath River; this step remains for subsequent calibration.

Overall Survival/Production

Finally, of course, we would like the model to predict outmigrant production correctly, but this will undoubtedly be a challenge. Unbiased estimates of main stem production are difficult to obtain from trapping data and may be “contaminated” with tributary production. It is worth stressing again that the field data itself contains considerable uncertainty.

Coronado and Hilborn (1998) reviewed coded wire tag return data for 1971 to 1988 from multiple hatcheries in the Pacific Northwest, Iron Gate among them. Region-wide, Chinook salmon survival declined in the mid-1970s and has not rebounded. Fall Chinook survival to age 3 returning to the Iron Gate hatchery in 1988 was given as approximately 1.75 percent. Perhaps we could derive an estimate of outmigrant production from the Iron Gate to Scott study area based on the Coronado and Hilborn (1998) estimate, but this will be complicated given our assumptions about what constitutes successful production (see following section).

As a last resort, we may be able to develop a relationship with subsequent year escapement, but of course this introduces all of the ocean dynamics, as well as harvest and straying, that are a undescribed processes.

Discussion on Model Parameterization

Interpreting Model Results

Because no true calibration is yet possible for this Klamath Salmod model application, the reader is urged to remember that simulated outmigration numbers and their attributes are best used not as absolute values, but rather as relative values (Prager and Mohr, 1999). Even if the model were fully calibrated, measurements for outmigrating salmon are imprecise and subject to poorly understood biases; therefore, the model might be expected to reflect any biases. Further, because this is not a full life cycle model including complex estuarine and ocean dynamics, nothing is known about what happens to salmon successfully migrating downstream from the Scott River, where other density-dependent phenomenon may constrain the populations. Salmod is clearly not an ecosystem model (*sensu* Link, 2002), but instead a single species model whose “predictions” are limited to that target species.

Uncertainty Inherent in Model Results

Models can be misused (Radomski and Goeman, 1996; Schnute and Richards, 2001). We have spoken at some length about the uncertainty and assumptions bound up in this application. Parameter values have come from a variety of sources representing studies in different locations and river settings, have been "extrapolated" across salmon runs, and in some cases, borrowed across species. One must be forever critical of what has been published. We are 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."

Model formulations are inexact approximations of the processes we believe to be governing populations, not necessarily the "truth." Models act as metaphors of reality and also as filters to isolate a signal from background noise in the data. But there are three types of potential errors inherent in fisheries models that frustrate this signal extraction (Schnute and Richards, 2001). The first is process error, referring to the model’s inability to capture the full range of dynamism in birth, death, and growth rates. The second is measurement error, referring to our inability to precisely measure what it is we are trying to model. The third element is model uncertainty, referring in the authors' context to our occasional inability to know whether the model does in fact cover the full range of possible phenomena that may occur to a fish stock. Collectively, these three types of potential errors indicate that there may be multiple, equally valid explanations to account for what we believe we have witnessed. As has been pointed out by modelers investigating the dynamics of Klamath River fall Chinook in the ocean, relationships can be spurious and fail with the addition of new data, relationships can be real, but environmental or recruitment stochasticity masks the relationship, or relationships may not be stationary, but change over time for unclear reasons, making that relationship exceedingly difficult to determine (Prager and Mohr, 1999).

Suggested remedies to these problems include vigilant skepticism, continued data collection to "disprove" the model, applying common sense, and implementing precautionary management strategies that are robust to fish stock failure (Schnute and Richards, 2001).

Drawing Inferences from Model Results

Walters (1986) reasons that we are always in the mode of needing to make policy choices, even when field experimentation is impossible or extremely difficult. Thus, choices will continue to be made based on inference. Inference is fine as long as we make our assumptions explicit–and that's what a model is all about. The Achilles heel, however, is that our assumptions, however carefully considered, may still be wrong (Schnute and Richards, 2001). For this reason, Walters (1986) further argues that there should always be an opportunity to rethink, revise, and expand the model.

With this in mind, we have given some thought to the evolutionary progression of model development and application (Table 18) shows that modeling, like any investigation, moves from general and suggestive to specific and credible (Holling and Allen, 2002). The reader will notice from Table 18 that validity is always provisional rather than essential for model utility (Rykiel, 1996). In our estimation, Salmod for the Klamath River is currently cycling between Stages 5 and 6, indicating that one can begin to explore "solutions" to management issues as long as one is clear that the model remains a hypothesis and skepticism is fostered. We believe the model rests on a sound theoretical footing, and most, but not all, of its parameters are tied to sound empirical data.

Table 18. Progression of model development and application stages.

Model development stage	Attributes	Model capabilities may be used in decisions to:
(9+) repeated calibration/ verification loop	Confidence-driven	Refine estimate of uncertainty/ Evaluation is ongoing/ Model becomes ever more trustworthy
•	•	•
(8) verification	Understanding-driven	"confirm"/strengthen/predict/or falsify; Continue to accumulate evidence; Uncertainty is poorly defined
•	•	•
(7) calibration	Knowledge-driven	"suggest" (assuming model is "calibratable"); gain precision
•	•	•
(6) parameterized using best river-specific data	"fact"-driven	"imply or infer" Can begin to explore "solutions" to issues, but must be clear that model remains a hypothesis
•	•	•
(5) testing	Plausibility?	Question perceptions; gain insight by identifying patterns Revise data and implementation
•	•	•
(4) parameterized from literature or general knowledge	Data-driven	"deduce" based on estimates and assumptions; Continue consensus building on model structure and expected behavior; gain realism
•	•	•
(3) formalization and implementation	Box-and-arrow-driven	Stimulate concrete thought about variables, relationships, constraints, temporal and spatial scale, and so forth; speculation
•	•	•
(2) conceptual formulation	Hypothesis-driven	"reason"
•	•	•
(1) opinion	Experience-driven	No real model

Though skepticism is always warranted, modeling applications can often point to interesting and potentially useful results. For example, on the Trinity River, Salmod has suggested pragmatic flow regimes (Bartholow, 1996; Bartholow and Waddle, 1995). A well-designed model can greatly aid one's thinking about the complexities of the real world and the attendant consequences of our collective assumptions (Schnute and Richards, 2001). What is essential is to set the model at risk and be vigilant in its adaptation to new understandings, which brings up another modeling value. This may be referred to as the "lie detector" benefit of modeling. When the model and measured data disagree, we know that one or the other–or both–are wrong. The ensuing process of questioning can be quite instructive, as we will see in reviewing the results presented in the following section.

Simulation Results

Habitat Availability

Salmod may be used to calculate the aggregate microhabitat availability throughout the entire 75-km study area by applying the results of the PHABSIM analysis. We have done so in a simplified manner by assuming that discharge was uniform throughout the Iron Gate to Scott River study reach. The resulting curves for each life stage (Figure 20) are comfortingly smooth, presumably because of the large number of transects used to develop each mesohabitat type's relationship and the smoothing we did. They indicate that, if water supply permits and management can control, fall and winter flows in the range of about 1,700 to 2,100 ft^3/s provide the greatest availability of spawning and incubation habitat, while spring flows in the range of 5,500 to 5,900 ft^3/s provide the greatest amount of juvenile rearing habitat. Incubation habitat does not decline with increasing flow due to our assumption that the eggs must simply remain wet, though scouring flows would eliminate incubation habitat above 13,000 to 14,000 ft^3/s (not shown on the graph). The curve set also indicates that fry habitat is more limited than pre- or immature smolt habitat, but recall from Table 14 that fry require less space per individual than do larger juveniles.

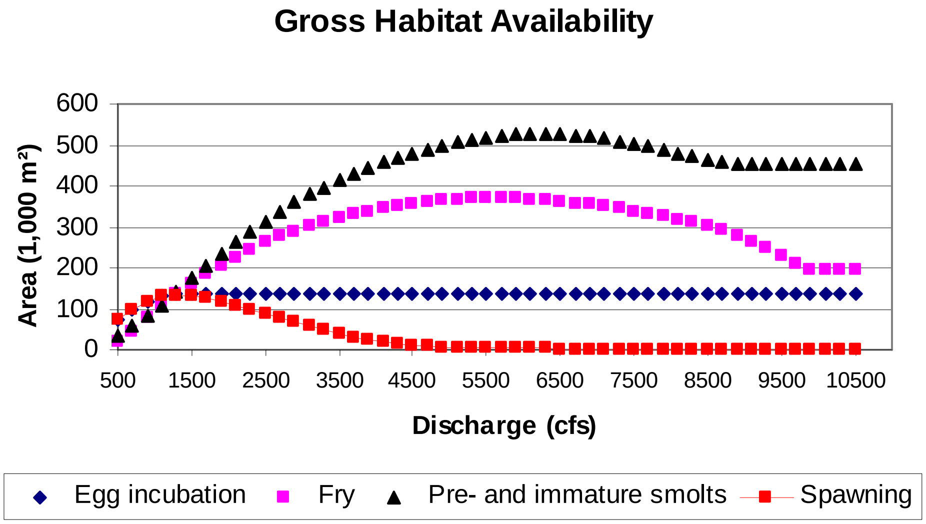

Figure 20. Gross habitat (m2) availability as a function of discharge through the entire study area. Accretions and effects of water temperature are ignored in this graph.

Note, however, that the portrayal in Figure 22 is oversimplified because it assumes that there are no accretions from Iron Gate to the Scott River, it completely ignores any effects that sustained flows may have on water temperature, and it does not account for the non-homogeneous distribution of habitats. In reality, median accretions from Iron Gate to the Scott River are about 450 ft^3/s, approximately one-half of which arises upstream of or from the Shasta River. Thus one might reasonably conclude that the curves in Figure 20 should be "shifted to the left" by about one half of the median accretion, or about 225 ft^3/s, if applied in a rudimentary manner.

The non-homogeneous nature of habitat availability is worth emphasizing. Figure 21 depicts the spatial distribution of eggs, fry habitat, and presmolt habitat throughout the study area during one year, each a weekly snapshot taken when their numbers peaked during that year. Though fry and presmolt habitat are well correlated, most of the eggs (and redds) are close to Iron Gate Dam. Redistribution of emergent juveniles is required to reduce habitat capacity constraints.

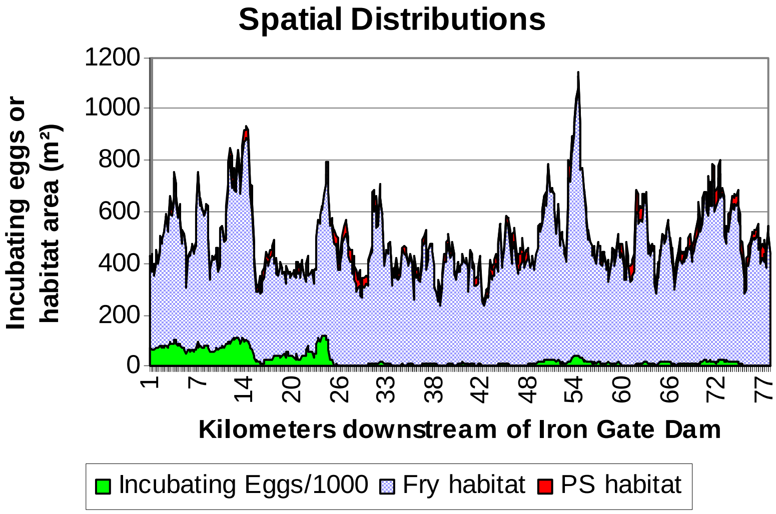

Figure 21. Comparison of spatial distribution of peak egg numbers (scaled to fit) compared to habitat availability (m2) for fry and presmolts (PS) during their respective peak weeks in a single simulation year. The values have been smoothed by averaging over 10 computation units.

Life-History Timing

The Salmod model was run for a 43-year period covering water years 1961 to 2003. For this period, the average life-history timing is shown in Figure 22; individual years may look quite different. As will be seen, adults seed the study area and then die as they spawn. Eggs accumulate as adults spawn and die, and then decline due to natural and environmental causes throughout the lengthy incubation period. The earliest fry emergence overlaps the egg incubation period. Two factors obscure clear discrimination of main stem fry emergence. First, water temperatures are not uniform throughout the Iron Gate to Scott reach; downstream water temperatures can average less than 1°C cooler near the Scott River during the spawning period. Second, juveniles, including fry, are added from tributaries (and the hatchery) throughout the spring period. Newly emerged fry grow and progress normally into the presmolt and immature smolt stages. Ultimately, most surviving juveniles exit the study area through seasonal outmigration.

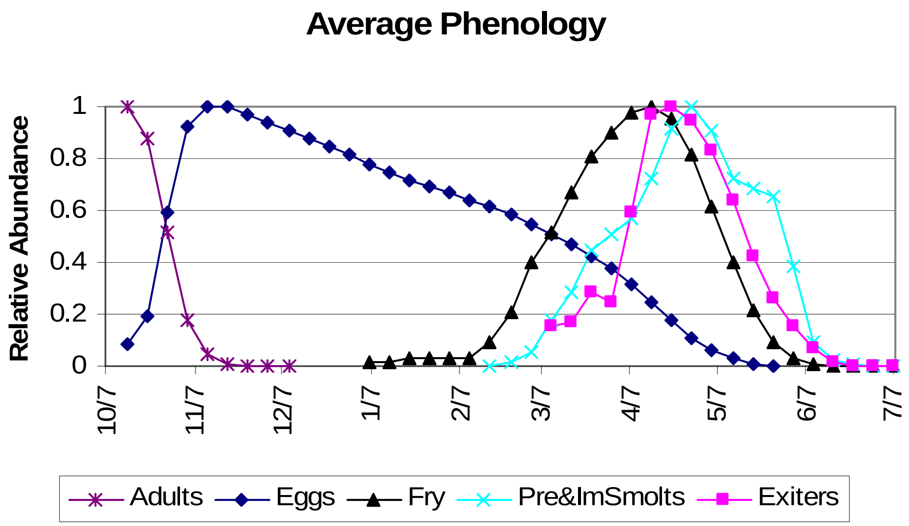

Figure 22. Average simulated life-history timing through the biological year for fall Chinook salmon in the study area. The scale is based on the maximum abundance of individuals in each stage.

Note that in the absence of a dynamic model, one might propose flow scenarios based solely on knowledge of the life-history timing and the PHABSIM results. This will be discussed in more detail later.

Model Fit to Measured Data

During initial simulations, small adjustments were made in the proportion of each life stage moving during each week during the seasonal outmigration period to roughly mimic the field measurements made at the most downstream trapping location (Kinsman) in our study area. Because these trapping data have not been expanded, we cannot compare the absolute magnitudes, but we can compare the values as an index (Figure 23). Though we did not expect an exact replication due to differences in averaging of the data sources, the model fit appears to capture the temporal trend in outmigration well, especially in the first several weeks of the period. The model does not reflect the oscillation apparent in the measured late April and early May timeframe, nor does it seem to reflect the “blip” measured in mid-May. We offer no explanation for these differences.

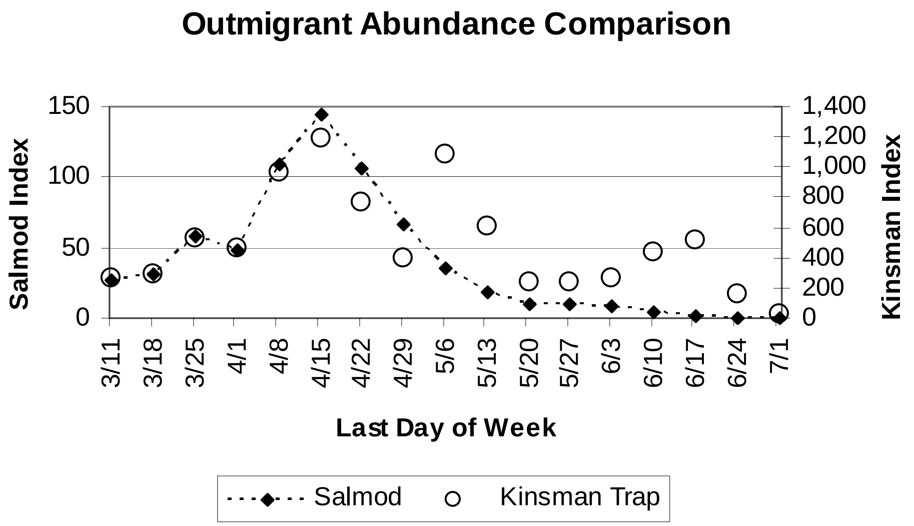

Figure 23. Comparison between Salmod's estimate of average weekly outmigration just upstream from the Scott River and the field measurement index at the Kinsman trap site. Data have been averaged for the period 2000 to 2004.

Figure 24 compares the length of outmigrants predicted by Salmod with the Kinsman trap measurements. Though the temporal trend in lengths agrees well until the last few weeks when there are few fish migrating, the absolute magnitudes diverge significantly by late May. We have not been able to satisfactorily explain this discrepancy. Obviously the difference may arise from one or more causes, including: (A) the model over predicts the juvenile growth rate, (B) the trapping data under sample larger fish (or over samples smaller fish), (C) we have not captured or have misrepresented some form of size-selective mortality, (D) juvenile emigration rates differ substantially from the parameter values we used, or (E) we made some other error, especially in interpreting tributary or hatchery fish lengths.

Because we have not seen such a large divergence in fish lengths in other modeling studies, we do not initially suspect Salmod's growth-rate parameterization, though we may have slightly overestimated the length of newly emerged fry, as shown in the first week's values in Figure 24. There is no evidence that mortality associated with disease affects larger fish more than smaller ones; if anything, the opposite is true (Scott Foott, written comm., 2006). The other possibilities remain to be further evaluated. However, though it is clear that Salmod may over-estimate production biomass, differences in juvenile growth alone are unlikely to significantly affect inferences about relative annual production potential.

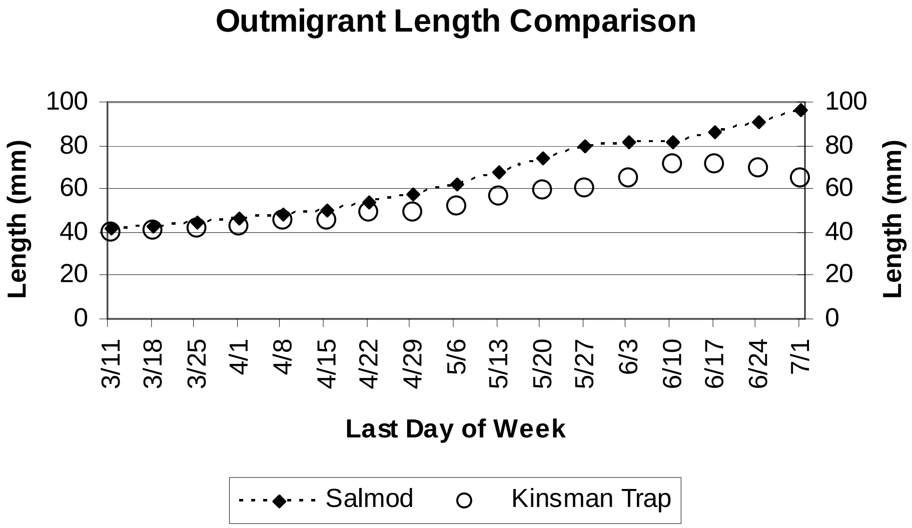

Figure 24. Comparison between Salmod's estimate of average weekly outmigrant length and field measurements taken at the Kinsman trap site. Data have been averaged for the period 2000 to 2004.

