

Klamath River Fall Chinook Stock-Recruitment Analysis

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EXECUTIVE SUMMARY

Introduction

At the June, 2005 meeting, the Pacific Fishery Management Council (Council) directed the Salmon Technical Team (STT) to conduct several analyses of Klamath River Basin natural fall Chinook using the best datasets available. The analyses to be performed included:

- 1) estimate the parameters of a Ricker-type stock-recruitment model, including an estimate of the spawner abundance expected to generate maximum sustainable yield;
- 2) a correlation analysis of production (survival) and river flow conditions during the juvenile freshwater phase; and
- 3) a correlation analysis of production and river flow conditions during the parent spawning period.

This report completes the assignment given to the STT. The executive summary provides a very brief review of the methods used in the analyses, and a summary of the results of those analyses. Both the executive summary and the main report present only the results of technical work assigned by the Council to the STT. The results presented here should not be interpreted as a recommendation by the STT to modify the Council's management objectives for Klamath River fall Chinook.

Methods

Stock-Recruitment Model

Three models were used to develop spawner reference point estimates assuming a Ricker-type stock-recruitment relationship. Model 1 used only parent spawner abundance as a predictor of subsequent brood recruitment. Model 2 included both parent spawner abundance and a measure of post-freshwater-rearing survival as predictors of subsequent recruitment. This measure of post-freshwater-rearing survival covered the period from the onset of juvenile outmigration in May-June, through the end of August of that same year. Model 3, under development by the Canadian Department of Fisheries and Oceans, is based on a meta-analysis of Ricker stock-recruitment relationships for Chinook salmon populations from the Oregon coast through Southeast Alaska, and uses accessible watershed area (5th order and higher streams) as a predictor of subsequent recruitment.

Correlation Analyses

While adequate time series of stream flow data in the Klamath Basin were available at a number of locations, wild production estimates were not available. Because of this lack

of direct measure of wild production, we used estimates of hatchery release survival as a surrogate for wild stock survival.

Correlation Analysis – Juvenile phase

Correlation analyses were performed between various river flow measures in the Trinity and Klamath Rivers and cohort-reconstructed release-to-age-2 survival rates of fingerlings released from the hatcheries on these rivers. Correlation analyses were performed on minimum, maximum, and monthly average daily flows during the parental spawning migration as well as the month of release to the release-to-age-2 survival rates.

Correlation Analysis – Adult phase

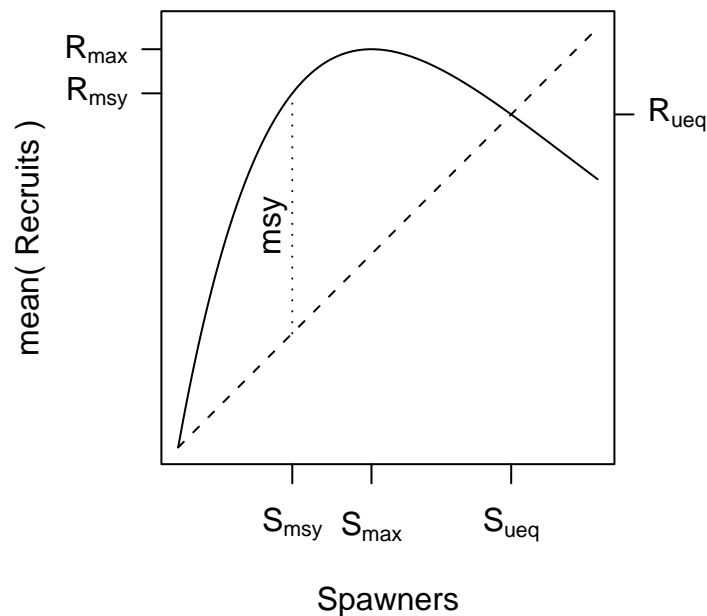
Because the survival of hatchery fish may not necessarily represent that of natural fish, we also performed a cursory examination of correlations between environmental measures and the Model 1 recruitment residuals. The environmental variables used were various measures of flow in the Klamath Basin.

Results

Stock-Recruitment Model

An example of a Ricker spawner-recruit curve and important points on that curve are shown in Figure ES-1.

Figure ES-1. Schematic of a Ricker stock-recruitment curve.



The peak of the curve represents the point of maximum production (R_{max}). The straight (dashed) line represents replacement, where recruitment equals the number of spawners. For any given parental stock size, the harvestable surplus is the difference between the recruitment curve and the replacement line. In the absence of fishing the relationship has an equilibrium spawning escapement at S_{ueq} where recruitment equals escapement. The point labeled S_{msy} represents the number of adult spawners that, on average, will generate maximum sustained yield (msy). Note that the harvestable surplus of the stock at S_{max} is less than the harvestable surplus at S_{msy} even though the number of recruits (R_{max}) is greater. The reference points resulting from the three models used to estimate the stock-recruitment parameters are provided in Table ES-1. Model 1 estimates S_{msy} at 32,700 (90% CI: 25,800 – 42,600). Model 2 estimates S_{msy} to be 40,700 (90% CI: 32,200 – 54,100). Model 3 estimates S_{msy} to be 70,900 (90% CI: 43,700 – 111,000).

Table ES-1. Spawner reference points for Ricker stock-recruitment Models 1,2,3.

Spawner Reference Point	Model 1 (parent spawners)	Model 2 (parent spawners, survival)	Model 3 (watershed area)
S_{ueq}	101,300	112,300	185,000
S_{max}	39,700	56,900	111,200
S_{msy}	32,700	40,700	70,900

Correlation Analyses

Correlation analyses were performed on minimum, maximum, and monthly average daily flows during the parental spawning migrations as well as the month of release, on the survival of hatchery fish to age 2. No significant relationships were found in any of these correlations. The strongest relationships were between survival of releases from Iron Gate Hatchery and flows during the months following release. However, the R^2 values were 0.25 or less, which suggests that only a small portion of the variability in age 2 survival rates can be explained by stream flow conditions.

No significant correlations were found between the Model 1 recruitment residuals and flow variables during the period of juvenile rearing and outmigration. However, significant positive correlations were found between several stream flow measures (e.g., monthly average discharge, minimum discharge, minimum 7-day average discharge, etc.) during the period when adults were migrating and spawning.

We examined the predictive potential of these relationships by incorporating some of these variables with the highest correlations into the spawner-recruit relationship as independent, explanatory variables. While incorporation of flow variables into the spawner-recruit explained more of the variability in recruitment, it decreased the significance of the fit, whether or not the hatchery survival was included.

Introduction

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- 1) estimate the parameters of a Ricker-type stock-recruitment model, including an estimate of the spawner abundance expected to generate maximum sustainable yield;
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Data Sources

The spawner and recruitment data used in this report are derived from cohort reconstructions provided by the Klamath River Technical Advisory Team. These data and methods have been recently revised (KRTAT 2002). Changes in data and methodology used in the cohort reconstructions were reviewed and accepted by the STT and SSC during their review of the new KOHM in 2001—2002. We used these data sets, updated through the most recent brood years available, for these analyses.

All streamflow data used in this report were obtained from published United States Geologic Survey (USGS) gauging station records (<http://waterdata.usgs.gov/ca/nwis/nwis>).

Methods

Three models were used to develop spawner reference point estimates assuming a Ricker-type stock-recruitment relationship. Model 1 used only parent spawner abundance as a predictor of subsequent brood recruitment. Model 2 included both parent spawner abundance and a measure of post-freshwater-rearing survival as predictors of subsequent recruitment. Model 3, under development by the Canadian Department of Fisheries and Oceans, is based on a meta-analysis of Ricker stock-recruitment relationships for a

number of west coast Chinook stocks, and uses accessible watershed area as a predictor of subsequent recruitment.

For the juvenile freshwater phase analysis, correlation analyses were performed on various river flow measures in the Trinity and Klamath Rivers to cohort-reconstructed age 2 survival rates of fingerlings released from their respective hatcheries.

For the adult spawning period analysis, correlation analyses were performed on minimum, maximum, and monthly average daily flows, and the Model 1 recruitment residuals.

Stock-Recruitment Models

Model 1: Ricker model.

A Ricker stock-recruitment model (Ricker 1954) was fit to all available spawner-recruit data for the natural stock of Klamath River fall Chinook salmon.

Assumptions

Several assumptions are made in proceeding with this analysis:

1. *Density dependent mortality.* For some time period prior to recruitment, the brood instantaneous mortality rate is proportional to the number of parent spawners (Ricker 1954).
2. *Stationarity.* The average stock-recruitment relationship is constant over time (Hilborn and Walters 1992), i.e., environmental conditions randomly affect survival, independent of stock size or time.
3. *Lognormal variation.* At any particular spawning stock size the variation in recruitment is lognormally distributed about its average, and acts multiplicatively. This is expected under the Central Limit Theorem of statistics if a combination of normally distributed, random factors affects the instantaneous mortality rate from egg to recruitment (Quinn and Deriso 1999)
4. *Measurement error.* Error in spawning stock size estimates (measurement error) is small relative to the range of spawning stock sizes observed (CTC 1999:section 1.4). Variation in realized recruitment at any particular spawning stock size (process error) dominates recruitment measurement error.
5. *Hatchery/Natural dynamics.* Estimates of spawning stock and recruitment are representative of a natural stock that can be considered independent of hatchery influences.

6. *Aggregate stock.* The contribution of fall Chinook sub-stocks in the Klamath basin is sufficiently stable that parameters for stock-recruit relationships can be adequately estimated by aggregating data.
7. *Reproductive potential.* The appropriate metric for spawning stock is abundance, independent of age, except for fish younger than age 3 which are not considered to be important to recruitment dynamics.

Methods

In general, the methods we used follow those outlined by the PSC Chinook Technical Committee (CTC 1999:section 1).

Data. Parent spawning stock, S , was defined as adult spawner abundance in Klamath Basin natural areas (outside hatcheries), and this data was obtained from the California Department of Fish and Game (CDFG 2005). Recruitment, R , was defined as the abundance of S progeny that survived to ocean age 3 in adult equivalent units (see Appendix A for details), and this data was derived based on the results of cohort reconstructions performed by the Klamath River Technical Advisory Team (as described in Goldwasser et al. (2001)).

Model/Estimation. A stochastic form of the Ricker stock-recruitment model (Quinn and Deriso 1999:equation 3.11, CTC 1999:section 1.6.1) was used to represent the data:

$$R = \alpha S e^{-\beta S + \varepsilon}, \quad \varepsilon \sim N(0, \sigma_\varepsilon^2), \quad (1.1)$$

with ε being a normally distributed error term. The model was fit to the data by first transforming it into a linear model

$$\log(R/S) = a + bS + \varepsilon, \quad (1.2)$$

and then using ordinary least-squares regression to estimate the parameters a , b , and σ_ε^2 .

The Ricker model parameters α and β were then estimated as

$$\hat{\alpha} = e^{\hat{a}}, \quad \hat{\beta} = -\hat{b}, \quad (1.3)$$

where a hat, “^”, denotes an “estimate”. The expected (mean) value, $E()$, of recruitment at a given spawner abundance, $R|S$, was estimated as

$$\hat{E}(R|S) = (\hat{\alpha} e^{\hat{\sigma}_\varepsilon^2/2}) S e^{-\hat{\beta}S} = \hat{\alpha}' S e^{-\hat{\beta}S}, \quad (1.4)$$

where the term $e^{\hat{\sigma}_\varepsilon^2/2}$ largely corrects for the bias arising from the fact that the expected value of e^ε is $e^{\sigma_\varepsilon^2/2}$; not 1 (Hilborn 1985). Given the $\hat{E}(R|S)$ function, three spawner abundance reference points were estimated (Ricker 1975:346–347).

