Population Dynamics of Klamath River Fall Chinook Salmon:  
Stock–Recruitment Model and Simulation of 
Yield under Management 

Report to Klamath Fishery Management Council  
by the  
Klamath River Technical Advisory Team  

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## Contents

List of Figures ............................................. iii

1 Introduction ........................................... 1

1.1 Present Management Strategy and Policy ................. 2

1.2 Detailed Objectives .................................. 4

2 Simulation Methods .................................... 5

2.1 May 1 Population Size ................................ 7

2.2 Abundance Estimation ................................ 7

2.3 Setting the Annual Management Regime and Fishing .... 8

2.4 Other Parameters Related to Harvesting ................. 10

2.5 Natural Mortality ..................................... 11

3 Stock–Recruitment Submodel ........................ 12

3.1 Data ................................................ 12

3.2 Model Form ........................................ 13

3.3 Estimates of Recruitment Parameters ..................... 14

3.4 Environmental Effects on Recruitment ................... 16

3.5 MSY and Recruitment Models ........................ 17

4 Simulations Run — Statistics Recorded .................. 17

5 Results .................................................. 19

5.1 Annual Catch ........................................ 20

5.2 Year-to-Year Variation in Catch ......................... 21

5.3 Frequency of Fishery Closures ......................... 22

5.4 Spawning Escapement Achieved ........................ 23

5.5 Tribal Share of Catch ................................ 25

6 Discussion ............................................. 26

6.1 Historical Comments on the Spawner Floor .............. 26
6.2 Modeling and its Assumptions ........................................... 27
   6.2.1 Assumptions about Recruitment ............................... 28
   6.2.2 Assumptions about Natural and Hatchery Stocks ........... 29
   6.2.3 Assumptions about Stock Structure ........................... 30
6.3 Conclusions ............................................................. 30
   6.3.1 Present Value of Spawner Floor ............................... 30
   6.3.2 Use of Minimum Spawner–Reduction Rate .................... 31
   6.3.3 Effects of Estimation Error ................................. 32

7 Acknowledgments ......................................................... 33
Sources Cited ............................................................... 34
List of Figures

1. Block Diagram of Simulations ................................ 6
2. Sensitivity of Simulations to Starting Values ...................... 8
3. Block Diagram of Klamath Harvest Rate Model .................. 9
4. Fitted Stock-Recruitment Model .............................. 15
5. Typical Frequency Distribution of Simulated Annual Catches .... 18
6. Median of Simulated Annual Catches vs. Spawner Floor ........ 20
7. Nonparametric CV of Simulated Annual Catch ................ 21
8. Proportion of Years Simulated Fishery is Closed ................ 23
9. Median of Simulated Annual Spawning Escapements under Management 24
10. Sensitivity Analysis on Median and Mean Escapement ........... 25
11. Median Proportion of Simulated Catch Taken by Tribes ........ 26
1 Introduction

A basic question about any fish stock is the nature of the stock-recruitment relationship. The process of replenishment through recruitment, with the density-dependent compensation it necessarily implies, is the force that makes fisheries possible. Thus, the study of stock and recruitment has occupied a central place in the fisheries literature.

Once a stock’s recruitment dynamics have been described, it becomes possible to model various management measures, either existing or proposed, for the purpose of estimating the long-term average yield expected under them. For example, one might estimate a stock’s maximum sustainable yield (MSY), which would require a recruitment model (explicit or implicit) and several other assumptions. Regardless of the management benchmark chosen, it is necessary in every case to understand recruitment (or to make assumptions about it) to progress from questions of yield per recruit to those of sustainable yield.

The Klamath Fishery Management Council (the Council) has assigned the Klamath River Technical Advisory Team (KRTAT) to conduct a modeling study of stock, recruitment, and yield of Klamath River fall chinook salmon. The objectives of such a study are understood to include evaluation of the present management policy, in particular the spawner floor, and possible alternatives. The present scheme of Harvest Rate Management was described in a previous report (KRTAT 1986) that introduced not just the concept of a spawner floor and relatively constant harvest rate, but also suggested the parameters and procedures for a management policy based on them. With the passage of time, additional data have become available that could be incorporated into a re-evaluation of some of the parameters of the 1986 report.

A preliminary report on the new assignment (KRTAT 1996), using computer simulation to explore possible ramifications of different values for the spawner floor, was discussed at a Council meeting in October, 1996. In the ensuing discussion, a number of areas were identified for improving the work, and it was agreed that a revision should be made. One specific area of improvement was that the simulations should include spawning over a realistic range of ages, rather than only at age 3.

In the time since the 1996 preliminary report was written, a comprehensive revision of
the Klamath Harvest Rate Model (KHRM) has been conducted (Prager and Mohr 1998). The revised KHRM and its embodiment as a computer program provided an age-structured model of management, fishing (including catch, incidental mortality, and allocation), and spawning that could be incorporated into the revised study of stock, recruitment, and yield. What remained to complete the assignment was to add a recruitment model, tie it to the KHRM framework, and to meld the two into a unified simulation model. Following that, of course, were the tasks of exercising the model, collecting appropriate summary statistics, and documenting the results. This report is intended to satisfy the assignment given to the KRTAT by the Council. As is explained in detail below, the modeling work included a stock-recruitment study followed by computer simulations of the stock, with simulation of spawning, fishing, and mortality at ages 3, 4, and 5.

1.1 Present Management Strategy and Policy

To put into context the questions addressed by this study, it is necessary to summarize the present scheme of management used for this stock. For clarity, we first define contrasting terms for different aspect of management. These terms are used throughout the report.

- We use the term management strategy to describe the overall management principles and framework in effect. Examples of management strategies are the use of a spawner floor and the existence of agreements on catch allocation.

- We use the term management policy to refer to specific numerical limits and constraints applied on an ongoing basis within the overall management strategy. Examples of management policies are a spawner floor set at 35,000 fish or an agreement that exactly 50% of catch be allocated to the Yurok and Hoopa Valley tribes.