Annual Production Potential

Figure 25 presents the annual time series of fall Chinook salmon production from the model simulation. Remembering that each simulation year begins with the same number of adult spawners and gets the same tributary and hatchery contribution, the model suggests that production potential has varied by a factor of about four to five regardless of whether one is more interested in numbers of fish or biomass. Interestingly, the period of the early 1990s was characterized by wide every-other-year swings that mark the highest and lowest values for the 43-year period. Clearly, accurate but unmodeled annual variation in the number of main stem spawners and tributary fish would serve to amplify these potential production estimates.

Biomass can be seen to roughly parallel the numbers of outmigrants, but not perfectly. This is a function of differing growth rates between years, largely attributable to the seasonal thermal regime. Figure 26 further illustrates the relationship between simulated production numbers and biomass and signifies that generalizations that one may develop using one measure apply well to both.

During the 1961–2003 period we simulated, the minimum production was approximately 330,000 and the maximum production was 1,580,000 fish. The median is slightly above the mean at 933,000 fish, signaling little variation in annual production–the occasional "busts" are not counterbalanced by exceptional "banner years." Overall, the average egg to main stem-origin smolt survival rate predicted by the Salmod model was about 5 percent, slightly lower than the value of 7 percent reported in the literature from multiple salmon streams north of the Klamath River (Bradford, 1995). To be truly comparable, however, it must be remembered that presmolts and smolts moving downstream from the Scott River still have another 233 km (145 mi) of river and estuary to negotiate, so it would be fair to assume that the model-predicted survival rate is even lower.

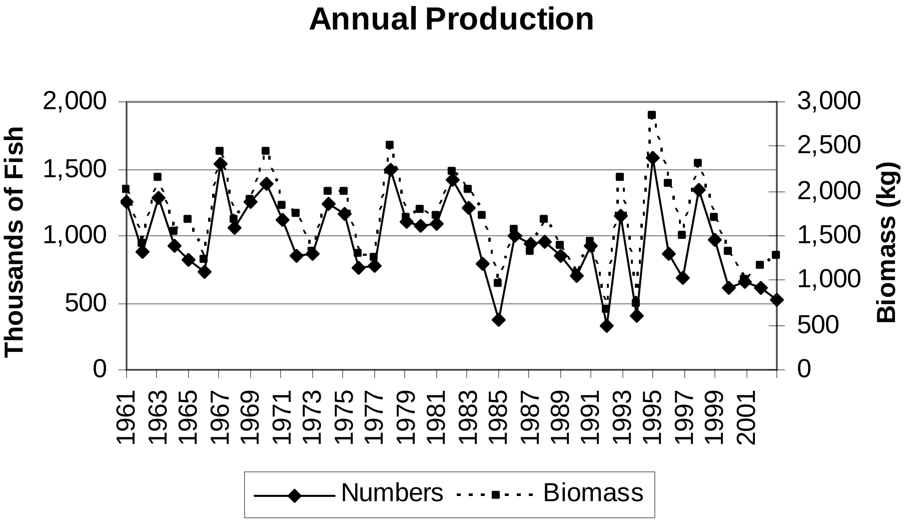

Figure 25. Time series of annual production potential by water year, both numbers of juveniles and their biomass, surviving to move downstream from the Scott River.

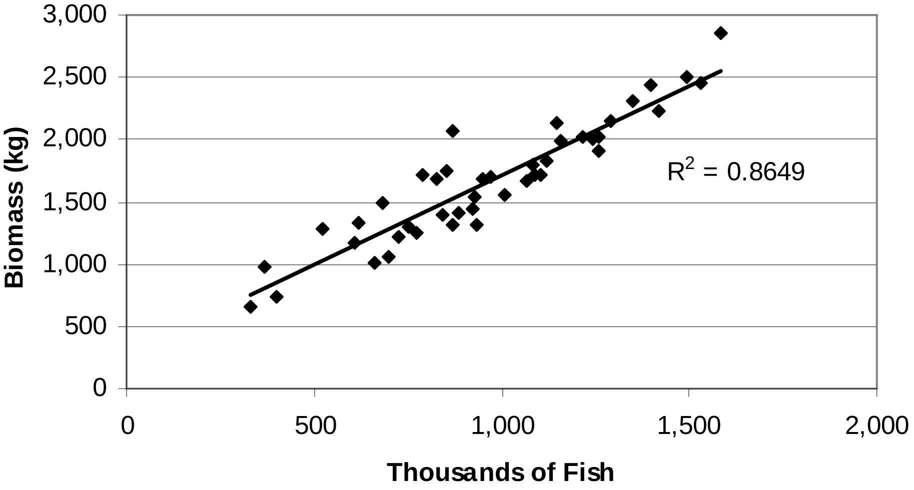

Figure 26. Relationship between annual production potential and biomass for the 43-year simulation period.

Causes of Mortality

Over the course of the 43-year simulation, production potential was reduced from the maximum possible by a variety of causes. A simple average across the simulation period suggests that fry and presmolt habitat-related mortality were the largest contributors to annual mortality after a somewhat expected high base mortality for eggs, followed by egg and fry temperature-related mortality (Figure 27). Remaining mortality causes other than superimposition begin to rank well down the list, in marked contrast to Salmod applications for other study areas, presumably because of the large number of juvenile Chinook salmon exogenously added to the model domain from the Shasta River and Bogus Creek. Said another way, since the main stem Klamath River has only about 22 percent of the adults estimated to spawn in either the main stem, Bogus Creek, or the Shasta River (California Dept. of Fish and Game, no date; though note that the recent conclusion that there are more main stem spawners than previously recognized may change this estimate), these other tributaries tend to overwhelm main stem production. Large numbers of tributary fish result in high habitat-related mortality estimated by the model occurring downstream from these tributary mouths. Predicted egg superimposition mortality, though infrequent through the years (see fig. 27), is higher than we expected and should receive some scrutiny for reasonableness in the future.

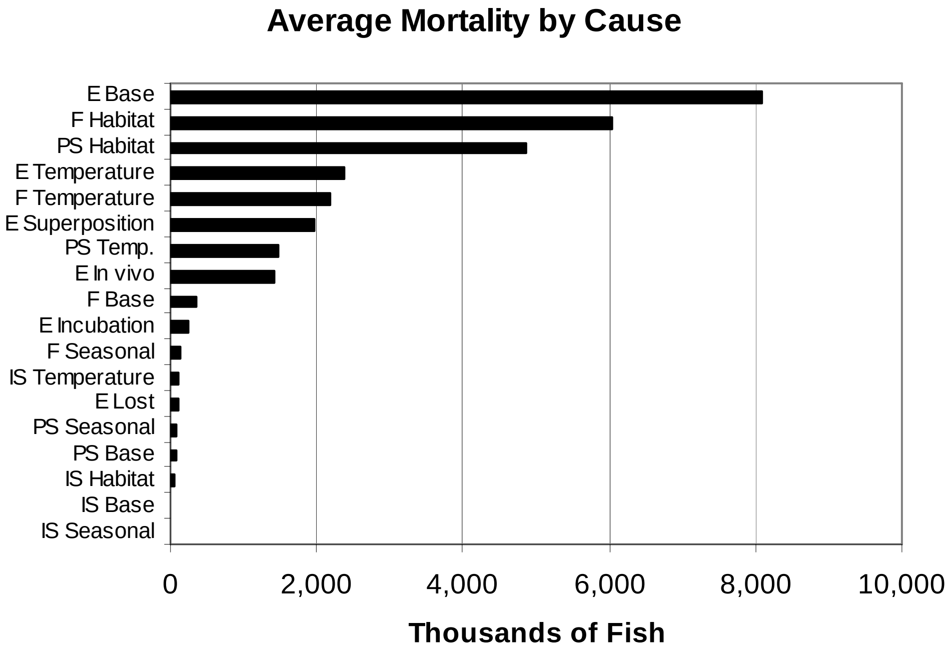

Figure 27. Average annual mortality by cause over the 43-year simulation period for eggs (E), fry (F), presmolts (PS), and immature smolts (IS). No mortality due to habitat or water temperature was predicted for adult spawners in the study area, but some ripe females did die unspawned.

It is also instructive to look at annual mortality in another way. Figure 28 shows the relative frequency or predictability of various forms of mortality, but presented in a somewhat unusual fashion. At the top of the graph appear those mortality events that occur with the lowest frequency or consistency. For example, “lost eggs” refers to mortality that occurs when many ripe females died prior to spawning due to a shortage of available spawning habitat. This was a relatively rare occurrence during the 43-year simulation in contrast to those forms of mortality that appear at the bottom of Figure 28 that take place with great regularity from year to year at roughly the same magnitude. Presmolt habitat-related mortality is the most consistent form of mortality predicted by the model.

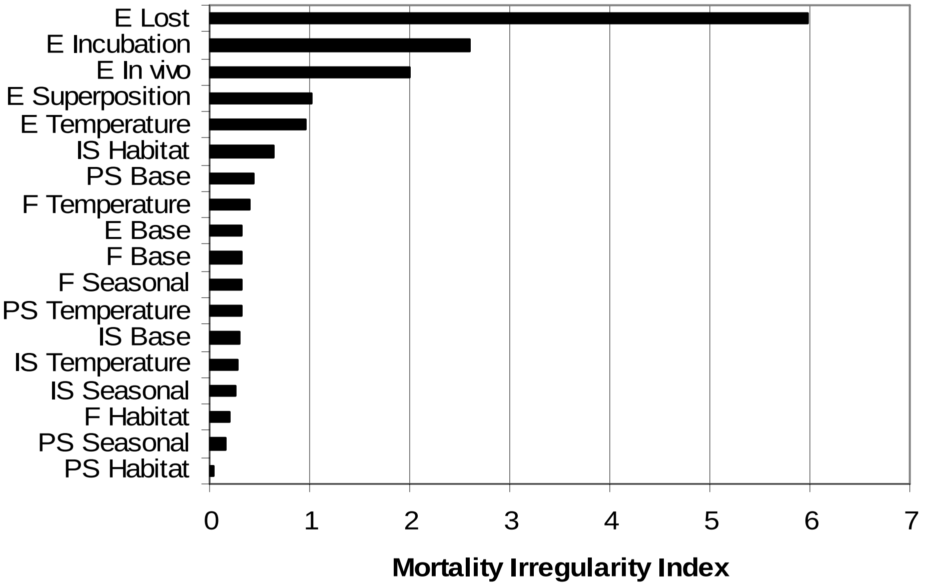

Figure 28. Mortality irregularity index showing the relative infrequency (and its inverse, the relative predictability) of annual mortality due to different factors. This index is the coefficient of variation (standard deviation divided by the mean) for the 43-year simulation. In other words, mortality to presmolts due to habitat constraints occurs year in and year out at approximately the same magnitude, whereas lost eggs was a very rare event of inconsistent magnitude.

Because habitat-related mortality appears to be a significant limiting factor in model simulations, it may be instructive to more closely examine past flow regimes associated with these limits. It is difficult to look at this issue comprehensively because of the dynamic nature of flows, their seasonal consistency (or lack thereof), and flow transitions from month to month or week to week. One way to synthesize the large data set is to look at exceedance plots depicting the probability of historical flows in different periods relevant to Chinook life-history. The following two graphs capture this information, Figure 29 for the spawning and early incubation phases and Figure 30 for the bulk of the juvenile rearing phase. Referring back to Figure 20, we can see that fall spawning flows from 1,000 to 2,000 ft^3/s, indicative of maximum habitat availability, occur frequently in Figure 29, but flows outside this range occur approximately 36 percent of the time. In contrast, spring rearing flows in the range of approximately 5,000 to 6,500 ft^3/s are quite rare (only about 20 percent of the time; Figure 30). This flow frequency perspective may shed some light on the dominance that juvenile rearing habitat constraints seem to play relative to spawning and incubation habitat limitations. A more extensive time-series analysis is outside the scope of this report, except insofar as Salmod captures these dynamics.

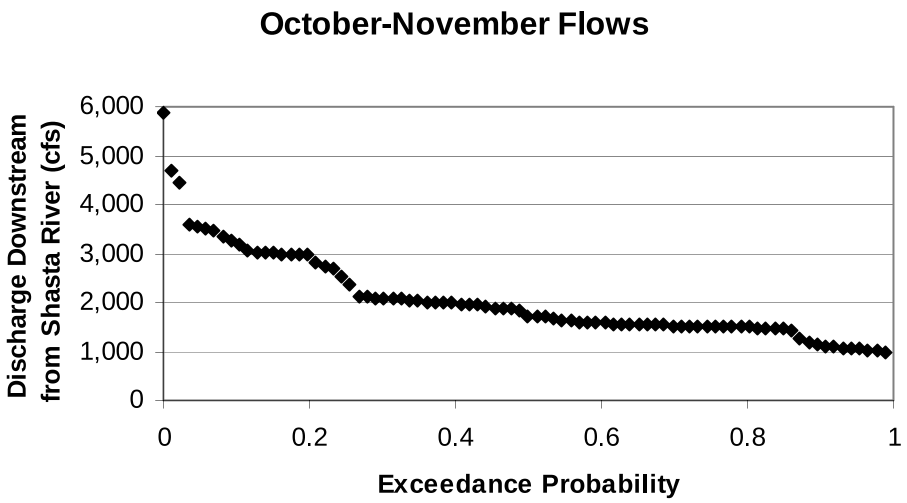

Figure 29. Probability of flow equaling or exceeding the given flow in the months of October and November immediately downstream from the Shasta River.

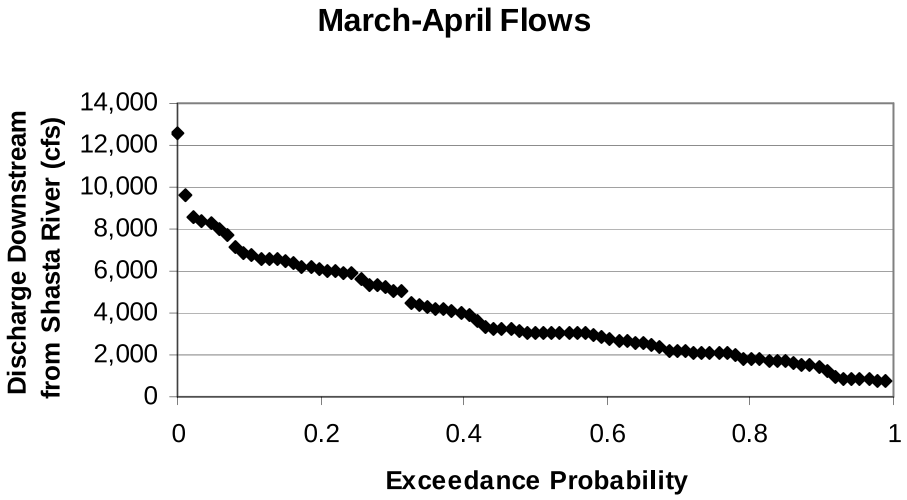

Figure 30. Probability of flow equaling or exceeding the given flow in the months of March and April immediately downstream from the Shasta River.

Figure 31 depicts some of the least consistent forms of mortality over time and is a good illustration of how total mortality is composed of sub elements of variable magnitude and frequency. Just because habitat limitations appear to dominate overall mortality, less frequent or severe causes should not be completely discounted as potentials for mitigation.

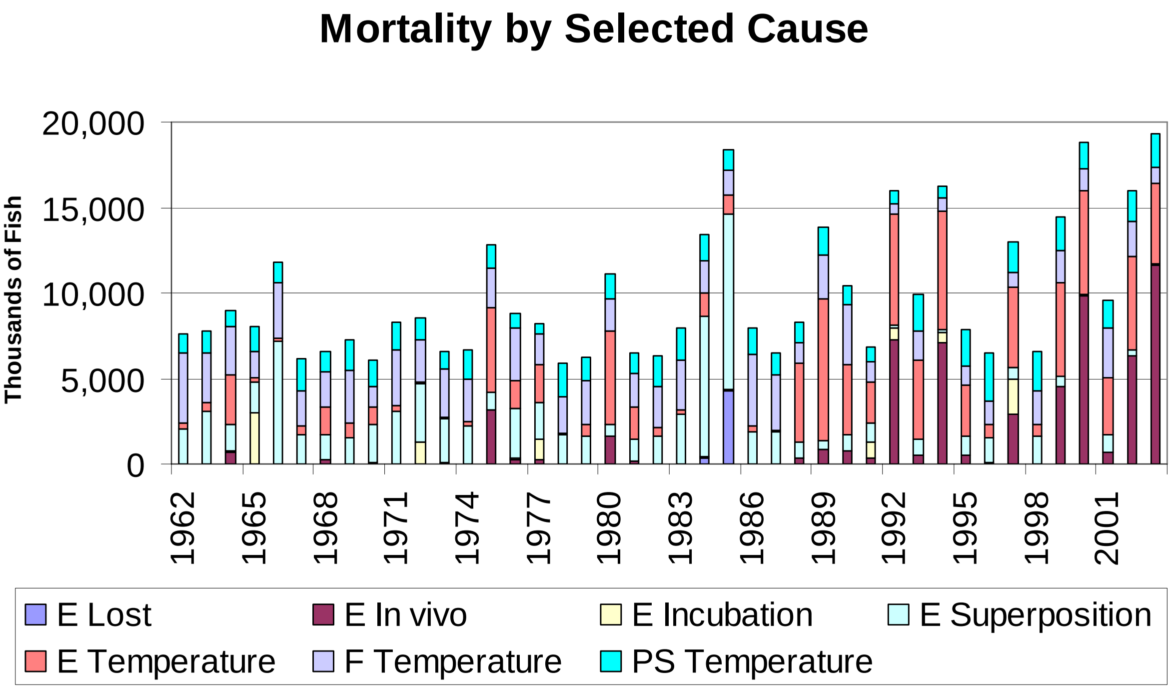

Figure 31. Time series of mortality from several of the less frequently consistent causes by water year. Shading progresses from the bottom of each bar to match the legend from left to right.

Effects of Water Delivery on Simulated Production Potential

One important variable to investigate has to do with the potential effect of annual water delivery downstream from Iron Gate Dam on simulated fall Chinook production. We use the term "water delivery" instead of "water supply" to indicate that this analysis draws no conclusion regarding variable water supply and consumptive use upstream of Iron Gate Dam. In relating annual production to water released from Iron Gate, we are oversimplifying any effects that arise from the variable accretions of the Shasta River and other minor tributaries, especially if the accretions do not mirror Iron Gate releases. As will be seen, we know that these accretions do affect the model's predicted production. We also acknowledge that quantifying water delivery as an annual value ignores important distinctions between intra-annual delivery patterns. However, we will look more closely at these seasonal phenomena when we examine the discrete causes of mortality.

