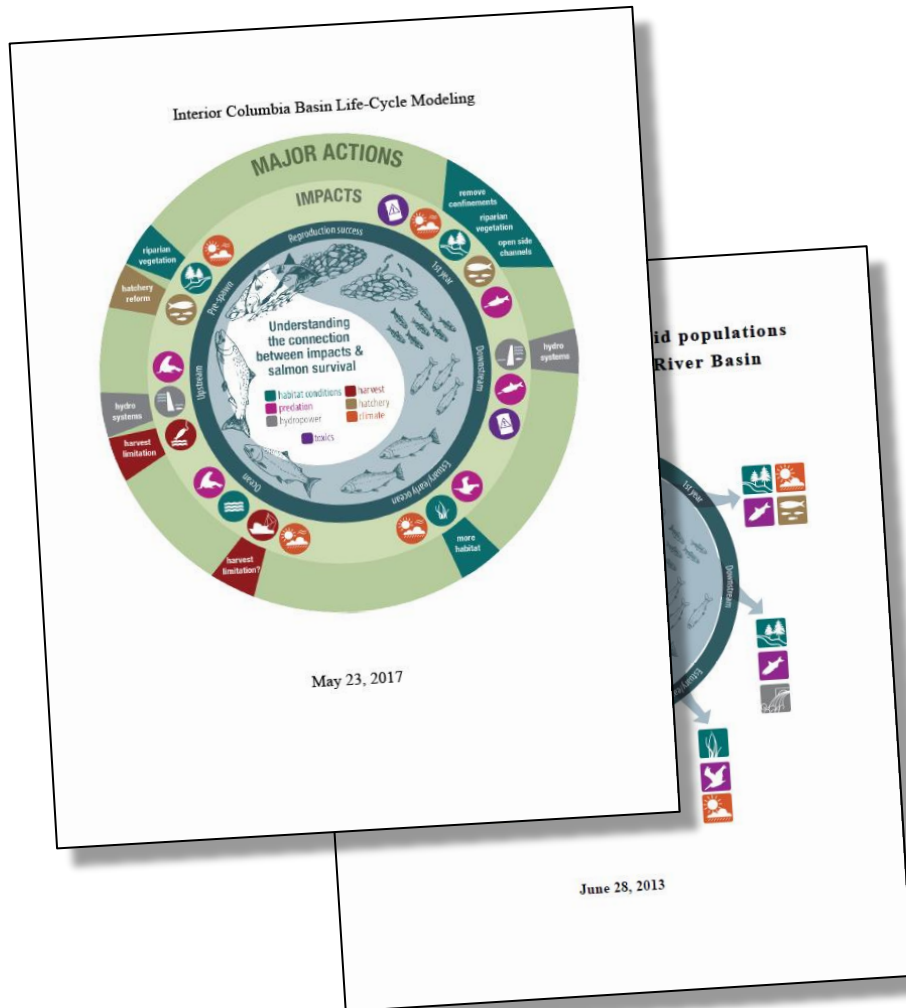


Independent Scientific Advisory Board

Review of NOAA Fisheries' *Interior Columbia Basin Life-Cycle Modeling* (May 23, 2017 draft)





Independent Scientific Advisory Board

for the Northwest Power and Conservation Council,
Columbia River Basin Indian Tribes,
and National Marine Fisheries Service
851 SW 6th Avenue, Suite 1100
Portland, Oregon 97204

Kurt D. Fausch, Ph.D., Professor of Fisheries and Aquatic Sciences, Department of Fish, Wildlife, and Conservation Biology at Colorado State University, Fort Collins, Colorado

Stanley Gregory, Ph.D., Professor Emeritus of Fisheries at Oregon State University, Corvallis, Oregon

William Jaeger, Ph.D., Professor of Applied Economics at Oregon State University, Corvallis, Oregon
(also serves on IEAB)

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Laboratory

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Conservation Biology and associate director of the Center for Watershed Sciences, University of
California, Davis.

Katherine W. Myers, Ph.D., Research Scientist (Retired), Aquatic and Fishery Sciences, University of
Washington, Seattle, Washington

Gregory T. Ruggerone, Ph.D., (ISAB *ad hoc*) Fisheries Scientist for Natural Resources Consultants,
Seattle, Washington

Laurel Saito, Ph.D., P.E., Nevada Water Program Director, The Nature Conservancy of Nevada, Reno

Steve Schroder, Ph.D., (ISAB Vice-chair) Fisheries Consultant and Fisheries Research Scientist (Retired),
Washington Department of Fish and Wildlife, Olympia, Washington

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British Columbia, Canada

Thomas Turner, Ph.D., Professor of Biology and Associate Dean for Research at the University of New
Mexico, Albuquerque, New Mexico

ISAB Ex Officios and Manager

Michael Ford, Ph.D., Director of the Conservation Biology Program at the Northwest Fisheries Science
Center, Seattle, Washington

Nancy Leonard, Ph.D., Manager, Fish, Wildlife, and Ecosystem Monitoring and Evaluation, Northwest
Power and Conservation Council, Portland, Oregon

Zach Penney, Ph.D., Fisheries Science Manager at the Columbia River Inter-Tribal Fish Commission,
Portland, Oregon

Erik Merrill, J.D., Manager, Independent Scientific Review, Northwest Power and Conservation Council,
Portland, Oregon

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ISAB Review of NOAA Fisheries'
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Executive Summary

In response to NOAA Fisheries' [request](#), the Independent Scientific Advisory Board (ISAB) reviewed a report titled *Interior Columbia Basin Life-Cycle Modeling* ([May 23, 2017 draft](#); LCM report). The life-cycle modeling is part of a proposed adaptive management strategy for evaluating alternative salmonid recovery actions in the Columbia River Basin. The LCM report builds on previous reports, which were reviewed most recently by the ISAB in 2013 ([ISAB 2013-5](#)). The report describes ongoing efforts to model the numerous factors affecting salmon and steelhead in the Columbia River Basin. Life-cycle modeling remains a significant challenge because of the complexity of the wide-ranging life histories of these fish and the many locations where fish are affected by human activities and the changing environment.

The ISAB is impressed with the growth and progress of the life-cycle modeling effort and the inclusion of investigators from several other agencies and organizations. The current LCM report has been expanded to include several areas recommended by the ISAB in earlier reviews, including new chapters describing methods for incorporating habitat variables, potential effects of toxics, and efforts to develop communication with managers. However, several components such as ocean, toxics, and communication are at early stages of development, and as acknowledged by NOAA Fisheries, non-native species are not covered. Because the various components are at differing stages of development, the report would be strengthened by descriptions and supporting illustrations of how the parts will be integrated or interact.

Models are always a tradeoff between realism and simplicity. In particular, many of the models in the LCM report do not include all sources of variation. Consequently, the models can be used for ranking scenarios, but their predicted results may not be accurate. The ISAB believes that going forward the authors of the LCM report need to clearly define scenarios to be tested, describe the assumptions in the model and the implications if those assumptions are incorrect, and provide measures of uncertainty and variability in model output. Additionally, models need to be validated by comparing outputs to real-world data. Many of the models presented in the LCM report rely on long term datasets, which highlights the value of the ongoing monitoring and evaluation needed to parametrize and validate models. Perhaps most important, modelers must provide a timeline for when and how the fully developed model will be ready to address specific management needs. In summary, the ISAB believes that the LCM report would benefit

from a “roadmap” for how the life-cycle models will serve policymakers and managers for which they are being developed.

The ISAB acknowledges the technical nature of our review of the LCM report and that the primary audiences are the LCM report authors and recovery and restoration practitioners who will use the model outputs in planning exercises. That said, the individual chapter reviews include sections on model goals and key findings, often thought-provoking, which should be of interest to a broad audience. To help summarize three key aspects of the models, the ISAB created Table 1, which contains our collective understanding of 1) species/ESU addressed, 2) key questions asked, and 3) outputs that could be useful to decision makers and managers.

Table 1. ISAB summary understanding of chapters in the life-cycle models 2017 report. Please see the individual chapter reviews for complete ISAB recommendations.

Title	Species/ESU	Key Questions	Outputs Useful to Decision Makers
2a. Review of capacity methods (Bond et al.)	Spring/Summer Chinook, steelhead (CRB-wide, but mostly Snake, mid- & upper Columbia)	How many juvenile salmonids can specific watersheds support?	Approaches to estimate juvenile rearing capacity in watersheds & to evaluate benefits of habitat restoration.
2b. Large scale geomorphic assessment for estimating parr abundance (Bond et al.)	Spring Chinook	How has the extent of mainstem & side-channel habitat changed historically in the CRB?	Assessment of potential parr rearing capacities of salmon & steelhead at the scale of CRB.
2c. Juvenile capacity modeling (Liermann & Bond)	Spring Chinook	Does habitat expansion provide a better estimate of parr capacity than watershed area? Are parr migrants (versus smolt migrants) in a population related to habitat capacity?	Model can estimate capacity in spring Chinook populations without smolt traps. Model predicts proportion of parr migrants based on watershed size. Output contributes to identification of watersheds that can benefit from habitat restoration.
2d. Movement & survival estimation (Saunders et al.)	Spring Chinook, Steelhead	Can mark-recapture data estimate life stage-specific survival of juveniles & density dependence? Can reach-specific estimates of movement & survival improve restoration designs?	Provides better estimates of movement & survival where data are available for 10-20 yr. Improves LCM accuracy & spatial resolution.
2e. Habitat restoration for spring Chinook (Paulsen & Fisher)	Spring chinook	What is relationship between parr-adult survival & cumulative effects of restoration projects? Has investment in restoration paid off by producing more adults?	Continued use of best habitat management will collectively improve salmon survival. Conclusions are cautious & do not prioritize among management practices.
3. Modeling Chinook ocean survival (Burke et al.)	Snake River spring/summer Chinook (wild, in-river migrating smolts)	Can environmental data effectively model ocean survival?	Model suggests that ocean survival may be related to sea surface temperature in winter, winter ichthyoplankton biomass, & coastal upwelling in spring.
4a. Hydrosystem spill scenarios: Grande Ronde Chinook (Lessard)	Spring/Summer Chinook in Grande Ronde Basin	What is impact of spill-flow scenarios on SARs, & long term adult returns?	Compare 12 scenarios of spill/flow on SARs & adult returns.

Title	Species/ESU	Key Questions	Outputs Useful to Decision Makers
4b. Hydrosystem spill scenarios (Faulkner et al.)	All salmonids; River system only (feeds into another model for ocean survival)	What is predicted in-river survival & SARs under flow/spill scenarios?	Compare effects of spill/flow scenarios on survival through hydrosystem
5. Toxics (Scholz et al.)	All salmonids; Pacific lamprey; all resident & non-native fish; invertebrates (i.e., aquatic life)	Where are toxicants in the basin? What are effects of toxicants on life stages of fish & invertebrates?	Identify data gaps on toxicants & their effects in the CRB.
6a. Pinniped predation in the lower Columbia River (Sorel et al.)	Spring/Summer Chinook	How does variable intensity of pinniped predation contribute to stock-specific mortality & travel time to BON?	Pinniped predation has important demographic & evolutionary implications for maintaining diversity in run timing. Data are critical for parameterizing LCMs.
6b. Effect of bird removal on smolt survival (Paulsen)	All salmonid stocks; Snake, Upper & Middle Columbia	Does reduced nesting habitat on East Sand Island reduce predation on smolts?	The impact of reducing birds from one extant breeding colony was modeled. The possible effects of reducing bird abundance in other colonies was not made.
6c. Food-web model linkage with life-cycle models (Benjamin et al.)	Spring Chinook; Methow River	What is relative importance of different biotic & abiotic interactions & processes on freshwater productivity? What are impacts of management actions & environmental changes on freshwater productivity?	Ultimately possible to simulate effects of restoration & environmental conditions on food web components, including salmon.
7. Adult-to-adult integrated population model (Buhle et al.)	Spring/Summer Chinook (Snake River Basin ESU)	How do measurement & process errors affect resiliency & quasi extinction threshold (QET)?	Important modeling approach for evaluating extinction risk of ESA-listed salmon. Can be modified to address other questions, e.g. effects of predation & harvest.
8. Snake River fall Chinook LCM (Perry et al.)	Fall Chinook	How do spawning aggregates contribute to the diversity & resiliency of the fall Chinook complex? How do juvenile freshwater life history strategies & emigration timing affect SARs? What factors contributed to the rebound in Snake River abundance?	Simulates effects of management actions & environmental conditions. Preliminary runs examined how recruitment of natural-origin juveniles varies with the number of female spawners. Preliminary results point to overcompensation.

Title	Species/ESU	Key Questions	Outputs Useful to Decision Makers
9a. Grande Ronde LCM (Cooney et al.)	Spring Chinook; Grande Ronde River	How will habitat restoration, hatchery supplementation, pinniped predation, & ocean conditions affect spring Chinook populations in four rivers of the Grande Ronde River basin?	Provides guidance on potential relative responses of spring Chinook to habitat restoration, hatchery supplementation, pinniped predation, & ocean conditions in Grande Ronde River basin.
9b. Wenatchee spring Chinook LCM (Jorgensen et al.)	Spring Chinook; Wenatchee River	How do harvest, habitat restoration, hydro operations, pinniped predation, & hatchery releases influence abundance?	Provides general guidance on the relative effects of pinniped predation, ocean conditions, hatcheries, harvest, hydro operations & habitat restoration.
9c. Predicting impacts of climate change (Crozier & Zabel)	Spring/Summer Chinook	How will climate change affect survival of Chinook?	Predicts probability of extinction for 9 populations of Chinook. Predictions are based on water temperature, water flow, & ocean conditions.
9d. ISEMP/CHaMP tributary habitat restoration (Saunders et al.)	Spring/Summer Chinook & Steelhead	How will abundance, survival, & persistence of salmonids respond to habitat restoration?	Predicts VSP parameters & QET at the subbasin scale for habitat restoration scenarios in three IMWs
9e. Yakima Steelhead LCM (Kendall & Frederiksen)	Steelhead/resident rainbow trout; Yakima River	Can population dynamics of resident & anadromous <i>O. mykiss</i> be better understood with LCMs?	Preliminary stage of development. Working with stakeholders to finalize management scenarios.
9f. Catherine Creek LCM (McHugh et al.)	Spring Chinook; Catherine Creek, Grande Ronde River	How will Chinook respond to land use, habitat restoration, hatchery supplementation, & regional warming?	Provides guidance on potential relative responses of spring Chinook to land use, habitat restoration, hatchery supplementation, & regional warming in Catherine Creek.
10. Do metapopulation processes influence salmon persistence? (Fullerton et al.)	Spring/summer Chinook	Is dispersal of Chinook populations within MPGs important to their recovery?	PDO caused synchrony among populations within ESUs. Identified strong vs. weak populations. Key gap is dispersal data.
11. Communication (Siegltitz et al.)	Not applicable	How can LCM results be conveyed to managers?	A draft Tier 1 fact sheet was provided. See chapter review for ISAB recommendations.

ISAB Review of NOAA Fisheries’
Interior Columbia Basin Life-Cycle Modeling
(May 23, 2017 draft)

Review Background

In response to a [May 5, 2017 request](#) from NOAA Fisheries, the Independent Scientific Advisory Board (ISAB) reviewed NOAA Fisheries’ *Interior Columbia Basin Life-Cycle Modeling* ([May 23, 2017 draft](#); LCM report). This is the ISAB’s second review of NOAA Fisheries’ life-cycle modeling effort. The first review took place in 2013 ([ISAB 2013-5](#)). As with the 2013 version, the 2017 LCM report represents a combined effort from modeling teams consisting of scientists from NOAA’s Northwest Fisheries Science Center, other federal, state, and tribal fish and wildlife agencies, and consulting firms. The suite of life-cycle models described in the LCM report were developed in response to NOAA’s 2010 Adaptive Management Implementation Plan ([2010 Supplemental FCRPS BiOp](#)) that called for expansion of models used in the 2008 Federal Columbia River Power System Biological Opinion (2008 FCRPS BiOp; also see [2014 Supplemental FCRPS BiOp](#), page 424). The models are intended to inform future FCRPS analyses and decision makers about the influence of restoration activities on the recovery and viability of ESA-listed salmon in the Columbia Basin.

The modeling effort described in the LCM report 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, spatial interactions, and effects of toxics. As in 2013, 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.

For this 2017 review, NOAA Fisheries asked the ISAB to consider progress made since the 2013 review and “the usefulness of the models for addressing the most timely and critical management questions.” NOAA Fisheries specifically asked the ISAB to consider the following questions:

- a) Are the model frameworks appropriate for exploring the effects of proposed management actions related to known limiting factors (habitat, hydro, harvest, hatcheries, contaminants, non-natives, others)?

For example, can the models be used for exploring how alternative scenarios of tributary habitat restoration could influence capacity and productivity?

- b) Are the modeling frameworks appropriate for analyzing alternative scenarios (i.e., different combinations of management actions)? Are they set up to make use of the best available data generated by the Fish and Wildlife Program (e.g., CHaMP and ISEMP, status and trends monitoring, IMWs)? Does the ISAB see any critical data gaps that if filled would further improve the models?
- c) Is the modeling framework structured in such a way that allows for incorporation of new information as it is obtained such as under future spill operations, ocean conditions and a changing climate?
- d) How could the modeling frameworks better account for potential impacts of key assumptions and uncertainties? How could the documentation and presentation of results (output) better clarify and communicate assumptions and uncertainties?

This review is organized to address these four questions and evaluate progress toward addressing issues and questions raised in 2013.

The ISAB's review was greatly aided by presentations from the modeling team at the ISAB's May 12, 2017 meeting and a follow-up question and answer session at the ISAB's June 23 meeting.

Summary Answers to NOAA's Questions

The ISAB provides brief answers of how the life-cycle model effort as a whole addresses the four NOAA Fisheries questions, and the ISAB's individual chapter reviews provide detailed assessments of how each model component addresses the questions.

a) Are the model frameworks appropriate for exploring the effects of proposed management actions related to known limiting factors (habitat, hydro, harvest, hatcheries, contaminants, non-natives, others)?

Partially. Many limiting factors are addressed in specific chapters, but some are not. Habitat, hydro, hatcheries, and predation are covered appropriately in several chapters (see Table 1). Harvest is considered in a few chapters but needs broader coverage in the life-cycle models. Non-native fish are not considered, which is a significant shortcoming, but the potential to model the effects of contaminants and climate change is illustrated (Table 1).

The ISAB was pleased to see a chapter dedicated to relaying the results of life-cycle modeling to decision makers. An "Outreach to Management" subcommittee was recently added to the Adaptive Management Implementation workgroup and is beginning to develop an outreach strategy. The ISAB suggests that the group consider more focus on developing the human-system model components relevant to the interventions considered when modeling actions to

achieve policy goals. The ISAB also strongly recommends including human-system modeling for all the life-cycle models (please see Programmatic Comments).

b) Are the modeling frameworks appropriate for analyzing alternative scenarios (i.e., different combinations of management actions)? Are they set up to make use of the best available data generated by the Fish and Wildlife Program (e.g., CHaMP and ISEMP, status and trends monitoring, IMWs)? Does the ISAB see any critical data gaps that if filled would further improve the models?

The ISAB believes that the authors did not develop sufficiently realistic scenarios to model, and thus, the full value of the life-cycle models is not realized. A framework to integrate the suite of scenarios was not provided, the sources or basis for the scenarios were not described thoroughly, and scenarios were represented inconsistently in the models. For example, ecological benefits of habitat restoration were represented as immediate and fully realized in one model, which we believe is highly unlikely, and gradual and successional in another model. Many of the models presented in the LCM report rely on long term datasets, which highlights the value of the ongoing monitoring and evaluation needed to parametrize and validate models. It is very difficult to translate habitat restoration actions into measurable fish responses because long term monitoring is not always available, but these monitoring data are critical to detect responses from restoration actions because those biotic responses reflect substantial natural variability in the environment and biological processes.

Models are always a tradeoff between realism and simplicity. Examples of this tradeoff are evident with several ISEMP/CHaMP models for the John Day and Entiat rivers, where a highly complex and realistic model that couples microhabitat selection by salmonids with stream hydraulics is used to estimate carrying capacity (abundance) for juvenile salmon, a key quantity in the life-cycle model. This model has been tested at a modest sample of sites in the Columbia River Basin (22 sites) and in Japan (20 sites), and holds promise to estimate capacity. However, annual predictions at several sites need to be coupled with long-term monitoring data to test and fine-tune the model further, if managers are to gain confidence in its predictions.

Data requirements for complex ecological relationships, such as ecosystem productivity and food web interactions, will always limit the application of bioenergetics models in river networks at the spatial and temporal scales required for resource management. Models of fish populations or communities in stream reaches or river networks in the Columbia River Basin inherently require simplification and coarse approximation of critical processes at scales relevant for management decisions. However, the ISAB emphasizes that these models are informative and one of the few approaches for representing complex interactions in river systems. Development and evaluation of life-cycle models require coordination with long-term monitoring programs and site-specific experimental measurements. The ISAB reviewers noted critical data gaps, and these are discussed in the individual chapter comments.

c) Is the modeling framework structured in such a way that allows for incorporation of new information as it is obtained such as under future spill operations, ocean conditions and a changing climate?

Yes, the ISAB believes that the modeling frameworks can typically incorporate new data and test new scenarios, involving such topics as climate change, ocean conditions, and changes in spill. The ISAB notes that the life cycle modeling team is a very talented group and they can readily adapt the models to address specific needs. For example, in response to the ISAB 2013 review of ISEMP/CHaMP life-cycle models, the authors presented methods and results for a few specific scenarios relevant to management of listed salmonids and expanded the analysis from one watershed to three watersheds.

d) How could the modeling frameworks better account for potential impacts of key assumptions and uncertainties? How could the documentation and presentation of results (output) better clarify and communicate assumptions and uncertainties?

All models must make assumptions, but it is often difficult to evaluate the importance of these assumptions. A standard way to assess impacts of assumptions is to analyze the sensitivity of a model to a range of values for parameters or to make a variety of alternate assumptions where the impact of failure of an assumption can be approximately quantified. A sensitivity analysis also will show which part of the model requires more attention—either through better modeling or more data. Sensitivity analyses often will show that processes in certain life stages (e.g., ocean survival) are much more important and least understood of all the life stage components.

Uncertainties can be handled similarly, with an important caveat. Often models cannot include all sources of variation (e.g., climate variables in the future) and are necessarily simplifications of reality (e.g., no compensatory responses). As a result, output from models may be less variable than would be seen in reality. This is particularly true for probabilistic output such as probability of extinction (quasi-extinction threshold; QET) which is likely underestimated for many models. Often “simple” components can be inserted into the life-cycle model to add additional variation or uncertainties (e.g., compensatory responses). The model is then applied under these additional scenarios to give a sense of how much more variation may be observed in reality.

Programmatic Comments

Habitat

The five sections of Chapter 2 address the capacity of various habitats to support different life stages of salmonids. The ISAB found the introductory section of the chapter (2a) to be informative. In this section, the investigators describe seven methods currently being used to estimate rearing capacity of juvenile salmon at several spatial scales in the Columbia Basin. The capacity of a watershed to support each life stage of salmon is important for identifying those life stages that may control overall abundance. The other sections of Chapter 2 address the relative merits of different approaches for estimating capacity and survival using different methods that are appropriate at different spatial and temporal scales. This evaluation is important to determine the best approaches to include in more complex models.

The six sections of Chapter 9 describe models that were developed to assess the combined effects of habitat actions with those of other limiting factors (e.g., hatchery supplementation, pinniped predation, climate warming), and five of the six models appear complete and capable of at least ranking scenarios based on single and combined effects.

Model types

The researchers developed three types of models, described as simple (Chapter 7), intermediate (Chapters 4a and 8), and complex (Chapter 9). It is important to understand that the NOAA simple model is a complex adult-to-adult model, which is “simple” only because it does not include prediction about life stages between the spawning parents and the subsequent return of their progeny as adults. The ISAB appreciates that these models are being developed by different researchers (and organizations) with differing data available. However, there are some unresolved questions about the value of the models. Answering these questions would help determine which models and analyses should be pursued, modified, or abandoned:

- Why do some decisions/questions need more complex models than others?
- When a simple model seems adequate to guide decisions, are other more complex models necessary?
- Is overlap or redundancy among models useful, given the widely differing approaches? How will the complete set of models be integrated?
- Are the models achieving the overall goals?
- Which of these models are (or are not) essential to our understanding the effects of management actions on the salmon life cycle?

- Given a wide range of potential management actions and the multiple criteria for selecting among them, will the models provide the information needed for calculating these metrics and choosing among the management options?
- At what scale can the life-cycle models guide management actions?
- What are the limitations as to how these models can be used and how the outputs can be interpreted?

Improving Analyses and Reporting

The ISAB appreciates having all of the LCM models presented in one report but suggests that Chapter 1 serve as a roadmap and foundation for the document by clarifying the organization of the report and key terms to be used throughout the report. The ISAB requests that, in the future, the chapters of the report be more detailed than a typical scientific paper and be more like a technical report that serves as backup for a future scientific paper. For example, in the Comparative Survival Study (CSS) each chapter is self-contained and slowly grows over time. Thus, each chapter in the LCM report should:

1. Be complete; that is, do not simply refer to previous papers, but rather include an explicit description of the model (typically a set of equations and simulation conditions).
2. List sources of data (e.g., give references to reports).
3. Perform model assessment and validation (e.g., compare outputs to observed data; check for lack of fit).
4. Explicitly state which parameters of each model are based on other studies and which are estimated from the data, and provide rationale/justification for the values or ranges of values of parameters and provide measures of their uncertainty.
5. Explicitly list assumptions; provide an assessment of whether assumptions are reasonable, and discuss implications of failure of assumptions.
6. Indicate if all levels of variability are included and the ramifications if they are not—this is especially important for estimating the risk of quasi extinction threshold (QET).
7. Include clear and complete definitions of scenarios and the details of how they were developed. For example, are the scenarios from regional plans or proposed management actions?
8. Discuss the limitations of the models. Are they suitable only for ranking the scenarios based on model results, or can they predict outcomes given forecasts for exogenous processes such as climate change and population growth?
9. Discuss next steps if the model is still in development, indicate when the model will be ready to address management questions, and identify the management questions it is designed to answer.

10. Discuss how the results of the model address management needs and appropriate applications of the model in decision making.
11. Include section(s) defining abbreviations, either for the whole document or in each chapter. Many members of the ISAB and other readers may not be familiar with abbreviations that are well known by the authors.
12. Include a glossary, which defines such terms as capacity and productivity, and use these definitions consistently in the document.

Model Products and Uses

In future iterations for each life-cycle model, it would be valuable to have a detailed representation of the anticipated model output metrics indicating how the results could be summarized for decision makers. This would promote two-way communication between researchers and decision makers. What metrics are intended to be generated? What outputs from the model are required to calculate those metrics?

As an example, for each life stage a set of possible interventions could be listed, including a set of relevant metrics for each such as costs and benefits of specific actions and affecting specific stakeholders, the distribution of those costs and benefits over time, and potentially the probability distributions for costs and benefits. The list of attributes or metrics could include other variables. One might begin with:

- A. Life stage 1
 - a. Possible intervention A
 - i. cost,
 - ii. benefit,
 - iii. proportion of costs affecting agriculture, etc.
 - b. Possible intervention B
 - c. Possible intervention C
- B. Life stage 2, etc.

An example from a different type of environmental assessment is presented below of an analysis of the range of potential interventions that could be implemented to reduce CO₂ emissions (Figure 1). The interventions are ordered from left to right by their estimated cost per ton of reduced CO₂. The width of each rectangle provides an estimate of the amount of reductions that could be achieved with this action at this cost. Presenting information in this way would allow policymakers to evaluate alternative actions. We envision that similar information on interventions for salmon restoration could be developed.

These estimates are imprecise, of course, because of the challenges of predicting human responses to policies and incentives. Predicting changes in ecological systems and salmon abundance in response to policy changes is also highly complex and uncertain, but a similar

figure could be developed for increases in fish abundance. For example, figures that show costs and fish abundance after 5, 10, and 20 years would be informative.

To indicate the net impact on various interest groups, a set of tables could be constructed, for example. Even if the tables contained mostly empty cells, sharing these templates among researchers and decision makers would stimulate productive feedback and improvements in the templates. This could also avoid unpleasant surprises, such as when researchers realize that a model element or metric critical for outcomes was not included at an earlier stage, and now cannot be included.

Global GHG abatement cost curve beyond business-as-usual – 2030

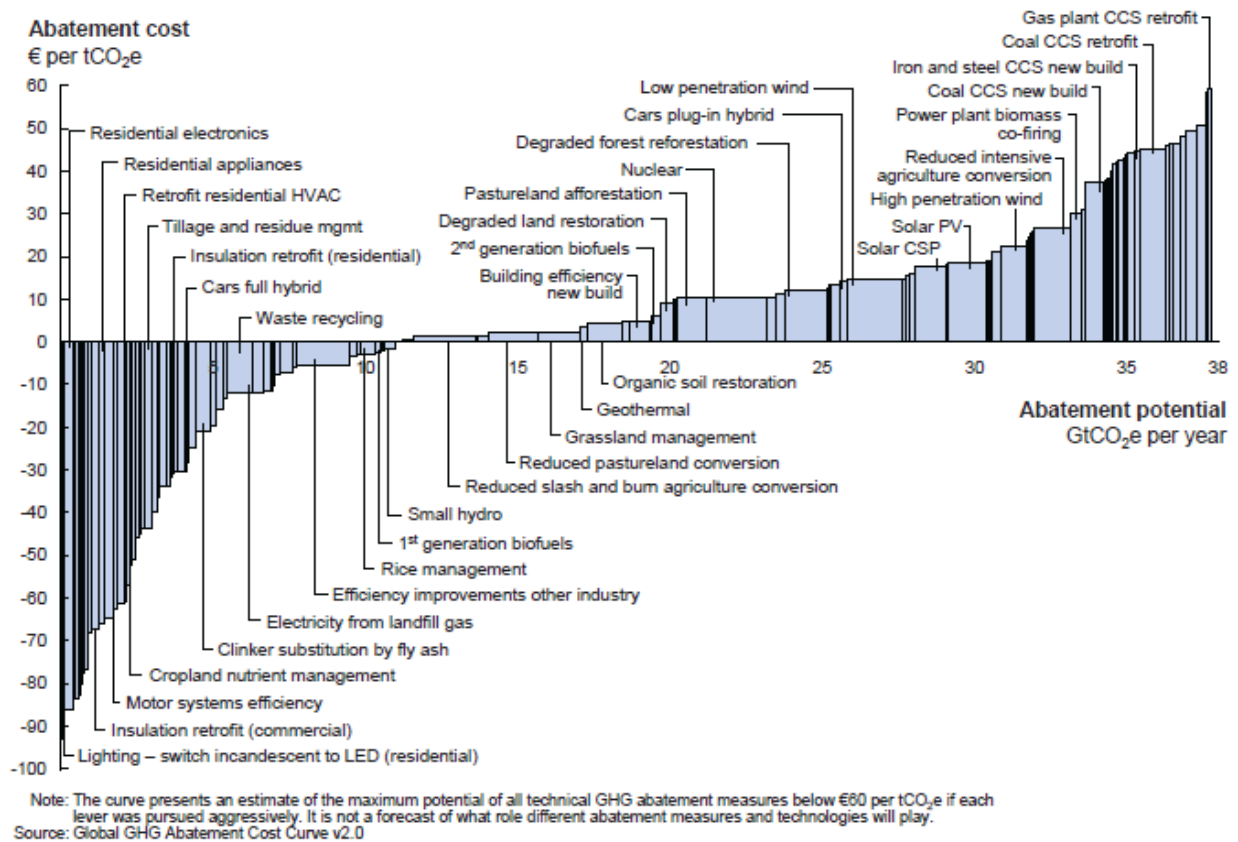


Figure 1. Example of estimated cost and scope of policies to reduce greenhouse gas emissions. Source: Nauc er and Enkvist (2009).

Incorporating Socioeconomics

The ISAB believes it would be useful for economic analysis and representation of human systems to have a closer connection and integration into the development of life-cycle models. The value of these life-cycle models will depend on whether they provide policymakers with the kinds of information needed to make decisions leading to successful fish recovery. Policymakers make decisions on behalf of society, where multiple objectives give rise to multiple criteria for choosing a course of action.

Economic Analysis

Societal objectives are often translated into criteria for policy analysis. These criteria include costs such as financial costs, private costs, government/public costs, opportunity costs, and non-market costs related to recreation, aesthetics, ethical or cultural values. They also include the timing of both benefits and costs, and the incidence, or distribution of benefits and costs across different communities and stakeholder groups. Risk and uncertainty, spillover effects, and unintended consequences can also be important for evaluating policy and management options. Although a wide range of behavioral social science considerations like these are recognized and regularly evaluated in economics, to the extent that other social considerations or phenomenon are recognized to be important in specific situations, a dedicated effort or inquiry may be warranted. If multiple actions are considered, are their benefits additive, complementary, or in conflict either socially or biophysically? The answers may depend on feedbacks in the biophysical system, the human system, or linkages between the two. Although some actions may be relatively straightforward (e.g., changes in spill, floodplain reconnection, channel meandering, addition of large wood), their evaluation for policy purposes may not be straightforward, given the need to evaluate, interpret, summarize, and communicate the results in ways that meet the needs of policymakers.

Without modeling human components, it may not be possible for these life-cycle models to adequately identify or quantify important metrics for policymakers. Identifying underlying causes of system changes that have adversely influenced fish populations is required to evaluate the range of possible actions to reverse the decline. Human responses can be as important as the biological responses when identifying the range of possible mitigation actions. Will human responses be large or small, costly or inexpensive? Because of the need for this kind of integrated approach, an economic analysis done separately, or after-the-fact, may fail to capture important relationships, processes, or potential actions. Modeling studies of complex coupled human- and natural-systems have demonstrated that a balanced, integrated approach can be extremely important to illuminate the critical linkages and feedbacks, as well as identify the range of actions under consideration (Bateman et al. 2013; Rabotyagov et al. 2014).