S_{msy} : the spawner abundance expected to generate maximum sustained yield

$$1 = (1 - \hat{\beta} \hat{S}_{msy}) \hat{\alpha}' e^{-\hat{\beta} \hat{S}_{msy}}. \quad (1.5)$$

S_{max} : the spawner abundance expected to generate maximum recruitment

$$\hat{S}_{max} = 1 / \hat{\beta}. \quad (1.6)$$

S_{ueq} : the spawner abundance expected at unfished equilibrium

$$\hat{S}_{ueq} = \log(\hat{\alpha}') / \hat{\beta}. \quad (1.7)$$

Various statistical diagnostics of the model's fit were assessed (see Appendix A for details).

Estimation bias and uncertainty measures for the model parameter and spawner abundance reference point estimates were derived using the bootstrap procedure described by the CTC (1999:18–19), except that regression residuals were re-sampled on the $\log(R/S)$ scale since it is on this scale that the errors are modeled as additive and of constant variance. The bootstrap number of trials was 100,000.

Results

Data. The $\{R, S\}$ data are presented in Appendix A Table A1. The extent of the current available data is for brood years 1979–2000, which yields 22 (R, S) data points. The range of S is (11649, 161793), a span equal to about 13 times the minimum observed S , which should provide sufficient contrast for estimation of the Ricker model parameters (CTC 1999:5). The range of R is (16213, 368159), and recruit-per-spawner ratios, R/S , range from (0.22, 22.42), again indicating sufficient contrast should be present in these data to allow for estimation of the Ricker model parameters (CTC 1999:5). All of the above supports analysis assumption 1. Figure 1 is a plot of R/S versus S , with the dashed line referencing replacement ($R/S = 1$). The two-digit numbers, xx , in the plot denote brood years (19 xx or 20 xx). Note that the highest R/S values have generally occurred at the lower S values, and that the lowest R/S values have generally occurred at the higher S values, which is consistent with the Ricker model presumption of density dependent mortality.

Model/Estimation. Figure 2 is a plot of the transformed data $\log(R/S)$ versus S , with the solid line representing the fitted model on this scale. The corresponding least-squares regression statistics are provided in Appendix A Table A2. The density dependent parameter estimate $\hat{\beta}$ is statistically significant ($p < 0.001$), and the R -squared value is 0.5571, which means that the Ricker model accounts for about half of the density independent model residual variation in $\log(R)$ (see Appendix A for the basis of this interpretation). Figure 3 is a plot of the untransformed (R, S) data, with the solid curve representing $\hat{E}(R|S)$, and the dashed line referencing 1:1 replacement. Note that there is considerable unexplained variation in R about the $\hat{E}(R|S)$ curve. The Ricker model parameter and spawner reference point estimates are presented in Table 1, along with associated 90% confidence intervals. All of these results presume the Ricker model is appropriate for these data. A variety of regression diagnostics (Appendix A Figures A1–A4) performed to address this presumption did not indicate a lack of model fit, or violation of analysis assumptions 1–3.

Ricker model

Figure 1. Recruits-per-spawner.

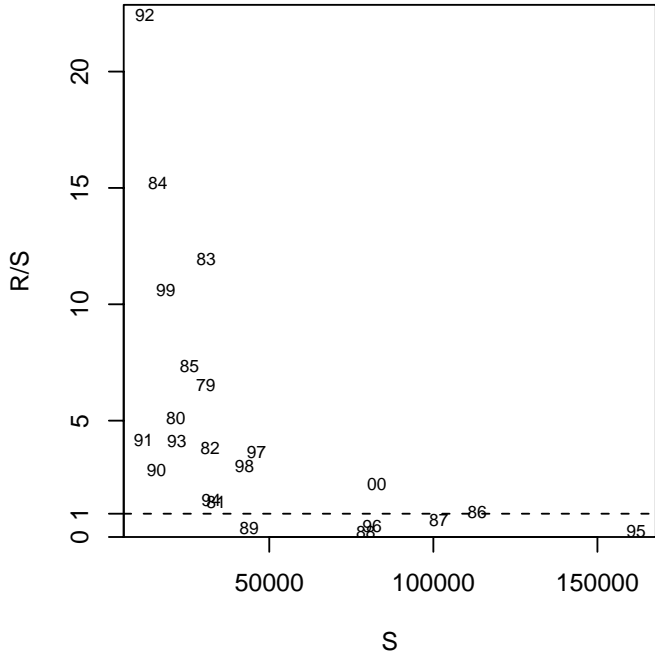


Figure 2. Transformed data and fitted model.

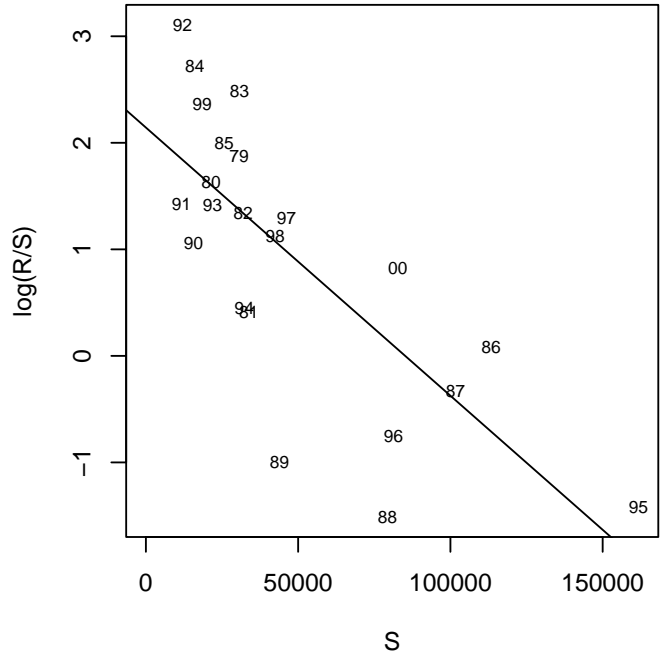


Figure 3. Expected value Ricker model.

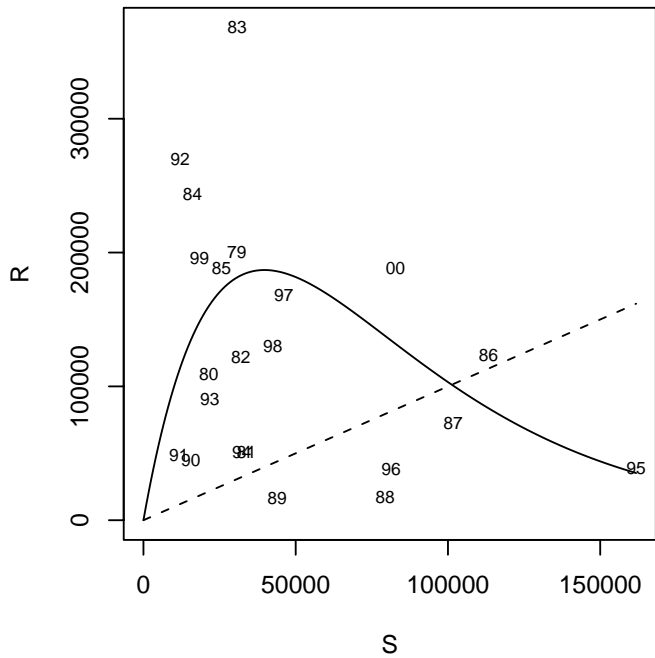


Table 1. Ricker model parameter and spawner reference point estimates.

Quantity	Point Estimate	90% Confidence Interval
α	8.5277	(5.2176–13.673)
β	0.000025171	(0.000017656–0.000033364)
σ_ε^2	0.81089	(0.39482–1.1170)
α'	12.791	(7.7302–19.201)
S_{msy}	32,700	(25,800–42,600)
S_{max}	39,700	(30,000–56,600)
S_{ueq}	101,300	(83,400–124,200)

Model 2: Ricker model w/ survival.

An index of early-life survival was incorporated into the Ricker stock-recruitment model of the previous section, and the model was fit to all available spawner-recruit data for the natural stock of Klamath River fall Chinook salmon.

Assumptions

The previous analysis assumptions (1–7) apply, in addition to the following one:

8. *Survival rate index.* The instantaneous mortality rate for Klamath Basin hatchery fingerlings from release to age 2 (four month period following release) is proportional to that of naturally produced outmigrants over this same period.

Methods

The assessment methods used for Model 2 build on those used for Model 1, and again generally follow the methods outlined by the PSC Chinook Technical Committee (CTC 1999:section 1).

Data. Early-life survival was estimated for hatchery fingerling cwt groups over the four-month period immediately following release (May—Aug) based on the results of cohort reconstructions performed by the Klamath River Technical Advisory Team (as described in Goldwasser et al. (2001)). For each brood year a weighted average, s' , of the survival rate estimates for Iron Gate Hatchery (IGH) and Trinity River Hatchery (TRH) fish was derived (see Appendix B for details).

Model/Estimation. Model 1 was extended to include early-life survival as a covariate as follows (CTC 1999:p.9–10):

$$R = \alpha S e^{-\beta S + \theta(s - \bar{s}) + \varepsilon}, \quad \varepsilon \sim N(0, \sigma_\varepsilon^2), \quad (2.1)$$

where $s = \log(s')$ and $\bar{s} = \text{mean}(s)$ over the 22 brood year data set. Notice that the productivity coefficient is now brood-year-specific, $\alpha e^{\theta(s - \bar{s})}$, and depends on the value of s . With the above parameterization, α now represents the productivity under average

conditions ($s = \bar{s}$). The model was fit to the data by first transforming it into a linear model

$$\log(R/S) = a + bS + c(s - \bar{s}) + \varepsilon, \quad (2.2)$$

and then using ordinary least-squares regression to estimate the parameters a , b , c , and σ_ε^2 . The Model 2 parameters α , β , and θ were then estimated as

$$\hat{\alpha} = e^{\hat{a}}, \quad \hat{\beta} = -\hat{b}, \quad \hat{\theta} = \hat{c}. \quad (2.3)$$

The expected value of recruitment at a given spawner abundance was estimated as

$$\hat{E}(R|S) = (\hat{\alpha} e^{\hat{\sigma}_\varepsilon^2/2}) S e^{-\hat{\beta}S + \hat{\theta}(s - \bar{s})} = \hat{\alpha}' S e^{-\hat{\beta}S + \hat{\theta}(s - \bar{s})}, \quad (2.4)$$

also dependent on s . Given the $\hat{E}(R|S)$ function, the three spawner abundance reference points, S_{msy} , S_{max} , and S_{ueq} , were estimated as:

$$1 = (1 - \hat{\beta} \hat{S}_{msy}) \hat{\alpha}' e^{-\hat{\beta} \hat{S}_{msy} + \hat{\theta}(s - \bar{s})}, \quad (2.5)$$

$$\hat{S}_{max} = 1 / \hat{\beta}, \quad (2.6)$$

$$\hat{S}_{ueq} = \left[\log(\hat{\alpha}') + \hat{\theta}(s - \bar{s}) \right] / \hat{\beta}. \quad (2.7)$$

\hat{S}_{msy} and \hat{S}_{ueq} were computed assuming average early-life survival ($s = \bar{s}$).