Figure 32 displays annual production against the backdrop of annual Iron Gate discharge. When conditions are either "dry" or "wet," production appears to be diminished. Production may be high when water delivery is "average," but average conditions are no guarantee of maximizing production; production can be lower in an average year than it is under drier or wetter conditions. (Note that we are, for the moment, ignoring important seasonal differences in discharge.)

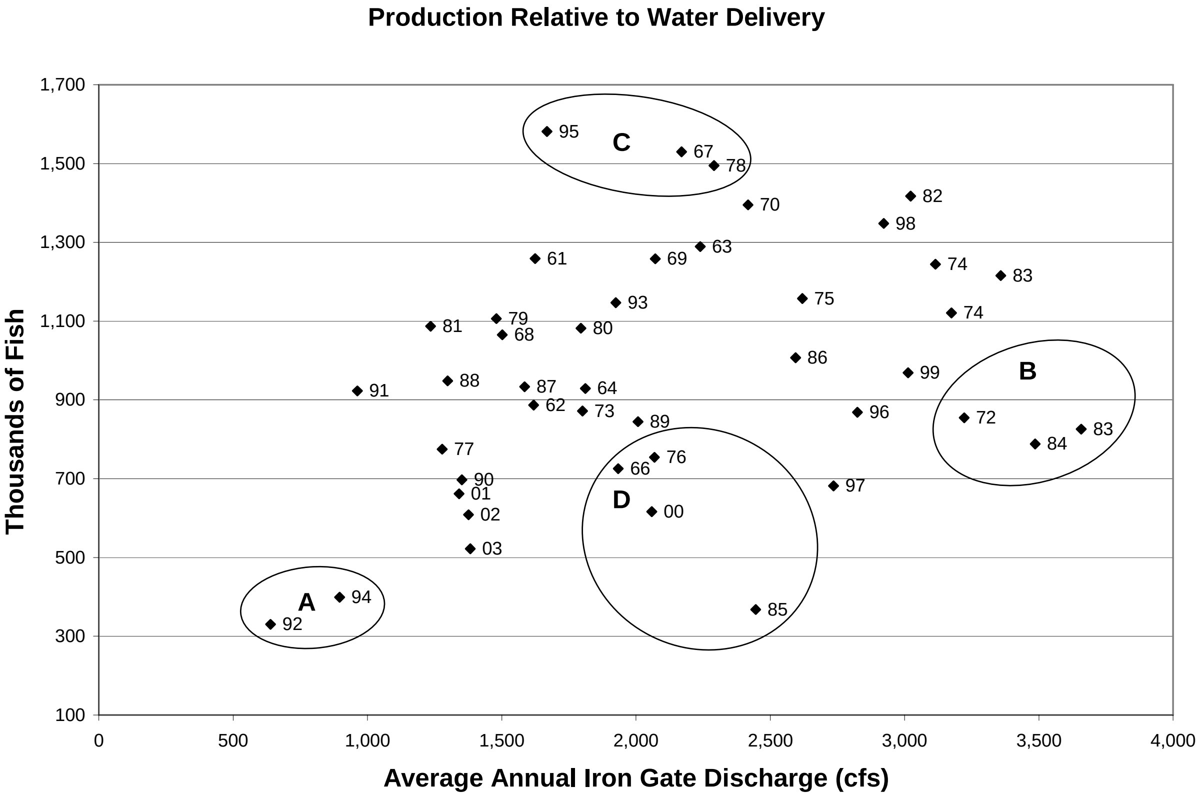

Figure 32. Annual production portrayed as a function of water delivery downstream from Iron Gate Dam. Numbers associated with each annual point refer to the water year. See text for an explanation of groupings.

Using figure 32, we examined several water years with relatively low simulated production, some associated with low annual delivery of water downstream from Iron Gate Dam and some with high delivery. These years were (Group A) 1992 and 1994, and (Group B) 1972, 1983 and 1984, respectively. We also chose three water years with relatively high simulated production clustered in the middle range of water delivery downstream from Iron Gate Dam. These years were (Group C) 1967, 1978, and 1995. Finally, we looked closely at four other years, (Group D) 1966, 1976, 1985, and 2000, also falling in the mid range of water delivery but exhibiting lower production potential than other mid delivery years. Our objective was to learn whether there was any commonality in these groupings.

Group A characterizes years of relative drought from the historical record. Careful examination of the simulated annual mortality for these years shows some similarities and some differences. Both years (1992 and 1994) had three to five times the average egg thermal mortality, both in vivo and during incubation, due to mean weekly water temperatures above 16.5°C before and during the initiation of the spawning period. Both years also had more than 2.5 times the average egg incubation mortality primarily associated with reductions in February flows significantly below flows available during the fall spawning period sufficient to dewater much of the previously used spawning habitat. Remaining causes of mortality were generally average.

Group B (1972, 1983, and 1984) characterizes years of relatively high water delivery. Like the drought years, these years had somewhat higher egg mortality than average, considering all forms of egg mortality. Some mortality was associated with redd-scouring flood flows downstream from the Shasta River instead of the flow reductions noted for Group A and some for superimposition. The year 1984 exhibited high thermal mortality on immature smolts. Mean weekly water temperatures in this year often exceeded 17°C by mid-June. It should be noted that temperatures regularly exceeded 17° in other years as well, but 1984 had a relatively cool spring, which may have delayed juvenile growth, which was then followed by a relatively hot summer. But fundamentally, Group B simply had average mortality from almost all causes. Thus, their production was simply average.

Group C (1967, 1978, and 1995) characterizes the mid range of water delivery and higher than average annual production. As might be expected, the commonality among these years was a general lack of higher than normal mortality. Some of these years exhibited slightly higher than average thermal mortality on either presmolts or immature smolts, or both, but none of these years was marked by high mortality on multiple life stages, especially the early life stages. Fall and spring flows in these years were not necessarily ideal (as judged by Figure 20), but did share some common characteristics. Flows generally increased steadily during the spawning season, giving rise to progressively more spawning habitat as the season advanced. Spring rearing flows were most often above 2,000 ft^3/s, and generally peaked in the neighborhood of 4,000 to 5,000 ft^3/s. All of these high production years did have higher than normal base mortality. This should be expected because there were simply more fish suffering the same mortality rate.

Group D (1966, 1976, 1985 and 2000) characterizes mid-range water delivery but depressed production and is perhaps the most interesting group of all. These years were unremarkable with respect to the "normal" thermal and habitat-related mortality noted for Groups A and B. Instead, the unifying factor for these years was depression due to the relatively infrequent forms of mortality. Each had two or more incidents of high mortality due to "lost eggs," in vivo egg mortality, egg incubation mortality, redd superimposition, egg thermal mortality, or immature smolt habitat-related mortality. The lowest production year, 1985, showed significant decreases in spawning habitat availability that led to exceptionally high lost eggs and superimposition mortality. It should be noted that Group D may or may not have had the same seasonal delivery pattern as years included in Group C. In the future, it would be intriguing to pursue this same sort of analysis, but with water delivery broken into seasonal groups, for example fall, winter, spring.

Effects of Water Temperature on Simulated Production Potential

Because of the predictable annual thermal cycle in the Klamath River, we know that high temperatures are likely to affect both the period of early fall adult upstream migration and egg incubation as well as late spring juvenile rearing (Bartholow and others, 2004). For this reason, and because we discussed water temperature effects to some degree in the previous section, we chose not to rely on a single annual index for water temperature. Instead, Figure 33 and Figure 34 attempt to isolate the individual effects of fall and spring temperatures on production.

Figure 33 illustrates the relationship, or lack thereof, between maximum weekly temperatures in the last two weeks of October and Chinook production. There may be a relationship, but this relationship does not appear to be statistically significant, though from model parameterization we would not expect to see much effect until temperatures exceeded

15°C. An analysis using quantile regression might be in order as this technique may better elucidate the true "limit" here. In other words, imagine fitting a "regression" line not through the middle of the cloud in Figure 33 but rather as a "cap" or ceiling on the cloud. Such a limiting cap would be apparent in the production decline evident above 14 or 15°C. A similar relationship appears in Figure 34. Again this relationship is not strong, but the effect of the increasing water temperatures above 10°C on the rate of disease-induced mortality does come through. In neither case would one conclude that water temperature is the decisive factor limiting freshwater production. Instead, one would surmise that many limitations are involved, both habitat and water quality.

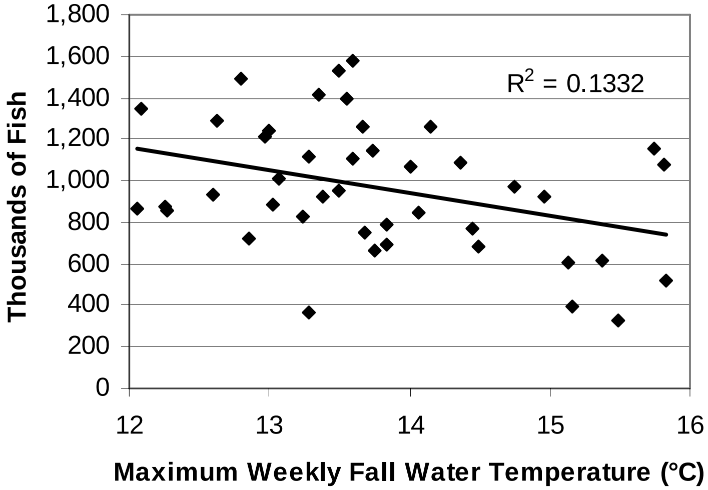

Figure 33. Annual production compared with maximum weekly water temperature in the last two weeks of October.

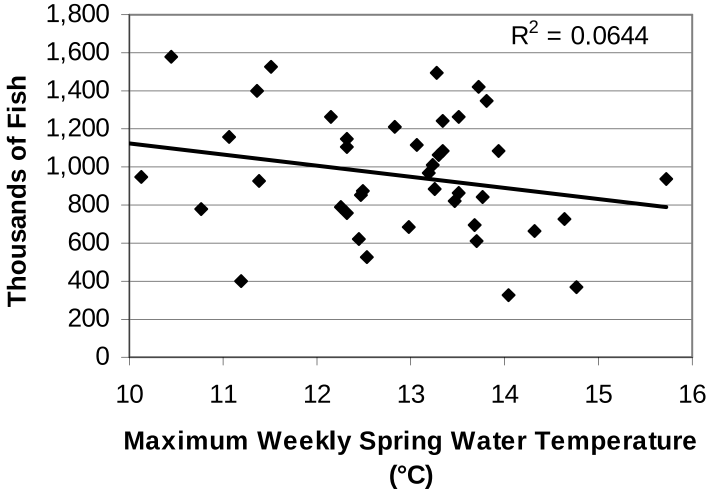

Figure 34. Annual production compared with maximum weekly water temperature in the first two weeks of May.

Bottlenecks?

So far we have sidestepped at least one important issue. We have seen that overall production seems to be related to the number and severity of the various forms of mortality that can occur to multiple life stages within a biological year. We have also seen that fry and presmolt habitat-related mortality are predicted to be the most significant and regularly acting forms of mortality. The reader may also recall that habitat-related mortality is a direct function of the specified habitat capacity because there is a maximum number of individuals that can occupy the habitat available each week for each non-egg life stage. This fixed limit could act as a so-called bottleneck, setting an absolute limit to the maximum production that could ever occur given the computed habitat availability. Bartholow (1996) found some evidence for this on the Trinity River. However, the specified habitat capacity is not as fixed as it sounds because of the model's movement algorithm, the dynamic nature of juvenile growth, the ever-changing habitat availability as a function of flow, and other factors (Bartholow and others, 1993). So the question becomes, "How much would any increased survival at the egg or fry stage likely persist through any subsequent habitat bottleneck at the fry and presmolt stages to increase production?" More simply, if you could save eggs or fry from thermal or incubation losses, would such action be effective in increasing juvenile production, or would subsequent juvenile habitat constraints preclude any increase?

In addition to the benefits of a sensitivity analysis listed in Appendix D, one may also infer which limitations, if relaxed, are likely to have payoff in terms of production. We have already seen from the sensitivity analysis (Appendix D) that egg thermal mortality has only moderate bearing on overall production, but it is not zero. Fry thermal mortality is far more sensitive, so we have some reason to believe that juvenile habitat constraints do not act as absolute limits.

Fortunately, a model such as Salmod can be used to directly answer this question by "turning off' egg mortality due to high temperatures. We ran the model after eliminating egg thermal mortality to see what effect this would have on overall production and found that between 0.5 percent and 7.5 percent of eggs so "saved" would contribute to outmigrant production, depending on the year, as currently parameterized. In other words, habitat limits still largely govern production potential but do not act as absolute bottlenecks–thermal effects can adjust production potential somewhat, especially in some years. Whether managing water to reduce egg or fry thermal mortality would be feasible or worth the effort remains an open question.

Summary of Important Modeling Inferences

Perhaps it is common sense that low production years are characterized by mortality affecting multiple life stages and involve both habitat-related constraints and higher than normal water temperatures. Neither fall nor spring water temperatures were decisively associated with limits on annual production, though in both cases the highest temperatures did appear to depress production. We believe this underscores the conclusion that reduced production is most closely associated with multiple causes involving both water temperature and habitat constraints. Neither alone is a sufficient explanation for significant decreases in simulated production.

It may be less obvious that both dry years and wet years were predicted to negatively impact egg incubation. Dry years were also associated with higher egg thermal mortality and wet years were unexpectedly associated with higher juvenile thermal mortality. We must make it clear that we draw no conclusion from this analysis that water delivery significantly affects or controls water temperature. Instead, it is likely that water temperature is primarily associated with seasonal meteorological conditions instead of water management (Campbell and others, 2001). Nonetheless, this remains for further investigation.

All things being equal, the model suggests that any action successful in mitigating forms of mortality that are both common and substantial may be expected to result in improved Chinook production. Mortality associated with limitations to presmolt and fry habitat fits this classification. Mortality associated with high water temperature also can be substantial but occurs far less predictably. It is clear that main stem flows, if available and properly regulated, have the ability to control the amount of habitat available for fry and presmolts precisely through time. The role that flow regulation may play in controlling water temperatures is far less clear.

The feasibility and relative effectiveness of alternative water management scenarios designed to minimize the collective constraints on Chinook salmon production remain for additional study. However, the principal hypothesis emerging from this analysis is that spring flows, which govern fry and pre-smolt habitat availability, may have the greatest utility in moderating production limitations.

Recommendations for Further Study

Several lines of investigation were highlighted as important for future study. Some apply to model parameter uncertainty, some to model process uncertainty or assumptions, and some to water management. In no particular order, let us try to summarize these important issues.

The effect of disease on juvenile mortality must be better understood. Fortunately, considerable effort is ongoing by others to study and quantify disease dynamics. Better ways to relate disease incidence and virulence to water temperature will likely prove worthwhile.

The model currently overestimates the juvenile growth rate. We have discussed potential reasons for this problem and suggest that some effort be devoted to pursuing a differential diagnosis to eliminate the source of this inaccuracy.

The model suggests that fry and presmolt habitat constraints collectively are major impediments to increased production. The model further suggests that habitat-related mortality should be the greatest in the few kilometers downstream from each of the major tributaries and the hatchery release site. A carefully executed field study may be able to confirm or reject this hypothesis.

Because presmolt habitat appears to be a major limiting factor, and we do not have a measured habitat capacity for presmolts in the Klamath River, we recommend that more effort be devoted to sampling juveniles larger than 55 mm in order to better estimate a river-specific capacity value.

The model suggests that tributary production significantly boosts overall production from the study area and that management of springtime limiting factors may be more important overall than those in the fall. However, we did not explicitly model these tributaries whose production in reality would also be influenced by fall river conditions, especially in vivo egg mortality. We may wish to consider a way of incorporating dynamic tributary production, especially as we move closer to model calibration.

The exact relationships between managed Iron Gate releases and downstream water temperature remain for investigation. We have at present unpublished modeling results that indicate that there is such a relationship, but it is simply not straightforward. We believe that this issue is worthy of further study and in fact are in the process of working on it.

It is important to resolve the issue with in vivo egg mortality. Does it exist? Is it significant on the Klamath River? Though this report suggests that flow (and possibly temperature) management in the spring is likely the key to improving Chinook salmon production, we continue to believe that we cannot completely overlook flow and temperature management in the fall. It may take some investigation of the Iron Gate hatchery records to be successful at putting this issue at rest, but it may well be important because any effect on holding adults will affect not only main stem spawners, but also tributary and hatchery spawners. In addition, opportunities for multiple-level temperature control, even if the volumes are small, remain for investigation.

Naturally, data collection sufficient to further calibrate and then validate, or invalidate, the Salmod model is important. It is clear from the data already collected by the USFWS at multiple locations that there is considerable mortality occurring between Iron Gate Dam and the Shasta River. This may be related to disease or other factors. We fully support continued efforts to understand and quantify outmigrant dynamics as well as fish abundance along the length of the study area.

The ongoing data-collection effort by the USFWS and others should continue to look for evidence for or against the influence that sudden changes in discharge (freshets) may have in stimulating juvenile outmigration. This phenomenon is certainly present in other river systems and we would be surprised if it is not true on the Klamath River. If such stimulation is evident, capturing the phenomenon in the model would add realism and potentially be quite valuable in designing effective flow regimes.

Because Bogus Creek appears to be a significant factor in Klamath River Chinook production, it is important to better quantify its contribution to the main stem. We have made what we believe is a reasonable assumption on the numbers of juveniles emigrating the main stem, but our assumption should be confirmed or replaced.

Some of our recommendations indirectly address the relative importance of Klamath River main stem production compared to the tributaries (principally the Shasta River and Bogus Creek in our study area) and the hatchery. There is no evidence that the main stem segment of the spawning population is declining relative to the tributaries. However, because main stem-specific production is small relative to these other sources, we raise the question of whether near-future river management may ultimately marginalize main stem production. This is not a question that can be answered effectively using Salmod or similar production models but instead must be addressed within the larger context of conservation biology because man-made alterations to the Klamath River Basin have progressively pruned one tributary or main stem segment's subpopulation after another from the genetic pool. To the degree that these subpopulations represent population "insurance" to the variety of hydrometeorological and channel-forming events that can occur, the issue should not be considered trivial lest cumulative effects put the entire population at risk of extinction.

An additional avenue of investigation that we have not pursued is to better understand the likelihood of ensuring two high production years in a row. Though not necessarily beneficial for ocean-type fall Chinook, developing a familiarity with the potential management implications for stream-type Chinook and coho salmon, both of which require favorable living conditions over the summer and through the next fall and winter, may be important.

We have not kept up on other salmonid modeling efforts underway on the Klamath River, specifically KlamRas and EDT. It might be fruitful to compare results among all three studies, identifying similarities and differences. Such an effort might reveal promising lines of investigation.

We offer one further observation. During the modeling to produce this report, we increased the number of spawners. Unfortunately we also changed some other parameters at the same time, making clear discrimination of the changes attributable to each problematic. Nonetheless, the increased population gave some indication that the relative magnitude of bottlenecks changed. This was also apparent in the sensitivity analysis. This model prediction could bear additional attention.

