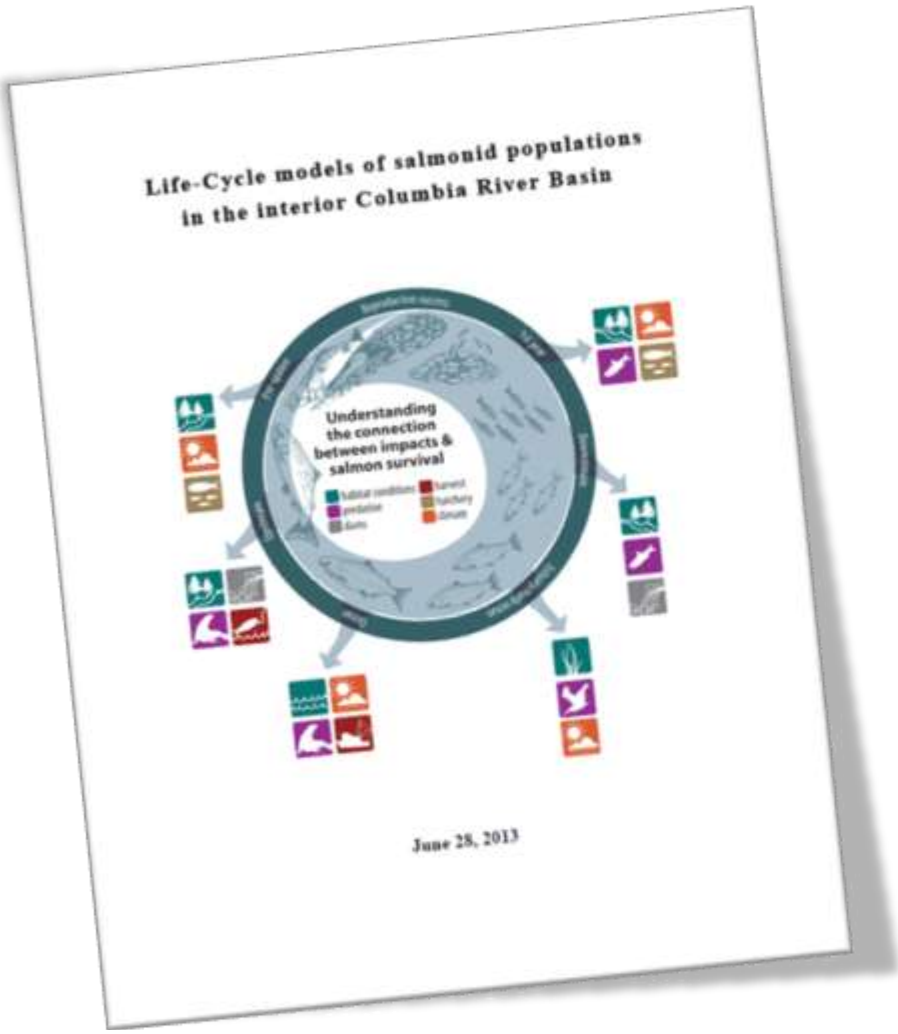
Independent Scientific Advisory Board

Review of NOAA Fisheries' *Life-Cycle Models of Salmonid Populations in the Interior Columbia River Basin*

(June 28, 2013 draft)



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Contents

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Executive Summary

In response to NOAA Fisheries' request, the Independent Scientific Advisory Board (ISAB) reviewed a draft document titled *Life-Cycle Models of Salmonid Populations in the Interior Columbia River Basin* (June 28, 2013; LCM document). The modeling effort described in the LCM document builds from previous efforts that modeled hydrosystem and climate effects on salmonid population viability, and expands those efforts to cover more populations and habitat actions, as well as improved representation of climate effects, hatchery spawners, and spatial interactions. Specific models are in various stages of development and will be updated as new data become available. Consequently, the technical content of the ISAB's review varies significantly depending on the status and content of the various models.

The report's Introduction briefly identifies past modeling efforts and describes new issues to be examined within the document. A general modeling structure is presented which is used to guide many of the models described in subsequent sections. Model metrics are stated to be consistent across models so that information may be shared. For example, the ocean and estuary submodels could be incorporated into models for upstream populations. The anticipated final models stemming from this effort may be expanded to encompass salmon evolutionary significant units (ESU), but it is not presently clear how the various models will be combined to address issues facing entire salmon ESUs. A key goal of life-cycle models is to inform decision makers about the influence of restoration activities on the recovery and viability of ESA-listed salmon in the Columbia Basin.

Habitat. NOAA Fisheries scientists and the ISAB recognize that linking mitigation actions to population responses of salmon is complex, data intensive, and highly challenging. Nevertheless, to demonstrate how existing data in the Columbia Basin may be used to evaluate effects of mitigation actions in tributary habitats on salmon population viability, the investigators present five modeling examples (Chapter 2). Three models target spring/summer Chinook in portions of the Snake River Basin, one model addresses spring Chinook in the upper Columbia River, and one model examines steelhead throughout the interior Columbia Basin. Some models, such as the Watershed Model in the Lemhi River that examines both steelhead and spring Chinook, are reportedly designed for implementation in subbasins throughout the Columbia Basin. All of these models are works in progress. Additionally, three other habitat

models and a fall Chinook run reconstruction effort are presented (Chapter 3), but these efforts are at very early stages of development.

A key information gap in all models is the lack of functional relationships showing how changes in habitat quantity and quality (i.e., from restoration actions) affect salmon survival or other population viability criteria. The investigators recognize this deficiency and are working to incorporate the available information to the extent possible. The ISAB also recognizes that development of these relationships is a major challenge because there are few examples in the literature that quantify population level responses of salmon to changes in habitat. The ISAB encourages broader collaborations with the Watershed Program in NOAA Fisheries and other experts on the freshwater ecology of salmon to develop quantitative fish/habitat relationships that could be incorporated within the life-cycle models. Although major challenges and data gaps remain with regard to these functional relationships, the ISAB believes that the life-cycle modeling approach is superior to the Expert Panel approach, which relies on untested hypotheses about the benefits of habitat changes for the recovery of salmon populations. Life-cycle models represent a means to test or explore these hypotheses while also examining sensitivity of uncertain parameters or measurements on desired outcomes. Information from life-cycle models can help with prioritizing restoration efforts.

