

Review of the National Marine Fisheries Service Draft Cumulative Risk Analysis Addendum

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EXECUTIVE SUMMARY

While the Independent Scientific Advisory Board's (ISAB) review of the Anadromous Fish Appendix (AFA) was underway, the National Marine Fisheries Service (NMFS) requested that the ISAB also review an addendum to that document, titled "A Cumulative Risk Analysis," and generally referred to as "the CRI." The ISAB found that:

1. The CRI represents a very recent undertaking for NMFS. We understand, therefore, that our review is as much an evaluation of the future potential for this approach as it is an evaluation of the results obtained thus far. The ISAB is favorably impressed with this new approach, and recommends that it be developed further. However, the substantive results that are reported in the CRI document seem preliminary and limited.
2. The CRI does not bring new "data" to the extinction analysis, and actually uses less data than were considered by the AFA for the calculation of extinction probabilities under present conditions.

The "data" that the CRI uses are derived quantities and estimates obtained from other projects; the uncertainties in these quantities, which in the opinion of the ISAB could be considerable, are not analyzed in the CRI. The CRI does not resolve the major outstanding uncertainties raised in the AFA, regarding "differential delayed mortality" or "extra mortality."

3. The CRI does not present an explicit synthesis of its own analysis and conclusions with those of the AFA or PATH.

Such a synthesis definitely is needed, since the AFA and the CRI documents come to quite different conclusions on several important points, and arrive at those conclusions via different kinds of analysis. Because the analyses use different techniques, and operate on different subsets of the data, some careful diagnosis is warranted to explain the different conclusions, and to choose between them in making actual recommendations for the eventual decisions that these documents are intended to support. The ISAB recommends that this be done.

4. The CRI brings a new element to modeling for salmon management decision support by announcing a policy of "transparency" in modeling and data analysis.
5. The present CRI document only partially lives up to the intention of achieving transparency, but it represents an important step in the right direction. The modeling package has a nice logical coherence, but it still involves some difficult technical steps that need more thorough documentation.

The web presentation so far is incomplete. And since the "data" are largely derived quantities obtained from other data analysis projects, simply listing those estimates does not provide enough of a paper trail to do justice to an evaluation of their uncertainties.

The ISAB considers the espousal of clarity and openness in the CRI an important contribution to the use of science for supporting a decision process. We hope that NMFS will follow through on

these good intentions. The model presented in the CRI needs to evolve a bit in the direction of greater complexity, to address a wider spectrum of possible interventions in greater detail, and this will add to the burden of documentation. Furthermore, some effort needs to be devoted to diagnosing reasons for the differences that may emerge between the results of the CRI modeling and other more complex and more detailed models, so as not to have a decision impasse when "the models disagree." We recognize that a commitment to thorough documentation of this sort will prove demanding of time and institutional resources, but we believe that the benefits to the quality of the science and the credibility of results are worth the institutional cost.

6. The CRI presents a new modeling package for estimating extinction probability and relating this to the life table and to the effects of possible interventions.

7. The new modeling package provides a clear logical framework that holds much promise. However, the actual implementation in the CRI document under review, seems very preliminary, and has some deficiencies that weaken its usefulness for the pending decision. The ISAB recommends continued development and application of this approach, recognizing, realistically, that this will require more time and resources.

The present version of the model has some structural limitations that merit future attention. The particular extinction model employed represents the population growth rate as a random variable with a constant distribution. This assumes no density dependence, no deterioration of viability at very small population sizes, and no sustained trends in population growth rate over time. In the long run, these assumptions are not tenable theoretically. And in the case at hand, the assumption of no trend appears to be contradicted directly by the data.

The exclusive focus on the linkage between mean growth rate and probability of extinction, in the program of analysis presented in the CRI, neglects the equally important linkage between variability in growth rates and the probability of extinction. More attention needs to be paid to factors, such as life history pattern, life history diversity, and metapopulation structure, that mediate between environmental variability and its expression in variation in salmon population dynamics.

8. The CRI presents an application of the modeling package to estimate extinction probabilities for the Snake River index stocks

9. The CRI largely corrects the most glaring shortcoming of the April 14, 1999 draft AFA, which reported implausibly low estimates of extinction risk. The CRI, significantly, shows quite high probabilities of extinction, if present conditions continue.

The ISAB believes that these estimates are still underestimates of the actual extinction risk, because the particular extinction model employed in the CRI program of analysis ignores the apparent declining trend in growth rates over time in the listed stocks, and does not incorporate a representation of the demographic, genetic, and ecological mechanisms which generally cause population viability to decline at very small population sizes.

10. With computed extinction probabilities as high as are shown with this preliminary analysis, there is no point to splitting hairs over the question whether the extinction probabilities are high enough to cause concern. The extinction probabilities definitely are high enough to cause concern.

But the calculation of extinction probability will also play a role in other questions, such as analysis of the delay option, or eventual evaluation of recovery plans, and in those applications the difference between the first cut analysis of extinction probability and a more detailed and biologically realistic analysis may well matter.

11. The CRI presents an application of the modeling package to identify, for the Snake River index stocks, which portions of the life history offer, theoretically, the greatest scope for reducing the probability of extinction

The CRI analysis shows that the risk reduction that would hypothetically be achieved by eliminating the remaining juvenile mortality within the migration corridor (not considering delayed effects) is considerably smaller than the risk reduction that would hypothetically be achieved by eliminating the remaining mortality in some other life history stages. But this theoretical comparison does not take account of feasibility of reducing the remaining mortality in the various life history stages.

12. The identification of life history stages with potential for mortality reduction to bring about reduced risk of extinction remains theoretical in the CRI, because the discussion of interventions to achieve improvements in survival (and reproduction) is pursued only superficially, and relates explicitly to defined management actions only in connection with in-river harvest, barging and passage mortality, to the neglect of effects of habitat on fecundity and rearing success, neglect of effects of hatchery production on wild populations, and without discussion of feasible measures to increase estuary and ocean survival.

The CRI program of analysis shows great promise as a framework for considering a broader spectrum of management options for salmon recovery; but this promise remains to be fulfilled.