Finally, our objective in this study has been to better understand the factors that have likely been instrumental in controlling freshwater production for Klamath River Chinook salmon. We have not yet addressed the full potential that alternative flow regimes may have for increasing production. Techniques to "design" favorable flow regimes would be capable of further illuminating the tradeoffs involved in how to "spend" a limited quantity of water throughout the biological year. This is an area of investigation of great potential utility and could target either flow regimes that are tailored to individual water supply or delivery scenarios, or toward flow regimes that may be of benefit regardless of water availability, or both. We do not believe that Salmod must be rigorously validated to begin this task.

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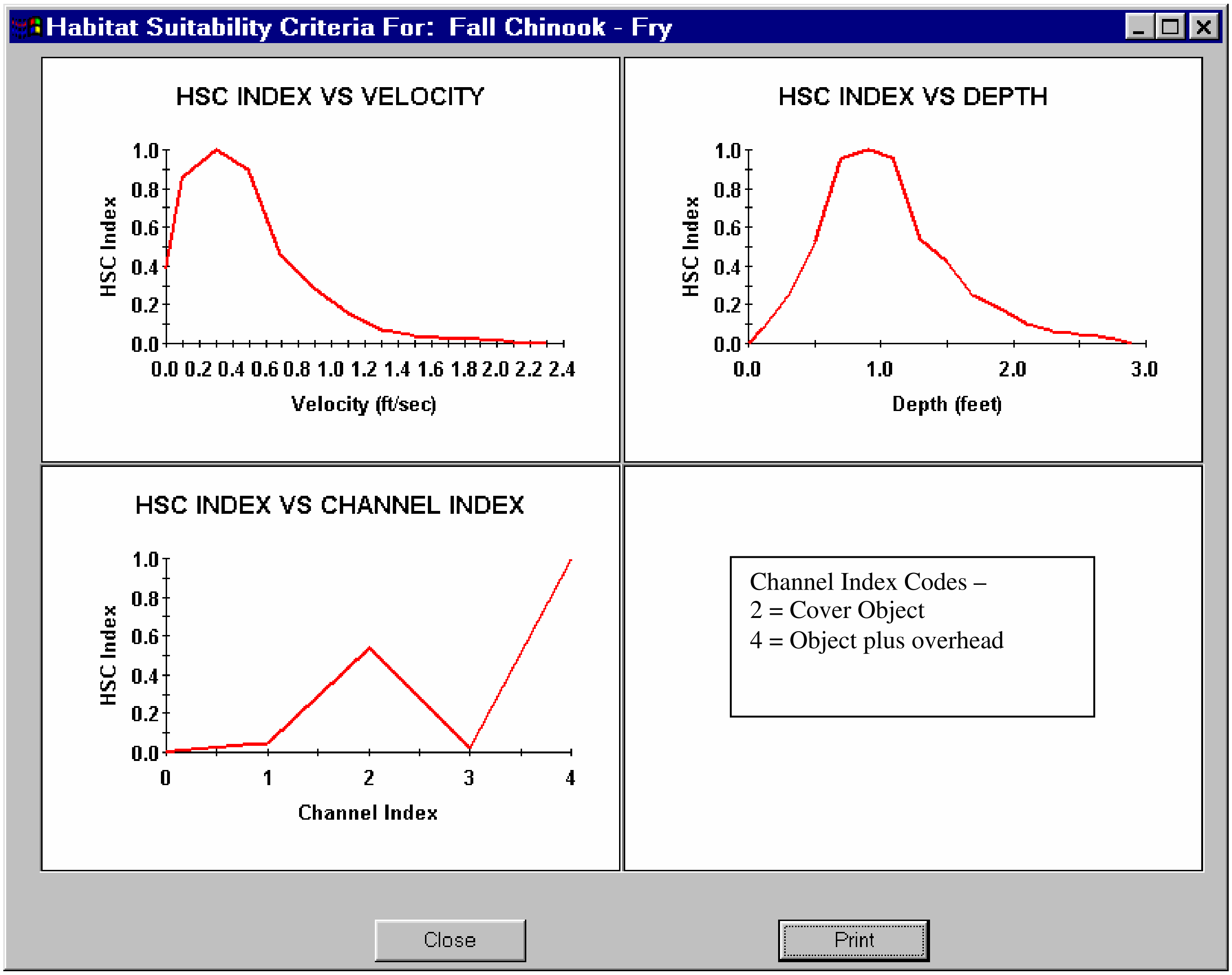
Appendix A. Salmod Input Files

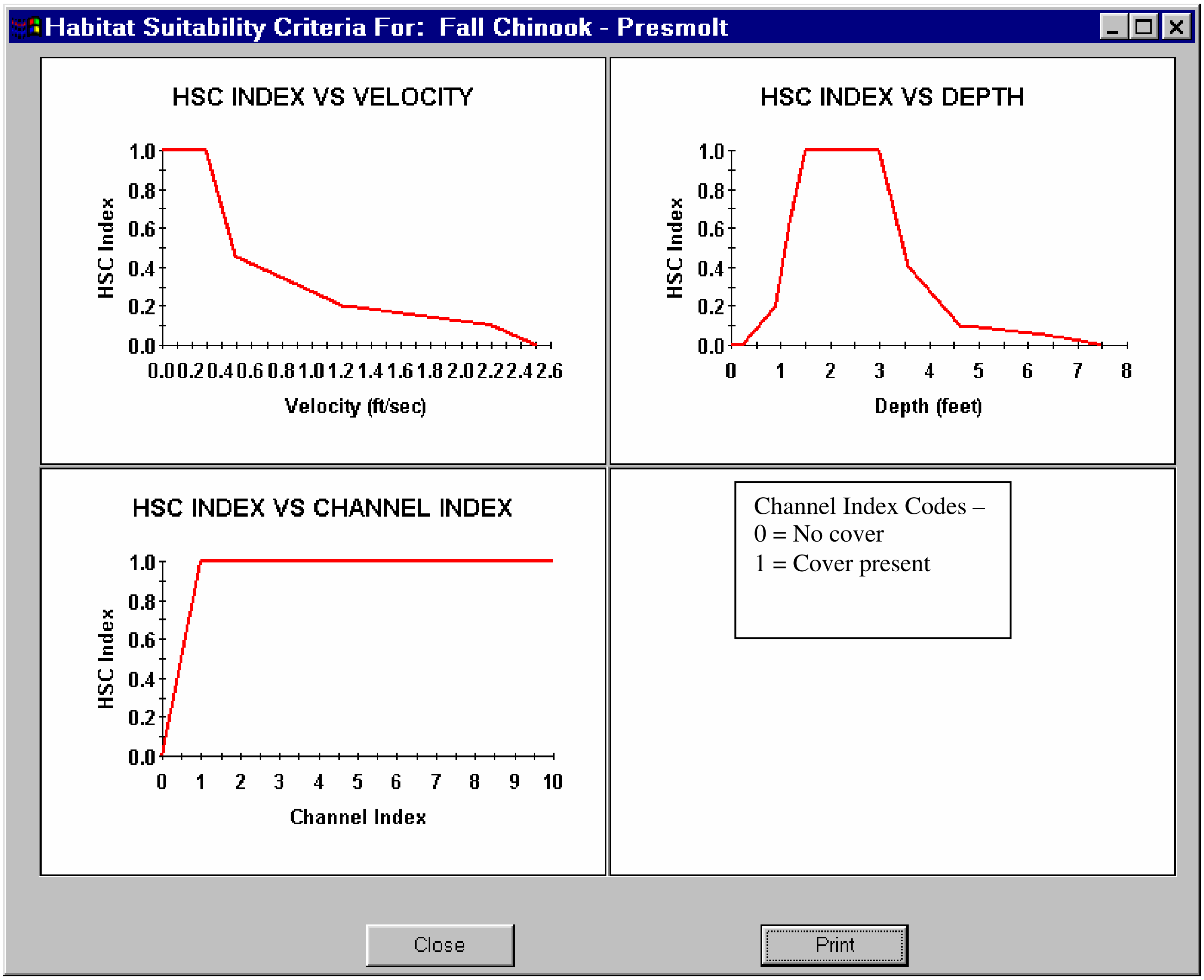
We will continue to update the Salmod model's parameter files as warranted by newly collected data. Complete Salmod input files accompanying the SIAM model may be downloaded from the Internet at *http://www.fort.usgs.gov/Products/Software/SIAM/*

Appendix B. Habitat Suitability Criteria



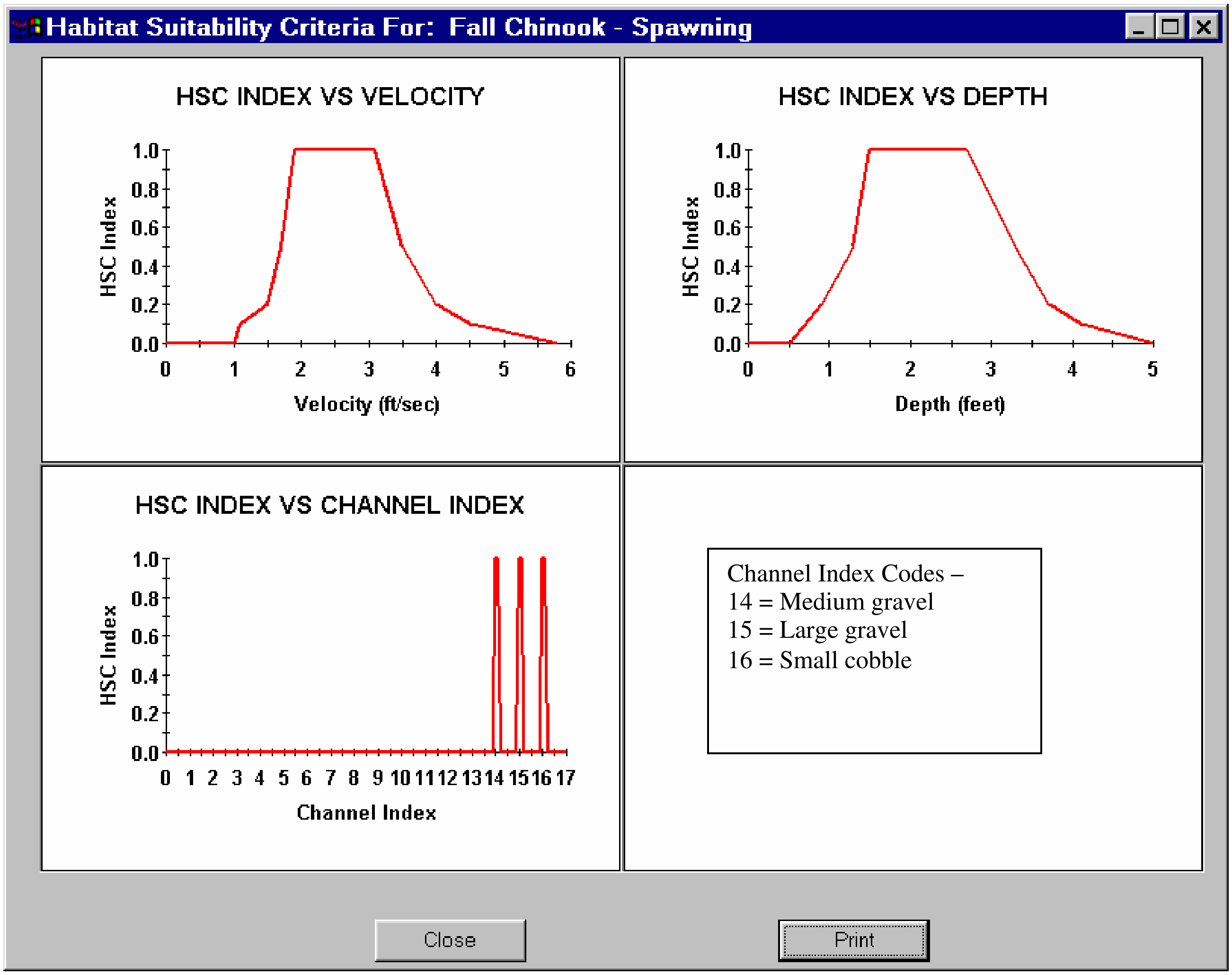
Channel Index Codes –
2 = Cover Object
4 = Object plus overhead

Figure B-1. Habitat suitability criteria for fry Chinook.



Channel Index Codes –
0 = No cover
1 = Cover present

Figure B-2. Habitat suitability criteria for presmolt Chinook.



Channel Index Codes –
14 = Medium gravel
15 = Large gravel
16 = Small cobble

Figure B-3. Habitat suitability criteria for spawning females–Chinook.

Appendix C. Flow in Relation to Weighted Usable Area

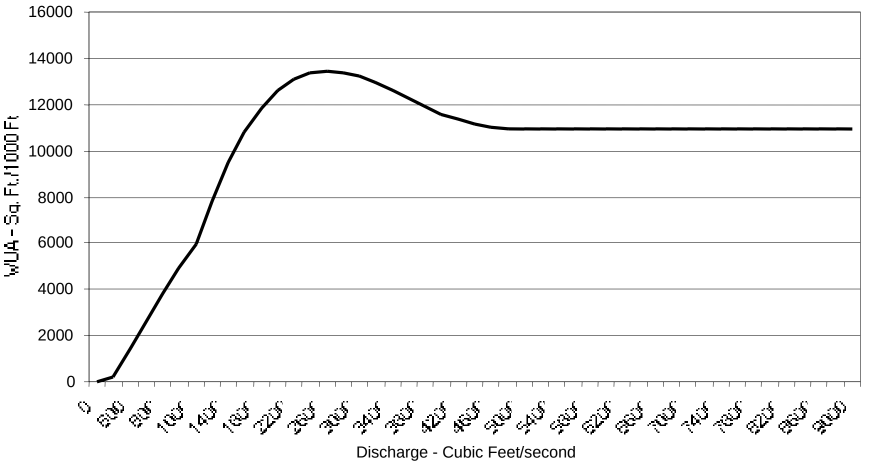


Figure C-1. Weighted Usable Area (WUA) for Fry in Low Slope Mesohabitat Type - Segment 1

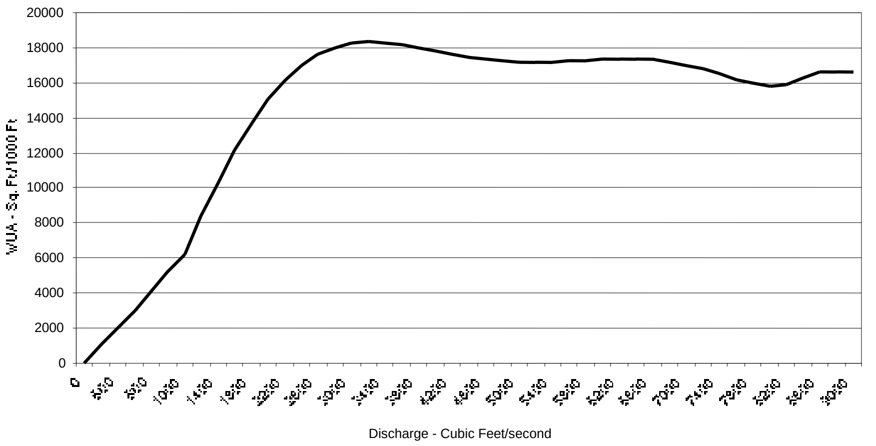


Figure C-2. Weighted Usable Area(WUA) for Presmolts in Low Slope Mesohabitat Type - Segment 1

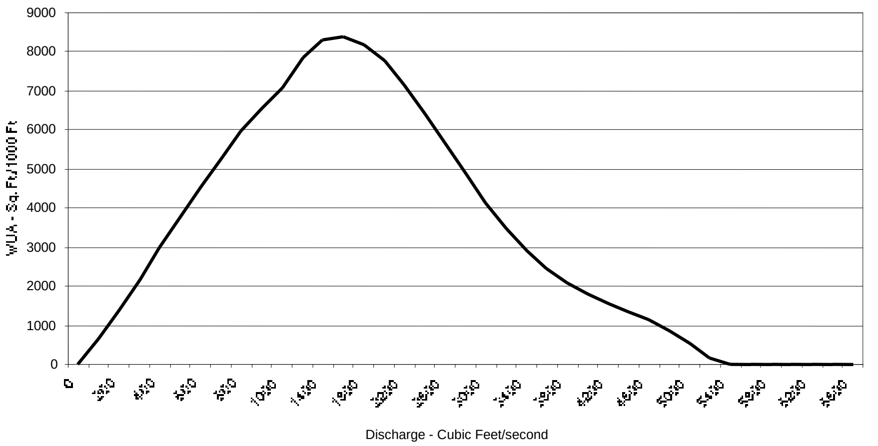


Figure C-3. Weighted Usable Area(WUA) for Spawning Females in Low Slope Mesohabitat Type - Segment 1

Figure C-4. Weighted Usable Area(WUA) for Eggs/Alevins in Low Slope Mesohabitat Type - Segment 1

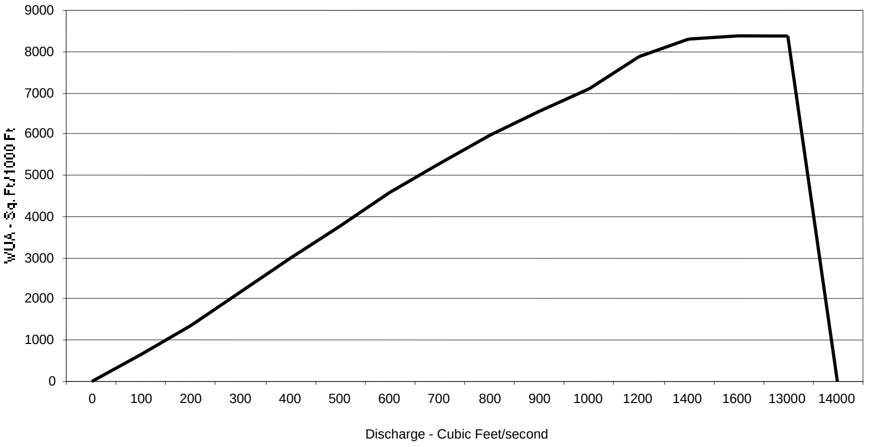


Figure C-5. Weighted Usable Area(WUA) for Fry in Moderate Slope Mesohabitat Type - Segment 1