While recognizing the fundamental need for quantitative fish/habitat relationships, one modeling approach (Section 2.3, 2.5) was developed to increase understanding of how changes in survival rates at various stages of the steelhead and Chinook life cycles could affect population abundance and viability. Model users can input changes in survival that might occur as a result of habitat restoration, hydrosystem changes, climate change, and so forth. These models incorporate results from the estuary and ocean submodels (see below), demonstrating some linkage between freshwater, estuarine, and ocean life stages.

Several statistical models provide strong empirical support for density dependent survival (Sections 2.1, 2.4, Chapter 4). This evidence provides support for the need to increase capacity and productivity of tributary habitats as a means to enhance salmon survival and abundance. As noted in previous ISAB/ISRP documents (e.g., ISAB 2011-4, ISRP 2011-14, ISRP 2013-11), evidence of strong density dependence in watersheds experiencing low population abundances relative to historical levels can be used to guide restoration efforts. For example, populations expressing steep density-dependent relationships at relatively low population densities could be targeted for potential restoration efforts. Likewise, a reduction in density dependence following restoration efforts may provide evidence of progress.

Hatchery Supplementation. Supplementation of wild salmon populations with hatchery salmon is a key, albeit controversial, strategy in the Columbia Basin for rebuilding depleted wild salmon populations. Chapter 4 describes a novel modeling approach for investigating the likely effects of hatchery supplementation on wild salmon population dynamics. This well-developed investigation used several decades of data for 23 Snake River spring Chinook populations. The ISAB commends the extensive use of existing data here and in many of the other models. This investigation provides compelling evidence indicating that numbers of hatchery salmon spawning in rivers accentuates density dependence such that lower survival offsets the anticipated benefits of supplementation for spring Chinook salmon. This modeling approach should be utilized for other species and watersheds when sufficient data exist, and the findings should be incorporated into other life-cycle models. Presently, only a few of the models incorporated effects from hatchery/wild salmon interactions, but none use findings from this investigation. We anticipate that this effort will be significant in informing policy and management in the Columbia Basin.

Estuary and Ocean. The estuary and ocean models (Chapter 5) partially build upon existing information, but both could be expanded to incorporate information provided by other estuarine and marine researchers. The estuary model focused only on avian predation. It is estimated that a 50% reduction in predation would lead to proportional increases in estuarine survival of 1.7% for Chinook and 11.5% for steelhead. This model did not include other key factors such as estuarine habitat restoration and predation by pinnipeds, but the investigators indicated these factors would be addressed in future iterations. Other than avian predation in the estuary, predation was not addressed in other models in the report (e.g., by pikeminnow, bass, catfish, walleye). The ocean model builds upon some earlier efforts on factors affecting Chinook and steelhead survival at sea, but it is likely that additional effort could refine and improve these relationships by considering additional variables examined by NOAA Fisheries ocean researchers.

Hydrosystem. Chapter 6 provides a very brief description of a hydrosystem survival model based on CSS and COMPASS models that can be used to evaluate hydrosystem scenarios. Considerable hydrosystem modeling efforts have occurred in the past (e.g., COMPASS, CSS), but the information presented here is insufficient to allow a scientific review. It is unclear how the hydrosystem model will be used to model specific scenarios mentioned in the report such as dam breaching and reservoir drawdowns.

Population Spatial Structure. Spatial structure and diversity are key elements of viable salmon populations. As part of the metapopulation framework for the life-cycle models (Chapter 7), the investigators examined 1) isolation of Snake River spring/summer Chinook salmon in relation to population “sources and sinks” and 2) correlation among Chinook population abundances in the upper Columbia and Snake rivers. The framework is a work in progress. The ISAB found the analyses provided scientifically interesting results and identified data gaps (e.g., information on fish movements is needed), but it is not clear how this effort furthers the goal of developing a full metapopulation model for spring/summer Chinook or for other races and species.

Climate Change. Climate change is recognized in the Columbia Basin as a major factor for restoration efforts to overcome if salmon populations are to become viable and robust. The Introduction identified previous modeling efforts that incorporated future climate change scenarios. Section 2.4 examined population responses of spring/summer Chinook salmon in the Salmon River Basin to projected changes in streamflow and temperature as a result of climate change scenarios. The conceptual approach was innovative. However, in its present state of development, the model relies on numerous assumptions and the investigators warn that current findings are highly preliminary and should not be used for decision making. Other aspects of climate change – such as potential changes in forest health, ocean acidification, and salmon survival at sea – were not discussed in the overall report.

Additional Factors. The life-cycle models addressed, to varying degrees, many of the issues facing salmon populations in the Columbia Basin. However, two key factors not addressed, and that may slow salmon recovery, are the widespread proliferation of nonnative species and continued use and discharge of toxic chemicals in the subbasins. These factors undoubtedly impact salmon populations, though effects at the population level may not be readily known. The ISAB encourages NOAA Fisheries scientists address nonnative species and toxic chemicals in subsequent life-cycle models.

Summary. The ISAB supports the decision by NOAA Fisheries scientists to seek peer review of the life-cycle modeling effort at this early stage. Life-cycle models can be complex and early feedback on model development is an important step. The investigators have shown progress, but there is much to do before the models can, for example, inform habitat restoration activities and decision making. Specifically, the incorporation of quantitative fish/habitat functional relations in tributaries and the estuary remains a key challenge. The hatchery supplementation model was innovative and informative; these findings should be incorporated into other models and the approach should be applied to other species and regions if data are available. The ISAB anticipates that the next iteration of models will provide greater coherence and integration among the modeling efforts, so that they may begin to address key questions. Furthermore, the overall modeling effort should explicitly identify its role in the adaptive management process within the Columbia Basin. Although significant challenges remain, building life-cycle models is an effective means for identifying data needs. These data needs should be fulfilled whenever possible. The ISAB looks forward to seeing further progress on this important endeavor in the near future.