To examine the benefit of including s in the recruitment model, the observed relationship between the two predictor variables s and S was explored, as was the relationship between the Model 1 residual variation in $\log(R/S)$ and that portion of s unaccounted for by S . The latter provides a direct gauge of the utility of including s in the recruitment model, and is complementary to comparison of the Model 2 versus Model 1 regression statistics.

The diagnostics previously described for Model 1 were also used as a check on the aptness of Model 2 (see Appendix B for further details).

Estimation bias and uncertainty measures for the model parameter and spawner abundance reference point estimates were derived using the bootstrap procedure previously described for Model 1.

Results

Data. The $\{s'\}$ data are presented in Appendix B Table B1. The range of s' over the 22 brood year dataset is (0.00043, 0.0625), and the range of s is (-7.76, -2.77). Figure 4 is a plot of the s_{IGH} and s_{TRH} time series, and the derived s . Typically, $s_{IGH} < s_{TRH}$. The s_{IGH} and s_{TRH} time series display a remarkable coherence (Figure 4) given the two series were independently derived.

Model/Estimation. The covariation between s and S is displayed in Figure 5. The solid line is the least-squares regression fit, which though marginally significant ($p = 0.0535$), has a low R-squared value of 0.1739 (Appendix B Table B2). The brood years corresponding to the six highest recruit-per-spawner values in the dataset are boxed in

Figure 5; the six lowest are circled. Model 1 assumes that high R/S values are entirely a result of low stock size (and random process error). Figure 5 strongly suggests that these high R/S values are partially accounted for by a relatively high early-life survival for those brood years. Similarly, Figure 5 suggests that the low R/S values associated with high stock-sizes are partially accounted for by a relatively low early-life survival for those brood years.

One measure of the value of incorporating s in the Ricker model is to answer the question: What portion of the Model 1 residual variation can be explained by that portion of s unaccounted for by S ? Figure 6 is a plot of the residuals of the Figure 2 model against the residuals of the Figure 5 model. High $\log(R/S)$ residuals are associated with high s residuals, and low $\log(R/S)$ residuals are associated with low s residuals. The solid line is the least-squares regression which is highly significant ($p < 0.0001$), and s accounts for 54.5% of the Model 1 residual variation (Appendix B Table B2). Thus, s is a significant predictor of recruitment success, above and beyond S , and should be incorporated into the stock-recruitment analysis in the form of Model 2.

The least-squares regression statistics for Model 2 are provided in Appendix B Table B2. On the whole, Model 2 is highly significant ($p < 0.0001$) relative to the density independent model, and the R-squared value substantially improves to 0.7986, which means that Model 2 accounts for about 80% of the density independent model residual variation in $\log(R)$ (see Appendix A for the basis of this interpretation). The coefficient of s in Model 2 is significant ($p = 0.00013$) and, in agreement with the Figure 6 analysis results, its inclusion accounts for 54.5% of the Model 1 residual variation (Appendix B Table B2). Figure 7 is a plot of the untransformed (R, S) data, with the solid curve representing the estimated Model 2 expected value assuming average early life survival, $\hat{E}(R|S, s = \bar{s})$, with the dashed line referencing 1:1 replacement. Recall that for Model 2, the Ricker curve is year-specific in that it depends on the value of s . Assuming $s = \bar{s}$, the Model 2 curve is less steep and descends less quickly than the Model 1 curve (compare Figures 3 and 7), which derives from the uneven distribution of s values across the range of S . The Model 2 parameter and spawner reference point estimates are presented in Table 2, along with their respective 90% confidence intervals. The \hat{S}_{msy} and \hat{S}_{ueq} values are conditional on $s = \bar{s}$. All of these results presume Model 2 is appropriate for these data. A variety of regression diagnostics (Appendix B Figures B2–B5) performed to address this presumption did not indicate a lack of model fit, or violation of analysis assumptions 1–3.

Ricker model w/ survival

Figure 4. log(survival) time series.

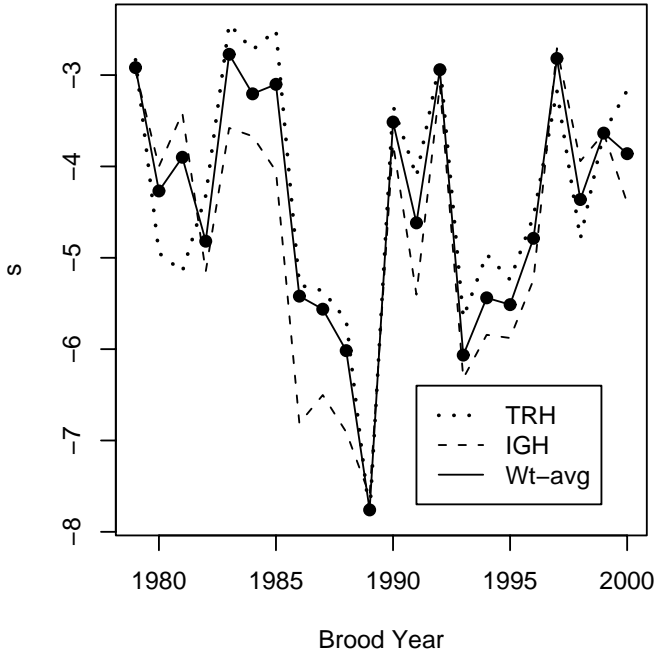


Figure 5. Covariation: log(survival) and S.

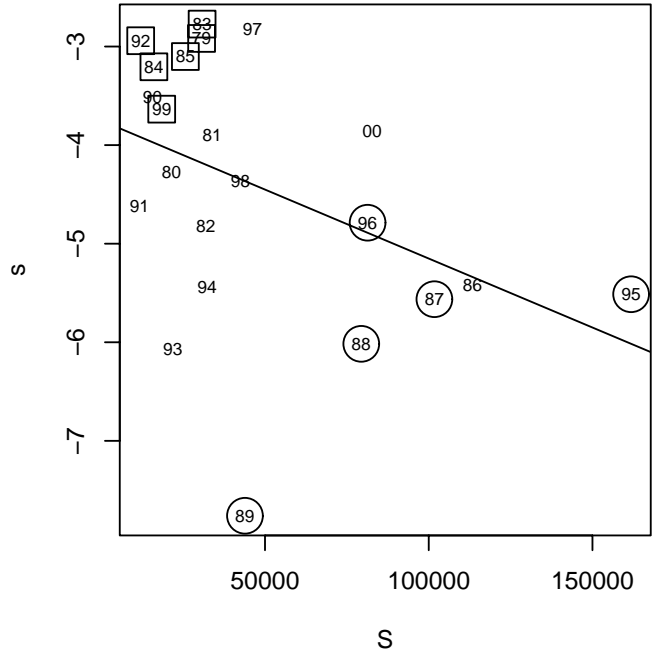


Figure 6. Covariation: log(R/S) and s, unaccounted for by S.

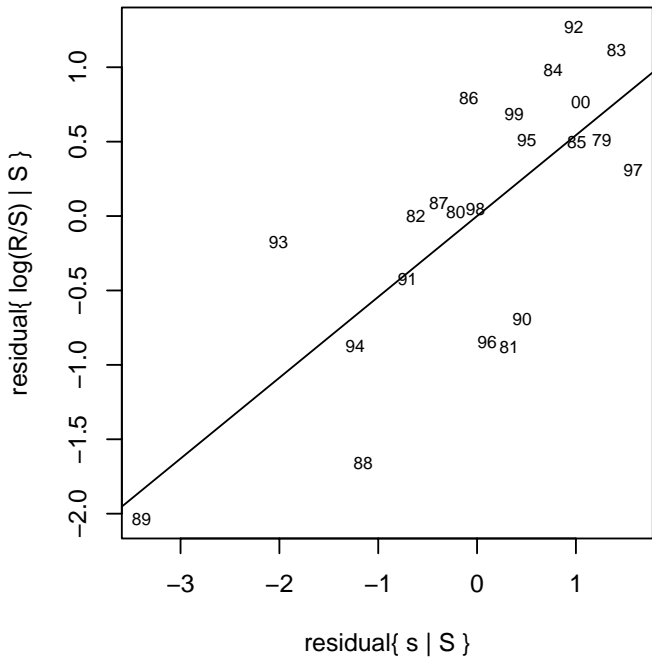


Figure 7. Expected value Ricker model w/ $s = \bar{s}$.

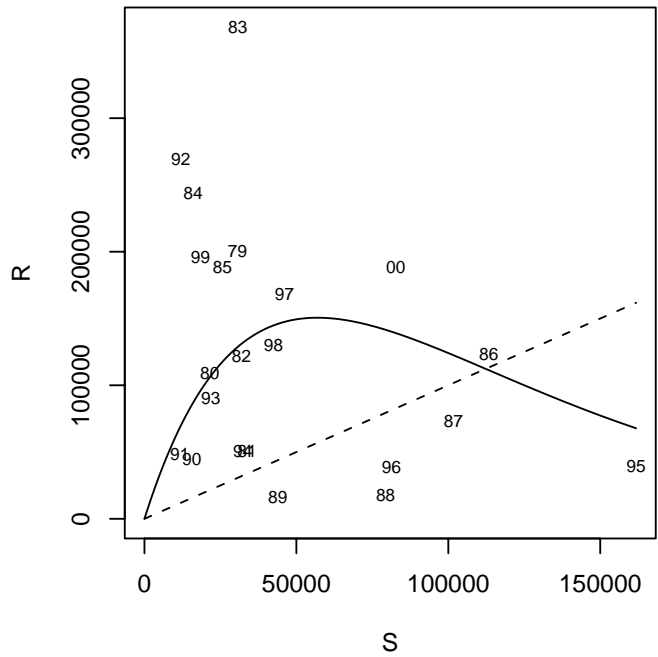


Table 2. Model 2 parameter and spawner reference point estimates.
 The \hat{S}_{msy} and \hat{S}_{ueq} values are conditional on $s = \bar{s}$.

Quantity	Point Estimate	90% Confidence Interval
α	5.9218	(4.1698–8.3184)
β	0.000017567	(0.000011879–0.000023564)
θ	0.54327	(0.37317–0.72115)
σ_{ε}^2	0.38821	(0.19045–0.48619)
α'	7.1904	(4.9564–9.7130)
S_{msy}	40,700	(32,200–54,100)
S_{max}	56,900	(42,400–84,200)
S_{ueq}	112,300	(91,500–142,400)

Discussion: Model 1, Model 2.

Assumptions

We first briefly discuss analysis assumptions 1–8 in light of the observed data and analysis results.

1. *Density dependent mortality.* The highest S/R ratios have occurred at lower levels of spawner abundance, and vice-versa, which is consistent with, though not necessarily proof of, density dependent mortality. As a result, the $\{S, R\}$ data are clearly more consistent with the density dependent recruitment models (Models 1 and 2) than a density independent recruitment model.
2. *Stationarity.* Background processes whose effects on mortality have not occurred randomly with respect to stock size during the period when the $\{S, R\}$ data was collected may seriously bias the estimated spawner-recruit relationship in terms of future predictions. Our analysis strongly suggests that the magnitude of density independent early-life survival over the four-month period following the onset of juvenile outmigration may not have been randomly distributed across the range of observed stock sizes (relatively higher s values were associated with lower S values, and vice-versa), and this is the rationale for including s as a covariate in the Ricker model. Other, currently unrecognized, factors may have influenced the observed $\{S, R\}$ relationship as well.
3. *Lognormal variation.* The Model 1 and 2 residual variation in $\log(R)$ is largely consistent with this distributional assumption.
4. *Measurement error.* There are currently 22 (S, R) data points, and the contrast within these data appear to be sufficient for identifying/estimating the parameters of a Ricker stock-recruitment relationship in the presence of measurement error. The actual contributions of process and measurement errors to the overall variation in R at any particular value of S are not presently known. Process error

was assumed to dominate recruitment measurement error. This assumption is precautionary, i.e., estimates of spawner reference points would be lower as the relative contribution of measurement error increases.