- We use the term annual management regime to refer to specific harvesting regulations approved by the Council for a year’s fishing season. An example of an annual management regime would be an approved ocean harvest rate, tribal quota, and river-recreational quota for a given year.
The Klamath fall chinook stock is presently subject to a management strategy known as Harvest Rate Management (KRTAT 1986), which is applied only to “natural” fish. This management strategy consists of taking the maximum number of adults (ages 3, 4, 5) possible, subject to the following rules:

1. Removals must not reduce the spawning escapement below a predetermined minimum or spawner floor.

2. Removals must not reduce the spawning escapement beyond a maximum allowable proportion, compared to the escapement with no fishing. That proportion is termed the maximum spawner-reduction rate.

3. Rule 1 may be tempered by application of a minimum spawner-reduction rate greater than zero, to allow a small amount of fishing when the fishery would otherwise be closed. (This is sometimes termed a de minimus fishery.)

4. The catch of the three fishery segments (ocean, river tribal, and river recreational) must be in accordance with predetermined sharing agreements, which at present allocate portions of the catch to the ocean fishery, to the river-recreational fishery, and to the Yurok and Hoopa Valley tribes as a unit.

Other issues, such as limiting the incidental take of endangered species and achieving a desirable season structure, may be considered in the actual fishery, but were not considered in this simulation study.

The use of a constant spawner-reduction rate (as well as an escapement floor) was originated the KRTAT (1986) report, which used the term “harvest rate” as a metric of fishing intensity. That the intent was a spawner-reduction rate can be seen on p. 7 of that report, which states: “…any of the combinations [of harvest rates] shown in Figure 4 …would allow

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2“Natural” fish is taken to mean fish, regardless of origin, that spawn in natural areas (not hatcheries) and descendents of such fish.

3This material is included to aid interpretation of the report. It should not be used as a definitive description of current management of this stock.
about 35 percent of potential adults to spawn.” We have adopted the term “spawner-reduction rate” as being less open to possible misunderstanding.

In applying the management strategy stated above, the following management policies are presently in effect:

- The spawner floor is 35,000 fish.
- The maximum spawner-reduction rate is 67%.
- The minimum spawner-reduction rate is zero (i.e., no *de minimus* fishery is part of current management).
- The proportion of the total catch allocated to the tribes is 50%.
- The proportion of the nontribal catch allocated to the river-recreational fishery is 15%.

Certain other mathematical constants used in the management of this stock, and therefore used in the simulations, might also be considered part of current management policy. Examples are natural and incidental mortality rates, sizes at age, and rates of maturity at age. The values used for such quantities are described as part of the simulation model in §2.4.

1.2 Detailed Objectives

As stated above, this study was undertaken to satisfy the Council's assignment. Thus, its specific objectives were to answer questions asked by the Council, either explicitly or implicitly, in their request and in subsequent discussions. Here, we set forth those questions as they are understood by the authors of this report. The questions fall into two sets.

The first set of questions addresses the specific level of the spawner floor. For example, what is the relationship between the spawner floor and the yield available from the fishery? Can the present floor result in achieving the maximum sustainable yield (MSY), or approximately MSY, from the stock? Would other values for the floor result in higher yields? What would be the tradeoffs, if any, associated with those higher yields? Is there any indication that the present spawner floor encourages overfishing? To answer such questions, computer simulations were undertaken with a range of values for the spawner floor.
The second set of questions addresses the closure of the fishery when the spawner floor cannot be met, or can be met only by an extremely limited fishing season. For example, what are the consequences to the stock of closing the fishery? What would be the consequences of allowing instead a nonzero minimum spawner-reduction rate (sometimes termed a \textit{de minimus} fishery), when the spawning-stock size is estimated below or near the spawner floor? How would implementation of a minimum SRR affect the long-term yield from the fishery? What would be the tradeoffs? What value of minimum SRR might be appropriate? To answer such questions, additional computer simulations were undertaken with a range of values for the minimum spawner-reduction rate.

2 Simulation Methods

In answering the Council’s questions, the authors have attempted to use the best scientific methodology available, subject to limitations of time, data, and other resources. A dedicated simulation model was programmed in Fortran and run under numerous scenarios. Results were analyzed both graphically and statistically. The main limitation encountered was the relative scarcity of data on the stock. In particular, the stock-recruitment series is relatively short, and there are apparently not sufficient data to serve as the basis of a simulation model that includes substock structure.

The basic components of the simulation model (Figure 1) include estimation of abundance from the true May 1 stock size, setting of annual management regimes, catch and incidental removals due to fishing, maturity, reduction in numbers by natural mortality, and replenishment due to spawning and recruitment. Implicitly, but not explicitly, included in Figure 1 are such processes as growth and vulnerability to the gear. However, such processes are discussed below, together with those explicitly identified.

The diagram describing the simulation model (Figure 1) has a labeled starting point but no stopping point. A simulation model such as this can be exercised for any number of years: the tradeoffs are increased execution time vs. increased information. Because results are presented in statistical form—as measures of central tendency, dispersion, or proportion, rather than year by year—the increase in information is quite limited after a certain simulation.
length. In this study, all simulations were run for 3,000 years. This long duration was not intended to represent a realistic management horizon, but rather to allow statistics on each management strategy to be computed precisely.

The remaining parts of this section describe the major components of the simulation model, roughly in the order shown in Figure 1. The exception is the recruitment component, which because of its importance is treated separately in §3. Later sections of this report describe the specific simulations made, the analytical methods used, and the results.
2.1 May 1 Population Size

Each year’s management of the stock begins by considering the population on May 1, and so does the simulation model (Figure 1). The simulated population is self-regenerating, so that each year’s May 1 population size is determined by the previous population trajectory and the recruitment model. Those (immature) fish that remain in the ocean after the prior year’s fishery are reduced by natural mortality, advanced in age by one year, and then form part of the May 1 population. The other part of that population is formed by new recruits, whose number is determined by application of the recruitment model to the spawning stock three years prior. Although this is not apparent from Figure 1, the recruitment model itself contains a stochastic (random) component, so that the same sized spawning stock can lead to different recruitments in different years.

