Viability Status of Oregon Salmon and Steelhead Populations in the Willamette and Lower Columbia Basins

Appendix E: Conservation Assessment and Planning Model (CAPM)

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Background

The following describes CAPM (Conservation Assessment and Planning Model) a population viability model that was developed to assist salmonid conservation and recovery planning in Oregon. The model's primary outputs are forecast probabilities of population extinction. Each forecast is performed under a specific set of assumptions concerning key variables such as reproductive rate, habitat capacity, environmental variability, critical population abundance, proportion of hatchery fish, and fishery related mortality rates. Values for these variables (and others contained within the model structure) can be set to represent current conditions for the population or they can be set to reflect alternate conditions that are expected to occur in response to the implementation of specific recovery strategies. Therefore, modeling results can provide insight into the likelihood of population extinction should conditions remain unchanged in the future and also the likelihood of population extinction should these conditions change in response to implementation of successful recovery strategies.

A wide variety of viability models have been used by conservation biologists to estimate the vulnerability of populations to extinction (Shaffer 1981, 1990; Murphy et al. 1990; Nickelson and Lawson 1998). CAPM represents yet another approach to estimating population viability. It was generally based on methodology described by Burgman et al. (1993) and Morris and Doak (2002). However, CAPM also draws on original methodologies described here for the first time here.

In general, CAPM forecasts the probability of population extinction by simulating wild spawner abundance over a future time period of 100 years. Depending on the average life age of the species, this requires the simulation of 20 to 33 cycles of spawners and subsequent recruits (100 years). CAPM relies on spawner-recruit functions to accomplish this. These functions predict recruits (offspring) from two variables: 1) the number of parents (spawners), and 2) an independent environmental index of cyclic variations in freshwater and marine survival. SNEG, an index of high elevation maximum snow depths, was used as the environmental survival variable. Although, several other survival related indices were considered for this purpose (e.g. PDO, OPI, and PNI), SNEG, when evaluated across all species, appeared to have the greatest power to explain observed variations in population recruitment.

As is characteristic of all population viability models, CAPM attempts to mimic the stochastic behavior of population recruitment as it occurs in nature. Without this stochastic component added to the model, recruitment functions will always yield the same value for recruits produced for each input value for spawner abundance. So for example, from a spawner escapement 500 fish, a specific recruitment function might predict 800 recruits would be produced. More importantly, each time a spawner abundance of 500 was seeded into the recruitment function, the forecast number of subsequent recruits would always be exactly 800. However, real fish populations don't behave this way. For example, the repetition of a 500 fish spawner escapement for say 10 years in a row, would most likely result in 10 different values for the number of

recruits produced. These recruit abundance values may average 800 fish, but random and unknown variations in annual survival could easily produce a range in the annual recruit number from 400 to 1200. Therefore, the inclusion of a stochastic component to CAPM, ensured that recruitment functions would produce a range of values from each spawner abundance level rather than the same answer over and over. It was assumed that inclusion of this stochastic element would produce a more accurate model of real populations and their vulnerability to extinction.

Although the stochastic component is not unique among population viability assessment (PVA) models, there are several features of CAPM that are perhaps atypical. The first is the use of an independent environmental variable (SNEG) within the recruitment function. This was done to obtain a more accurate mathematical description of the biological recruitment process observed for each population. Secondly, rather than using only one recruitment model to simulate population recruitment, CAPM uses three. It was assumed that in doing so the adverse consequences of case by case inaccuracies of data fits to a particular recruitment function could be reduced. Thirdly, a probability of extinction was calculated for each set of recruitment function parameters estimated via the bootstrap process (description to follow). Therefore, CAPM results for each run of the model consist of many estimates of probability extinction for each population. The range, median and distribution of these extinction probabilities is used to help gauge model results in terms of uncertainty with respect to how well the shape of the recruitment curves fit observed population data.

Key topics discussed in this summary of CAPM are: 1) the population recruitment function, 2) fitting population recruitment curves, 3) addition of stochastic effects, 4) assumptions about future conditions, 5) program mechanics, and 6) model output.