13. The CRI presents an application of the modeling package to consider specifically whether dam breaching alone, or habitat improvement and harvest reduction without dam breaching, are likely to reduce the extinction risk significantly

The conclusions presented in the CRI explicitly consider two questions: (a) Is it likely that dam breaching alone could raise the average growth rate enough to reduce the extinction risk significantly? (b) Is it likely that habitat improvement and harvest reduction by themselves could raise the average growth rate enough to reduce the extinction risk significantly? The tentative answer of the CRI to both questions is "possibly yes" for fall chinook and steelhead; but it seems to be a qualified "probably no" for spring/summer chinook.

14. The ISAB does not find the scope of the CRI analysis of effectiveness of dam breaching versus effectiveness of habitat improvement and harvest reduction to be entirely satisfactory. The prospects for risk reduction through modification of artificial production operations needs to be

evaluated as well. And, logically, the analysis should also evaluate the prospects for significantly reducing risk by the action of dam breaching AND addressing habitat and harvest and hatcheries.

15. The high probabilities of extinction that the CRI shows for many of the stocks should raise the sense of urgency about the management decisions bearing on hydrosystem operations, possible dam breaching, and other interventions as well.

16. The ISAB is not comfortable with the apparent drift toward delay of the actual decisions about the management decisions bearing on hydrosystem operations, possible dam breaching, and other interventions as well.

The possibility that there is no time to lose in beginning to implement management experiments, while there are still enough local populations of listed stocks to work with, should put a premium on a deeper and more detailed analysis of the options. The ISAB believes that the stakes are high enough to warrant a detailed formal probabilistic decision analysis.

INTRODUCTION

In a letter dated August 9, 1999, from Usha Varanasi, NMFS requested that the Independent Scientific Advisory Board (ISAB) review the scientific adequacy of the draft "Cumulative Risk Analysis," prepared as an addendum to the draft "Anadromous Fish Appendix," (AFA), itself prepared as an appendix to the US Army Corps of Engineers (COE) document, the "Lower Snake River Juvenile Salmonid Migration Feasibility Study," which is to be part of an Environmental Impact Statement. The draft Cumulative Risk document we received, dated September 9, 1999, is formatted as "Section 9," with the Section title, "A Cumulative Risk Analysis." The document, generally referred to as "the CRI," describes an analysis strategy for attempting to evaluate management options for their likely effects on listed stocks of Snake River Salmon.

The CRI proposes an analysis strategy that would serve as an alternative or complement to the PATH-based analysis, presented in the April 14, 1999 draft AFA that the ISAB recently reviewed (ISAB Report 99-6, October 12, 1999). That draft of the AFA focuses the evaluation specifically on hydrosystem management options. The CRI considers the same hydrosystem management options, but also proposes that its analysis strategy could serve as an analytical framework for considering a broader range of management options in the broader context of salmon recovery planning.

The charge to the ISAB, in the letter from NMFS, stated a list of eight questions to help guide the review of the CRI. These are the same eight questions that the ISAB was asked in connection with the AFA. Given that the CRI will be a chapter of a new draft of the AFA, we can best address the questions from NMFS by considering what the CRI adds to the analysis already presented in the April 14, 1999 draft of the AFA, and considering how the additions affect the conclusions of the combined package.

GENERAL IMPACT OF THE CRI

Briefly, the CRI largely corrects the most glaring shortcoming of the April 14 draft AFA with respect to extinction analysis, and, significantly, shows quite high probabilities of extinction, if present conditions continue. This result is what we would expect from a sensible analysis of the available information.

The CRI does not bring new data to the extinction analysis, and actually uses less data than the AFA for the calculation of extinction probabilities under present conditions. It is not surprising, therefore, that the CRI does not resolve the major outstanding uncertainties raised in the AFA, regarding "differential delayed mortality" or "extra mortality," because data gaps are at the heart of these uncertainties. In fact, one of the most important functions to be served both by the AFA and CRI is their potential use in "surgical" identification of the data gaps that have the greatest influence on the present uncertainty about management decisions for salmon restoration.

The CRI program of analysis does have definite advantages of clarity and tractability, compared to the analysis in the AFA. Also, the CRI program of analysis brings life history information not used by the AFA to its analysis how factors in different life history stages can affect the population

growth rate. For these same reasons, the CRI program of analysis shows great promise as a framework for considering a broader spectrum of management options for salmon recovery. But this promise remains to be fulfilled, as of this moment, for the actual analysis presented in the CRI document under review is sketchy and tentative, and leaves many important scientific questions undecided.

The implications for the conclusions of the combined AFA/CRI package are unclear. The CRI draft of September 9, 1999, does not present an explicit synthesis of its own analysis and conclusions with those of the AFA draft of April 14, 1999. Such a synthesis definitely is needed, since the two documents come to quite different conclusions on several important points, and arrive at those conclusions via different kinds of analysis. Because the analyses use different techniques, and operate on different subsets of the data, some careful diagnosis is warranted to explain the different conclusions, and to choose between them in making actual recommendations for the eventual decisions that these documents are intended to support.

Implications for Weighing the Merits of Dam Breaching

Even within the narrower context of the CRI document itself, the scope of the conclusions seems rather meager. One might think that acknowledgement of the high probabilities of extinction for many of the stocks would raise the sense of urgency about the management decisions bearing on hydrosystem operations, possible dam breaching, and other interventions as well. But the continuing uncertainty about the efficacy of the respective management options seems to discourage decisiveness in the conclusions of the CRI.

The ISAB is not comfortable with this apparent drift toward delay of the actual decisions. We think it important that discussions of uncertainty about effectiveness of management interventions be accompanied by thoughtful analysis of the possibility that there is no time to lose in beginning to implement management experiments while there are still enough local populations of listed stocks to work with.

The CRI document does confront these issues more directly than the AFA, and does so in a lucid way. The quantitative consideration of the probable relative effectiveness of in-river harvest reductions compared to the migration corridor survival increases expected from dam breaching, is a welcome contribution in clarity.

Highlighting the uncertainty about effects of dam breaching outside the migration corridor is candid, but not especially helpful to the decision at hand. The CRI does not remove any of the uncertainty about the validity of the other "hypotheses" about factors contributing the Snake River salmon decline, beyond setting mathematical upper limits on the magnitude of possible improvement for survival in each life history stage. The analysis does not address possible influences of hatchery operations beyond the possible predation by hatchery steelhead smolts on chinook smolts. The analysis does not address habitat degradation, or combinations of hatchery, habitat and hydropower operations. The CRI analysis does provide interesting insight about how large the changes in average survival rates would have to be at various stages in the life cycle in

order for the changes to contribute appreciably to salmon recovery. But this is only part of the story on possible interventions.