In addition, life-cycle model projections of future trends in salmon and steelhead populations based on static assumptions may lead to inaccurate and overly optimistic conclusions. Therefore, assumptions about future changes in climate, population, economic activity, land use, and other external drivers should be realistic and described explicitly. In the case of land use change, the interactions of population growth, economic structural change, land use regulations, zoning, infrastructure development, and other factors will interact to determine how land use changes will evolve and how these changes will affect salmon and steelhead life cycles. A range of approaches are possible for projecting land use change including those used in economics, geography, regional science, and planning. In cases where future system change is highly uncertain, “scenario planning” approaches can also be useful (Polasky et al. 2011; NRC 2014).

The ISAB believes that the LCM report should describe how the life-cycle models will serve policymakers and managers for which they are being developed. This should include a description of 1) how human systems will be integrated with the biophysical system, 2) how exogenous changes in the system (e.g., climate change, population growth) are represented, 3) how and when the full range of restoration actions will be identified and defined, and 4) how responses to those actions will be estimated, evaluated, and validated. The ISAB recommends development of a separate economics and human systems chapter or sections within each LCM chapter. Assumptions about the human system should be explained, as well as the sets of metrics and analyses that are part of the models and future trajectories, to provide a vision of how these essential components are incorporated or integrated with life-cycle models. Additionally, these economic and human systems components would benefit from an economic review.

Section References

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ISAB Comments on Life-cycle Model Chapters

Chapter 1. Introduction

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General Comments

Chapter 1 is informative, especially in describing how this latest version of the LCM report addressed ISAB questions and suggestions from the previous review ([ISAB 2013-5](#)). In addition, sections of Chapter 1 provide context and definitions for other chapters in the report. For example, the definitions beginning on page 8 are very helpful. However, the chapter would benefit from additional definitions of terms that are used in this chapter as well as throughout the report (i.e., QET, VSP, RM&E, etc.). In particular, a clear explanation of how the quasi-extinction threshold (QET) is defined and used in the life-cycle models would be very helpful. The report as a whole appears to be written with an assumption that readers are very familiar with life-cycle models and are fish scientists. Many ISAB members, and many future users of the report, are not fish scientists.

The ISAB believes that the Introduction should answer several questions. Why are the models needed? For example, the models are intended to inform future FCRPS analysts and decision makers about the influence of restoration activities on the recovery and viability of ESA-listed salmon in the Columbia Basin. What are the objectives of the models (e.g., to understand the effects of management decisions on VSP)? To what extent do the existing life-cycle models cover key management issues? The Introduction also needs a better description of how the chapters in the report fit together or how they are envisioned to come together in the future. The discussion of the types of models (simple, intermediate, complex) was informative, but how, for example, do toxics (Chapter 5) relate to one or more of these model types? Perhaps a table listing the chapter, topic, status of model development and future directions would give the reader a clearer picture of how the chapters relate to each other (see Table 1 in the Executive Summary)?

The example of Wenatchee River spring Chinook (beginning on page 8) caused some confusion. It appears that this is an example of how the various models (simple, intermediate, complex) will be used in determining the risk of extinction (QET) and measuring recovery (viable salmonid population parameters, VSP). The lead sentence (bottom of page 7), “With this round of modeling, we plan to express model outputs in terms of VSP scores” suggests that this example illustrates how life-cycle model outputs from the other tributaries will be evaluated. If this is correct, a more explicit statement about this would be helpful, and referring back to VSP and QET as anticipated endpoints in each chapter would help to unify the report. It is also a bit

confusing why these apparent endpoints for the Wenatchee modeling are presented in the Introduction, but then none of these analyses are used in Chapter 9b on Wenatchee Chinook salmon.

ISAB Recommendations

The following are questions or comments that the ISAB has about specific parts of the Introduction. Please also see the Programmatic section of this report.

- A. Page 1, paragraph 5: It is not accurate to say that Chapter 5 “presents a population model of the impacts of toxic exposure of population success.” Previously published modeling exercises are mentioned and cited, but the modeling is not discussed nor are results of the model presented in Chapter 5.
- B. Page 1, last paragraph: “In regard to ecological interactions, we have expanded out (sic) modeling substantially. The avian predation section (Paulsen, Chapter 6b) has been updated with recent analyses.” Chapter 6b describes the collection of data on predation but does not present it in the life-cycle model framework.
- C. Page 4, last paragraph: In addition to asking managers for the “type of information they need,” it would be prudent to ask them about the areas of focus they are interested in. Also, in regards to the last sentence: “We have begun to compile some useful information (e.g., maps and fact sheets) that can help managers better understand what types of products we are producing.” It would be more valuable for the managers if the life-cycle model authors asked the managers what products they need.
- D. Page 4, first paragraph: Is there any verification/justification of the appropriateness of “borrowing” data? Or is it just assumed that such borrowing is appropriate without any justification?
- E. Page 5, paragraph on non-indigenous species: Is this really the only area that the authors did not cover in the 2017 life-cycle models? Or do the authors mean that it’s the only area mentioned by the ISAB that was not covered?

Chapter 2.a. Habitat: Review of capacity methods

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1. Goal

A primary goal of conservation biologists and managers of Columbia Basin salmonids is to estimate the potential response of populations to habitat restoration and management actions. One approach for achieving this goal is to quantify the upper limit of salmon densities (or abundances) that a habitat or watershed can support so that benefits of restoration and/or management actions can be predicted. When a habitat is fully seeded, the maximum density (or abundance) it can support is often described as "capacity." In this introductory chapter, the investigators describe seven methods currently being used to estimate rearing capacity of juvenile salmon at several spatial scales in the Columbia Basin (spawning capacity is addressed to a lesser extent). These approaches for estimating capacity range from empirical fitting of stock-recruitment data to mechanistic models that employ functional responses to estimate maximum abundance at one or more life stages. Mechanistic models include geomorphic estimates of habitat availability coupled with maximum fish densities associated with each habitat type and food web models that consider energy flow through the aquatic community. The goal of this chapter is to "review and compare all seven methods to benefit those using capacity estimates in modeling exercises or evaluating the benefits of restoration or management scenarios, as well as those collecting the data used to estimate capacity." This review chapter aims to help guide the execution of the most appropriate method for estimating capacity given different management and conservation needs.

2. Key model findings

The capacity of a watershed to support each life stage of salmon is important for identifying those life stages that may control overall abundance. Seven methods for estimating salmon capacity are described, compared, and evaluated. The habitat and fish data requirements and scalability (applicability) of the seven capacity approaches are compared in Tables 2 and 3 (p 52, 57). Table 1 identifies the chapter in which the method is applied in a life-cycle model along with the watershed, species, and life stage. These summary tables are very informative.

The habitat expansion approach (e.g., sum of habitat area X maximum density in each habitat) was viewed by the investigators to be relatively simple (fewer data requirements) and could be used to estimate changes in capacity in response to habitat restoration. However, the habitat expansion approach does not readily incorporate environmental variability such as temperature and flow. Maximum fish density in each habitat type is challenging to accurately estimate, and so the habitat expansion approach seems best viewed as an index of capacity. The habitat expansion approach assumes that maximum density is constant across different units of the

same habitat type, apparently without consideration of habitat quality. It seems juvenile salmon dispersal associated with size and age may cause capacity of a population to be overestimated if maximum densities are summed and fish are essentially counted more than once. The authors suggest that this approach "should be restricted to data points most closely associated with spawning reaches."

In contrast, stock-recruit (S-R) models incorporate environmental variability and can be used to estimate recent capacity of the population, but they do not readily predict future changes in capacity in response to habitat restoration. S-R models can be used to predict whether current habitat and environmental conditions have the capacity (and intrinsic productivity) to support a viable population or minimum threshold abundances (e.g., see questions raised by authors of Chapter 9d). This information can be used to predict changes in capacity and/or intrinsic productivity levels needed to achieve population viability goals. Residuals from the S-R model can be used to test for potential shifts in productivity and capacity in response to a significant management action(s).

Several approaches (S-R, net rate of energy intake [NREI], and dynamic food web) were considered to be specific to the watersheds where they were developed and not easily extrapolated to other watersheds. Most approaches require large amounts of habitat data. In contrast, fish data requirements were considered to be low for habitat expansion, NREI, habitat suitability, and dynamic food web approaches. NREI and habitat suitability approaches had the highest "resolution," i.e., results could be developed for specific (small) stream reaches. S-R models were viewed to have low "resolution," but they reflected the overall habitat conditions used by the stock. Ultimately, the use of these approaches will depend on the question of interest and data availability.

3. Progress toward addressing ISAB recommendations from 2013

This 2017 model component does not have a corresponding 2013 model component, so specific comments are not available for comparison. However, the section was developed partially in response to the ISAB's 2013 recommendation for the NOAA modelers to work with their Watershed Program. This chapter recognizes the importance of capacity at each life stage and how limited capacity at one stage can constrain overall population growth.

4. Applicability to management decisions, alternative scenarios, and adaptive management

This chapter reviews seven methods for estimating freshwater rearing capacity and/or spawning capacity of salmonids in Columbia Basin watersheds. The chapter should be useful to managers seeking to understand the relative attributes of the seven approaches, data requirements, and basic methodology, but improved clarity of the text is needed to allow managers to readily understand the approaches. The capacity estimation methods are deployed in other chapters, as referenced in Table 1.

Capacity estimates are a critical component of life-cycle models, which can be used for evaluating and predicting potential benefits of habitat restoration, alternative management actions, and for providing insights for adaptive management. Capacity estimates at specific life stages can be used to identify those life stages that are most limiting to population growth. The review characterizes limitations of each method, which is important for fishery scientists considering measurement of this challenging determinant of fish population abundance. For example, it describes the fundamental problem that most models assume that populations are at equilibrium, when in the real world the environment in which the fish live varies randomly (i.e., is stochastic) and fish populations are affected by many factors other than capacity.

5. Compatibility with best available data and flexibility to incorporate new data

Tables 2 and 3 compare habitat and fish data requirements and scalability (applicability) to other areas of the seven approaches. Data needs and scalability vary with the approach, so it is important to apply the approach that best fits the question and available data. Information is presented evenhandedly, and the report does not inappropriately advocate for one approach over the others. The approaches are implemented in other chapters of the life-cycle model report.

6. Treatment and communication of assumptions and uncertainties

A key goal of this chapter is to identify the assumptions, uncertainties, and limitations of the seven approaches for estimating salmon capacity. The text is often theoretical and technical, but it provides a good overview of the underlying assumptions, data requirements, and uncertainties associated with each method. One notable exception is that the chapter does not describe how capacity is calculated using the stock-recruitment model, other than in very general terms. This is needed because not all readers will be fishery scientists who work with salmon, and capacity estimates may vary with the type of S-R model, e.g., Beverton-Holt versus Ricker. Stock-recruitment models are almost never used for resident salmonids and other freshwater fishes.

The review includes excellent tables that summarize data needs and resolution of approaches for measuring capacity. A similar table of the major types of assumptions and uncertainties of the different approaches would be useful. The review described many of the limitations and uncertainties associated with each approach, but it rarely described the magnitude of variability or error in different measures. Where these have been published, it would be useful to provide the reader with information on the associated magnitude of error that has been observed (e.g., Aquatic Trophic Productivity (ATP) model analysis by Bellmore et al.).

We highlight an important statement by the authors: “One of the most critical challenges of estimating capacity is matching the spatial grain and extent of interest with an appropriate method for estimating capacity at that extent, or extrapolating local estimates to larger spatial scales relevant to management.” In many ways, this is the most basic challenge for life-cycle

modeling. This is especially true for species like Chinook salmon where their diverse life history (fry, parr, smolt migrants) seemingly evolved as a means to reduce density dependence and ultimately increase population capacity.

The section on Microhabitat Models (P. 36) is overly positive about the use of Weighed Usable Area (WUA) as a measure of habitat. The studies of John Williams (Williams 2010a, 2010b, 2010c) and others have shown some hidden biases in the technique (e.g., non-random transects) that make WUA determinations less reliable than generally recognized. Furthermore, few studies have demonstrated a relationship between WUA and numbers of fish present in the habitat. These issues are also relevant to the habitat expansion approach that often borrows maximum fish density from other watersheds.

Figure 3 shows a stacked graph of capacities for Sacramento winter-run Chinook salmon in Sacramento River, Yolo Bypass, Delta, and Bay habitats. These habitats are largely encountered by Chinook salmon migrating sequentially from the river to the Bay. Therefore, it seems to be misleading to show cumulative (stacking) habitat capacity that might be interpreted as the overall capacity of this system to support winter-run Chinook salmon. This figure, as presented, detracts from other important statements indicating the need to identify specific life stages that have low capacity and limit overall production. Oddly, the figure caption indicates Bay habitat to have the lowest capacity for supporting Chinook salmon even though river and Delta habitats have been severely degraded by human activities.

It is a minor issue, but the review did not mention the effect of disease or parasites on applications, such as the habitat suitability index. Sources of disease and different vulnerabilities to diseases and parasites across the region or even watersheds introduce additional uncertainty in application of these approaches for productive capacity.

7. ISAB Recommendations

The chapter is an excellent introduction for researchers, managers, and decision makers. Following some additional editing to clarify text, the chapter should be understood by a relatively broad (and motivated) audience. Some of the information on the dynamic food web model was better described in this chapter than in Chapter 6c.

Specific recommendations for this chapter include:

- A. The authors should continue to develop supportive material and synthesize information on critical aspects of estimating capacity (e.g., magnitude of observed error or variability in estimates, sensitivity to abiotic and biotic factors). In particular, it would be beneficial to summarize how well the various approaches worked when applied to the specific situations that are identified in Table 1 of the chapter.
- B. The authors need to add a section that clearly and completely describes how stock-recruitment models are used to estimate capacity and productivity, to match sections

for the other six methods, because many readers are not fishery scientists who work with salmon.

- C. The terms capacity, production, and productivity should be clearly defined in the report, and used consistently throughout all the chapters (see editorial comments).
- D. Capacity is primarily described here as fish density or abundance, though the chapter does mention biomass (numbers x average weight). It may be worthwhile to further discuss growth and emigration responses of salmon in relation to salmon density and capacity. Growth and emigration are important life history characteristics or "strategies" of salmon that enable salmon to increase capacity beyond that in the natal river. Other chapters describe downriver dispersal as fry, summer parr, and fall parr in addition to overwintering near the natal area. To what extent do the capacity models incorporate life histories that disperse downstream across the seasons? How can this information be used to guide and evaluate habitat restoration potential for fry and parr that have dispersed downriver versus fish that have remained in the natal watershed?
- E. Although this chapter focuses on various methods for estimating salmon capacity in Columbia Basin, it would be worthwhile to compare current salmon abundances with these capacity estimates (perhaps in a different chapter). To what extent are existing abundances approaching or exceeding capacity in the existing environment? A review of density dependence in the Basin indicated many salmon and steelhead populations may be exceeding capacity (e.g., R/S is often less than 1; [ISAB 2015-1](#)), and it would be worthwhile to further examine this question with new data and approaches.
- F. Additionally, it may be worthwhile to compare values produced from the different approaches for a specific area, if possible, and discuss the attributes of the approaches in regard to the goals of the life-cycle models. Can mechanistic-based models be used to accurately predict absolute capacity (abundance), or are they best used to compare scenarios, e.g., current capacity versus post-restoration capacity?

8. References

- Williams, J.G. 2010a. Lost in space, the sequel: spatial sampling issues with 1-D PHABSIM. *River Research and Applications* 26:341-352.
- Williams, J.G. 2010b. Sampling for environmental flow assessments. *Fisheries* 35:434-443.
- Williams, J.G. 2010c. Comment on Gard (2009): comparison of spawning habitat predictions of PHABSIM and River2D models. *International Journal of River Basin Management* 8:117-119.

Chapter 2.b. Habitat: A habitat expansion approach to estimating parr rearing capacity of spring and summer Chinook in the Columbia River Basin

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1. Goal

Representation of habitat characteristics to model the distribution and abundance of fish is a critical component of life-cycle models because floodplain conditions and side channel habitats are major influences on fish populations. Availability of geomorphic information frequently limits application of life-cycle models at the large spatial scales of river basins or subbasins. The goal of this chapter is to develop methods to predict current side channel habitat area and historical side channel area based on estimates of current and historical floodplain widths. The ultimate goal is to develop approaches that allow geomorphic characterization for the river networks of the Columbia River Basin that are currently accessible to spring Chinook. These geomorphic characterizations will be used to estimate river habitat area throughout the Columbia Basin, contemporary and historical side channel area, effects of floodplain reconnection on side channel habitat, and current rearing capacity and effects of restoration scenarios on rearing capacity for spring Chinook parr in currently accessible areas of the Columbia Basin. Readers should note that the term “habitat expansion” is somewhat confusing because the authors are referring to expansion of habitat estimates to estimates of potential fish abundance or capacity rather than actually exploring expansion of the areal extent of available habitat for spring Chinook salmon.

2. Key model findings

The authors predicted the geomorphic structure and areal extent of mainstem (non-side channel) habitats based on basin geomorphology, geology, hydrology, and land use. Small streams (< 8 m bankfull width) were assumed to be single thread channels, and side channel area in large streams and rivers was estimated based on geomorphic characteristics, geology, hydrology, and land use. Wetted width and bank-to-bar ratios were estimated well ($R^2 = 0.82$, 0.68 , respectively). The random forest classification model predicted the presence of side channels with 74% accuracy and little bias. Floodplain width was an important predictor of side channel presence and amount. The analysis indicated that contemporary side channels comprise 13% of the total wetted habitat area but more than 41% of the high value rearing habitat. Estimates of historical side channel habitat were 34% greater than contemporary estimates. Three methods were used to estimate capacity in terms of fish density: relationships between habitat type and Chinook parr densities (habitat expansion method), quantile regression of observed fish densities in the Columbia Basin using habitat type and area, and estimates based on habitat relationships from mid-summer snorkel surveys in the Salmon River.

The habitat expansion method applied the maximum reported Chinook parr densities for six types of habitats (side channel, mainstem bank, mainstem bar, mainstem mid-channel, small stream pool, small stream riffle) to the estimated area of those habitat types in each stream segment in the Columbia Basin that was accessible to Chinook salmon. Chinook parr capacity was estimated by quantile regression for 63 subbasins in the Columbia Basin using ISEMP data to relate fish densities to habitat area projections. The quantile regression method estimated higher capacity for spring Chinook parr than the other methods.

Contemporary side channel habitat accounted for 37% of total capacity for spring Chinook parr across the Columbia Basin. Historical estimates of spring Chinook parr capacity were 13% greater than estimates for contemporary conditions. Analyses of restoration scenarios estimated that conversion of either rangeland alone or rangeland and croplands to natural cover within the floodplain would increase spring Chinook parr capacity by approximately 8% but up to 25% in some basins. The small differences between historical and current capacity and the relatively small effect of restoration actions may reflect the lack of factors other than geomorphology in the model. The authors noted that the model does not include important habitat features such as riparian vegetation or large wood. Food resources are not addressed directly in the models and are assumed to be reflected in overall, large-scale monitoring data and habitat relationships derived from such data.

3. Progress toward addressing ISAB recommendations from 2013

This 2017 model component does not have a corresponding 2013 model component, so specific comments are not available for comparison. However, this 2017 model component was developed partially in response to the ISAB's 2013 recommendation for the NOAA Fisheries modelers to work with their Watershed Program.

4. Applicability to management decisions, alternative scenarios, and adaptive management

The model is an ambitious attempt to estimate habitat availability from large-scale landscape data available throughout the Columbia Basin. Clearly such an analytical tool would allow decision makers to compare alternative management scenarios and identify potential recovery trajectories to inform adaptive management. Recent advances in remote sensing, environmental modeling (e.g., temperature), and networks of environmental empirical data increase the likelihood that such projections would be sufficiently accurate to estimate habitat conditions across the region. Questions of the magnitude of errors and factors related to errors are quickly apparent, but these questions or concerns do not negate the potential utility of this approach.

This modeling study is designed to provide a broad-scale picture of the current habitat situation throughout the Columbia Basin compared to historical conditions as background for managers. The study is focused on mainstem, side channel, and floodplain habitat. The goal is partly to provide managers with an idea of where restoration efforts might be concentrated (by habitat

type and region) and make predictions of potential capacity of habitat for juvenile Chinook rearing with and without restoration. Early results indicate that the most “bang for the buck” will be in restoring side channel and floodplain habitats. The modeling also provides an analytical tool to prioritize field studies of both hydrology and salmon habitat use. Analyses of restoration scenarios with the initial models should be viewed cautiously. The model currently is largely a model of coarse scale geomorphic influences on spring Chinook parr capacity and does not account for many factors that determine stream productivity. Utility of the models will be improved by future refinement to include effects of water quality, temperature, riparian vegetation, large wood, sedimentation, substrate composition, potential food resources, active channel widths, and better estimation of floodplains and side channels. The authors noted several of these factors (riparian vegetation, large wood, temperature, active channel width) are planned for future model development.

5. Compatibility with best available data and flexibility to incorporate new data

This is a broad-scale study based on data from satellite imagery. As the authors point out, their analysis consequently is lacking in some details (e.g., habitat changes caused by dams, thermal regimes, large wood habitats). The study is compatible with using such data for confirmation of results when it becomes available. The approach is basically developed to take advantage of the best available data. It would only be strengthened by new and better data, remote sensing technologies, and analytical methods. Projections of spring Chinook parr capacity would be improved with additional detailed field measurements, which currently are limited in scope and availability and take considerable effort to obtain. As the authors indicate, their modeling needs validation by field studies in both hydrology and salmon habitat use; the study indicates where such research might be most valuable.

The authors identified several future modifications and improvements, including development of approaches to provide better channel estimates in areas with bank modification, areas with hydromodified banks below impoundments, better data on parr densities in side channels, incorporation of effect of large wood, additional LIDAR data and use of on-the-ground estimates from monitoring programs, and incorporation of water temperature in models for estimating parr fish capacity. Future refinements should include continued assessment of error in classification, side channel estimation, and seasonal changes in inundation.

6. Treatment and communication of assumptions and uncertainties

The authors are very candid about weaknesses; typical comments include:

“Our estimates of bankfull width for main stem channels were in general larger than those estimated by Beechie and Imaki (2014). However, we have not yet validated the precision of our satellite imagery based measurements with field measurements.”

“Hydromodified banks in particular may be prominent in areas below impoundments or with substantial urban development and road density, and have the potential to substantially decrease rearing capacity.”

“Current remote sensing techniques that rely on satellite imagery are often too coarse to estimate finescale features.”

Assumptions and uncertainties are well spelled out, but the authors do not directly address the resolution of their estimates of fish capacity and the applications for which these model projections would be appropriate. The fish capacity estimates generated by the three approaches are based on broad assumptions and coarse resolution data to extrapolate juvenile density data to habitats across the Columbia Basin and sum them to estimate capacity.

Each of the three methods has major limitations. The habitat expansion approach divides rearing habitat into six habitat types and assigns a fixed average maximum density to each type based on beach seining or electrofishing data. Variability in the observed "capacity" in each habitat type are not provided (but may be in unpublished reports unavailable to readers). Beach seining and electrofishing provide substantially different estimates of juvenile salmon abundances, but no information is provided to explain how these data are integrated to provide estimates of abundance. Use of the gear types is restricted to certain types of habitat, and each type is selective for different sizes and life stages of fish. Catch rates also are strongly influenced by season, e.g., fry migrants, summer parr migrants, fall parr migrants, smolt migrants, and therefore distance from the natal spawning area. Snorkeling estimates are strongly affected by habitat type, water clarity, and fish behavior. None of this is discussed by the authors. How was fish density measured across each reach in the quantile regression approach in the Willamette Basin? The assumption of 5200 parr per hectare seems especially crude. How useful is this metric when evaluating various types of habitat restoration? The authors note that they hope to include components of habitat quality in the model in the future, but they give no description of the likely magnitude of this source of error or uncertainty.

The chapter assesses the response of juvenile spring Chinook capacity to two types of restoration: rangeland alone and rangeland and cropland. The two restoration scenarios were not described in detail, providing little or no information on the specific assumptions, data sources, and habitat relationships. Rangeland and cropland restoration also restores water temperature, riparian vegetation, large wood, sedimentation and substrate composition, and food resources; but none of these factors are represented in the model. As a result, the model may substantially underestimate changes in juvenile Chinook salmon capacity in responses to the two forms of restoration. Furthermore, these two types of restoration are a subset of the range of restoration practices in the Columbia Basin. The authors should explain this to readers and provide a context for interpreting their results. For example, to what extent has habitat restoration during the past 25 years altered capacity estimates based on these three capacity

approaches? What level of restoration is realistic over the next 25 years and to what extent will capacity increase? Is the Columbia Basin habitat capacity really only 13% below historical capacity? If not, explain the limits of this geomorphic analysis more clearly when presenting the findings. How would restoration that targets habitat quality (salmon productivity) rather than habitat type (and capacity) fit into the use of this information by regional managers?

7. ISAB Recommendations

The approach has great potential for regional analysis. The ISAB suggests the following:

- A. Future research should refine the accuracy of channel characterization and application of models and data on fish habitat relationships. In particular, influences of habitat quality (e.g., temperature, riparian vegetation, large wood, sedimentation and substrates, food resources) need to be included in the model or explained clearly in the discussion of model results.
- B. Critical assumptions about floodplain function and land-use types should be verified and refined.
- C. The restoration scenarios assessed in the report were relatively simplistic. More thorough development and definition of scenarios and description of specific types of actions would make the analyses more informative and valuable. Refining empirical information on the effect of restoration practices on habitat types would strengthen the model. Selectively ground truthing results of scenario analyses (such as those shown in figures 15-20) would strengthen application of the projections of where restoration efforts would have the greatest benefits to juvenile Chinook salmon.
- D. The objective to “estimate current rearing capacity and the effects of restoration scenarios on rearing capacity for spring Chinook parr in currently accessible areas of the [Columbia Basin]” was largely ignored in the description of methods and discussion of results. Managers and decision makers will focus on the results of the scenarios and guidance from the authors would greatly improve the managers’ understanding and application. The authors should carefully explain the context and limitations of their analyses, including significant factors that are not included in the model and the potential magnitude of their effects on model projections. The authors could work directly with decision makers and managers to refine and develop scenarios to be evaluated with the model. In such scenario development, the authors should explicitly document the assumptions, data sources, relationships, and links to regional strategies that are included in the scenarios.

Chapter 2.c. Habitat: Juvenile capacity modeling

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1. Goal

The goal of this project is “to investigate the utility of using a habitat based metric of Chinook parr capacity to explain patterns in juvenile production.” This goal and the objectives could be expanded and refined to better inform the reader of what follows in the chapter. For example, it seems the key objectives are to test (1) whether the habitat expansion approach (Chapter 2b) provides a better estimate of parr capacity than does measuring watershed area, (2) whether the slope of the relationship between estimated parr capacity and habitat-based capacity is one (also please explain for the reader why this is important), and (3) whether the proportion of parr migrants in a population is related to habitat capacity.

2. Key model findings

The parr habitat index for spring Chinook salmon performed substantially better than basin area, explaining more than twice as much of the variability in estimated capacity (apparently based on stock-recruitment relationships) than watershed area only. This finding, in general, is expected because the habitat index contains more information specific to parr rearing, and watershed area is a maximum potential value. Nevertheless, a key finding was that the habitat index explained approximately 49% of the fish-based capacity estimates across 22 populations. In other words, approximately 51% of the variability in salmon capacity remained unexplained by the habitat expansion index, indicating the need for incorporating additional explanatory variables in order to better predict salmon population capacity.

The proportion of parr that migrated out of the natal basin in fall tended to be higher for basins with smaller parr habitat indices; larger habitat capacities supported more overwintering in the natal area. Parr migrants ranged from less than 5% of total parr production for the relatively large Methow River to close to 75% of total parr production for the relatively small Marsh Creek. The parr habitat index explained about 40% of the variability in the proportion of parr versus smolt (yearling) migrants. Inclusion of environmental or other landscape variables may help refine this relationship between parr migrants and habitat capacity. Habitat capacity below the trap area, which is especially important for parr migrants, did not appear to be considered in this analysis even though this downstream habitat contributes to the capacity of the population, i.e. maximum juvenile population abundance supported by the habitat.

Average over-winter and spring survival of parr, which was measured from the natal river trap (first growing season) to the first dam (the following spring), ranged from ~20% to 40% based on PIT-tag data. In contrast, spring-time survival of natal area smolts from the trap to the first

dam was ~40% to 70%. Year-to-year trap-to-dam survival tended to be correlated among the 22 populations, especially for parr emigrants that overwintered downstream of the natal area traps. The ratio of parr survival to smolt survival may serve as an approximate estimate of over-winter survival, indicating ~30% to 70% over-winter survival depending on stock.

3. Progress toward addressing ISAB recommendations from 2013

This 2017 model component does not have a corresponding 2013 model component, so specific comments are not available for comparison. However, this 2017 model component was developed partially in response to the ISAB's 2013 recommendation for the NOAA Fisheries modelers to work with their Watershed Program.

4. Applicability to management decisions, alternative scenarios, and adaptive management

The relationship between parr capacity and the parr habitat index, stemming from 22 populations, can be used to predict maximum parr production in natal areas of other basins without smolt traps. Since the index can also be calculated based on a hypothetical restored basin, where human impacts are removed, the benefits of restoration actions can be estimated and expressed in terms of parr capacity (i.e., juvenile production at full seeding) and compared with current conditions. This investigation appears to provide an important refinement of the habitat expansion approach discussed in Chapter 2b. However, there is uncertainty in the capacity estimates for the area above the traps and this estimate does not include downstream habitat used by parr migrants.

Predicting the proportion of fish that emigrate at different life history stages provides information to managers on the degree to which over-winter habitat in the natal river basin versus downstream areas is important. This information can help guide the location and type of restoration actions. Overall, the estimation of parr capacity is important for management decisions, scenario evaluations, and possible implementation in adaptive management cycles. However, the model should be used cautiously while recognizing the uncertainties in modeling results.

Chinook salmon have a variety of life history strategies that effectively increase the overall rearing capacity for the populations. This investigation examines capacity of the natal river upstream of the fish trap. Many parr emigrate downriver to overwinter somewhere between the natal watershed fish trap and the first dam. This leads to the question: what is the capacity of this downstream habitat for supporting Chinook salmon stemming from a variety of upstream populations? In other words, what does the habitat expansion approach in Chapter 2b say about parr capacity downstream of the fish traps and how do the number of parr migrants compare with these capacity estimates?

5. Compatibility with best available data and flexibility to incorporate new data

The investigation appears to use best available data for spring Chinook salmon parr and smolts collected at traps, but more information on the influence of habitat quality on capacity estimates in each habitat type is needed. In general, there are few if any limitations on incorporating new data as long as they are collected with standard regional protocols.

6. Treatment and communication of assumptions and uncertainties

The authors described their assumptions, uncertainties, potential weaknesses, and possible improvements throughout the description of the model. The ISAB provides a number of recommendations below to help improve communication of assumptions and uncertainties.

7. ISAB Recommendations

- A. Please provide more detail about the estimation of parr capacity for each habitat type. How is quality of habitat in each type considered in this analysis given that quality will likely vary in watersheds where the parr capacity approach might be applied? What is the variability in parr capacity estimates associated with each habitat type in the habitat expansion approach discussed in Chapter 2b and used in Chapter 2c? Fig. 4 provides plots of smolts versus spawners and the hockey stick model provided capacity estimates for each random draw for smolts. Was total parr capacity modeled in the same way and used in Fig. 2 (Y-axis), or is capacity in Fig. 2 based only on smolts? Please clarify. The text also states that summer parr rearing capacity was estimated using density values in Chapter 2b. These values and their underlying assumptions should be shown here to allow this report to stand alone.
- B. The model (P. 5) applied the average standard deviations of survival estimates for other years or all populations where estimates of variance were not available (about 25%). We suggest looking at the effects of using the highest standard deviations for these missing data as a more conservative assumption.
- C. The investigators identified several future steps to improve the models. We encourage the investigators to continue to refine the models by incorporating additional explanatory variables (environmental and watershed characteristics) that affect the estimates of capacity or survival. Do fall parr size, smolt size, or stream gradient contribute additional information about the capacity of the basins to support salmon?
- D. An interesting finding is that basins with smaller capacities tended to produce relatively more parr migrants than smolt migrants. Does this relationship help explain why the slope of the estimated parr capacity to parr-habitat capacity is less than one? Does the fact that this slope is less than one raise concerns when applying the habitat expansion index to other watersheds? Please provide more discussion regarding implications of

the statement: "When the slope is less than one, the relationship is non-linear with less predicted capacity per unit of habitat index as the habitat unit index increases." To what extent was the observed parr capacity (Y-axis, Fig. 2) greater or smaller than the parr habitat index, i.e., where is rearing capacity approached?

- E. Using raw (non-standardized) values would help the reader evaluate the ability of the parr habitat index to approximate observed capacity values. For example, when the model was forced through the origin the slope was only 0.11. Does this mean that observed capacity was only 11% of the parr habitat index?
- F. The relationship described in this chapter examines capacity upstream of the fish trap in the natal watershed, but many parr emigrate downriver and rear somewhere upstream of the first dam, as briefly discussed in this chapter and many other publications (see a partial list below). What is the capacity of this downstream overwintering area to support these parr migrants? What is the capacity of the natal watershed and the downstream habitat to the first dam for supporting parr migrants plus smolt migrants? Please discuss habitat capacity for fry and parr migrants, which are very important life strategies, and how the life-cycle modeling effort can incorporate these fish in addition to habitat associated with smolt migrants. Can the life-cycle models be used to inform habitat restoration decisions in the natal watershed versus downstream areas that support parr migrants?
- G. Which Chinook salmon populations have greater overall smolt-per-spawner productivity (fish counted at 1st dam, i.e., parr migrants plus smolt migrants): stocks with a higher or lower proportion of smolt migrants? What does this tell us about habitat in the natal watershed versus downstream habitat?
- H. Provide a time series for each subbasin of the following ratio as a means to evaluate the extent to which habitat is fully seeded each year: $(\text{number of parr})/(\text{parr habitat capacity})$. To what extent does this metric explain the proportion of parr migrants, size of parr migrants, size of smolts, and total smolts (at 1st dam) per spawner?
- I. For Fig. 2, it may be worthwhile to show actual units rather than standardized units along the X-axis since a goal of this analysis is to apply this relationship to other watersheds where parr capacity has not been estimated. What are the units for the Y-axis? Is it correct to assume that basin area (middle panel) excludes habitat upstream of the anadromous zone? In Figs. 2 and 5, we suggest changing "Standardized log Parr Index" to "Standardized log Parr Habitat Index" just to emphasize that this is a habitat index of capacity.
- J. How well do the parr capacity estimates generated in this analysis compare with parr capacities generated by the other two approaches described in Chapter 2b?