ISAB Review of NOAA Fisheries' *Life-Cycle Models of Salmonid Populations in the Interior Columbia River Basin*
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Background

At NOAA Fisheries' request and as called for in the NOAA's 2009 Adaptive Management Implementation Plan (AMIP), the ISAB reviewed a draft document titled *Life-Cycle Models of Salmonid Populations in the Interior Columbia River Basin* (June 28, 2013; LCM document). The life-cycle models described in the LCM document were developed in response to NOAA's AMIP that called for expansion of models used in the 2008 Federal Columbia River Power System Biological Opinion (FCRPS BiOp). The 2008 BiOp used life-cycle models to examine the effects of hydro actions on population viability under a range of future climate scenarios. The AMIP modeling effort expands the number of populations examined, models effects of habitat mitigation actions, improves representation of climate effects, includes the effects of hatchery spawners, and models spatial interactions. The LCM document represents a combined effort from modeling teams consisting of scientists from NOAA's Northwest Fisheries Science Center, the U.S. Geological Survey, consulting firms, and state and tribal fish and wildlife agencies. NOAA Fisheries emphasized to the ISAB that the LCM document was a work in progress. The models will be updated to take advantage of the many field studies currently underway or planned that will strengthen the database supporting the models.

The ISAB was greatly aided in this review by presentations from the modeling teams at the ISAB's June and September 2013 meetings.

The ISAB's review is provided in two parts: a primary report summarizing findings on each section of the LCM document and an appendix with technical and editorial comments. Because the LCM document is a work in progress and the ISAB anticipates an iterative review role, the ISAB's comments are primarily directed to NOAA Fisheries and the modeling teams to improve the next round of modeling and documentation. The appendix, in particular, is intended for the modeling teams (see ISAB 2013-5A).

In reviewing each LCM document section, the ISAB considered the following questions:

1) Are the goals and objectives of the model(s) clearly stated?
2) Are the specific approaches and methods scientifically sound and clearly written? Are there any significant conceptual flaws?

3) Do the models make appropriate use of the data? Are the data sufficient to build and make effective use of the model? If not, what types of data need to be collected to answer the question and develop the model?
4) Is the report clearly written? Are the methods described in sufficient detail for a reader to understand and replicate what was done? Are assumptions and uncertainties about the analyses clearly described? For example, do the authors identify the strengths and weaknesses of the model, and accuracy and precision of model output?
5) Is the level of complexity of the models appropriate? Does the model output, characterized by metrics on initial conditions, population performance, and population dynamics, allow comparisons among populations and across scenarios within populations? Did they conduct appropriate sensitivity analyses?
6) Is the role of the model in adaptive management clearly identified?

The ISAB's answers to these questions for each LCM document section are provided in the appendix and summarized in the main body of the report. The appendix is available in a separate downloadable file: www.nwcouncil.org/media/6890798/ISAB2013-5A.pdf.

Review of Chapter 1. Introduction

Chapter 1 focuses on the development of life-cycle models and provides an overview of the general form of many models that are described in subsequent chapters. The form is a standard matrix model with stochastic components. Some notation and a set of common metrics that will be used to characterize population performance are introduced. A very brief overview (one paragraph) is provided on the chapters that follow.

There has been considerable effort on life-cycle or related modeling in the Columbia Basin for more than two decades. Some of that effort is referenced in the overview part of the introduction. The modeling history has been one of conflicting views (see ISAB 2001-1, ISAB 2008-1), but this conflict is not discussed here. Life-cycle modeling is clearly important, and it would help to provide more detail on past efforts and to clarify how this new effort is stepping beyond or building on past efforts. What has been learned and where are the critical uncertainties or limitations? *(Note that the introduction to Chapter 4 provides a nice example for the specific topic of hatchery effects.)* The real challenge is not building more complex and sophisticated life-cycle models, but to parameterize models in an objective and meaningful way, particularly for the early life history stages that represent key linkages between habitat and population performance.

Because the first chapter sets the tone for subsequent chapters, the basic terms and symbols used in this and other chapters need to be defined and used consistently throughout the report. For example, the definition of productivity varies among ecological sciences and among sections within this report. The ISAB's Appendix covers additional issues with notation (ISAB 2013-5A).

The output metrics are standard, for the most part. The outputs need to reflect reality and be reasonably predictive. The challenge is to balance the complexities associated with life-cycle dynamics, environmental influences on those dynamics, and ease of use and understanding by managers. For example, it is unclear how the risk of quasi-extinction (QE) is extracted from Figure 4.

The Introduction emphasizes the importance of developing relationships between juvenile productivity and habitat conditions (Section 1.4). While this focus is right, some chapters tend to gloss over the linkage between the parameter estimates and habitat conditions, or they focus on conditions they can estimate and ignore those they cannot (e.g., Chapter 2.2). Some rely on complex extensions of limited information to fit the critical functions (e.g., Chapter 2.4). Each chapter needs to explicitly state how habitat conditions are or are not included in their model and identify data gaps when appropriate.

Important work in later chapters, which begins to conceptualize models for specific places and to estimate some of the necessary parameters, is very briefly summarized in the Introduction. It would be helpful for the Introduction to address questions such as: How was it decided which models to develop? What is the time frame for the modeling efforts? What is the anticipated endpoint for the final models? Also missing is an overview of the success and failures of each of the models in the report. It would be very useful to have a Table summarizing the questions and outcomes of these modeling efforts, and how the results will be used to improve the plight of fish populations in the Columbia Basin (and elsewhere). This would help to establish the credibility of the life-cycle modeling approach for the general reader, to ascertain how much of the salmon life cycle we understand and to identify critical uncertainties and information needs.

Recommendations

1) Add a section describing how this modeling effort differs and improves on past modeling efforts. What will be the limitations of this approach (e.g., dealing with climate change, contaminants, nonnative species, and other predators)?
2) Standardize notation throughout the working groups, especially the definitions of fish age (refer to the Appendix for more details).

3) Provide a more detailed overview of the individual models developed as part of this project, along with the key questions to be answered and their outcomes (successes and failures).
4) Provide a summary of how well the individual components of the life cycle are understood based on the modeling efforts and what knowledge is missing.
5) Provide an overview of key data gaps that have emerged from the modeling efforts.

Review of Chapter 2. Examples of Freshwater Habitat Relations in Life-cycle Models

2.1: Grande Ronde spring Chinook population models

Goal: The primary focus of this study is to update and expand the ICTRT's (2007) matrix model by developing more detailed models specific to each of four Chinook populations (Catherine Creek and the Upper Grande Ronde, Minam, and Lostine rivers). The ultimate objective is to use the more detailed models to assess natural sustainability and potential for restoration.

Key findings: This study is a major contribution in synthesizing and documenting field data collected with many years of effort. The analysis suggests that the freshwater productivity of juvenile Chinook can be strongly density dependent, as in the Upper Grande Ronde population, and provides additional justification for freshwater habitat restoration actions there.