Implications for Weighing the "Delay" Option

One might also think that the acknowledged high probabilities of extinction should put a premium on a deeper and more detailed analysis of the "delay" option in the forthcoming Biological Opinion on hydropower operations. The CRI has taken a big step in the right direction by calculating more plausible estimates of extinction probability, but the other components of a thorough analysis of the costs and benefits of delay still are absent from the combined AFA/CRI package.

The ISAB is concerned that the delay option may appear attractive by default, without adequate consideration of the probable range of consequences of delay, and without consideration of the costs of dealing with those consequences. In particular, the costs of a last ditch effort, conducted in a crisis atmosphere, to attempt to save the populations after their situation has deteriorated even further than at present might well exceed the costs of taking preemptive action now.

The ISAB believes that the stakes are high enough to warrant a detailed formal probabilistic decision analysis for the delay option. Such an analysis should start with a statement of commitments regarding the monitoring and experiments that will be done during the delay period, and presentation of a proposed decision tree specifying what management actions should be taken, and on what time table, depending upon the results of the monitoring and experiments. The analysis should attempt to be realistic in estimating the institutional time lags in implementing decisions, and the physical and biological times scale of probable responses to interventions. The analysis could then investigate the probabilities of extinction and recovery, and the likely magnitude of the required intervention effort, with such a system of monitoring and decision rules in place, compared to extinction and recovery probabilities, and intervention effort, under other plans or decision schedules. We recommend that this analysis be given immediate priority.

COMMENTS ON THE SPIRIT OF THE CRI

The avowed guiding principle of the CRI is to keep the modeling simple enough, and hierarchically organized, so as to maintain "transparency." It is hoped that transparency in the analysis will facilitate a more productive style of scientific discourse, in what is, admittedly, a contentious setting. To this end, it is proposed in the CRI that the "data" and the "models" be publicly accessible on the web.

The ISAB considers this espousal of clarity and openness laudable, and hopes that NMFS will follow through on these good intentions. We recognize that such a commitment to thorough documentation will prove demanding of institutional resources, as the models and analyses invariably evolve in the direction of greater complexity and realism; but we believe that the benefits to the quality of the science and the credibility of results are worth the institutional cost.

The present CRI document lives up to these intentions only partially. The document does not list a web site for the data or the models. As of October 28, 1999, the CRI effort was described on the NWFSC site at www.nwfsc.noaa.gov/cri, but the data link and model link for the extinction analysis only brought up the spreadsheets for the Marsh Creek stock (as in the CRI document itself), not the other populations.

Appendix A of the CRI provides a sample spreadsheet of the extinction risk analysis for one stock (Marsh Creek), but the results in the spreadsheet (average $\lambda=1.33$, probability of extinction within 10 years=0.095) do not agree with the results for the Marsh Creek stock in Table 9-6 in the main body of the text (average $\lambda=1.25$, probability of extinction within 10 years=0.15). The "data" for checking the extinction risk analysis for the other stocks are not provided. For the one stock with a paper trail, some aspects of data treatment in the analysis, such as removal of jacks from the counts, and whether both sexes are included in the time series of counts of spawners used for estimating the parameters of the extinction model, are puzzling and inadequately explained.

The "data" in any case are not actually data, in the sense of actual observations, but are derived quantities, drawing on the same compilations of estimates, generated by PATH, and used by the AFA. Backtrailing these run-reconstructions to the actual measurements and counts on which they are based, and conducting a statistical analysis of the error variance and possible bias in the run-reconstruction numbers, especially the breakdowns by age and sex, will be a larger undertaking, but this should be done. We believe it reasonable to assume that the measurement error is large, until proven otherwise.

The CRI document states that sensitivity analyses showed that uncertainties in the input quantities to the extinction risk analyses were not important to the results, but these sensitivity analyses are not described in detail and their results are not presented. *Prima facie*, we would think that measurement error will bias the estimate of some input quantities, particularly "sigma squared," and this in turn would bias the estimate of the extinction probability.

Appendix B of the CRI shows the steps in the assembly of an estimated Leslie matrix for each of the spring/summer chinook index stocks. Here, too, there are references and citations for input values used, but these input values are themselves estimates, not really data, some are actually "guesstimates," many are not specific to any one of the index stocks, and the text does not make clear what periods of time the various component estimates actually pertain to. For example, the values chosen neglect known differences in egg size and number with the age of the spawner. The use of an old generic rule of thumb in place of a real measurement of marine survival is especially disconcerting, in light of the importance of that factor. Notwithstanding this remoteness of the values from documented raw observations, and despite the evident uncertainty attached to many, their uncertainty is not examined, nor is it propagated through the analysis.

The thoroughness of documentation that is necessary for a really adequate check of something as complicated as a population extinction analysis is probably not fully appreciated. The CRI references the publication by Dennis, et al. (1991) as the model used and the basis for the calculation of results. But equation [16], on page 119 of that publication, the key equation for calculating the probability of extinction, or quasi-extinction, before a specified time horizon, has a

mistake: the plus sign in the argument of the second normal cdf term (Φ) should be a minus. The related equation [A.5] in the appendix to the paper has the signs correct.

Verifying the matter is not helped by notational confusion in the treatment of the relevant distribution (inverse gaussian) in the most recent edition (2nd, 1994) of Johnson, Kotz, and Balakrishnan, the natural text to consult. There, on page 261, the key substitution of variables in transforming the Brownian motion notation, equation [15.1], to the canonical form, eq [15.4a], used by Dennis, et al., has typographic errors, meaninglessly defining the greek letter nu, " $\nu=d/\lambda$," whereas the needed substitution is for a script v , $v=d/\mu$. The interested reader is further advised that Johnson, et al., use the parameter μ to designate what, in the notation of Dennis, et al., would be symbolized as x_d/μ ; Kotz, et al., use the parameter x to designate what Dennis, et al., symbolize as t ; and Kotz, et al., use the parameter λ to designate what, in the notation of Dennis, et al., would be $(x_d/\sigma)^2$ while Dennis et al., use λ for another purpose, as, in their notation, the quantity:

$$e^{\mu+\sigma^2/2}.$$

In the actual event, our attempts to duplicate the calculations of extinction time in Step 3 of Appendix A, accepting the values of "slope from regression" and "sigma squared," agreed to the 4th digit for "avg. Lambda," the 3rd digit for "mean time to extinction," and to 1 part in 200 for probability of quasi-extinction within 10 years, using the corrected version of equation [16] from Dennis et al, and assuming that the "sigma squared" reported in Step 3 of Appendix A of the CRI is the unbiased estimate, not the maximum likelihood estimate, and converting this to the maximum likelihood estimate for use in the Dennis equation for the distribution of time to quasi-extinction. Obviously, explicit statement of the equations used, in a clear notation, would be an aid to review.