- K. On page 42, the authors state: “Chinook in some CRB watersheds may be far enough below capacity that even local sampling may not detect evidence of density dependence or capacity.” The authors also state “Our estimates demonstrate only modest losses in habitat area, and hence capacity, from historical to current estimates.” However, a review of density dependence in the Columbia Basin, based on a number of recent publications and technical reports in the Basin, suggests that there is considerable evidence for density dependent growth and survival, and emigration (to some extent) ([ISAB 2015-1](#)). In ISAB 2015-1, we noted that it is difficult to separate changes in salmon production associated with productivity versus capacity, unless the parameters are being estimated via a recruitment curve.
- L. The ISAB encourages the investigators to discuss the following statement in greater detail: “This can be used to help prioritize basins for restoration. Those basins that appear to be limited by capacity and not productivity (due to lower downstream survival) would tend to be better candidates for parr habitat restoration.” When conducting habitat restoration, it may be difficult to isolate the effects of the action on capacity versus productivity, unless the action is removing a migration barrier that has clearly limited capacity. Such an action to increase capacity can cause reduced productivity if the new habitat is lower in quality compared with the existing habitat. It would be worthwhile to further discuss both capacity and productivity.
- M. The Discussion should further evaluate the following ambitious claim that was provided in the Introduction: “Here, all of the potential habitat metrics have been condensed into this single metric of capacity before the modeling process. Instead of focusing on which components of the physical habitat are important we explore how this capacity metric performs and illustrate how the metric in combination with the fish data can be used to make predictions about juvenile population dynamics across the different basins. Through this modeling we can account for density dependence, incorporate different life-history strategies, and estimate aggregate survival over most of the freshwater residence.”
- N. As noted in the Discussion, much more information can be extracted from these data to evaluate factors affecting survival and key restoration actions. The ISAB encourages the investigators to pursue more analyses while also considering published studies based on similar datasets in the Basin:
- Connor, W.P., A.R. Marshall, T.C. Bjornn, and H.L. Burge. 2001. Growth and long-range dispersal by wild subyearling spring and summer Chinook Salmon in the Snake River Basin. *Transactions of the American Fisheries Society* 130:1070-1076.

- Copeland, T., and D.A. Venditti. 2009. Contribution of three life history types to smolt production in a Chinook salmon (*Oncorhynchus tshawytscha*) population. *Canadian Journal of Fisheries and Aquatic Sciences* 66:1658-1665.
- Copeland, T., D.A. Venditti, and B.R. Barnett. 2014. The importance of juvenile migration tactics to adult recruitment in stream-type Chinook salmon populations. *Transactions of the American Fisheries Society* 143: 1460-1475.
- Walters, A.W., K.K. Bartz, and M.M. McClure. 2013b. Interactive effects of water diversion and climate change for juvenile Chinook Salmon in the Lemhi River Basin (USA). *Conservation Biology* 27:1179-1189.

Chapter 2.d. Habitat: Movement and survival based on mark-recapture data

[View Chapter](#)

1. Goal

The report describes analysis of mark-recapture data to better estimate survival and movement probabilities and relate them to stream habitat conditions and potential habitat restoration. The report also describes approaches to account for density dependence.

2. Key model findings

The investigators demonstrated the application of the Barker model to analyze discrete and temporally continuous mark-recapture data to estimate stage-specific probabilities of survival and movement of juvenile salmonids. They used data for steelhead from the Middle Fork of the John Day River to illustrate the approach and demonstrate how it can be integrated into life-cycle models. The model was used in the John Day River to assess potential benefits of restoration approaches designed to (1) create cooler summer temperatures and (2) increase structural complexity (see Chapter 9d. ISEMP/CHaMP life-cycle models).

The report used a multi-state model to estimate movement probabilities from different reaches of the Entiat River. They found that fish left reaches with less off-channel habitat from summer to winter and they moved less from reaches with extensive side channel and floodplain habitat.

The investigators' use of mark-recapture data for parameterizing productivity parameters in stage-specific Beverton-Holt models is limited because these habitats are rarely at carrying capacity, even though populations often exhibit density dependence. Because survival in stage-to-stage transitions can be influenced by density-dependent dynamics, the Beverton-Holt model must be adjusted for different productivity, termed Beverton-Holt productivity equivalent. The productivity equivalent can be estimated if survival is known from years that are assumed to be close to carrying capacity. The authors solved for a productivity equivalent in the life-cycle model that gave values similar to those observed in the mark-recapture measurements. In the John Day River, this process estimated that the stream reaches were at 25% of capacity during the years that were sampled.

The authors also developed an approach for rivers where there are few life stages of fish. The authors used survival from mark-recapture data and also estimated survival based on abundances of different life stages. Using a Bayesian framework to estimate productivity and quantile regression forest to estimate parr capacity based on habitat characteristics, they estimated survival of spring and summer Chinook juveniles moving from the Lemhi River through Lower Granite Dam, demonstrating the ability to adjust for density dependence in mark-recapture estimates of survival.

3. Progress toward addressing ISAB recommendations from 2013

This 2017 model component does not have a corresponding 2013 model component, so specific comments are not available for comparison. However, this 2017 model component was developed partially in response to the ISAB's 2013 recommendation for the NOAA Fisheries modelers to work with their Watershed Program.

4. Applicability to management decisions, alternative scenarios, and adaptive management

The report describes statistical methods for using mark-recapture (PIT-tag) data to better estimate survival and movement probabilities related to stream reach habitat conditions, including habitat restoration. The report also describes approaches used to account for density dependence. They used data from the Middle Fork of the John Day River to illustrate the approach. They also observed that survival had to be adjusted for productive capacity in life-cycle models. These relationships are extremely important in life-cycle models, and the approaches for using mark-recapture data and PIT tagging movement data provide necessary information for modeling. The investigators suggest that this new approach may provide an effective means for prioritizing restoration actions. The focus of the report is not to determine or model patterns of movement and survival across the Columbia River watershed but "rather outlines how tagging data can be used to address restoration applications and identify critical uncertainties regarding the estimation of demographic rates and their integration into LCMs." As a demonstration project, it largely succeeds.

5. Compatibility with best available data and flexibility to incorporate new data

The approaches inform the design of field studies to measure survival and movement and help determine relationships between habitat quality and demographics. This would add value to the existing PIT tag database. If the new or additional studies follow similar protocols and spatial distribution of marked fish, the analyses and modeling are compatible with new data. Application of these data to life-cycle models would be improved with results from other locations and fish species. The potential is demonstrated with two examples. Presumably the data can be used to generate scenarios and improve adaptive management.

6. Treatment and communication of assumptions and uncertainties

The authors discussed the assumptions, uncertainties, and limitations of their approach. They provided suggestions for future studies and improvement of the analyses and modeling. The authors acknowledged that there are artifacts associated with PIT tagging, such as lost tags. Another critical concern that the authors did not acknowledge is the differential effects of PIT tagging on different sizes of fish. The 60-100 mm juveniles likely experience greater handling mortality than fish >100 mm. This is a major challenge for applying this approach with subyearling and yearling juveniles, parr versus smolts, and species like steelhead which outmigrate at a wide range of sizes. The investigators should be aware of studies indicating

additional mortality caused by PIT tags, as indicated by Knudsen et al. (2009) and Tiffan et al. (2015). The Comparative Survival Study works extensively with PIT tag data and is currently investigating PIT tag-related mortality. Also see a review paper by Klimley et al. (2013) on the use of electronic tagging to provide insights into salmon migration and survival.

The investigators hypothesize that restoration actions in specific valley segments of the natal stream would reduce over-winter movement out of the stream, thereby allowing more fish to overwinter in higher quality habitat, leading to overall greater survival. Survival of parr migrants versus smolt migrants is an important question. To what extent is it better to emigrate as parr in the fall, as many spring Chinook do, versus overwinter in the natal watershed? Movement has been described as a density-dependent response by other investigators, such as Copeland et al. (2014). If habitat in lower reaches is degraded and leads to lower survival of parr migrants, would it be better to focus restoration on the lower river habitats where parr overwinter?

7. ISAB Recommendations

- A. The ISAB recommends continued refinement of these approaches for developing survival and movement information for life-cycle models based on mark-recapture studies.
- B. The study should be continued with the goal of contributing to the understanding of movement and survival of juvenile salmonids across basins.
- C. The authors should provide a discussion of their findings and provide guidance for decision makers and managers to help them understand the importance of these approaches and the potential applications in management decisions.
- D. The authors should provide a list of future research needs that may be worth considering.

8. References

- Copeland, T., D.A. Venditti, and B.R. Barnett. 2014. The importance of juvenile migration tactics to adult recruitment in stream-type Chinook salmon populations. *Transactions of the American Fisheries Society* 143:1460-1475.
- Klimley, A.P., P.T. Sandstrom, B. McFarlane, S. Lindley. 2013. A summary the use of electronic tagging to provide insights into salmon migration and survival. *Environmental Biology of Fishes*, 96:419–428; DOI 10.1007/s10641-012-0098-y ([pdf](#)).
- Knudsen, C., M. Johnston, S. Schroder, W. Bosch, D. Fast, and C. Strom. 2009. Effects of passive integrated transponder tags on smolt-to-adult recruit survival, growth, and behavior of hatchery spring Chinook salmon. *North American Journal of Fisheries Management* 29:658–669.

Tiffan, K. F., R. W. Perry, W. P. Connor, F. L. Mullins, C. D. Rabe, and D. D. Nelson. 2015. Survival, growth, and tag retention in age-0 Chinook salmon implanted with 8-, 9-, and 12-mm PIT tags. *North American Journal of Fisheries Management* 35:845–852.

Chapter 2.e. Habitat: Habitat actions and Chinook parr-adult survival

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1. Goal

The goals are clear: “the present analysis attempts to examine the relationship (if any) between putatively beneficial habitat actions and fish survival. It updates our 2005 analysis referenced above, and extends it from parr-smolt survival to adulthood (fish returning to Lower Granite dam as one-ocean jacks or 2+ ocean adults).” This statement is satisfactory but might be more strongly stated as “The goal of this study is to determine the relationship (if any) between collective habitat actions and salmonid survival.” In other words, is the huge investment in habitat restoration projects reflected in improved survival of salmonids in the parr through adult stages?

2. Key model findings

The basic idea of this modeling exercise is to examine parr-to-smolt and smolt-to-adult survival, taking advantage of the large numbers of tagged wild juveniles in diverse streams, to determine if, on a broad scale, stream restoration projects make a difference. The conceptual model tested is that numerous restoration projects on many streams result in a net increase in the number of adult spring-run Chinook salmon returning to spawn. The data set was generated by lumping and simplifying data from many restoration projects over a broad area. This was appropriate because the projects were diverse and not designed with this kind of analysis in mind. While more complex models have been used in the past, the use of log-linear regression models was highly appropriate given the nature of the data, with potential for robust results. The key findings were that over a large scale, restoration projects increased survival of parr and smolt Chinook salmon, although the translation of this increased survival to adults was less clear.

3. Progress toward addressing ISAB recommendations from 2013

This 2017 model component does not have a corresponding 2013 model component, so specific comments are not available for comparison.

4. Applicability to management decisions, alternative scenarios, and adaptive management

The study does not really address individual management actions but suggests that cumulative effects of many diverse actions that increase size of parr at age have a positive effect on adult populations. Thus, any management action that increases growth rates of parr and therefore increases survival can be regarded as appropriate. The study essentially says “keep using the

best habitat management practices and collectively they will make a difference in salmon survival.”

The investigators nevertheless are appropriately cautious in their conclusions. They recognize that there are few studies that quantify benefits of habitat restoration on salmon survival and abundance. Therefore they examine available data for spring/summer Chinook salmon in the Snake River Basin as the first approach to quantifying benefits, if any. However, as noted by the investigators, a drawback to the approach is that habitat action is simply defined as the number of habitat actions in a watershed where one action could represent a suite of actions within one year; size and type of habitat actions was not considered because data do not exist or are not readily available. As a result, the analysis does not provide information on the type of habitat actions that are likely to produce larger parr and higher survival rates, although an effort was made to relate different types of restoration programs to benefits to salmonids.

The study examined six types of restoration (authors said five types but listed six): riparian plant and bank restoration, livestock grazing, rearing habitat improvement, fish passage improvement, increased flow, and water quality restoration. The analysis assumed that all actions would be immediately and equally beneficial, but the authors acknowledged this would not be true for several restoration types, such as riparian plantings. It is likely that the assumption would not be valid for at least three of the restoration types (riparian plant and bank restoration, livestock grazing, water quality restoration), and it often is not valid for rearing habitat restoration actions. It is not surprising therefore that results at this level were equivocal.

Several other aspects of the analysis also raise questions. The Lemhi River population was removed from the populations analyzed because it had more than twice the number of actions of the next highest location. The authors justified this decision because many of the actions had occurred on smaller tributaries and they suggested that the areas accessible to spawning Chinook could have been saturated with restoration actions. There is no empirical or analytical basis to support this judgment and removal by the authors. Additionally, all projects regardless of length or area of restoration were considered equal. No data were provided about the spatial extents of the actions. Quantitative information on the types of restoration actions was not provided either in the text or in an appendix.

The authors seem to be aware of these problems and note that their analysis is a simple, initial approach. Although it is encouraging that the analysis documented higher survival in populations with higher numbers of restoration actions, decision makers should consider alternative explanations before concluding that this study demonstrates that restoration actions have increased survival. Nevertheless, the analysis is worthwhile and a good start on a broader investigation.

The modeling was not designed to test alternative scenarios, although the data set possibly could be used to look at responses at a watershed scale in watersheds where different restoration approaches were used. As the authors indicate, their results on survival probabilities have some use for increasing the realism of life-cycle models. The data gaps include (1) a need for intensive study of one or two watersheds that could actually detect changes in marine survival of fish produced by restored reaches and (2) applying the model to other broad areas in the Columbia Basin.

5. Compatibility with best available data and flexibility to incorporate new data

The data are lumped and transformed in the process because they come from diverse sources of varying quality; however, the data are the best available. The modeling can and should incorporate new data on restoration projects as it becomes available. However, it would presumably only be sensitive to fairly large changes in management and many of the weaknesses of the analysis or limitations on interpretation would still apply.

6. Treatment and communication of assumptions and uncertainties

This modeling was really designed to address one major uncertainty: is the huge investment in habitat restoration paying off by adding more adult Chinook salmon to the fishery or overall population? While the approach makes the results much easier to understand and the report tries to avoid over-estimating significance of model results, there are many uncertainties associated with it.

One perplexing aspect of this study is that Chinook salmon survival is estimated from the PIT-tagging trap to the first dam or to the adult stage, whereas all habitat actions included in the study occurred upstream of the downstream-most tagging site. In other words, survival is estimated primarily after most juvenile salmon would have experienced improved habitat conditions. The investigators suggest that size of salmon at tagging is a key factor leading to increased survival, but linear correlations (Table 4) indicate the relationship between salmon length at tagging and number of habitat actions is very weak (r values: 0.10, 0.19, 0.16). Based on these linear correlations, habitat actions explained up to only 3.6% of the variation in salmon length at the time of tagging.

Likewise, linear correlations are quite weak between the three salmon survival metrics (parr-to-smolt, parr-to-adult, smolt-to-adult) and the number of habitat actions (-0.06, 0.18, 0.22), indicating habitat actions only explained up to 4.8% of the variability in salmon survival. Furthermore, the negative correlation between parr to Lower Granite Dam survival is troubling because it implies survival declined with increasing number of habitat actions.

Table 5 presents what appear to be multiple regression coefficients. The parr-to-smolt survival model includes mean month of tagging even though this variable is not significant ($P = 0.72$). All three models show very high adjusted R^2 values (0.55-0.78) stemming from the two (or three)

independent variables. The high amount of variability explained by these models is surprising given the very low correlations presented in Table 4. Presumably the high R^2 values stem from the inclusion of a year effect (Y) and index variables (P) in the model (see page 14), but there is no mention of these two factors. Additional model diagnostics are needed to address potential collinearity among independent variables and autocorrelation of model residuals. This is especially important because number of habitat actions and year are highly correlated relative to other factors in the regression models (Table 4).

Figure 5 compares mean survival values for three stocks experiencing the fewest habitat actions with three stocks experiencing the most habitat actions since 1992. The text notes that watersheds with few actions are relatively pristine whereas watersheds with many actions are relatively degraded. However, Figure 5 shows that salmon parr-to-adult survival in the degraded habitats with many actions typically is greater than that for the relatively pristine areas with few actions. This finding suggests that something might be confounding the results of this study (e.g., stream size). Based on the modeling results, the investigators state that a population with 100 actions would experience a 21% increase in parr-to-smolt survival and a 230% increase in parr-to-adult survival compared with a population that received no habitat actions. They associate the high SAR benefit relative to parr-smolt benefit to increased fish size associated with habitat actions, yet Table 4 indicates <1% of the variability in SAR was explained by salmon length.

The investigators noted that approximately 33% of the estimated survival values were 0% even after releasing the prerequisite number of PIT-tagged fish. Were these low survival estimates associated with fewer tags released from watersheds with fewer habitat actions?

The investigators did not consider density dependence or the potential effects of hatchery supplementation. Many studies in the Snake River Basin now show density dependent survival, growth, and emigration (see review by [ISAB 2015-1](#)). Failure to account for density dependence could cause spurious results.

Are the investigators confident that all of the PIT-tagged fish are wild-origin fish? Ocean Chapter 3 (p. 3) states that <3% of PIT-tagged Snake River spring/summer Chinook detected at Bonneville Dam were wild-origin fish. Inclusion of hatchery PIT-tagged fish would bias the results. Were transported fish used in the analysis?

Finally, while the authors addressed several assumptions and sources of uncertainty, the discussion did not address the consequences for making decisions based on the conclusions if the assumptions were incorrect or if the analysis did not represent the nature of on-the-ground restoration. Two major assumptions that are difficult to accept are that all restoration actions are immediately and equally beneficial and that there is no systematic bias in the basins where more actions occurred. Three of the six types of actions almost certainly would require 5-50 years to have a complete functional response. Attributing increases in survival to these actions

is highly questionable. The analysis assumes there is no difference in baseline survival between locations where few actions occurred and locations where many actions occurred, but it is likely that large numbers of actions occurred in areas where greater responses were expected and additional management decisions potentially influenced the outcome. It is possible that basins with many actions were more likely to show positive responses. It was assumed that the fact that locations with more actions supported larger fish, reflected the benefits of the actions. It is equally possible that the larger size illustrated the bias toward locations where greater responses were likely because of characteristics of the habitat and watershed and perhaps because of lower fish densities that resulted in faster growth.

7. ISAB Recommendations

- A. The study seems to provide evidence that investment in restoration projects is paying off for spring Chinook salmon. The authors nevertheless need to be very careful when interpreting the results; they need to conduct model diagnostics and critically examine the models for spurious results, as indicated in Section 6 above. A study should be planned that takes into account, for example, age and other characteristics of restoration projects
- B. There is also a need for studies that more conclusively demonstrate the mechanism proposed (increased growth and survival of parr). The study needs to show that restoration leads to increased size at age because the current study implies that greater size led to higher SAR. So a key is the extent to which restoration increases growth after controlling for density and environmental conditions.
- C. The ISAB believes the authors should provide more thorough and critical discussion of their assumptions and assess inherent biases or possible associations between numbers of actions and types of actions. This could be accomplished by comparing conditions in basins with low numbers of actions to basins with high numbers of actions.
- D. Authors should consider alternative representations of the extent and functional responses of restoration actions. Functional responses of shade or wood could be adjusted based on age of riparian plantings. Livestock grazing effects could be adjusted temporally based on literature values for rate of channel recovery. Actions to reduce sedimentation could be adjusted for relative contribution to sediment delivery and spatial extent of the action. At the very least, information about the habitat action types and extents could be provided in a table or appendix.

Chapter 3. Ocean/Estuary survival based on PIT-TAG data

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1. Goal

The goal is to better address marine survival and covariates so that life-cycle models can be used to explore potential future climate change scenarios and management decisions. Work to achieve this goal is at an early stage. A new survival dataset (PIT tag data) and analytical approach (logistic regression) were used to model the effect of environmental covariates on survival probability of individual fish (binomial response) of wild in-river Snake River spring/summer Chinook (outmigration years 2000-2013). Models will be applied to a second data set (Upper Columbia River spring Chinook) in the future.

2. Key model findings

Preliminary data, methods, and model results indicate that recent ocean survival can be effectively modeled using environmental data from multiple sources and seasons. The top explanatory variables were (1) the first principal component of the Northwest Fisheries Science Center's stoplight chart variables, which are ocean physical, biological, and ecosystem indicators of juvenile salmon early ocean survival in the Northern California Current, (2) sea surface temperature in winter, (3) winter ichthyoplankton biomass, and (4) coastal upwelling in spring. The ranking of "top" variables was based on an information theoretic approach to model selection and multi-model inference.

3. Progress toward addressing ISAB recommendations from 2013

In 2013, the ISAB recommended that the modelers:

Estuary

- 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.

Ocean

- 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.

The investigators are exploring a new approach; thus, it is not surprising that many of the ISAB's issues raised in 2013 are not considered in this new chapter. The ISAB's 2013 recommendations for the estuary are not addressed, although some of the parameters investigated might reflect estuary conditions (see below). The new PIT tag dataset cannot be used to evaluate estuary and ocean survival parameters separately. There is no indication of collaboration with estuarine investigators to solve the complex problem of estimating the effects of estuary habitat restoration on survival, life history diversity, and population viability of salmon and steelhead.

The ISAB's 2013 ocean recommendations are partially addressed by the investigators' continued exploration and evaluation of parameters that explain variability in ocean survival. The regression models are not specific to ocean age; thus, the assumption of constant ocean survival (0.8) after the first ocean year is not considered in this chapter. Regardless, the ISAB agrees that modelers should not assume a constant late marine mortality. The investigators are clearly working with other NOAA ocean researchers to determine the best indicators of ocean survival.

4. Applicability to management decisions, alternative scenarios, and adaptive management

The investigators discuss various ways in which the new analysis might be adapted to life-cycle models for alternative scenarios analyses of future climate change. But it is too early in the process to determine applicability to management decisions and adaptive management. They do not mention the analysis of climate change scenarios (Chapter 9c), which uses a new ocean survival module in the life-cycle model (Chapter 1) based on PIT-tag data, environmental data, and regression models (Chapter 3; see ISAB review of Chapter 9c).

5. Compatibility with best available data and flexibility to incorporate new data

The PIT tag data used in the analysis are an improvement over SAR data, which need to be adjusted for in-river survival. The statistical approach is largely limited to populations that have sufficient PIT tag data. Adequate PIT tag data are available only since 2000, a much shorter time series compared with coded-wire tag (CWT) data; this limits the range in ocean conditions examined by this new model. The investigators focus on Snake River spring/summer Chinook salmon, largely because there is a wealth of PIT tag data, and there are life-cycle models for this

stock. This population group likely uses estuarine and oceanic habitats differently than other species of salmon and steelhead; therefore the findings may not be readily applicable to other populations and species.

As discussed by the investigators, the PIT tag data have some limitations. The results presented here involve wild-origin Chinook salmon that were not transported around dams in barges. How do the findings compare for transported wild fish or for in-river hatchery fish? A direct comparison with survival values based on CWT data likely would be very different, because migration timing cannot be considered with CWT data, most CWT fish are hatchery origin, and CWT survival values include in-river mortality.

The investigators consider a long list of potential covariates, largely reflecting ocean conditions. Many of the spatially explicit environmental variables reflect ocean conditions during the juvenile (early ocean) life stage. In the search for informative environmental variables, have the authors considered/evaluated seasonal spatially explicit variables that reflect ocean conditions during other life stages, particularly environmental conditions related to ocean age/size at maturation and adult run timing? As discussed by the investigators, it would be worthwhile to incorporate age structure into the survival analysis. Faster growing juveniles spend less time at sea, leading to higher survival, in part because the fish mature at a younger age. Can this modeling approach be adapted to approximate mortality after the first year in the ocean?

Very few variables used in the analysis seem to be related to the estuary. Columbia River flow and perhaps insulin-like growth factor may relate to growth and survival in the estuary. If funding is available for the long term, NOAA might consider development of new indices that relate to the estuary, e.g., salmon residence time and growth in the estuary via otolith microchemistry analysis. The current model will likely provide very little or no information related to benefits of restoration efforts in the estuary. Are there estuarine restoration variables that NOAA might consider for this model even though the time series may be too short at present to detect a significant effect?

PIT-tag data typically include information on fish length at the time of tagging. It would be useful to incorporate fish length at Bonneville Dam (BON), but how this might be estimated is not clear. Could sampling of wild origin smolts in the Snake River Basin be used as an index of body length at BON? Can a bird predation index be developed for consideration? We note that the COMPASS model has a predator density component. Juvenile salmon abundance at BON is a metric that could be tested in the model to account for possible density dependence in the estuary. It is not likely to be significant because smolt density is probably relatively constant given the nearly fixed number of hatchery fish that are released. The ISAB notes that the COMPASS model has a smolt density component. Can the models described in this chapter be linked to the COMPASS model?

6. Treatment and communication of assumptions and uncertainties

The authors do a good job of communicating assumptions and uncertainties in the data and analysis, as well as potential approaches to including or excluding ocean environmental parameters in life-cycle models.

The investigators present a reasonable justification for excluding hatchery Chinook salmon from the analysis: the survival ratio of wild versus hatchery salmon varies from year to year. The greatest difference was during the first three years; thus, the ratio fluctuated around 1. However, hatchery fish also produce many mini-jacks which can bias survival upward because they do not overwinter in the ocean. The investigators provide a good discussion of mini-jacks and how they might influence the analysis. Fortunately, few mini-jacks are produced by wild-origin Chinook salmon; the percentage of wild origin mini-jacks should be documented. Likewise, the investigators should provide rationale for excluding transported salmon.

Some of the environmental variables used in the analysis are not clearly defined, for example, the winter sea surface temperature use (described as "arc", with no explanation). The first principal component (PC1) from the NOAA stoplight chart is a key variable to predict survival. What does this PC1 variable tell us about ocean conditions affecting survival?

Julian date is incorporated into each model. Logically, this variable accounts for the potential mismatch between migration timing and estuary/ocean conditions. The Cumulative Survival Study (CSS) analyses also show that date of migration is very important to survival. However, could inclusion of Julian date in the model reduce the explanatory power of other variables? If so, what are the model results when Julian date is removed? Also, is there an interaction between Julian date and other explanatory variables?

7. ISAB Recommendations

- A. Continue to explore this approach with more model runs, including consideration and evaluation of new explanatory variables, alternate time series of survival data, and potential linkage to other models (e.g., COMPASS) that incorporate density dependence (see section 5 of this review), and repeat analyses as the PIT tag data set grows, assuming that PIT tagging will continue on a large scale.
- B. Attempt to develop a model structure that predicts ocean age structure and survival or accounts for age structure while predicting estuary/ocean survival.
- C. Continue to work closely with estuary and ocean researchers and managers to determine spatially explicit and life stage-specific indicators of estuary and ocean survival of salmon and steelhead.

- D. Use life-cycle models to better understand the potential effects of future estuary/ocean conditions with the goal of adjusting actions in the Basin to achieve greater benefits and/or efficiencies.
- E. Could inclusion of Julian date in the model reduce the explanatory power of other variables? If so, what are the model results when Julian date is removed? Also, is there an interaction between Julian date and other explanatory variables?
- F. Some of the environmental variables used in the analysis are not clearly defined, for example, winter sea-surface temperature "arc." The first principal component (PC1) from the NOAA stoplight chart is a key variable to predict survival. What does this PC1 variable tell us about ocean conditions affecting survival?
- G. The percentage of wild origin mini-jacks should be documented. Likewise, the investigators should provide rationale for excluding transported salmon.

Chapter 4.a. Integrated population model of the Grande Ronde Basin

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1. Goal

This chapter continues the development of the life-cycle model for spring/summer Chinook in the Grand Ronde basin. No new features were added to the life-cycle model in 2017. However, they used the life-cycle model to evaluate the impact of 12 alternative spill-flow combinations on SARs and long-term abundance of spring/summer Chinook out to 2050 after initializing the model with empirical number of spawners from 2010-2014. These population projections are used to compute the performance measures such as long-term average SARs and long-term average abundance.

They also investigate the relative benefit of improvement in juvenile passage vs. improvements in spawning productivity and capacity of the habitat to support spawners.

2. Key model findings

They conclude that:

- greatest benefits to SARs occur in scenarios with highest spill and lowest flow,
- relative return abundance appears to be mostly limited by capacity of the habitat to support the fish.

In particular, they describe in Discussion section that the most significant simulated benefits to SARs occur at the lowest flow levels with spill levels at the highest total dissolved gas limit (TDG; limit spill levels to 125% TDG at all eight Snake and lower Columbia dams). It was also shown that low flows are predicted to contribute more significantly to increases in SARs to the mouth of the Columbia at BiOp or 115/120% TDG than at higher levels of spill. The life-cycle model also predicted that the highest TDG limit spill level (125% TDG) produced a larger incremental benefit to SARs at higher assumed flow levels than at lower flow levels.

3. Progress toward addressing ISAB recommendations from 2013

This is a new addition to the NOAA-led life-cycle model and thus was not part of the ISAB's 2013 review. However, this model component was developed as part of the Comparative Survival Study (CSS), and the ISAB reviewed a summary of the effort provided in Chapter 2 of the CSS 2016 Draft Annual Report (see [ISAB 2016-2](#)). The ISAB raised a number of issues in that review, which the CSS responded to in Appendix J of their [final 2016 Annual Report](#). The main concerns

from the ISAB revolved around (a) not incorporating stochasticity in all parameters during forward projections, and (b) incorporating density dependence at only one life stage.

For example, the ISAB noted that the analysis of alternative spill scenarios held certain aspects of the simulations fixed rather than allowing them to vary and so the results may not reflect the total variability. The CSS noted that this was deliberate because the goal was to compare the performance measures among the 12 spill/flow combinations and not to quantify uncertainty in predicted outcomes of a single scenario. Presumably while the addition of further stochasticity will spread out the results, it may not affect the mean average long-term abundance or mean long-term average SARs, and so comparisons among the 12 scenarios using these performance measures will likely not be affected. However, the simulated outcome should not be used to estimate the probability of quasi-extinction which may depend greatly on including all sources of variation.

Similarly, this report uses 2010, 2009, and 2011 as “typical” of low, average, and high flow years, respectively. These three years represent a range of flow conditions relative to the historical data (1929 to 2012) and so provide a reasonable contrast among flow years. The three years also represent operations that reflect the most recent configuration and operation of the FCRPS. As noted above, this will result in a reduction in stochasticity in each water year and for the same reasons, comparisons among scenarios are informative, but variability within a scenario is likely understated. Consequently, the ISAB acknowledges that among scenarios, comparisons of the average long-term abundance and the average long-term SARs will likely provide a meaningful comparison.

The current model includes density dependence only at the spawner-to-smolt interval. It may be useful to include density dependence elsewhere in the lifecycle, e.g., when considering predator control measures. The CSS pointed out that the model also has the capability of detecting density dependence in the estuary/early ocean stage, but the model fitting did not detect any density dependence. Future versions of the model may include density dependence effects at different life stages, but the data may not have the quality and quantity to detect such effects.

Another potential issue is the impact of assuming a fixed 20% transportation proportion for all prospective spill scenarios. This was necessary because the transportation proportion during model fitting was taken as “given” from the CSS reports and not modeled as a function of other covariates. Is there evidence that the proportion of transported smolts depends on spill/flow and, if so, what is the impact of ignoring this relationship? For example, if a lower proportion were transported at higher spill levels, then more fish would be subject to in-river survival rates and delayed mortality from powerhouse contacts, which may reduce the apparent benefit of higher spill. This would seem to be relatively easy to simulate by adding a new column to Table 2 for the proportion transported that varied by spill level to see the potential impact of such a relationship.

4. Applicability to management decisions, alternative scenarios, and adaptive management

This modeling approach provides a nice contrast to the COMPASS results, also in this chapter. It is not clear if the spill/flow scenarios are directly comparable – it would be very helpful to employ COMPASS and this life-cycle model using the same spill/flow scenarios to better understand if the two models agree in their findings and if not, why not.

This life-cycle model will be useful to evaluate the AVERAGE response to management scenarios but less useful to evaluate performance measures that depend on stochastic variation such as the probability of quasi-extinction. As such, this model is useful as a first ranking of scenarios on these two long-term performance averages.

Because the variability is likely understated in a particular scenario for future responses, it will be difficult to evaluate if failure of actual performance measures differ from predictions. Consequently, adaptive management decisions will have to be based on long-term averages (say 10 years) after implementation.

5. Compatibility with best available data and flexibility to incorporate new data

The modeling approach is sophisticated and uses data appropriately. It can be recalibrated fairly quickly as new data (of the same type) are collected. The framework appears to be flexible enough to allow for new types of data (e.g., density dependence at other life stages), but it is difficult to evaluate the technical difficulty of implementation. At the moment, it does not appear to be possible to model the proportion transported as a function of covariates (such as spill) for prospective simulations, but this feature should be straightforward to add to the existing model.