5. *Hatchery/Natural dynamics.* The adequacy of this assumption (independence) is contingent on the stray rate of hatchery fish into natural areas, particularly in the proximity of the Klamath Basin's two production hatcheries. If the stray rate were to increase in the future, and the offspring of these spawners are not as fit as their natural-origin counterparts, the currently estimated spawner-recruit curve would be overly-optimistic of the productivity of the "natural" stock.
6. *Aggregate stock.* Differing maturation schedules and river conditions for the Klamath and Trinity River stocks argue for conducting separate spawner-recruit analyses for the two systems. However, the available data are insufficient to reliably conduct such an analysis. Even so, if one of these two sub-basin stocks has a lower productivity than the other (or if this is true of any other stock sub-units), then managing according to the composite \hat{S}_{msy} may seriously deplete, and even extirpate, these less productive stock sub-units over time (Walters and Cahoon 1985).
7. *Reproductive potential.* Failing to account for age 2 fish on the spawning grounds is unlikely to have significantly affected the analysis conclusions. Data are insufficient to determine if the recruit-per-spawner ratio is a function of the age-sex composition of the adult (age 3 and older) spawning stock.
8. *Survival rate index.* The proportionality assumption cannot be directly confirmed, but if this rate primarily reflects early-life marine environmental conditions, then it is entirely plausible (discussed further below). The explanatory power of s as a predictor of natural-stock recruitment variability was clearly significant, and consistent with this assumption.

Model 1 versus Model 2.

The Model 1 (Ricker without survival) estimated recruitment curve is rather steep near the origin ($\hat{\alpha}_1 = 8.5$) which, in and of itself, is indicative of a rather productive stock, especially considering that the age of recruitment in our analysis was defined as ocean age 3 (September 1). However, the Model 1 estimated spawning stock size resulting in maximum recruitment, $\hat{S}_{max,1} = 39,700$, seems rather low for a basin of this size, and is nowhere near the value predicted under the habitat-based meta-analysis recruitment model for West Coast Chinook presented in this report. The Model 1 estimate $\hat{S}_{msy,1} = 32,700$ is 2,300 fish less than the current minimum spawner floor value of 35,000. This is consistent with the findings of the KRTAT (1999) which suggested, based on a Model 1 spawner-recruit curve fit to the 1979–1993 brood year data, that S_{msy} was between

30,000 and 35,000 fish, depending primarily on the level of imprecision in preseason ocean abundance forecasts.

In contrast, the Model 2 (Ricker with survival) estimated recruitment curve corresponding to the average value of s is less steep and descends less quickly than the Model 1 curve. This derives from the apparent non-random distribution of s with respect to S for the years examined in this analysis. Generally, s was relatively high for those brood years produced at low stock abundances, and thus under the average s observed for the entire dataset, the expected productivity will be reduced when compared to that of Model 1. The Model 2 productivity estimate ($\hat{\alpha}_2 = 5.9$) is 30% less, and $\hat{S}_{max,2} = 56,900$ is 40% greater, than the Model 1 estimates as a result. The unexploited equilibrium spawner stock size under the two models is similar. The Model 2 estimate under average survival conditions is $\hat{S}_{ueq,2} = 112,300$, which is 11,000 fish higher than $\hat{S}_{ueq,1}$. For Model 2, again assuming average survival conditions, $\hat{S}_{msy,2} = 40,700$, which is 5,700 fish more than the current minimum spawner floor value of 35,000. Other $\hat{S}_{msy,2}$ values would result under alternative assumptions about the magnitude of s . For example, a more risk-averse value of s might be considered during periods of poor early-life survival conditions.

The statistical support for both density dependent models was strong relative to a density independent recruitment model. Recruits-per-spawner declined with increasing spawning stock size consistent with the Model 1 and 2 assumption of density dependent mortality. The estimated density dependent parameters for Model 1 and 2, $\hat{\beta}_1$ and $\hat{\beta}_2$, respectively, were statistically significant, as was the Model 2 survival coefficient, $\hat{\theta}$. Fifty-six percent of the density independent model residual variation in $\log(R)$ was accounted for by Model 1; 80% was accounted for by Model 2. The incorporation of the covariate s into the Ricker model accounted for 55% of the Model 1 residual variation in $\log(R)$, with $\hat{\theta}$ being statistically significant at the $p = 0.00013$ level. This one additional parameter in the model provided an as good or better fit than Model 1 to 20 of the 22 (R, S) data points (exceptions were brood years 1979 and 1997). The significance of s implies that the stationarity assumption may have been violated for Model 1 (time-dependent α a function of s). The statistical support for including s as a covariate in the Ricker model is compelling.

Early-life survival

As discussed by the CTC (1999:10), the fitted stock-recruitment relationship can be strengthened by including marine survival as a covariate. This also holds true for measures of survival during density independent freshwater life-stages. The relationship will be strengthened when the variation in the survival measure unaccounted for by S correlates well with the $\log(R/S)$ Ricker model residuals, as was demonstrated for the survival index s proposed here ($r = 0.74$).

The hatchery fingerling release-to-age-2 survival rate was selected as a surrogate index for the survival rate of progeny from natural spawning escapement. No comparable time series of survival estimates is available for the natural stock. The use of the s time series in our analysis does not require that the hatchery and natural stocks have equivalent survival rates, but only depends on the assumption that the survival of both stocks varies proportionately and synchronously.

The independently derived $\{s_{IGH}\}$ and $\{s_{TRH}\}$ time series were strongly coherent, and clearly suggestive of an annual effect. There are three plausible sources for this effect: (a) hatchery effect; (b) downstream migration effect; or (c) early-life marine effect. A hatchery effect seems unlikely for an annual signal in that the hatcheries are independently operated, but would have to have the same relative annual effect on s each and every year. A downstream migration effect also seems questionable for an annual signal in that the majority of the downstream migration route for the two hatchery stocks is in different river systems (although annual climatic events may shape the environment in both systems similarly). An early-life marine signal seems the most plausible. This is the environment shared by both hatchery stocks, and when coupled with the fact that IGH and TRH hatchery fingerlings take only about three weeks to outmigrate, this suggests that s may primarily reflect early-life marine survival (first three months), and explain why s correlated so well with recruitment success for the natural stock.

Model 3: Habitat-based methods for estimating stock-recruit reference points

The potential of the Klamath watershed to produce Chinook can be evaluated through an assessment of suitable habitat. In 1985, the California Department of Fish & Game estimated a range for the optimum spawning escapement for the Klamath basin of between 40,100 to 105,900, based on expert opinion of field biologists (Hubbel and Boydstun 1985). More recently, in June 2005, the Pacific Salmon Commission's Chinook Technical Committee accepted a habitat-based method for estimating maximum sustained yield (MSY) escapement levels. The method, under development by the Canadian Department of Fisheries and Oceans (CDFO), is based on a meta analysis involving stock-recruit models for several stocks along the coast (Chuck Parken, CDFO, personal communication August, 2005). In its present form, the CDFO model estimates the spawning escapements associated with MSY, maximum production, and unfished equilibrium (S_{msy} , S_{max} , and S_{ueq} , respectively) using a single variable, accessible watershed area (square kilometers for 5th order and higher streams for stocks with ocean-type life histories). The current watershed area for 5th order and higher streams in the Klamath Basin below impassable barriers is estimated as 16,561 square kilometers.

Methods:

CDFO's approach is derived from a meta analysis of Chinook salmon populations from the Oregon coast through Southeast Alaska using Ricker stock-recruitment relationships, assuming multiplicative, lognormal error:

$$R = \alpha * S * e^{-\beta * S} \exp(\varepsilon)$$

where R = recruitment

S = spawners

α = slope at origin

β = the capacity parameter

ε = lognormal process error with mean 0 and variance σ^2

For each Ricker stock-recruitment relationship the biological reference points of S_{msy} , S_{max} , and S_{ueq} were calculated and the relationship between the reference points and habitat was estimated assuming an allometric relationship with a single habitat parameter, accessible watershed area (WA):

$$y = a * WA^b * \exp(\varepsilon) \quad (3.1)$$

The relationship was estimated by linear regression using the log-transform of the model:

$$\log(y) = \log(a) + b \log(WA) + \varepsilon \quad (3.2)$$

Parameters were estimated separately for ocean and stream-type Chinook. Twelve stocks¹ were employed to estimate parameters for ocean-type Chinook in the CDFO Habitat Model.

Reference points ($y = S_{msy}, S_{max}, S_{ueq}$) are calculated using the following equation:

$$\hat{y} = WA^{\hat{b}} * e^{\log(\hat{a}) + (\frac{\hat{\sigma}^2}{2})} \quad (3.3)$$

Table 3. Parameter values for the CDFO Habitat Model reference points for ocean-type Chinook are presented in the following table:

<i>Parameter</i>	$y = S_{msy}$	$y = S_{max}$	$y = S_{ueq}$
$\log(a)$	2.240	2.170	3.560
B	0.911	0.962	0.875
σ^2	0.158	0.206	0.138

¹ The ocean-type stocks included in the meta analysis included the Chehalis (WA), Cowichan (BC), Harrison (BC), Humptulips (WA), Lewis River (CR), Nehalem (OR), Queets (WA), Quillayute (WA), Siletz (OR), Situk (AK), Siuslaw (OR), Skagit (WA).

Results:

Substituting the estimated watershed area for the Klamath (16561 square kilometers) and the parameters from Table 3 into equation (3.3), yields estimates for the reference points of: $S_{msy} = 70,900$, $S_{max} = 111,200$, and $S_{ueq} = 185,000$.

Table 4. Point estimates and confidence intervals for S_{msy} and S_{ueq} based on the Habitat Model provided by CDFO staff²:

	S_{msy}	S_{ueq}
Point estimate	70,900	185,000
Coefficient of Variation	0.29	0.27
Percentiles	5th = 43,700 10th = 48,100 25th = 57,600 50th = 69,900 75th = 85,100 90th = 101,000 95th = 111,000	5th = 118,000 10th = 130,000 25th = 153,000 50th = 184,000 75th = 219,000 90th = 259,000 95 th = 283,000

Discussion:

The Klamath River system encompasses a watershed area of nearly 13,000 square miles (~ 33,500 square kilometers) and continues to be a major producer of Chinook salmon (USFWS 1979). Since 1981, the combined natural and hatchery production of fall chinook has ranged from a low of 67,700 in 1992 to 1,448,900 in 1986 (September abundance of age 3 and 4 fish) while natural spawning escapements of adults has ranged from 11,600 in 1996 to 161,800 in 1995 (KRTAT 2005, STT 2005). Production has been highly variable; data employed in the STT's stock-recruitment analysis indicate that production of natural-origin Klamath fall Chinook has ranged from a low of 16,200 for the 1989 brood to a high of 368,200 for the 1983 brood.