ISAB comments: The refined life-cycle model appears to be well-reasoned and conceptually sound. It can be used to explore the population-level consequences of management actions or future scenarios that affect juvenile survival (perhaps reflecting the quality of habitat) and/or carrying capacity (reflecting the quantity of suitable habitat). The capability to model salmon productivity and carrying capacity separately is a significant conceptual improvement over procedures currently being used in the Expert Panel process in which a linear relationship is assumed between changes in habitat condition (expressed as a percentage of optimal condition) and changes in salmon survival. The statistical analysis of various factors affecting recruitment (parr per spawner) seems incomplete (see Key Gaps). The speculation that variation among streams in the measured ratio of early to late migrants is an artifact of fish trap placement casts doubt on the representativeness of samples, and thus, on the entire juvenile enumeration effort and all of the survival analyses that are based on these enumerations.

Key gaps: More analysis is needed to determine reasons for the strikingly greater density dependent growth and survival of parr in the Upper Grande Ronde. For example, it seems that the steeper, (extrapolated) negative slope for the Upper Grande Ronde in Figure 10, from which greater density dependent survival is inferred, might arise just from overestimating the amount of ***suitable*** habitat in the Upper Grande Ronde during the AQI standardization step. The statistical analysis of various factors affecting recruitment (parr per spawner) also seems incomplete; the various factors in Figure 3 should be considered jointly to increase statistical power and to explore potential interactions. Potentially confounding time series effects should be investigated or ruled out.

Recommendations:

1) Consider (and if possible, rule out) alternative explanations for the apparently stronger density dependence in the Upper Grande Ronde Chinook population.
2) Improve statistical analyses of factors potentially affecting recruitment of parr-per-spawner and consider the implications of bias due to trap placement.

2.2: ISEMP Watershed Model for spring/summer Chinook salmon and steelhead in the Salmon River Subbasin

Goal: This section describes how the ISEMP Watershed Model has been refined to incorporate tributary-specific data on factors affecting freshwater productivity of salmon. The current model is used to simulate habitat restoration scenarios and to predict corresponding changes in adult Chinook abundance in the Lemhi River. The ultimate goal is to apply a generalized version of the Watershed Model in other subbasins and to guide monitoring design.

Key findings: Considerable work has been done in the Lemhi River to support the refinement of life-cycle modeling outlined in this chapter, both as part of ISEMP but also through a substantial history of work by others. Life-cycle modeling in the Lemhi could become a powerful tool to help interpret results generated in monitoring and research. It could also help to prioritize and guide future work in both restoration and evaluation.

ISAB comments: This report is an outline of a work in progress rather than a compelling example of the utility of the updated ISEMP Watershed Model. The modeling and discussion of how changes in habitat affect salmon survival seem very preliminary. No doubt the modeling has potentially important applications in the Lemhi, but the conclusions seem largely speculative without a more complete analysis of uncertainty, sensitivity of results to the assumptions, and a detailed logical account of how the models might be adapted to include additional information that will become available in the future. It would be useful to include more discussion of what has actually been learned about fish-habitat relationships in the Lemhi, how that has or could be incorporated in the models, and some examples of how other scenarios would help to learn something more specific or to resolve important uncertainties. There are no analyses of uncertainty or sensitivity, yet it seems critical to consider this uncertainty in order to prioritize and focus future work.

Key gaps: A major deficiency in this draft is the relative lack of detail and confusing presentation of the work: it is not clear how the general model has been refined and adjusted or how empirical data are used to parameterize the new version of the model; terminology is unclear and used inconsistently; and the simulation scenarios are incompletely described and hard to understand. Much of the refinement of the general model to the application in the Lemhi basin is apparently based on other reports that were not easily accessible to the ISAB.

Recommendations:

1) Discuss what has been learned about fish-habitat relationships, and include some examples of how running scenarios could inform specific issues or resolve important uncertainties.
2) Include more analysis or discussion of uncertainty and sensitivity to help prioritize and focus future work; continue to evaluate (and peer review) modeling efforts in this system to guide further efforts in the Lemhi and elsewhere.

2.3: Upper Columbia River spring Chinook salmon

Goal: The goals of this section are not stated explicitly, except for the sentence, "*One of the goals of developing this model is to characterize the impact of habitat actions on survival and subsequent impacts on population dynamics.*"

Key findings: The simulation scenarios provide a basic sensitivity analysis in which selected parameters of interest are adjusted separately to determine outcomes for fish population metrics, consistent with procedures described in Chapter 1. Population metrics are shown to be very sensitive to assumptions about ocean survival. Even so, improved freshwater survival during the prespawning and spawner-to-parr phases (assumed to be achievable through habitat restoration) could substantially reduce extinction risk despite poor ocean survival.

ISAB comments: These efforts to model life history diversity and habitat relationships in the Wenatchee River seem surprisingly preliminary, given the investment in ISEMP and CHaMP programs for the Wenatchee and Entiat rivers. Fish-habitat relationships are not actually incorporated into this version of the ICTRT life-cycle model, and habitat actions are not specifically addressed within the current draft. We presume that models incorporating more explicit fish-habitat relationships are still being developed and will be presented in the near future.

Key gaps: Instead of predicting population responses to habitat restoration actions, the simulation scenarios only illustrate various assumed consequences for survival. It seems that the data or conceptual tools are still inadequate to examine quantitatively how freshwater habitat causes changes in Chinook abundance, recruitment, or extinction in the Wenatchee system.

Recommendations:

1) Clearly state the goals and objectives; consider how this model might be used in the adaptive management cycle to improve decision making and to assist with the delisting of ESA-listed fishes.
2) Refine this model to explicitly include functional relationships between habitat actions and fish survival (and submit for peer review).

2.4: Population responses of spring/summer Chinook salmon to projected changes in stream flow and temperature in the Salmon River Basin, Idaho

Goal: This study develops modeling and statistical techniques to investigate how freshwater survival of Chinook in the Salmon River is affected by fish density and components of climate change, particularly temperature and flow. A life-cycle model incorporating inferred functional relationships between freshwater survival and climate variables is then used to assess the viability of nine Chinook populations under several downscaled climate projections stemming from published climate models.