6. Treatment and communication of assumptions and uncertainties

This report is fairly detailed as to the assumptions made as part of the model building and fitting. Modeling decisions to keep some parameters fixed appear to be reasonable as long as interest focuses on among-scenario comparisons of long-term average abundance and long-term average SARs. However, there is some concern that keeping the proportion transported fixed rather than depending on spill (or other covariates) may not fully reflect the impact of the scenarios. The discussion should include cautions to the reader about using this current model to infer statistics such as probability of quasi-extinction which require stochasticity in all parts of the model.

7. ISAB Recommendations

- A. While no significant changes are suggested, the next iteration should examine the potential problem with proportion of smolts transported being related to spill levels and report on likely impacts of keeping the proportion of smolts transported fixed.

- B. The current model evaluates density dependence only at the spawner-to-smolt stage. It may be useful to include density dependence elsewhere in the life cycle, e.g., when considering predator control measures if data are available. If data are not currently available, what forms of data are needed?

Chapter 4.b. Hydro Modeling: The COMPASS Model for assessing juvenile salmon passage through the hydropower systems on the Snake and Columbia rivers

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1. Goal

This section contains two reports.

The first report presents the COMPASS model outputs for the base conditions (80 years of Columbia River hydrology data from BPA HYDSIM) and alternative hydro management scenarios. The COMPASS system models the river channel, reservoir filling and depletion, dam passage routes based on flow and operations, etc. The model then predicts biological variables such as fish travel time, in-river survival, and arrival-time distribution at Bonneville. The arrival-time output is then input into another (unspecified) model to estimate the smolt-to-adult return (SAR). Five different management scenarios were investigated – baseline (Base), which includes current configurations and operations of the dams; three scenarios (Opt1, Opt2 and Opt3) had minor modifications to baseline, including slightly higher levels of spill; and a final scenario (ORPIv2) with higher levels of spill throughout the migration season. Model runs predicted the effects of these management scenarios on the biological variables.

In the second report, the authors develop models based on PIT-tag data to describe the distribution of arrival time at Bonneville Dam (BON) of specific populations of Snake River spring Chinook and steelhead. Principle Components Analysis (PCA) was used to reduce 18 monthly flow predictors to a smaller set. These reduced variables and water temperatures at Lower Granite Dam (LGD) were used as predictors of arrival time at LGD. The COMPASS model was then used to predict biological variables such as survival, SAR, proportion transported, etc., for salmon and steelhead from the various populations and population groups from LGD onwards. For this exercise they used only the Base condition from the COMPASS model, not the four management scenarios.

2. Key model findings

The first paper reported that differences between hydro management scenarios for the various COMPASS output statistics were smaller than the year-to-year variability within scenarios. Mean in-river smolt survival of the five scenarios ranged from 0.5500 (Base) to 0.5624 (Opt2), or by about 1.2 percentage points. SARs for in-river fish ranged from 0.01730 (ORPIv2) to 0.017489 (Opt 2). SARs for transported fish were consistently lower and ranged from 0.00704 (Opt3) to 0.00714 (Opt 1). Only the proportion of fish entering the transport system varied to any large amount (0.315 to 0.407). These findings suggest the proposed alternatives have little

effect on survival of Snake River spring Chinook salmon. Findings for steelhead also indicated small differences in survival associated with the management scenarios.

These results are at odds with work conducted under the Comparative Survival Study (CSS) that looked at the impact of spill. The authors suggest that the failure of COMPASS to show a large benefit to increased spill is due to the fact that sub-models that form part of COMPASS (e.g., the effect of spill on routing of fish at the dams) largely did not identify spill as an important predictor (see below). Also, COMPASS only looked at the benefits of increased spill on in-river survival and did not consider impacts on delayed mortality in the ocean as is done in the CSS model.

The second paper reported that predicted in-river survival and SARs were affected for the late migrating Chinook stocks (lower survival and more fish transported). This raises the question: how do these fish compensate for late migration timing and low survival in order to be viable, or do these late migrating stocks have lower population status?

3. Progress toward addressing ISAB recommendations from 2013

The first paper assumes that the reader is familiar with the COMPASS models and presents only a high-level summary of the model. This makes it difficult to review the document and to assess the findings. Too little information on the modeling approach is provided in this first report to determine if it addresses the ISAB recommendations from 2013.

It would be helpful to present a diagram showing how all of the parts fit together, e.g., distribution of smolts at LGR that feed into a dam passage model, then into the river until the reservoir, then a reservoir model, etc. For each part, the authors should indicate the data sources used to fit the important predictors in the model. For example, the authors claim that the failure of COMPASS to show any large benefits to spill is due to spill not being an important predictor. However, is this because there was a large contrast in the spill values in the data fitting steps and spill did not appear to be an important predictor, or was this because the contrast in spill values in the existing data was so small that it was impossible to extract an impact of spill? If spill also impacts survival in the ocean, how much of the benefits of spill occur in-river vs in-ocean?

The arrival distribution of smolts at Bonneville is fed into another (unnamed) model that provides SAR estimates. What factors influence this ocean-survival model? Are they held constant for all 80 water years? It is quite possible that the factors that impact the SAR model are related to the water years, e.g., are poor ocean conditions associated with low-flow years. No information was provided on this part of the process.

At this point, it would be helpful to step back and provide quantitative estimates on how each part of the river system affects survival. For example, if dam passage mortality represents only 10% of the total mortality from LGR to BON, then the negative findings of the impact of spill are

much more understandable. Similarly, how much does the arrival distribution at BON affect SARs relative to changes in SARs from changing other components of the model? Without this information it is difficult to evaluate the rationale and conclusions of the authors.

The second paper appears to be new. The paper is not written in a scientific style which makes it difficult to review. For example, the information provided on modeling the arrival distributions of fish at LGR is difficult to understand. Is it possible to alter the arrival distribution at LGR? Would doing so change the output from a model run for a particular water year by 1%, 10%, 50%? Given the large differences due to water years, perhaps this level of modeling is superfluous.

The statistical models are very complex with each having from 13 to 23 explanatory variables. Is collinearity or over-parameterization an issue? With so many predictor variables, the model fits are very good, but this does not mean they will be good for predicting future migration timing. Given the somewhat limited number of PIT tagged fish, to what extent does measurement error in the observed timing distribution affect predictions?

Variability in predicted median arrival day at LGR over the 80-day period is very high, ranging from day ~80 to 140, i.e., 60 days (Fig. 5). How does this compare with the observed data? Smolts have behavior such that late migrating fish tend to migrate faster. Was behavior fully incorporated into the model across the 80-year period?

4. Applicability to management decisions, alternative scenarios, and adaptive management

The COMPASS model (first report) provides a high-level way to assess management scenarios. Each particular run does not involve stochastic relationships so the variability in the responses is not provided. Therefore, while the average performance is acceptable, there is a high risk of extinction when no adults return due to stochastic fluctuations.

Although the main results showed only a small impact of the scenarios on the performance measure when averaged over all 80 water years, how did the scenarios perform in high-, regular- and low-flow years? Perhaps the poor showing is due to the difficulty in manipulating spill in low-flow years and these are swamping the results? Or perhaps in the baseline scenario the distribution of performance measures is unrelated to flow whereas in the high spill scenarios the distribution of the performance measures is highly related to flow and both cases have the same average (over the 80 water years).

The COMPASS model could be very helpful for managers to see the relative impacts of each part of the system on the total mortality and to judge if management decisions have the potential for small or large impacts (see above).

It is not clear how to incorporate the COMPASS results into an adaptive management cycle. Suppose that the actual in-river survival (as measured by CSS) differs considerably from that

predicted by COMPASS. Without any stochastic component, it is difficult to evaluate if this anomalous response is just normal variation or requires rethinking management actions.

The second report describes a complex statistical approach for predicting the migration timing distribution of spring Chinook salmon and steelhead at Lower Granite Dam (LGR). This information can be used in subsequent predictive models that use arrival distributions as inputs. The COMPASS model and other analyses indicate salmon survival is influenced by migration timing. However, given the very small difference in survival values among the five management scenarios in the first report, will this new information have significance for management actions? What management actions can occur to benefit these late migrating stocks and will the actions be meaningful?

The second report in the chapter is well positioned to explore the four alternative scenarios described in the first report, but this was not done. Based on the Discussion section of the second report, it appears that the authors are continuing to fine tune treatment of empirical data before proceeding into scenario testing.

The report notes that in-river survival and SARs predicted by COMPASS were most sensitive to the late migrating Chinook stocks (lower survival and more fish transported). This raises the question: how do these fish compensate for late migration timing and low survival in order to be viable, or do these late migrating stocks have lower population status?

For both reports, it is not clear how scenarios were generated. It would be helpful to know how the four alternate management scenarios were chosen for the first report and why the CSS spill experiment was not modeled.

5. Compatibility with best available data and flexibility to incorporate new data

This is difficult to evaluate given the cursory presentation for the COMPASS model. It does appear that each part of the COMPASS model can be modified as new data arrive (revising the parameter estimates). Can they use existing data on, for example SARs or proportion transported, to test the COMPASS predictions?

The second report describing the modeling of arrival distributions at LGR appears to be a “work in progress” because there are several technical issues that need to be resolved, such as counting parameters when comparing models using AIC, maintaining monotonicity in the estimated quantiles, or dealing with uncertainty in the two-step modelling process. The approach appears to be very flexible, but there is a danger that it is too flexible and that most of the complexity just happens to be related to fitting data noise.

6. Treatment and communication of assumptions and uncertainties

Several key assumptions were never explicitly stated. For example, the COMPASS model does not appear to include stochasticity, i.e. the same output is obtained if a run for a particular model year is repeated. This mean response may not fully reflect the risks to the population.

The authors describe a hierarchical model which likely entails some shrinkage in the reservoir survival estimates, but the amount of shrinkage is not made clear. For example, if there are 10 reservoirs and a separate survival rate is estimated independently for each reservoir, the “range” between the lowest and highest estimated survival rate will be larger compared to the “range” of the same estimated survival rates when a hierarchical component is added. The variability in individually estimated reservoir survival rates includes both reservoir-to-reservoir and normal stochastic variation of the estimated survival rates within each reservoir. The hierarchical model separates the two and so the estimated variability in survival rates among reservoirs under a hierarchical model is “smaller” than the composite variability—this is called “shrinkage.”

The model that predicts subsequent ocean survival based on arrival distribution at BON is not described. Given the large ocean mortality, this omission is troubling and the lack of a spill effect may be related to this sink.

The statistical models in the second report are very complex (i.e., contain many explanatory variables). The assumptions and consequences of failures of assumptions need to be carefully explained.

7. ISAB Recommendations

- A. [Report 1] Add a diagram showing all of the parts of COMPASS and how they fit together.
- B. [Report 1] Provide more information on the ocean-survival model that predicts SARS.
- C. [Report 1] Present information on the relative impact of the different parts of the hydrosystem on the performance measures, e.g. what fraction of total mortality is due to dam passage versus reservoir migration versus survival at sea?
- D. [Report 1] Use the COMPASS model to investigate the spill experiment proposed by the CSS and Fish Passage Center as another scenario. If the CSS analyses seem to indicate a larger benefit of spill, this needs to be fully explained. For example, is this difference in findings due to different impacts of spill on ocean survival or lack of contrast in data used to derive effects of spill? Compare and contrast the two modeling approaches.
- E. [Report 2] Improve the second report so that it is presented in a scientific rather than a high-level description format. The second report appears to be a “work in progress” because there are several technical issues that need to be resolved.

- F. [Report 2] A justification for the (very) complex modeling of arrival timing at LGR is needed.
- G. Is the model over-parameterized relative to the data used?
- H. What are the impacts of measurement error on the observed timing distributions?
- I. Variability in predicted median arrival day at LGR over the 80-day period is very high, ranging from day ~80 to 140, i.e., 60 days (Fig. 5). How does this compare with the observed data?
- J. Smolts have behavior such that late migrating fish tend to migrate faster. Was behavior fully incorporated into the model across the 80-year period?
- K. What assumptions are being made and what are the impacts of failure of these assumptions?
- L. [Report 2] Integrate the new model described in the second report with the COMPASS model in the first report and describe the extent to which the five management scenarios affect survival metrics across the 80-year period modeled in the second report.
- M. Examine survival estimates by stock and timing group (early, average, late). Discuss implications for managing the hydrosystem.
- N. Given the very small difference in survival values among the five management scenarios in the first report, will this new information have significance for management actions?
- O. What management actions can occur to benefit these late migrating stocks and will the actions be meaningful?
- P. [Reports 1 & 2] The introduction in the second report should describe how it relates to COMPASS (first report) and how the model outputs relate to the life-cycle model. These comments are similar to those from the ISAB in 2013. The 2013 concerns about lack of detail with which to judge the COMPASS model still need to be addressed.
- Q. [Reports 1 & 2] Provide rationale for the scenarios chosen in each report.

Chapter 5. Toxics as an Obstacle to Salmon Recovery in the Columbia River Basin

[View Chapter](#)

1. Goal

The goal of this chapter is to summarize the literature on toxic chemicals as limiting factors for the recovery of salmon and steelhead in the Columbia River Basin. This is not a comprehensive review but rather a description of how human land uses have altered freshwater and estuarine habitats by changing the chemical environment. The chapter does not present any existing models.

2. Key model findings

The chapter does not present any model results, although models were mentioned in section 5.e (Population-scale benefits of reducing toxics across the Columbia River Basin for ESA-listed salmon). These models are presented in published papers and the authors are NOAA biologists. Reportedly, the models were used to make theoretical population-level projections of the effects of contaminants on Chinook salmon in the Salmon and lower Willamette rivers. The chapter, however, is a review of studies completed by NOAA researchers for the most part.

3. Progress toward addressing ISAB recommendations from 2013

This is a new component to NOAA's life-cycle model that addresses a gap identified in the ISAB's 2013 report: "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 to address nonnative species and toxic chemicals in subsequent life-cycle models."

The ISAB appreciates the 2017 addition of a toxics section as a step forward in the modeling effort. The chapter is composed of several sections that summarize current knowledge, issues, data gaps, and recommendations for three types of contaminants—current-use pesticides, legacy contaminants (e.g., PCBs, DDT), and chemicals of emerging concern (CECs, e.g., pharmaceuticals, plasticizers) from wastewater. The ISAB hopes that the recommendations in the chapter for filling the large gaps in our understanding of contaminant effects on individual fish and fish populations come to fruition and lead to modeling efforts that can be integrated with the existing life-cycle models.

4. Applicability to management decisions, alternative scenarios, and adaptive management

The report is too preliminary and non-quantitative to contribute substantially to adaptive management processes. The review is a good start but does not include many available studies

of toxic substances and their effects on salmon. The report provides limited or no discussion of several toxic substances, such as heavy metals, even though there are numerous studies on their occurrence in the Columbia Basin and their effects on salmon. The ISAB understands that the authors were not comprehensive for good reason—the literature is huge, albeit often consists of laboratory studies on species like fathead minnows.

At the end of each section the authors present several recommendations to fill existing data gaps in our understanding of the effects of contaminants on salmon. The following statement summarizes the current situation: “The final theme reflects the current reality – i.e., environmental health science for salmon (ecotoxicology) is not keeping pace with existing and emerging data gaps.” (Chapter 5, page 4). The ISAB believes that filling these gaps is essential to developing a life-cycle model that will provide managers with a reasonable approximation of the real world threats to salmon recovery.

5. Compatibility with best available data and flexibility to incorporate new data

The ISAB believes that the authors of this chapter have access to the best available data and that, because there are no models yet linked to life-cycle models, there is maximum flexibility to incorporate new data. The three approaches to investigating toxics in the Columbia Basin in this Chapter (chapter section 5b: pesticides in salmon; 5c: persistent organic pollutants [POPs] in salmon; and 5d: CECs) provided a good synthesis of issues with these toxics in the Columbia Basin. Chapter 5b and 5c were fairly comprehensive, but Chapter 5d did not seem very complete. It also would be useful to have a review of water quality in the Columbia Basin (i.e., where the pesticides, POPs, and CECs have been found and in what quantities) to identify areas of threat for salmon, for example, see Fig. 1c in Naiman et al. (2012).

6. Treatment and communication of assumptions and uncertainties

No model is presented in the chapter, so there are no assumptions. The chapter is dedicated to the vast uncertainties surrounding our understanding of contaminant effects on salmon recovery. Perhaps the authors could address uncertainty and information gaps systematically and prepare matrices of toxics and the quality and extent of available information on their effects on aquatic organisms, including salmon.

7. ISAB Recommendations

- A. The report omits large portions of the available information on toxic substances and their effects in the Columbia River Basin. Major studies by USGS, EPA, state agencies, municipalities, and university researchers are not included. A literature review or summary of water quality measurements in the Columbia River Basin as part of Section 5.d would strengthen this section, which was not as informative as Sections 5.b and c.
- B. Section 5.e mentions models reportedly used to make theoretical, population-level projections of the effects of contaminants on Chinook salmon in the lower Willamette

River and the Salmon River tributary of the Snake River (Spromberg and Meador 2005; Mebane and Arthaud 2010). However, the models were not presented in any detail. It would be informative for the authors to include more detail, or reasons for the lack of detail, and a discussion of how these models might be modified to be compatible with the life-cycle models. Also, Loge et al. (2006) used a dose-structured population dynamics model to predict as high as 18% increased disease mortality in salmon exposed to chemical and non-chemical stressors during outmigration in the Columbia Basin. Could models that appear to show compounding mortality factors be incorporated in a life-cycle model?

- C. The authors mention studies that have identified specific contaminant effects on, for example, life-stage-specific survival or interaction with the aquatic food web by, for example, reducing prey availability or reducing the salmon's ability to capture the prey (page 6). Could these documented effects be linked to existing life-cycle models to explore "what if" scenarios?

8. References

- Loge, F., M. R. Arkoosh, T. R. Ginn, L. L. Johnson, T. K. Collier. 2006. Impact of Environmental Stressors on the Dynamics of Disease Transmission. *Environmental Science and Technology*, 39(18):7329-7336.
- Naiman, R.J., J.R. Alldredge, D. Beauchamp, P.A. Bisson, J. Congleton, C.J. Henny, N. Huntly, R. Lamberson, C. Levings, E.N. Merrill, W. Pearcy, B. Rieman, G. Ruggerone, D. Scarnecchia, P. Smouse, and C.C. Wood. 2012. Developing a broader scientific foundation for river restoration: Columbia River food webs. *Proceedings of the National Academy of Sciences (USA)* 109 (52):21201-21207.

Chapter 6.a. Population-specific pinniped predation

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1. Goal

This section provides estimates of survival of returning adult Chinook salmon as they pass upstream from the Columbia River Estuary to Bonneville Dam. A key source of mortality at this life stage is predation by pinnipeds, and measures of pinniped abundance are included as independent (predictor) variables in linear and logistic regression models. Other variables, such as time of estuary entry (e.g., spring vs. summer runs), source population, climate variables, and temperature are also included in four submodels that address different predictors of salmon arrival and survival in the lower river.

2. Key model findings

Analyses are organized into four submodels, each addressing different questions about salmon survival, date of entry into the estuary for different stocks, travel time from the estuary to Bonneville Dam, and environmental correlates of survival and travel time. Key findings are (1) apparent survival of Chinook salmon declines as pinniped density increases, (2) fishes that enter the lower river earlier (i.e., spring run Chinook) have higher risk of mortality from pinniped predation; however, (3) there are survival advantages for late migrating natural origin Chinook above Bonneville, (4) there is inter-annual variation in estuary arrival time, but the chronological sequence of appearance of different runs/populations is maintained, and (5) fish migrating in cooler river water had slower travel times than fish migrating in warmer water.

3. Progress toward addressing ISAB recommendations from 2013

This is a new report component that was added to the 2017 version of the life-cycle model and was not in the 2013 version. In 2013, the ISAB recommended that the estuary component of the model include a pinniped predation component. The Introduction to the 2017 life-cycle model describes the rationale for including this pinniped component, “California Sea lions have expanded their presence in the Columbia River estuary to become a major threat. Accordingly, we have developed a module that covers population-specific mortality due to the presence of sea lions.”

In 2016, the ISAB released a Predation Metrics Report ([ISAB 2016-1](#)) that recommended approaches to measure the effects of predation on Columbia River Basin salmon and steelhead. Accordingly, the specific goal of the analysis in this chapter was to estimate survival of adult Chinook salmon from the mouth of the Columbia River to Bonneville Dam as a function of their migration timing and other factors. Analyses were designed such that results could inform life-

cycle models and allow for more insight into mortality from predation compared to the generalized model (that does not attempt to partition mortality sources) that is currently employed. In a time series that spans 2010 to 2015, proponents evaluated survivorship directly by tagging returning salmon at Astoria and then by counting tagged fish at Bonneville Dam. Annual data collection included spring and summer runs. From these data, survivorship, travel time from estuary to dam, and identity (hatchery vs. natural origin, sex, body size/condition, genotype) of survivors were determined. As discussed below, fish identity could be particularly important because traits that influence run timing are heritable and vary across watersheds within the Columbia Basin. Thus, management actions that aim to maintain life history variation must consider differential predation pressure over time.

The tag-recapture approach employed has applicability to life-cycle models to the extent that sample sizes of fish encountered at Astoria can reasonably be increased. Increased sample sizes could help identify whether hatchery fish are subject to higher predation probabilities and how predation pressure aligns with maintenance of variation in run timing among spring/summer Chinook salmon. Efficacy and predictive power depend on the density and quality of mark-recapture data, and how this information is incorporated into the life-cycle model. It was noted that life-cycle models already include variables for baseline levels of adult estuarine mortality.

4. Applicability to management decisions, alternative scenarios, and adaptive management

The question of direct applicability to management is not strictly relevant to this chapter since this is not a life-cycle model component. However, in combination, managers could use this information to estimate when stocks of up-river spring/summer Chinook are expected to enter the Columbia River, how long it is likely to take them to migrate to Bonneville Dam, and what mortality losses are anticipated. In the current stage of model development, estimates of how adult survival may vary under different environmental and biological conditions can be generated. Thus, it should be possible to predict how adult survival changes under different abiotic and biotic regimes and conditions. Such predictions would need to be linked to comparable estimates (with and without fisheries) of survival from Bonneville to natal spawning areas. This would allow managers to assess consequences of possible management actions and other scenarios in the lower river.

Scenario testing can be used to guide future management actions making adaptive management possible. The consequences of alternative management practices (e.g., removal of pinnipeds) on Chinook survival would need to be appraised. Results of these evaluations could then be used to assess the benefits of implemented actions. That is, did they lead to increases in survival and is the magnitude of any increased survival great enough to bring about a noticeable change in adult numbers on spawning grounds? This additional analysis should consider the density-dependent relationship between spawners and production of smolts, which can be strong in some watersheds. Additionally, these appraisals would make it possible

to validate the predictive capacities of the existing sub-models and possibly lead to further refinements (e.g., the use of different independent variables) in the models.

5. Compatibility with best available data and flexibility to incorporate new data

The proponents appear to have made extensive use of numerous appropriate data sets when creating each of their four sub-models. For example, they used data collected on adult salmon PIT-tagged as juveniles to document stock arrival timing at Bonneville Dam. They found inter-annual variation in arrival time at the mouth of the Columbia River, dependent on ocean and riverine conditions. Despite this variation, the order in which stocks entered the river remained chronologically consistent across multiple years. PIT-tag detection data collected at Bonneville was used to assess how many days it took adults to travel from the mouth of the river to Bonneville. Genetic Stock Identification tools were used to determine the stock origins of the tagged fish. This combination of approaches allowed proponents to determine overall survival rates of specific stocks. It also made it possible to compare adult mortality rates at different times throughout the migration period.

The four sub-models were developed to estimate potential effects of pinniped predation on adult Chinook survival from the mouth of the Columbia River to Bonneville Dam. One module was created to determine whether there was a consistent chronological order to arrival times of distinct spring/summer Chinook populations. Another examined how ocean and riverine conditions affected arrival time. A third module examined how environmental factors affected fish travel time between the Columbia River mouth and Bonneville Dam. The last module estimated mortality rates of each population over the course of the adult migration period.

Each submodel incorporated biological and environmental statistics and variables to estimate parameters. Additional or different statistics other than those reported were tried (and rejected) before determining the most suitable models. Consequently, flexibility exists to incorporate new statistics or factors into each model. Proponents used the Akaike Information Criterion (AIC) to measure the relative quality of each of their models. If new statistics were added, it is assumed that AIC methods would be repeated to determine model suitability. In summary, the data sources used in the models appear to be appropriate, care was taken to evaluate the relative quality of competing models, and models are constructed so that new statistics can be added and tested for their contribution to the explanatory power of the model.

6. Treatment and communication of assumptions and uncertainties

In some ways, the report is preliminary and does not fully address data sources, robustness to violation of some assumptions, demographic effects (potential for compensation or depensation), and evolutionary effects of differential predation of pinnipeds on spring/summer Chinook salmon. For example, proponents should be more explicit about where and how pre-2012 survival data were obtained and used. Small sample sizes in the tag-recapture study (and other data sets) are an important limitation, and this should be explicitly addressed with

regards to impact on analysis and the assumptions that small sample sizes necessitate (i.e., constant variances). In short, this report should “stand alone” with regards to data, assumptions, and interpretations such that reviewers and readers can reasonably assess the validity of conclusions.

Some assertions were not well supported. For example, mortality due to handling and tagging is presumed to be equal in all years, without discussion of how variable mortality might affect estimates. Small sample sizes necessitated simplifying assumptions like constant year effects across populations and constant variances within populations across years, but discussion was limited on robustness to violation of these assumptions.

7. ISAB Recommendations

- A. The proponents should investigate how small sample sizes affect assumptions that need to be made and conclusions drawn from the models.
- B. They should also specify how many cohorts were released and when they were released to help illustrate how well the entire migration period was covered by the mark-recapture study. It would be helpful to provide some explanation of how stock identity will be determined when adult PIT tagging is not done. For example, DNA samples from a proportion of adults could be collected as they pass over Bonneville Dam to obtain information on stock composition in lieu of PIT-tag information.
- C. One predictor of in-river survival is the log-transformed 7-day running mean number of pinnipeds hauled out at Astoria. However, predation efficiency of pinnipeds could vary by location in the lower river. For example, predation efficiency might be relatively high just downstream of Bonneville Dam. The proponents should consider total counts or just counts of California sea lions at Bonneville in the mortality model.
- D. Additionally, the overall abundance of adult salmon in the river may influence prey selectivity of pinnipeds. Was adult abundance (as estimated by BON counts) considered as a possible factor in the survival model? Additionally, they should consider the abundance of alternate prey, such as smelt or shad.
- E. The Hosmer-Lemeshow Goodness-of-Fit Test was used to see if the model developed for in-river mortality fit the data. The number of groups used to pool the data is typically 10 in these analyses. However, the number of groups can affect p -values in this test. Were different group numbers tried to confirm goodness of fit?
- F. The ISAB also recommends some specific areas for future development of the study and implementation of results in life-cycle models:
 - i. Apply the results to existing life-cycle models, as recommended by the authors and [ISAB 2016-1](#) (Predation Metrics Report) and evaluate the risk of extinction

caused by pinniped predation and tradeoffs between fishing mortality and this predation mortality and the risk of extinction.

- ii. Extend the model to include parameters for marine mammal predation on adult salmon and steelhead in the Columbia River Plume. Explore spatial variation in predation pressure in the plume and lower river.
- iii. Investigate relationships of fishing and marine mammal predation on adult salmon. It is well known that seals and sea lions feed preferentially on salmonids caught by hook and line and in commercial and research net fishing gear.
- iv. Investigate relationships of forage fish density and marine mammal predation on adult salmon and steelhead survival.
- v. Develop methods to investigate marine mammal predation on the juvenile freshwater/estuary/early ocean life stage.

Chapter 6.b. Avian predation management effects

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1. Goal

There are two goals for this section: (1) evaluate impacts of reduced avian nesting habitat on East Sand Island on fish predation, and (2) determine whether compensatory mortality can be reliably detected.

2. Key model findings

Management actions reduced Caspian tern and cormorant nesting habitat to one third of its 2010 area by 2016. Although the method was not described, the authors used a Bayesian estimate that combines PIT-tag detections on East Sand Island, detection rates for the tags, and deposition rates. The authors concluded that reducing nesting habitat indirectly reduced avian predation on focal salmonids at East Sand Island. The paper presents a straightforward analysis to estimate effects of reductions of nesting habitat on predation proportions of focal salmonids. Estimated proportions of smolts consumed by birds on East Sand Island were reduced by as much as 50% for 7 of 8 stocks (sockeye, fall Chinook, spring Chinook, and steelhead from the Snake and upper Columbia rivers) examined over the six-year time series. No detectable changes were observed for Snake River sockeye, but only two years of pre-management data were available, which may have limited power to detect pre- and post-management trends in this species.

In the second part of the chapter, the estimated proportion of sockeye and Chinook consumed are small enough that compensatory mortality is “hidden” by the noise in the data. Conversely, predation proportions for steelhead appear to be large enough that a more refined analysis looking for compensatory behavior is warranted.

3. Progress toward addressing ISAB recommendations from 2013

In 2016, the ISAB released a Predation Metrics Report ([ISAB 2016-1](#)) that recommended approaches to measure the effects of predation on Columbia River Basin salmon and steelhead. The authors cite the ISAB report regarding prey selectivity but did not use recommended approaches.

4. Applicability to management decisions, alternative scenarios, and adaptive management

Management actions were effective in directly reducing bird nesting habitat, and the authors concluded that reducing nesting habitat indirectly reduced avian predation on focal salmonids at East Sand Island. These results, however, cannot be generalized to the entire system. It is

possible that bird predation simply became more intense elsewhere in the system. This section indicates that similar analyses at other colonies are in progress. The ISAB looks forward to the larger-scale and systemwide analysis of fish mortality from avian predation. If the predation ratio was converted to a “per bird” basis, then some estimates of total bird predation from all colonies may be possible.

While the results presented in the report are interesting, the question of compensatory response still needs to be addressed to properly evaluate whether reductions in avian predation are improving SARs. Integration of avian predation rates (or survival to invulnerable size) into life-cycle models offers one approach to account for variation in mortality rates and whether or not compensation is occurring. This section would benefit from additional modeling (e.g., multiple colonies) and development and evaluation of scenarios relating to managing avian predation.

5. Compatibility with best available data and flexibility to incorporate new data

The analysis of predation proportions uses sound statistical methods and should be continued. It could incorporate additional information such as energetic needs of the birds in a straightforward fashion. Table 6B.1 is a good summary of the effectiveness of the management program in reducing predation rates for some salmonid stocks. However, integration of avian predation into a life-cycle model that accounts for other sources of mortality and potential compensation will be crucial to better understand effects of avian predator control ([ISAB 2016-1](#)). This was not done in this section, and it was difficult to evaluate how well the models could be expanded into an integrated life-cycle model.

6. Treatment and communication of assumptions and uncertainties

This was a high-level summary of work conducted and does not include an in-depth discussion of assumptions and uncertainties. There are other methods to estimate compensation based on returns of marked fish (as discussed in the [ISAB 2016-1](#) report) but feasibility of these methods to estimate compensatory effects was not discussed in this chapter.

7. ISAB Recommendations

- A. Convert proportional consumption estimates to a “per bird” basis and extrapolate to other islands to get a rough estimate of total proportion of the salmonid populations consumed by avian predators.
- B. Plan and implement a simulation study to investigate the level of compensatory behavior that is detectable given changes in avian predation and inter-annual variation in SARs.
- C. Develop and evaluate scenarios on management of avian predation throughout the Basin and impacts on the fish populations. In 2016, the ISAB released a Predation

Metrics Report ([ISAB 2016-1](#)) that recommended approaches to measure the effects of predation on Basin salmon and steelhead. The section authors cite the ISAB report regarding prey selectivity but did not use any of the recommended approaches from that report. These recommended approaches need to be evaluated to determine if they are feasible for the evaluation of bird predation on salmonids.

- D. Explicitly incorporate and integrate avian predation proportions into life-cycle models. Treatment of the issue of compensatory effects is crucial to integrating predation into the life-cycle model. If compensation is not explicitly treated, a simple linear response to intensity of avian predation will be erroneously obtained and this may misinform managers about the benefits of controlling avian predators.

Chapter 6.c. Incorporating food web dynamics into life-cycle modeling

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1. Goal

The goal of this section is to describe a model that incorporates biotic interactions with fish responses to physical habitat in a food web model that is then linked with a life-cycle model for spring Chinook salmon to estimate size and number of smolts in the Methow River. The ultimate intent of the food-web model is to evaluate impacts of management actions and environmental conditions on freshwater productivity (i.e., food-web dynamics and performance of specific food-web members).

2. Key model findings

The Aquatic Trophic Productivity (ATP) model is a dynamic mass-balance food-web simulation model that mechanistically models the food web and performance of food-web members (i.e., fish, aquatic invertebrates, detritus, periphyton) in response to physical habitat conditions, riparian vegetation conditions, and marine nutrient subsidies delivered by adult salmon. This food-web model is linked to the freshwater portion of a life-cycle model to simulate the effects of changes in freshwater conditions on Chinook salmon survival and abundance. The linked models predicted 88 smolts/adult, a 25% survival for smolts migrating through the Columbia River from the mouth of the Methow River and past Bonneville Dam, and average smolt size of 9.8 g. The predicted values for the smolt/adult ratio and percentage survival were underestimated compared to empirical and Comprehensive Passage Model estimates, respectively, but average smolt size was similar to measured data.

3. Progress toward addressing ISAB recommendations from 2013

Considerable progress has been made with the food web model and linkage to a life-cycle model since the last report, and proponents were successful in creating a clearer and simpler description of their model with much more detail than in the 2013 report. The approach is impressive and appears well-thought out, making good use of literature and information from studies in a region where location-specific data are not available.

However, this section still did not have sufficient detail to provide an adequate review of the modeling approach without gathering information from other reports or resources referenced in the chapter. In particular, it was unclear how simulated changes in riparian vegetation conditions and in-stream physical habitat conditions drive changes in the food web that, in turn, affect growth, survival, and abundance of salmon. Some background on the model, currently provided in section 2a, would have helped to build better context and allow for a

more detailed review. A key problem is that although the authors described the food web (ATP) model and life-cycle model in some detail (although there are many details not described), they presented only a few results in a two-panel figure so that most predictions cannot be evaluated.