Population Recruitment Function

As stated earlier three equations were used to simulate population recruitment. The first of these was based on the Beverton-Holt recruitment model (Beverton-Holt 1957). The second function was the Ski recruitment model. This is a previously undescribed recruitment curve that is similar to the Beverton-Holt (BH) model. However the Ski (SK) curve builds to maximum recruit capacity more rapidly than the BH model for each increment in spawner abundance, from mid-range spawner levels upward (Figure D1). The Crowbar model, also a previously undescribed recruitment curve, was the third function used by CAPM. The Crowbar (CB) function is similar to the SK function however it has a unique feature in that reproductive rates at very low spawner abundance levels decline rather than increase (Figure D2). As a consequence maximum recruits per spawner typically occur at higher spawner abundance levels than for either the BH or SK curves. Essentially the CB curve has built-in depensation, while the BH and SK curves do not. Mathematically these three recruitment functions are described by the following equations:

$$\text{Beverton-Holt:} \qquad R_t = (a * S_t) / (1 + (a / b * S_t)) \qquad\qquad (1)$$
$$\text{Ski:} \qquad R_t = b * (1 - \exp(-(a / b * S_t))) \qquad\qquad (2)$$

Crowbar: $R_t = b * \exp((- b * \exp(- 1)) / (a * S_t))$ (3)

Where R_t = the total number of adults produced from the spawners of a particular year (t), S_t = number of spawners in year t, a = maximum recruits per spawner, b = and capacity of habitat expressed as maximum possible recruits.
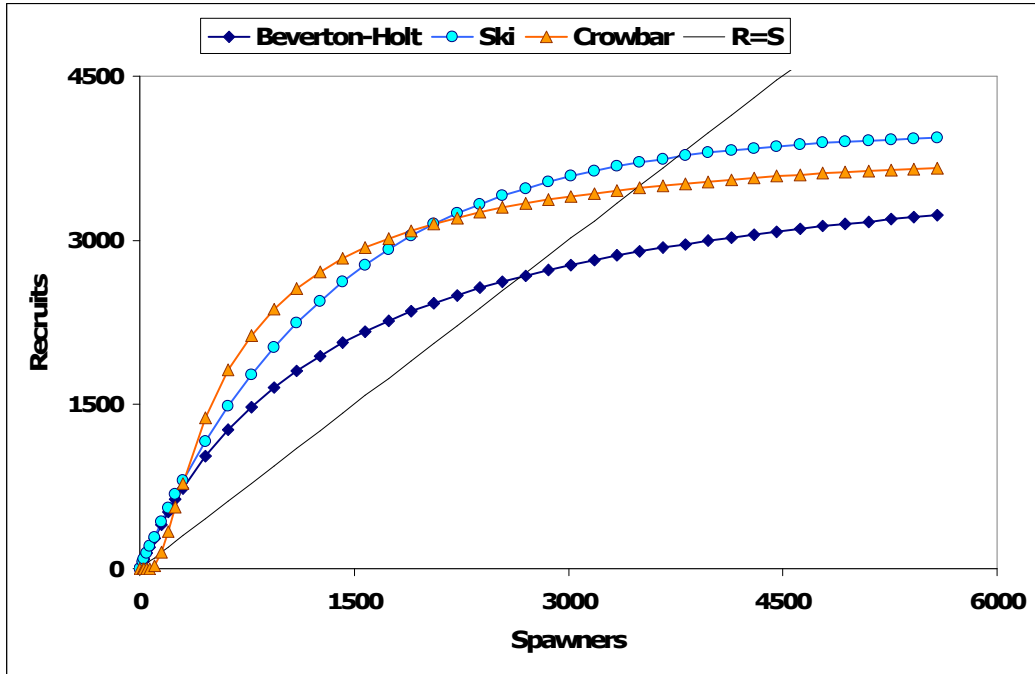

