



Fisheries and Oceans
Canada

Pêches et Océans
Canada

Ecosystems and
Oceans Science

Sciences des écosystèmes
et des océans

Canadian Science Advisory Secretariat (CSAS)

Proceedings Series 2021/045

Pacific Region

Proceedings of the Pacific regional peer review of the evaluation and update of biologically-based targets for enhanced contributions to Chinook populations

**August 31-September 1, 2017
Nanaimo, British Columbia**

**Chairperson: Lesley MacDougall
Editors: Steven Schut and Lesley MacDougall**

Fisheries and Oceans Canada
Science Branch
3190 Hammond Bay Road
Nanaimo, BC V9T 6N7

Foreword

The purpose of these Proceedings is to document the activities and key discussions of the meeting. The Proceedings may include research recommendations, uncertainties, and the rationale for decisions made during the meeting. Proceedings may also document when data, analyses or interpretations were reviewed and rejected on scientific grounds, including the reason(s) for rejection. As such, interpretations and opinions presented in this report individually may be factually incorrect or misleading, but are included to record as faithfully as possible what was considered at the meeting. No statements are to be taken as reflecting the conclusions of the meeting unless they are clearly identified as such. Moreover, further review may result in a change of conclusions where additional information was identified as relevant to the topics being considered, but not available in the timeframe of the meeting. In the rare case when there are formal dissenting views, these are also archived as Annexes to the Proceedings.

Published by:

Fisheries and Oceans Canada
Canadian Science Advisory Secretariat
200 Kent Street
Ottawa ON K1A 0E6

[http://www.dfo-mpo.gc.ca/csas-sccs/
csas-sccs@dfo-mpo.gc.ca](http://www.dfo-mpo.gc.ca/csas-sccs/csas-sccs@dfo-mpo.gc.ca)



© Her Majesty the Queen in Right of Canada, 2021
ISSN 1701-1280
ISBN 978-0-660-40449-3 Cat. No. Fs70-4/2021-045E-PDF

Correct citation for this publication:

DFO. 2021. Proceedings of the Pacific regional peer review of the evaluation and update of biologically-based targets for enhanced contributions to Chinook populations; August 31-September 1, 2017. DFO Can. Sci. Advis. Sec. Proceed. Ser. 2021/045.

Aussi disponible en français

MPO. 2021. *Compte rendu de l'examen par les pairs de la région du Pacifique sur l'évaluation et mise à jour des cibles biologiques aux fins de contributions améliorées aux populations de saumon quinnat; du 31 août au 1 septembre 2017. Secr. can. de consult. sci. du MPO. Compte rendu 2021/045.*

TABLE OF CONTENTS

SUMMARY.....	iv
INTRODUCTION	1
REVIEW.....	1
PRESENTATION OF WORKING PAPER	1
PRESENTATION OF WRITTEN REVIEWS	2
JEFF HARD	2
PATRICK O'REILLY.....	3
AUTHORS RESPONSE TO REVIEWERS	3
GENERAL DISCUSSION	4
EPIGENETICS.....	4
RELATIVE REPRODUCTIVE SUCCESS (RRS).....	5
PHOS (EFFECTIVE VS CENSUS).....	5
SELECTION AND OTHER MODEL PARAMETERS	5
CLARIFICATION OF PNI.....	5
MODEL STOCHASTICITY.....	6
DEFINITION OF WILD AND IMPACTS OF STRAYING.....	6
FUTURE WORK CONSIDERATIONS	6
OTHER CONSIDERATIONS	6
CONCLUSIONS.....	6
REVISIONS FOR WORKING PAPER	7
ACKNOWLEDGEMENTS	7
APPENDIX A: TERMS OF REFERENCE.....	8
APPENDIX B: WORKING PAPER ABSTRACT	10
APPENDIX C: AGENDA.....	11
APPENDIX D: PARTICIPANTS	13
APPENDIX E: WRITTEN REVIEW BY JEFF HARD	15
APPENDIX F: WRITTEN REVIEW BY PATRICK O'REILLY.....	28

SUMMARY

These Proceedings summarize the relevant discussions and key conclusions that resulted from a Fisheries and Oceans Canada (DFO), Canadian Science Advisory Secretariat (CSAS) Regional Peer Review meeting of Aug 31-Sept 1, 2017 at the Pacific Biological Station in Nanaimo, B.C.