Hubbel and Boydston (1985) reported that CDFG established a spawning escapement goal of Klamath fall chinook of 115,000 adults (97,500 natural spawners plus 17,500 hatchery spawners) in 1978. The goal, which represented the average number of spawners observed during the 1960s, was subsequently adopted by the PFMC to guide the development of its fishery management plans. Until the mid 1980s, escapements averaged less than 35% of the goal and some groups began to express concerns that the goal was not appropriate for current conditions within the watershed. This controversy led to the creation of the Klamath Fishery Management Council in 1986 and the availability of resources to increase the information basis for management of this stock. In response to concerns for adverse impacts to the fishing industry that would result from

² Estimates provided by CDFO staff, Chuck Parken, pers.com. Confidence intervals were generated using bootstrap methods involving resampling of regression residuals.

strict adherence to the 97,000 escapement goal, the PFMC reduced the goal to 86,000 and adopted a plan to rebuild escapements to attain the 115,000 goal over a period of years (Amendment 9 to the Council's Salmon Fishery Management Plan). In 1986 and 1987, natural escapements exceeded 100,000 adults, but then remained well below the original goal of 97,000 except in 1995 (Figure 8).

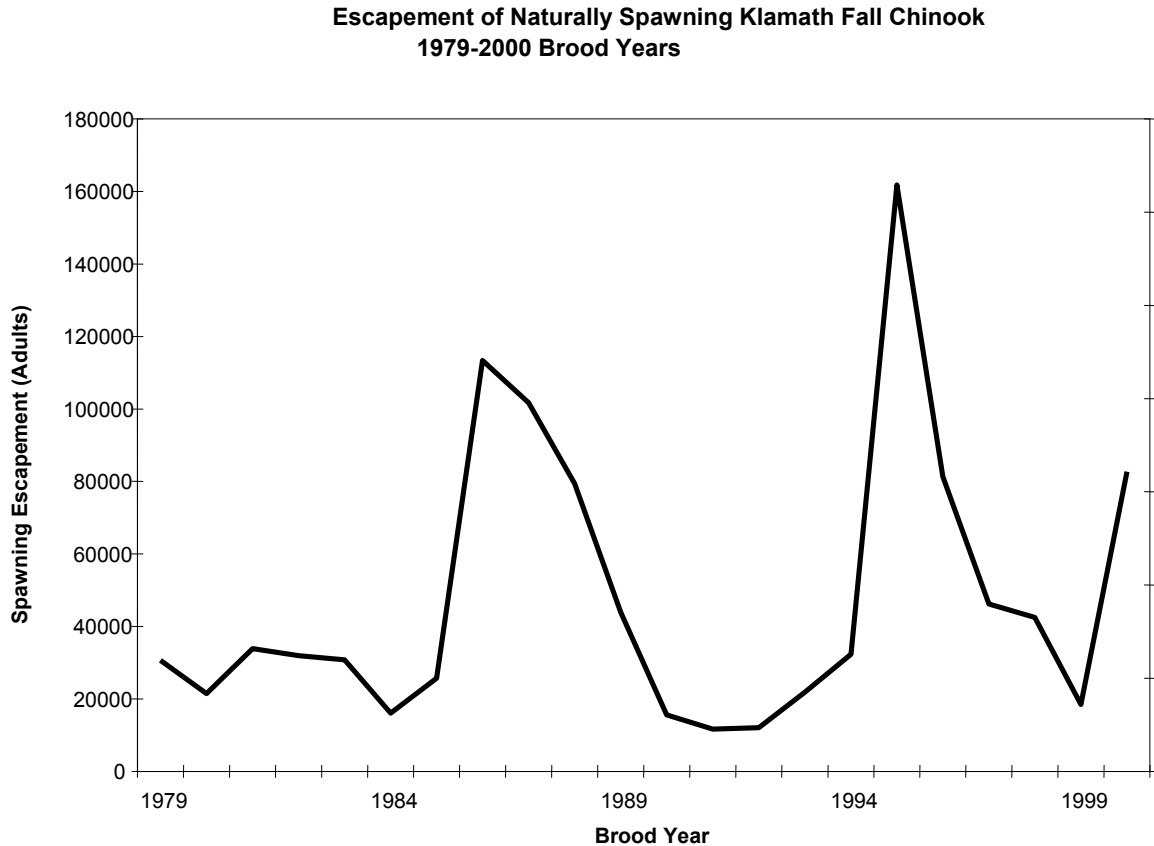


Figure 8. Natural spawning escapements for Klamath fall chinook for the 1979 to 2000 brood years

Production from these three years, when the escapement exceeded the original goal of 97,000 spawners, was poor; only the 1986 brood had production that exceeded spawning escapement. It is unclear, however, if the cause of this poor production is due to compensatory effects of spawning escapement or the coincidence of adverse environmental conditions resulting in poor survival of progeny. A survival index, based on estimated survivals of fall chinook fingerling releases from Iron Gate and Trinity hatcheries indicates that very low survival of brood year progeny coincided with high spawning escapement levels (Figure 9). Both escapement and the survival index were highly variable during the time period for which data are available to perform stock-recruitment analyses. Production from any given level of spawning escapement can vary

substantially from average expectations. Considerable uncertainty remains over whether the results from stock-recruitment analysis can reliably predict future production from spawning escapement levels over the long term.

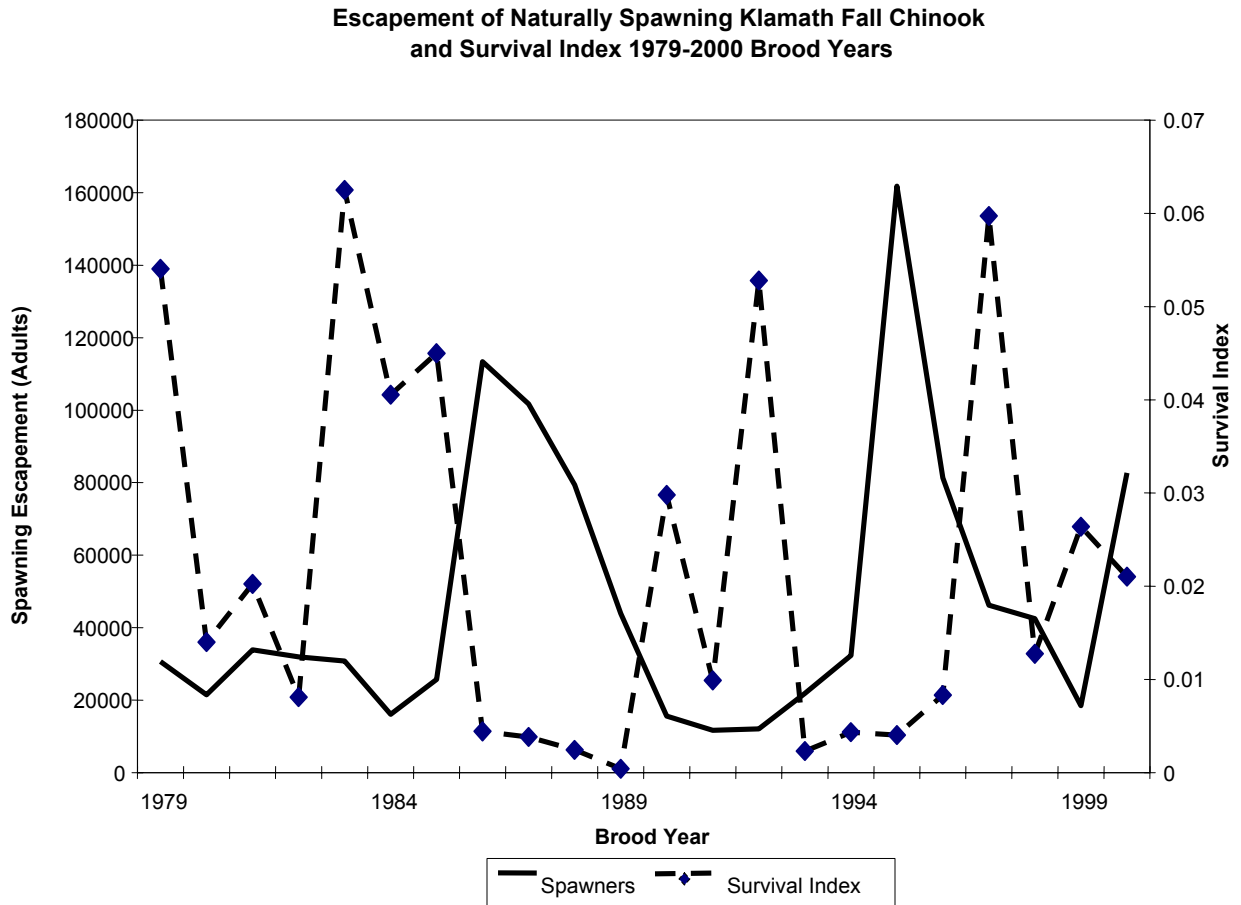


Figure 9. Natural spawning escapements for Klamath fall chinook and survival index for the 1979 to 2000 brood years

Available information about the productivity and capacity of Klamath fall Chinook is conflicting. The stock-recruitment analyses suggest that data for the 1979-2000 broods indicate that S_{msy} is likely to lie within the range of 25,800 to 54,100. On the other hand, historical information indicates that the Klamath basin was capable of supporting large runs of Chinook salmon and that spawning escapements averaged 97,000 during the 1960s. The CDFO habitat model indicates that an S_{msy} of 70,900 adults would be expected, and that estimates of S_{msy} and S_{ueq} derived from stock-recruitment analysis using the data for the 1979-2000 broods lie well outside computed confidence intervals.

It is nearly certain that other factors influence the production of fall Chinook from the Klamath River Basin. Water quality studies indicate that dissolved oxygen and water temperatures in the Klamath River reach conditions that are stressful and even lethal to salmon. A massive fish kill observed in 2002 spurred numerous investigations into the cause. Concerns have been raised as to the effects of water management and diversion on ecosystem functions in the Klamath basin. There are indications that water flow conditions may affect survival of fingerling fall Chinook releases from Iron Gate Hatchery. There are also indications that environmental conditions have changed in the Klamath basin since the 1960 and that they will continue to change in the future.

Bartholow (2005) found evidence that water temperatures in the Klamath River has been increasing at about 0.6 C per decade since the 1960s, that the season of high temperatures stressful to salmon has lengthened over a month during the same period, and that the average length of the Klamath mainstem with cool summer temperatures has declined by about 8.2 km/decade. Bartholow concluded that if the trends continue, recovery of salmonids in the Klamath will become increasingly problematic.

Correlation Analyses – Juvenile Survival and Freshwater Flows

A review of potential sources of data and prior analyses of flow and temperature conditions on the Klamath and Trinity rivers was conducted. Long time series of flow data are readily available at a number of locations within the Klamath and Trinity basins on the USGS web site (<http://waterdata.usgs.gov/ca/nwis/nwis>). However there were no comparable time series of temperature data available. Flow data was used from the gauging station at Hoopa on the Trinity River and at Orleans on the Klamath River. These were the lowest gauging stations where the two rivers were separate. Flow data were also available on the mainstem Klamath River near Klamath, but the time series of discharge data from this station has missing data. In addition attempts were made to locate a time series of juvenile production estimates from natural areas in the Klamath and Trinity River basins. Juvenile sampling in the basin has been conducted sporadically and only in recent years has this sampling been done in such a way that production estimates could be made. However these recent production estimates were not yet available from the investigators for our analysis. Because of this lack of direct measure of wild production we decided to explore the use of hatchery survival as our only available surrogate for the wild stock survival.

