Part V. APPENDIX
Stock-Recruit Analysis of Hoh River Wild Winter-Run Steelhead Data
For Brood Years 1978 to 1999
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I. Raw Data and Data Reconstruction for Analysis.

Data for Hoh River wild winter-run steelhead was obtained from Washington Department of Fish and Wildlife in a Microsoft Excel ® file named "HohRiver_WSH120705.xls". The file included spawner escapement data for brood/spawning years 1978 to 2005, and wild run size data for spawning return years 1980 to 2005. Assuming that the majority of recruits are ages 4 to 6 as in the nearby Quilleute River system, this permitted spawner-recruit data to be calculated for 22 brood years, 1978 to 1999.

No age or repeat spawner data for wild recruits was provided, so I made the assumption that both age-composition and repeat spawning frequency of Hoh River adult recruits was identical to that of the Quilleute River for which annual age and repeat spawner data is available for the same period. Based on the data for this period, wild Quilleute River winter steelhead adults have the following age composition: Age-4: 0 .4725, age-5: 0.467, and age-6: 0.0605. The average proportion of repeat spawners is 0.1094 (standard deviation 0.0465).

To estimate recruits from the wild run data I employed the assumptions about age composition and proportion of repeat spawners as follows. All age-4 adults are first-time spawners. Consequently, the average proportion of each annual wild run consisting of repeat spawners (0.1094) is composed exclusively of 5 and 6 year olds. The proportion of all 5 and 6 year olds in each run is 0.5275 (0.467 + 0.0605). In order for this proportion to contain repeat spawners comprising 0.1094 of the total run, 0.2074 must be repeat spawners (0.1094 = 0.5275*0.2074). Therefore, for each year I multiplied the wild run size by 0.4725 to derive the number of 4-year olds in the run, by 0.3701 (=0.467*(1-0.2074)) to obtain the number of 5-year old first-time spawners in the run, and by 0.048 (0.605*(1-0.2074)) to obtain the number of 6-year old first time spawners. Each of the estimated age-4, -5, and -6 first-time spawners for each return year was then assigned to the appropriate brood (spawning) year. The recruits in each age class for each spawning year were then summed to provide total recruits for each spawning year in the data set between 1978 and 1999. The resulting data is listed in Table A1. Recruits are plotted against spawner numbers together with the one-to-one replacement line and two different parameterizations of the Ricker equation in Figure A1.

II. Data Analysis and Results.

I performed a Bayesian analysis to fit the Hoh data to the following stock-recruit models: 1) the Ricker (R = alpha*S*exp(-S/beta)*e, where R is recruits, S, spawners, alpha and beta the model parameters, and e is log-normally distributed, residual error (normally distributed in the natural logarithmic space)); 2) the Beverton-Holt (R = alpha*S/(1+beta*S)*e; and, 3) Schnute-Kronlund (R = alpha*S/[(1+gamma*beta*S)$^{1/gamma}$]*e, where gamma is a third parameter that governs the shape of the fitted curve, ranging from Ricker when gamma = 0 to Beverton-Holt when gamma = 1).

Parameter estimation was conducted using the Bayesian inference program SWL (Sampling Weighted Likelihood), a Fortran program written by Dr. Daniel Goodman, Ecological Statistics Work Group, Department of Biology, Montana State University. Uniform distributions spanning a broad range of plausible parameter values were employed on all parameters for each model. 5 million random combinations of parameter values were drawn, and for each combination the model likelihood of the spawner-recruit data was calculated and assigned to each parameter. For each parameter, the range of the prior distribution was divided into 100 discrete non-overlapping bins and total likelihood values assigned to each parameter cumulated within each bin, then summed across all bins to permit reporting of both posterior probability mass values for each discrete interval (bin) and posterior cumulative probabilities. The 5 million random draws were sufficient to produce smooth posterior distributions of the parameters.

When data sets are sufficiently informative, the Schnute-Kronlund model can be helpful in determining whether the data conform closely to the Ricker or to the Beverton-Holt model or to an intermediate model. In the present case, neither the Ricker nor the Beverton-Holt models were strongly favored. The posterior distribution of the shape parameter gamma spanned most of the space of the prior distribution between 0 and 1. Approximately 70% of the probability mass was concentrated in the center of the range between 0.20 and 0.75. The posterior mean was 0.47 with a posterior standard deviation of 0.24. There were several modes between 0.35 and 0.64, with the largest mode at 0.39. Thus, not only was there no clear support for either the Ricker or the Beverton-Holt model, there was no clear support for a single intermediate model. Reasons for this are discussed below. However, it should be noted that this result from fitting the Schnute-Kronlund model indicates that caution should be used in interpreting the results of the following analyses.