DFO's Pacific Region Salmonid Enhancement Program (SEP) has long standing enhancement guidelines for hatchery program that integrate multiple biological and socioeconomic objectives. Key policy and scientific advancements have been made since the implementation of the existing enhancement guidelines. The purpose of this peer review process is to provide science based advice on genetically based targets for enhanced contributions to Chinook Salmon populations that reflects new Canadian policy, new genetic information, assessment tools, and measurement metrics for the genetic effects of hatchery rearing and enhancement on wild fish.

A working paper on genetically based targets for enhanced contributions to Canadian Pacific Chinook salmon populations was presented for peer review. The regional peer review included the following discussions following presentation of the paper: context, appropriateness of Proportionate Natural Influence (PNI) and the model presented, chosen model parameters, and subsequent sensitivity analyses. The discussion was varied, and often focused on the implementation implications of the recommendations, and how the advice should address this. These implementation considerations were deemed out of the scope of the advice being requested. The general consensus is that the use of PNI and the modelling effort were appropriately matched to the objectives stated in the terms of reference, and the paper was accepted as written with very minor changes. Future work was discussed such as categorizing current hatcheries using PNI.

In-person and web-based participation included Fisheries and Oceans Canada (DFO) Staff from Science, Ecosystem Management and Fisheries Management sectors; and external participants from NOAA, First Nations, non-governmental organizations, and recreational fishing interests.

The Research Document and Proceedings will be made publicly available on the [Canadian Science Advisory Secretariat](#) website.

INTRODUCTION

A Fisheries and Oceans Canada (DFO) Canadian Science Advisory Secretariat (CSAS), Regional Peer Review (RPR) meeting was held August 31 and September 1, 2017, at the Pacific Biological Station in Nanaimo to evaluate genetically based targets for enhanced contributions to Canadian Pacific Chinook salmon populations.

The Terms of Reference (TOR) for the science review (Appendix A) were developed in response to a request for advice from DFO Ecosystems Management Branch, specifically the Salmon Enhancement Program. Notifications of the science review and conditions for participation were sent to representatives with relevant expertise from NOAA, First Nations, non-governmental organizations, and recreational fishing interests.

The following working paper was prepared and made available to meeting participants prior to the meeting (Abstract provided in Appendix B):

Withler, R., Bradford, M., Willis D., and Holt, C. 2017. Genetically Based Targets for Enhanced Contributions to Canadian Pacific Chinook Salmon Populations. CSAP Working Paper 2013SEP02.

The meeting Chair, Lesley MacDougall welcomed participants, reviewed the role of CSAS in the provision of peer-reviewed advice, and gave a general overview of the CSAS process. The Chair discussed the role of participants and the definition and process around achieving consensus decisions and advice. Everyone was invited to participate fully in the discussion and to contribute knowledge to the process, with the goal of delivering scientifically defensible conclusions and advice. It was confirmed with participants that all had received copies of the Terms of Reference, the background information, and supporting documents.

The Chair reviewed the Terms of Reference and the Agenda (Appendix C) for the meeting. The Chair then reviewed the ground rules and process for exchange, reminding participants that the meeting provided an opportunity for participants to provide feedback on the proposed framework. The rapporteur for the meeting was Steven Schut.

Members were reminded that everyone at the meeting had equal standing as participants and they were expected to contribute to the review process if they had information or questions relevant to the materials being discussed. In total, 39 people participated in the RPR (Appendix D).

REVIEW

Working Paper: "Genetically Based Targets for Enhanced Contributions to Canadian Pacific Chinook Salmon Populations." by Withler, R., Bradford, M., Willis D., and Holt, C (2013SEP02).