Figure D1. Recruitment curves for three spawner-recruit functions used within CAPM for an example where maximum recruits per spawner (a) equals 3.0 and maximum habitat capacity (b) equals 4,000.
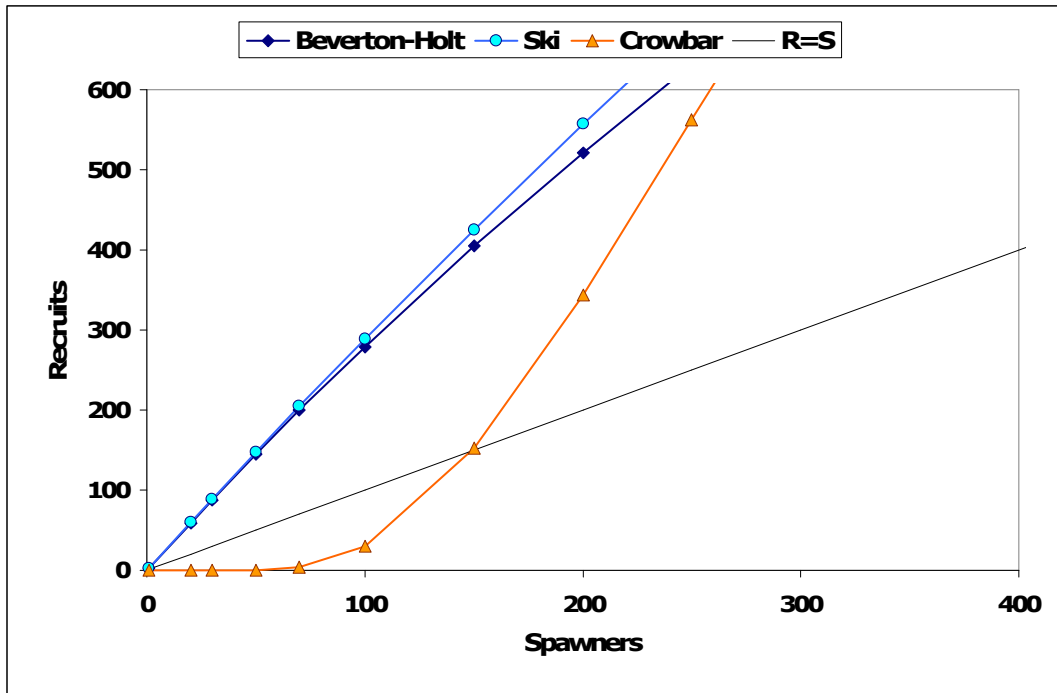
Figure D2. Recruitment curves for three spawner-recruit functions used within CAPM for an example where maximum recruits per spawner (a) equals 3.0 and maximum habitat capacity (b) equals 4,000, (same as Figure D1, but expanded to better compare functions at low spawner abundance levels).

As noted earlier, the CAPM recruitment functions included an environmental variable, SNEG. The inclusion of this variable changed the recruitment relationship from the 2-dimenisional curve of Figure D1, to a 3-dimensional recruitment surface as illustrated in Figure D3. Mathematically the inclusion of this second variable modifies the recruitment Equations 1, 2, and 3 to the following:

BH: $\quad R_t = (a * S_t) / (1 + (a / b * S_t)) * (\exp(c * SNEG_{t+m}))$ $\qquad$ (4)
SK: $\quad R_t = b * (1 - \exp(- (a / b * S_t))) * (\exp(c * SNEG_{t+m}))$ $\qquad$ (5)
CB: $\quad R_t = b * \exp((- b * \exp(- 1)) / (a * S_t)) * (\exp(c * SNEG_{t+m}))$ $\qquad$ (6)

Where R_t, S_t, a, b are as defined in previously (Equations 1, 2, and 3) and c = the parameter for the snow index $SNEG_{t+m}$ for the year t+m, where t = spawner brood year, and m = a modification number that best aligns the index to the recruitment performance of the species and region. The value for m ranges from +2 to -2.

The snow index (SNEG) was derived from the maximum annual snow depths observed at Mt. Rainier and Crater Lake National Park sample sites from 1945 to present. These annual average snow depths were then converted so they were expressed as a deviation from the 1945 to 2007 average. A negative value in the resulting data set meant the maximum depth was less than the 1945-2007 average; a positive value meant the snow depth measurement was greater than the 1945 to 2007 average. The SNEG index was calculated as the 7-year moving average of these data. Therefore the 1948 SNEG year was the average of annual snow deviations from 1945 to 1951, the 1949 SNEG year the average of annual data from 1946 to 1952, and so forth until the last index point for the