Despite the uncertainty regarding model form all three models had relatively narrow and broadly overlapping posterior distributions for equilibrium abundance. The posterior distributions of residual error (sigma) were very similar for all three models. The standard deviations of the posterior distribution of the alpha parameter and equilibrium abundance were slightly smaller for the Ricker model than for either the Schnute-Kronlund or the Beverton-Holt models even when the former was fit with the shape parameter (gamma) constrained to the posterior modal value of 0.39. For these reasons I conducted the remaining analyses using the fit to the Ricker model. Given the uncertainty regarding model form and the similarities of the posterior distributions of equilibrium abundance, similar results would likely obtain if fits to the alternative models were employed instead.

An examination of Figure A1 and Table A1 reveals that positive recruitment (greater than 1:1) has occurred across the range of escapement levels reported in the data set. The largest recruitments (between 4700 and 5200) have occurred at spawner abundances between 1700 and 3100. However strong recruitment has occurred at spawner levels approaching 4000. Further, there is little if any hint of strong density dependence at escapements up to 4000. Only one data point at an escapement of almost 4600 (in 1983) displayed a recruitment level that fell below the replacement line, and this point was only marginally below replacement (recruit-to-parent ratio = 0.971). This makes it nearly impossible to determine the strength of density dependence over the range of escapements observed. It also makes it difficult to estimate with much certainty where the equilibrium level is, except that it is likely that escapements at or above the equilibrium level have not been observed in the data set. This is largely why the data provide such little information about the shape (model form) of the stock-recruit relationship for this population over the time period covered by the data.

There is only one data point (1979) where the level of escapement fell below 2000. Seven data points occur a escapement levels between 2000 and 2400 and these exhibit recruitments ranging from about 3300 to 4800. This results in a significant degree of uncertainty regarding the value of the alpha parameter of the stock-recruit models, the productivity of the population at low abundances. There is even less information about the possibility of depensation at very low spawner levels.

The results of the Ricker stock-recruit analysis are presented graphically in Figures A2 – A6. Posterior means, standard deviations and modes are given in the legends to the figures, but are summarized here. The central 50% of the posterior probability distribution of alpha lies approximately in the interval [3.1, 3.83]. The mean (standard deviation) is 3.53 (0.0536). The mode is 3.35.

The central 50% of the posterior probability distribution of beta (the spawning stock size at which maximum recruitment occurs) lies approximately in the interval [2850, 3600]. The mean (standard deviation) is 3403 (682). The mode is 3112.

The central 50% of the posterior probability distribution of sigma (residual, process error) lies approximately in the interval [0.12, 0.165]. The mean (standard deviation) is 0.159 (0.028). The mode is 0.157.

Equilibrium abundance (EQ) is a derived parameter determined jointly by the values of alpha and beta according to the equation EQ = Ln(alpha)*beta.[1] The central 50% of the posterior probability distribution of equilibrium abundance lies approximately in the interval [3900, 4200]. The mean (standard deviation) is 4153 (290). The mode is 4010. The 95th percentile posterior value is 4570. That is, there is a 5% probability – given the data, the model, and the prior distributions – that the equilibrium abundance level for the population is greater than 4570.

[1] The posterior probability distribution of EQ was generated by calculating the value of Ln(alpha)*beta from the pairs of alpha and beta values randomly drawn from the prior distributions for alpha and beta, calculating the likelihood of each of those pairs of values having produced the stock-recruit data points, and assigning each of those likelihood values to the calculated value of EQ and cumulating those values in discrete bins as for the primary parameters.