Correlation analyses were performed on various river flow measures in the Trinity River and Klamath Rivers to cohort reconstructed age 2 survival rates of fingerlings released from their respective hatcheries. Correlation analyses were performed on minimum, maximum, and the monthly average daily flows during the parental spawning migrations as well as the month of release to age 2 survivals. The strongest relationship was the Klamath River minimum flows during and immediately after the month of release. However the R^2 value was just over 0.20 which suggests that only a small portion of the variability in age 2 survival rates could be explained by river flow conditions. It is likely that hatchery operations have more effect on survival than does flow alone. A more

through analysis of fish health and handling conditions at time of release for individual batches of fish may better isolate the effect of flow on survival. Hatchery reports contain more information about fish disease and success of release than does the RMIS data. In some cases the RMIS data contain errors such as the date of release and fail to detail conditions that would affect juvenile survival. Considerable detective work would be necessary to verify the accuracy of the release data. Even if this was done there would still be the problem of determining if survival of the hatchery stock represents survival of the wild stock.

Correlation Analysis – Ricker Model Residuals and River Flow

Because the survival of hatchery fish may not reflect survival of natural fish, another approach taken by the STT was to examine correlations between environmental variables and the residuals of recruitment from that predicted by the Ricker spawner-recruit relationship without incorporation of the hatchery survival index (Table 5).

Table 5. Correlations between residuals from predicted recruitment and monthly average daily discharge during adult spawning migration and juvenile rearing and outmigration.

Month	Brood year	Year of outmigration
March		-0.007
April		0.019
May		0.054
June		0.087
August	0.298	
September	0.408*	
October	0.400*	
November	0.375*	
December	0.066	
Sept-Oct	0.439*	

* $p < 0.05$ (one-tailed test)

No significant correlations with discharge were observed during the period of juvenile rearing and outmigration, but significant correlations were observed during the period of adult migration and spawning. These correlations, though significant, are weak, and are similar in magnitude to those between discharge and the hatchery survival index. Because the strongest correlations were observed with average daily discharge in September and October, we also computed the correlation between recruitment residuals and daily flow averaged over both months, and found that it had a higher correlation than daily discharge averaged over each month individually (Table 5).

In an attempt to see if there was some other aspect of flow that may have better predictive ability, we also examined correlations between the recruitment residuals and the maximum and minimum daily and weekly discharge for the basin as a whole and for each river (Klamath and Trinity) individually monthly mean flow for each River separately. These variables are highly correlated with each other, and showed similar patterns of

correlation with recruitment residuals. The highest correlation observed (0.625) was with the minimum daily flow in the month of November.

To investigate the predictive capability of these relationships, we included them as independent variables in the spawner-recruit regression.

$$\log(R/S) = \alpha + \beta X + \varepsilon,$$

Where β is a vector of coefficients and X is a vector of predictor variables (spawners, survival index, and flow variables). While inclusion of flow variables marginally improved the fit of the spawner-recruit relationship (Table 6), the improvement was less than that of including the survival index. In every case examined, when flow variables were included in the regression, the loss of degrees of freedom resulted in lower overall significance of the fit, than the same model without the flow variables included.

Table 6. Results of including hatchery survival index and flow variables in the spawner-recruit regression.

Model (predictor variables)	Adjusted R²	d.f.	F
Spawners (S)	0.535	20	25.16
S + log(survival)	0.777	19	37.66
S + Sept-Oct flow	0.616	19	22.57
S +log(survival) + Sep-Oct flow	0.814	18	26.24
S + Nov minimum flow	0.622	19	18.28
S + log(survival) + Nov min flow	0.782	18	26.14

Because including flow variables in the spawner-recruit relationship resulted in lower significance of the overall regression, we did not pursue further investigations with flow relationships.

Literature Cited

- Bartolow, J. M. 2005. Recent Water Temperature Trends in the Lower Klamath River, California. *North American Journal of Fisheries Management* 25:152–162.
- CDFG (California Department of Fish and Game). 2005. Klamath River Basin fall Chinook salmon spawner escapement, in-river harvest and run-size estimates 1978–2004. Unpublished memorandum. California Department of Fish and Game, Trinity River Project Office, Arcata, CA.
- CTC (Chinook Technical Committee). 1999. Maximum sustained yield or biologically based escapement goals for selected Chinook salmon stocks used by the Pacific Salmon Commission's Chinook Technical Committee for escapement assessment, Volume I. Pacific Salmon Commission, Joint Chinook Technical Committee Report. TCCHINOOK (99)-3.
- Goldwasser, L., M. S. Mohr, A. M. Grover, and M. L. Palmer-Zwahlen. 2001. The supporting databases and biological analyses for the revision of the Klamath Ocean Harvest Model. Unpublished report. National Marine Fisheries Service, Southwest Fisheries Science Center, Fisheries Ecology Division, Santa Cruz, CA.
- Hilborn, R. 1985. Simplified calculation of optimum spawning stock size from Ricker's stock recruitment curve. *Canadian Journal of Fisheries and Aquatic Sciences*, 42:1833–1834.
- Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics, & uncertainty. Chapman and Hall, New York.
- Hubbell, P.M. and L.B. Boydstun. 1985. An assessment of the current carrying capacity of the Klamath River Basin for adult fall Chinook salmon. Inland Fisheries Division, California Department of Fish and Game, October 9, 1985.
- KRTAT (Klamath River Technical Advisory Team). 1999. Population dynamics of Klamath River fall Chinook salmon: stock-recruitment model and simulation of yield under management. Technical Report to Klamath Fishery Management Council. U.S. Fish and Wildlife Service, Yreka Fish and Wildlife Office, Yreka, CA.
- KRTAT (Klamath River Technical Advisory Team). 2002. Ocean abundance projections and prospective harvest levels for Klamath River fall Chinook, 2002 season. Technical Report to Klamath Fishery Management Council. U.S. Fish and Wildlife Service, Yreka Fish and Wildlife Office, Yreka, CA. March 8, 2002.
- KRTAT (Klamath River Technical Advisory Team). 2005. Ocean abundance projections and prospective harvest levels for Klamath River fall Chinook, 2005

season. Technical Report to Klamath Fishery Management Council. U.S. Fish and Wildlife Service, Yreka Fish and Wildlife Office, Yreka, CA.

Quinn, T. J., II, and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, New York.

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

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada, Bulletin No. 191*.

STT (Salmon Technical Team). 2005. Review of 2004 ocean salmon fisheries. Pacific Fishery Management Council. Portland, OR.

USFWS (United States Fish and Wildlife Service). 1979. Final Report. Hoopa Valley Indian Reservation. Inventory of reservation waters fish rearing feasibility study and a review of the history and status of anadromous fishery resources of the Klamath River Basin. USFWS, Arcata Field Station, Arcata, CA. March 15, 1979.

Walters, C.J. and P. Cahoon. 1985. Evidence of decreasing spatial diversity in British Columbia salmon stocks. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1033–1037.

Appendix A: Model 1

Data. The $\{R, S\}$ data are presented in Table A1. BY denotes brood year; $N_{3,Sept1}$ denotes the abundance of progeny spawned by S in calendar year BY that survive to become ocean age 3 on September 1 in calendar year $BY + 3$; $R = R_3 + R_4 + R_5$ denotes recruitment and is equal to $N_{3,Sept1}$ in adult equivalent units. That is, R_a is the number of $N_{3,Sept1}$ that would have been expected to spawn at age $\{a = 3,4,5\}$ if no fishing would have occurred:

$$R_a = N_{3,Sept1} \left[\prod_{j=3}^{a-1} (1-v_j)(1-m_j) \right] (1-v_a)m_a(1-r_a), \quad (A1)$$

where $v_a = 1 - \prod_{t=Sept}^{Aug} (1-v_{at})$ is the annual natural mortality rate at age a absent fishing; v_{at} is the age a natural mortality rate in month t ; m_a is the age a maturation rate (taken to occur on August 31); and r_a is the age a out-of-basin stray rate. The $\{m_a, a = 3,4,5\}$ are also year-specific. Values of $N_{3,Sept1}$, $\{v_{at}\}$, $\{m_a\}$, and $\{r_a\}$ were provided by the Klamath River Technical Advisory Team.

Table A1. Klamath River fall Chinook stock-recruitment data set.

BY	$N_{3,Sept1}$	R_3	R_4	R_5	R	S	R/S
1979	423701	42235	137103	21360	200698	30637	6.6
1980	236144	28082	56102	25246	109430	21484	5.1
1981	106338	16737	26354	7877	50968	33857	1.5
1982	277850	17331	61442	43414	122187	31951	3.8
1983	776743	73352	259838	34969	368159	30784	12.0
1984	512171	46576	181026	16450	244052	16064	15.2
1985	391378	52017	119909	16796	188722	25676	7.4
1986	256532	29759	84135	9353	123247	113359	1.1
1987	148910	20399	50415	2167	72981	101717	0.7
1988	37029	2871	13010	1569	17450	79385	0.2
1989	33368	4921	9962	1330	16213	43869	0.4
1990	85146	29185	13186	2539	44910	15596	2.9
1991	91590	29578	18478	457	48513	11649	4.2
1992	526545	129836	132474	7368	269678	12029	22.4
1993	177305	40102	48124	1984	90210	21858	4.1
1994	99535	24195	24978	1667	50840	32333	1.6
1995	72062	28271	10703	229	39203	161793	0.2
1996	74965	17305	21052	51	38408	81326	0.5
1997	327575	84784	76782	6523	168089	46144	3.6
1998	253386	62628	66021	1634	130283	42488	3.1
1999	406036	74558	89368	32271	196197	18456	10.6
2000	386121	60997	112628	14912	188537	82729	2.3

Model/Estimation. Basic regression statistics for the fitted model are presented in Table A2.

Table A2. Model 1 regression statistics.

Model	Coef.	Estimate	Std. Err.	t-value	Pr(> t)
$\log(R/S) = a + bS + \varepsilon$	a	2.143e+00	3.079e-01	6.962	9.31e-07
	b	-2.517e-05	5.018e-06	-5.016	6.62e-05
Residual standard error: 0.9005 on 20 degrees of freedom.					
F-statistic: 25.16 on 1 and 20 degrees of freedom, p-value: 6.625e-05.					
R-squared: 0.5571.					

We note that the Ricker model could be alternatively fit using least-squares regression as $\log(R) = a + \log(S) + bS + \varepsilon$, with an implicit coefficient of 1 for the $\log(S)$ term (in other words, by treating $\log(S)$ as an “offset”). Note that the hypothesis to be tested $H_0 : b = 0, H_1 : b \neq 0$, has an equivalent interpretation under both transformations. The base model under H_0 is $R = \alpha S e^\varepsilon$; density-independent recruitment. The model under H_1 is the Ricker model; density-dependent recruitment. The base model under consideration therefore is not a constant recruitment model, $R = \alpha e^\varepsilon$; which isn't a submodel of either formulation. While the $\log(R/S)$ transformation is convenient, it is often noted that with S appearing on both sides of the equation correlation will be induced between $\log(R/S)$ and S , even if $\text{covariance}(R, S) = 0$. Though true, both transformations lead to the same point estimates and residual sums-of-squares terms, and thus both transformations lead to equivalent regression R-squared and F-statistic values as these are functions of the residual sums-of-squares terms (M. S. Mohr³, unpublished). To emphasize, R-squared is the fraction of the density-independent model residual variation, in $\log(R/S)$ or $\log(R)$, that is accounted for by introduction of the density-dependent term, bS . It is not the fraction of variation in R accounted for by the Ricker model.