Overall our impression is that the CRI draft under review shows a well-thought-out first cut at implementing a commitment to documentation of data and methods, where good judgment has been exercised in setting priorities on the initial effort; but still it is only a first cut, on an initial effort, and far from complete.

Similarly, the CRI draft shows a well-thought-out first cut at developing a relatively simple, powerful, tractable, and potentially flexible modeling approach, but this too must be viewed as preliminary. In evaluating the stated conclusions of the CRI, it is wise to recall McCullagh and Nelder's (1983:8) three principles of model application: (1) "...all models are wrong; some, though, are more useful than others and we should seek those," (2) "Modeling in science remains, partly at least, an art," and (3) It is prudent "...not to fall in love with one model to the exclusion of alternatives."

The model presented in the CRI needs to evolve a bit in the direction of greater complexity, to address a wider spectrum of possible interventions in greater detail. Furthermore, some effort needs to be devoted to diagnosing reasons for the differences that may emerge between the results of the CRI modeling and other more complex and more detailed models, so as not to have a decision impasse when "the models disagree."

COMMENTS ON THE LOGIC OF THE CRI PROGRAM OF ANALYSIS

The technical logic of the CRI program of analysis links a stochastic extinction model and a deterministic demographic projection model. The linkage involves some subtle points, because of the differences between stochastic models that explicitly represent real variation in the phenomenon, and deterministic models that average over the variation and represent the dynamics as if the true rates were constant at the average value. The main steps of the linkage, as conducted in the CRI are:

1. Estimate the probability of extinction from estimates of the population size, and the mean and the variance of the population growth rate.
2. Estimate the birth rates and survival rates associated with various stages of the life history, and use these as elements of the age structured population projection matrix responsible for the average growth rate of the population.
3. Computationally explore the effects of changes in vital rates at specific life history stages on the average population growth rate resulting from the projection matrix.
4. Score the value of changes in vital rates at specific life history stages by computing the change in probability of extinction that results from the accompanying change in the mean growth rate, assuming other parameters are unchanged.
5. Evaluate the prospects that various feasible interventions actually can bring about the respective changes in vital rates at specific life history stages.

This analytical program provides a clear logical framework that holds much promise. The ISAB recommends continued development and application of this approach, recognizing, realistically, that this will require more time and resources.

The present implementation of this approach, however, in the CRI document under review, seems very preliminary, and has some deficiencies that weaken its intended use for application to the eventual "1999 Hydrosystem Decision." The greatest shortcomings are in steps 1, 4 and 5, as defined above. Briefly: the extinction model employed in step 1 ignores the apparent declining trend in growth rates over time in the listed stocks, and has no relation to changes in habitat quality or quantity; exclusive focus on the linkage between mean growth rate and probability of extinction, as in step 4, neglects the equally important linkage between variability in growth rate and the probability of extinction; and the evaluation of feasible interventions, proposed in step 5, is pursued only superficially in the present draft of the CRI, and relates explicitly to defined management actions only in connection with in-river harvest, barging and passage mortality, to the neglect of effects of habitat on fecundity and rearing success, neglect of effects of hatchery production on wild populations, and without discussion of feasible measures to increase estuary and ocean survival.

The superficial and selective evaluation of feasible interventions creates a peculiar impression. The conclusion developed in the CRI, that there is little room left for significant improvement in

components of the life history that take place within the migration corridor, naturally directs hope and attention to the ocean and estuary and pre-migration components of the life history, and the possible influences of hatchery production, ocean harvest practices, migration corridor history, flow management, and natural variation on these life history stages. But the interventions under consideration in the EIS that the AFA/CRI package will be appended to are solely management of hardware in the migration corridor. If the implication is that we can relax our concern about the need for further improvement in management in the migration corridor because there could hypothetically be such a high return on improvement elsewhere, the argument is curiously incomplete. Such an argument really needs to be accompanied by discussion identifying the interventions that are available to achieve that improvement in demographic rates outside the migration corridor, and outlining the decision contexts where a commitment to those interventions might be expressed by the appropriate institutions.

Our more detailed comments on the respective steps in the CRI chain of logic are presented in the following section.

COMMENTS ON SOME OF THE TECHNICAL STEPS IN THE CRI ANALYSIS

Estimation of Extinction Probability

In the CRI, the extinction calculation is carried out with the "Dennis model." The "Dennis model" is described in a now classic publication by Dennis, et al. (1991). That publication develops a self-contained extinction analysis package in two stages. The first stage, an estimation stage, is a distinctive statistical procedure for estimating 3 necessary parameters from a regression operation on a time series of population censuses. The second stage, a prediction stage, uses these parameter estimates to compute characteristics of the distribution of time to extinction, using a standard Brownian motion model borrowed from physics.

The estimation stage of the Dennis model collapses the data on the population into estimates of three quantities: (a) the "average population growth rate," (b) the variance in the population growth rate, and (c) a starting population size. With these three estimated quantities, the prediction stage of the Dennis model calculates extinction probabilities (and the distribution of extinction times), based on the assumption that the dynamics are essentially equivalent to the physical model of diffusion with drift, with an absorbing lower barrier, and no upper barrier. Biologically, these assumptions translate more or less into an assumption of no density dependence of any kind in the dynamics, and an assumption that the achieved instantaneous population growth rate during a short time period is randomly sampled from a normal distribution, where the distribution does not change over time.

Of course these assumptions are not tenable in the long run: population growth must slow as a population experiences resource limitation near carrying capacity, and population growth must become more volatile at the opposite extreme of very low population sizes, where random processes affecting sex ratios, population structure, and individual birth and death events play a

more important role. Further, the regression of spawner per recruit values against brood year, in Figure 9-2 of the CRI, makes it clear that, at least for this period from 1980 to 1994, the time series of growth rates for the index stocks of Snake River spring/summer chinook salmon has been far from a random sampling of a stationary distribution: there has been a marked downward trend in the growth rates of all stocks.