Key findings: Chinook populations in the Salmon River may vary widely in their vulnerability to climate change. Most, but not all populations, showed reduced carrying capacities under warmer conditions, despite the high altitude and somewhat pristine environment of the Salmon River basin. These results may be the best that can be achieved with the limited information currently available. Unfortunately, many assumptions were required to represent complex life histories in the complex, multistage statistical analyses. For this reason, the authors warn that their current results should not be used as predictions for decision making.

ISAB comments: The conceptual approach is innovative, and the techniques developed in this study are potentially useful for simulating the impacts of climate change on salmon productivity. However, the data and modeling are (as yet) too limited in scope to provide realistic results that can guide habitat restoration or other management actions. Relying solely on statistical relationships without understanding the mechanisms involved seems risky; in-depth exploration of the mechanisms that are assumed or implied, and how they might be validated, is needed.

Key gaps: The conclusions from the simulations rest on extrapolations from an inherently limited data set. The authors note important caveats in the discussion, but more detailed exploration of the uncertainties and the sensitivity of the results to the parameter estimates would be useful to guide further field and modeling work.

Recommendations:

1) Consider how errors (or uncertainty) in estimates of fish abundance might affect conclusions that are based on statistical differences in how well complex models fit the (questionable) data.
2) Discuss likely biological mechanisms behind the statistical results that are extrapolated in the modeling.
3) Test predictions from the statistical models by acquiring empirical data on parr density and experimental support for functional relationships between fish survival and habitat variables associated with climate change.
4) Collect data to test and model additional functional relationships (e.g., those involving winter ice, disease, predation, competition from non-native fishes).

2.5: Life-cycle matrix models to evaluate productivity and abundance under alternate scenarios for steelhead populations

Goal: This model expands the 2007 ICTRT matrix model with updated data and additional steelhead populations. It is used to estimate steelhead abundance and extinction risk at 25 and 100 years in the future.

Key findings: The analysis is essentially a sensitivity analysis exploring the effect of changing (assumed) survival rates at different life stages. Scenarios are labeled as habitat, hydrosystem, climate change, and such, but there are no functional relationships linking management actions, habitat restoration, or changes in climate to changes in survival. Moreover, validation of the model results is not possible. The simulation results do suggest that plausible (but assumed) improvements to adult and juvenile freshwater survival could have large benefits for some populations at risk, potentially offsetting the declines in abundance and increases in quasi-extinction risk caused by recent changes in ocean conditions due to climate change.

ISAB comments: As stated by the authors, this life-cycle model demonstrates potential to increase understanding of how changes in survival rates at different stages of the steelhead life cycle can affect population abundance trends and viability. The modeling framework is quite flexible and can be made to accommodate scenarios of survival changes at multiple life stages. Although many scenarios could be modeled, one of particular interest is the combined effect of all improvements in survival that could be effected by improved management; for example, increases in survival owing to improved habitat, reduced harvest, improved downstream survival through dams, and improved estuary survival via reduced avian predation. The assumption that population subunits (that are only partially isolated from other subunits) will be demographically representative of the entire population seems questionable, and results could be misleading. Under-representation of high-elevation populations (for which data are lacking) also might be misleading. The ISAB encourages further exploration of other climate/ocean indices (beyond the PDO and coastal upwelling) that may be related to growth and survival of juvenile steelhead during the first-year offshore phase in the Gulf of Alaska.

Key gaps: These models do not yet include functional relationships between freshwater habitat conditions and juvenile and pre-spawning adult survival. The modeling of life history variation also seems preliminary as resident life histories and iteroparity are not considered. Hatchery supplementation and the effects of hatchery/wild interactions are not included. The current modeling effort does highlight the need to collect additional data on the abundance of resident rainbow trout (*O. mykiss*) and the contribution of rainbow trout to steelhead productivity (an issue being addressed by another model that is under development and described in Chapter 3.4).

Recommendations:

1) Simulate additional scenarios to determine the extent to which cumulative improvements due to all plausible management and habitat restoration actions could compensate for decreased productivity due to changes in climate.
2) Continue development of the model to consider the abundance of resident rainbow trout and their contribution to steelhead productivity.
3) Refine estimates of ocean survival by considering additional ocean/climate indices that may explain patterns of growth and survival of immature steelhead in the ocean.

Review of Chapter 3. Models under Development

3.1: Snake River basin fall Chinook salmon run reconstruction as a basis for multistage stock-recruitment modeling with covariates

Goal: This chapter describes how juvenile and adult passage at Lower Granite Dam will be reconstructed for use in a yet-to-be-developed stock-recruitment model.

ISAB comments: The run reconstruction is complicated by numerous factors, including incomplete counts of salmon at the dam and releases of unmarked hatchery salmon. A similar model is built for the juvenile run reconstruction.

The written portion seems to present a reasonably rational accounting for run reconstruction, but it is all "verbal" with limited formal model development (e.g., it is missing a set of equations). The figures are helpful in understanding the logic, but the text lacks sufficient detail to reproduce the results. The models are currently implemented in spreadsheets making it difficult to audit or to extend the models.

There are many data sources used in the run reconstruction, but only data that provide direct information are used. Because of the model structure, data that provide indirect information cannot be incorporated into the model. For example, the run counts from downstream dams do provide some information about the counts at Lower Granite Dam, but this information cannot be incorporated into the current model.

Model outputs will include the run reconstruction along with measures of precision. The latter are to be generated using bootstrapping, but it is not clear that all sources of uncertainty will be incorporated. For example, how will the period when counts are not made be bootstrapped? How well is each of the input data values determined? Are there additional (possibly hidden) sources of uncertainty in the raw data that imply a simple bootstrapping of the raw data will miss this uncertainty?

No sensitivity analyses are presented.

Recommendations

1) Perform sensitivity analyses to understand which data sources are most critical for model performance.
2) Identify any data gaps. (i.e., are there some data, which if available, would greatly improve the reconstruction?)

3) Convert the spreadsheet implementation to computer code (such as R) which is easier to audit and is more easily modified.

3.2: Methow River Intensively Monitored Watershed: incorporating food webs into the life cycle

Goal: This section attempts to describe a comprehensive modeling approach to incorporate food webs into life-cycle models. The current document describes an ambitious undertaking, at a very high level.

ISAB comments: The current condition of this section made it very difficult to follow and to evaluate. For example, how are the modeling precepts and design (section 3) applied in the model development? There are many figures that show conceptual models, but it is unclear how these are linked together.