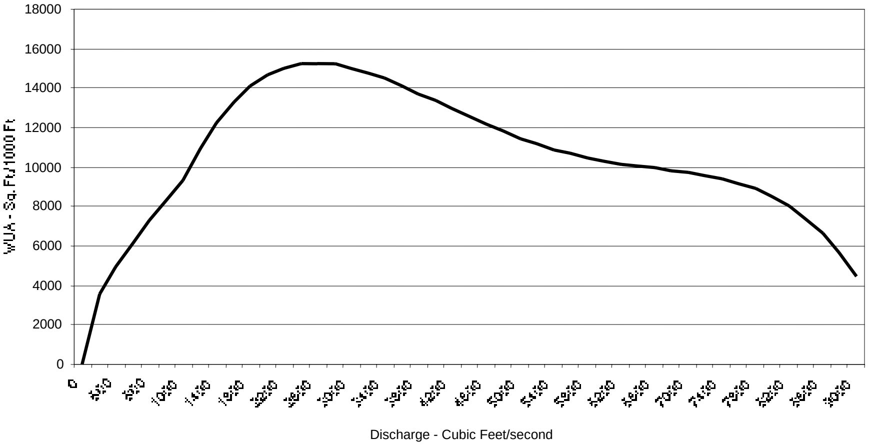
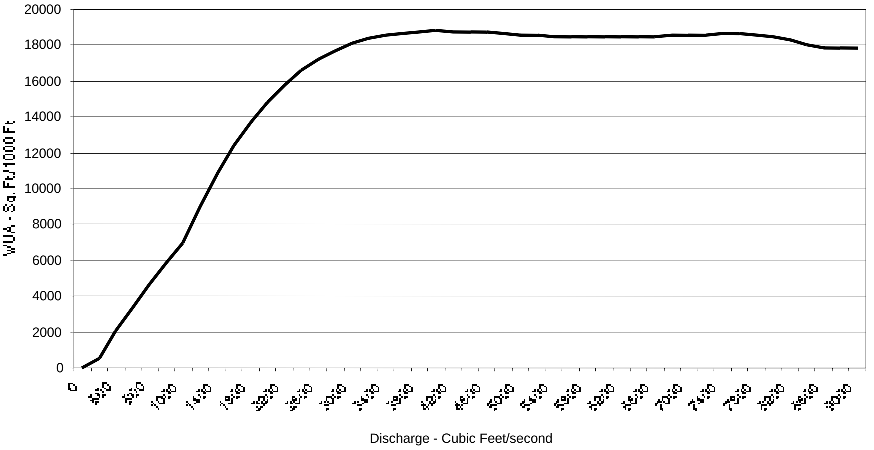


Figure C-6. Weighted Usable Area(WUA) for Presmolts in Moderate Slope Mesohabitat Type - Segment 1



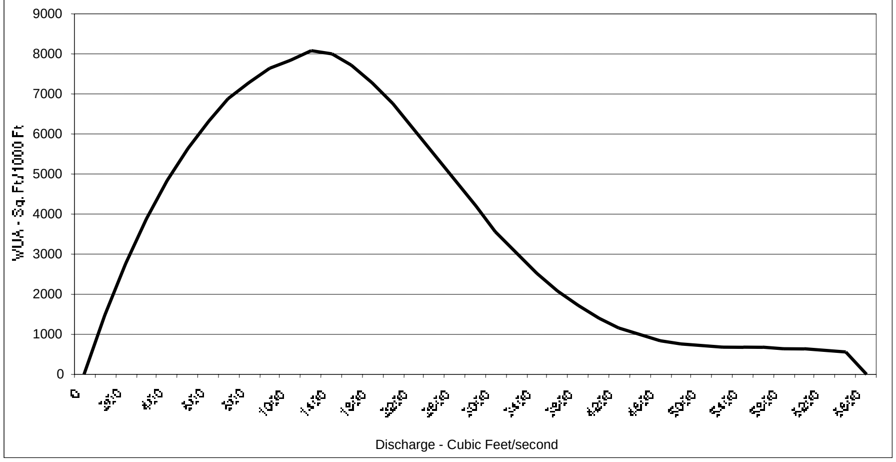


Figure C-7. Weighted Usable Area(WUA) for Spawning Females in Moderate Slope Mesohabitat Type - Segment 1

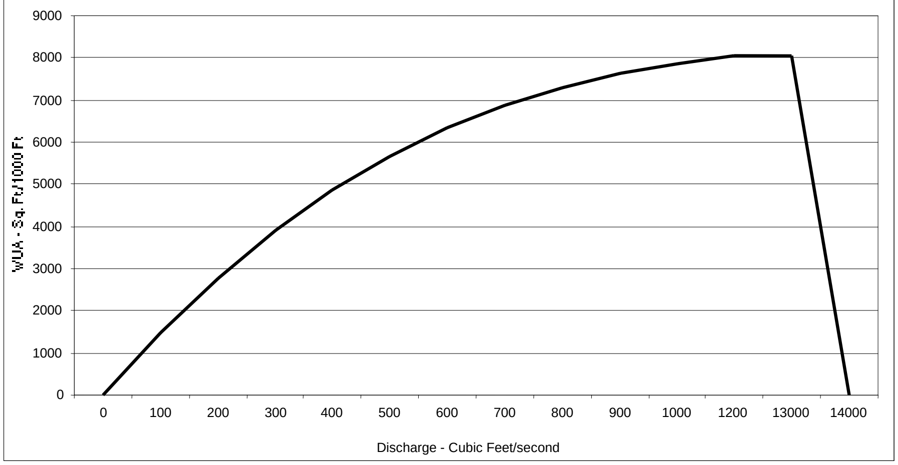


Figure C-8. Weighted Usable Area(WUA) for Eggs/Alevins in Moderate Slope Mesohabitat Type - Segment 1

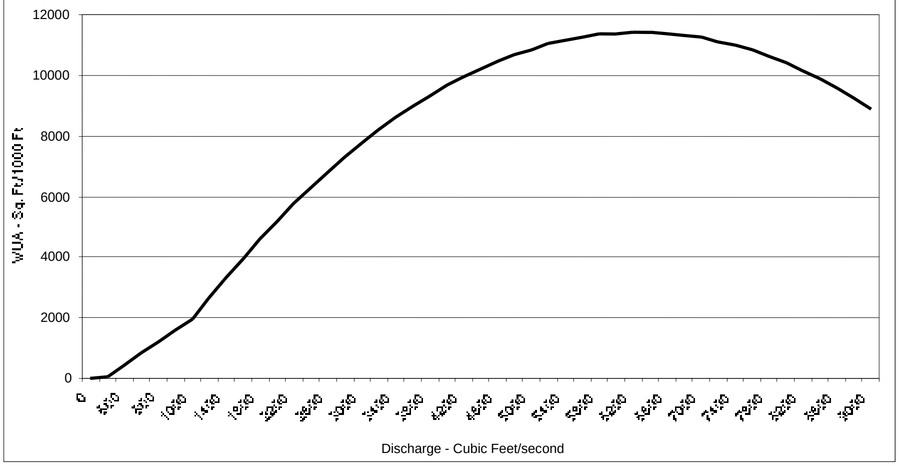


Figure C-9. Weighted Usable Area(WUA) for Fry in Backwater Mesohabitat Type - Segment 1

Figure C-10. Weighted Usable Area(WUA) for Presmolts in Backwater Mesohabitat Type - Segment 1

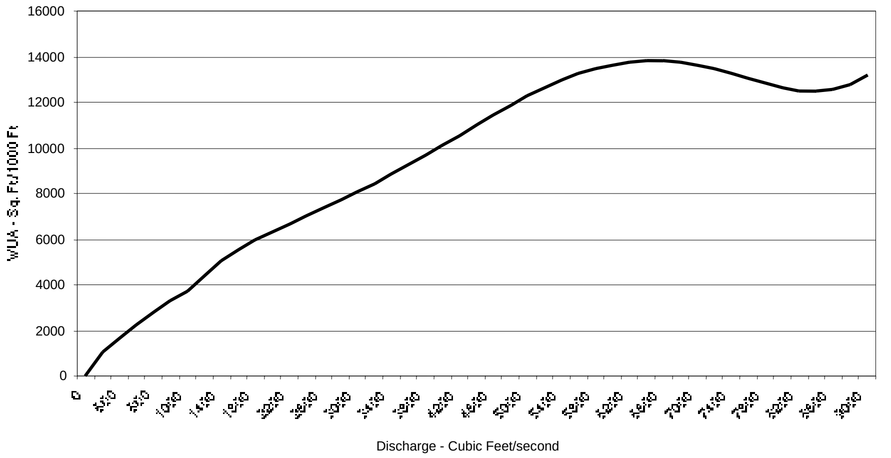


Figure C-11. Weighted Usable Area(WUA) for Spawning Females in Backwater Mesohabitat Type - Segment 1

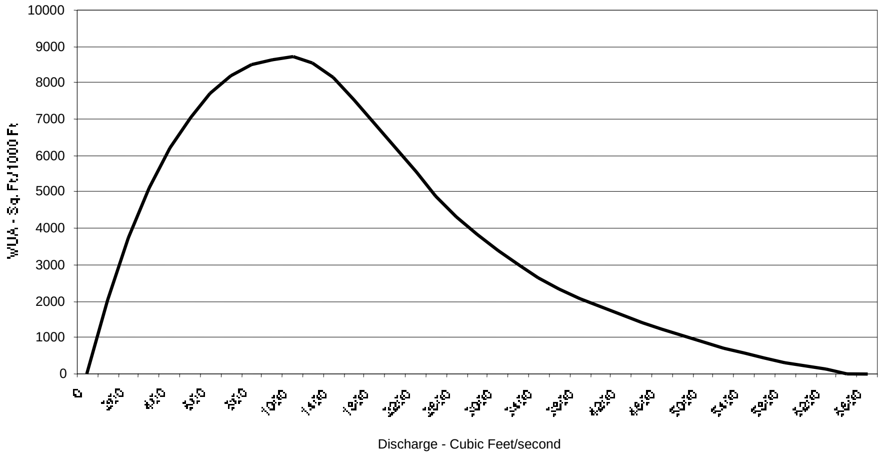


Figure C-12. Weighted Usable Area(WUA) for Eggs/Alevins in Backwater Mesohabitat Type - Segment 1

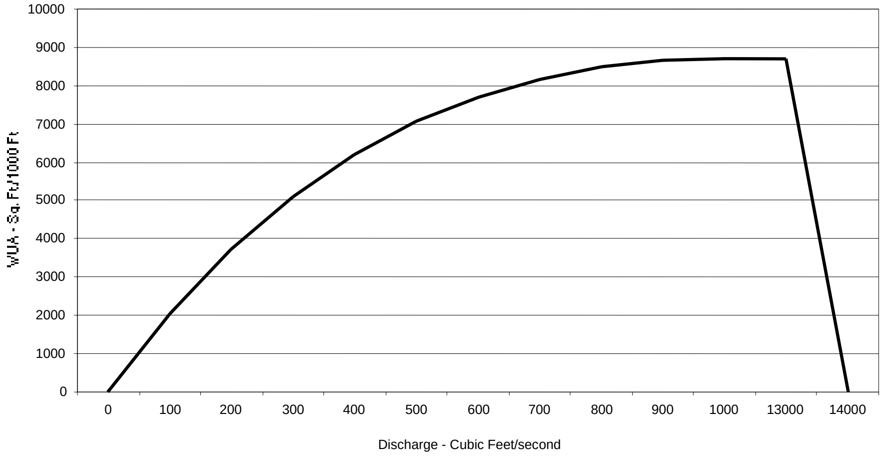


Figure C-13. Weighted Usable Area(WUA) for Fry in Steep Slope Mesohabitat Type - Segment 1

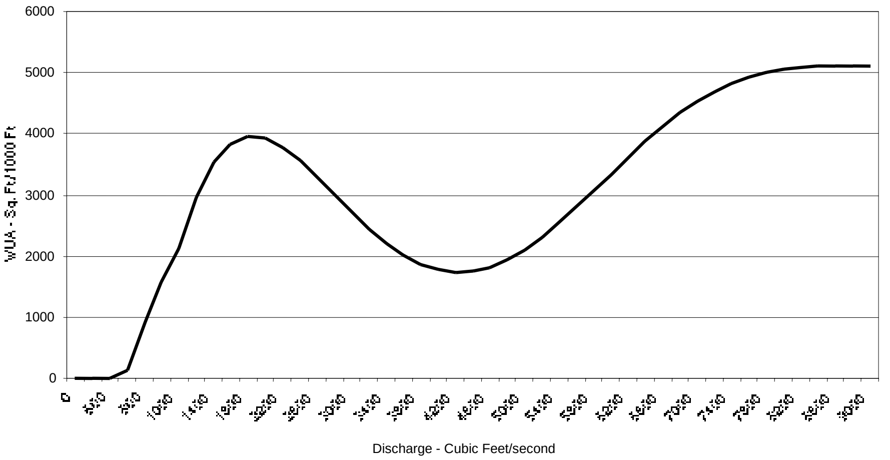


Figure C-14. Weighted Usable Area (WUA) for Presmolts in Steep Slope Mesohabitat Type - Segment 1

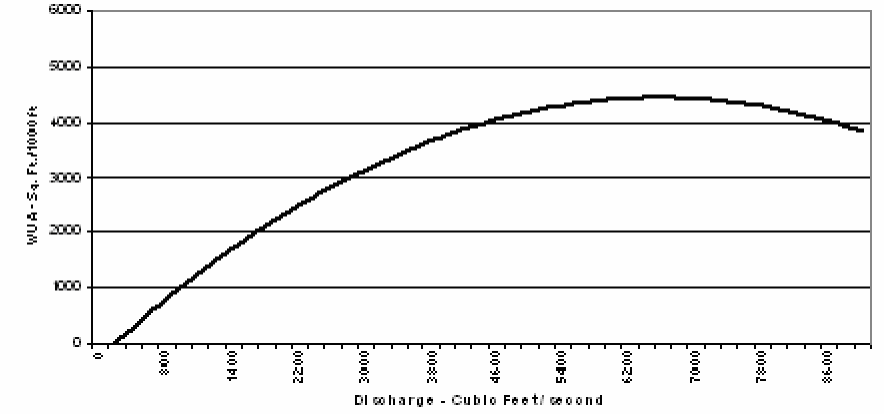


Figure C-15. Weighted Usable Area(WUA) for Spawning Females in Steep Slope Mesohabitat Type - Segment 1

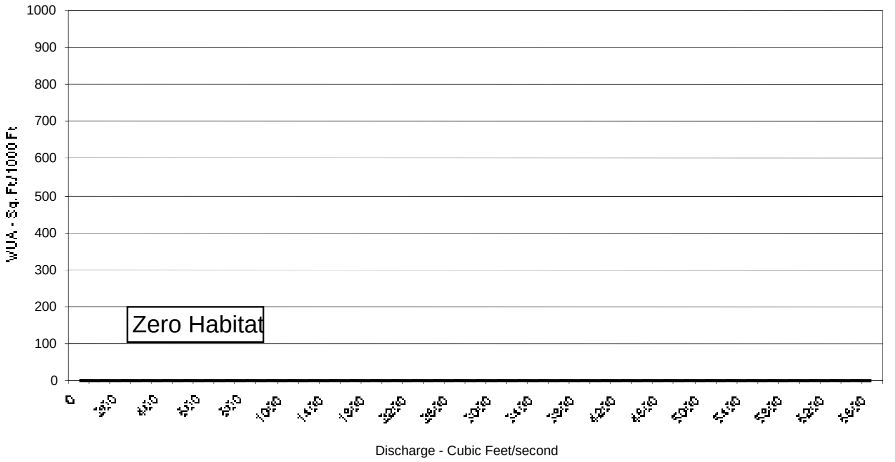


Figure C-16. Weighted Usable Area(WUA) for Fry in Split Channel Combined Mesohabitat Types - Segment 1

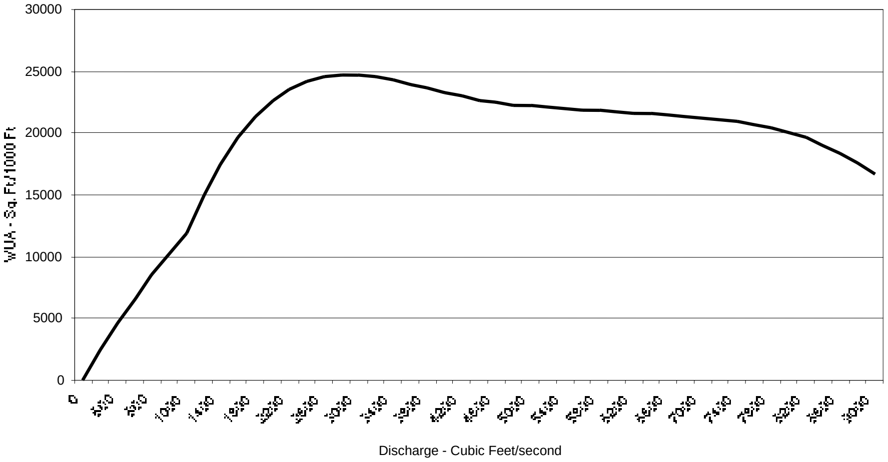


Figure C-17. Weighted Usable Area(WUA) for Presmolts in Split Channel Combined Mesohabitat Types - Segment 1

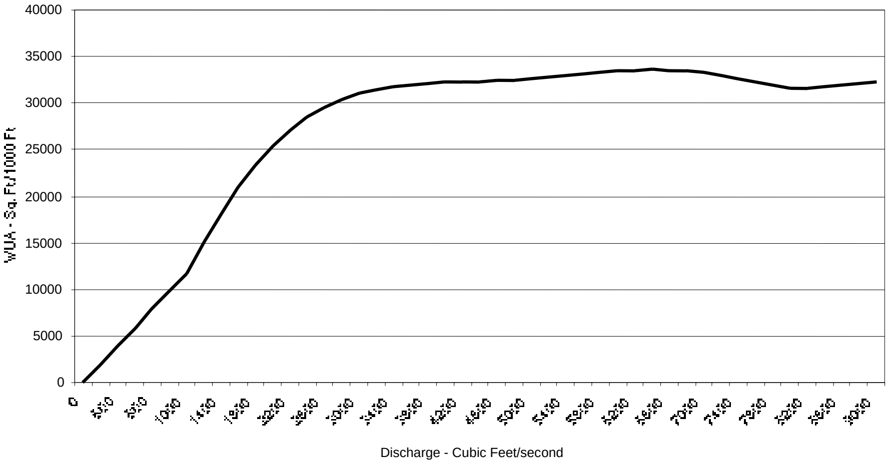


Figure C-18. Weighted Usable Area(WUA) for Spawning Females in Split Channel Combined Mesohabitat Types - Segment 1

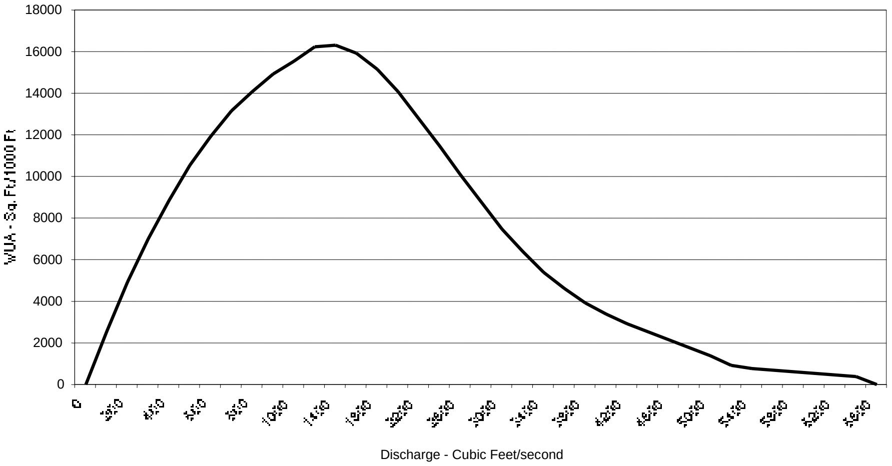


Figure C-19. Weighted Usable Area(WUA) for Eggs/Alevins in Split Channel Combined Mesohabitat Types - Segment 1