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2004 SNEG year which was the average of the years 2001 to 2007. As illustrated in Figure 4D these 7-year averages show both a cyclic pattern and a downward slope since the 1950s.
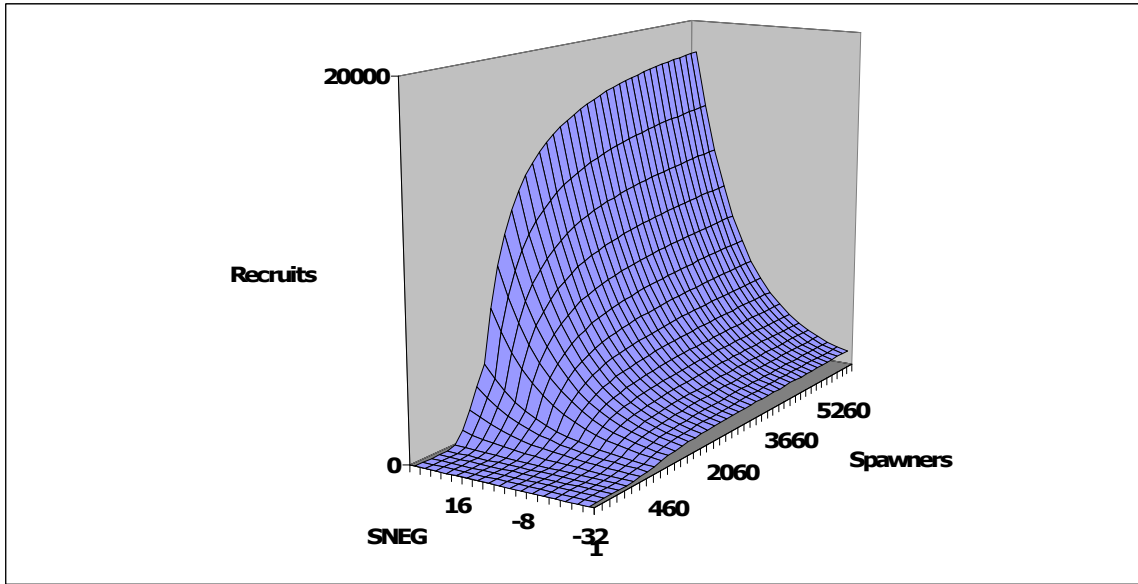

Figure 3D. Illustration of Crowbar recruitment function with SNEG variable added (a = 3.0, b = 4,000, and c =0.05)
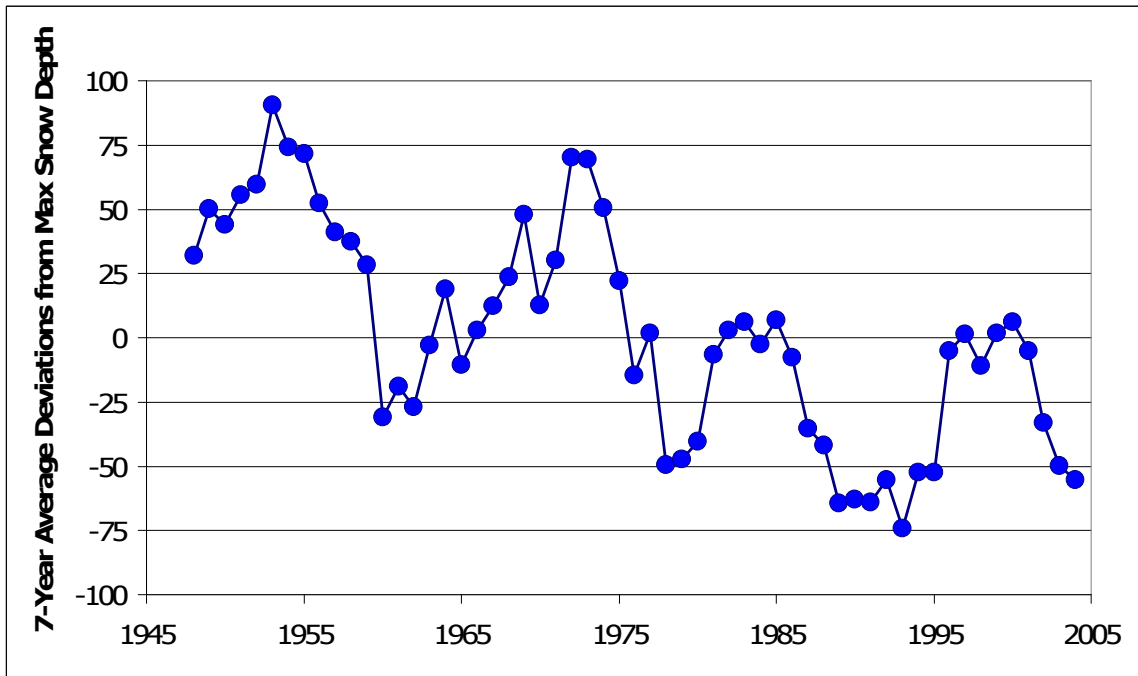

Figure 4D. SNEG 7-year moving average index of annual maximum snow depths, expressed as deviations (cm) from 1945 to 2007 mean maximum snow depth; snow data are from annual measurements averaged for two high elevation monitoring stations, Mt. Rainier and Crater Lake.