It is also unclear exactly how the food web will be applied to life-cycle modeling. For example, Bellmore et al. (2013) discusses Methow River food webs, but this chapter contains no food web data, and there is no information on how food webs will be linked into the salmonid life cycles. The Intensively Monitored Watershed (IMW) project has been active for several years, but this modeling effort (Chapter 3.2) is apparently new. The current document reads more like a proposal to incorporate food webs into life-cycle models than a description of accomplishments.

Near the end of the report (p. 21), the authors present their conclusion that salmon have a net negative effect on periphyton production (via a combination of bringing marine-derived nutrients but also disturbing substrate with their redd-building activities), but no details on the model nor data analysis are presented to support this conclusion. Appendix A describes the Ricker recruitment models for the populations. However, there are few data and much of the density dependence seen may rest on a single data point. There was no discussion of the uncertainty in the fit from these sparse data, nor any discussion of the fit of alternate models with no density dependence.

Recommendations:

1) Prepare a more formal report.
    a. Revise the report through significant reorganization, simplification, and editing to clarify what are high level conceptual views of the model, what models have been implemented, and which are still in the planning stages.

b. Provide more evidence for the conclusion that salmon have a net negative effect on periphyton production.
c. Provide more detail on fitting data with Ricker model.

3.3: Catherine Creek life-cycle model with policy optimization

This is a very brief description (two pages) of a model that will be developed that includes many individual life stages, each influenced by habitat conditions and other variables. Movement between life stages will be modeled using a Beverton-Holt (BH) model to include density dependence (if needed). Each of the BH models can include covariates specific for that life stage. The stochastic model then can be used to predict how changes at each life stage (e.g., improvement in habitat) affect future population trajectories. This can be used as a planning tool to see which changes have the biggest impact.

No actual model is presented, nor are any preliminary results, so it is difficult to review this section except at a high level. The ISAB did receive a presentation and user's manual from Chris Jordan (Habitat Modification Effects on Salmonid Population Dynamics) that might describe this model in more detail, but a review of this document is not included here.

Recommendations:

Prepare a more formal document that describes the model structure and how it can be used.

3.4: Yakima River steelhead and other *Oncorhynchus mykiss* populations

Goal: This section describes two models: 1) a life-cycle model that describes abundance, age structure, and expression of anadromy in steelhead over time, and 2) a model that investigates influences of various factors on the expression of anadromy in steelhead. The first model is at the population level, while the second model examines fine scale differences in environmental variables on distribution.

ISAB comments: The models are not described in detail in this report because several cited papers provide a fuller discussion. Nevertheless, the overview is clearly written. The first model does very well at predicting abundance trends in the upper Yakima River basin. The model also shows it is important to model interactions between anadromous and resident *O. mykiss*, and to model the effect of different smolt-to-adult survival (SAR) values on anadromy.

The second model suggests that higher summer base flow levels generally favor resident individuals and that the effect of temperature is complicated.

Key gaps: The authors candidly discuss that there is no modeling of the impact of environmental factors on the relative number of migrants vs. residents. At the moment, different populations in different spatial areas are subject to different environmental variables, and so there is complete confounding of population and environmental effects. To resolve these issues, the authors make some very sensible recommendations on further model development.

Data gaps and model limitations are discussed in Courter et al. (2010) but not in this report. The authors did perform some sensitivity analysis on their models. For example, the SAR and proportion of steelhead produced by crosses appear to be confounded. Additional sensitivity analyses are needed to see what other relationships are confounded.

Recommendations:

1) Continue refinement of the model as suggested in the report, including: (1) incorporate a life history tactic that maximizes fitness with growth, modeled as a change in body length, weight, and lipid content, (2) model how changes in freshwater conditions affect the proportions of anadromous and resident fish, and (3) develop single-sex models because of differential expression of anadromy in male and female fish.
2) Perform additional sensitivity analyses to see what other relationship are confounded. What data would be needed to inform confounded relationships? Are these data available or can they be collected?

Review of Chapter 4. Hatchery Impacts

4.1: Impacts of supplementation on population dynamics of Snake River spring/summer Chinook salmon

Goal: The authors present a novel modeling approach for investigating potential effects of hatchery supplementation on "wild" salmon population dynamics. This is an important issue in the Columbia Basin and in other regions of the Pacific Northwest. The manuscript applies several decades of data for 23 Snake River spring Chinook populations to several population models and uses a statistical approach to identify the best-supported models.

Key findings: The investigation provides empirical evidence that reinforces earlier observations and concerns by the ISAB, ISRP, and others that supplementation may only result in replacement of existing natural salmon production rather than adding to it (ISAB 2003-3, ISRP/ISAB 2005-15, ISRP 2011-14). The key findings include strong evidence for density dependent survival and evidence for even stronger density dependence in response to increasing numbers of spawning hatchery spring Chinook salmon. The investigators conclude that supplementation of streams with hatchery spring Chinook salmon may have a benign or beneficial effect when spawner abundances are very low, but supplementation may limit the rate of rebuilding spring Chinook populations or limit the capacity of the wild population to respond to improved environmental conditions.

ISAB comments: The ISAB finds that the investigators provide compelling evidence to show that numbers of hatchery salmon spawning in the rivers accentuates density dependence such that anticipated benefits of supplementation may not be realized for spring Chinook salmon. The investigators use a large informative dataset spanning many years and many salmon populations in the Snake River Basin. The modeling approach developed by the investigators is sophisticated and novel. Although the analysis cannot distinguish between genetic versus environmental effects of supplementation, as noted by the investigators, it provides important findings about overall effects of supplementation. The analysis should provide important information for policy and management planning in Fish and Wildlife Program amendments, the artificial production strategy, harvest management, and the FCRPS BiOp. The report and analyses are insightful and demonstrate attention to detail. Nevertheless, as is common in ISAB reviews, we provide a number of suggestions and comments in the Appendix. We hope that the authors will find these comments useful when further developing the manuscript for publication.

Key gaps: The investigators make use of an extensive dataset spanning many years, but the quality of data, including changes in methods to obtain the data, could be described in greater detail.

Recommendations:

1) Consider how the evidence for density dependence, which is shown to occur at low spawning densities, should be used to further guide habitat restoration efforts in the Snake River Basin, e.g., populations showing strong density dependence at low spawning levels might be targeted for restoration.
2) Use the analyses to identify levels of parent spawners (natural vs. hatchery origin) needed to sustain productive spring Chinook populations in each watershed. This could be reported in an appendix.
3) Identify additional salmon species and populations in the Columbia River Basin where data are sufficient to apply this approach.