In 2013, the ISAB recommended providing “more evidence for the conclusion that salmon have a net negative effect on periphyton production,” and “more detail on fitting data with Ricker model.” However, neither recommendation was addressed in this section. The ISAB recognizes that it may be difficult to address these issues in the high-level summary presented in this section.

4. Applicability to management decisions, alternative scenarios, and adaptive management

The proponents argue that their model will be useful for management application, but the model is not yet sufficiently developed to do this. They state that “the model is not intended to produce precise predictions or forecasts of fish populations, but rather to capture the important processes assumed to be at play in an explicit, model-based framework” (p 12). Therefore, it is unclear from this report how knowledge gained from this modeling work will improve management. For example, does the model show that more focus should be placed on floodplain restoration that supplies energy to the food web, rather than on instream habitat structures that may have unknown benefits for juvenile salmon survival?

Linking meso-scale food web processes with fish growth and condition, standing stocks, and abundances of focal species would be an important achievement. It would permit detailed prioritization of management activities such as habitat restoration, and suggest improvements to monitoring and adaptive management programs. An important step forward is to identify key milestones that must be met such that the model could inform management decision making. It is also important to address uncertainties introduced by linking this ATP model to the life-cycle models, especially with respect to model validation and compounding of uncertainties.

5. Compatibility with best available data and flexibility to incorporate new data

The combined ATP model and life-cycle model would, in theory, allow predicting how salmon and other species would respond to a wide variety of changes in management, climate, disturbance, and other factors from the most basic first principles of ecology—that is, constructing an entire food web and then resolving the effects of that on salmon life history. However, this requires substantial data from many sources, presumably of varying quality.

If it is possible to combine the models effectively, even at a level that allows only comparison of alternatives (rather than matching empirical data exactly), then it would be highly useful as a comparison to other models that do not incorporate the trophic basis for fish production and abundance. While complex, the overall model can be continuously improved with new and

improved data. The incorporation of the trophic basis for salmon production into our understanding of the salmon ecosystem would be a major accomplishment.

The approach uses literature-reported values and equations to apply the life-cycle model approach, which seems like a good approach. However, a lot of detail is missing. For example, what is the currency to evaluate whether restoration has been successful in a food web context? Is there dynamism in the model that relates to flow conditions and other drivers? What sort of scaling issues do these researchers expect? How are decomposition, transfer, and assimilation rates determined? The importance of these factors is not clear and sensitivity analysis is warranted.

6. Treatment and communication of assumptions and uncertainties

The model is complicated and includes interacting submodels and parameters. Thus, it is difficult in any short treatment to adequately address assumptions and uncertainties. The Results and Discussion section describes inconsistencies that raise broad concerns about the accuracy of the model. Discrepancies between model predictions and empirical observation could confuse the reader rather than providing a high-level summary of the model efficacy as the proponents intended. The model appears to predict weight of salmon through smolting fairly well, but not migration timing. Overall, too few results were presented to evaluate model predictions.

The brief text is mainly about assumptions and data sources, not about uncertainties. The chapter indicates that the model can predict trophic dynamics, at least of juvenile salmon, in the Methow River, which is an achievement, but it needs more comparisons with empirical studies for validation. In addition, there is likely to be considerable uncertainty in extending the model to other river systems, but this is not discussed.

A thorough assessment of assumptions and uncertainties would require more detail on what parameters are used to adjust the model, and what their values were set at for the results provided. This information was not described clearly such that reviewers could identify what “knobs” are used to adjust the model. The proponents stated their intent to do sensitivity analyses, but it is unclear how those would be done and used to inform food web modeling and coupling with life-cycle models. For example, would the sensitivity analysis be done on the ATP model, the life-cycle model, or both? Would mortality values in Table 2, and alpha values in Table 1 be investigated with a sensitivity analysis?

Additional reference to be considered:

Tunney, T.D., S.R. Carpenter, and M.J. Vander Zanden. 2017. The consistency of a species' response to press perturbations with high food web uncertainty. *Ecology*. doi:10.1002/ecy.1853

7. ISAB Recommendations

- A. The organization of this section is much improved compared to the 2013 report, but more complete detail on the modeling is needed to allow more complete evaluation. In particular, the authors do not report the mechanisms by which changes to instream habitat or riparian conditions affect the food web and life cycle of salmon. In addition, they presented few results (only a two panel figure) so that model predictions cannot be adequately evaluated against empirical data.
- B. Justifications and explanations of the modeling approach described in Chapter 2a should be included in this chapter, so that it can stand alone.
- C. The food web modeling effort is promising, but the many model components need validation before it can be widely used to judge the effects of restoration or changes in flow or temperature or ocean conditions on salmon populations. Examples of how the model would be used to assess the effects of restoration or changes to environmental conditions are also needed.
- D. Identify key milestones that must be met such that the model could inform management decision making.
- E. Develop some predictions and address uncertainties based on well-designed sensitivity analyses and validation with empirical data.
- F. Address scaling and non-independence issues associated with integrating 1 km habitat sections to an entire watershed and applying the approach to other watersheds.

Chapter 7. Simple Population Model: Using integrated population models to evaluate natural and anthropogenic risk factors for Pacific salmon

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1. Goal

The goal of this new investigation is to evaluate the use of integrated population models (IPM), which have rarely been used for Pacific salmon, for evaluating salmon population resiliency and risk of extinction. A key benefit of IPMs is that they account for measurement and process errors, and this can improve the precision and accuracy of parameter estimates. In this application, the investigators examine the degree of density-dependent compensation of spring/summer Chinook salmon from the Snake River Basin and examine population resiliency and risk of quasi-extinction compared with estimates based on a traditional approach (i.e., run reconstruction).

2. Key model findings

Data from 24 spring/summer Chinook salmon populations over a ~60-year period were modeled using routine run reconstruction (RR) methods and compared with the IPM approach that accounted for measurement and process error. The IPM approach indicated that the salmon populations were less productive and less constrained by density dependence at low abundances compared with results of the RR models that did not account for error. In other words, declining abundances when abundance was already low did not lead to as much of an increase in productivity (compensation) based on IPM compared to when error was ignored in RR models.

A key finding is that the probability of extinction is considerably higher when measurement error is modeled and accounted for via an IPM. The authors state that the IPM can be adapted to other life stages where data exist (e.g., juveniles) and to the evaluation of risks associated with pinniped predation and fishery harvests. The key implication is that some salmon populations may be at greater risk of extinction than previously thought.

3. Progress toward addressing ISAB recommendations from 2013

In 2013, the ISAB recommended that the modelers:

- 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.

The 2017 modeling effort is completely different from the 2013 effort by these investigators. The new effort considers density dependence, but it does not yet discuss specific actions related to habitat restoration as a means to reduce density dependence (Recommendation 1). The new analysis does not yet estimate spawning levels spring/summer Chinook salmon need to sustain productive populations in each watershed, but it probably could be used to do so (Recommendation 2). The model currently does not address the effects of hatchery salmon on the productivity of natural salmon. The new effort does state that the IPM approach can be adapted to other species and other applications in the Columbia Basin, including harvest management and predator impact analysis. The authors should also identify if other life-cycle modeling efforts by NOAA scientists should adapt the IPM approach. Under what situations is the IPM approach best suited, and for which is it inappropriate?

4. Applicability to management decisions, alternative scenarios, and adaptive management

The Integrated Population Model described in this study has rarely been adapted to Pacific salmon. The model provides a state-space modeling approach for estimating uncertainty (measurement versus process error), leading to new estimates of intrinsic productivity and capacity of the populations that are important to management decisions about ESA-listed salmon. The model should provide reliable estimates of credible intervals as long as the process model is well specified.

In this study, accounting for measurement and process error led to reduced productivity (and compensation) at low abundances, less resilient salmon populations, and higher risk of extinction. The investigators note that the model can be adapted to other life stages and scenarios including salmon harvest management and evaluation of pinniped predation on viability of spring Chinook salmon. As model development incorporates more complex processes, e.g., inclusion of parr, smolts, etc., the model should perform well with reliable data, and it can impute data when data are missing. This model application did not incorporate adaptive management, but it seems possible that the modeling results could be used to inform adaptive management decisions and the model can be refined as more data or information become available.

5. Compatibility with best available data and flexibility to incorporate new data

The empirical statistical model appears to be using the best available data for spring/summer Chinook salmon in the Snake River Basin. The model appears to be a powerful and flexible

method that is compatible with best available data and can readily incorporate new data. The authors note that the model can borrow information from data-rich populations to help inform information on data-poor populations. A discussion of whether this could produce biased results would be useful.

The previous review ([ISAB 2013-5](#)) mentioned the potential impacts of changing data collection methods on the spring/summer Chinook model. More discussion of this issue would be worthwhile. Is there any evidence that measurement error has increased or decreased over time?

The investigators mention that some life-cycle models assume that Chinook salmon spending 3+ years in the ocean have a survival rate of 0.8 per year based on Ricker (1976). The ISAB agrees that investigators should not assume constant 0.8 annual survival for older Chinook salmon because there is very little, if any, information to support this partitioning. The assumed annual ocean survival rate of 0.8, i.e., ocean mortality rate of 0.2, for older age groups of Chinook salmon can be traced back to Major (1984), who cites Ricker (1976), but this value was not reported by Ricker (1976).

6. Treatment and communication of assumptions and uncertainties

If age composition of returning adults is known (with some measurement error), as is typical when brood tables are developed for stock-recruit analyses, it is not clear why recruitment age is parameterized or why survival and maturation probabilities need to be specified (Page 7). For example, it is not clear how equation 5 (and equation 8) considers what we know are factors influencing age at maturation, such as growth, gender, and the fact that additional mortality occurs among fish spending additional years at sea. How well does equation 5 (and equation 8) predict known age of each population?

The investigators state that the model makes no assumptions about the age structure of hatchery-origin adults because there are few age data for hatchery salmon. However, the Snake River Compensation Program has estimates of age composition of hatchery (and wild) spring Chinook salmon for many stocks, e.g., Tucannon River, Salmon River, Imnaha, Clearwater River, Powell, etc. Furthermore, there is considerable information showing that hatchery male Chinook salmon mature at an earlier age than wild male Chinook salmon.

It is not clear why age composition of adult hatchery salmon is needed for the model because the model should be focusing on recruitment from natural spawners (natural origin and hatchery origin fish that spawn in nature). Estimates of p_{HOS} are used to subtract hatchery-origin returns from total fish spawning in the river. It does not appear that the model is attempting to account for spawner age as part of the recruitment analysis (older females produce more eggs and larger eggs), especially given that the oldest age group (age 6) is excluded because it is rare (in reality, these big fish can produce many progeny).

The IPM quantifies measurement versus process error, and measurement error seems to be much greater than process error. What types of measurement error were most important? In recent years, when hatchery production has increased, does it contribute significantly to measurement error? If so, given the IPM results indicating measurement error can mask risk of extinction, does this mean that hatchery strays, which affect accuracy of recruitment estimates, lead to higher risk of extinction in those systems with hatcheries than previously estimated?

The investigators note that the IPM model “did a good job of capturing the historical dynamics of Snake River spring/summer Chinook populations (examples shown in Fig. 1).” For plots of recruits per spawner, many of the observation points and 95% credible intervals were beyond the model’s predicted intervals, and model residuals were often biased in one direction for successive years. Please discuss. Also explain why R/S is not considered an observed quantity whereas spawner counts that also involve multiple calculations and expansions are considered observed quantities. The final report, or an appendix, should show plots for each of the populations rather than just 3 of 24 populations. This information may be important for individual populations and watersheds.

P. 14. What does it mean that "Observation error in spawner abundance was greater (posterior mean and 95% CI of σ_{obs} : 0.67, 0.63-0.72) than the unique process error in recruitment (σ : 0.25, 0.21-0.30)"? Process error of recruitment seems to be low because overall recruitment was correlated among the populations. What is the observation error in recruitment? Please clarify the assumptions underlying estimates of process versus observational error.

Figure 2 shows that maximum recruitment (capacity) tends to be slightly higher for the IPM versus RR model. However, capacity is reached more slowly with the IPM versus RR model, indicating less compensation and less population resilience in the IPM model. Figure 1 shows that R/S is typically higher for the RR model (orange points), implying that spawner density in Figure 1 is typically less than 5 per ha, since R/S is less for the IPM when density is below 5 per ha. To clarify Figure 1, the authors might consider standardization of the units (e.g., spawners per ha) or present both. For 2C, the authors might show R_{max} in standard rather than log units. A plot of R/S versus spawners would help readers recognize the compensatory effect of reduced spawners on increased R/S, which is a key issue when comparing the IPM and RR findings.

In Figure 2, is it realistic to have some R_{max} densities (fish per ha) that are so low, e.g., ~0.01 to 1 fish per ha? Alternatively, some populations seem to have very high R_{max} densities. It would be worthwhile to discuss these seemingly unique populations, including the relationships with habitat conditions. How do these estimates of intrinsic productivity and R_{max} densities compare with more robust spring/summer Chinook populations in other regions? Do these parameters seem reasonable?

The predicted future simulations (no harvest, no supplementation) have very wide credible intervals that span the range of past observed values, but the median response seems to approach an R/S of 1, i.e., replacement (Figure 2). Given the wide prediction intervals, are the model predictions useful? Additional discussion of these findings would be worthwhile. Figure 5 is an important contribution to this discussion because it indicates additional mortality (e.g., harvest) would cause many populations to decline.

One of the arguments for the IPM models is that they deal better with assumptions and uncertainties. On page 3, the text states that IPM models “fully capture all of the uncertainty in the data” (underlining added for emphasis). As the mantra goes, “all models are wrong” because they must simplify reality, so this statement should be qualified, perhaps to specify what data in the IPM models are fully explained. Nevertheless, the authors have made a good case for how IPM models are able to deal with uncertainties that traditional RR models are not as able to represent.

7. ISAB Recommendations

This chapter was well-written and organized. Recommendations and questions are listed below for consideration by the investigators. We recognize that some recommendations may be beyond the scope of this chapter. Additional suggestions are described above.

- A. Ricker models typically provide lower estimates of intrinsic productivity, leading to lower optimal harvest rates and higher spawning escapement goals in managed fisheries, compared with Beverton-Holt (B-H) models. For this reason, some scientists have recommended the use of the Ricker model when setting conservation harvest policies even when overcompensation is not present. Would the findings presented here change much if a Ricker model was used instead? How might the risk of extinction change if a Ricker model was used, given that a Ricker model is viewed as a more conservation-based model?
- B. The implications of accounting for measurement error in the stock-recruitment analysis seem to be substantial. The text stated that “Observation error in spawner abundance was greater (posterior mean and 95% CI of σ_{obs} : 0.67, 0.63-0.72) than the unique process error in recruitment (σ : 0.25, 0.21-0.30). However, overall recruitment process error was dominated by the shared cohort effect.” More discussion on how well the IPM model estimated observation error and how well the B-H model fit data at low spawning abundances would be useful, e.g., in the region where spawner density per ha was less than 5.
- C. Consider the discussion of measurement error effects on density dependence by Hilborn and Walters (1992) and Walters and Ludwig (1981) when evaluating stock-recruit curves, and explain whether the IPM analysis is consistent with these findings. They note that measurement errors make recruitment appear to be less affected by spawning

stock, leading to optimum harvest rates that are too high and spawning escapement goals that are too low. Bias will be greater when the range in spawning stock is relatively small (p. 287 of Hilborn and Walters 1992). Walters and Ludwig (1981) state, “if density dependence is weak, the effect of observation errors is to overestimate the amount of density dependence. This leads to overexploitation. On the other hand, if density dependence is strong, then observation errors lead to underexploitation.” The chapter seems to imply that accounting for measurement error will consistently lead to lower productivity. Is this correct?

- D. Evaluate the effect of hatchery spawners on productivity and capacity, and the effect of hatchery spawners on the risk of extinction given that hatchery spawners likely contribute to measurement error. Do the findings suggest that hatchery salmon have lower productivity?
- E. Estimate spawning escapement values that lead to maximum recruitment using both B-H and Ricker models (assuming you also evaluate the IPM using a Ricker model). Figure 2c shows this in log density units, but absolute values would be useful in a table along with population name and recent data on current spawning abundances. To what extent is R_{max} being achieved by natural and hatchery-origin spawners? This analysis would be very informative for evaluating the effect of pinniped predation on spring/summer Chinook salmon (Chapter 6a). For example, effects of predation may be minimal if spawning abundances lead to R_{max} .
- F. Further explain how well the model captures age structure of these Chinook salmon, assuming it is using modeled values rather than observed values to construct brood tables. Provide original and modeled brood tables for each population in an appendix. Include numbers of hatchery origin fish in the spawning escapement.
- G. The text states a very high coefficient of determination (0.85) between the log of observed spawner numbers and those estimated by the IPM, shown in Figure 1. What is this telling us beyond the fact that the two series are highly correlated? Is the unexplained variation due to both observation error and process error?
- H. While the chapter is well written, a more thorough discussion of assumptions, uncertainties, and potential pitfalls in using and interpreting the results of IPM would be useful. To what extent might the prior distribution for capacity pull the asymptote up or down? In equation 7, each population is partially pooled with other populations (via the ϕ -term) so that information is borrowed from other populations. Please discuss errors in variables that now depend on the errors in measurements for this population plus errors in other populations.

- I. Briefly discuss situations and/or specific salmon populations in the Basin where the IPM model should be used instead of the existing model. Should it be used instead of other models in this life-cycle model report?
- J. Continue efforts to adapt and apply the IPM to evaluate effects of pinniped predation and harvest mortality on viability of salmon populations. Continue to develop the IPM that includes the juvenile life stage.

8. References

- Hilborn, R., and C.J. Walters. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall, Inc. New York.
- Major. 1984. Yield Loss of Western Alaska Chinook Salmon Resulting from the Large Catch by the Japanese Salmon Mothership Fleet in the North Pacific Ocean and Bering Sea in 1980. North American Journal of Fisheries Management 4A:414-430.
- Ricker, W.E. 1976. Review of the rate of growth and mortality of Pacific salmon in salt water, and noncatch mortality caused by fishing. Journal of the Fisheries Research Board of Canada. 33:1483-1524.
- Walters, C.J. and D. Ludwig. 1981. Effects of measurement errors on the assessment of stock-recruitment relationships. Canadian Journal of Fisheries and Aquatic Sciences. 38: 704710.

Chapter 8. Intermediate Model: Building a state-space life-cycle model for naturally produced Snake River Fall Chinook Salmon

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1. Goal

The goal of this chapter is to describe the current status and structure of a two-stage life-cycle model for Snake River fall Chinook. The model is designed to track how adult abundance affects juvenile production and how juvenile life histories and abundance affect the production of adults.

2. Key model findings

Substantial progress has been made on the model since 2013. Details on the structure, assumptions, and uncertainties associated with a two-stage state-space Bayesian life-cycle model are presented. A description of an ideal two-stage life-cycle model for Snake River fall Chinook is first described. Then the authors' current life-cycle model is contrasted to the ideal condition. Additions and refinements to the model based on this comparison are described. Results from an initial version of the model are presented to indicate the types of retrospective and predictive outputs the model will provide once it is completed.

One of the important findings from these preliminary outputs was the realization that juvenile abundance estimates made at Lower Granite Dam were underestimating the abundance of natural origin juveniles. This in turn was inflating smolt-to-adult survival (SAR) values. New methods of determining juvenile abundance were developed to correct this bias and are now being applied to previously collected data. Other planned refinements include developing methods that can be used to generate estimates of uncertainty in adult abundance, the prevalence of different juvenile outmigration strategies, and age and sex of returning adults. The authors also anticipate adding components that will allow modeling the effects of separate spawning aggregates, hydrosystem operations, and ocean conditions on the population dynamics of Snake River fall Chinook salmon.

3. Progress toward addressing ISAB recommendations from 2013

In 2013, this model was characterized as being under development, and the ISAB recommended that the modelers:

- 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.

Progress since 2013:

- 1) Significant improvements in model development have been made, and the current version of the life-cycle model is undergoing further improvements. It does not appear, however, that sensitivity analyses have been performed. No analyses were done to provide a weighting of the importance of input data. Because the authors rely on data provided in other reports, often with no estimates of uncertainty, they must assume the extent and form of the statistical distribution of that uncertainty. The distributions that they use follow standard procedures in the literature.

Once the model has undergone additional refinement, a sensitivity analysis is highly recommended. Such an analysis would help determine which types of data may need further monitoring efforts. For example, would it be worthwhile to have more accurate estimates of (1) pHOS, (2) hatchery versus wild smolt abundances, (3) age-0 Chinook counted at Lower Granite Dam that overwinter in the river rather than entering the ocean at age-0, and (4) Chinook salmon harvested in fisheries in Alaska, British Columbia, Westcoast, and in-river?

- 2) Data gaps have been identified. For example, the potential bias in underestimating natural juvenile abundance and the consequent overestimation of SARs is clearly stated. To resolve this issue the proponents have developed a parametric method for estimating daily detection of PIT-tagged juveniles. This appears to fill an important data gap. However, there are still issues in assessing the number of naturally produced fish because they are indistinguishable from unmarked hatchery fish. This results in strong assumptions in estimating uncertainty in adult abundance and in outmigration strategy, components fundamental to model predictions. We urge the authors to consider collecting DNA samples on unmarked juveniles collected at Lower Granite Dam. Parentage-base-tagging is being applied to all the Snake River fall Chinook hatchery fish. Thus, such samples could be used to assess the reliability of the new method being used to estimate the origin of juveniles collected at the dam. Collecting similar DNA samples from unmarked adults intercepted at Lower Granite Dam should also be contemplated as they could be used to help estimate the abundance of hatchery and non-hatchery origin fish.

- 3) The model has been implemented in the runjags package of R using three MCMC (Markov Chain Monte Carlo) chains. The authors used the Rubin-Gelman diagnostic to evaluate convergence, which is often a major issue when using MCMC simulations. The model is now properly coded and can be readily modified. Standard, well-tested Bayesian methodology is being used.

4. Applicability to management decisions, alternative scenarios, and adaptive management

Outputs from the preliminary model showed its potential use in management, and once the model is fully developed it will be a valuable tool. Relationships between the abundance of natural origin females and the production of naturally produced juveniles showed clear signs of density dependence. For instance, the predicted median female spawner abundance level producing maximum recruitment (S_{max}) was estimated to be around 7,300 fish (with 95% confidence intervals of 4,910 – 10,621). Due to abundant returns of natural-origin adults in 2010-2014, S_{max} was exceeded and juvenile production from naturally spawning females decreased. A noticeable decline in productivity, the number of juvenile out-migrants produced per female, was also observed as female spawner numbers increased. The authors stress that these observations should be viewed with caution as other factors may be contributing to these trends. Nevertheless, when fully fitted and operational, the model could be used by managers to help establish biologically based escapement levels and to evaluate the degree of overcompensation at high spawning levels (i.e., fewer adult returns with increasing parent spawners). Additionally due to its two stage structure, the impacts of management actions such as adjusting flow, river water temperatures, and modifying passage structures on juvenile and adult survival can be predicted to help guide adaptive management.

5. Compatibility with best available data and flexibility to incorporate new data

Because the authors are using a state-space Bayesian framework coded in R and JAGS, the model is flexible and will be able to incorporate new data as it becomes available. Several examples were used to illustrate how new information could be inserted into the model. In one instance, sea surface temperature was used as a covariate to see if this factor influenced SAR values. The model revealed that as winter sea-surface temperatures increased, SAR values decreased. In another instance, the importance of juvenile out-migration timing on productivity was modeled. This covariate disclosed that productivity declined as the fraction of the juveniles that emigrated late in the season increased. Similar analyses with different covariates appear to be possible.

6. Treatment and communication of assumptions and uncertainties

The comparison of the ideal two-stage space model with what has been developed to date revealed many of the challenges and uncertainties of the current life-cycle model. Additional assumptions and uncertainties were described and in many instances plans are being made to address them through additional modeling or retrospective data analyses. Detailed equations

were provided to guide a reviewer through the model framework. Nevertheless, knowledge of the use of hierarchical Bayesian frameworks and implementation using the MCMC samplers was assumed.

7. ISAB Recommendations

- A. Continue to develop measures of uncertainty or observation error on (1) juvenile passage by origin and life history type, (2) adult abundance, (3) age and sex of adults, and (4) ocean and in-river harvest. Perform a sensitivity analysis to help delineate the factors that have the greatest impact on model performance. Consider collecting DNA samples on unmarked juveniles collected at Lower Granite Dam. Parentage-base-tagging is being applied to all the Snake River fall Chinook hatchery fish. These samples could be used to assess the reliability of the new method being used to estimate the origin of juveniles collected at Lower Granite Dam. We also encourage the authors to incorporate data after the 2014 adult return year (e.g., 2015) because these data should now be available.
- B. Please provide a brood table for natural Chinook salmon that was constructed from this effort and include the proportion of females in the return and numbers of smolts by age produced by the spawners.
- C. Use the model to (1) estimate spawning levels leading to maximum sustained adult returns, (2) evaluate the effect of pHOS on salmon productivity, (3) estimate potential additional harvest if “surplus” hatchery fish could be efficiently harvested, i.e., hatchery fish beyond what is needed to fully seed spawning areas.
- D. When future revisions to the model description are produced, please address the following questions:
 - i. Adult female Chinook salmon typically have different ocean age proportions than male Chinook salmon, because, for example, females tend to delay maturation. Gender is included in the model (equation 10). Does this model allow different age structure for each sex? If not, to what extent might this affect results?
 - ii. Clarify equation 11. Why are harvest and broodstock collection applied only to natural spawners and not hatchery fish?
 - iii. On page 12 it is stated “In the observation model, we use estimates of uncertainty where available and assume values for the magnitude of observation error where estimates of uncertainty are unavailable.” Please contrast this approach with the IPM model approach where uncertainty was modeled.
 - iv. Page 13 - Why is no observation error assumed for hatchery adults at Lower Granite Dam whereas error is assumed for natural origin at Lower Granite Dam?

- v. Page 14 - Clarify how brood return statistics were calculated for years 1992-2003. What information was known for these years and what information was not known? The point is that if some key information needs are known, such as dam counts and harvests of natural Chinook, then uncertainty will likely be less than if everything is unknown.
- vi. “We modeled SAR as a function of sea surface temperature during the winter following ocean entry of subyearling juveniles.” Why ignore sea surface temperature for yearlings? Why not consider other key variables used in the ocean model, while recognizing that fall Chinook will use nearshore marine and ocean habitats differently than spring/summer Chinook (Chapter 3)?
- vii. What are the SAR trends for hatchery and natural adults?
- viii. Smolts per spawner decreased as the fraction of age-1 migrants increased, as expected (p. 22). However, a more important question is whether overall life-cycle productivity declined as the fraction of age-1 migrants increased. Also, how is productivity associated with ocean age?

Chapter 9.a. Grande Ronde spring Chinook populations: Juvenile based models

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1. Goal

The goal of the modeling effort was to update life-cycle models for four Grande Ronde River basin spring Chinook salmon populations. Three years of additional data were incorporated into the models for the four subbasins. Data were particularly lacking previously for the Upper Grande Ronde population. The models were used to explore scenarios for habitat restoration, hatchery supplementation, pinniped predation, and ocean conditions and climate change.

2. Key model findings

Inclusion of the three additional years of data improved model performance in the upper Grande Ronde, though changes to the fitted relationships for summer parr to spring migrant survival for the Catherine Creek, Minam, and Lostine River populations were slight. The populations continued to exhibit strong density dependence. The authors have less confidence in the spawner to summer parr function for the Upper Grande Ronde population and are considering alternative approaches to deal with the limited data.

Based on model predictions, habitat restoration actions in targeted high and moderate priority reaches would reduce short term quasi-extinction risk modestly and increase average abundance over the long term. Without hatchery supplementation, populations would fall below the quasi-extinction threshold. Increased pinniped predation beyond current rates would increase extinction risk, and stock productivity would have to be approximately doubled to achieve a high persistence probability. While actions related to habitat restoration, hatchery supplementation, and pinniped predation could reduce short term quasi-extinction risks, future adverse changes in ocean or other environmental conditions would require substantial additional actions to meet long-term abundance objectives.

3. Progress toward addressing ISAB recommendations from 2013

In 2013, the ISAB recommended that the modelers:

- 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.

In response to Recommendation 1, the document addresses the sparse data for the Upper Grande Ronde River Chinook salmon population. The investigators state that data quality for the Upper Grande Ronde watershed is lower than the other three watersheds, and so findings for the Upper Grande Ronde are less certain. Four years of new data were added for each population in the Grande Ronde life-cycle model. The Upper Grande Ronde and Catherine Creek populations both show very strong density dependence during the spawner to summer parr stage and the parr to smolt stage. Aquatic habitats in these subbasins have been degraded more than in the other Grande Ronde watersheds.

Statistical analyses of factors responsible for recruitment of parr per spawner were improved, and the report discusses the effect of trap placement on the analysis. The investigators considered the small number of fry that emigrate below the trap and note that these fish apparently have high mortality, largely in response to water withdrawal in that reach. The investigators have not been able to directly include environmental co-variates in the stock-recruit model, but they have been considering changes to temperature and flow that stem from habitat restoration based on information from CRITFC and ISEMP contractors. Several restoration scenarios involving the spawner to parr and smolt stages were evaluated.

4. Applicability to management decisions, alternative scenarios, and adaptive management

The models are informative and provide useful tools for analysis of alternative scenarios, management decisions, and use in an adaptive management process. The models considered scenarios related to habitat restoration actions, effects of hatchery supplementation, pinniped predation, and ocean conditions. However, one of the major weaknesses of the chapter is the overly simplistic description of scenarios. The authors do not clearly explain how scenarios were developed, how regional and local decision-making processes influenced the specific scenarios, or how future scenarios will be developed. The policy or management actions being modeled need to be defined clearly and in detail. Though several scenarios are related to regional strategies, the document needs to stand alone and provide adequate information for the reader to understand the specifics of the actions or conditions represented in the scenarios.

The management actions associated with the scenarios are represented in the biophysical models, but the coupling with human systems is weak. The scenarios do not account for changes in human populations, either in the study basins or downstream reaches. Future human impacts in terms of land use, fishing pressure, hydrosystem demands, sea lion hazing, water quality and quantity, or other factors are not incorporated into the model or its evaluation.

5. Compatibility with best available data and flexibility to incorporate new data

The team has used data from their watersheds and regional sources effectively. They have developed new studies to provide critical data and demonstrate a willingness to strengthen the model with new information. The model update incorporated four more years of data. The

model is flexible enough to incorporate scenarios of habitat restoration, pinniped predation, and ocean conditions.

6. Treatment and communication of assumptions and uncertainties

The chapter is written as a brief update of the 2012 model rather than as a more comprehensive, standalone report. While the model and findings are useful, the report should be written as a comprehensive formal report before broader dissemination. A more formal approach would have facilitated communication.

Assumptions and uncertainties were typically described and uncertainty was incorporated into the models, but a systematic description of assumptions and uncertainties was not provided. It was difficult to completely understand the model findings because the text was limited and labels for the various model scenarios were not defined in several figures. Graphs, tables, and acronyms are incomplete and difficult to understand (see Figure 7 as an example).

The authors considered climate change and how the models could be applied to explore the implications of climate change on fish populations. Another major strength of the modeling is the temporal adjustment of responses to restoration actions. Several of the life-cycle models in other chapters assume that restoration actions are immediately effective, which is impossible and makes the outcomes of the models far less credible. The Grande Ronde modeling effort developed a plausible phased representation of habitat recovery, an approach that should be used in other life-cycle models.

7. ISAB Recommendations

- A. The report should be revised to communicate its findings more clearly. The models appear to be highly applicable to management decisions under different scenarios, but the report is in draft form and is not understandable by a fish biologist who is not intimately familiar with the region and analyses, or by a broad audience who may ultimately use it.
- B. The modeling approach should be described thoroughly. The chapter should stand alone without requiring the reader to refer to previous reports or publications.
- C. The report should clearly explain how scenarios are developed and how regional and local decision-making processes influenced the specific scenarios or will influence future scenarios. Specific values used in the scenarios should be reported and the assumptions, definitions, and sources of the scenarios should be provided.
- D. Graphical and tabular presentation of results should be clear, complete, and easy for the reader to understand. Symbols and acronyms should be clearly explained. Details of the model or scenarios should be explained in the text rather than figure captions.

- E. The report should provide a discussion of the results. The chapter should provide guidance for decision makers and managers to help them understand the context and limits for using these results in management decisions and the potential future applications of the model in management decisions.

Chapter 9.b. Wenatchee River spring-run Chinook salmon life-cycle model: hatchery effects, calibration, and sensitivity analyses

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1. Goal

The authors state that the goal of their model is to “develop a comprehensive tool to help us understand the potential population level responses to a range of diverse management actions and environmental change.” To accomplish that goal an age-structured stochastic life-cycle model that tracks population abundance at five life stages across diverse habitats is being assembled. Whenever possible, demographic information obtained from Wenatchee spring Chinook are being used to parameterize the model. The model is designed to evaluate the effects of inadvertent hatchery domestication, climate change, hydrosystem alterations, harvest rates, pinniped predation on adults, ocean conditions, and freshwater rearing habitat attributes on the population dynamics of Wenatchee spring Chinook. Additional components that largely deal with interactions between habitat conditions and juvenile capacity and productivity are under development and will be added to the model in the future.