In the first few years of simulation, before the model itself supplies May 1 population numbers, they must be supplied a priori. To meet this need, simulations were started at the following population sizes, which are on the order of population sizes recently observed: 70,000 fish of age 3; 20,000 fish of age 4; and 1,000 fish of age 5. To remove any sensitivity of the simulation results to these starting values, the first 300 years’ results from each simulation were discarded before analysis. The long duration of each simulation also served to remove the effects of starting values. Finally, sensitivity runs were conducted with much lower and much higher starting values, and no appreciable differences in results were noted (Figure 2).

2.2 Abundance Estimation

The next process in the simulation model (Figure 1) is abundance estimation. In the actual fishery, preseason abundance is estimated by statistical methods based on cohort analysis and linear regression analysis. [The procedure is briefly reviewed by Prager and Mohr (1998).] An important fact is that the preseason estimates of abundance, like abundance estimates of any fish stock, are not perfect. The dichotomy between management, which is guided by imperfect estimates of stock size, and fishing mortality, which is applied to the actual stock, can lead to stock dynamics quite different from those expected under perfect knowledge. This situation is well suited to study by simulation modeling.
Figure 2: First 30 years of age-3 abundances from simulations otherwise identical but with high, normal, or low starting population sizes. Results for ages 4 and 5 are similar.

To explore the consequences of error in abundance estimation, it was assumed that the estimates are median unbiased, but subject to lognormal random error, and thus imprecise. Because little is known about the level of imprecision in the actual estimates, four levels of imprecision were used in the simulations: coefficients of variation (CVs) of zero (no imprecision), 25%, 50%, and 75%. The means by which this imprecision was brought into the simulation are described in the following section, together with related aspects of the simulated management and fishing.

### 2.3 Setting the Annual Management Regime and Fishing

These two processes, although separately represented in Figure 1, are treated together here because they are closely related, both conceptually and in the simulator. The processes are tied together through the Klamath Harvest Rate Model (KHRM), a management model that was devised to implement the suggestions of the KRTAT (1986) report and that is presently used for annual management of this stock (Prager and Mohr 1998). The KHRM (Figure 3), a box model that follows the stock through an entire fishing season, is used to define annual
Figure 3: Logic flow of the Klamath Harvest Rate Model (KHRM), used for management of Klamath River fall chinook. The KHRM is incorporated, in slightly modified form, into the simulator used here. [Source: Prager and Mohr (1998).]
management regimes⁴ that meet the management strategies and policies described earlier. As a byproduct of setting the annual management regime, the KHRM also helps determine what type of season will occur, among four alternatives: (1) a closed season; (2) a season limited by the spawner floor; (3) a season limited by the maximum spawner-reduction rate; or (4) if a minimum spawner-reduction rate is in effect, a season subject to that rate.

The regime-setting and harvesting components of the KHRM were used in this study to mimic the actual management procedures used, but were modified to introduce error into the simulated estimation of May 1 abundance (Figure 1). To each year’s simulated “true” May 1 stock size⁵, random error was added to create an “observed” stock size. Using this “observed” stock size, the management regime was set. This management regime was then applied to the “true” stock size, resulting in catch, incidental mortality, spawning escapement, and some surviving fish remaining in the ocean (Figure 1).

2.4 Other Parameters Related to Harvesting

Simulation of the stock required defining values for parameters representing several other biological and management processes. This section describes those that are intrinsically related to harvesting of the fish, and are thus identical to parameters of the KHRM. Although not all shown in Figure 1, all such parameters are described here, at least briefly. The values used are those used in recent applications of the KHRM and other management models for this stock. More rigorous definitions of these quantities are given by Prager and Mohr (1998).

Vulnerability to the gear at age is defined separately for ocean and river fisheries. For the ocean fisheries, proportions used were 0.88 for age-3 fish, 1.0 for age-4 and age-5 fish. In modeling the river fisheries, the proportions used were 0.59 for age-3 fish, 1.0 for age-4 and age-5 fish.

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⁴An annual management regime for this stock includes target values for the ocean contact rate, tribal catch, and nontribal river catch. The ocean contact rate may be translated by further modeling into a time-and-area structure for the ocean season.

⁵“True” and “observed” are placed in quotation marks here to emphasize that they refer to the simulated, not the actual, stock.
The *proportion legal* at age in the ocean fishery was set at 0.8 for age–3 fish and 1.0 for age–4 and age–5 fish. These values reflect the current 26-inch size limit.

When fish of less than legal size are hooked in the ocean fishery and released, a proportion die: this is termed *shaker mortality*. The value used for shaker mortality in this study was 0.25, the same value used by the PFMC in its work. Shaker mortality applies to age–3 fish only; it is assumed that, because age–4 and age–5 fish are all of legal size, they do not experience shaker mortality.

The *proportion mature* at age is used in modeling to apportion fish between those that remain in the ocean and those that take part in the fall spawning migration (river run). In this study, the fractions used were 0.378 for age–3 fish, 0.935 for age–4 fish, and 1.0 for age–5 fish.

*Dropoff mortality* occurs when a fish is hooked, then lost from the hook unintentionally, and it dies as a result of the encounter. Following the practice of the Pacific Fishery management Council, we calculated dropoff mortality as 5% of the number of fish contacted in the ocean, 8% of fish contacted by tribal fisheries, and 2% of fish calculated by river–recreational fisheries. [For computations of the number of fish contacted, see Prager and Mohr (1998).]

The *proportion spawning in natural areas* is a component of management models such as the KHRM. This quantity is required because although the “natural” stock is managed separately from the stock of hatchery-produced fish, when quotas are set, they are for both “natural” and hatchery fish. For lack of more detailed data, the proportion is set to an age– and year–independent constant. In the present simulations, the proportion was set to unity; i.e., the modeled stock was the “natural” stock only. This was appropriate because the recruitment model was based on naturally spawning fish, as are the management policies.

### 2.5 Natural Mortality

Natural mortality was applied to overwintering fish as a simple proportional loss of 20% per year, applied to the transitions from age 3 to 4 and age 4 to 5. As all age–5 fish are mature, and the species is semelparous, no transition to age 6 occurs. At ages younger than 3, natural mortality is subsumed into the recruitment model.
Table 1: Data used to fit stock–recruitment model of Klamath River fall chinook. Spawners and recruitment are measured in thousands of fish. Relative weights used to compute weighted spawning stock are 1.000, 1.548, and 1.992 for age 3, 4, and 5 fish, respectively.