Fitting Population Recruitment Curves

Fitting the recruitment curves to the observed data was a two step process. First a baseline data set of spawners, recruits, and SNEG index values was constructed. Because the SNEG index was not population specific, it was easily obtained following methods previously described. However, spawner and recruit data sets were more difficult to develop. For many populations, there are either no data or too few years of data to perform a recruitment analysis. Where sufficient data exist there were often data gaps of unknown hatchery fish fractions that had to be resolved in order to build a useable data set. The steps involved were specific to each population and are reported, along with the resulting data sets, in Appendix B. However, there several common and important elements to this data set building process that should be highlighted.

One of these important elements is that "spawners" are defined as the total of both wild and naturally spawning hatchery fish. When hatchery fish occur in the data base they are not given a reproductive success "discount" to correct for their likely reproductive inefficiency compared to wild fish. This discounting step was not taken for several reasons. First, it is not clear how much discount to apply. Second, such discounts may not appropriately account for the full impact of naturally spawning hatchery fish on subsequent population productivity. For example, in those studies showing large reproductive differences in reproductive success between naturally spawning hatchery fish and wild fish, a sizable portion of the naturally produced smolts were offspring of hatchery spawners. However, the marine survival of those natural smolts having hatchery parentage is typically less than those from wild parents. Therefore, there is likely a density dependent effect of hatchery spawners on smolt production, that can not be accounted for by applying a simple discount to hatchery spawners proportional full life history reproductive differences between hatchery and wild spawners.

Another important feature of the recruitment curve fitting was the estimation of brood year specific recruits from spawner escapement data. The number of recruits produced by each brood year of spawners was estimated by reconstructing each production group using the following relationship:

$$R_t = \sum [(A_j * S_{t+j})/(1 - F_{t+j})] \qquad\qquad (3)$$

where R_t represents the number of naturally produced (wild) recruits by fish that spawned in year t, A_j is the proportion of fish having age j at spawning (j = 2, 3, 4, 5, 6, 7), S_{t+j} is the number of wild spawners in year t + j, and F_{t+j} is the cumulative fishing mortality rate for the return of fish that spawned in year t + j.

The second step of fitting the recruitment curves was estimating the parameters for each equation and capturing the uncertainty associated with these estimates. Recruitment equation parameters were estimated via multivariate non-linear regression using the DataFit software developed by Oakdale Engineering (Oakdale, Pennsylvania). The DataFit software parameter estimation algorithm is based on the Levenberg-Marquardt method described by Marquardt (1963). Because the errors were assumed to be log-normally distributed, the form of the recruitment equations upon which the regression

analyses were performed were modified to the lognormal form as follows, where ϵ_t represents the lognormal error term.

BH: $Ln(R_t) = Ln(a) + Ln(S_t) - Ln(1 + (a / b * S_t)) + (c * SNEG_{t+m}) + \epsilon_t$ (7)

SK: $Ln(R_t) = Ln(b) + Ln(1 - exp(- (a / b * S_t))) + (c * SNEG_{t+m}) + \epsilon_t$ (8)

CB: $Ln(R_t) = Ln(b) + ((- b * exp(- 1)) / (a * S_t)) + (c * SNEG_{t+m}) + \epsilon_t$ (9)

The regression input data as used for CAPM consisted of a table with the first two columns containing the annual values for the predictor variables S (spawner abundance) and SNEG (snow index) and the third column the corresponding values for the response variable Ln(R) (natural log of recruits). Each row of the data table represented the observations associated with one brood year.