Figure A6 shows the log residuals (Ln(Actual Recruits/Predicted Recruits)) from a Ricker model using the posterior modal values for alpha and EQ from the Bayesian analysis. The associated Ricker model curve is plotted in Figure A1 and labeled 'Modal Ricker Fit'. The posterior mode of EQ was used rather than the posterior mode of beta for the following reasons. There is a strong negative correlation between the alpha and beta parameters inherent in the Ricker model (as well as in the Beverton-Holt and Schnute-Kronlund models). Consequently, the individual posterior modal values of alpha and beta are not likely to be the modal values of the *joint posterior* of alpha and beta. This latter value is the most probable (under the model, the data, and the priors) pair of alpha and beta values. It is unlikely that the most probably values of alpha and of beta individually will also be the most probable pair.

The joint posterior mode of alpha and beta can be tracked using a derived parameter that is directly dependent on both alpha and beta, such as EQ. This does not, however, provide the separate values of alpha and beta that generate particular values of EQ. To provide an approximate decomposition of values of alpha and beta for the modal value of EQ I proceeded as follows. The coefficient of variation (standard deviation/mean) of the posterior distribution of alpha was smaller than the posterior of beta (0.152 vs. 0.200), indicating that alpha is slightly better defined under the model than beta. Therefore, I determined the value of *beta**, defined as the value of beta that yields the posterior modal value of EQ given the posterior modal value of alpha. (Beta* = EQ-mode/Ln(alpha-mode).) Applying the posterior modal values for alpha (3.345) and EQ (4010) yields a value for beta* of 3321 (compared to the posterior modal beta value of 3112). I then used alpha and beta* in the Ricker equation to predict recruits for the Hoh spawner series. Thus the equation employed was R = 3.345*S*exp(-S/3321). I then examined the log residuals from these prediction by plotting them against spawner year as shown in Figure A6.

The residuals show a pronounced and steady decline from the start of the data set in spawner year 1978 to 1991, switching from positive to negative residuals during this interval in spawner year 1985. This was followed by a slower rebound that peaked with modestly positive residuals in 1997 before again declining steadily in 1998 and 1999. This does not appear to be a cyclical pattern, since the rebound period where residuals were positive is much shorter than the initial period of decline during which residuals were positive and generally of greater magnitude than the peak residuals of 1996 and 1997 in the brief rebound period.

Rather, it appears that midway through the period 1978 to 1991 there was a shift (downturn) in recruitment dynamics. This is suggested by noting in Table A1 that during the latter half of the downturn period when residuals were negative escapement levels were below 3000 (between 2000 and 3000) in all years but 1985 when 3228 were estimated to have spawned. If this is the case, then there are at least two periods with distinct stock-recruit dynamics contained in the data set, not one as is implied by the fitting procedure (as discussed in the body of this report). Consequently, as discussed in the body of the report there is too little data (too short a time series) to expect to estimate with much accuracy any of the component stock-recruit relations that likely have governed the population at different times during the period of record.

It is important to note, however, that the two significantly positive residuals from 1996 and 1997 occurred at escapements of 2340 and 3008 and that the slightly negative residual for 1998 was associated with a data point that had a positive recruitment of 3857 from 3689 spawners and even the smallest residual of 1999 was associated with a positive recruitment of 3324 from 3095 spawners. This suggests that equilibrium abundance may not have changed greatly from the range estimated in the model posterior for EQ.

III. Conclusion.

It appears that the Hoh winter-run steelhead population was in a period of decline at the beginning of the collection of spawner-recruit data and that the decline continued through the 1980s. There may also have been a shift in stock-recruit dynamics to a less productive state during the period of decline. Factors responsible for such a decline could include interactions with hatchery steelhead plantings, unaccounted harvest, and shifts in ocean survivals. Research should be directed at these and other potential factors.

Despite the uncertainties attending the stock-recruit analysis of this data set, the data contains evidence that the population remains modestly productive and has a spawning capacity much larger than the current escapement goal of 2400. Both life history diversity and system capacity should be encouraged by raising the target escapement threshold to above 3500. The 95th percentile of the posterior cumulative distribution of EQ under the Ricker model is 4570. The value of beta associated with this value and the modal value of alpha (3.35) is 3780 (4570/Ln(3.345)). If the true equilibrium population size was 4570 and the true value of alpha was 3.345, maximum recruitment (= 4652) would occur at an escapement level of 3780. The curve associated with this alternative parameterization of the Ricker model is plotted on Figure A1 and labeled '95%_EQ_beta'. This would not be an unreasonable target escapement to begin a management process that would encourage this population to recover lost diversity, productivity, and capacity.