2. Key model findings

Three areas of model development, hatchery effects, calibration, and sensitivity analysis have occurred since 2013 when the model was last reviewed. Research performed in the Wenatchee River has shown that the relative reproductive success of hatchery fish is lower than that of natural origin spawners. These results were used to develop the model component that estimated the domestication discount that was applied to naturally spawning hatchery origin fish. The calibration procedure was initiated to adjust model outputs to observed values of smolt and adult abundance, but as noted below, the calibration process may need revision. The goal was to identify parameter values that generated simulated data with characteristics similar to observed data. Factors included in the calibration were parr-smolt survival, ocean survival after the first year at sea, upstream survival of adults, and pre-spawning mortality. A “global” sensitivity analysis showed that model outputs were most sensitive to three factors: ocean survival after the first year, parr-to-smolt survival, and adult survival through the hydrosystem. To illustrate the current capability of the model, the authors presented the results of seven scenarios where alterations in either management or environmental conditions were simulated. In these model runs, hatchery production, in-river harvest rates on adults, incubation and juvenile rearing habitat conditions, spill rates through dams in the mainstem during the smolt migration, pinniped predation on adults, and ocean conditions were varied.

3. Progress toward addressing ISAB recommendations from 2013

In 2013, the ISAB recommended that the modelers:

- 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).

Progress since 2013:

- 1) The goals and objectives of the model are clearly described. Additionally, the model is being developed so that the effects of alternative management options can be estimated through simulation. Thus, it has the potential to be an important adaptive management tool. Some discussion was directed toward how the model could be used to help make decisions leading to the delisting of Wenatchee spring Chinook salmon. This discussion could be improved by indicating how trends or trajectories in smolt and adult abundance will be incorporated into an adaptive management cycle.
- 2) Not much attention in the model is currently being paid to specific factors that influence egg-to-smolt survival (except for the hatchery progeny discount) through outmigration. Consequently, model utility is limited to actions governing hatchery management and predator control. Yet spawning and rearing areas are the focus of substantial habitat restoration in the Wenatchee subbasin. To rectify this deficiency, additions to the model are now being made so that functional relationships between habitat restoration actions and fish survival can be estimated. This effort is at a preliminary stage. However, the authors indicate that they plan to model relationships between habitat conditions and egg-to-fry survival, juvenile capacity, life-history diversity, and over-winter survival. It also seems fruitful to consider incorporating elements from food web and metapopulation models into this part of the life-cycle model.

A scenario that examined the possible effects of floodplain and side channel reconnection and road removal on juvenile capacity was presented. Improvements to habitat were modeled indirectly by using assumed changes in capacity produced by work done by Bond et al. (2017). We encourage the authors to continue this work. It has the potential to offer insights on possible effects of climate change and various habitat restoration actions.

4. Applicability to management decisions, alternative scenarios, and adaptive management

This model has the potential to be useful to managers. The effects of a single management alternative or the combined effects of a suite of management alternatives can be simulated by

the model. These simulations are designed to help expose the expected relative impact of one or more management actions on the abundance and extinction risk of Wenatchee spring Chinook. However, many of the parameter values are fixed (see Table 5) with only a few parameters “estimated” through an ad-hoc calibration procedure. Consequently the true uncertainty in the output is likely understated and the Quasi Extinction Risk is certainly understated. Comparisons with a “no action” alternative should also be included (e.g., in Table 7) if possible. Given the many assumptions and fixed parameter values, the outputs should be used in a qualitative fashion only, e.g., to rank actions in terms of effectiveness. It would be difficult to assign a quantitative gain to any of the scenarios that were performed.

Similarly, it will be difficult to use the model in its current stage of development for adaptive management, because it will be unknown whether a failure to see a predicted response to a management action in the real world is due to stochastic variability or to inadequacy of the life-cycle model.

5. Compatibility with best available data and flexibility to incorporate new data

The proponents indicate that a significant amount of research and monitoring has taken place in the Wenatchee subbasin, particularly in the Chiwawa River. Thus, whenever possible, the model has been parameterized by time series data obtained from studies conducted in the Wenatchee subbasin. The model appears to have the flexibility needed to incorporate new information. For example, the proponents indicate that the life-cycle model structure is flexible enough so that it can accommodate either time series or averages as input data. At present, the authors are planning on integrating new data into their model from numerous sources. Data from ISEMP/CHaMP, Bond et al. (2017), USGS flow gauge readings, and the results of studies on species composition, abundance, distribution, survival, and growth conducted by state, federal, tribal, and other entities, for example, are being sought for potential use in the model. The goal for expanding the current model is to identify the habitat and ecological factors that drive the survival and movement of juvenile and adult Wenatchee spring Chinook. The authors should consider, however, that egg-to-smolt transitions may be complicated by microhabitat partitioning and other factors. Additionally, some environmental variables appear to be confounded which could suggest correlations when in fact they do not exist. Other challenges will be to incorporate fish-habitat, metapopulation, and dynamic food-web models. Future reports should be explicit in how this will be done and tested.

6. Treatment and communication of assumptions and uncertainties

Each component of the model is well explained. Details are also provided on the calibration method and sensitivity analyses. Model assumptions are described along with candid explanations of uncertainties. A few questions, however, still need to be addressed. For example, parameter values that are fixed in the model are shown in Table 4, but it was not clear where these values were obtained and how applicable they were to Wenatchee spring Chinook.

Moreover, comparison between simulated and observed abundances was not done. This made it difficult to know how well the model fit observed data. Because many parameters are fixed, uncertainty in many of the results is likely understated. This caveat needs to be clearly communicated to the reader. The risk of over-parameterization caused by the incorporation of multiple and possibly confounded data sets and sub-models also needs to be discussed. An overfit model will likely generate spurious predictions and therefore affect model outcomes and recommendations to managers.

7. ISAB Recommendations

- A. Substantial progress has been made on the model since it was reviewed in 2013. The main recommendation is to continue on the course undertaken and to prepare a manuscript from these efforts for a peer-reviewed journal, when this first stage of modeling is complete. Some components of the model and the approaches taken will need further explanation and development, however, before a manuscript can be prepared. For example, Table 4 shows that water transit time and upwelling are used as covariates [presumably for $s_3(t)$] but this is never described. The fertility functions $F(t)$ and the management choices for number of hatchery or natural origin brood stocks also need to be described with equations showing how these were implemented.
- B. Additionally, the calibration procedure should be revisited. It appears that only four parameters were “estimated” from the calibration procedure (Table 2) with the rest of the parameters fixed at certain values as shown in Table 5. As it stands, the calibration procedure may not perform as intended. The use of the empirical likelihood forces parameter values towards the mode of the empirical likelihood function rather than trying to fit observed data.
 - i. In general, there are two ways in which models of this type can be calibrated. First, a Bayesian state-space formulation (the underlying stages of the life-cycle model) is linked with an observation model (the time series data) as has been done in other chapters. The calibration/estimation process compares the observed and actual time series of observations (and not the marginal distributions of the time series). This process would then automatically generate posterior samples that match the distribution and autocorrelation of the observed data.
 - ii. The second method is known as Approximate Bayesian Computation (ABC) and is similar to what was done in this report. In ABC, a measure of discrepancy between the summary of the model output and the summary of the target data is used to weight the model inputs. For example, a goodness-of-fit measure comparing the distribution of the modelled abundance to the distribution of the observed abundances could be such a discrepancy measure. A major difficulty with the ABC approach is combining several discrepancy measures. The use of ABC discrepancy

measures rather than the state-space approaches must be thoroughly justified as the model time-series of, e.g. abundance, is never directly compared to the observed time-series.

- C. The authors indicate that fish-habitat relationships developed by ISEMP/CHaMP, NWFSC, and WDFW will be incorporated into the Wenatchee model. We encourage them to make this a priority. Such data will help parameterize the portions of their model that examine the potential effects of habitat restoration actions on egg-to-smolt survival, an area that needs further development.
- D. Although the upper tributaries of the Wenatchee River are in relatively pristine condition, their capacity to support juvenile spring Chinook appears to be restrained by three factors: (1) the narrowness of the valleys which limits the availability of floodplain and side channel habitat, (2) cold water temperature regimes that limit annual growth, and (3) nutrient poor habitats that likely restrict the prey resources available to juvenile salmonids. The first two factors are not easily changed. However, local managers believe that nutrient enhancement either by the addition of salmon carcasses or by carcass analogs might offer a possibility of increasing juvenile capacity in these habitats. When nutrients should be added, where they should be added, what appropriate loadings might be, and whether cold temperatures limit their effectiveness are some of the questions that the Wenatchee life-cycle model could potentially address if it were expanded to address these questions. Such an expansion would provide managers with estimates of the potential benefits derived from various levels of nutrient enhancement and help determine if this tactic is one that should be pursued.

Chapter 9.c. Themes of climate impacts on Columbia Basin salmon: Multiple limiting factors, correlation in climate drivers, and cumulative life cycle effects

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1. Goal

This paper develops a life-cycle model to predict the persistence of nine populations of spring/summer Chinook salmon in the Columbia Basin under scenarios of climate change. Population vulnerability was tested under three scenarios of scaled temperature change and three scenarios of hydrologic flows, based on data obtained from global climate models and previously reported or published data. New data on the relation between sea surface temperature and ocean survival, stemming from Chapter 3, were added to improve model performance.

2. Key model findings

The paper presents a complex age-based matrix population model wherein climate-driven rates of survival are impacted by potential future temperature and flow projected in global climate models. When the model was tested against historical data (the testing set), model output fell within 84% of the confidence intervals to demonstrate that it would adequately model current trajectories of the nine Chinook salmon populations, but it is unknown whether the model predicts well under future regime shifts that fall outside of historical data. Key model outputs included parr-smolt survival as a function of temperature and flow, and smolt-to-spawner survival.

The nine Chinook salmon populations responded with some differences to climate-driven changes in river flow and temperature. Under the most likely climate projections into the second half of this century, all populations went extinct. Life-stage specific survival changed with warming: parr-per-spawner and parr-to-smolt survival increased because of reduced density-dependent effects and faster growth, whereas survival during upstream migration decreased. Sea-surface temperature had the greatest effect on survival, with survival during the marine phase of life being the main factor affecting quasi-extinction risk. The model was not entirely complete when presented to the ISAB and some findings are preliminary.

3. Progress toward addressing ISAB recommendations from 2013

In 2013, the ISAB recommended that the modelers:

- 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).

The authors have addressed several issues that were raised by the ISAB in 2013. However, work remains to include uncertainty in projections of fish abundance. The model is fit to spawner-abundance data, without considering the uncertainty in the estimates from published reports. The model structure appears to be a modification of an age-based matrix model (page 4) and the equations that are presented (page 5) do not include error terms. Although matrix models have been useful in identifying vulnerable life stages, they have been less useful as a predictive tool for estimating population abundance because they do not readily incorporate uncertainty.

The model relies largely on statistical relationships between climate variables and components of the life-cycle model. Modeled values of juvenile production have been compared to independent results from PIT-tagged fish (item 3 in the above list). However, Figure 5 appears to show that the new data points are consistently over or under-predicted values in each stream. In contrast, Figure 7 (page 23) shows that the model fits recent data well in 7 of the 9 cases, but for Loon Creek and Camas Creek there is little evidence of density dependence and those poor fits propagate through the results. The authors should provide an explanation for this apparent disparity.

Developing the exact biological mechanisms that drive the statistical relationships at each stage of the life-cycle model is likely difficult because of the lack of data at this level. The authors have a very brief discussion of why potential biological mechanisms are not used (item 2) on page 18. The authors acknowledge that they lack mechanistic models to explain how flow and temperature alter survival of parr-to-smolts, an important component of the life-cycle model. In the interim, they rely on “robust” statistical correlations. However, many models that initially fit well have fallen apart as more data are added to the model over time and the correlations disappear.

The authors have obtained parr-to-smolt survival data from PIT-tagged fish as requested in the previous ISAB 2013 review. The model results based on these data provided notable differences in estimated spawner abundance and thus, quasi-extinction risk. To fit the model better, they added a new factor to the model, a modified s_3 (see matrix, equation 1, p. 4) that altered the early ocean survival of smolts based on comparing mean observed spawner counts with PIT-tag estimates. This is an important disparity that should be explained. The ISAB wonders if the

lower survival of PIT-tagged fish may reflect tag loss and tag mortality, as described by Knudsen et al. (2009) and other studies.

There does not appear to be any additional data on other covariates requested in the last ISAB review (item 4).

4. Applicability to management decisions, alternative scenarios, and adaptive management

The model output seeks to provide the probability of extinction risk under several scenarios of climate change. Figure 9, page 27, indicates that the largest populations face the lowest extinction risk. Because the model predicts that all populations will be extinct by mid-century, it is important to be sure that the model is sufficiently developed to support such an important prediction. The model (very briefly discussed—see below) seems to fit the last 20 years of data reasonably well (see Figure 8, page 24). However, the model is so complex and so briefly explained that the reader has to assume that the model represents parsimony over the existing data even in face of an extra term introduced to improve the fit of the PIT-tag data that predicts subsequent adult abundance.

The results in Figure 9 are very worrisome: under current conditions three of the nine populations already have more than a 50% chance of quasi-extinction. Are these results in accordance with any other estimates of extinction risk for these populations? The results seem to provide at least a rank ordering when alternatives are presented, but sometimes (e.g., three populations in Figure 10) the results are opposite to what is expected and little discussion is provided in the paper as to why this occurred. The key message in Figure 11 is that although climate change may be “beneficial” by producing some juvenile fish, ocean conditions will be so poor as to wipe out all the gains. Any fish that do make it back as an adult also have a small reduction in survival while migrating up through the hydrosystem. So ocean conditions are the big driver—something which no management actions can be taken to improve!

What isn't considered in this type of model is the buffering against risk that might come from connectivity between populations, even if small.

5. Compatibility with best available data and flexibility to incorporate new data

It can be argued that the authors are using the best available data. For example, they are using current Global Climate Model predictions and the available data on PIT-tag survival estimates. However, these data may not be adequate to provide reasonable projections because of the uncertainty of the precipitation data, the integration of daily model components with monthly June temperatures at Bonneville Dam, the short time series of PIT tag-based survival estimates, patterns in the residuals, and such.

From the pattern of residuals, it is clear that the process model is incomplete. The presentation on page 4 shows that they are using an age-based matrix model, which has fixed parameters for survival (s), fecundity (F), and proportion mature (b). One limitation of a strict matrix model

approach is that density dependence is not included in the parameters. For example, if food is scarce in the ocean and that results in less growth, then fecundity may be decreased, but F is a constant in these models. So even though they can make the models more complex, they may not be making them more flexible.

This model is very complex and the technical details are either in other papers or not presented in this paper. However, the model seems to fit the last 20 years of data reasonably well (see Figure 8) with the caveats that the credible intervals in the figure are very wide.

The model is currently using a Leslie-type matrix approach, and some revisions would be needed if life-stages were separated. It is not clear how the relationship between each individual stage and climate data was fit, but these models can be made flexible enough that additional variables could be added.

6. Treatment and communication of assumptions and uncertainties

Many assumptions are made in the fitting process. Some of these are presented in other reports and not given in this paper. Other assumptions (e.g., assuming temperature and flow values for the entire Salmon River rather than using stream-specific values) are briefly described in the chapter with some justification. How sensitive are the results to assuming a common value for temperature and flow for all populations rather than population specific values? There must be some data available to show the congruence between the basinwide values and the population specific values to justify using the basinwide values. This issue was raised in the previous review but was not addressed.

Other assumptions (e.g., to match projections with empirical data, an extra multiplier s_3 was created [p 10]) are presented with minimal explanation to the development or estimation of the adjusted s_3 . Presumably Figure 8 shows that the problem is fixed, but it is uncertain whether the fit seen in Figure 8 is all due to the $s_3(t)$ term. The requirement for this term would seem to indicate a systematic bias in the model fitting for marine survival, and the cause of this potential bias is not addressed.

We were unable to track uncertainty and how error was included beyond just a differences in simulated discrete populations. Equations are presented with little indication of error or discussion of its distributional form. On page 2 the authors mention a 2006 publication that states that there is autocorrelation in marine survival, s_0 , but the matrix model does not include autocorrelation as it steps through time. Without reading their previous papers, we cannot tell how they are calculating likelihoods. It would help to have more detail and equations.

It would help if the authors tracked uncertainty that propagates through the model. Figure 8, page 24, shows that the model predictions do fit previous observations, albeit with very wide credible bands (on the logarithmic scale). Managers would not have much faith in such predictions given the order of magnitude in the uncertainty.

The paper states that it relied upon ocean survival data developed from PIT tags and a survival model developed by Burke et al. (Chapter 3). Burke et al. excluded both hatchery fish and transported fish, leaving a relatively small sample size of wild-origin fish that spanned only 14 recent years (2000-2013). These details should be discussed here, along with data used to model the juvenile life stages. For example, did modeling of in-river juvenile life stages rely upon both hatchery and wild Chinook salmon, and if so, how might hatchery fish affect the findings given that juvenile hatchery Chinook salmon likely use habitats differently from natural salmon? Survival at sea is reported to be the dominant factor influencing extinction risk, but the model is built upon a fairly limited time series of survival at sea that may reflect only a small component of future climate change. The Burke et al. survival models also incorporated Julian date of migration, which was not discussed here.

7. ISAB Recommendations

- A. The authors have done a great deal of work on this paper and are to be commended. However, if they seek to publish it, more explicit detail on the modeling is needed. It is currently too terse for a journal submission. More details of the individual steps of the life-cycle model are needed. The original model was published almost 10 years ago, but this paper appears to be a substantial revision so that the original publication may no longer be relevant.
- B. Additional details on how the climate scalar works in practice are needed, similar to those given in the [presentations](#) to the ISAB at our June 23, 2017 meeting.
- C. Provide additional details on the PIT tag data used as discussed above.
- D. As noted in the paper (pages 4 and 10), values for other parameters need to be updated given the new marine survival estimates that are being used. We encourage the investigators to incorporate variable age at maturation and associated fecundity in the model. Faster growth in freshwater and/or the ocean can lead to earlier age at maturation, which likely leads to higher overall survival (less risk of mortality while spending an additional year at sea) but lower fecundity. These tradeoffs are an important aspect of Chinook salmon life history and how Chinook salmon respond to changing environmental conditions and to density dependence.
- E. Obtaining valid estimates of quasi-extinction probabilities depend on the model incorporating all sources of variation. This model has many areas where there is uncertainty about parameter estimates and the authors have often included variability during the projections. The authors should do a sensitivity analysis to see which sources of uncertainty have the most impact on the estimated quasi-extinction probabilities to ensure that uncertainty is properly accounted for and is realistic for these important parameters.

8. Reference

Knudsen, C., M. Johnston, S. Schroder, W. Bosch, D. Fast, and C. Strom. 2009. Effects of passive integrated transponder tags on smolt-to-adult recruit survival, growth, and behavior of hatchery spring Chinook salmon. *North American Journal of Fisheries Management* 29:658–669.

Chapter 9.d. ISEMP/CHaMP life-cycle models – Entiat, John Day, Lemhi, habitat actions

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1. Goal

The Integrated Status and Effectiveness Monitoring Program (ISEMP) together with the Columbia Habitat Monitoring Program (CHaMP) developed a life-cycle model to assess the effects of habitat restoration in Columbia River tributaries on salmon and steelhead. This chapter presents the model and its applications in three watersheds: the Middle Fork John Day River for steelhead, Entiat River for Chinook salmon, and a preliminary model for Lemhi River Chinook salmon.

The model is a stage- or age-structured life-cycle model based on Beverton-Holt population dynamics that can incorporate temporal, spatial, and pure stochasticity in input parameters, as well as correlation among input parameters. The model can also account for multiple sites, as well as fish movement among sites if data are available.

A key aspect of the model is the use of mechanistic models based on microhabitat selection by juvenile salmonids to optimize their net rate of energy intake (NREI models). The NREI models were coupled with hydraulic models to estimate the carrying capacity of habitats for juvenile salmon (i.e., their abundance) under specific conditions. This capacity, along with estimates of productivity (recruits/spawner) based on empirical survival estimates, provided the parameters needed for the Beverton-Holt model for these life stages. A different model, termed the Habitat Suitability Index model, was used to estimate carrying capacity for adult spawners. Both juvenile and adult capacity were then extrapolated to entire river networks based on models relating it to temperature, primary production, channel and valley geomorphology, and riparian vegetation.

When fully developed, the models were used to estimate the effects of various habitat restoration actions (e.g., placement of large wood, restoration of riparian vegetation that shades streams and reduces temperature, restoration of channel and floodplain complexity, reconnection of tributaries for spawning and rearing) on salmon life cycles and viability of their populations.

2. Key model findings

Models were developed for three different basins and two different species, so the key findings are addressed separately.

Middle Fork John Day (MFJD) River Steelhead model – the model was parameterized and used to assess two main scenarios of restoration of riparian vegetation to reduce water temperature (a “best-case” scenario and one based on riparian restoration to 2008, once mature) and one scenario of addition of large wood structures to increase habitat complexity. Key assumptions include (1) that the ratio of juvenile steelhead survival at temperatures estimated under current and restored conditions is the same as the ratio of freshwater productivity (smolts/spawner) under these temperature regimes, and (2) the improvement in survival of juveniles with vs. without large wood additions is the same as the estimated increase in abundance of juveniles.

The model outputs for escapement and total life cycle productivity (spawner-to-spawner) had similar ranges as empirical data, but the means were substantially lower than the empirical data, causing concerns about accuracy of the model. A key finding was that lowering temperature under the “best case” scenario of riparian restoration had the largest effects on increasing abundance (capacity) and productivity (smolts/spawner?), whereas the effects of current riparian restoration or large wood additions were similar and substantially less. However, all three scenarios reduced the quasi-extinction risk below the 10%-per-100-year threshold.

It is difficult to know the sensitivity of the model to key assumptions like those above, and many others, given the very large number of linked models and parameters. In addition, the magnitude of treatments (or their cost) may or may not be similar. Hence, a possible conclusion is that large wood additions can have important effects on capacity and productivity, especially if they can be produced through judicious riparian forest management. However, in this basin where temperature is on the brink of lethal levels (24-25 °C max summer temperature) and also influences nonnative smallmouth bass invasion (see Lawrence et al. 2014, *Ecological Applications*), management of riparian vegetation to increase shading could be more cost effective. The possible effects of both combined were not modeled, but could be.

Another key assumption not addressed is that juvenile overwinter survival is not influenced by addition of large wood structures that increase habitat complexity. Given that steelhead must survive two to three winters, large wood structures may have a greater effect as refuges during this key stressful period than as structures that provide optimal positions for summer foraging.

Entiat River Chinook salmon model – This model has the same structure as the one for the Middle Fork John Day, and was used to estimate effects of current and proposed habitat improvement actions in four segments in the lower river and a major tributary with different geomorphology. Estimated abundance for the Entiat River model was expanded to the watershed scale using a sampling design (GRTS design) rather than being based on models that related it to temperature and larger-scale riparian and geomorphic variables as in the Middle Fork John Day River model.

Key assumptions include that hatchery Chinook introductions and harvest in the ocean or rivers have minimal effects on the population dynamics, even though much is known about the fitness effects from hatchery introductions in the Wenatchee River, which is an adjacent basin.

The three scenarios evaluated included a baseline of no habitat improvement; those improvements already implemented (creating side-channel habitat—adding large wood and boulders); and those actions plus a 2% increase in Chinook salmon survival. This last scenario is based on empirical data showing that habitat structures increased overwinter survival (see previous model where this effect was omitted).

The model produced an estimate of spawner abundance below the actual values and did not reproduce the apparent increasing trend in spawner escapement (see Fig. 9) whereby the population met or exceeded the recovery target 2 or 3 years since 2000. All three scenarios predicted a high risk of extinction, although the third scenario (habitat improvement plus increased survival) reduced the risk somewhat. Nevertheless, extinction was still the most likely outcome under all scenarios. Overall, the relatively modest habitat improvements included in the model (although not all those conducted to date were included) are predicted to have little effect on reducing extinction probability of this population, even if they increase survival. This result is qualitatively similar to that predicted for the Middle Fork John Day River, where habitat restoration was projected to have modest effects.

Unfortunately, the model so far has been used to assess the effects of only a subset of habitat improvements installed to date, apparently owing to the intensive work required to survey stations and model these effects based on accurate digital elevation models (DEMs). More work is needed to model the remaining improvements.

Lemhi River Chinook Salmon model – the main focus of this model was to assess the effects of enhancing spawning and rearing habitat in the mainstem and reconnecting tributaries dewatered by diversions in their downstream reaches on private lands. Less data are available than for the other two basins, so only the freshwater portion of the life cycle was modeled (spawners, parr, and smolts to Lower Granite Dam). Future work is planned to “close the loop” and include the rest of the life cycle from smolts to subsequent spawners.

Data on adult escapement, summer parr abundance, and smolt abundance were modeled based on empirical data, using a Bayesian analysis, and used to fit Beverton-Holt models.

The two scenarios considered were the current situation and the increase in parr abundance (capacity) owing to reconnecting five tributaries during 2009 to 2012. Results showed that reconnecting these tributaries—despite increasing parr abundance (capacity) by an estimated 132,000 fish—would increase smolts per spawner by only 10% and with substantial uncertainty. Future modeling is planned to include the rest of the life-cycle of these salmon and incorporate spawner escapement numbers and age structure.

Overarching findings – A key finding across all three models appears to be that some habitat restoration efforts, such as additions of large wood and boulders in the Middle Fork John Day and Entiat rivers, and reconnecting tributary habitats in the Lemhi River, are estimated to have modest effects on fish abundance, survival, or productivity, and hence on population persistence, at least if implemented at the scale and scope modeled. Other restoration actions, such as “best case” riparian restoration in the Middle Fork John Day River, that could reduce water temperature below the 25 °C threshold over long river segments, are estimated to have much greater effects. This points to the value of these kinds of integrated life-cycle models for planning large and expensive restoration projects. The addition of relative economic costs of the scenarios, even if these were estimated relatively crudely, would make these models and the scenarios evaluated highly useful for managers.

3. Progress toward addressing ISAB recommendations from 2013

In 2013, the ISAB recommended that the modelers:

- 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.

The original report apparently addressed models only for the Lemhi River, whereas the current one describes models for three watersheds. It presents specific details on the models developed for each watershed, and the methods and results for specific scenarios relevant to management of listed salmonids in each one. Methods to include uncertainty and measure sensitivity are described for each model, although many more analyses could be considered. More work is needed in each basin, such as to include modeling of all habitat restoration in the Entiat River and to “close the loop” and include data on adult spawners in the Lemhi River. The models are useful to estimate the impact of management actions, but given the lack of fit noted below the findings must not be taken too literally.

Since 2013, several key papers from the CHaMP/ISEMP projects have been published (e.g., Bennett et al. 2016; Wall et al. 2016, 2017; McHugh et al. 2017) addressing in part the ISAB’s concerns about lack of peer review.

4. Applicability to management decisions, alternative scenarios, and adaptive management

The models are aimed directly at analyzing alternative scenarios relevant to management decisions in each river and hence could be useful for adaptive management. They now include the capacity to simulate complex fish behavioral responses to habitat restoration, flexibility in migration behavior of different steelhead life histories, and distributions in the river network. In

addition, the central model now links geomorphic and hydraulic models with energetic models (NREI) and habitat suitability models (HSI), and these, in turn, to restoration scenarios or actions. As a result, it has greatly improved the usefulness of the models to evaluate scenarios and help make management decisions.

Nevertheless, the use of NREI and HSI requires substantial amounts of empirical data. Several chapters in this report describe approaches for credibly representing these relationships or processes based on remote sensing or regional data, but it will remain challenging to accurately model fish responses at different spatial scales from reaches to watersheds and across the entire Columbia River Basin.

Specific concerns about applying the models include:

- a) A more thorough description of the approaches used to develop scenarios is needed, before exploring them with the model.
- b) The first two models used only 200 simulations (of which 20 were discarded for the “burn in” period) which implies that estimates of quasi-extinction risk (QER) have considerable uncertainty (on the order of at least 4 percentage points for 19 times out of 20) so that an estimated QER of 12% may not actually be different from the 10% target. Consequently, small changes in QER may be artifacts of the number of simulations run.
- c) As noted in the first model, the output of means from the life-cycle model (p. 14) is considerably lower than actual data for both escapement and spawner-to-spawner ratios. Consequently, estimates of QER may not be reliable. The impacts of changes in habitat are interesting, but the realism of the changes is unknown. How is this model better than simply asking the impact of a specified increase in capacity? In many cases, the latter (via a sensitivity analysis) may be more useful to managers to indicate the scope of changes (e.g. to carrying capacity) that would be needed to have a meaningful impact upon a population. Perhaps both approaches would be useful in conjunction.
- d) Because of the lack of fit for escapement and spawner-to-spawner ratios, it is unclear how useful these models will be in adaptive management. Suppose that the results from an action do not provide the anticipated effect. It would not be clear if this is a problem with the model or just stochastic variation. Overall, the basic framework of the life-cycle model is useful for ranking alternative scenarios but not for absolute predictions.
- e) The models appear to indicate that the modest habitat restoration done so far is not effective at increasing salmon abundance or productivity. However, the assumptions made about no effect of habitat on overwinter survival in the MFJD and the inability to model all of the habitat restoration actions in the Entiat call this conclusion into question to some degree. Likewise, it is unclear how the scope and costs of different

actions compare. For example, what was the real scope of wood additions modeled in the MFJD in terms of percentage of channel treated (this was unclear), and what is the cost of this work compared to the much larger scope of hypothetical systemwide riparian restoration that is estimated to alter temperatures markedly? The difficult part is estimating the type and amount of restoration actions needed to achieve the productivity and capacity targets.

- f) Eventually, more careful work is needed to include a full range of policy options (e.g., changes to fishing pressure, hatchery interactions, hydro, etc.) and combinations of different management actions.
- g) In the future, policy or management actions need to be defined very specifically, and include actions that are realistic. For example, for the MFJD, the T1 “best-case scenario” appears to be hypothetical and therefore may not be useful for policy analysis purposes.
- h) Ideally, biologists and biological modelers would work with socioeconomic scientists to calibrate even more complete models of coupled human-natural systems. Please see Programmatic Comments.

5. Compatibility with best available data and flexibility to incorporate new data

The models appear to be highly flexible and able to incorporate new data. In all three cases, the authors discussed the next steps they plan to integrate additional data or scenarios. Because there is little model fitting and most parameter values were extracted from the literature, when new data are available they can be readily incorporated. However, the steelhead model for the MFJD requires a tremendous amount of information and has many assumptions. How applicable is this approach to steelhead in other watersheds?

6. Treatment and communication of assumptions and uncertainties

These models include a very large number of submodels, each with many assumptions. The authors addressed various assumptions and considered the sensitivity of the outputs to some of them but not others. Several additional assumptions not addressed by the authors are described in the Key Finding section above, such as the assumption for the Middle Fork John Day River that additions of large wood would affect only summer rearing energetics but not overwinter survival.

Specific concerns about assumptions and uncertainties include:

- a) Extrapolation beyond the bounds of the parameters, whereby predictions are made about future outcomes using data collected in the past when conditions were different than those predicted for the future. For example, the scenarios involving temperature changes in the MFJD used the existing models for capacity vs temperature to extrapolate to the new thermal regimes (page 11) but this assumes that the existing

data provide sufficient information for the new thermal regime. Has this been validated?

- b) A brief but comprehensive explanation of the assumptions and uncertainties associated with the foraging and bioenergetics components of the Net Rate Energy Intake Model (NREI) is needed. Moreover, are the outputs of the model sensitive to NREI estimates, so that the huge efforts to gather data and model this metric are warranted, or would a simpler approach be sufficient?
- c) The life-cycle models are based on expected values and so do not include variability due to stochastic processes such as survival. For example, the Watershed Model User's Guide.docx (available from the web site) has details on the life-cycle model presented as a series of *R* statements and it appears that the expected number surviving to the next life-stage is always computed using expected values. This implies that the observed variability is likely too small and that the QER is likely underestimated.
- d) It was difficult to review the first two models (MFJD and Entiat rivers) because of a lack of detail on the actual life-cycle model and on which parts of the model are based on data versus speculation.
- e) A brief summary of the life-cycle model structure should be added to these reports so each report can stand alone and be complete.
- f) For models in the first two rivers, there does not appear to be any model fitting to data. Parameters are chosen based on published values and put together in a life-cycle model (which is never explicitly defined) and the model is run. The authors claim that the models seem to work but also note (page 14) that the model had a "lower central tendency" when compared to actual data. What was the cause of this apparent bias?
- g) The authors state (p 2) that correlation among the input parameter values will be accounted for, but never specify any details on how these are estimated. For example, how is the correlation in in-river survival and ocean survival estimated or specified? From the Watershed Model User's Guide.docx, it appears that a random effects model on the parameter value is used to enforce this correlation for a selected parameter set.
- h) Middle Fork John Day River:
 - 1) This model needs an equivalent of Table 4 from the Entiat River model showing the parameter values used and from where they were extracted.
 - 2) On page 8, it is unclear how steelhead "predictions" are translated into estimates of juvenile rearing capacity using a fish placement algorithm. Is this at the reach scale? Perhaps some of this is explained in Wall et al. (2016) and should be summarized here.

- 3) Benefits from riparian restoration can include increased insect production, inputs of organic matter and large wood. Addition of wood might change the thermal regime by causing more hyporheic flow and affect spawning habitat in addition to rearing habitat. How can these factors be considered in the model?
- i) Entiat River:
 - 1) Some of the parameter estimates (assumptions) used in the life-cycle model for the Entiat River seem unrealistic. For example, egg-to-fry survival appears to be high at 0.492. Research in the Chiwawa River suggests that a value of 0.20 to 0.25 is more appropriate.
 - 2) The habitat capacity/meter values also seem unrealistic. When spawner densities are low, redd sizes in spring Chinook can be up to 7 m², there will be spaces between redds, and not all stream areas are suitable for redds. Thus, the 309 eggs/meter value seems high.
 - 3) Territorial behavior in fry, parr, and yearlings also make the habitat capacity values/meter for each of those life stages appear high. For example, it is hard to envision that any habitat could support 13 yearlings per meter. These values should be validated by field work. The food resources capable of supporting those individuals may exist, but behavioral interactions would likely cause dispersion making the predicted capacities higher than they should be.
 - j) Lemhi River: In this model, parr capacity is essentially determined by the Bayesian prior (page 39) indicating that there was no information from the data to estimate this parameter. Is this owing to a lack of data or an indication that this parameter is non-identifiable given that none of the data points apparently have parr abundance values close to capacity? The model also simulates the effect of habitat reconstruction indirectly by increasing the median of the prior distribution (page 42) rather than a formal model as was done in the other two rivers.
 - k) In the Entiat and Lemhi rivers, Chinook capacities are estimated for both fry and parr life stages. Does the model consider migrant fry and parr, i.e., fish that leave the natal watershed? How? If not, how might this important life history strategy for increasing capacity affect model findings? Earlier NOAA chapters discuss parr and smolt migrants, the abundances of which are often density dependent. Also, fall parr migrations tend to be greater in smaller watersheds, as a percentage of the total population.