<table>
<thead>
<tr>
<th>Brood year</th>
<th>Spawners $S$</th>
<th>Total Recruitment $R$</th>
<th>log $R/S$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>age 3</td>
<td>age 4</td>
<td>age 5</td>
</tr>
<tr>
<td>1979</td>
<td>11.74</td>
<td>16.68</td>
<td>2.22</td>
</tr>
<tr>
<td>1980</td>
<td>9.10</td>
<td>9.77</td>
<td>2.61</td>
</tr>
<tr>
<td>1981</td>
<td>27.05</td>
<td>6.05</td>
<td>0.76</td>
</tr>
<tr>
<td>1982</td>
<td>14.42</td>
<td>16.27</td>
<td>1.26</td>
</tr>
<tr>
<td>1983</td>
<td>19.19</td>
<td>11.10</td>
<td>0.49</td>
</tr>
<tr>
<td>1984</td>
<td>7.39</td>
<td>8.31</td>
<td>0.37</td>
</tr>
<tr>
<td>1985</td>
<td>13.13</td>
<td>10.23</td>
<td>2.32</td>
</tr>
<tr>
<td>1986</td>
<td>94.69</td>
<td>17.35</td>
<td>1.32</td>
</tr>
<tr>
<td>1987</td>
<td>43.64</td>
<td>54.78</td>
<td>3.30</td>
</tr>
<tr>
<td>1988</td>
<td>41.93</td>
<td>35.85</td>
<td>1.61</td>
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<tr>
<td>1989</td>
<td>17.79</td>
<td>24.56</td>
<td>1.52</td>
</tr>
<tr>
<td>1990</td>
<td>5.05</td>
<td>9.98</td>
<td>0.57</td>
</tr>
<tr>
<td>1991</td>
<td>4.14</td>
<td>7.28</td>
<td>0.23</td>
</tr>
<tr>
<td>1992</td>
<td>3.07</td>
<td>8.64</td>
<td>0.32</td>
</tr>
<tr>
<td>1993</td>
<td>18.66</td>
<td>3.03</td>
<td>0.17</td>
</tr>
</tbody>
</table>

The natural mortality rate of 20% was chosen, because it is currently used in management of the stock. The report introducing the Harvest Rate Management strategy (KRTAT 1986) assumed that the natural mortality rate was 25% annually. Both in KRTAT (1986) and in this study, natural mortality was assumed to occur between fishing seasons, which corresponds to a Type I fishery in the terminology of Ricker (1975).

3 Stock–Recruitment Submodel

A recruitment submodel was used to provide a self-regenerating simulated population. This submodel was based on a fitted Ricker recruitment model with stochastic component. Data and modeling techniques used are described in the following sections.

3.1 Data

Stock and recruitment estimates (Table 1) were originally provided by Alan Barracco [Califor-
nia Department of Fish and Game (CDFG), Rancho Cordova, California, personal communica-
[79x687]tion], and were updated by the authors from reports of the Pacific Fishery Management Council
and the KRTAT. Recruitment estimates are derived annually by CDFG from cohort reconstruc-
tions and define recruitment as the number of 3-year-old progeny of natural spawners found
in the ocean on May 1. The number of spawners of ages 3, 4 and 5 in natural areas (i.e., not
in hatcheries) is estimated annually by subtracting the estimated hatchery returns from the
estimated total escapement.

3.2 Model Form

Development of this submodel began with the stock-recruitment function of Ricker (1975),

\[ R = \alpha S \exp(-\beta S), \]

where \( R \) is recruitment, \( S \) is the spawning-stock size, and \( \alpha \) and \( \beta \) are parameters of the
model. One interpretation of this model is that \( \alpha \) represents individual fecundity, and \( \beta \),
which reduces recruitment at larger spawning-stock sizes, represents cannibalism or other
negative effects on the young fish by their parents. This functional form has been used widely
in fishery science, particularly in analyses of salmonid populations.

Dividing both sides of equation 1 by \( S \), a model of spawning success, defined as the ratio
\( R/S \), is obtained:

\[ R/S = \alpha \exp(-\beta S). \]

Equation 2 is often referred to as a “recruits per spawner” model, as it expresses directly the
recruitment relative to spawning-stock size, as a function of that same spawning-stock size.

Taking (natural) logarithms of equation 2 results in a model of log spawning success:

\[ \log(R/S) = \alpha' - \beta S, \]

where \( \alpha' = \log(\alpha) \). This linear transformation is the usual form in which the Ricker model
is fit to data. In the present study, equation 3 was fit by ordinary-least-squares regression,
assuming normal additive errors, to obtain the recruitment submodel for this study. The error assumption is equivalent to that of lognormal multiplicative errors in equation 1. The use of lognormal error in this context is supported by studies including that of Peterman (1981) and is recommended by standard texts in fishery science [e.g., Hilborn and Walters (1992)].

A remaining question is the correct unit of measurement for spawning–stock size. The quantity $S$ in equations 1 through 3 can be in numbers of fish ($S_n$) or in biomass ($S_w$). For this stock, these quantities are defined as $S_n = \sum_{a=3}^{5} N_a$ and $S_w = \sum_{a=3}^{5} w_a N_a$, where $w_a$ are relative weights at age. Indeed, different units are at times used for each side of (2) and (3). On the left-hand side, $S_w$ is likely to be used, as fecundity is often roughly proportional to body weight; on the right-hand side, $S_n$ is often used to quantify cannibalism or similar effects. For this study, we fit models with all four combinations of $S_n$ and $S_w$, using $w_a = \{1.0, 1.548, 1.992\}$ for $a = \{3, 4, 5\}$ respectively. (These values were calculated from data on observed weights at age.) The results were not markedly different. Nonetheless, as we observed the best fit using $S_w$ on both sides, that model was used for the simulations.

In incorporating the recruitment function into the simulation, normally distributed random was error added to the log spawning success obtained from equation 3. The mean of the error was zero, and the standard deviation was the root mean-squared error from the regression. To constrain the stochasticity to a more realistic range of values, random numbers of more than $\pm 2$ standard deviations were discarded.