TABLE A1. Hoh Wild Winter Steelhead Spawners and Recruits for Spawning Years 1978 - 1999

Spawning Year	Spawners	Recruits
1978	3002	5113
1979	1723	4956
1980	2660	4874
1981	2224	4806
1982	3984	4356
1983	4593	4463
1984	3670	4547
1985	3228	3963
1986	3000	3911
1987	2908	3857
1988	2906	3858
1989	2808	3605
1990	2390	3403
1991	2783	3403
1992	2061	3663
1993	2053	3632
1994	2239	3620
1995	2204	3859
1996	2340	4337
1997	3008	4595
1998	3689	3935
1999	3095	3307

Figure A1.

Modal Ricker is the fit to the data of the Ricker model using the modal value of alpha (3.345) and beta* (3321) the value of beta at the modal value of alpha and the modal value of equilibrium abundance (4010) 95%_EQ_beta is the fit of the Ricker model using the modal value of alpha and the value of beta associated with the 95th percentile value of the cumulative posterior distribution of equilibrium abundance of the modal Ricker fit (95% EQ = 4570, 95%_EQ_beta = 3780). See text for further explanation.

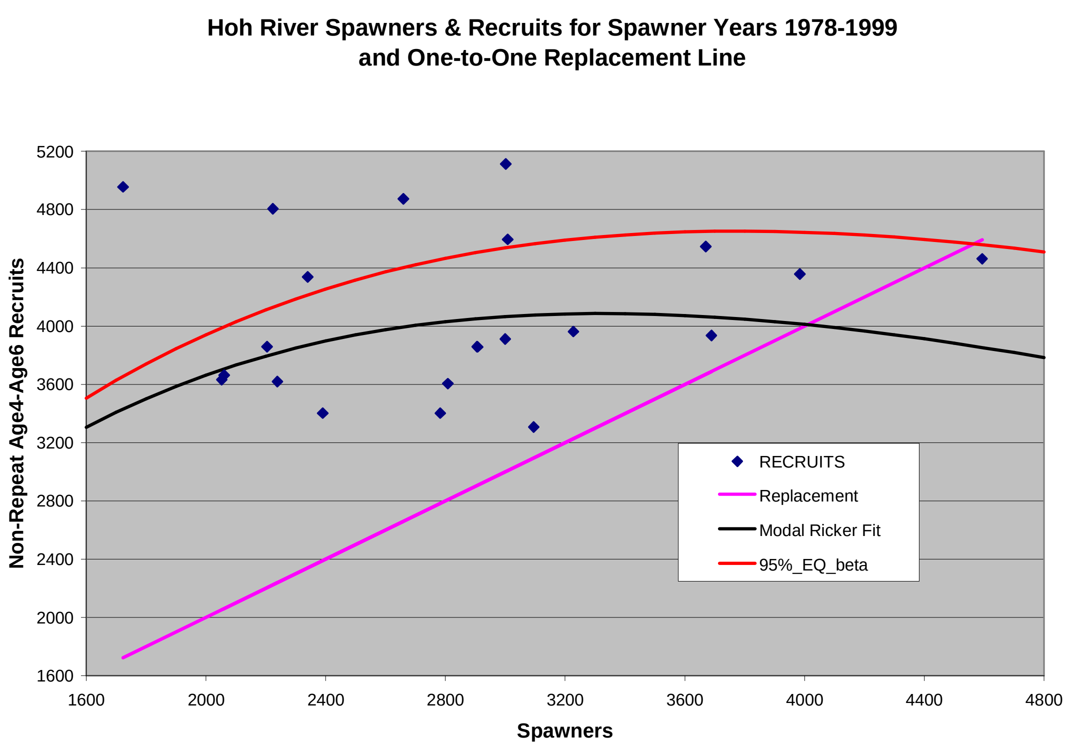

Figure A2.

Posterior Distribution of Ricker alpha parameter from fit to Hoh winter steelhead run data for brood years 1978- 1999. Prior on alpha: uniform (1.0, 8.0), beta: uniform (500, 10000), residual standard deviation, sigma: uniform (0.05, 2.0). Posterior mean (standard deviation) = 3.53 (0.0536). Posterior mode = 3.35.