Review of Chapter 5. Estuary/Ocean

5.1: Estuary

Goal: The authors' goal is to illustrate life-cycle effects of a 50% reduction in estimated avian predation mortality in the Columbia River estuary on population parameters and ESU-level population performance. Estimated avian predation mortality is assumed to be constant (published values of 3.4% for yearling Chinook and 18.7% for steelhead). In the life-cycle model, terms for 1st-year ocean survival (S_3 for Chinook or S_{O1} for steelhead) are modified to include explicit terms for estuary (S_{EST}) and ocean (S_{EO}) survival. S_{EST} includes avian (M_A) and non-avian (M_{NA}) sources of mortality. M_A includes predation by terns (M_T) and cormorants (M_C). The authors refer readers to Chapter 2 for life-cycle modeling results using the estuary survival parameter. The authors note (p. 326) that future models will look at other sources of smolt mortality, adult mortality (by pinnipeds), and effects of habitat restoration on population viability.

Key Findings: A 50% reduction in estimated avian predation mortality resulted in proportional increases in estuarine survival of 1.7% for Chinook and 11.5% for steelhead.

ISAB comments: The incorporation of an estuarine survival term into NOAA's life-cycle matrix model is clearly important but is still a work in progress. Estimating improvement in population viability due to habitat restoration in the estuary is an important goal for the Council's Fish and Wildlife Program. Achieving this goal will be a major challenge that requires extensive collaboration between life-cycle modelers and experts in the estuarine ecology of salmon.

Key Gaps: (1) No specific parameters for other (non-avian) sources of estuarine mortality such as estuarine habitat changes, contaminants, and food web effects; (2) no population-specific parameters; (3) no information on year-to-year variation or other types of variation (e.g., density dependence) in parameters; (4) no evaluations of the appropriate level of model complexity; (5) only limited comparisons among populations and across scenarios within populations (Ch. 2); (6) only limited analyses of sensitivity of the model to different values of the parameters; and (7) no simulations to develop adaptive management approaches.

Recommendations

1) Continue to develop and evaluate estuary survival parameters for the life-cycle model that are separate from freshwater and ocean survival.
2) Work closely with the Lower Columbia River Estuary Partnership (LCREP) and others involved in estuarine research, monitoring, and evaluation to advance accurate solutions to the complex problem of estimating the potential effects of estuary habitat

restoration on survival, life history diversity, and population viability of salmon and steelhead.

5.2: Ocean conditions

Goal: The authors' goal is to provide details on modeling of ocean survival for spring/summer Chinook and steelhead populations. Briefly, population-specific 1st-year ocean survival is calculated from smolt-to-adult survival (SAR). Ocean survival after the first ocean year is assumed to be constant (0.8, Ricker 1976). Functional relationships between 1st-year ocean survival and candidate indicators (based on previous studies) are developed. Candidate indicators include water travel time (WTT) downstream from the fish's natal Basin to the estuary, and monthly (spring and summer/fall) Pacific Decadal Oscillation (PDO) and the Pacific coastal upwelling indices. Previous analyses for Snake River spring/summer Chinook salmon, Wenatchee spring Chinook salmon, Snake River steelhead, and Umatilla River steelhead are updated with additional years of data, and new relationships for Yakima River steelhead are developed. Predictions of survival were used in the life-cycle modeling (Chapter 2).

Key Findings: For Snake River spring/summer Chinook, the functional models reasonably capture year-to-year variability in 1st-year ocean survival and demonstrate high variability in ocean survival and relatively low ocean survival during 1977-1997. Key findings for other Chinook populations and steelhead populations are not discussed. However, fits of steelhead models are not as good as those of Chinook models and are relatively poor for Umatilla River (mid-Columbia) steelhead. Overall, life-cycle model results (Chapter 2) indicate strong effects of estuary/ocean conditions on population metrics, highlighting the need to further develop habitat-specific survival terms for the estuary and ocean to better address questions related to the potential effects of restoration actions in the Basin.

ISAB comments: This chapter section provides a brief summary of activities conducted but does not represent a fully described, cohesive paper at this time. The nuances of the data and interpretation are not laid out in detail. There are potentially significant conceptual flaws in the selection of appropriate indicators of ocean survival related to the complex ocean life histories and ocean distribution and migration patterns of Columbia River steelhead and Chinook salmon. Adding additional complexity to the estimates of ocean survival and consideration of additional indicators of ocean conditions may improve explanatory and predictive capabilities of the model.

Key Gaps: (1) No scientific justification for the methods other than to cite previous work; (2) lack of species- and population-specific estimates of ocean survival after the 1st ocean year; (3)

need for more thorough selection and evaluation of potential ocean indicators for both early (1st ocean year) and later ocean life stages; (4) no evaluation of the appropriate level of model complexity; (5) limited comparisons among populations and across scenarios within populations (Chapter 2); (6) limited analyses of sensitivity of the life-cycle model to changes in ocean survival (± 10%, Chapter 2); and (7) no simulations to develop adaptive management approaches (Chapter 2).

Recommendations

1) Continue to develop species-, population-, and life stage-specific parameters for ocean survival that capture how variability in ocean conditions affects salmon and steelhead in ways that, if not considered explicitly, would mask the potential benefits of restoration actions in the Basin.
2) Evaluate the assumption that ocean survival after the first ocean year is a constant (0.8; Ricker 1976).
3) Work closely with NOAA ocean researchers and others involved in ocean research to determine the best indicators of ocean survival of salmon and steelhead. Use the model to better understand the potential effects of future ocean conditions with the goal of adjusting actions in the Basin to achieve greater benefits and/or efficiencies.

Review of Chapter 6. Hydrosystem Survival

Goal: This section provides a general description of the hydrosystem survival model that can be used to evaluate hydrosystem scenarios. Updated estimates of hydrosystem survival are calculated using recent estimates of in-river survival, percent transported fish, and effective D based on the 2012 CSS study report. The model runs use the most recent five year set of annual system survival estimates and are identified as placeholders to demonstrate how the model can incorporate more detailed tributary habitat components.