The procedure for estimating equation parameters and the associated standard deviation of the residuals entailed more than performing a single DataFit-based regression analysis of a population's data set. Instead, a Monte Carlo bootstrapping procedure was used to repeatedly sample the population data set. A regression analysis was then performed on each data set sample using the same DataFit-based nonlinear regression routine. This meant that for every bootstrap sample an estimate of recruitment equation parameters and associated standard deviations were generated for all three recruitment curves (BH, SK, and CB). Therefore, if 500 bootstrap samples were drawn, 500 parameter and standard deviation estimates for each of the three recruitment equations would be generated. The primary purpose of this extended bootstrap procedure was to better understand the range and magnitude of possible errors in estimating recruitment equation parameters.

Simulating Population Recruitment - Addition of Stochastic Effects

An important element of simulating population recruitment within CAPM was the inclusion of random variation in the recruitment process. This element was intended to represent the effect of natural variations in annual recruitment and be consistent with the assumption that for real populations, the recruitment process is not a simple, unwavering deterministic process. To accomplish this, the error term (ϵ_t) in equations 7, 8, and 9 was replaced with a number (dev_t) randomly drawn from a normal distribution having a mean of zero and standard deviation equal to the regression standard deviation. Each time one of these equations was used within CAPM to simulate population recruitment; a new random number was drawn and used to calculate a new value for dev_t. This randomly fluctuating component of the recruitment equation was the primary source of stochasticity for CAPM population abundance simulations and ultimately estimates of extinction risk.

Simulating Population Recruitment – Snow Data

Each estimate of population recruitment within CAPM requires a value for SNEG. Therefore, for the population simulation portion of this model it was necessary to generate 100-year sequences of the SNEG index in manner that was consistent with observed SNEG values of the past Figure 4D. The method implemented within CAPM to do this begins by randomly selecting 120 snow depth values from a normal distribution

having a mean equal to the 1945-2007 maximum snow depth value (442 cm) and a standard deviation from the same period (101 cm). For most model runs each pool of random numbers was adjusted downward to make the starting snow conditions equal to the average snow depth conditions of the last 30 years (1977 to 2007). This adjustment entailed subtracting the difference between 1977-2007 snow average and the 1945-2007 snow average (37cm) from each random number. In addition, CAPM was also capable of performing model runs that assumed a downward long-term trend in maximum snow depth. To implement this capability within a model run, each randomly picked snow depth value was adjusted downward by subtracting: (the slope of the downward trend expressed as change in snow depth per year) x (year number in model run sequence -1). For example, in year 2 of the simulation, if the change rate was expected to be -0.5cm per year and then the snow depth value would be adjusted downward by -0.5cm. In year 3, the adjustment would be – 1.0 cm, for year 4, -1.5cm, and so forth.

Once the string of randomly selected snow depths had been selected and adjusted, they were converted to be deviations by subtracting from each, the 1945 to 2007 mean snow depth (37cm). Model run values for SNEG were then calculated as the moving 7-year averages of this string of annual snow depth deviations. The same string of SNEG values were used for each bootstrap sample and associated parameter estimates.

Assumptions about Future Conditions

Like all viability models, CAPM is build around assumptions concerning the future conditions a population will likely experience. Since model runs are meant to simulate a future time period lasting 100 years, these future condition assumptions are usually critical to extinction probabilities forecast by the model. As reported here, CAPM results were generally based on the assumption that future conditions would approximate those experienced by populations from 1977 to 2007. The primary way for doing this was as previously described, constructing the simulation values for the SNEG index such that they would be representative of the 1977 to 2007 observations.

However, with respect to harvest and naturally spawning hatchery fish, the simulated future conditions were not always intended to represent those observed from 1977 to 2007. For fishery harvest the reason for this was that fishery impacts prior to the 1990s were higher than those of the most years and those anticipated in the future. For example, lower Columbia coho experienced cumulative harvest rates of 75% to 90% prior to 1990. Since 1990, these rates have been reduced and it is unlikely that for wild fish they will exceed 25% in the future. The assumed fishery impact rates used for all model runs are consistent for those presented earlier in **Table 8** of this report.

The second departure from past conditions is the way hatchery fish were treated. In many populations the presence of hatchery fish on the spawning grounds has been a significant, yet highly variable feature. Most evidence suggests that naturally spawning hatchery fish tend to lower the overall natural reproductive rate for mixed populations of hatchery and wild fish compared to populations comprised only of wild fish.