Regression model graphical diagnostics are presented in Figures A1–A4 that examine the appropriateness of analysis assumptions 1–3. Numbers that appear within Figures A1–A4 denote brood year order within the time series (i.e. “1” represents *BY* 1979, “2” represents *BY* 1980, ... , “22” represents *BY* 2000). Figure A1 is a plot of the normalized residuals versus fitted values; a horizontal band of points symmetric about the value 0 is expected under the Ricker model (assumption 1). Figure A2 is a quantile-quantile (Q-Q) plot of the observed versus residuals expected for a normally distributed error term; a straight line is expected under the model (assumption 3). Figure A3 is a plot of Cook's distance which is a measure of the relative influence of each data point on the regression parameter estimates. Figure A4 is a plot of the autocorrelation function (ACF) versus lag, which examines the dependence of the model residuals on time; correlations contained within the two dashed lines are statistically insignificant; for lag 0 the correlation is 1 by definition (assumption 2).

³ National Marine Fisheries Service, Southwest Fisheries Science Center, Fisheries Ecology Division, Santa Cruz, CA.

Diagnostics: Ricker model

Figure A1. Residuals vs fitted.

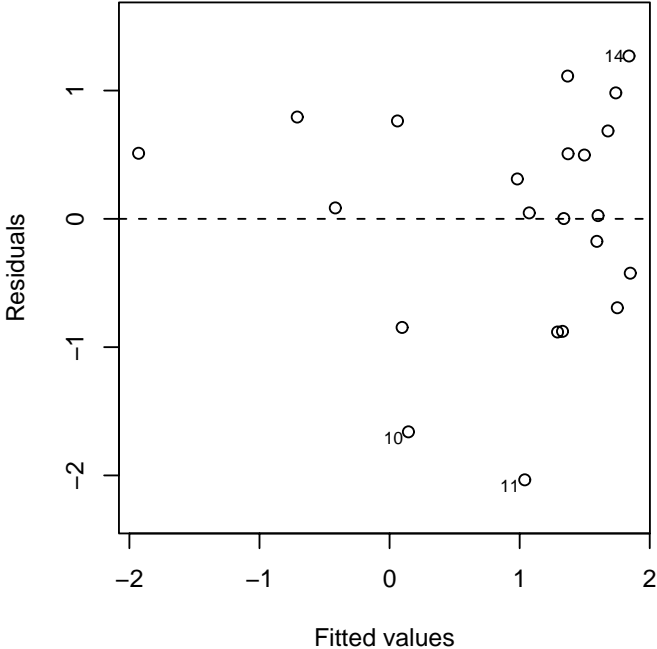


Figure A2. Normal Q-Q plot.

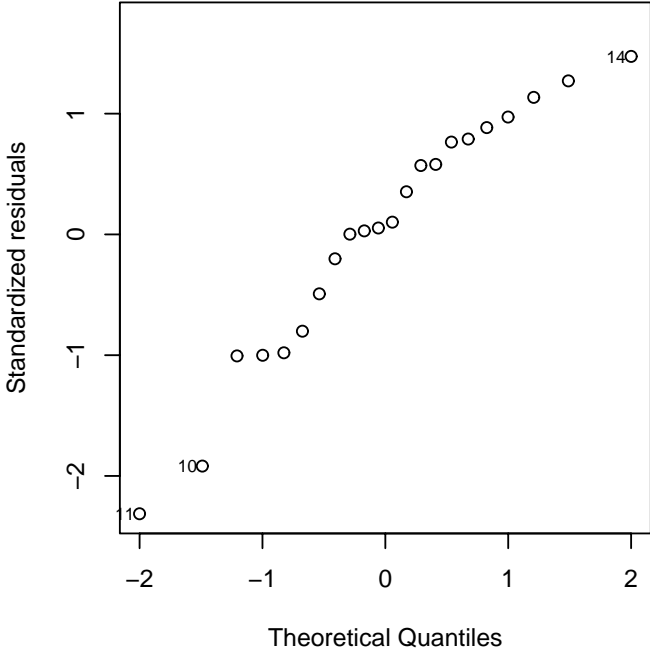


Figure A3. Cook's distance.

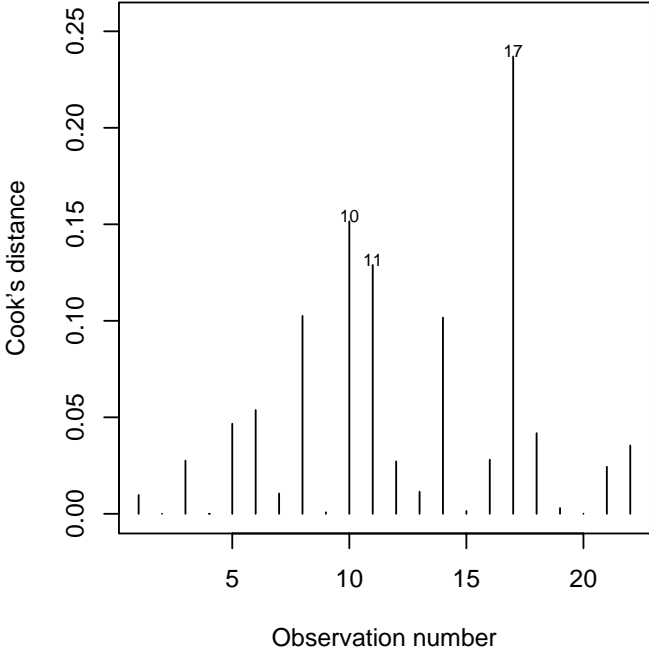
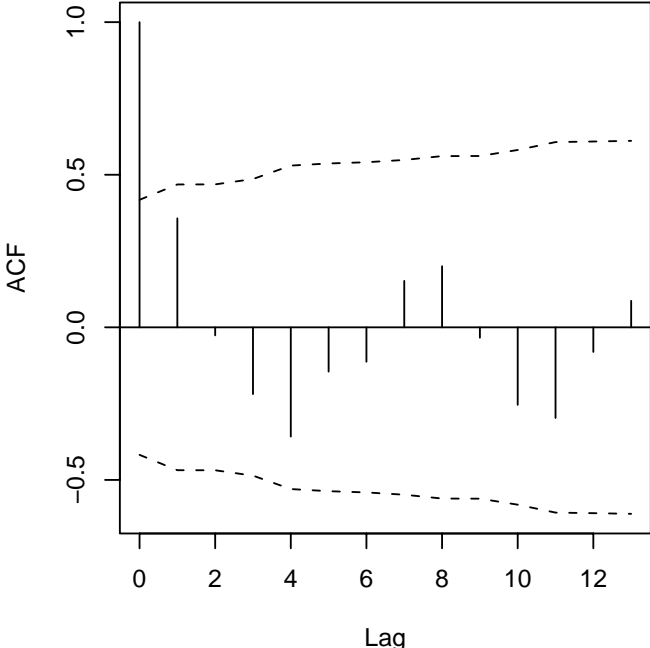


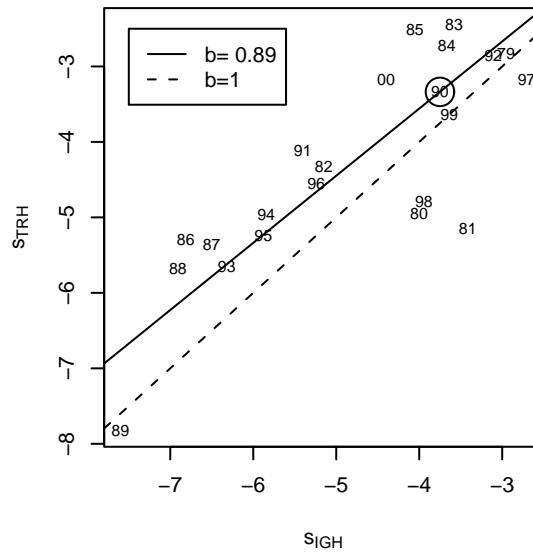
Figure A4. Residual autocorrelation.



Appendix B: Model 2

Data. The $\{s'_{IGH}\}$ and $\{s'_{TRH}\}$ sets of survival rate estimates were independently derived based on the results of cohort analyses performed separately on fingerling cwt groups released from the two hatcheries. For a given brood year and hatchery, s' was computed as the estimated abundance of fingerling releases that survived to the onset of age 2 (approximately four months after release, on September 1) divided by the initial number released. Brood-year-specific estimates of s' for each hatchery are available for all of the $\{R, S\}$ dataset brood years, except for $s'_{TRH,1990}$. The log of the estimates, s_{IGH} and s_{TRH} , for each brood year are plotted against each other in Figure B1. The two time

Figure B1. log(survival): TRH vs IGH.



series of estimates are well correlated ($r = 0.80$). The solid line in Figure B1 depicts a least squares regression fit through the origin:

$$\hat{s}_{TRH} = 0.89s_{IGH} ; \quad (B1)$$

the dashed line is a 1:1 reference line. The regression was used to impute the missing value of $s_{TRH,1990}$ based on the value of $s_{IGH,1990}$. The imputed data point is circled in Figure B1. The full $\{s'_{IGH}, s'_{TRH}\}$ dataset, including the imputed value, is presented in Table B1.

Because the stock-recruitment analysis is not sub-basin-specific, the two estimates for each brood year must be combined in a way thought to be most representative of the composite natural stock. The most appropriate weighting would be natural stock sub-basin-specific age-two recruitment of each brood, but that data is unavailable. A proxy measure for this would be natural stock sub-basin-specific spawning escapement of each brood (across ages), but sub-basin-specific natural area spawner age composition data

Table B1. Klamath River fall Chinook early-life survival data set.