This deterioration in recruits per spawner needs more analysis. It resonates with the "extra mortality" hypotheses considered in the AFA, but not analyzed in the CRI. The causes behind the deterioration in recruits per spawner must be critical to the decline of the stocks. This is important enough that it should motivate some analysis of the dynamics of the period prior to the 1980 brood year. The choice of 1980, in the CRI, as a cutoff for the beginning of the period when dam hardware and operation assumed its modern configuration is, in any case, an oversimplification: hardware, and the rules for operation, have continued to change.

The Assumption of Zero Trend

The regression based parameter estimation process of the "Dennis model" assumes that there is no trend with time in the growth rates. If there is a trend, the estimate of the "sigma" term gets inflated from lack of fit, and the "slope from regression" term ignores the trend and delivers an estimate of the "average growth rate" as if it were constant, overestimating the future average growth rate in the case of a negative trend (as we have here). Then, if a trend is operating, calculation of the distribution of extinction times, under the Dennis model, proceeds with these corrupted estimates of dynamic parameters and does not adjust for the fact of the trend. To quote Dennis, et al., "assume that the elements... change with time in the form of a (multivariate) stationary time series....this assumption excludes populations experiencing non-stationary fluctuations in demographic rates, such as decreasing survival or reproduction rates due to diminishing habitat."

The consequences for the extinction probabilities, and extinction times, are quite large. Consider the 11 complete spawner to spawner cycles reported for the Marsh Creek index stock from the 1980 through 1990 brood years. The summary statistics of the actual eigenvalues for these 11 realizations of a projection matrix are: mean=1.001, variance=0.125, corresponding approximately to a mean instantaneous rate of -0.065 and a variance in the instantaneous rate of 0.140. Using these values for statistics of the instantaneous rate in the Dennis calculation of extinction time gives a probability of 0.27 for quasi-extinction (defined by 30 adult equivalents for the total population with overlapping generations) within 20 years (about like the non-overlapping generation calculation described in the CRI).

Now consider the last 6 of those 11 complete brood years. The summary statistics of the actual eigenvalues for these 6 realizations of a projection matrix is: mean=0.754, variance=0.029, corresponding approximately to a mean instantaneous rate of -0.316 and a variance in the instantaneous rate of 0.076. Using these values for statistics of the instantaneous rate in the Dennis calculation of extinction time gives near certainty (probability=0.999) for quasi-extinction within 20 years. That is, pooling the 11 brood years as if they were drawn from the same constant distribution gives a 27% probability of extinction within 20 years, but treating the last 6 brood years as if they were representative of a new dynamic regime that continues into the future gives

essentially 100% extinction within 20 years. If we interpret the shift observed in the 11 brood years as a continuing trend, so that the eigenvalues would continue to decline further in the future, extinction would be faster yet.

Brood Line Dynamics

The Dennis model uses two dynamic parameters in the calculation of distribution of time to extinction. These parameters can be specified as the "average population growth rate," and the variance in the population growth rate. It must be understood that the regression operation used for estimating these two quantities is entirely phenomenological: it is based on observations of gross population size in a time series. These estimates are not obtained through a model of demographic mechanism: that would require a dissection of birth rates and survival rates followed by a synthesis of these components into a summary rate for the population.

The use of the Dennis model in the CRI departs from this mode of operation by attempting to track brood lines, rather than the population as a whole, as the fundamental unit. The CRI proceeds by calculating an average return rate for each brood year, and construing the dynamics as if the generations did not overlap. This does not distort the estimate of the growth rate very much, but it appreciably inflates the apparent variance of the growth rate (reflected in the value returned for "sigma squared"), compared to the variance in the growth rate of the actual population. This is because the actual dynamics of population growth with overlapping generations averages the realized growth rate of several brood years in assembling the population of spawners each year, and this averaging smoothes out a lot of the independent variation between brood years.

The strength of the averaging in reducing the effective variance increases with the spread in ages at which adults return to spawn in the life history of the particular stock. The force of the averaging in reducing the effective variance also depends on the extent to which the variance is driven by random year effects that operate primarily on young individuals, rather than on returning adults regardless of age. It is believed that a large amount of the variation affecting salmon dynamics does operate primarily on the young life stages since brood year strength varies widely, but brood year strength for adults returning at young ages is a good predictor of brood year strength for the later returns (Hankin, 1990; Percy, 1992).

The distortion of parameters owing to "decomposition" of brood lines from a population with overlapping generations is partially absorbed by the CRI by defining "quasi-extinction" as "brood line extinction." More precisely, "quasi-extinction" is defined in the CRI as zero returning spawners in any single year. Of course zero returning spawners in any single year is more probable than total extinction of the population, since a year with zero returning spawners can occur when there are still good numbers of non-adult fish still alive at other stages.

In fact, this peculiar use of the Dennis model does seem to provide a reasonable approximation for predicting the probability of a year with zero spawners, as can be seen by comparing an overlapping generation model for the Marsh Creek stock, with the analysis reported in the CRI. For this particular overlapping generation model (not using the Dennis machinery), and assuming stationarity (contrary to the observation of a strong downward trend), the probability of total

extinction within 20 years is very small (0.001, which agrees fairly well with the value 0.003 returned by the prediction stage of the Dennis model if it uses the dynamic parameters estimated from the overlapping generation model), but the probability of a year with zero returning spawners is substantial, 0.31, in the overlapping generations model, comparable to the probability 0.27 reported in the CRI analysis.

Perhaps of greater concern in the suppression of effects of overlapping generations in the model is the fact that this will obscure some potentially important effects of life history pattern. Recall that the variance reducing property of overlapping generations increases in effectiveness with the spread in ages at reproduction. If there is a shift toward return at younger ages, this will reduce the effectiveness of the variance averaging, and make the population more vulnerable to extinction. There are indications that many salmon stocks in the Pacific Northwest are returning to spawn at smaller sizes and younger ages, and with lower fecundity than previously (Ricker, 1981), and hatchery stocks generally return at smaller sizes and younger ages than their wild counterparts.

Density Dependence

One more limitation of the Dennis model, that needs to be borne in mind if it is adopted for continued use, is the absence of density dependence. Note that density dependence should manifest itself both at population sizes larger than at present, and at population sizes smaller than at present. The population sizes of the index stocks are already so small that perhaps we should not be worried at the potential introduction of bias by neglecting to allow vital rates to become more favorable as "crowding" diminishes even further.