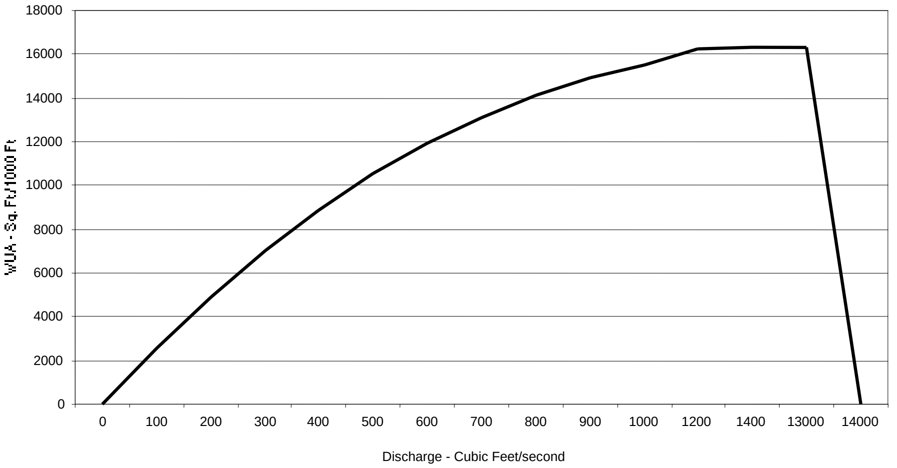


Figure C-20. Weighted Usable Area(WUA) for Fry in Side Channel Combined Mesohabitat Types - Segment 1

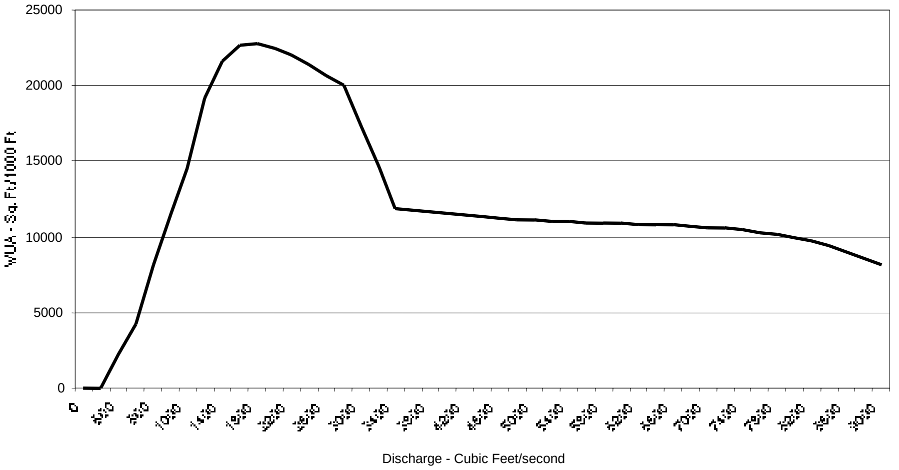


Figure C-21. Weighted Usable Area(WUA) for Presmolts in Side Channel Combined Mesohabitat Types - Segment 1

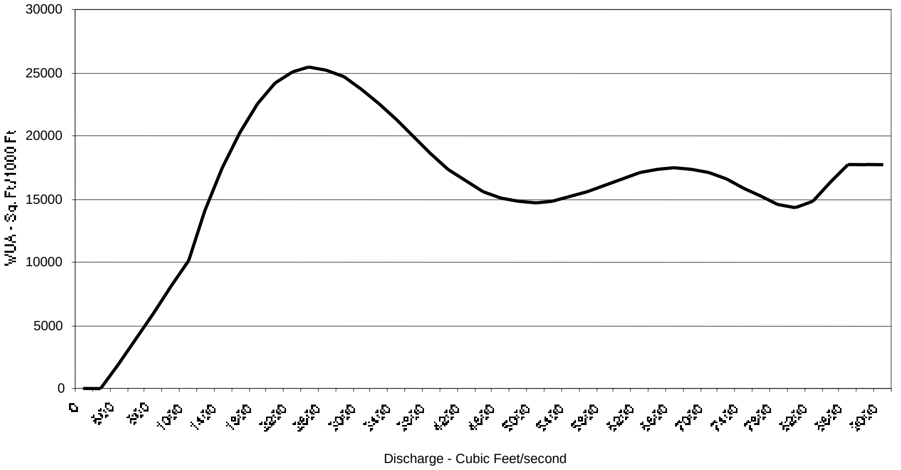


Figure C-22. Weighted Usable Area(WUA) for Spawning Females in Side Channel Combined Mesohabitat Types - Segment 1

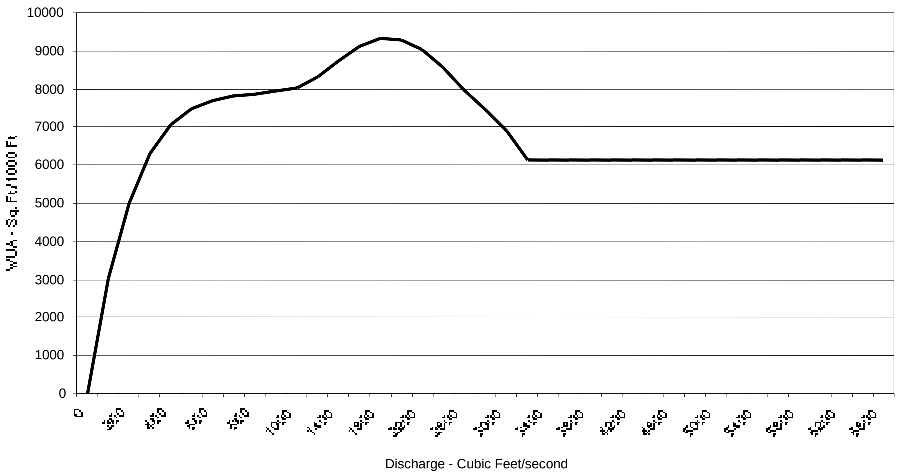


Figure C-23. Weighted Usable Area(WUA) for Eggs/Alevins in Side Channel Combined Mesohabitat Types - Segment 1

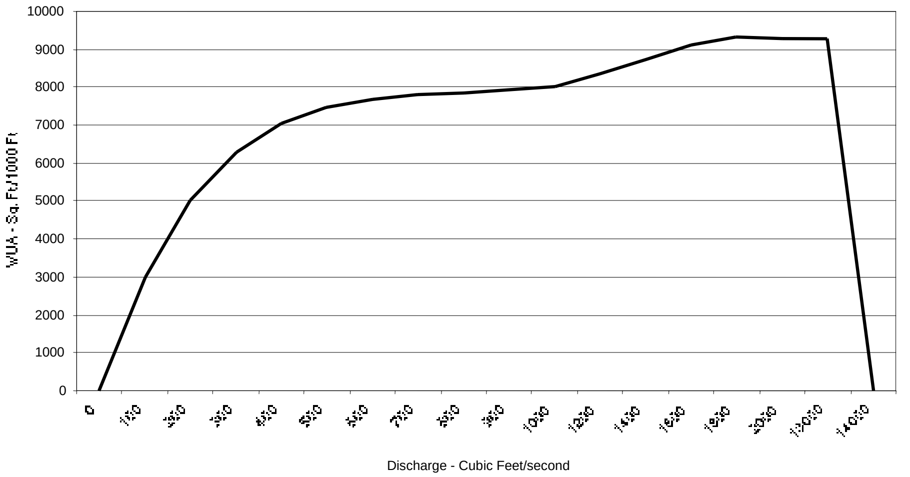


Figure C-24. Weighted Usable Area(WUA) for Fry in Low Slope Mesohabitat Type - Segment 2

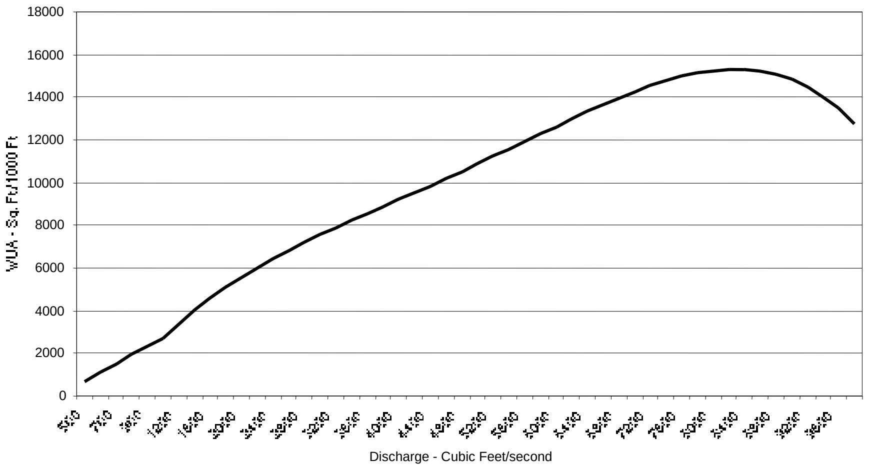


Figure C-25. Weighted Usable Area(WUA) for Presmolts in Low Slope Mesohabitat Type - Segment 2

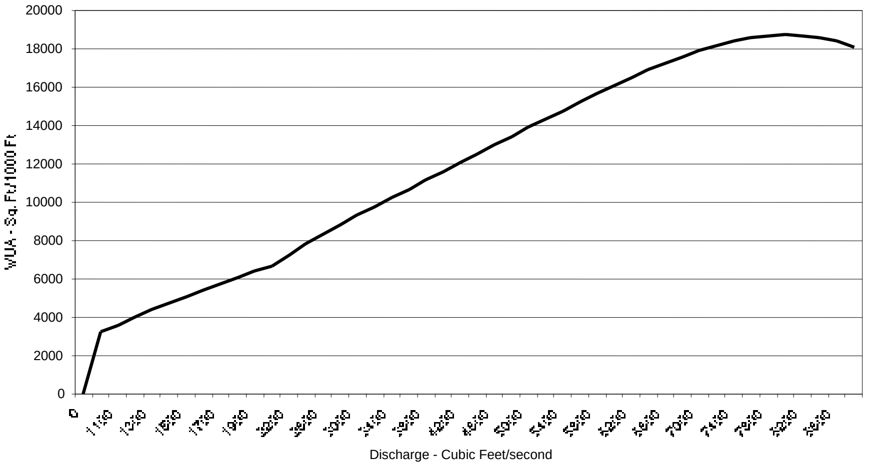


Figure C-26. Weighted Usable Area(WUA) for Spawning Females in Low Slope Mesohabitat Type - Segment 2

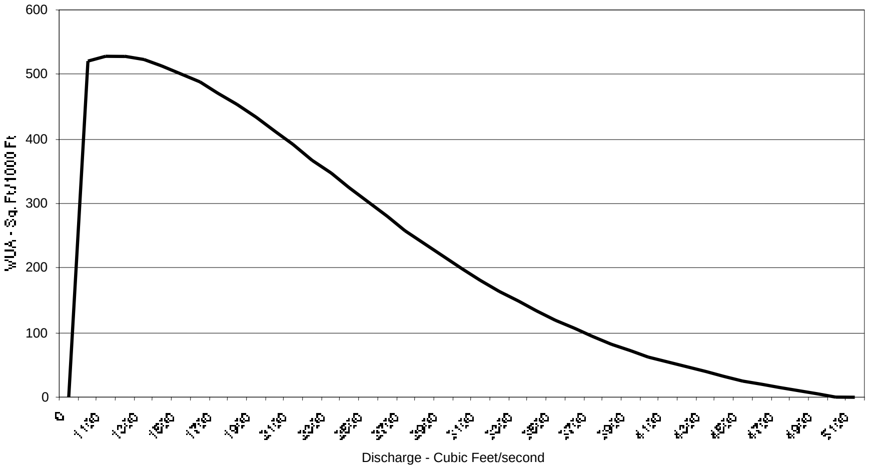


Figure C-27. Weighted Usable Area(WUA) for Eggs/Alevins in Low Slope Mesohabitat Type - Segment 2

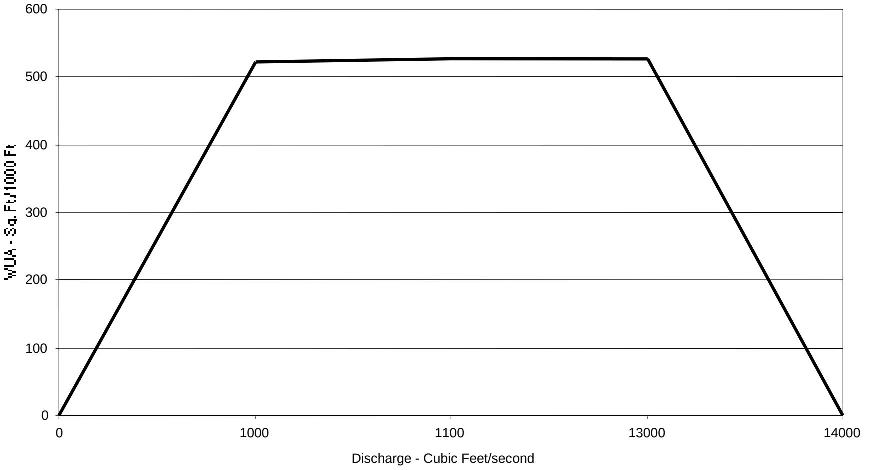


Figure C-28. Weighted Usable Area(WUA) for Fry in Moderate Slope Mesohabitat Type - Segment 2

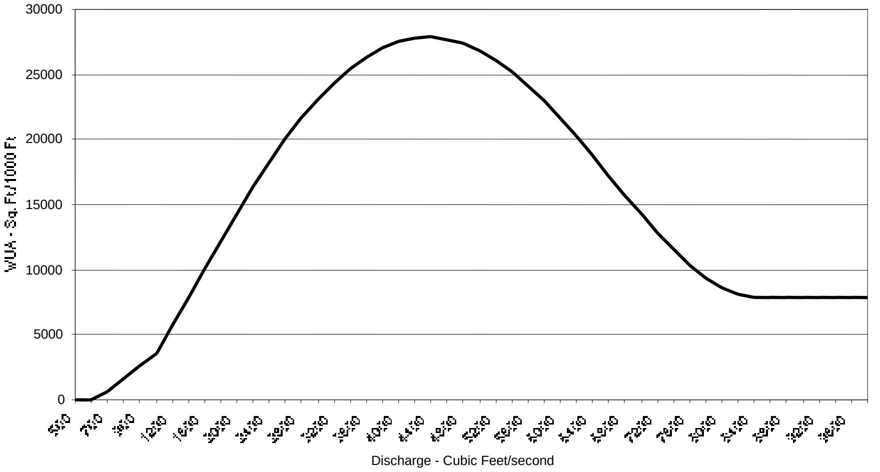


Figure C-29. Weighted Usable Area(WUA) for Presmolts in Moderate Slope Mesohabitat Type - Segment 2

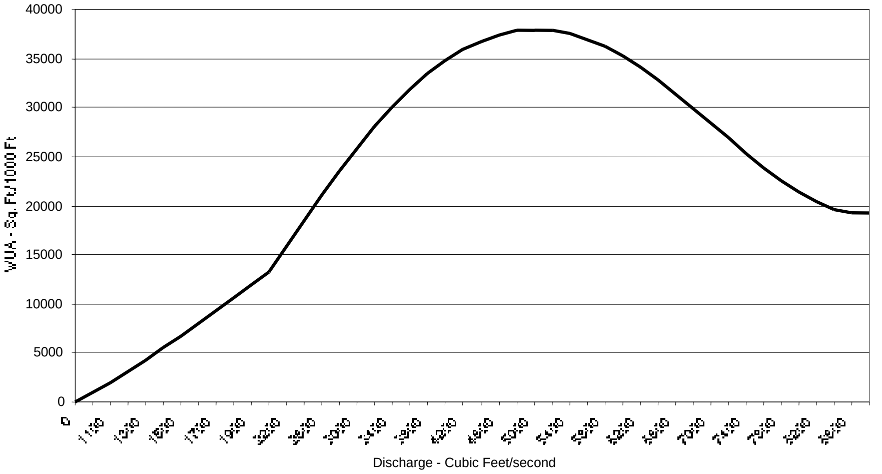
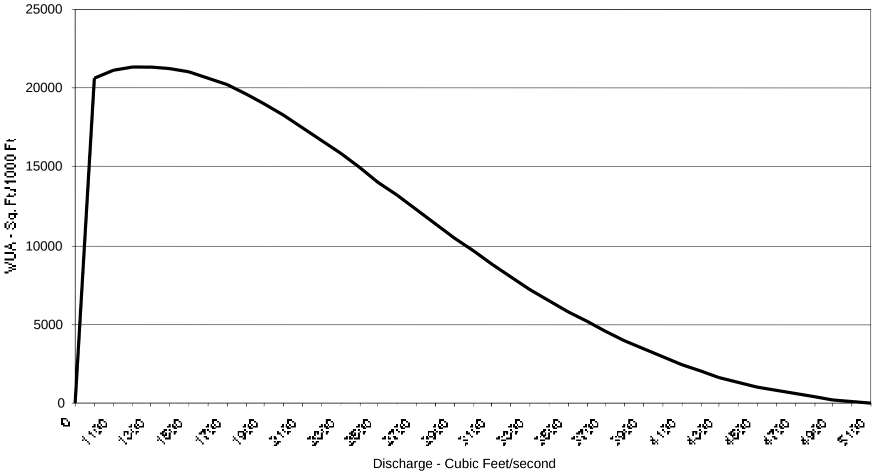


Figure C-30. Weighted Usable Area(WUA) for Spawning Females in Moderate Slope Mesohabitat Type - Segment 2