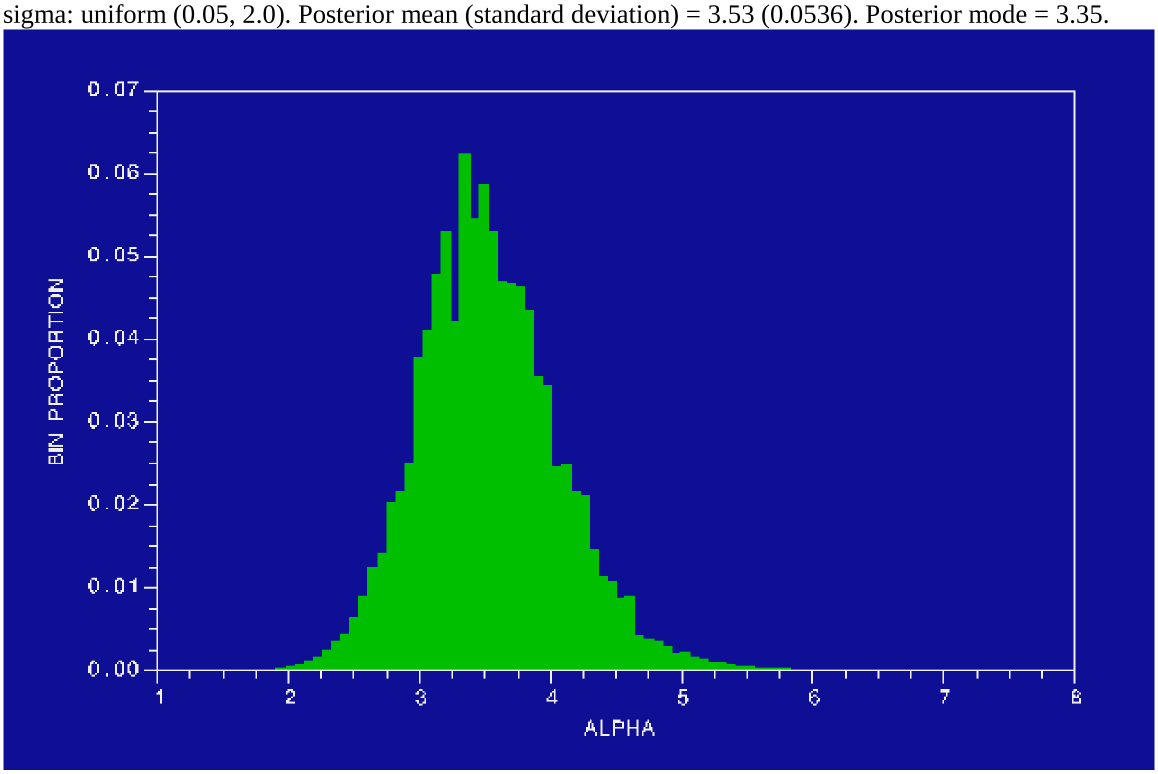

Figure A3.

Posterior Distribution of Ricker beta parameter from fit to Hoh winter steelhead run data for brood years 1978- 1999. Prior on alpha: uniform (1.0, 8.0), beta: uniform (500, 10000), residual standard deviation, sigma: uniform (0.05, 2.0). Posterior mean (standard deviation) = 3403 (681). Posterior mode = 3112.