But at the other end of the spectrum we do need to pay attention to habitat mediated ceilings on population size. The Dennis model does not incorporate any such ceiling, and if the long run growth rate (which will be defined below) is not negative, the model allows a fraction of the probability cloud of population sizes to grow to infinity, thereby escaping any probability of extinction. Needless to say, this is biologically (and physically) unrealistic. In the parameter ranges for the Marsh Creek stock, this phenomenon is not coming into play. We do not have the "data" to know if this is operating with the other stocks. But we do know that if conditions improve, either through natural environmental change or good management, then the stocks will be operating in a dynamic regime where this phenomenon does play a role, and where, therefore, the Dennis model would be an inappropriate analytical tool.

In general, we would advise caution in the adoption of a one-size-fits-all modeling approach in a technical area as complicated (and assumption-ridden) as extinction modeling. There is a lesson to be drawn from the experience of the comparison study reported by Mills, et al., (1996), where several "canned" PVA programs in common use were applied to a single data set, yielding disparate results.

Quasi-extinction

The CRI uses one standard in its model as a surrogate for biological extinction: extinction of a brood line defined by the brood line dropping to one or fewer individuals. This may set too low a standard. It is likely, on biological grounds, that at population sizes larger than one effective spawner in a given year, certain genetic, demographic, behavioral, and ecological processes begin to erode the viability of the population. The expected consequence of this combination of factors is variously termed "depensation" or an "Allee effect." Such reduced viability at low population sizes makes the actual probability of extinction considerably higher than would be predicted by a model assuming density independence (like the Dennis model).

It is customary, for this reason, to use models, such as the Dennis model, to predict the distribution of time to reach "quasi-extinction" levels corresponding to population sizes substantially larger than 1 or 2. There is not, however, a clear scientific consensus on what precise population size really should define quasi-extinction. For the benefit of decision-makers who will attempt to use the CRI to arrive at practical conclusions, the CRI ought to consider a range of definitions of the quasi-extinction level, present the rationale for each, and calculate the probability of quasi-extinction associated with each.

Because it is hoped that the CRI modeling framework will eventually be applied for many kinds of salmon management decision, besides the limited menu directly addressed in the AFA, it would also be worthwhile for NMFS to consider different candidate levels defining quasi-extinction appropriate for making decisions about different kinds of interventions. For example, what definition of quasi-extinction would be most informative for making the decision to take a stock into captive breeding? This might not be the same as the best quasi-extinction definition for triggering a decision to reduce harvests, for example.

Average Growth Rates

The CRI reports an "average growth rate" computed from the Dennis model. The estimation stage of the Dennis model estimates a mean and variance of the infinitesimal (instantaneous) growth rate. The prediction stage of the Dennis model computes the distribution of times to extinction, assuming that the distribution of instantaneous growth rates is normal, with, in the Dennis notation, mean μ and variance σ^2 where μ is estimated by the regression slope from the estimation stage, and σ^2 is estimated from the regression residuals. The normal distribution is a standard feature of molecular diffusion models (Brownian motion) in physics, but the application to salmon, even as an approximation, is just a guess. The 11-year record of run reconstructions at our disposal is too small a sample to determine what distribution is really appropriate here.

Biologically and physically, instantaneous rates of population growth do not correspond closely to real features of salmon life history, where the life cycle takes several years, most major stages of the life cycle are keyed to seasonal events, and where the principal real variation in rates is interannual. In other words, on time scales less than a year, the details of salmon population growth do not have much in common with the mechanisms of the Dennis model.

Conventionally we often represent population growth as an annual factor of increase, called a finite rate, or a discrete time rate, or sometimes symbolized as λ . This rate is related to the age specific birth rates and survival rates of a population projection matrix (Leslie matrix) according to the "characteristic equation." The finite rate is the dominant eigenvalue of that matrix.

There is a mathematical conversion between instantaneous and finite rates of growth. For constant growth, the conversion is very simple. In the Dennis notation, with constant instantaneous growth μ the finite rate is $\lambda = e^\mu$, and conversely $\mu = \ln(\lambda)$. For variable growth, however, the conversion is extraordinarily complicated, and depends on the variance of the growth rate and on the nature of the distribution of that variation.

If the instantaneous rates have a normal distribution (which is an assumption of the Brownian motion model), with mean μ and variance σ^2 the conversion is

$$\text{mean}(\lambda) = e^{\mu + \frac{\sigma^2}{2}}$$

and

$$\text{var}(\lambda) = e^{2\mu + \sigma^2} (e^{\sigma^2} - 1)$$

and conversely

$$\mu = \ln(\text{mean}(\lambda)) - \frac{1}{2} \ln \left(\frac{\text{var}(\lambda)}{\text{mean}(\lambda)^2} + 1 \right)$$

$$\sigma^2 = \ln \left(\frac{\text{var}(\lambda)}{\text{mean}(\lambda)^2} + 1 \right)$$

If the instantaneous rates do not have a normal distribution, there is no exact general equation for the interconversion, but there are Taylor series approximations, which are increasingly accurate as the variance becomes smaller:

$$\mu \cong \ln(\text{mean}(\lambda)) - \frac{\text{var}(\lambda)}{2\text{mean}(\lambda)^2}$$

and

$$\sigma^2 \cong \frac{\text{var}(\lambda)}{\text{mean}(\lambda)^2}$$

The former relation was applied to population dynamics by Lewontin and Cohen (1969), the latter by Tuljapurkar (1982).

It is generally believed that the estimate of $mean(\lambda)$ computed in this way from the regression on population sizes in the estimation stage of the Dennis model, is also approximately equivalent to the "average lambda" obtained as the eigenvalue of the Leslie matrix formed from "average values" (i.e., averaged over a period of time) of the age specific birth rates and survival rates. Tuljapurkar (1982) developed some formulas relating the approximate variance in eigenvalues of the year-specific Leslie matrices to the pattern of year-to-year variation in the age specific entries in the matrix.

The CRI takes the approach of estimating "mean (λ)" both from the Dennis model and from the dominant eigenvalue of a Leslie matrix of average age specific vital rates. The discrepancy in the two values reported for the Marsh Creek index stock is very large: 1.3335 from Dennis estimation, versus 1.092 from the Leslie matrix. But this discrepancy is within the formal uncertainty bounds of the Dennis calculation (because the sample of years is so small); and informal appraisal of the many uncertainties in the "data" plugged into the Leslie matrix suggests large uncertainty there as well.