7. ISAB Recommendations

- A. Carefully define the meaning of all terms, especially capacity and productivity, in every case, so that there is no chance that readers will be confused. Without this, few readers will understand the models or the meaning of this substantial body of work.
- B. A brief summary of the life-cycle model structure should be added for each of the three models. See the specific comments above.
- C. Prepare a short paragraph explaining more comprehensively the basic premises of the NREI model, its assumptions, and how it has been validated and how successful this validation has been, based on Urabe et al. (2010) and Wall et al. (2016). This model is a key component of the life-cycle models described here, but many readers will be either uninformed about it or skeptical about its accuracy.
- D. Address key assumptions noted above for each model, such as two key assumptions described for the MFJD model: (1) that the ratio of juvenile steelhead survival at temperatures estimated under current and restored conditions is the same as the ratio of freshwater productivity (smolts/spawner) under these temperature regimes, and (2) the improvement in survival of juveniles with vs. without large wood additions is the same as the estimated increase in abundance of juveniles.
- E. In at least a qualitative way, compare the scope and cost of different scenarios, such as in the MFJD the hypothetical maximum restoration of the riparian zone versus placement of large wood in only some segments or at modest density. Also address how useful both actions together could be in reaching recovery goals.
- F. Include caveats such as that riparian restoration and wood additions have benefits beyond temperature and summer rearing habitat, respectively. Address how these benefits could be incorporated into the model.
- G. The life-cycle models described here require considerable data input, but many of these data are not available for other watersheds. Please address how these life-cycle models can be used to inform restoration actions to achieve recovery in watersheds where the data required are limited?
- H. In the future, these models should be used to estimate the increase in productivity and capacity needed to achieve recovery goals. These values will be useful to guide the types and amount of habitat actions needed to reach recovery (assuming factors not modeled remain constant).
- I. Despite the limitations, these models are an important first step in trying to estimate the effect of actual changes to the habitat. Work should continue, but much more model validation is needed, especially given the apparent bias in abundance and

spawner-to-spawner ratios seen in the model for the MFJD. It would be helpful to identify what sources of data are needed to fit the “missing parts” of the models so that studies can be established to collect this information.

Chapter 9.e. Yakima River *Oncorhynchus mykiss* populations

[View Chapter](#)

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1. Goal

The immediate goal is to better understand population dynamics of sympatric populations of resident and anadromous *O. mykiss* in the Yakima River. Ultimately, the goal is to produce an *O. mykiss* life-cycle model that can be used here and elsewhere in the Columbia Basin

2. Key model findings

A new approach to life-cycle modeling of *O. mykiss* is being developed to address stakeholder issues and alternative management scenarios for steelhead and resident rainbow trout in the Yakima River. Meetings with stakeholders are underway, and the model is being coded into R programming language.

3. Progress toward addressing ISAB recommendations from 2013

The authors appear to be addressing past ISAB recommendations as they continue to develop a life-cycle model that includes both resident and anadromous *O. mykiss*. The authors briefly review four different life-cycle models, all previously reviewed in 2013 (Chapters 2.5 and 3.4; text and citations nearly identical). They state that they will “integrate” the four models, which is a new approach, but no methods for model integration are provided. Funding from the Yakama Nation will allow them to continue with model development, and portions of the model that were originally in a Microsoft Excel spread sheet are now being coded in the R programming language.

4. Applicability to management decisions, alternative scenarios, and adaptive management

The authors are meeting with stakeholders to address these three issues. They list five scenarios that will guide their final development of the integrated model, but this is a work in progress. Among these are simulations of the response of Yakima River *O. mykiss* to (1) predicted effects of climate change, (2) new spill and flow regimes in the Yakima River and in the mainstem of the Columbia River, (3) newly opened habitat in the Manastash River and above Cle Elum Lake, (4) variation in ocean conditions, and (5) changes in avian and pinniped predation. Results from these and other model scenario runs are expected to guide management actions associated with the Yakima River Biological Opinion, Yakima River Integrated Water Resource Plan, and in the Climate Adaptation Plan for the territories of the Yakama Nation.

5. Compatibility with best available data and flexibility to incorporate new data

The authors seem to be keenly aware of existing data and the need to incorporate the best available data to parameterize their model. One of their main objectives is to be able to adapt the model as new data become available. A considerable amount of information has been collected on Yakima steelhead and resident rainbow trout over the past 25 years. Consequently within-basin data can be used to parameterize much of the new model.

In some cases, however, data from the Yakima subbasin may not be available. In that circumstance, it would be prudent to validate these inputs whenever possible. For instance, it is assumed that interbreeding rates of 25% are likely to occur between resident rainbow trout and anadromous steelhead. This value is based on observations made on steelhead spawning in two Olympic Peninsula streams. In both streams a temporal decrease in anadromous males over the course of a spawning season allowed some resident males to spawn with anadromous females. The authors' review does not state whether late spawning anadromous females in the Yakima River also face a scarcity of anadromous males. If so then this assumption may be reasonable, and, if not, it should be validated by examining extant data or via new fieldwork.

To produce a model that can be used elsewhere in the Columbia Basin, the authors recognize that their model will have to be flexible enough to accommodate environmental conditions and migration pathways that are idiosyncratic to the populations that are being modeled.

The ISAB appreciates the authors' desire to consider physiological factors driving the smolt decision window. The authors may be interested in a few citations listed in our editorial comments (see Appendix).

6. Treatment and communication of assumptions and uncertainties

The authors do a good job of communicating assumptions and uncertainties associated with the four life-cycle models. They are motivated to combine the existing models to reduce or take into account the assumptions and uncertainties contained in the individual models. After the model has been completed, they plan to parameterize the model with "known data" to confirm its ability to produce reliable outputs. Sensitivity analyses are also planned to understand which life stages drive variation in the expression of anadromy and residency in freshwater. Sensitivity analyses will be used to identify confounding variables that influence both the dependent variable and other independent variables. These steps will help determine what additional refinements might be needed in the newly crafted model.

7. ISAB Recommendations

The proposed approach of integrating components of four extant steelhead models and producing an integrated life-cycle model seems appropriate.

- A. Some clarification on a few issues would be helpful. Will Beverton-Holt recruitment curves be used to estimate survival between egg deposition and age 1, between age 1 and 2, etc.? Because strong density dependent effects have been observed while the fish reside in freshwater, it seems logical to use a Ricker recruitment model. Will possible effects of the kelt reconditioning program in the Yakima River be included in the new model? Do data exist to help estimate how environmental factors in the Yakima River influence pre-spawning mortality? Or will information from other basins be used to create a model component that can examine relationships between flow, water temperature, and other variables and pre-spawning mortality?
- B. Complete development, calibration, and validation of the integrated Yakima steelhead life-cycle model, and apply it to management and climate-change scenarios.
- C. Adapt the Yakima life-cycle model to a general model that can be used for other populations.

Chapter 9.f. Catherine Creek spring Chinook life-cycle model

[View Chapter](#)

1. Goal

The goal of this investigation was to (1) further develop a life-cycle model for Chinook salmon to assess restoration opportunities within the Catherine Creek and Upper Grande Ronde River watersheds, (2) modify the models to incorporate hatchery supplementation, and (3) use the models to assess Chinook salmon population responses to scenarios of land use, habitat restoration, hatchery supplementation, and regional warming.

2. Key model findings

The parameterization of the life-cycle model for spring Chinook salmon in Catherine Creek closely reflected stage-specific (i.e., freshwater vs. marine) and total life-cycle productivity. In spite of the complex sources of data and relationships, patterns of smolts per female spawner in the modeled dataset closely mirrors those in ODFW's 20-year sampling dataset.

Changes in juvenile carrying capacity in response to alternative habitat scenarios resulted in changes in abundance of natural origin adults. Scenarios that included maximum stream cooling without projected climate change effects exhibited 30-40% increases in spawner abundance. The scenario that included future climate change but no riparian vegetation restoration projected a 30% reduction in spawner abundance. The scenario that ceased all hatchery supplementation efforts after 20 years resulted in the rapid extinction of natural origin adults. The Catherine Creek Chinook population is apparently entirely dependent on supplementation from the integrated hatchery program, without which it will rapidly collapse (within 5 years).

3. Progress toward addressing ISAB recommendations from 2013

In 2013, the ISAB recommended that the modelers, "Prepare a more formal document that describes the model structure and how it can be used."

The document clearly and succinctly describes the model structure and output and clearly states the assumptions and limitations. The authors have produced three peer-reviewed publications that describe their models (Justice et al. 2017, White et al. 2017, and McHugh et al. in press) and explore Chinook salmon responses to alternative scenarios. This effort is a positive response to the 2013 recommendation by ISAB. The model structure and assumptions are described in Appendix A, but future application of their model will require additional details on model sensitivity, uncertainty, and limitations.

4. Applicability to management decisions, alternative scenarios, and adaptive management

The authors have demonstrated the utility of their models in recently published explorations of alternative scenarios of land use, fishery management, and climate change. The models are valuable contributions to management of these watersheds, and the authors could collaborate with the Grande Ronde Model Watershed to develop a formal and ongoing link to the adaptive management process for the Model Watershed Project. They developed several scenarios of restoration practices, land management, and climate change, which showed that potential restoration actions could increase adult spawners, no action would result in decreased abundance, projected climate changes would lead to substantially lower spawner abundance, and populations would be extirpated rapidly without hatchery supplementation.

The scenarios chosen were important to management and reflect topical issues for combating the effects of climate change. The models have substantial potential to address fishery management alternatives related to habitat restoration and hatchery supplementation. Additional model development will be critical to applying these models in future management decisions. The simulations are overly simple in the current form. The authors state this, but not strongly. It will be important to develop the models based on the nature of management decisions for which they are used (e.g., required level of accuracy, spatial detail, error or uncertainty, timeframe, related social processes and decisions). The model structure will allow that application and development, but additional model construction or modification will be required.

5. Compatibility with best available data and flexibility to incorporate new data

The authors used an extensive dataset and also explicitly address the importance of obtaining new data from stakeholders and incorporating it into future modeling. The data they are using are taken from current research and monitoring and appear to be the best available data for these simulations. In some cases, where there are no data (e.g., survival of the two parr strategies), the authors point out data gaps that need to be addressed if possible.

6. Treatment and communication of assumptions and uncertainties

Many simplifying assumptions were made, but these were explicitly stated and carefully detailed in the text and two appendices. They also suggested alternative approaches that might be used in the future. Sensitivity analysis of the model was not discussed or provided.

Several critical but unrealistic assumptions include:

- Overwinter survival is equal in both the tributary reaches and the valley reach
- Benefits of restoration are immediate (impossible) and time scales of changes are equal for all practices

- Future human populations, land use, water consumption, delivery of toxic substances, and other anthropogenic effects are the same as the present and do not change.

The investigators acknowledged the weakness of several of these assumptions. Future modeling efforts should address these weaknesses and provide more thorough description of the scenario details, assumptions, data sources, and the process that was used to develop them.

Only 100 simulations were run for each scenario. This is substantially lower than required to represent variation in most models, though more runs might not define the uncertainty better given that standard deviations in the input data were all in similar ranges. This may explain why the boxplots have similar quantile ranges. Also, the time period for the simulations was short, only 30 years. The authors should evaluate the variance in model outputs across a range of simulation intervals or present the results if such analyses have been conducted. Also, some important modeled variables apparently were input as deterministic quantities, such as capacity, fecundity, and smolt releases (Appendix A).

The time series density plots of natural-origin Chinook salmon returns to the Catherine Creek adult trap (Figure 3) exhibited little change in final abundance relative to starting abundance. While the mean or median abundance for the different scenarios were similar and had similar trends, their variance differed among scenarios. While variance is extremely important and is related to the risk of extinction, the minima for the different scenarios did not differ greatly over the 30-year simulations, and the only scenario that exhibited a greatly different standard deviation was *CLIM*. While this indicates that warming climate trends could have negative effects on Chinook populations, there is no explanation or discussion of why this scenario had low variance.

7. ISAB Recommendations

Overall, the authors conducted a well-planned life-cycle model iteration for the Catherine Creek population and provided clear guidance for taking the next steps to improve the model and further consider issues of management interest.

- A. Model performance should be assessed further. This would include sensitivity analyses, effects of numbers of simulations and time period for model runs, and additional validation based on empirical information from the watersheds. Human decision making and spatial and temporal variation in those actions should be evaluated in future scenario development.
- B. Model structure can include the improvements suggested by the authors and incorporate human processes either in the model or in alternative scenarios.
- C. The investigators acknowledged the weakness of several of their assumptions. Future modeling efforts should address these weaknesses (particularly the immediate full

benefit of restoration actions) and provide more thorough description of the scenario details and process that was used to develop them.

- D. We encourage the authors to put more mathematical details into the report or its appendix so that the simulation can be better understood. The report provides code, but it appears to be almost “pseudocode”, not true R code.

Chapter 10. Metapopulation: Assessing salmon spatial structure and metapopulation dynamics

[View chapter](#)

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1. Goal

The goals of this chapter are to (1) review the literature on metapopulation processes and how common they are among salmon populations, and (2) describe options for modeling these processes in the Columbia River basin at the scale of ESUs and MPGs to aid in planning for recovery of multiple populations of listed salmonids that are potentially linked by dispersal and subject to stochastic risks.

2. Key model findings

The modeling completed is described in two papers recently published, reported under “Phase 1 Research Completed.” The first showed that time series abundance of 24 populations in the Upper Columbia and Snake River ESUs of spring/summer Chinook salmon were influenced by the Pacific Decadal Oscillation, and dynamics were consistent within an ESU, thereby supporting the spatial structure of the ESU (Jorgensen et al. 2016). The second paper used a variety of data on dispersal among populations to show that, as in the first paper, the spatial structure matched ESU designations, but that lack of data or uncertainty in dispersal estimates had the strongest influence on results, more so than uncertainty in abundance estimates (Fullerton et al. 2016).

The authors present three research options for future modeling efforts to determine how spatial metapopulation processes (MP) might influence recovery planning: Research Option 1) use a set of existing population-level life-cycle models to determine whether a set of subpopulations can be viable without dispersal among them (no MP); Research Option 2) develop an integrated population model (as described in other chapters) for multiple populations simultaneously and test sensitivity of the viability of Major Population Groups (MPG) to dispersal among them (MP included); and Research Option 3) develop an individual-based model where decisions by individual fish drive dispersal and hence metapopulation processes are an emergent property (MP derived from individual behavior).

The authors are apparently developing a model in HexSIM for the third option, but models are only proposed for the other two options. If these latter efforts are ongoing they were not described. They are seeking guidance from the ISAB on which options will be most fruitful before proceeding.

3. Progress toward addressing ISAB recommendations from 2013

The authors met the goal of providing a succinct review of what is known about salmonid metapopulation biology, including anadromous and land-locked populations of several species. As expected, there are more simulation studies than those that are parameterized with empirically derived distribution, abundance, dispersal, and extirpation rates. Data quantity, quality, and spatial evenness remain an important limitation for predictive metapopulation modeling for salmonids. Influential studies were identified, and attention was paid to new literature on the subject.

The authors are to be commended for publishing two papers on their efforts in the intervening four years since the 2013 report. These papers are milestones in the sense that they address metapopulation dynamics in the Columbia Basin when data are sparse and allow for some conclusions to be drawn. Jorgensen et al. (2016) explicitly addressed how limitations in the quality and completeness of time series data could affect conclusions about synchrony of population dynamics across subpopulations. This analysis showed that long-term data on spawner abundance corroborates existing classification of stocks at the ESU level. They conjecture that some of the findings at the MPG level are a result of shared exogenous influences but provide no details. For example, do these “distant cousins” move through the hydrosystem together? How similar is the arrival pattern at Bonneville? Do these populations return to Bonneville at the same time as adults? The CSS should have some of this information, some data on arrival timing of juvenile spring Chinook are described in Chapter 4b, and some for arrival timing of adult spring Chinook may be available as part of the study described in Chapter 6a.

The finding by Fullerton et al. (2016) that missing data on dispersal has large consequences on estimating metapopulation structure is, in retrospect, not too surprising, but what implications does this have for the tagging/genetic programs currently in place? Can genetics be used to examine metapopulation structure and the rate of strays entering the population? Much new research using single-nucleotide polymorphisms (SNP) is being done on this topic. In addition, if elucidating the metapopulation structure is important, what is the magnitude of the changes in programs that are needed? How long will it take to collect these data (e.g., 10 years)?

Temporal variation (annual, decadal oscillations, episodic events) and effects of press and pulse disturbances on local productivity, straying rates, and identity as source or sink is a major area where long time series are required. This distinction between exogenous influences and demographic connectivity as promoting synchrony is interesting. It suggests the grim possibility that a large-scale press disturbance like climate change could force synchronous dynamics despite appropriate management of the metapopulation. Distinguishing these two sources of synchrony seems like a priority. This work may inform the research on climate change discussed in Chapter 9c.

4. Applicability to management decisions, alternative scenarios, and adaptive management

It is a bit unclear how applicable the results of the published work, or that considered in the next steps, will be to management decisions via analysis of alternative scenarios. The five MPG-level criteria are relatively simple to assess and so serve as a good initial screening tool, but it is not clear what the next steps are. Is a major research program needed to further assess MPGs that satisfy these five criteria or do these five criteria provide enough “safety” that further assessment is not needed (see research question (1) on page 13)? Is the extent of the missing data on dispersal so large that many years (>10) of further data collection are needed?

Research Option 1 appears to be a low-cost option with high probability of completion.

Research Option 2 appears to be highly dependent on the availability of dispersal data, which the authors admit is notoriously sparse but could be modeled using a distance decay function. The sensitivity analysis “to evaluate the extent to which results might differ under a range of dispersal hypotheses” likely is the most useful for application in management and adaptive management because it would set some approximate bounds on the dispersal needed to keep a stable meta-population. Nevertheless, because the approach imposes population boundaries and dispersal rates at the outset, it may be most useful for scenario testing, especially for metapopulation response to habitat restoration, reintroductions, harvest rates, and combinations of these.

Research Option 3 is more speculative, and ISAB members were not convinced of the benefits of this approach. Computation times are long (10s of hours per scenario—see page 20) and the data requirements appear to be enormous to develop sensible rule sets other than by trial and error. Therefore, it is unclear what insight this will provide for management. Insufficient information was presented here to properly evaluate this option.

Overall, the report should more explicitly connect modeling outcomes to decision points for management, including (1) relative influences of integrated hatchery fish as a source for the metapopulation, (2) relative abundance of wild source subpopulations and connectivity to other subpopulations, (3) avoidance of synchronization of demographic processes across subpopulations, (4) when and where to re-establish extirpated subpopulations, and (5) the role of habitat restoration (core habitat and connectivity, when applicable).

5. Compatibility with best available data and flexibility to incorporate new data

As described in 2013, a key data gap is the rate of dispersal among populations (Fullerton et al. 2016), but nothing presented here suggests that effort has been made to collect these data. The method of Jorgensen et al. (2016) can be readily extended to incorporate more years of data and new data types. However, it is not clear how the ensemble methods in Fullerton et al. (2016) can deal with new types of data. For example, how are genetic similarity vs. tag-recapture data combined, considering that they are based on different time scales? Moreover,

how would similarity based on rare-element signatures be incorporated, given that this has yet another time scale?

Research Option 1 can be extended by including new life-cycle models as they are developed. Research Option 2 is mostly simulation based and so existing data are sufficient. It was not possible to evaluate Option 3 properly, but ISAB members suspect that virtually none of the existing data (e.g., CSS) are useful for these models.

6. Treatment and communication of assumptions and uncertainties

Other than the discussion of lacking data on dispersal, there was little discussion of assumptions and uncertainties. Spawning abundances are measured with error, so what is the impact of measurement error on the results of Jorgensen et al. (2016)? Similarly, dispersal data likely have a large temporal random component (year-specific effects) so the results from a single year may not be that useful. What is the effect of year-specific factors on dispersal data and what is the recommended “minimum” number of years of data needed?

The assumptions and uncertainties of the life-cycle model for Research Option 1 are well known. More detail is needed for Research Option 2. Very little information was presented for Research Option 3. Likewise, a reference is needed for “dynamic factor analysis” (p 11).

7. ISAB Recommendations

- A. It is not clear what the next steps are in addressing the five MPG criteria. Is a major research program needed to further assess MPG that satisfy these five criteria or do these five criteria provide enough “safety” that further assessment is not needed?
- B. Following on Jorgensen et al. (2016), what is the effect of measurement error on estimated meta-population structures?
- C. Following on Fullerton et al. (2016), address the magnitude of the changes in programs that will be needed to collect the appropriate dispersal data and how long this will take. What is the effect of annual variation in dispersal on the outcomes of models using data from only one or a few years?
- D. For Research Option 2, address whether Comparative Survival Study data can be used to evaluate whether exogenous influences affect findings at the MPG level.
- E. For Research Option 3, please provide more detail on the IBM approach. Perhaps a future tutorial session for the ISAB is needed?
- F. The report should more explicitly connect modeling outcomes to decision points for management.

Chapter 11. Communication with managers

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1. Goal

Although a goal and rationale for the outreach activity is not clearly stated, the general goal of the chapter is to recognize the importance of communication, identify the challenges to communicating complex scientific information regarding the full salmon life cycle to policy makers, and outline an approach to improve communication about the life-cycle models and their results. As stated in the Introduction, this chapter specifically provides a summary of the Outreach to Management Subcommittee's basis, approach, and draft materials

2. Key model findings

The ISAB's report *Using a Comprehensive Landscape Approach for More Effective Conservation and Restoration* ([2011-4](#)) emphasizes the importance of public outreach as an integral part of ecosystem restoration efforts. This chapter recognizes the importance of communicating progress of the life-cycle models to decision makers. It broadly describes some of the approaches that will be taken.

3. Progress toward addressing ISAB recommendations from 2013

This is a new chapter that was not included in the 2013 LCM report but is relevant because of the importance of communicating scientific findings to diverse audiences.

4. Applicability to management decisions, alternative scenarios, and adaptive management

This chapter is broadly written and looks like a first attempt at addressing this topic. It does not discuss specifically how the authors would engage diverse audiences. It states that it is targeted at communications with decision makers but describes three tiers of communication. The rationale for needing three tiers of communications is not described, nor who the audiences might be for these communications.

The chapter is not tied to management decisions, alternative scenario analyses, or adaptive management, although it could be with some rewriting. The ISAB believes that questions related to applicability to management decisions, alternative scenarios analysis, and adaptive management frameworks that an audience might like to have addressed by the communications materials could include:

- a) How will the models be used together? This is a critical question and one that the NWFSC is actively pursuing in a scientific context. The answers are not yet available, and integration of these models is complicated and has some risks (e.g., over-

parameterization, inherent uncertainties, compounded uncertainties through model processes and assumptions), but there are potentially important payoffs (e.g., a comprehensive predictive framework that can evaluate and prioritize management actions and trade-offs). The integration of models is worth doing, particularly if there are intermediate milestones to full integration of models (i.e., life-cycle model, metapopulation, food webs, and such).

- b) Do the models represent advances from previous work? Life-cycle models are important aggregators and integrators of past work. They are parameterized from real data, often gathered from diverse studies.
- c) What role will the models play in recovery plan implementation and the FCRPS Biological Opinions? And “Can the models assist in evaluating progress toward or limitations in attaining accomplishments?” It should be clearly articulated that models require ground-truthing and on-the-ground monitoring to evaluate outcomes and validate predictions.
- d) Will the models be helpful in prioritizing actions? Yes, if implemented correctly. These models can be a key tool in comparing scenarios and prioritizing actions.

5. Compatibility with best available data and flexibility to incorporate new data

There is no discussion of compatibility with the best available data and flexibility to incorporate new data. Although this question is related to model approaches in other chapters, it still applies to this chapter because any communication with managers should be able to convey new developments and incorporation of new data. The Introduction stated that a strategy for communicating “progress” of the life-cycle models had been developed by the Adaptive Management Implementation Plan (AMIP) workgroup, so that would imply an ongoing type of communication, which could include such things as an electronic newsletter and a regular blog series. However, ongoing communication is not discussed.

Introducing new data, concepts, and models is challenging, especially if new approaches lead to new conclusions or altered decision points. Policy makers are usually most interested in stable conditions and non-moving targets with respect to incorporating scientific data and interpretations into documents and action. The “best available science” clause of ESA is sometimes invoked by scientists, but it is important for scientists to clearly link new findings to old results and explain how they came to different (or the same) conclusions.

6. Treatment and communication of assumptions and uncertainties

The chapter describes how uncertainty can make communication of life-cycle models more difficult. Explaining uncertainty and variability is something scientists do not do well in general, so it requires continuous effort.

However, how assumptions and uncertainties will be communicated to managers is unclear in this Chapter. It is difficult to convey these ideas to policy-makers without them feeling as if no solid conclusions have been obtained through the scientific process. Translation of model findings and outcomes depends on communication of uncertainties of life-cycle model in a way that allows effective decision making (see Polasky et al. [2011] for discussion of decision theory). These communications should also identify key data gaps and challenges of conflicting management directions of stakeholders, including clear articulation of where decisions in a portion of the basin may affect basinwide outcomes.

7. ISAB Recommendations

- A. This chapter should include more focus on developing the human-system model components relevant to the interventions considered when modeling actions to achieve policy goals. In some cases only cost estimates are needed, but in other cases, other socioeconomic aspects such as indirect or spillover effects, lagged responses, and human behavioral responses should be included. Are land use changes anticipated that will affect the models results? Economists and others conduct policy analysis to develop the relevant aspects of the human system that have impacts on fish and that are needed to fully address the consequences of alternative policies. The template for “final products” could help improve communication and assess what needs to be communicated.
- B. The Chapter should clarify the role of ISAB review and the peer-review publication system. Policymakers and other audiences cannot be expected to judge the quality or validity of these complex models. ISAB reviews are signals of quality, so it is worth recognizing that these are critical channels for communication between researchers and policymakers.
- C. Poor communication will limit the usefulness of high quality research and policy analysis, just as high quality communication will be of limited value if the policy analysis is poor quality. Communication with decision makers is needed both as an integral part of the life-cycle model research program and to communicate the results of the research to multiple audiences. As an example of this important spectrum from applied, multi-disciplinary research to policy analysis and communication, we note the excellent work done at the Public Policy Institute of California ([PPIC](#)) Water Policy Center. They produce numerous briefs, reports, public events, panel discussions, as well as in-depth policy analysis and applied economics in reports such as Escrivá-Bou et al. (2017). The PPIC approach typically starts with a long, often book-length report, which is released accompanied with 10-, 5-, and 1-page versions, and a blog or two, all with eye-catching graphics, and all written clearly without jargon. While PPIC targets policy makers, most of their material is suitable for a broader audience and is available for downloading on

their web site. The key to their success is using multiple approaches and adapting their information dissemination to their diverse audiences.

- D. The subcommittee could address communications with others besides just decision makers, including restoration practitioners, which are separate from decision makers, and the general public because they may also influence decision makers.
- E. We suggest adding more citations to the Introduction and “hurdles to communication” section from the substantial literature about communicating science, including suggestions on effective means to do so. The chapter could address alternative communication strategies (e.g., “story telling” approaches; Dahlstrom 2014), and tailoring communication to avoid misunderstanding. ISAB ([2011-4](#)) also includes suggestions about communication. It is important to recognize also how incentive problems can influence the communication and interpretation of information in public agencies (Vestergaard 2010; Imperial and Yandle 2005). Also see this [link](#) to a memo that was circulated to the ISAB in the past that includes some thought-provoking suggestions for communicating conservation.
- F. As a programmatic item, a forward-looking plan for linking life-cycle model results, economic models and results, policy analysis, and communication, would be very useful. This could include a plan to involve both policy analysis and communication expertise as part of these programs. Please see Programmatic Comments.
- G. The Chapter could convey a recognition that science informs policy. In general, policymakers want to know what response is expected from an action (which is what life-cycle models can provide), whether the expected response was achieved (monitoring), and what should be changed if the response is undesirable or different (adaptive management).
- H. The Chapter should also discuss the importance of the two-way communication needed between scientists and policy makers, and among natural science researchers, economists, policy analysis specialists, decision-makers, and managers. This iterative process of model development, results, interpretation, and two-way communication is highlighted in ISAB/ISRB [2016-1](#), Appendix A. For example, rather than solely considering how life-cycle modelers should convey science to decision makers, the Chapter should address what the decision makers would like to know from models.
- I. Regarding the three tiers of materials, it was not possible to evaluate their effectiveness. More detail is needed regarding (1) why the different tiers are needed and (2) who the audiences are for each of the tiers. The ISAB suggests that each of the materials describe why life-cycle models are needed and why it matters. For Tier I, it was assumed that “they” are life-cycle models. The reference to “advancement from

before” was unclear so it was difficult to evaluate if this was an effective question for this tier.

8. References

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Appendix: Editorial Comments by Chapter

Chapter 1. Introduction

1. Page 1, paragraph 4 – “With COMPASS, Zabel et al. (Chapter 4b) have...” The correct citation is Faulkner et al.
2. Figure 2 – the figure caption needs better explanation. It appears the model was run 9X without changing any of the baseline parameters. So, is the mean (+/-SE) of the red dots a measure of variability inherent to the model? Also, the y-axes should be the same in all graphs. Is “abundance” the number of fish?
3. There is inconsistent notation throughout this chapter, e.g., Life-Cycle model or life-cycle model. Abbreviations are not always defined, e.g., MSFMA and VSP on page 7, QET on page 8.
4. The term “out modeling” is used twice on page 1. Should this be “our modeling”? If not, what is “out modeling”?
5. Page 6, first sentence: Shouldn’t you also include improvement of the models in addition to the analytical framework as part of the adaptive management?
6. Page 7, sentence that begins with “All ESA listing...” Is this statement about the Sacramento River delta system or the Columbia River Basin? Is it really true that ALL ESA listing and status decisions are supported with full life-cycle models for the respective basin you are referring to?
7. Page 8, “Run” definition: How do you decide on the number of years for a run? Is sensitivity analysis used to assess uncertainty?
8. Page 8, sentence that starts “We determined this by fitting a Gompertz model...” Is “this” referring to “50 spawners” or “productivity” or what? If it is not referring to “50 spawners,” how did you decide to use 50 spawners?
9. Page 9, sentence beginning with “Accordingly...” Did you “measure” the abundance from the model output? If so, is “measure” really the right word?
10. Figure 6, left plot: Shouldn’t this figure have the same response surface as Figure 4? Why does it look different?

Chapter 2.a. Habitat: Review of capacity methods

1. Page 7, definitions: Suggest using “or” rather than the slash for clarity, assuming that it is “production” or “yield” and not “production divided by yield.” This comment also goes for “Productivity/Productive capacity.”
2. Page 7, definitions: Capacity is first defined as “production” which was defined above as biomass produced per unit area per unit time, but then in the next sentence it is defined as population size. Which is it? Regarding the definition of capacity, many readers may not link this definition to an S-R relationship and understand the implications of “long-term average asymptotic production...” It will be very important to be specific in using the terms capacity, production, and productivity throughout the document to avoid confusion, especially by readers not familiar with stock-recruitment models for salmon.
3. Page 11: What is an example of a habitat classification system?
4. Page 26: What methods are being referred to as “both” in the last sentence of the first paragraph?
5. Page 31, third sentence of first paragraph: Please clarify – if one reads the sentence as written, it seems like it is stating a necessary result – if you’re adding something to the direct interaction, it will result in more than the direct interaction
6. Pages 33-34: Text in this section to the sentence that starts with “Drift-foraging bioenergetics models...” seems repetitive with earlier text in this Chapter and is unnecessary.
7. Page 34: The rest of the text on this page, while useful, seems less organized and difficult to follow.
8. Page 36, second to last sentence of first paragraph: How do the authors know that the models produce errors that are equal to or less than measured values? If measured data are input into models, the models have errors due to those measured data.
9. The sections on HSI and NEI models were not so easy to follow and contained ambiguous language.
10. Page 39 and elsewhere (e.g., p. 46): Use of the word “simply” seems inappropriate. Despite saying “simply” here and other places in this chapter, the authors go on to describe complexities or challenges of obtaining adequate data.
11. Page 41, second paragraph that begins with “Samples of invertebrate...” This section is confusing and hard to follow. What is “Ryan’s section”?

12. Page 42, sentence that starts with “Finally, these models could be used...” This sentence and the next one are difficult to follow. Is “cover” a single variable that is accounting for multiple habitat features?
13. In Table 3, define “resolution” (i.e., specific reach versus entire are occupied by population). The qualifier "none" for resolution does not seem appropriate. For S-R, resolution is at the population or stock scale.
14. Table 2. Output metric. “Maximum abundance” may be more appropriate than simply “abundance.” The S-R model also provides an estimate of intrinsic productivity. Spatial grain: is this the same as resolution in Table 3? Spatial grain of "none" does not seem appropriate for S-R models. For S-R, is spatial grain at the population or stock scale?

Chapter 2.b. Habitat: A habitat expansion approach to estimating parr rearing capacity of spring and summer Chinook in the Columbia River Basin

The Discussion was overly brief in some sections and would benefit from better organization, including the use of topic sentences for each paragraph.

Chapter 2.c. Habitat: Juvenile capacity modeling

The report contains numerous grammatical errors. The report should be edited to improve readability.