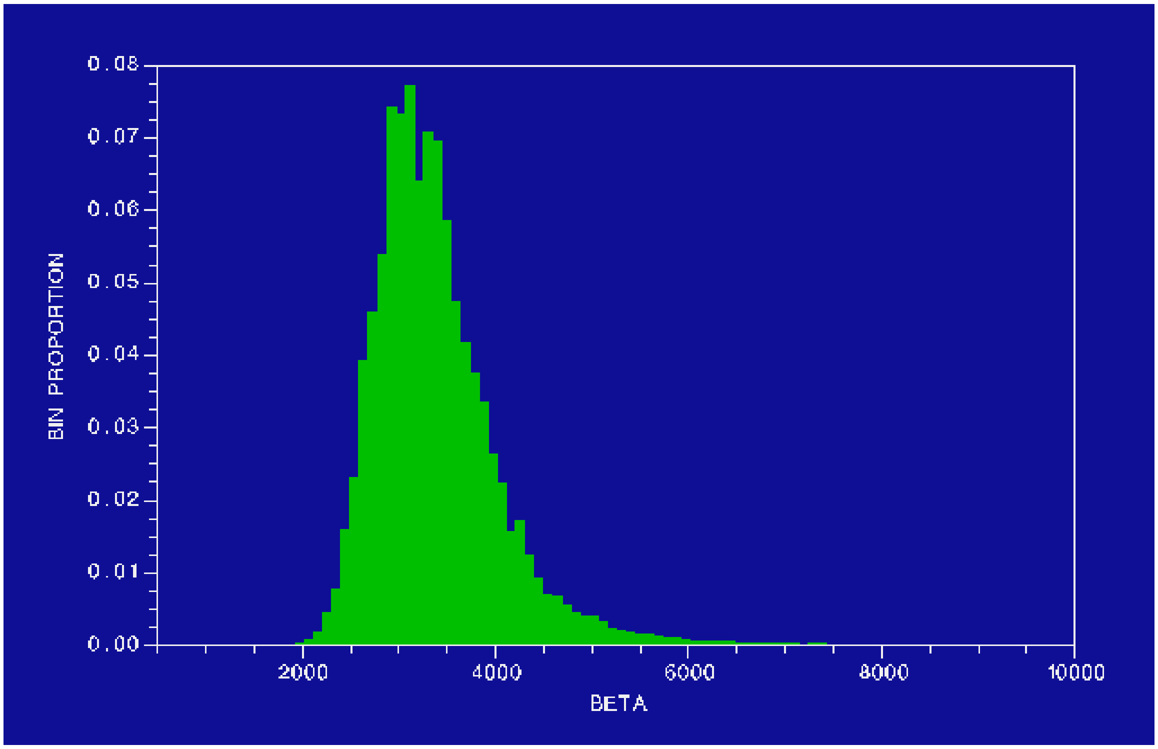

Figure A4

Posterior Distribution of Ricker sigma parameter from fit to Hoh winter steelhead run data for brood years 1978- 1999. Prior on alpha: uniform (1.0, 8.0), beta: uniform (500, 10000), residual standard deviation, sigma: uniform (0.05, 2.0). Posterior mean (standard deviation) = 0.159 (0.028). Posterior mode = 0.157.