Comparing the table of "average growth rate" values from the extinction model in the CRI (Table 9-6) and the table of average growth rate estimates from analysis of the demographic projection matrices (Table 9-11), we see that substantial discrepancies are the rule, not the exception. Bear in mind that the effects of these growth rates compound over time, so discrepancies of even a few percent quickly lead to big differences in projected population size.

Effect of Average Growth Rate on the Population Dynamics

If the mathematical relation of the "average growth rate" to measurable parameters is dauntingly complicated under conditions of variable growth, the functional role of the "average growth rate" in determining the fate of the population is even more complicated, and somewhat counterintuitive. It turns out that the "average growth rate," as defined here, does not govern the long run growth of the population.

Viewed from the perspective of the instantaneous rate, it is μ , the average of the instantaneous growth rates that governs long run growth. Converting to a finite rate over a unit time interval gives e^μ as the finite (discrete time) equivalent of the long run growth, whereas $mean(\lambda)$ is approximately:

$$e^{\mu + \frac{\sigma^2}{2}}$$

Viewed from the perspective of annual factors of increase, the long run growth rate is governed by the geometric mean of the annual rates, not their average. The geometric mean is e raised to the power of the average of the logarithms of the factors of increase. For a lognormal distribution of factors of increase, which would result from a normal distribution of the logarithms of the factors of increase, which would result from a normal distribution of instantaneous rates with mean μ , the geometric mean is exactly e^μ .

Another way to put this, from the perspective of the distribution of annual factors of increase, without assuming that the distribution is exactly lognormal, is that, using the Taylor approximations, the long run growth rate, which is the geometric mean of the factors of increase, is approximately the quantity:

$$mean(\lambda) \times e^{-\frac{var(\lambda)}{2mean(\lambda)^2}}$$

Note that the quantity in the exponent is invariably negative if there is any variation in the growth rates, since variances and quantities squared must be non-negative. Note also that the exponential term will have a larger negative exponent (and therefore be a smaller value) as the variance in λ increases.

In other words, the long run growth rate of a population will be less than the "average growth rate" by an amount that increases with the variance of the growth rate.

The predicted future of a population undergoing random growth is a probability distribution of population sizes. Some measure of location of the "center of gravity" of that distribution is given by projection of the initial population according to the long run growth rate. For the Dennis model, the median of the probability distribution of future population size is simply the starting population size projected according to the long run growth rate. Therefore, generally, the location of the "center of gravity" of the distribution of future population size will be a smaller value than that projected by the "average growth rate," and the amount by which it is smaller will increase with the variance in growth rate.

Thus, there are two components to the probability of extinction. One is the trend governed by the long run growth rate, and the other is the dispersion in the predicted population sizes governed by the variance in the growth rate. Neither of these components is governed solely by the average growth rate. Interestingly, because of the fact that the long run growth rate is smaller than the average growth rate, a population can have a long run declining trend, and therefore be headed for certain extinction, even though its "average growth rate," expressed as a multiplicative factor of increase, is greater than 1.

And both components of the probability of extinction are affected by the variance in growth rate. A large variance in growth rate contributes to the probability of extinction in two ways: by depressing the long run growth rate (so there is a trend toward extinction), and by increasing the dispersion in the distribution of future population sizes (so that a larger fraction of the distribution overlaps the extinction threshold).

Effects of Growth Rate Variation on Extinction Probability

All three of the input parameters of the extinction model used by the CRI (starting population size, "average growth rate," and the variance in population growth rate) affect the predicted probability of extinction and time to extinction in the extinction model. Thus it is possible to ask: "If we held two of these inputs constant at some particular value, and varied the third, how much would the probability of extinction change?" The CRI pursues this question by holding the starting

population size and variance in population growth rate constant, and changing the input value of "average growth rate." In this fashion it delivers a mathematical answer to the question: how much would the "average population growth rate" have to increase in order to get the extinction risk down to some specified level.

Three warnings are in order about this mathematical exploration. First, the "average population growth rate" that is being examined in this mathematical exercise is the phenomenological average growth rate of the extinction model. This is not necessarily exactly equivalent to the growth rate that comes out of the Leslie matrix of average age specific birth rates and survival rates.

Second, the "average population growth rate" from the extinction analysis is a mathematical construct that does not comport exactly with our intuitive understanding of how an average rate should summarize the process. Note that 6 out of 7 of the spring/summer chinook index stocks in Table 9-6 of the CRI show strongly positive "average growth rates," of 8% to 48% annual increase, but these stocks have all been declining markedly during the period covered by the data.

Third, for a population with a positive "average population growth rate," the extinction probability is very sensitive to the variance in population growth rate. Indeed, if there were zero variance, and each of the index stocks had grown at a constant rate, equal to its respective "average growth rate" since 1980 as reported in Table 9-6, six out of the seven stocks would have recovered by now (more than quadrupled in number since 1980), and the seventh would still be almost at its 1980 numbers. If the variance is that important, it would be instructive to hold starting numbers and "average growth rate" constant in the analysis, and ask how much the variance needs to be reduced in order to achieve an acceptably low probability of extinction.

We can pursue exactly that question with the information presented for the Marsh Creek stock in Appendix A of the CRI. Using nominal CRI parameter values of 1.335 for the "average lambda," 84 individuals for the starting population, and a value 1.177 for the variance in lambda (back calculated from the CRI values of -0.0407 for the slope of the regression, and 0.6598 for sigma squared), the prediction stage of the Dennis model gives a probability of 0.110 for quasi-extinction (defined again as 1 individual) within 10 years (the CRI lists the probability as 0.095, probably because of the conversion to a maximum likelihood estimate for the variance). The following table shows the effects on the extinction probability of reducing the variance in lambda, while keeping the average lambda and the starting population constant.

Variance in Lambda	Probability of quasi-extinction with 10 years
1.177	0.110
1.1	0.085
1.0	0.057
0.9	0.035
0.8	0.019
0.7	0.008

In short, a reduction of the variance in the growth rate from 1.2 to 0.7 reduces the probability of quasi-extinction from more than 0.1 to less than 0.01, all other things being equal (which is to say, with the "average growth rate" no better than at present). With the variance held constant, the same effect could be obtained by raising the average growth rate to slightly over 1.5.