### 3.3 Estimates of Recruitment Parameters

The fitted spawning–success submodel was

$$\log(R/S_w) = 2.106 - 0.02329 S_w,$$

with root-mean-squared error of 0.997. The units of $R$ are thousands of fish, and of $S_w$, thousands of fish, weighted as explained in §3.2. The fitted model of log spawning success, plotted with the observed data in Figure 4a, exhibits moderately good fit, with an adjusted $R^2$ statistic of 43%. The fit was highly statistically significant ($F = 11.5, P < 0.005$). The equivalent equation in terms of stock-size and recruitment, pictured in Figure 4b, is
Figure 4: (a) Fitted model of logarithm of spawning success of Klamath fall chinook, with data and 90% confidence interval on estimated individual values. (b) Corresponding Ricker recruitment curve.

\[ R = 8.218 S_w \exp(-0.02329 S_w) \]  \hspace{1cm} (5)

with the units of \( R \) and \( S_w \) as in equation 4. It is interesting to note that the KRTAT (1986) report used high- and low-productivity Ricker curves to bracket the productivity of this stock, and that the coefficient \( \hat{\beta} = 0.0233 \) in equation 5 is quite similar to that of the low-productivity
estimate in that report ($\hat{\beta} = 0.0244$ after adjustment from fish to thousands of fish). In addition, our estimate of $\hat{\alpha} = 8.2$ is not far from the earlier report’s assumption of $\alpha = 10.0$. Because of this close correspondence, our Figure 4b is remarkably similar to the low-productivity curve shown in Figure 5, Curve B, of KRTAT (1986).

### 3.4 Environmental Effects on Recruitment

In the previous draft report (KRTAT 1996), an environmental covariate was found to provide a sizable variance reduction when included in equation 3. The use of that covariate was explored in the present study, but it was not found statistically significant, and it provided very little variance reduction. It is not uncommon in fisheries research for an apparently strong environmental relationship to fail with additional data. This failure could reflect one of several underlying situations:

- The relationship was spurious, and the addition of data has made that clear, or

- The relationship is real, but the stochasticity of the environment or in fish recruitment is large enough to mask the relationship at present (Goodyear and Christensen 1984), or

- The stock-recruitment relationship is not stationary, so that detection of an environmental covariate is exceedingly difficult

Unfortunately, there is no way to distinguish these possibilities other than waiting for more data. Even more data may not make the matter clear if nonstationarity is involved. Based on the exploratory results indicating no significant environmental effect, a recruitment model without environmental effects was used.

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6The previous year’s annual rainfall anomaly at Eureka, which was misidentified in that report as the rainfall anomaly in the year of spawning.
3.5 MSY and Recruitment Models

Under the Ricker model and given certain assumptions, equilibrium MSY can be estimated from equation 1 by defining the equilibrium yield $Y_e$ attainable from a spawning-stock size $S$ to be the excess of recruitment over parent spawning-stock size:

$$Y_e = R - S.$$  \hspace{1cm} (6)

The three main assumptions necessary for equation 6 to be valid are—

- The stock is semelparous.
- All spawning is by a single age class.
- The age of spawning and age of recruitment are the same.

Under those assumptions, MSY is by definition the highest value of $Y_e$ attainable from a particular stock-recruitment relationship. In the Ricker formulation, a closed-form solution for MSY given $\alpha$ and $\beta$ does not exist. However, the maximum of $Y_e$ can be found by differentiating equation 6 with respect to $S$ and locating the point where the derivative is zero, which is the point $S = S_{\text{MSY}}$. Substitution into equation 1 or equation 2 will give the corresponding value of MSY. This was done in the earlier draft report (KRTAT 1996), in which the simulations met the assumptions listed above.

It is inconvenient, but true, that MSY cannot be so simply defined when more than one age participates in spawning. In this study, simulations included spawning at ages 3, 4, and 5, rather than just at age 3 as in KRTAT (1996). For that reason, no attempt was made to provide a formal estimate of MSY. Instead, stochastic simulations were used to estimate long-term average yield from the fishery under a variety of management policies.

4 Simulations Run — Statistics Recorded

To address the Council’s questions, a 3,000-year simulation was made corresponding to each combination of the following values:
Figure 5: Typical frequency distribution of simulated total annual catches (under present management policy), assuming measurement error of 15%. Distribution is approximately lognormal.

- Spawner floors from 15,000 to 50,000 fish, at intervals of 5,000 fish
- Minimum spawner-reduction rates from zero to 20%, at intervals of 5%
- Estimation imprecision of the starting (May 1) population size from a CV of zero to a CV of 75%, at intervals of 25%

In all cases, the maximum spawner-reduction rate was set at 67% (the present management policy). For each combination of values examined, the following summary statistics were computed:

- Median and nonparametric coefficient of variation (NPCV)\(^7\) of annual catch in each fishery segment (ocean, tribal, river-recreational)

\(^7\)The NPCV is an analog of the parametric coefficient of variation (CV). The CV and the nonparametric CV are both ratios in which the numerator is the central range that contains 38.3% of the frequency distribution and the denominator is a measure of central tendency. In the parametric CV, the range is one standard deviation; the measure of central tendency is the mean. In the nonparametric CV, the range is the difference between the 30.85\(^{th}\) percentile and 69.15\(^{th}\) percentile, and the measure of central tendency is the median.
• Median and NPCV of annual “natural” escapement

• Number of years with each fishery outcome: closed, limited by minimum SRR, limited by spawner floor, or limited by maximum SRR

The median was used in this study to characterize results because, when a quantity has a skewed distribution, the mean is a misleading measure of central tendency (Sokal and Rohlf 1981). A few high values can influence the mean dramatically, so that it is not a good estimate of the most common value. Furthermore, those few high values are likely to change in repeated simulations, increasing the standard error of the mean. In our simulation, the distributions of simulated total annual catch (Figure 5) and related quantities were typically quite skewed, most likely because the recruitment function was lognormal. Thus, median values were chosen for presentation of results.