Chapter 2.d. Habitat: Movement and survival based on mark-recapture data

The chapter reads like a rough draft. Several sections were difficult to follow or sentences were confusing. For example, on page 6 the text reads “The stage-specific parameterization of the life-cycle model for the Middle Fork John Day hottest to specifically evaluate the potential impacts of habitat restoration actions targeting water temperature reduction (e.g., vegetation plantings additional water allocation) as well as construction of large Woody structures in tributary and mainstem habitats (results summarized in Chapter 9.d, see McHugh et al. 2017 for details).”

The report does not provide a Discussion section and ends abruptly with a brief Future Research Needs section.

Chapter 2.e. Habitat: Habitat actions and Chinook parr-adult survival

1. Page 5, Parr data. Even though the tagging procedure is covered in earlier publications, a brief description of the source of the fish would be helpful, especially noting that the fish were wild-captured parr.
2. Page 8, paragraph 2. Five problem areas are actually six.
3. Page 12, paragraph 2, lines 6-9. "We believe" should be replaced with more substantial wording, if no citation is available e.g., "professional judgment:"
4. Page 19, paragraph 2. The analysis comparing the three rivers with the most restoration actions with the three with fewest actions is not easy to accept. As the authors point out, they are comparing small headwater streams with medium sized rivers. A better comparison might be the three highest with the three lowest streams that are similar to the modified streams.
5. Page 20, paragraph 2, Discussion. There is still a heavy reliance on expert judgment, especially for interpretation of models; phrase is not needed.
6. Information on habitat actions (types, extent) should be provided in an appendix.

Chapter 3. Ocean/Estuary survival based on PIT-TAG data

The chapter introduction (first paragraph) could be improved by providing readers with a broad overview of what is known and needs to be known in order to incorporate information on estuary/ocean conditions into life-cycle models. In addition, the introduction could briefly discuss and direct readers to other chapters of the report pertaining to this issue.

Chapter 4.a. Integrated population model of the Grande Ronde Basin

1. p. 4, first paragraph: What is the value of the estimated fish guidance efficiency and is it static in all simulations? What is the source of value(s) used?
2. Figure 1: what are the units of the y axes?

Chapter 4.b. Hydro Modeling: The COMPASS Model for assessing juvenile salmon passage through the hydropower systems on the Snake and Columbia rivers

1. Page 3. The section on random effects for reservoir survival is very unclear. The random effect for reservoir survival is modeled using a hierarchical structure, but it is not clear how survival in the reservoir was grouped. Is this over multiple species? Is this over multiple stocks? Is this over multiple years for the same species? The authors also state “the observed [sic] survival (Cormack-Jolly-Seber [CJS] estimates) follow a lognormal distribution conditional on the latent random survival effects.” The survival is not observed (otherwise you would not need to estimate it). Is the log-normal distribution on the logit-scale? Otherwise you could have actual survival larger than 1.0 because the log-normal distribution has no upper bound. Again, at what scale are the CJS estimates computed for each stock?
2. Page 3. How do more time steps lead to more “accurate” travel time computations? Do you mean “finer” (i.e., in terms of hours rather than days)?
3. Page 52 second paragraph “We do not have sufficient PIT tag data to fit separate travel time, survival, or SAR models for the different population groups.” Should this be “...different populations.”?
4. Figures. General improvements are needed for all figures. Be consistent in adding extra colored lines for the means across the figures. The boxplot graphs are not well described in the captions—it appears that they are range, 0.05 and 0.95, mean, etc.? What are the small circles scattered about? What is the horizontal dashed line?

Chapter 5. Toxics as an Obstacle to Salmon Recovery in the Columbia River Basin

1. Page 1, Introduction: Goal statement would be better stated as a positive (i.e., what it is, rather than what it is not). The sentence “Rather, the sections...” doesn’t seem to properly describe what the chapter covers because it does not really describe influences on freshwater and estuarine habitats, but the impacts on salmonids. Later in the introduction on page 3 there is a goal mentioned about developing a modeling framework; perhaps that should be stated at the beginning of the chapter.
2. Introduction section: Text emphasizes impacts on juvenile salmon, but, as mentioned later in the chapter, there could be impacts on other life stages that could affect salmon recovery. For example, on page 3, the text mentions impacts on salmon physiology

including nervous system and reproductive biology, which seems like effects on more than just juvenile salmon.

3. Page 2: “The third section (5.d) is a discussion of wastewater and risks to salmon, including an introduction to chemicals of emerging concern (CECs). These are contaminants that are relatively new to salmon habitats in the Columbia Basin, and are often poorly studied.” Do we know that CECs are “new” to habitats or is it just that we are new at looking for and finding them?
4. Page 6, end of first paragraph: Suggest rewording “While the response of salmon to chlorpyrifos has been well studied...describing the consequences of pesticide exposure” because other pesticides have not been as well studied for salmon either. The end of the sentence implies that pesticide exposure has been well studied for salmon.
5. Page 6, first sentence of second paragraph: For clarity, we suggest changing “much of their prey thereby limiting somatic growth” to “much of salmon prey, thereby limiting somatic growth in salmonids” if we understood this sentence correctly.
6. Page 8, last sentence of second paragraph: Please clarify what is meant by “limiting their ability” – what is “their”?
7. Page 9, third sentence: What is meant by “These” in sentence that begins “These provide a better...”?
8. Page 10 and rest of this section: Please define what is meant by “wide area” in this section and Table 5.b.2.
9. Page 11, last paragraph: Please provide the methods used to create Figure 5.b.3.
10. Page 12-13, Recommendations: It seems like a literature review would also be helpful for developing a prioritized list of pesticides (second to last bullet). Also, would some experiments be helpful for understanding impacts of pesticides on salmonids and other species of concern?
11. Figure 5.b.3: Add a legend for color gradation.
12. Table 5.b.1: It looks like the % of Total column is for each category of pesticide; please clarify in caption or column title.
13. Table 5.b.2: Please cite the source of information in this table.
14. Table 5.b.2 on page 17. Are "Mosquito Control" and "Wide Area Use" land uses or activities that take place across all land uses?
15. Page 18: We suggest defining what “lipophilic” means.

16. Page 18, first sentence of last paragraph: Add “some” or “most” before “POPs” because there are some POPs whose toxicity is not as well known.
17. Page 19, next to last sentence of first paragraph: The statement that “POPs tend to be lipophilic” contradicts statement on previous page that POPs are lipophilic.
18. Page 21, middle paragraph and Figure 5.c.2: If the concentrations measured in fish are lower farther downstream even though POPs persist and bioaccumulate, does this mean that the fish with the high concentrations are dying and not making it downstream or that they are somehow losing some of the POPs?
19. Page 23, last sentence: Are you referring to the EPA study with “This study...”?
20. Page 24: Since eulachon have high lipid content, wouldn’t they accumulate more POPs? If so, doesn’t this contradict statement in fourth sentence that the levels would be below critical body concentrations? If our thinking is incorrect, please provide some clarification about why the levels would be low.
21. Table 5.c.1: Suggest defining abbreviation of CBR in caption
22. Figure 5.c.2: Are these the same data from Table 5.c.1? What is the source for the data shown in this figure? Are the images at the bottom of the figure relevant to the figure? If so, please explain.
23. Figure 5.c.3: The legend is not showing in our copy of the document so it is difficult to interpret the figure
24. Page 34, text on mixing zones: The text about “overlap within this and other salmon habitat and migration corridors” is confusing. Are you talking about overlap between states versus overlap within states? Perhaps some clearer definition of what is meant by “overlap” would help.
25. Page 37, end of second sentence: Suggest adding “in freshwaters” after “particularly vulnerable to the effects of contaminants” to clarify that they are vulnerable in freshwater.
26. Page 37, third to last sentence of first paragraph: Please add a reference or two for the juvenile salmon diet being a “well-established exposure route.”
27. Page 37, reference to Quinn (2005) in last sentence of first paragraph: Is this reference for 2-year outmigration? If it is for exposure, it should be moved to end of sentence.
28. Page 37. “However, during their up to 2-year outmigration to the ocean (Quinn 2005), juvenile Chinook salmon may exceed this exposure time.” This doesn’t seem accurate. Perhaps a more accurate statement would be “...during their two years in freshwater preparing for and outmigrating to the ocean...”?

29. Page 38, last bullet: Please reword this recommendation for clarify. What are the physiologic endpoints referred to here? Are they the same thing as “markers”?
30. Page 39: The title of “Background” seems misnamed. This section seems to be making some recommendations, not providing background.
31. Page 39, fourth sentence of “Background” section: What is a “toxic insult”?
32. Page 42, first sentence of section on “Population-level effects of remediation...” Suggest addition “potential” between “evaluate” and “impacts” (i.e., “evaluate potential impacts”) because the impacts suggested here are based on model predictions.
33. Citation in references for Meador 2014 is incomplete.

Chapter 6.a. Population-specific pinniped predation

A few typographical errors were identified in supplemental tables:

1. In Supplementary Table 1, total tag numbers for 2011 should be 372 not 374, in 2012 total tag numbers should be 369 and not 372, and the total number tagged in 2013 should be 69 and not 72.
2. In Supplementary Table 3, there were errors in the total number PIT tagged juveniles that returned to Bonneville Dam from 2001-2016. The total for the Upper Grande Ronde should be 92, for Lostine River it should be 215, for Marsh Creek 313, for Secesh 514, and for the Imnaha 1201.

Chapter 6.b. Avian predation management effects

Avoid the use of the term “rate” and use the term “proportion” instead. A “rate” is measured per unit time. These estimates are simple proportions of the run that are predated.

Chapter 6.c. Incorporating food web dynamics into life-cycle modeling

1. Some attention is needed to spelling and grammar throughout.
2. Suggest adding information in the model description on how nutrients, in-stream physical habitat, and riparian vegetation are modeled.

3. Table 1: Equation for “Nontarget Fish” has subscript of L in it that is not defined. In Bellmore et al. (2017), L indicates “Non-native snail.” Is that what it indicates here? If so, the authors should also describe how non-native snails fit into the food web.
4. Page 7, first sentence: Suggest rewording to “...salmon arrive on 01 July, hold for two months and eventually spawn on 01 September (Table 2).”
5. Page 8 – the meaning of the following sentence was unclear: “We estimate the number of juveniles the system can support (Ns) by multiplying the juvenile abundance by the amount of organic matter assimilated by an average size juvenile and dividing by respiration.”
6. Page 9, second paragraph, next to last sentence: Should this be “...which is consistent with smolts in many spring Chinook populations”? Please reword to be clear.
7. Page 9, second paragraph, last sentence: How does survival during the smolt stage take into account dam passage? Provide more detail on how this is done. Some more clarity is needed about “and ending with Bonneville Dam.” This sentence was hard to understand.
8. Page 9, last paragraph, first sentence: Please describe what is meant by “We allowed the model to equilibrate (burn-in).”
9. Page 10, second sentence after in first paragraph of “Results and Discussion”: What is “This value” that is referred to here? Please reword for clarity.
10. Page 10 – First sentence of Results and Discussion: Do you mean that the empirical number of spawners from weekly redd surveys was 2.5 times the value used, of 9 spawners? More importantly, if this is the case, why was the empirical number not used to start the model at this step?
11. Same paragraph: Clarify what is meant by “which we normalized to estimate the average number of redds per km and assumed two adults...”
12. Further on in that same paragraph, if smolts/adult predicted by the model are about one tenth of that actually measured, then it seems like something more drastic than a 9% change in survival (from 25 to 34%) must be driving such a large change. Likewise, if the empirical estimate of 34% survival for migrating smolts was available, then why was this not used in the model?
13. In the last paragraph on page 10, more explanation is needed about the potential for different patterns of migration, such as downstream into the Columbia mainstem to rear vs. complete rapid smolting to the ocean.
14. Page 11: “Tagged fish were not detected moving downstream near the mouth during mid-summer.” The meaning is unclear. Do you mean during September when the figure shows that the model says they should?

Chapter 7. Simple Population Model: Using integrated population models to evaluate natural and anthropogenic risk factors for Pacific salmon

1. Page 2, near bottom: Three issues are listed not two.
2. Page 3, last paragraph: Please provide the species for the studies cited here as having similar features to the IPMs presented in the chapter (i.e., Newman et al. (2006), etc.).
3. Page 10, paragraph before Equation 13: What are “vague priors”?
4. Page 12, 15: How is the quasi-extinction threshold (QET) determined, e.g., a four-year running mean of 50 spawners?
5. Page 14, Results: Although it is reasonable for the authors to focus on the multiple-population findings of the models, it would be helpful to have one sentence to explain why and how the results of individual population models compared to these results or are less relevant. In other words, what do outlier populations tell us about those populations compared to the majority of populations?
6. Page 17, last sentence of top paragraph: The sentence refers to comparison with mechanistic models. It would be helpful if the authors could elaborate on what mechanistic models they are referring to and the meaning of this sentence.

Chapter 8. Intermediate Model: Building a state-space life-cycle model for naturally produced Snake River Fall Chinook Salmon

It seems that age-0 and age-1 smolts are called "early season" and "late season" juveniles, respectively. The text would be much easier to understand if early and late season juveniles were referred to as age-0 and age-1 migrants based on their age at ocean entry.

Chapter 9.a. Grande Ronde spring Chinook populations: Juvenile based models

1. The report appears as a rough draft. For example, not all figures are cited in the text, they are cited out of order, and most importantly, most cannot be understood from their captions. Citation of references was unfinished with notes for “ref” or “lit” to be inserted. Acronyms are not explained, and spelling, grammar, and punctuation are incorrect. Much jargon is used without explanation. Experienced salmonid ecologists from outside the

Columbia River basin would have difficulty understanding much of this report. Only salmon biologists with extensive prior knowledge of this modeling could understand it, but this is probably not the only intended audience. This detracts greatly from the extensive effort to create the models and evaluate the scenarios. As a result, readers are prone to become frustrated before reaching the results and are unable to understand those results and their implications. This problem was noted in the 2013 review and still remains.

2. The nature of the scenarios and their evaluations are confusing. Specific values used in the scenarios are not reported and the assumptions, definitions, and sources of the scenarios are not provided. For example, the pinniped scenario represented “a) current status, b) current status with continuation of recent increases in estimated pinniped predation, and c) a two-fold increase in productivity (either from survival or capacity improvements) combined with recent level pinniped impacts.” What are the predation rates represented in the scenario? Does “continuation of recent increases in estimated pinniped predation” mean continued rate of increase in predation or continued increased predation?

Chapter 9.b. Wenatchee River spring-run Chinook salmon life-cycle model: hatchery effects, calibration, and sensitivity analyses

This chapter was clearly and concisely written. Below is a short list of areas where further clarification is needed.

1. Page 10, last sentence: Given that NORs cannot be managed, apparently, what flexibility is there for managers? Doesn't the table just show what PNI is, given different levels of NORs?
2. Page 16, top half: It would be good to remind readers the meaning of AR(1), which is an autoregressive model with a one-year time lag. It also would be good to specify that this autocorrelation is a temporal autocorrelation.
3. Page 17, Table 3: Are the numbers in parentheses in the right column the mean and variance of these distributions? Specify this in the caption, if so.
4. Page 19, “The joint likelihood for a given model run, n , was the product rather than the sum because the density estimates came from distributions fitted to untransformed observations.” This statement needs to be revised—likelihoods are always multiplied regardless whether observations are transformed or not.
5. Page 23, “Parameter ranges from which we sampled were typically set by using the 95% confidence interval of the estimated parameter.” How were these confidence intervals obtained? The calibration procedure is ad-hoc and does not generate any sort of uncertainty about any parameter.

6. Page 33, line 7: Should “reduced” be “increased”? It was also confusing why the hatchery program was first reduced in scenario 1 and then increased again in scenario 6, the rationale should be explained here.
7. Page 35, Figure 10: A reasonable question to ask is whether any single action alone could reduce the probability of quasi-extinction to 0.50 or less, especially if this analysis could also account for the negative effects of domestication by hatchery fish. This latter point was unclear when interpreting this figure, although it may have been partly addressed in the next paragraph on the bottom of page 35.
8. Page 37: This report did an excellent job of providing definitions of acronyms and explanations of key underlying concepts, which was greatly appreciated. One point where this could be improved is for VSP scores, by providing a brief summary of how these are calculated and what they mean.
9. Page 38, Figure 13 caption: Define extinction contours. Are these the probability of falling below the quasi-extinction threshold?
10. Page 39, Figure 14: It would be better to maintain the same Y-axis scales among the panels, so the reader could see the shift more clearly.
11. Page 44 and beyond: The term leverage is overused as jargon.
12. Page 52, Figure A6: Define the grey shaded area, in the caption
13. Page 52, six lines from bottom: Affect, instead of effect.

Chapter 9.c. Themes of climate impacts on Columbia Basin salmon: Multiple limiting factors, correlation in climate drivers, and cumulative life cycle effects

1. p. 5. The model assumes constant late marine survival (0.8). It is not clear why early marine survival needs to be split from late marine survival, although it is reasonable to align oceanographic variables with Chinook salmon smolts during their first year at sea. As discussed when reviewing Chapter 7, the ISAB recommends that investigators not assume constant 0.8 annual survival for older Chinook salmon because there is very little, if any, information to support this partitioning. The assumed annual ocean survival rate of 0.8, i.e., ocean mortality rate of 0.2, for older age groups of Chinook salmon can be traced back to Major (1984, North American Journal of Fisheries Management 4A:414-430), who cites Ricker (1976), but this value was not reported by Ricker (1976).
2. p. 8. They count 7 parameters for the spawner-to-smolt relationship. We count 6 (3 from equation 3 which generates c_2 , then p_1 , p_2 , c_1 from equation 2).

3. p. 8. Survival drawn from a log-normal distribution. This seems odd as survival probabilities are limited between 0 and 1, but a log-normal distribution ranges from 0 to infinity. What stops the simulation from choosing survival values > 1 ? Also, log-normal distributions are usually parameterized by the mean and standard deviation (SD) on the LOG scale but the authors give the mean and SD on the anti-log scale so it is difficult to envision the shape of the distribution.
4. p. 15. The paper needs to include a detailed explanation of how the climate scalar works as they did in the follow-up webinar. An illustrative example showing how the time series fluctuated with different climate-scalar values would be helpful to communicate to managers how this was modeled.
5. There was some inconsistency in the detail of parameters used. Equation 4 was made explicit in using a log-normal error structure as was the AR(1) model in equation 5, while s_3 appears to be a simple scalar.
6. p. 24. There appears to be a typo on Figure 8. The time scale sequence on the x-axis is 1988, 1998, 2008, and 1989.
7. General comment: To understand this paper on its own, the reader needs more detailed equations.

Chapter 9.d. ISEMP/CHaMP life-cycle models – Entiat, John Day, Lemhi, habitat actions

1. General comments: Please ensure that all acronyms are defined, such as Visual Basic QCI, so that all readers can understand the text. Many are not statisticians or modelers or even fish biologists, per se.
2. “User-specified” and “user-defined” are overused and often can be deleted to simplify the writing. Specified and defined are sufficient.
3. The Watershed Model User's Guide.docx document indicates that Normal or Dirchelet distributions are used to model parameter uncertainty, but this chapter indicates that a beta distribution is used. Which is correct?
4. The chapter would benefit from some common reorganization and formatting using the “best” presentations from each watershed. For example, the equivalent of Table 2 of the Entiat River model should be presented for each of the three models. The detailed model formulation from the model for the Lemhi River should be present for the other two rivers.

5. P 4 – Please clarify “After their first spring out of the gravel (i.e., as age-1 pre-smolts)....” Do you mean simply the spring when they are age-1?
6. P 6, line 8 – the term “capacity” needs to be defined up front, because it is used several ways. For example, the meaning of “...inform capacity input needs” is unclear at this point. Cite references for “published demographic parameters” (line 9), unless these are given below. See line 13 for an example of the use of capacity without definition. For example, do you mean abundance, or density, or the potential abundance or density with sufficient spawners?
7. P 6, line 11 – The parameter “ p ” is used liberally here and below for several types of “productivity” often without further definition about whether it refers to smolts/spawner (freshwater productivity?) or spawners/spawner (recruits/spawner, as adults/adult). Please clarify this in every case. For example, on p. 10, both kinds of productivity are clearly described and used, but in other cases the meaning is unclear.
8. P 6, line 19 – Avoid jargon, such as using “insight” when you mean “data”. Readers will understand the text if it is simple and clear, but may not otherwise.
9. P 8 – If “normalized capacity” y_i is in units of fish/m but L_i is in units of km, then total capacity cannot be the product.
10. How are steelhead “predictions” translated into an estimate of juvenile rearing capacity using a fish placement algorithm—presumably at the reach scale? More explanation of the model described in Wall et al. (2016) may be called for.
11. P 9, Fig 3. This figure is descriptive and helpful, but the inset in the box needs to be increased in size, and the parameter or unit “M” defined (millions of fish?).
12. P 10 – Here again, to avoid confusion, it would be wise to specify that abundance means adult spawner escapement and productivity means smolts/adult (which could be defined as freshwater productivity). However, this is a case where productivity was defined as smolts/adult, but then the field data are described as spawner/spawner. Readers will be confused.
13. P 11, five lines from the bottom – Define again the meaning of p and S here, so the reader is not confused. More important, justify the assumption that the ratio of smolts/spawner at the two temperatures is the same as the ratio of survival measured at the two temperatures over the 60-day period tested by Bear et al. (2007).
14. P 12, Table 1 – Under Scenario W1, what is the meaning of “productivity scaled proportionally.” Proportionally to what? Capacity?
15. P 13 – Have the wood structures already been added, or are they planned? Do the simulated wood structures at the 8 mainstem and 9 tributary sites cover a large or small

proportion of the length and area of these channels? Later, in Results, the reader learns that these occur in 3.4 km of stream, but this fact should be moved to this point. However, in the Discussion the reader learns that wood structures are modeled over a third of the model domain, but how this was determined is not explained.

16. What are the “wood frequency targets” specifically, for this basin, or these segments? Please explain in simple terms what “porous topography” means. Does the extrapolation of NREI capacity estimates with wood additions assume that wood structures are installed throughout the entire length modeled?
17. How sensitive are the model results to the assumption that the increase in survival is the same as the increase in abundance? For example, NREI refers to summer rearing habitat, based on the bioenergetics of the cost of holding focal points and the benefits from food delivery. However, fish also need to live through the winter, and so survival overwinter may depend on the habitat complexity provided by the wood structures (as shelter from flow and cover from predators) rather than on the energetics. Therefore, structures might appear from the model output to have little effect on summer carrying capacity but could strongly affect winter carrying capacity. These are steelhead, many of which spend several winters in fresh water (i.e., 90% smolt at age-2 or 3, so 2-3 winters). This caveat should be acknowledged. For an alternate approach, see the model for the Entiat River, where an increase in overwinter survival was modeled in sections with better habitat (p. 27).
18. P 15 – Are the changes in temperature described changes in the maximum or mean, and measured over what period? Is Figure 3 noted here actually Figure 5? What productivity is being referred to here? Freshwater?
19. P 16 – The authors claim that the effects of wood addition were minimal, but the increase in spawner escapement of T2 was also only about 100 more spawners, so this conclusion seems a bit misleading. Both T2 and W had similar effects on abundance, productivity and extinction.
20. Figure 5 caption – Describe the meaning of the shading and the upper and lower bounds in the figure. In the SQ panel, there is no solid horizontal line, at least no straight one, and indeed there are two solid lines, but explanation is lacking.
21. Figure 7 – This figure is far too small to read, isoclines are not labeled sufficiently or explained in the caption, and no isoclines are shown for T1.
22. P 21 – Perhaps you mean splash damming, but this should be defined for readers who won't know, or left out since log drives may be sufficient explanation.
23. P 22 – In the description of Valley Segment 1, it is unclear whether, for example, the high-gradient reach is upstream or downstream, and in which Valley Segment each lies. This problem persists throughout the bullets.

24. P 23, line 4 – do you mean unreliable?
25. Figure 8 caption – describe the subreaches and the different colors for them, as well as the symbols like VS1A.
26. P 24, bottom – here again, the meaning of “stage-specific productivity values” is unclear. Are these really just survival from one life stage to another, such as egg-to-fry survival probability? If so, please explain this clearly, probably near the beginning of the manuscript as well as reiterating it here.
27. P 25 – define S_{OAg} and m_g .
28. P 26 - Since the Entiat is close to the Wenatchee River, where much is known about the effects of hatchery fish, why not include fitness effects of hatchery fish based on those data?
29. The meaning of the VSP scores would be most helpful if it were moved up to the point where this metric is reported for the MFJD model.
30. P 27 – Describe the relevance of a 2% increase in survival here rather than later.
31. The sentence beginning “To estimate habitat capacity....” is quite complex and many readers will get lost. Are you referring to two different methods, one for modified sites and one for those not modified? If so, then it would be better to describe these in separate sentences.
32. Table 4 – What references were consulted for the estimates of fecundity and habitat capacity for fry and yearling/subyearling fish?
33. P 29 - The baseline scenario predicts a mean of 231 spawners, with relatively little variation, but the actual data appears to show an increasing trend, especially since 2000, with several years >500. Should the baseline scenario match this increasing trend? Could ocean conditions account for this variation in observed escapement? What modification of the model would be needed to help reproduce this aspect of the empirical data?
34. Figure 12 - Why are the number of spawners declining over time, especially in Scenario 2?
35. P 32 – If not all habitat improvement actions have been modeled, then the conclusion that the effect of the subset that was modeled is modest needs to be modified.
36. Figure 13 caption – Define all the items in the legend clearly, such as Full and No.
37. P 34 – Fig. 13 indicates that PIT tag detectors are located many other places in addition to near rotary screw traps, so this should be explained. “Remote site juvenile enumeration and tagging surveys” is not clear.

38. P 35 – Here again, the meaning of productivity, production, and capacity are confusing, and it is unclear whether they mean the same things as for the other two river basins. Consistent terms and definitions are critical for this chapter. Instead of “state variables” and “realized transition probabilities” which are terms primarily used by modelers, it would be best to refer to these as abundance and survival, if indeed they are.
39. Is there a reference for the branching model, either as a general model type or for this specific model?
40. P 37 – Any parameters in these five equations that were not defined above need to be defined here, such as c_{QRF} . Is “escapement” the same as number of spawners (S)? Which symbol equates to “spawner-to-parr capacity”? The reader who is not a statistician will need more explanation.
41. P 39 – “The posterior for parr capacity is strongly determined by the prior, whose CV was chosen arbitrarily; however, the other parameter estimates are robust to values of σ_{cQRF} as high as 0.5. As the lognormal prior on cSJ becomes more diffuse and thus more skewed, the posterior mean increases, but the posterior median changes very little and the remaining parameters are stable.” It would help readers to use less statistical jargon here, if that is possible. What meaning should the average reader take away from these statements?
42. P 39 - Juvenile Chinook have not yet been observed in the reconnected tributaries, and intrinsic productivity for these reconnected tributaries is assumed to be the same as other streams. Explain in simple terms how reconnection of these streams (i.e., greater capacity) also increased productivity (smolts per spawner) without altering intrinsic productivity (i.e., Figure 17). For example, this finding apparently stems from relaxation of density dependence at a given spawner abundance since spawners are distributed over a larger area. A key assumption here, as noted in the text, is that spawners will eventually colonize the reconnected tributaries.
43. The Lemhi model “infers that none of the observed escapements have come close to saturating the watershed with parr. In contrast, there is reportedly little evidence of density dependence in the parr-to-smolt period.” What happened? Did parr leave the watershed to rear downstream of the study area, or did parr die leading to low density dependence during parr to smolt stage?
44. (conclusions), the text seems to conflict with the above statement (on P. 40) and with Figure 16: “This simple two-stage model of freshwater juvenile production suggests there is moderate density dependence in the spawner-to-parr transition and weak density dependence in parr-to-smolt survival.” Figure 15 suggests weak density dependence during the spawner to parr stage after adjusting for measurement error. In contrast, Figure 16 shows moderate density dependent survival during the parr to smolt stage after adjusting for measurement error. Please clarify.

45. Figure 14 – It would be clearer if units were defined for intrinsic productivity and capacity in each panel. Is capacity in the lower left panel, for example, thousands of spawners?
46. References – Many references are incomplete.

Chapter 9.e. Yakima River *Oncorhynchus mykiss* populations

1. A diagram of the proposed integrated model, methods used to integrate the four models, and a table of input parameters needed to run the integrated model would be useful (see ISAB's programmatic comments for more detail on what needs to be included in every chapter).
2. Page 3, line 8: Currently this line reads as "1990. Multiple time a year and each year since 1991, Upper Yakima River juvenile *O. mykiss*..." Should this be "Multiple times each year and every year since 1991..."?
3. Page 7, end of first paragraph: "For the model runs, three pairing events were simulated annually: anadromous males spawned preferably with anadromous females, resident females spawned with resident males, and 21-25% of anadromous females were fertilized by resident males." Does this take into consideration a mix of anadromous and resident males spawning with a single female?
4. Page 20, first line: Currently this line reads as "to build a model that can important [import?] these factors."
5. Page 21: The last scenario is "Changes in smolt survival around Bonneville Dam as a result of changes in pinniped predation due to changes in management actions." Should this be adult survival?
6. Page 22, first line: Currently this line reads as "proportion of steelhead produced by crosses are likely compromised." The type of cross needs to be added.
7. Page 23, first line: Currently this line reads as "and more severe overwintering conditions. Thus, they are less likely to have a strong a strong..." Delete the extra a strong.
8. References: The proponents might find the following publications useful:
 - Graves D., A. Maule. 2012. Modeling water temperature in the Satus and Toppenish Watersheds of the Yakima River Basin in Washington, USA. Climate Change, doi:10.1007/s10584-012-0643.

- Hardiman, J.M. and M.G. Mesa. 2013. The effects of increased stream temperatures on juvenile steelhead growth in the Yakima River Basin based on projected climate change scenarios. *Climate Change*, doi:10.1007/s10584-012-0627-x.
- Hatten J.R., T.R. Batt, P.J. Connolly, A.G. Maule. 2013. Modeling effects of climate change on Yakima River salmonid habitats. *Climate Change*, doi:10.1007/s10584-013-0980-4.

Chapter 9.f. Catherine Creek spring Chinook life-cycle model

The document was carefully prepared, so comments are relatively few:

1. Fig. 1 – Why is there an arrow from Spawners back to Ocean Stages? Don't all spawners die?
2. P 11, first incomplete paragraph – Extensive work on the fitness effects of hatcheries has been done in the Wenatchee basin, so why not use those data to approximate these effects for this life-cycle model? In addition, please provide a reference for the statement “Further, previous analyses suggest that where differences may exist, they are either inconsistent and on average compensating...”
3. p 12 – The first bullet point was unclear, which reads “The proportional changes in juvenile carrying capacity reflecting the Justice et al. (2017) habitat scenarios translated into a natural origin adult abundance response that was similar on a rank-order basis...” Similar to what rank order?
4. P 12 – Here and elsewhere, avoid jargon like “vegetation/restoration wise...”
5. Table 2 – Spell out more words in the right-most column heading, and define this in the caption. Summary statistics for both hatchery and natural spawner returns could be included. Two graphs in Figure 2 are not needed. They are the same thing. We recommend using the log scale and clearly labeling the y-axis.

Chapter 10. Metapopulation: Assessing salmon spatial structure and metapopulation dynamics

1. P 2 – If the two goals for the analysis laid out in the quote from the AMIP (2009) plan will drive this chapter, then they should be highlighted more effectively. Many other lists are

introduced between this point and p. 11 where the goals are discussed again, which may divert attention of readers and ultimately confuse them.

2. P 6 & 7 – A very useful paper is Kanno et al. (2014; *Freshwater Biology*), which describes a “demogenetics” approach combining PIT tags and antennas with parentage analysis to evaluate importance of tiny tributaries to persistence of a brook trout population studied for a decade or more in Massachusetts. This paper could also be cited as an example of metapopulation processes in brook trout, in the sentence where efforts for various species are discussed. We note that it is cited in Fullerton et al. (2016).
3. P 8 – We found the two sets of four questions each under “Research Needs and Guiding Questions” to be confusing. They are presented before the two phases of work are presented, and the three options for modeling envisioned, and so divert attention away from the main goals. They cause the reader to forget the AMIP goals described above, which are later the main focus. Perhaps this section should go at or near the very end of the document, if they represent the next steps?
4. P 10 – the MPG-level criteria here are repeated in Table 1, but Table 1 is not cited here. One or the other seems sufficient.
5. Then, under “Phase I Research Completed”, the authors return to the AMIP objectives for spatial analysis, but the reader is likely to be confused because many other lists and objectives have been presented in the intervening text. See comment about P 8, for two of those lists, which likely could be moved or removed to improve clarity.
6. P 11 – After the first sentence in the section titled “Phase I Research Completed”, it would be wise to list the two papers already published that have addressed these objectives, to be certain that the reader doesn’t miss the point. In addition, it would be wise to avoid using statistical jargon such as “latent variables”, to ensure that the document is as clear to non-statisticians as possible. Do you mean that the PDO accounted for some kind of joint variation in the time series? A better description is needed.
7. P 14 – Four questions are posted to assess the first four MPG-level criteria, but the sentence starting “*The last criterion (5)...*” is confusing because the criterion or question is not presented.
8. P 15 – Many readers will be confused by the statistical jargon in “For instance, the residual covariance matrix from an integrated population model across 24 populations in this ESU retained spatial structure that was not accounted for by other factors in the model (Eric Buhle, pers. comm.)” What does “retained” mean in this context. Can this result be described more simply, so more readers can be informed?
9. P 21 – The authors outlined three options, but then four points are made here, again likely confusing readers.

10. Literature Cited – some references are not complete.

Chapter 11. Communication with managers

1. The sample document included in the review is attractive and presents good information. The wheel of actions and impacts is visually interesting, but the life cycle of the salmon is still rather cryptic. It might be helpful to use graphics that explain the salmon life cycle, or definitions of the graphics that are in the center of the wheel.
2. At the beginning of the chapter, the authors define “decision makers” and say they will hereafter refer to the collected group as such, but later use “policy makers.” Please be consistent.
3. The bullet about inclusion of a summary was confusing. Where would this summary be included?
4. The chapter mentions the ISAB review in several places, but it was unclear how the ISAB review would be connected with the communications with managers.