<i>BY</i>	s'_{IGH}	s'_{TRH}	S_{KR}	S_{TR}	S_{UN}	w_{KR}	w_{TR}	s'
1979	0.0522	0.0589	21141	8028	1468	0.725	0.275	0.0540
1980	0.0183	0.0071	12383	7700	1400	0.617	0.383	0.0140
1981	0.0329	0.0058	17517	15340	1000	0.533	0.467	0.0202
1982	0.0058	0.0133	21177	9274	1500	0.695	0.305	0.0081
1983	0.0279	0.0870	12230	17284	1270	0.414	0.586	0.0625
1984	0.0255	0.0656	9420	5654	990	0.625	0.375	0.0405
1985	0.0174	0.0814	12166	9217	4294	0.569	0.431	0.0450
1986	0.0011	0.0050	15893	92548	4919	0.147	0.853	0.0044
1987	0.0015	0.0047	26511	71920	3286	0.269	0.731	0.0038
1988	0.0010	0.0034	29783	44616	4987	0.400	0.600	0.0024
1989	0.0005	0.0004	10584	29445	3839	0.264	0.736	0.0004
1990	0.0235	*0.0356	7102	7682	812	0.480	0.520	0.0298
1991	0.0045	0.0164	5905	4867	877	0.548	0.452	0.0099
1992	0.0447	0.0575	4135	7139	754	0.367	0.633	0.0528
1993	0.0018	0.0035	13385	5905	2568	0.694	0.306	0.0023
1994	0.0029	0.0070	20003	10906	1424	0.647	0.353	0.0043
1995	0.0028	0.0053	79851	77876	4067	0.506	0.494	0.0040
1996	0.0053	0.0106	31755	42646	6925	0.427	0.573	0.0083
1997	0.0668	0.0419	29015	11507	5622	0.716	0.284	0.0597
1998	0.0194	0.0083	16407	24460	1621	0.401	0.599	0.0128
1999	0.0263	0.0265	10883	6797	777	0.616	0.384	0.0264
2000	0.0123	0.0421	58388	24340	0	0.706	0.294	0.0211

* imputed value: $\hat{s}'_{TRH,1990} = \exp(0.89s'_{IGH,1990})$.

isn't available prior to 1991, and also differing maturation schedules for Klamath River and Trinity River fall Chinook (and thus exposure to fisheries) would confound the relation between sub-basin-specific age-two recruitment and brood spawning escapement. Instead, the hatchery-specific survival rate estimates were weighted proportional to the sub-basin-specific natural area parent spawner abundance (age 3 and older) of that brood year (i.e., proportional to sub-basin initial production). These spawner abundances are listed in Table B1, with S_{KR} and S_{TR} denoting Klamath and Trinity Basin natural area spawner abundance (age 3 and older), respectively. Prior to 2000, there is a small number (typically < 10%) of natural area spawning fish that were accounted for, but for which the spawning sub-basin was unspecified, and these fish are listed in Table B1 as S_{UN} . Together: $S_{KR} + S_{TR} + S_{UN} = S$. Given these data, the weights were calculated as

$$w_{KR} = \frac{S_{KR}}{S_{KR} + S_{TR}} \quad \text{and} \quad w_{TR} = \frac{S_{TR}}{S_{KR} + S_{TR}}, \quad (\text{B2})$$

from which the brood-year-specific survival rate weighted average was computed as

$$s' = w_{KR}s'_{KR} + w_{TR}s'_{TR} \quad (\text{B3})$$

(Table B1). Finally, we note that the interannual variation in s' substantially exceeds the intrannual variation in s'_{KR} and s'_{TR} , and thus the Model 2 overall results should be fairly insensitive to the choice of weights.

Model/Estimation. To evaluate the significance of the Model 2 parameter θ , and thus the significance of Model 2 versus Model 1, an F-statistic for the nested submodel was used:

$$F = \frac{(RSS_1 - RSS_2)/(df_1 - df_2)}{RSS_2 / df_2}, \quad (B4)$$

which is distributed as $\mathcal{F}(df_1 - df_2, df_2)$ under the basic model structure if $\theta = 0$, where RSS_i is the residual sum-of-squares under Model i ($i = 1, 2$), and df_i is the associated degrees of freedom. The analogous R-squared value

$$\text{R-squared} = 1 - \frac{RSS_2}{RSS_1} \quad (B5)$$

measures the fraction of Model 1 residual variation accounted for by the introduction of s into the model. Basic regression statistics for the fitted models are presented in Table B2.

Table B2. Model 2 regression statistics.

Model	Coef.	Estimate	Std. Err.	t-value	Pr(> t)
$s = a + bS + \varepsilon$	a	3.751e+00	4.184e-01	-8.965	1.92e-08
	b	-1.400e-05	6.820e-06	-2.052	5.35e-02
Residual standard error: 1.224 on 20 degrees of freedom. F-statistic: 4.211 on 1 and 20 degrees of freedom, p-value: 5.349e-02. R-squared: 0.1739.					
$\text{resids}\{(R/S) S\} = a + b * \text{resids}\{s S\} + \varepsilon$	a	0	-	-	-
	b	5.433e-01	1.110e-01	4.896	8.72e-05
Residual standard error: 0.6073 on 20 degrees of freedom. F-statistic: 23.98 on 1 and 20 degrees of freedom, p-value: 8.724e-05. R-squared: 0.5452.					
$\log(R/S) = a + bS + c(s - \bar{s}) + \varepsilon$	a	1.779e+00	2.263e-01	7.859	2.18e-07
	b	-1.757e-05	3.820e-06	-4.599	1.96e-03
	c	5.433e-01	1.138e-01	4.772	1.32e-04
Residual standard error: 0.6231 on 19 degrees of freedom. $H_0 : b = c = 0 a$. F-statistic: 37.67 on 2 and 19 degrees of freedom, p-value: 2.449e-07. R-squared: 0.7986. $H_0 : c = 0 a, b$. F-statistic: 22.78 on 1 and 19 degrees of freedom, p-value: 1.324e-04. R-squared: 0.5452.					

Model 2 regression diagnostics are presented in Figures B2–B5 that examine the appropriateness of analysis assumptions 1–3. These are the same diagnostics that were used for Model 1. The interpretation of Figures B2–B5 are described in Appendix A.

In Figure B6, the Model 1 fit (dashed curve) is contrasted with the brood-year-specific Model 2 fit (solid curves). There is one plot for each brood year, with the brood year label marking the respective (R , S) data point. For all brood years except 1979 and 1997, Model 2 provides an as good or better fit to the observed (R , S) data than does Model 1 without the s covariate. The highest R/S values (brood years 1983, 1984, 1992) at low S values are now partially accounted for by the relatively high early-life survival following outmigration for those brood years. The lowest R/S values (brood years 1988, 1989) are now partially accounted for by the relatively low early-life survival following outmigration for those brood years.

Diagnostics: Ricker model w/ survival

Figure B2. Residuals vs fitted.

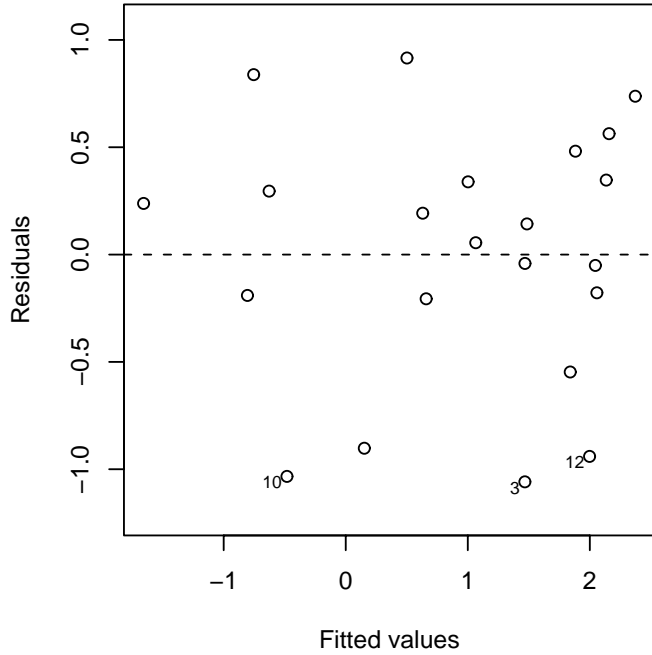


Figure B3. Normal Q-Q plot.

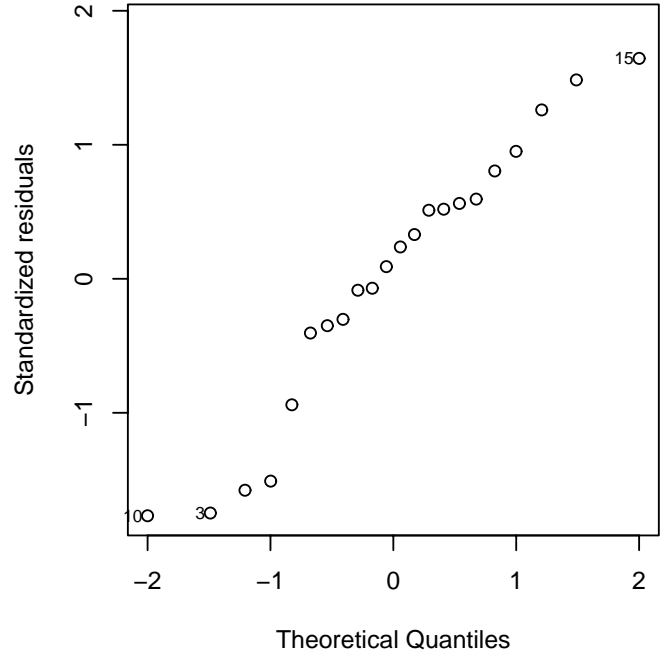


Figure B4. Cook's distance.

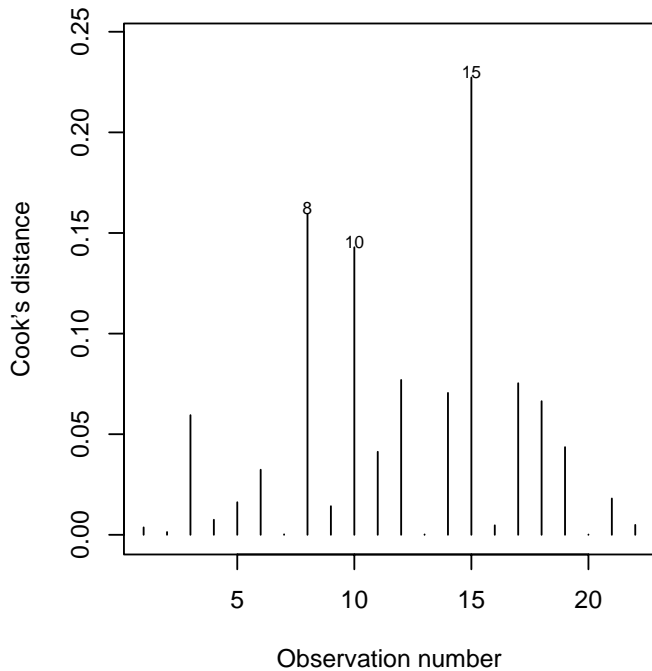


Figure B5. Residual autocorrelation.

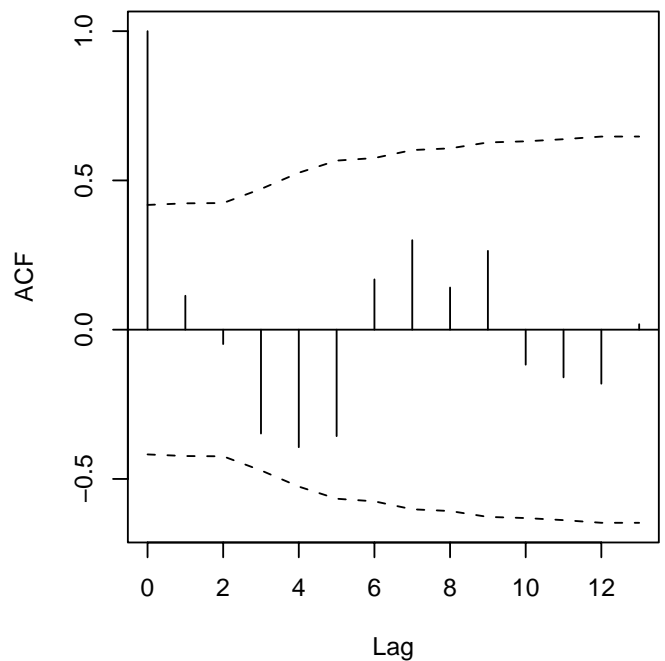


Figure B6. Brood-year-specific Ricker w/ survival.