In addition to the summary statistics presented in the next section, detailed results were collected from a subset of simulations. Those results were examined both graphically and numerically, as a quality-assurance measure on the simulation program.

5 Results

This section contains a summary of the simulation results with only slight interpretation. The implications of the results to the Council’s questions are given in section §6.3.

A few comments apply to all results equally. Because all results come from simulations, the word “simulated” will not be repeated constantly. When comments are made about the actual fishery, that will be made clear. Results are presented in numbers (or thousands) of fish. The reader is urged to place more weight on the relative results of different simulation scenarios than the absolute result of any one scenario or group of scenarios. This recommendation is made because experience has shown that simulations such as these are more likely to compare alternatives correctly than they are to give realistic results in absolute numbers.
Figure 6: Simulated median annual catch of Klamath-River fall chinook salmon under various management policies. Precision of May 1 (preseason) abundance estimation given above each panel. Symbols indicate level of minimum spawner-reduction rate (see text).

5.1 Annual Catch

The median annual catch obtained under management was relatively insensitive to the value of the spawner floor. The median catch increased slightly with increasing spawner floor up to a spawner floor of about 30,000 or 35,000; it then decreased markedly with further increases in the spawner floor (Figure 6). The median annual catch also was quite insensitive to the value of the minimum spawner-reduction rate, with little or no pattern to the results, suggesting that any differences are largely due to chance (Figure 6).

The strongest determinant of the median annual catch, among the variables simulated,
Figure 7: Nonparametric coefficient of variation (NPCV; footnote, p. 18) of simulated annual catch of Klamath–River fall chinook salmon under various management policies. Precision of preseason abundance estimation above each panel. Symbols indicate level of minimum spawner–reduction rate (see text).

was the estimation precision of the May 1 stock size. Compared to perfect knowledge (Figure 6a), catch was reduced by about 20% by a CV of 50%, and reduced by about 25% to 30% by a CV of 75%. It seems reasonable to believe that measurement precision in the actual fishery is near one of these latter figures.

5.2 Year-to-Year Variation in Catch

It has been recognized, e.g., by Clark (1985) and by KRTAT (1986), that a management policy maximizing long-term yield may result in large annual fluctuations in catch, which would be
undesirable in most fisheries. Thus, in simulating management policies, we look not just at average catch, but its variability. The year-to-year variation in catch in this study, as measured by the NPCV, varied moderately with the spawner floor (Figure 7). The NPCV of annual catch was lowest (about 80%) at the lowest spawner floors, probably because in those cases the fishery was least often limited by the floor. The NPCV of annual catch did not increase markedly until the spawner floor reached about 30,000 to 35,000 fish. Above those values, it increased more sharply as the spawner floor increased.

The NPCV of annual catch was quite insensitive to the minimum spawner-reduction rate. There was little change in year-to-year variability with changes in the minimum spawner-reduction rate, and what change there was exhibited little or no discernible pattern.

The estimation precision of May 1 stock size was a strong determinant of the variability in annual catch. At the present spawner floor of 35,000 fish, the NPCV of annual catch increased from about 100% under perfect estimation of May 1 stock size to about 140% under estimation of May 1 stock size with 75% CV. A similar increase occurred under other spawner floors as well (Figure 7).

5.3 Frequency of Fishery Closures

An important aspect of any management scheme is the possibility of fishery closure due to low stock size. Under the present management policy (i.e., minimum spawner-reduction rate of zero), closure can take place at low stock sizes, because maintenance of the spawner floor is an absolute requirement. However, if the minimum spawner-reduction rate were to be set above zero, by definition the fishery would never be closed. (One can envision that in reality rare instances of extremely low recruitment might still force closure, but it would not be expected routinely.)

In the simulations, the frequency of fishery closure under present policy (of a minimum spawner-reduction rate of zero) varied systematically with both the spawner floor and the precision of estimation of May 1 stock size (Figure 8). As one would expect, the frequency of closure was an increasing function of the spawner floor: with no estimation imprecision (the most optimistic case), the frequency of closure increased more or less linearly from about
2.5% to about 18% as the spawner floor increased from 15,000 fish to 50,000 fish. This pattern occurs because stock sizes that can meet higher spawner floors are less common than stock sizes that can meet lower floors. At the present spawner floor of 35,000 fish, closure occurred about 8% of the time under perfect estimation of May 1 stock size.

As the precision of estimating May 1 stock size worsened, the expected proportion of closed years increased. At a floor of 35,000 fish, but with an estimation CV of 75%, the frequency of closure increased was about twice that observed under an estimation CV of zero. The increase was proportionally less at lower values of the spawner floor and proportionally greater at higher values.

5.4 Spawning Escapement Achieved

Another important aspect of a management scheme is the level and consistency of spawning escapement expected under it. Under the present maximum spawner-reduction rate of 67%, the median annual escapement varied systematically with both the spawner floor and the level of imprecision in May 1 stock-size estimates (Figure 9). The median escapement achieved,
Figure 9: Median simulated annual “natural” spawning escapement of Klamath–River fall chinook as a function of management policy. Precision of preseason abundance estimation given above each panel. Symbols indicate minimum spawner-reduction rate (see text).

even at low stock sizes, was quite insensitive to the value of the minimum spawner-reduction rate, at least in the range of values considered. The escapement was sensitive, however, to the level of imprecision in estimating May 1 stock size, both at low and high values of the spawner floor (Figure 9).

The abrupt change in slope observed in Figure 9a prompted a sensitivity exercise to verify that this was not due to a implementation error. In Figure 10, both the median and mean of annual escapement are plotted agains the value of the spawner floor, for various values of the maximum spawner-reduction rate. In this sensitivity exercise, the estimation imprecision of may 1 stock size and the minimum spawner-reduction rate were both assumed to be zero.
Figure 10: Sensitivity analysis of (a) median and (b) mean simulated annual “natural” spawning escapement of Klamath-River fall chinook salmon. “SRR” is spawner-reduction rate. Assumes perfect stock-size estimation, and is thus over-optimistic; see Fig. 9 for more realistic results.