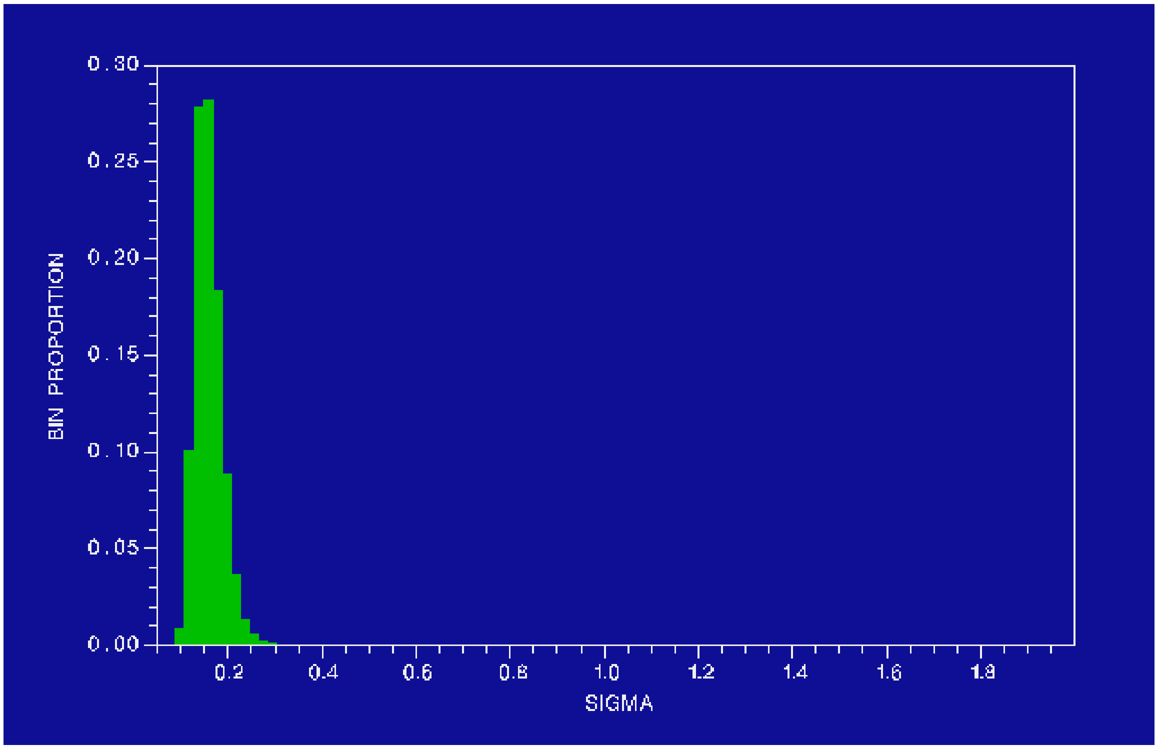

Figure A5.

Posterior Distribution of Ricker equilibrium parameter from fit to Hoh winter steelhead run data for brood years 1978- 1999. Prior on alpha: uniform (1.0, 8.0), beta: uniform (500, 10000), residual standard deviation, sigma: uniform (0.05, 2.0). Derived parameter value; posterior distribution derived from the joint posterior distribution of alpha and beta using the equation "equilibrium = Ln(alpha)*beta." Posterior mean (standard deviation) = 4153 (290). Posterior mode = 4010.

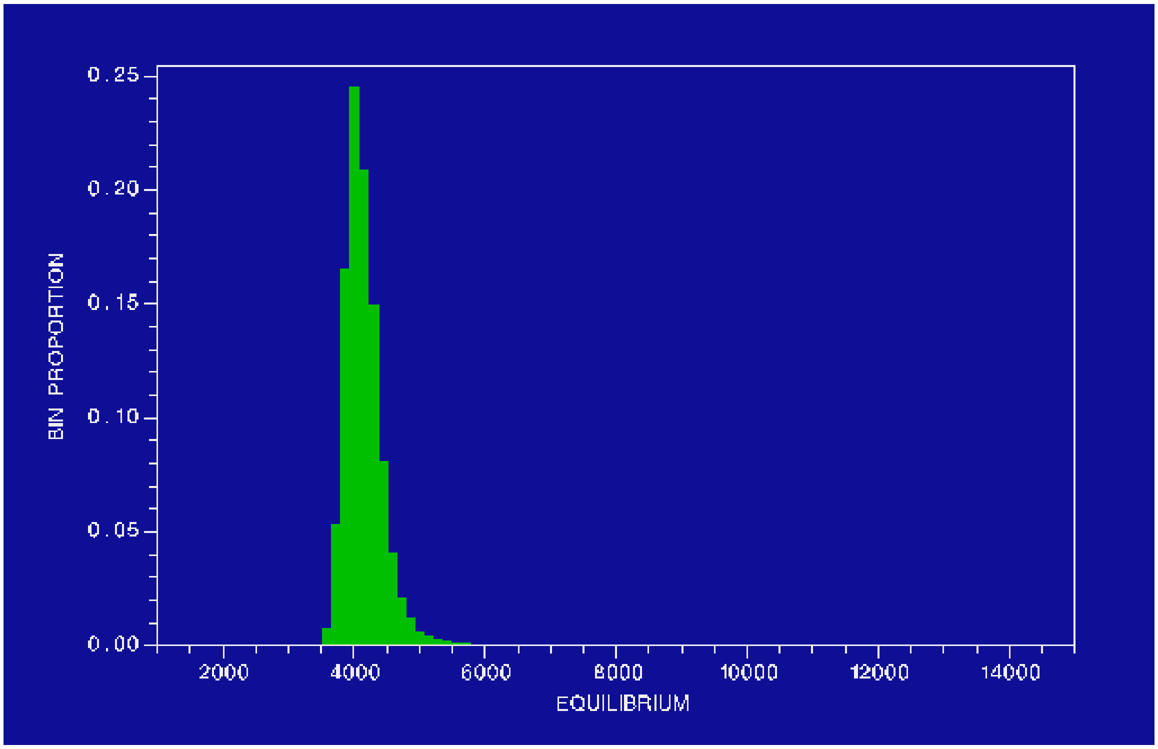

Figure A6.

Natural logarithm of residual error from posterior modal values of alpha and beta* of the Ricker stock recruit equation fir to Hoh wild winter steelhead data for brood/spawner years 1978 to 1999. See text for explanation of parameter *beta**.