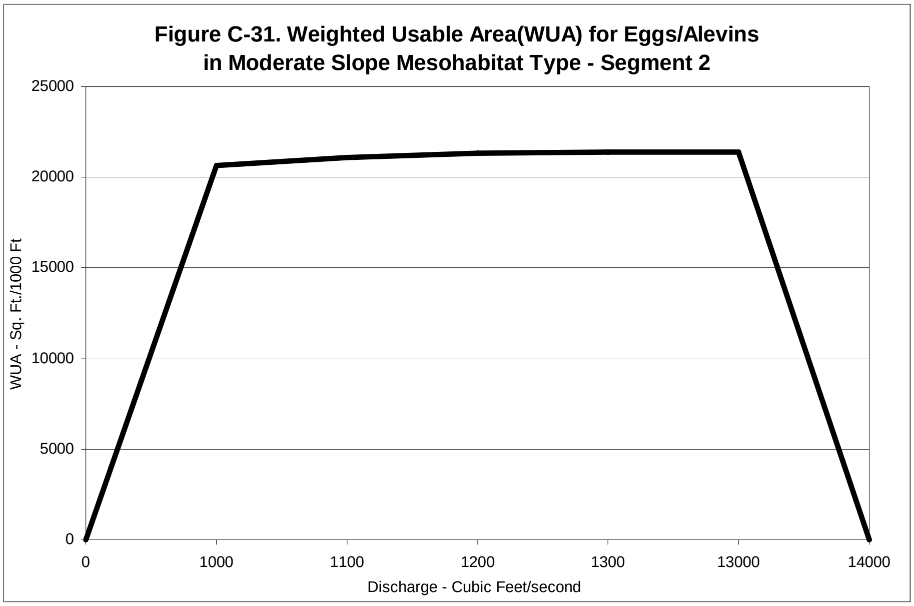


Figure C-31. Weighted Usable Area(WUA) for Eggs/Alevins in Moderate Slope Mesohabitat Type - Segment 2

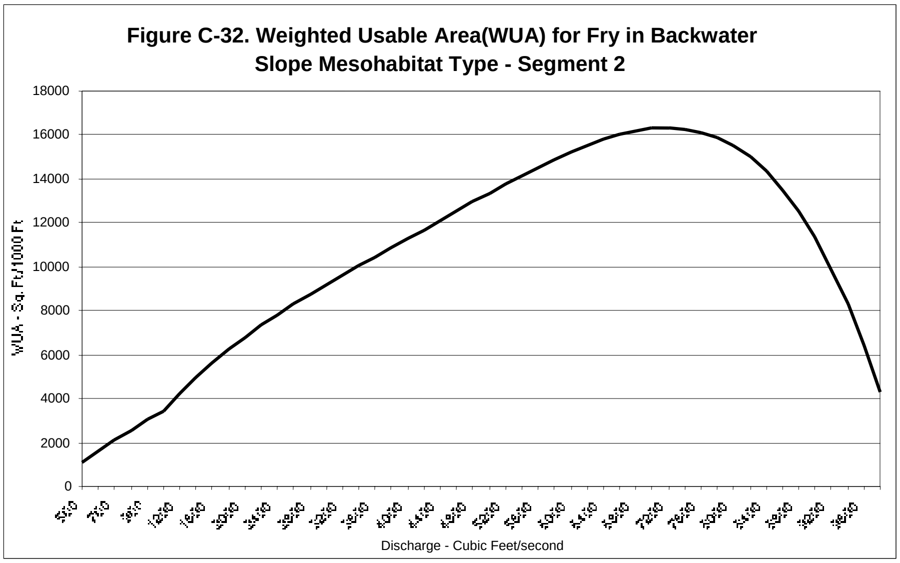


Figure C-32. Weighted Usable Area(WUA) for Fry in Backwater Slope Mesohabitat Type - Segment 2

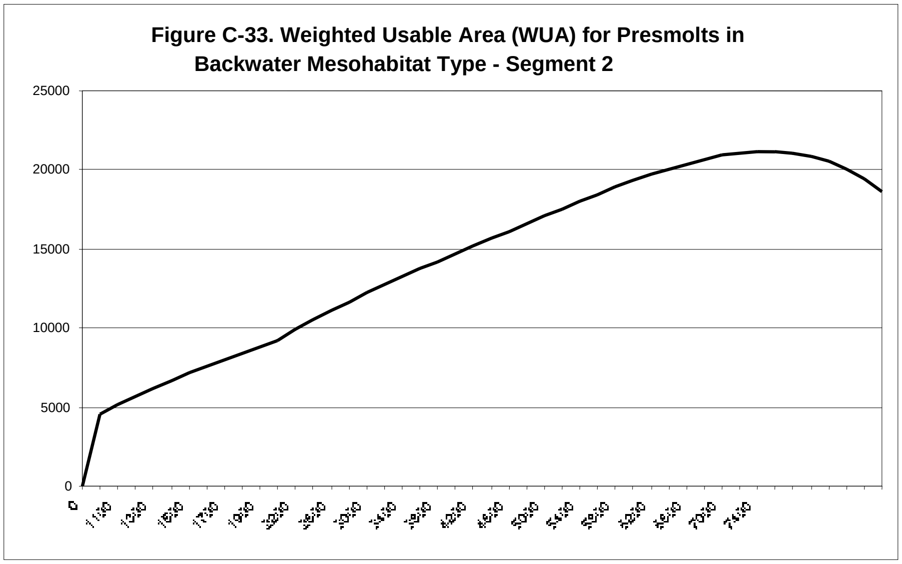


Figure C-33. Weighted Usable Area (WUA) for Presmolts in Backwater Mesohabitat Type - Segment 2

Figure C-34. Weighted Usable Area (WUA) for Spawning Females in Backwater Mesohabitat Type - Segment 2

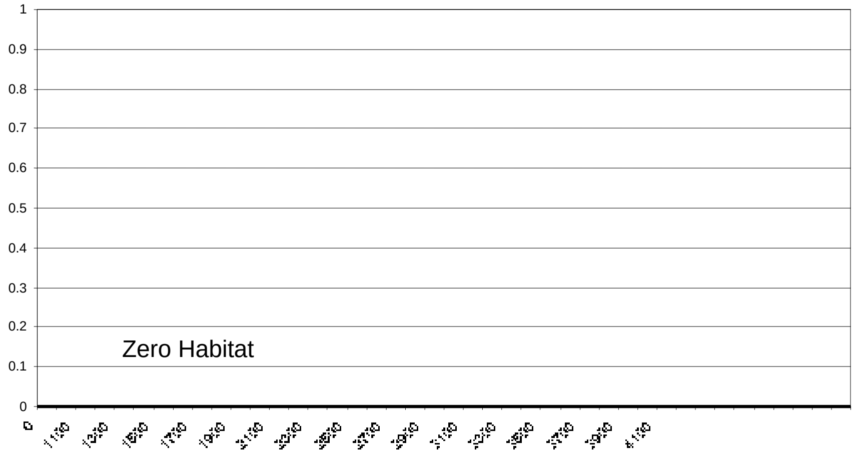


Figure C-35. Weighted Usable Area (WUA) for Fry in Steep Slope Mesohabitat Type - Segment 2

Figure C-36. Weighted Usable Area(WUA) for Presmolts in Steep Slope Mesohabitat Type - Segment 2

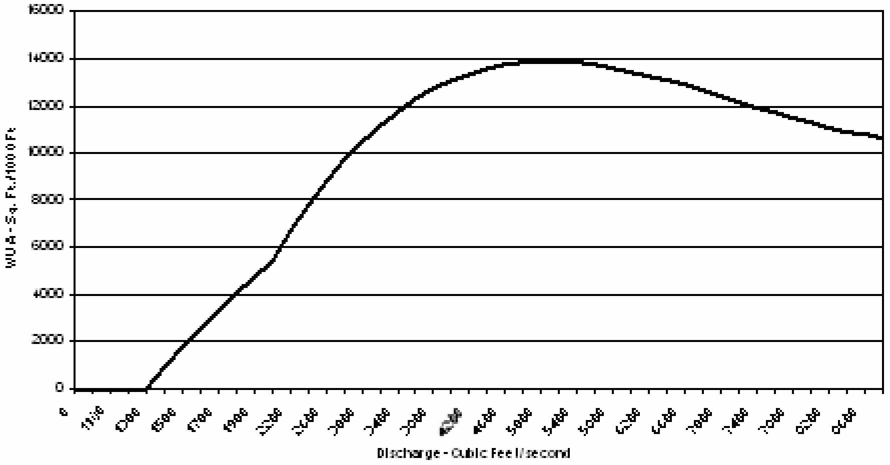


Figure C-37. Weighted Usable Area (WUA) for Spawning Females in Steep Slope Mesohabitat Type - Segment 2

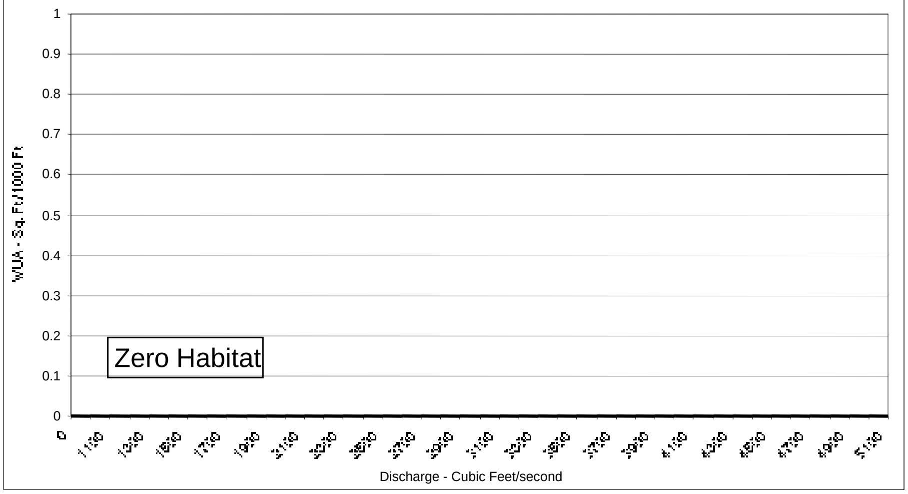


Figure C-38. Weighted Usable Area (WUA) for Fry in Split/Side Channel Combination Mesohabitat Type - Segment 2

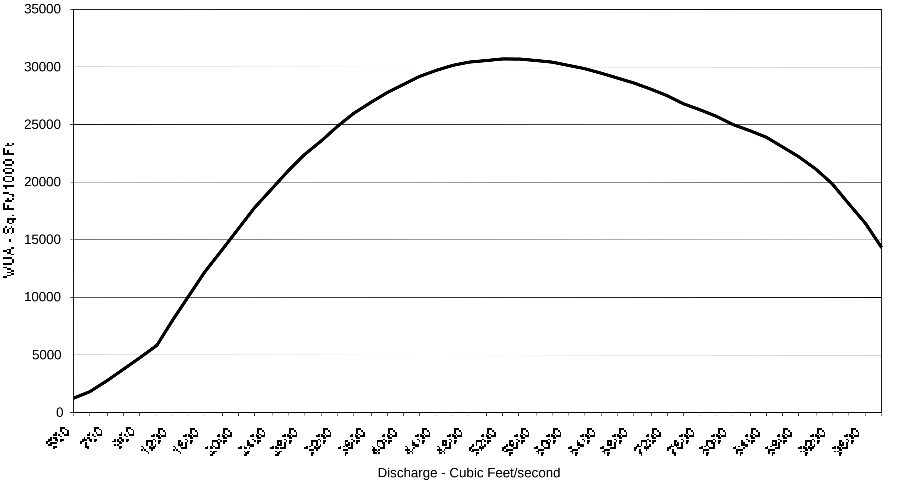


Figure C-39. Weighted Usable Area (WUA) for Presmolts in Split/Side Channel Combination Mesohabitat Type - Segment 2

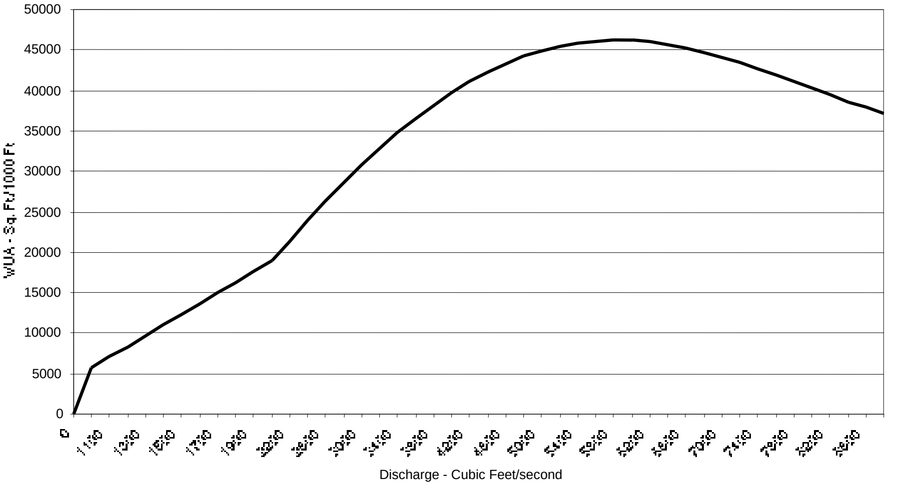


Figure C-40. Weighted Usable Area (WUA) for Spawning Females in Split/Side Channel Combination Mesohabitat Type - Segment 2

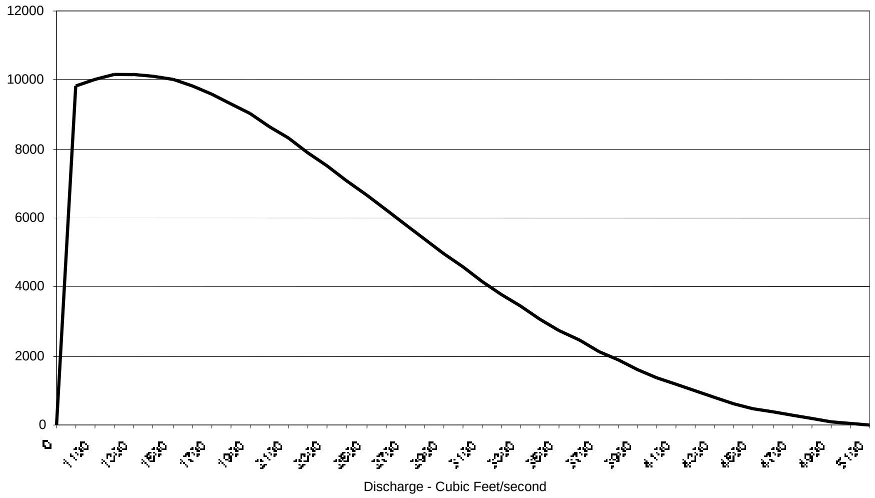
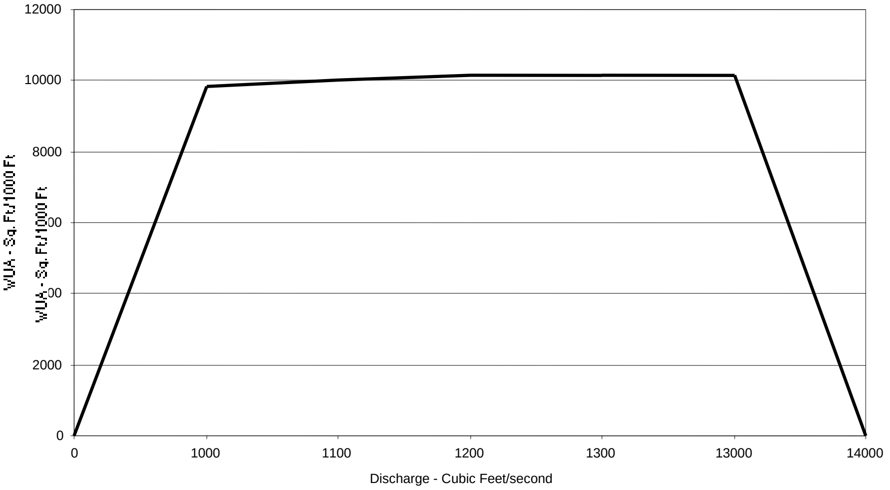


Figure C-41. Weighted Usable Area (WUA) for Eggs/Alevins in Split/Side Channel Combination Mesohabitat Type - Segment 2



Appendix D. Salmod Sensitivity Analysis

Salmod is a mathematical model constructed from a series of variable inputs, equations, and parameters that attempts to describe and quantify fall Chinook salmon production potential on the Klamath River downstream from Iron Gate Dam. Variables are defined as those external driving factors (flow, water temperature, and spawner seeding density) that vary from time step to time step or year to year. Parameters are essentially fixed values controlling internal model computations. It is important to understand uncertainties in both model variables and parameters, but in this initial sensitivity analysis (SA) we are targeting model parameters. Sensitivity to flow and temperature variability has been addressed in another stage of the historical analysis.

Model parameters are subject to many sources of uncertainty including errors of measurement, absence of information, and poor or partial understanding of important biological mechanisms. These limitations necessarily tax our confidence in model predictions. Good modeling practice requires that the modeler provide an evaluation of his or her confidence in the model, a portion of which involves assessing uncertainties associated with all model inputs.

Sensitivity analysis is one tool that can be used to:

- Apportion the relative variation in model output to variation in model inputs, qualitatively or quantitatively.
- Identify those parameters that may be in the greatest need of additional empirical data collection.
- Identify factors that may prove useful in subsequent model calibration.
- Identify insensitive variables that require little further attention.
- Establish defensibility in the sense that reviewers are increasingly asking for sensitivity analysis as a component of a thorough modeling analysis.

Methods

These are the general steps followed in conducting a SA for Salmod on the Klamath River:

1. Specify the model output of interest. It is important to select only one or a few of the many outputs produced by a model and identify this as the output of interest. In our case, the key value chosen was the total annual number of fall Chinook outmigrating downstream from the Scott River. Though we could have chosen biomass, we elected to choose numbers of fish because we felt that this would be more widely understood by all stakeholders and we relied on this metric during subsequent modeling analysis.

2. Select the inputs of interest from the full suite of possibilities, focusing on the most likely sensitive factors. Salmod has literally many hundreds of input values. If every single value were subject to variation, it would be very difficult to make sense of the voluminous results. For this reason, we grouped values into sets that were subsequently treated as single factors. For example, Salmod has a set of x,y coordinates that describe the relationship between mean weekly thermal exposure and mortality rate for each life stage. Rather than test the sensitivity of each coordinate pair, we shifted the whole set of coordinates “left and right” by 2°C for each life stage.

3. Choose the amount of variability for the selected factors. There is no single standard technique in performing a sensitivity analysis. Parameter variation is typically specified either as

proportionate (for example ± 10 percent) or through a "reasonable range" (for example from a low to high "probable" or "expected" value). We have chosen the reasonable range approach for most parameters, but we also used the proportionate approach when could not clearly identify the reasonable range.

Note that using both techniques can result in measures of sensitivity that are difficult to compare. For example, adjusting the calendar date of downstream pre-smolt migration by ±1 week may not be directly comparable to varying the temperature that initiates spawning by ±2°C because the units of variation differ. In addition, it should be clear that we may have overestimated the variability range for some parameters and underestimated the range for others, regardless of the approach. A comprehensive list of parameters and the variability assigned to them, along with other information, is given in the table.

4. Choose variation technique. The simplest and most common sensitivity analysis varies one parameter at a time, executing the model repeatedly to quantify any differences in key model outputs. The next level of complexity calls for variation of more than one parameter at a time, typically from a joint probability distribution that attempts to describe how the parameters might vary in tandem. However, it is often the case that such a joint probability distribution is itself unknown. We chose the single factor approach due to its simplicity. Under the presumption that all uncertain factors are susceptible to "correct" determination, and have the same cost to remove uncertainty, this so-called first-order sensitivity analysis identifies the factor(s) most deserving of better field or experimental measurement.