The median values (Figure 10a) show similar patterns, with the position of the abrupt change in slope varying by maximum spawner–reduction rate. The mean values (Figure 10b) also vary by maximum spawner–reduction rate, as expected, but more smoothly. This seems to confirm that the pattern seen in Figure 9a is correct.

5.5 Tribal Share of Catch

With lognormal measurement error, as simulated here, a pertinent question is whether quota management, as used in the river fisheries, will behave differently from contact-rate management (analogous to management by fishing mortality rate), as used in the ocean fisheries. This question was examined by computing the median proportion of the catch taken by the tribes. Because the river–recreational take is proportional to that of the tribes, results would be identical, except for scaling. The results (Figure 11) suggest that the target sharing agreement is indeed achieved on average, and that its being achieved is quite insensitive to the value of the spawner floor or to the amount of measurement imprecision present. An unexpected result was that the presence of measurement error increased the tribal share of catch slightly; however the increase was extremely small.
Figure 11: Median proportion of simulated annual catch of Klamath–River fall chinook salmon taken by the Yurok and Hoopa Valley tribes. (Target value is 50%.) Estimation imprecision in May 1 abundance is shown above panels. Symbols indicate level of minimum spawner-reduction rate (see text).

6 Discussion

6.1 Historical Comments on the Spawner Floor

A floor of 35,000 naturally spawning adult fall chinook was adopted in 1986 as part of the Harvest Rate Management strategy for the Klamath River. As stated in the report issued at that time (KRTAT 1986), the spawner floor of 35,000 was “intended to protect the production potential of the resource in the event of several consecutive years of adverse environmental conditions.” It replaced a goal of 115,000 adult spawners (of which 17,500 were to be natural spawners), which was believed too high for habitat conditions. The goal of 115,000...
had not been met in any year since its adoption in 1978. The report remarked that “a minimum spawning escapement of 35,000 natural spawners would be higher than any natural escapement since 1978, [escapement] levels that have been widely regarded as too low for the basin.” It also stated, based on the analysis of available data, that Klamath chinook were being overfished and that a reduction in harvest rate would increase the long-term yield from the resource (KRTAT 1986, p. 7).

Other spawning goals or estimates of spawning capacity have been made for this basin. The Trinity River Restoration Program has a goal of 62,000 naturally spawning fall chinook (J. Barnes, pers. comm.). No goal has been established for the larger Klamath River portion of the basin, but in an appendix to KRTAT (1986), an estimate was made that “low and high estimates of the total numbers of adult fall chinook spawners needed to achieve optimum utilization of currently available habitat [in the Klamath River system below Iron Gate Dam are] 64,610 and 129,850 fish, respectively” (Hubbell and Boydstun 1985).

6.2 Modeling and its Assumptions

The use of computer simulation offers opportunities, while it also raises certain pitfalls. In its favor are two main points: first, the ability to explore different courses of action without experimenting on real, and possibly quite valuable, systems; and second, the ability to use models that, while simple compared to reality, are nonetheless not amenable to analytical solution. Both of those qualities were valuable in the present study. The less favorable aspect of simulation modeling stems from its being in all cases a highly simplified representation of reality, in which important factors may have been omitted through the need to simplify. This most often occurs when detail is omitted for lack of data. Such simplifying assumptions, it is clear, are not unique to simulation modeling, but are also part of modeling in general, and perhaps of all forms of scientific endeavor.

This study was no exception to the general case, as the available data were quite limited, both in precision and in extent. The study relied upon major simplifications, including assumptions about the biology of the species and its stock structure (e.g., lack of substocks, no influence of hatchery fish). For these reasons, extrapolation of the results presented to the
actual stock should be made with full consideration of the consequences of possible omission of important processes. Some of the major assumptions of this modeling study were these:

- The Ricker model was assumed to be a reasonable model of spawning success, and its parameters were assumed to be constant through time.
- The spawning and recruitment estimates used were assumed representative of a wild stock that can be considered independent of hatchery influences.
- Any spawning by fish younger than age 3 was assumed to be insignificant.
- It was assumed that fish from the Trinity and Klamath systems could be lumped into a single analysis without losing important features of their dynamics.
- The management regime is followed without exception.

6.2.1 Assumptions about Recruitment

Estimating a stock’s long-term yield and other long-term responses has always been an imprecise science, in large part because it always depends on a model of recruitment, which in reality is a highly stochastic process. (Gulland 1983) summed up the situation this way:

> It should be stressed to begin with that any fish stock is part of a complex natural system. It is therefore very difficult to state with any certainty what the effects of any action will be. Some of the problems … [include] the effects of changes in adult stock abundance on the average level of subsequent recruitment. The scientist, and those he is advising, must therefore accept the fact that a comprehensive assessment of the long-term effects of any pattern of fishing is difficult, and is likely to be subject to inaccuracies.

In considering recruitment, the main assumptions of this study were that the model is a reasonable representation of the factors influencing spawning success and that the model’s parameters are constant. The main source of variability in the model was derived from the variability in the data set, which was assumed to be random. However, one could hypothesize nonrandom sources of error, as well. Examples of nonrandom effects would include
rates of incidental mortality that varied with the relative abundance of year-classes; rates of spawning success for natural spawners that depended on the quantity, health, or timing of hatchery releases; or a variable proportion of fish that spawn naturally, depending on the relative abundance of hatchery fish in the mixed population. Any such effects that have varied systematically, rather than in a random and independent manner from year to year, would tend to increase the level of uncertainty in the results presented here. They also might bias the simulations, as the influence of such nonrandom quantities cannot be presumed to have an average of zero in future years. This is equivalent to the model’s parameters changing through time, and would cause the results of management actions on the real stock to differ from those observed in the simulations.

In discussing recruitment, it should also be noted that the “natural” spawning escape-ment has included many hatchery fish in those years of high abundance when the hatchery closed its gates during the spawning season, thus forcing some fish of hatchery origin to spawn in natural areas. This occurrence would complicate the stock-recruit relationship by inflating estimates of “natural” spawning-stock size. The ultimate statistical effects would depend on whether the spawners of hatchery origin were similar in spawning success to those of natural origin, or not. If not, stock-recruitment function based on existing data would not be entirely correct under present hatchery management practices, in which hatchery managers prevent hatchery fish from spawning in natural areas.