However, in terms of natural offspring produced, hatchery fish may also make a substantial contribution, especially when they represent more than 50% of the natural spawning population.

The net effect of increased spawners and decreased reproductive rate as a result of naturally spawning hatchery fish is difficult to evaluate. However, for the purposes of understanding extinction risk and recovery potential, the key question is whether the wild fish would able to sustain themselves without 'reproductive support', should this 'support' indeed be a net positive benefit. As self-sustainability is the key question, we have chosen to make two conservative assumptions about future conditions as it relates to hatchery fish. First, that the recruitment parameters estimated during the period when hatchery fish were present in the past, are assumed to be representative of the wild fish in the population. Second, only wild fish are assumed to be present in the future and as a consequence their persistence dependent only on their ability to be self-sustaining. In this way the results obtained from the modeling exercise reflect our best estimate of the potential of the wild fish to maintain themselves in the future.

In reality, it is expected that substantial improvements in the natural reproductive rate will occur in many populations because the proportion of naturally spawning hatchery fish has been greatly reduced in recent years. For example, winter steelhead populations in the upper Willamette ESU. Also, it is possible that in places where naturally spawning hatchery will continue to occur (e.g. coho in the Youngs Bay streams), a portion of the naturally produced fish will be dependent on the reproductive contribution of stray hatchery fish.

However, the key question to be addressed by the viability modeling effort was: "if we assume the productive capacity of the population observed over the past 30 years is representative of wild fish, would such a population be self-sustaining in the future with no hatchery fish present." This is a conservative way to ask the question because it assumes any possible negative impact of past interactions with hatchery fish will continue and yet the future contribution of stray hatchery fish to the production of naturally produced offspring would be eliminated.

Program Mechanics

The CAPM is a program written in Visual Basic linked to nonlinear regression fitting algorithms provided by DataFit software. An Excel spreadsheet provides the user interface for data input, model run set up and display of the results. Starting with a population data set, CAPM proceeds through a series of calculations to produce multiple estimates of extinction probability. As stated earlier, the result is a distribution of extinction probabilities rather than a single estimate. The key steps in this series of calculations and the order in which they occur for the populations examined in this report are outlined in the following description.

After the raw population data and model conditions are entered, the program generates multiple estimates of the parameters for each of the three recruitment equations via the

bootstrap process. For viability estimates 300 bootstrap samples were drawn as described earlier. Each of these bootstrap samples was fit to the three recruitment equations using the DataFit software. The net result was 900 parameter sets (i.e., 300 samples x 3 recruitment equations). For each parameter set, CAPM simulated a future 100 year sequence of population abundance. The starting abundance for each of these 100 year simulations was set to equal the value for recruitment equation parameter for capacity, b, as described in Equations 7, 8, and 9. These 100-year simulations were repeated 500 times for each parameter set. The number of 100-year simulations that were found to incur an 'extinction event', was then divided by 500 to obtain a probability of extinction for the parameter sample. This process was repeated until probabilities of extinction probabilities were obtained for all parameter sets. This modeling protocol was computer intensive and time consuming as it essentially required the simulation of 45 million years of population growth and abundance (i.e., 500 repetitions of a 100 year simulation period, for each of 900 parameter sets).

The definition of an 'extinction event' was the occurrence of an average spawner abundance that was less than a population specific Critical Risk Threshold (CRT). Conceptually the CRT, was defined the level, below which the recruitment processes and the likelihood of population rebound was judged to be uncertain and potentially unlikely. The population specific CRT values for all populations are given in Table __. The period of years used for calculating the average abundance to test against the CRT was equal to the average age of spawners in the population. So for example, for coho a 3-year average was used and for summer steelhead a 5-year average was used. In summary, the detection of an 'extinction event' occurred if within the 100-year simulation of spawner abundance numbers, there was a sequence of years equal to the average age of the species (e.g. 3 years for coho) with an average abundance less than the CRT value.

The process of simulation recruitment under the CAPM also involved an assumption that at extremely low spawner abundance levels recruitment would totally fail. In other words, no recruits would be produced. This reproductive fail point was set at 20% of a population's CRT. So for example, the reproductive fail point for Clackamas coho was assumed to be 60, which is 20% of the CRT value of 300. Therefore, within the CAPM population simulations, zero recruits would be predicted for any simulated spawner escapement of Clackamas coho less than 60 fish.

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