We conclude that the year-to-year (or brood-to-brood) variation in realized recruits per spawner is an important contributor to the decline of the Snake River stocks. Investigation of the causes of this variation, and examination of the potential for management to reduce this variation, should be undertaken. In this light, the focus in the CRI on "average growth rate" in the analysis of the projection matrices is only part of the story.

PERSPECTIVE ON THE USES OF EXTINCTION MODELS

The extinction analysis in the CRI, using the "Dennis model," is a reasonable starting place, but it is important to recognize that it is only a starting place. With computed extinction probabilities as high as are shown with this preliminary analysis, there is no point to splitting hairs over the question whether the extinction probabilities are high enough to cause concern. The extinction probabilities definitely are high enough to cause concern.

But the calculation of extinction probability will also play a role in other questions, such as analysis of the delay option, or eventual evaluation of recovery plans, and in those applications the difference between the first cut analysis and a more detailed and biologically realistic analysis may well matter. Consider, hypothetically, an investigation of the implications of a ten-year delay. It is not enough to quantify the probability that a stock will go extinct during those ten years. The analysis also needs to factor in the subsequent probability of extinction for the stocks that survived the ten-year period; and it needs to factor in how the stocks, in their predicted status at the end of the ten-year period, are likely to respond to management interventions that may be implemented at that time. These considerations require a deeper analysis, and they may require more precise analysis.

The machinery of the Dennis model can illustrate some of the relevant phenomena in a crude way. Using CRI parameter estimates for the Marsh Creek stock, the probability of quasi-extinction within ten years is 0.11. Does this mean that the total risk from selection of the delay option now is a 0.11 risk of quasi-extinction? Hardly. At the end of the ten years there may be new information that points to some promising management options, but realistically the time required to decide to implement this management intervention may take another five years. From the present starting conditions, the probability of quasi-extinction within 15 years, with the Dennis formula, is 0.21, so the prospects actually are twice as bad as given by the ten-year prediction. And at the end of the fifteen years, when the hypothetical intervention is adopted for implementation, and assuming that quasi-extinction has not yet taken place, will the surviving population probably be no worse off than it is at present? Hardly. The Dennis prediction formula gives 47 as the median population size (actually size of the brood line, if we recall the way the CRI modifies the Dennis model to apply to brood lines) after fifteen years. Roughly a halving from the starting population. And if, realistically, ten more years must elapse before the biological response to the new intervention manifests itself,

what is the probability that a population that survived the first 15 years will survive the next ten? If we use the median population at 15 years to initialize a new Dennis model prediction for ten more years, the probability of quasi-extinction in those ten years is 0.17, rather worse than the prospects for the first ten years. Overall, the probability of quasi-extinction during the total 25-year interval (the first five years of delay, the next five years to adopt a decision, and the remaining ten years until the intervention begins to show fruit) is 0.36. Given the way probabilities compound in this kind of analysis, we would want a higher certainty that the details of the model are appropriate.

Similarly, metapopulation issues require a more sophisticated treatment. It is not enough to simply apply a 0.1 probability of extinction threshold at the single stock level, rather than a 0.01 threshold, just because there may be ten subpopulations to the metapopulation. The extinction probability for the entire metapopulation relates to the extinction rates for the subpopulations in a way that depends, among other things, on correlation between the dynamics of the subpopulations. Figure 9-2 of the CRI indicates high correlation, which will increase the vulnerability of the metapopulation to extinction, all other things being equal. The importance of correlation adds to the interest in extending a more detailed analysis farther back than 1980.

IMPLICIT CONCLUSIONS OF THE CRI DOCUMENT

The CRI does not present an explicit synthesis of its new conclusions with those of the AFA to recommend a bottom line for the EIS that it will serve. The CRI does present two summary statements internal to the CRI analysis, one in section 9.4.4 beginning on page 17, and another in section 9.8 on page 22. The form of the argument is interesting but incomplete. The argument asks two questions: (1) Is it likely that dam breaching alone could raise the average growth rate enough to reduce the extinction risk significantly? (2) Is it likely that habitat improvement and harvest reduction by themselves could raise the average growth rate enough to reduce the extinction risk significantly? The tentative answer of the CRI to both questions is "possibly yes" for fall chinook and steelhead; but it seems to be a qualified "probably no" for spring/summer chinook.

We are struck by three questions of our own, in appraising this summary in the CRI.

1. Would the answers be the same if the analysis considered the effects of interventions in reducing population growth rate variability, as well as effects expressed in raising average growth rates?
2. Where would artificial production fit in the equation?
3. What would emerge from analyzing the prospects of reducing risk by the action of dam breaching AND addressing habitat and harvest?

The logical analytical framework that is evolving under the title of the Cumulative Risk Initiative should be capable of addressing these three questions. We suggest that NMFS should attempt to address them before developing definitive recommendations for the 1999 Hydro Decision.

BIBLIOGRAPHY

Dennis, B., P.L. Munholland, and J.M. Scott. 1991. Estimation of growth and extinction parameters for endangered species. *Ecol. Monogr.* 61:115-143.

Hankin, D.G. 1990. Effects of month of release of hatchery-reared chinook salmon on size at age, maturation schedule and fishery contribution. ODFW Info. reports Number 90-4. 37 pp.

Johnson, N.L., S. Kotz, and N. Balakrishnan. 1994. Continuous Univariate Distributions. Vol. 1. 2nd edition. John Wiley & Sons, NY.

Lewontin, R.D., and D. Cohen. 1969. On population growth in a randomly varying environment. *Proc. Nat. Acad. Sci. USA* 62:1056-1060.

McCullagh, P., and J. A. Nelder. 1983. Generalized Linear Models. Chapman and Hall, London.

Mills, L.S., S.G. Hayes, C. Baldwin, M.J. Wisdom, J. Citta, D.J. Mattson, and K. Murphy. 1996. Factors leading to different viability predictions for a grizzly bear data set. *Conservation Biology* 10:863-873.

Percy, W.G. 1992. Ocean Ecology of North Pacific Salmonids. Washington Sea Grant Program. Univ. Wash. Press. Seattle, 179pp.

Ricker, W.E., 1981. Changes in the average size and age of Pacific salmon. *Can. J. Fish. Aqu. Sci.* 38:1636-1656.

Tuljapurkar, S.D. 1982. Population dynamics in variable environments. III. Evolutionary dynamics of *r*-selection. *Theor. Pop. Biol.* 21:141-165.