6.2.2 Assumptions about Natural and Hatchery Stocks

Can the “natural” stock be modeled as unaffected by hatchery dynamics? This study could not address that question, but interpretation of the results depends upon it. As mentioned in the preceding paragraph, an influx of hatchery strays could affect the apparent productivity of the stock and could thus bias estimates of the stock-recruitment relationship. This aspect of the problem appears intractable without changes in hatchery operations (e.g., marking all, or a constant fraction of, hatchery fish) or large increases in sampling effort. Even those might not answer the question, as the concept of a “natural” stock itself is changed by large and prolonged supplementation by hatchery fish. Finally, the use of a constant factor to divide the
observed stock into “natural” and hatchery components is a probably unrealistic feature of present management models which has by necessity been incorporated into our simulations.

6.2.3 Assumptions about Stock Structure

Lumping together all stocks in the Klamath–Trinity basin was done for lack of data on substocks, even on that large scale. As is always the case with a stock composed of multiple subpopulations, the relative strength of the subpopulations varies through time, and there is an element of risk specific to using stock-wide management goals. Under such goals, it may be possible to seriously deplete, or even extirpate, certain local subpopulations and thereby reduce the long-term productive potential of the overall stock. This would seem to call for caution in implementing a positive minimum spawner-reduction rate (*de minimus* fishery), if one is indeed implemented.

6.3 Conclusions

To the degree the simulations presented above are representative of the actual stock, it is possible to answer, at least guardedly, the questions asked by the Council.

6.3.1 Present Value of Spawner Floor

Several aspects of the results shed light on the appropriateness of the current spawner floor of 35,000 fish. The maximum of the spawner-recruit curve occurs at about 43,000 fish, weighted by age (Figure 4b). If a strong majority of the spawning stock is of age 3, as would be expected under exploitation, this is equivalent to only slightly fewer than 43,000 fish, unweighted. This figure in turn can be related to the spawner floor by noting that, with realistic values of measurement uncertainty, the simulated natural escapement attained was somewhat less than the spawner floor in effect (Figures 9c and 9d). These observations suggest that reducing the spawner floor below 35,000 would move the stock on average to a portion of the recruitment curve (Figure 4b) where strong recruitments are less likely to occur.

In terms of yield available from the fishery under the current management strategy, the current value of the spawner floor seems to be an near-optimal choice. The median yield
obtained in the simulated fishery was relatively insensitive to the value of the spawner floor, but declined somewhat above about 30,000 to 35,000 fish (Figure 6). Thus, a higher spawner floor would be expected to reduce the median yield attained in the actual fishery, while a lower spawner floor would provide less of a safety margin against poor recruitment but provide very little, if any, gain in yield.

In terms of fishery stability, the current floor seems to be a middle-of-the-road policy. Reducing the floor in the simulated fishery resulted in a small to moderate reduction in the variability of catch from year to year, and increasing the floor increased that variability (Figure 7). The same was true of the proportion of years closed (Figure 8); however, setting the minimum spawner-reduction rate higher than zero (i.e., establishing a de minimus fishery) could eliminate closures entirely, and might be a more constructive way of increasing stability than reducing the spawner floor itself.

The results of this study suggest that the present spawner floor of 35,000 is a prudent one. Decreasing it seems unlikely to bring substantial increases in yield. Sissenwine et al. (1988) found that persistence of a stock (at exploitable levels) under strong environmental variation does require higher escapements than simple models may predict. The KRTAT (1986) report did explore recovery after a series of three poor years, and found that such recovery was quicker and more complete, and led to higher yields, when a spawner floor of 35,000 fish was in place. The finding all support retention of the current escapement floor.

6.3.2 Use of Minimum Spawner-Reduction Rate

Our results tend to support the use of a minimum-spawner reduction rate greater than zero as a tool to eliminate closures. Such a policy had very little, if any, discernable effect on average catch (Figure 6), year-to-year variability of catch (Figure 7), or average natural escapement. At the same time, if applied to the actual fishery, it has the potential to eliminate a significant number of fishery closures.

The use of a positive minimum spawner-reduction rate to provide a small fishery in place of closures also seems to be supported by the simulation results. If such a policy should be adopted, it is suggested that a small value, perhaps 10% or 15%, be adopted at first. Although
the present results showed no adverse effects of a rate of up to 20%, this is precisely the sort of measure that could potentially damage the substock structure of the species, leading to reductions in long-term yield.

6.3.3 Effects of Estimation Error

It is widely accepted that fishery management must operate in an uncertain environment, and that lack of perfect knowledge can change the expected effects of management strategies and policies (Sissenwine et al. 1988). In this study, the inclusion of uncertainty was incorporated into the recruitment function and also as uncertainty about the true size of the preseason (May 1) stock of fish. This latter uncertainty was simulated here in a rather straightforward way as lognormal errors in the May 1 stock-size estimates. (We will call this measurement imprecision.) Although simple, this seems a reasonably realistic method of simulation, given the lack of a comprehensive study on the subject. The simulation results illustrate the potential negative effects of measurement imprecision and, conversely, the potential benefits to be realized from improved sampling and estimation.

Estimation imprecision reduced realized catches from the simulated stock significantly (Figure 6). Relatively small levels of imprecision, represented by a 25% CV, had almost no effect. However, as the imprecision increased to 50% and 75%, the realized catches decreased up to 31%. The year-to-year variability in catches also increased sharply under estimation imprecision (Figure 7).

In the simulations with the minimum spawner-reduction rate set to zero, the frequency of closures also increased sharply as measurement imprecision increased. This occurred at all values of the spawner floor, and at the present floor could lead, under the simulated conditions, to a doubling in the proportion of years closed.

Finally, the presence of significant measurement imprecision reduced the natural escapement realized under all spawner floors (Figure 9). This has the potential to move to an undesirable region of the spawner-recruit curve, which is probably why the average catch under high measurement imprecision is reduced.

The simulation results on measurement imprecision demonstrate the value of improved
information. Better data and estimates would be expected to increase the average yield from the fishery, to reduce the fluctuation in year-to-year yield, and to increase the escapement.

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