5. Generate a matrix showing the maximum sensitivity in model outputs from parameter variation. Again, we have chosen a simple design. We begin with the base simulation which contains our current best estimate of parameters. Then we make two other simulation runs, one with the high estimate and one with the low. Computing the biggest percentage change in outmigrant numbers (high minus base or low minus base) provides a measure of the maximum sensitivity for this parameter. In addition, having three points for each parameter (high, base, low) enables us to examine whether variation in each parameter causes a linear or non-linear response. We do not discuss this last point further here.

6. Repeat Step 5 for a variety of year types. Following the philosophy of looking for the maximum possible sensitivity, we also wanted to make sure that we examined a variety of different year types, from wet to dry and hot to cold. Thus, we repeated the sensitivity calculation for a three-by-three matrix representing these conditions by drawing on categorized years. Years were chosen using SIAM's yearly sort function and a previous analysis that provided maximum June air temperature and inflow to Upper Klamath Lake. The selected years are shown in the following table:

	Hot	Avg	Cool
Wet	1998	1982	1971
Avg	1985	1995	1976
Dry	1977	1988	1981

As before, we chose the maximum sensitivity for each parameter across all nine year types.

7. As previously noted, the single factor variation scheme prevents the detection of interactions among parameters. That is, in examining the sensitivity of one parameter, we accept the risk of remaining ignorant about important model dynamics if some or all of the remaining parameters were different than their base value. A prime example of this in our case is that the model might behave very differently, depending on the number of adult spawners used to seed

the system. With low numbers there might be little in the way of juvenile habitat-related mortality, but with higher seeding levels there may be a lot. Because of this, we repeated Steps 5 and 6 for the case where there were two times the average number of spawners used in the base case, once again choosing the maximum sensitivity values.

To summarize, we choose the maximum parameter sensitivity across three different cases: (a) base compared with high and low parameter estimates, (b) across nine year types, and (c) with a base and high number of spawners. Finally, we have displayed each parameter's relative sensitivity by scaling all sensitivity values to a maximum value of 100 for simplicity.

Findings

The following figure summarizes the findings. Parameters are arrayed in order of their relative sensitivity and arbitrarily divided into high, medium, and low categories. Highly sensitivity parameters were judged as those essentially demanding extra scrutiny. Parameters of lesser sensitivity are still important but are not likely to dominate Salmod's predictive ability. Parameters with low sensitivity warrant little scrutiny at this time.

Discussion

We were not surprised by the sensitivity of fry and presmolt weighted usable area (WUA). There is inherent uncertainty here (Gard 2005), and the results reflected our liberal 0.5 to 2X weighting. Similarly, habitat capacity values in essence reflect exactly the same uncertainty and must be accurately calculated from the best data available. Juvenile thermal mortality rates are also well described as highly sensitive. Fortunately, these are known with greater certainty. Fry and presmolt weekly seasonal movement distance are likely sensitive solely because they are, by default, just less than the study area length, meaning that outmigrating fry exit in either one or two weeks. (In fact, we reduced the computed presmolt sensitivity, believing it to be an artifact of the study area, not the actual parameter.)

More surprising were the several factors that in one way or another relate directly to species life-history timing, specifically:

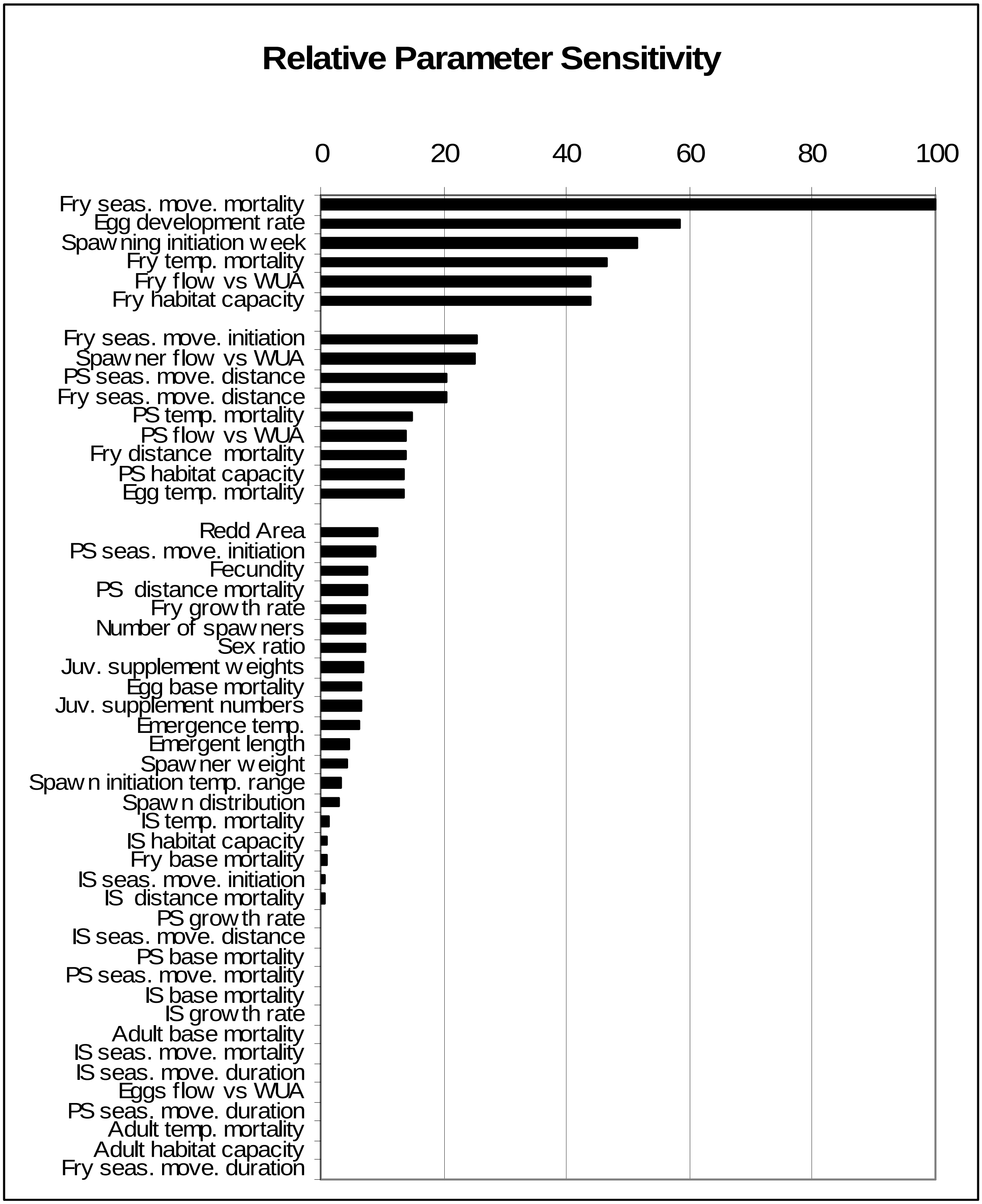
- Egg development rate
- Spawning initiation week
- Fry seasonal movement initiation

These factors, collectively, account for much model sensitivity (variance) and highlight the need to carefully verify event timing and triggers. Perhaps this should not have been surprising because Bartholow (2005) had shown that timing was a key determinant in predicting relative survival for the four races of Chinook salmon in the Sacramento River. Clearly establishing these timing factors will reduce the model's uncertainty.

Sensitivity analysis by itself does not address the issue of model realism. In other words, one might identify a parameter that has little influence on simulated model outcomes, but if the value is "wrong" it will detract from the believability and trust in model results regardless. In addition, one must be cognizant that in complicated, multi-parameter models, errors in one parameter may be masked by errors in other parameters without significantly affecting model behavior. Should one choose an apparently sensitive parameter as a management focus, it would be wise to test that sensitivity as a hypothesis before a full-scale effort.

Sensitivity analysis also can be used to address the model's internal structure. In our opinion, that is not our principal objective here. However, we must not lose sight of the fact that Salmod attempts solely to represent the freshwater dynamics and is not a full life-cycle model.

It is important to remember that sensitivity analysis does not in any way identify parameters that are wrong. The model may well be, and should be, sensitive to parameter changes. A different form of sensitivity analysis that could be pursued is what might be called the ultimate sensitivity analysis where one would examine how parameter variation might lead to a change of decision in using the model. This would require much additional work, but certainly what we have been doing is a sensitivity analysis of the variables, flow and water temperature, and how that variation may have affected historical salmon production.


Relative Parameter Sensitivity
0
20
40
60
80
100
Fry seas. move. mortality
Egg development rate
Spawning initiation week
Fry temp. mortality
Fry flow vs WUA
Fry habitat capacity
Fry seas. move. initiation
Spawner flow vs WUA
PS seas. move. distance
Fry seas. move. distance
PS temp. mortality
PS flow vs WUA
Fry distance mortality
PS habitat capacity
Egg temp. mortality
Redd Area
PS seas. move. initiation
Fecundity
PS distance mortality
Fry growth rate
Number of spawners
Sex ratio
Juv. supplement weights
Egg base mortality
Juv. supplement numbers
Emergence temp.
Emergent length
Spawner weight
Spawn initiation temp. range
Spawn distribution
IS temp. mortality
IS habitat capacity
Fry base mortality
IS seas. move. initiation
IS distance mortality
PS growth rate
IS seas. move. distance
PS base mortality
PS seas. move. mortality
IS base mortality
IS growth rate
Adult base mortality
IS seas. move. mortality
IS seas. move. duration
Eggs flow vs WUA
PS seas. move. duration
Adult temp. mortality
Adult habitat capacity
Fry seas. move. duration

Structural Elements	**Klamath-specific**	**Status**	**Uncertainty**	**Sensitivity Range**
Study Area	Yes	Considered fixed, IGD to the Scott River.	Downstream fate (including estuary and ocean) are considerable.	None
Flow and Temperature Reaches	Yes	Considered fixed. Eleven reaches, well matched to hydrology and thermal characteristics of the river.	Relatively minor.	None
Mesohabitat Typing Data and Downstream Sequence	Yes	Considered fixed. Derived from detailed habitat mapping.	Any misclassifications considered random.	None
Life Stage Nomenclature and Length Class Breakpoints	Yes	Well defined. Some investigators may use slightly different values.	Considered minor. May be explored later.	None
Initiation of Biological Year	Yes	Begins October 1.	Some adults may be in study area somewhat prior to October 1.	None
Hatchery Supplementation	Yes	Recent average defined by California Department of Fish and Game	Is not dynamic across years/conditions	±10%
Tributary Supplementation	Yes	Recent average defined by California Department of Fish and Game	Is not dynamic across years/conditions. Uncertainty regarding Bogus Creek values.	±10%
Driving Environmental Variables	**Klamath-specific**	**Status**	**Uncertainty**	**Sensitivity Range**
Flow and Water Temperature Values	Yes	Come from SIAM (MODSIM and HEC-5Q).	Aggregation to weekly time-step masks peaks. May need to test with measured data to the degree possible.	None. Will be a different exercise.
Parameters	**Klamath-specific**	**Status**	**Uncertainty**	**Sensitivity Range**
Q:WUA Quantification (Life stage-specific)	Yes	Available from PHABSIM.	Magnitude (y-axis)	0.5 to 2 times
			Flow-dependence (x-axis)	Did not vary
Weight:Length Relationship	Yes	Well defined.	Agrees well with Sacramento River.	None
Spawning Initiation Temperature	No	Klamath values are a subset of literature-derived values.	Upper value could be important, not lower value on Klamath	± 2°C "shift"
Spawning Spatial and Temporal Distribution	Yes	Well defined, but using multi-year average for all attributes. Could differ given differences between carcass and redd counts.	Distribution through study area	None
			Initiation timing (x-axis)	± 1 week
			Duration or "peakedness" (x-axis)	± 1 week
Spawner Density and Characteristics	Yes	Have hatchery and carcass count data. Likely to be representative of main stem study area.	Number of adults	± 10%
			Sex Ratio (actually spawners to non-spawner ratio)	± 10%

			Size (weight)	± 10%
Fecundity	No	From Lewiston Hatchery, but agrees well with older Klamath-specific data.	Could perhaps improve with values from Iron Gate Hatchery.	± 10%
Redd Area	Yes	Well defined.	Calculated from data.	4.25 ± 1.4 m^2
Superimposition Option	No	From Trinity.	Considered random.	None
Egg Development Rate	No	From reliable literature.	Some uncertainty in hatch to pre-emergent timing; may need to adjust during calibration.	± 2°C "shift"
Emergent Length	Yes	From field measurements, but not explicitly to estimate this parameter.	Contains some uncertainty.	35 ± 4.5 mm
Emergence Temperature	No	Literature derived, but for Atlantic salmon. Experts disagree.	Fair uncertainty.	± 2°C "shift"
Juvenile Growth Rates (Life stage-specific)	No	Well defined literature values that have worked well on other rivers.	Some uncertainty because values derived from ad lib feeding.	± 2°C "shift"
Freshet Movement Attributes (Life stage-specific)	Not yet used on Klamath	Other rivers see demonstrable effects, both for spikes and drops.	Trigger	Use existing model options
			Distance moved	± 10%
			Mortality	± 10%
Seasonal Movement Attributes (Life stage-specific)	Yes, for timing and distance	Values derived from other applications and may be adjusted during calibration.	Initiation timing	± 1 week
			Duration	± 1 week
			Distance moved	± 10%
			Mortality	± 10%
Base Mortality Rates (Life stage-specific)	No	Values derived from Trinity River.	Uncertainty due to endemic disease.	± 10%
Thermal Mortality Rates (Life stage-specific)	No	Values are composites from multiple literature sources.	Uncertainty due to many causes.	± 2°C "shift"
Habitat Capacity (Juvenile Life stage-specific)	Partial	Klamath-specific for fry; literature for other juveniles; guess for adults.	Uncertainty from multiple causes.	0.5 to 2 times
Habitat Capacity Movement Dynamics	No	Several assumptions.	Considered fixed assumption of the model.	None
Habitat-related Distance Moved Mortality Rate (Life stage-specific)	No	Derived from Trinity and Sacramento Rivers.	Much uncertainty. Will vary only the distance to 100% mortality.	0.5 to 2 times

Appendix E. Fahrenheit to Celsius, and Celsius to Fahrenheit Conversion Chart.

°F	°C	°F	°C	°F	°C	°F	°C	°C	°F	°C	°F
32.0	0.0	52.5	11.4	73.0	22.8	93.5	34.2	0.0	32.0	20.5	68.9
32.5	0.3	53.0	11.7	73.5	23.1	94.0	34.4	0.5	32.9	21.0	69.8
33.0	0.6	53.5	11.9	74.0	23.3	94.5	34.7	1.0	33.8	21.5	70.7
33.5	0.8	54.0	12.2	74.5	23.6	95.0	35.0	1.5	34.7	22.0	71.6
34.0	1.1	54.5	12.5	75.0	23.9	95.5	35.3	2.0	35.6	22.5	72.5
34.5	1.4	55.0	12.8	75.5	24.2	96.0	35.6	2.5	36.5	23.0	73.4
35.0	1.7	55.5	13.1	76.0	24.4	96.5	35.8	3.0	37.4	23.5	74.3
35.5	1.9	56.0	13.3	76.5	24.7	97.0	36.1	3.5	38.3	24.0	75.2
36.0	2.2	56.5	13.6	77.0	25.0	97.5	36.4	4.0	39.2	24.5	76.1
36.5	2.5	57.0	13.9	77.5	25.3	98.0	36.7	4.5	40.1	25.0	77.0
37.0	2.8	57.5	14.2	78.0	25.6	98.5	36.9	5.0	41.0	25.5	77.9
37.5	3.1	58.0	14.4	78.5	25.8	99.0	37.2	5.5	41.9	26.0	78.8
38.0	3.3	58.5	14.7	79.0	26.1	99.5	37.5	6.0	42.8	26.5	79.7
38.5	3.6	59.0	15.0	79.5	26.4	100.0	37.8	6.5	43.7	27.0	80.6
39.0	3.9	59.5	15.3	80.0	26.7	100.5	38.1	7.0	44.6	27.5	81.5
39.5	4.2	60.0	15.6	80.5	26.9	101.0	38.3	7.5	45.5	28.0	82.4
40.0	4.4	60.5	15.8	81.0	27.2	101.5	38.6	8.0	46.4	28.5	83.3
40.5	4.7	61.0	16.1	81.5	27.5	102.0	38.9	8.5	47.3	29.0	84.2
41.0	5.0	61.5	16.4	82.0	27.8	102.5	39.2	9.0	48.2	29.5	85.1
41.5	5.3	62.0	16.7	82.5	28.1	103.0	39.4	9.5	49.1	30.0	86.0
42.0	5.6	62.5	16.9	83.0	28.3	103.5	39.7	10.0	50.0	30.5	86.9
42.5	5.8	63.0	17.2	83.5	28.6	104.0	40.0	10.5	50.9	31.0	87.8
43.0	6.1	63.5	17.5	84.0	28.9			11.0	51.8	31.5	88.7
43.5	6.4	64.0	17.8	84.5	29.2			11.5	52.7	32.0	89.6
44.0	6.7	64.5	18.1	85.0	29.4			12.0	53.6	32.5	90.5
44.5	6.9	65.0	18.3	85.5	29.7			12.5	54.5	33.0	91.4
45.0	7.2	65.5	18.6	86.0	30.0			13.0	55.4	33.5	92.3
45.5	7.5	66.0	18.9	86.5	30.3			13.5	56.3	34.0	93.2
46.0	7.8	66.5	19.2	87.0	30.6			14.0	57.2	34.5	94.1
46.5	8.1	67.0	19.4	87.5	30.8			14.5	58.1	35.0	95.0
47.0	8.3	67.5	19.7	88.0	31.1			15.0	59.0	35.5	95.9
47.5	8.6	68.0	20.0	88.5	31.4			15.5	59.9	36.0	96.8
48.0	8.9	68.5	20.3	89.0	31.7			16.0	60.8	36.5	97.7
48.5	9.2	69.0	20.6	89.5	31.9			16.5	61.7	37.0	98.6
49.0	9.4	69.5	20.8	90.0	32.2			17.0	62.6	37.5	99.5
49.5	9.7	70.0	21.1	90.5	32.5			17.5	63.5	38.0	100.4
50.0	10.0	70.5	21.4	91.0	32.8			18.0	64.4	38.5	101.3
50.5	10.3	71.0	21.7	91.5	33.1			18.5	65.3	39.0	102.2
51.0	10.6	71.5	21.9	92.0	33.3			19.0	66.2	39.5	103.1
51.5	10.8	72.0	22.2	92.5	33.6			19.5	67.1	40.0	104.0
52.0	11.1	72.5	22.5	93.0	33.9			20.0	68.0		