ISAB comments: Chapter 6 is very brief and provides insufficient details for a scientific evaluation. The authors may be assuming that material in other chapters, as well as COMPASS and CSS reports, provide details needed for a complete ISAB review. Reference to specific elements within these other materials, along with some additional detail is needed before this chapter can receive a meaningful review. For example, it is unclear how the hydrosystem model will be used to model specific scenarios such as dam breaching and reservoir drawdowns. Also, explicit examples of adaptive management applications should be readily available.

Review of Chapter 7. Quantifying Spatial Structure of Interior Columbia Basin Salmon Populations

7.1: Introduction: toward a metapopulation model

Goal: This section provides the background and justification for the other two sections in Chapter 7, and a brief overview of some relevant literature on salmon metapopulation biology. Two goals in the 2009 FCRPS AMIP called for 1) developing metapopulation models that can identify populations at risk of extinction owing to isolation and 2) analyzing temporal concordance among populations arrayed across space. These goals stem from a need to develop metapopulation models to help guide more strategic management.

Key Findings: This section provides a brief overview of the next two sections, and thus has no findings. It describes the development of a metapopulation framework for the life-cycle models as a work in progress.

ISAB Review comments, including key gaps: The ISAB agrees that analyses to explore the spatial structure of Columbia Basin salmon populations are potentially useful in guiding restoration actions and highlighting key research needs. However, it was not clear after reading this first section and the next two how these new analyses further the goal of developing a full metapopulation model for spring/summer Chinook or for other races and species.

Recommendations:

1) Provide a more comprehensive review of what is already known about metapopulation biology of salmon, especially in the Columbia Basin, and the critical issues and priorities for further work.
2) Provide a stronger context for the two sections that follow. They are potentially useful for understanding large-scale structure of populations, but it is not clear that they could be used directly to inform a functioning metapopulation model or enhanced life-cycle model.
    a. For example, can the analysis of different dispersal models with a method from graph theory (adapted from Schick and Lindley 2007) be used to parameterize the dispersal matrix that will be needed for a refined metapopulation model?
    b. Can the synchrony analysis inform the covariance matrix that will be needed in a metapopulation model at the spatial scales at which populations are likely to interact demographically?
3) Describe the larger vision. Do the individual projects feed directly into a new metapopulation model, or did a prototype metapopulation model suggest these

individual projects? Are these part of a strategic effort following from a careful prioritization of critical information needs?

7.2: From genes to landscapes: using multiple data sources to identify spatial conservation priorities for Chinook salmon in the interior Columbia River basin

Goal: Four different metrics are developed to assess isolation among Snake River spring/summer Chinook salmon subpopulations. These are used to determine how different measures of isolation alter our understanding of sources and sinks and, in turn, the implications for alternative conservation actions (e.g., improving habitat, reducing hatchery fish). Subpopulations that are at least moderately isolated from each other allow higher persistence of metapopulations because each is buffered from degradation or catastrophes that affect other subpopulations.

Key Findings: In general, the four metrics give very different results about the potential and actual dispersal among Chinook salmon populations. They show that fish within Major Population Groups (MPG) are more closely related than with those in other MPGs. Further analysis suggests that increased or decreased hatchery influences would have the greatest effect on the metapopulation structure of these populations. The overall conclusion is that more monitoring of fish movement using more and better tags is needed to assess dispersal and connectivity among the populations.

ISAB Review comments, including key gaps: The discussions of each modeling approach provide a useful overview of the limitations, assumptions, and logic for each. This is a potentially useful step toward a more complete understanding of dispersal required for development of metapopulation models. Unfortunately, the available data are limited, and the results across the different models are not convergent. The basic conclusion (i.e., that we need to know more about dispersal) does not add much, and the conclusion that populations may be tied more strongly within than among MPGs seems self-evident. The authors conclude that increased monitoring efforts are needed to improve understanding of dispersal mechanisms, but it is not clear that the critical assumptions of the models can be addressed to allow selecting among them for use in conservation. Still, experience with the different approaches could become useful as more relevant/complete data become available in the future. As such, this is really a pilot analysis.

As suggested under comments to 7.1, the work does not fit directly within the existing life-cycle modeling framework, although data required for this analysis may become relevant to more complex metapopulation models in the future. The analytical methods may also be useful in and of themselves as a means of identifying populations and actions that could become priorities for conservation management in the future.

Recommendations:

1) The authors should carefully evaluate how to proceed with this effort. Although an interesting exercise, the conclusions do not reveal much more than better data are needed. While an excellent analytical effort, ultimately the results are unconvincing because they are highly sensitive to the inputs and difficult to interpret.
2) Revise the title to reflect the idea of testing alternative measures of dispersal among threatened salmon populations, the Introduction to describe how this study fits within the LCM project, and the Discussion to indicate how the findings could guide future work.

7.3: Spatial covariance of interior Columbia River spring/summer Chinook salmon from abundance data

Goal: The authors use a multivariate autoregressive state-space modeling framework to assess the correlation in abundances of wild spawning Chinook salmon across several populations in the upper Columbia and Snake rivers, for which >50 years of abundance data are available. The goal is to understand more fully how the populations are structured across space.

Key findings: The authors conclude that, in general, the analysis supports most of the current ESU designations for these salmon, although in certain cases, abundances of wild spawners are correlated even among distant populations. They speculate on why this may be and suggest that further analyses are needed.

ISAB Review comments, including key gaps: This is a very interesting and innovative analysis. In general the results are new and potentially quite useful in consideration of the large-scale structure and diversity of salmon populations in the Columbia Basin. The finding that the abundances of spawners is related most closely to the PDO index, lagged to the year during which most of the Chinook are in fresh water, seems a key result and potentially of broad interest to managers. It is less clear that the results actually inform more complex life-cycle or metapopulation models that are the general focus of the entire report. The reviewers also had some questions about the utility of the extrapolated data sets that are based on a variety of estimation methods and of uncertain quality. Those concerns may be mitigated by the scale of the analysis (e.g., looking for big trends), but they warrant more detailed discussion and some consideration of the potential influence of the errors.

Recommendations:

1) Clarify how this effort will be linked back to the larger life-cycle modeling framework.
2) Address how limitations in the quality and completeness of the time series data could affect the results.
3) Address how uncertainty in the age-class structure of populations could affect the strength of the correlation with the lagged PDO.
4) Link the findings to adaptive management, if possible. How can this work potentially inform a model that allows evaluating conservation management alternatives at the metapopulation or landscape/riverscape scale?

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