Rapporteur: Steven Schut

Presenters: Ruth Withler, Mike Bradford, David Willis, and Carrie Holt

PRESENTATION OF WORKING PAPER

Presentation of the working paper was divided into five sub-presentations on different components of the work, and all four authors presented different portions of the presentations.

David Willis provided an introduction to the working paper including an overview of the Salmon Enhancement Program (SEP) in BC, and the reasons for the original SEP Request Science

Information and Advice. He included information on the size and scope of the regional Chinook enhancement program, ties to the Wild Salmon Policy and the process of socioeconomic decision making in activity planning. The outcomes and advice from this peer review process will be used in future planning exercises, but it is important to identify that the implications for application of this advice is not within the scope of the current review.

The second presentation, by Ruth Withler, was an overview of the state of knowledge on the genetics of Pacific Salmon enhancement. She focused her discussion on the observed impacts of hatchery enhancement on phenotypic expression in wild populations. Genetic effects can be grouped into demographic change and fitness related effects. The presentation focused on mechanisms and metrics for changes in fitness including environmental and epigenetics in addition to genetics. Ruth discussed the challenges and general approaches to population genetic management in mixed hatchery/wild Salmon populations. She finished with a discussion of long term genetic consequences of enhancement.

Mike Bradford presented the third section on guidelines for the management of genetic risk. He focused his discussion on the Proportionate Natural Influence (PNI) an heuristic used to quantify the wild/hatchery genetic equilibrium in wild populations. The presentation covered the application of PNI in the United States by the Hatchery Scientific Reform Group (HSRG) and some discussion of the application of this approach in Canada.

In the fourth presentation Carrie Holt described the simulation model that was used in the working paper. She described the model components, parameters and assumptions used to predict changes in PNI metrics relative to different hatchery management actions. She then presented a series of figures demonstrating the predicted relationship between management actions and PNI outcomes. The results of a diversity of sensitivity analyses formed a significant component of this presentation, which concluded with a discussion of model limitations including uncertainties in the simulation modelling exercise, effects of the assumptions on outputs, appropriate and inappropriate uses of PNI.

Carrie Holt also presented the 10 recommendations in the working paper grouped under 3 different principles of development of goals for hatchery influenced populations, scientifically defensible hatchery programs and ongoing monitoring and evaluation.

PRESENTATION OF WRITTEN REVIEWS

JEFF HARD

Please refer to Appendix E for full written review.

Jeff Hard appreciated the approach taken and the thoroughness of the modeling conducted by authors. He acknowledged the limitations of the work in general were mostly the result of the limited scope of the objectives. Beyond that most of his comments related more to future work or were more editorial in nature.

Main Considerations

1. The approach of the model and the use of PNI are relatively simplistic tools; limited in their ability to accurately predict or incorporate the broader scope of genetic risk posed by salmon hatchery propagation. Authors should clarify that differences in performance of hatchery and wild fish in the natural environment can reflect several environmental and genetic factors.
2. Model is not explicitly genetic; in its focus on a generic phenotype, the relationship between PNI and fitness is complex and can be difficult to characterize adequately.

-
3. PNI is very sensitive to proportion of hatchery spawners in the wild (pHOS) and accurate estimation of this is difficult.
 4. Model does not account for the legacy effects of hatchery propagation or longer term, cumulative genetic change.
 5. The use of a deterministic model over a very long period of time is insensitive to the natural fluctuations that can occur in many of the model parameters. Recommend an expanded sensitivity analysis; ultimately, the use of a stochastic model merits development.
 6. Selection parameters (directional vs. stabilizing) and Relative Reproductive Success require further investigation to support the way they are used in the model.
 7. Authors should include guidance on how to evaluate the tradeoff between genetic risk from hatchery propagation and increased abundance to support harvest.

PATRICK O'REILLY

Please refer to Appendix F for full written review.

Patrick O'Reilly introduced himself as a geneticist, not a modeler. He also noted that very few rivers along the East coast of Canada (Maritimes and Gulf regions) are now stocked at all with Atlantic salmon, and that *in most instances* where hatcheries are used, stocking is carried out primarily for conservation purposes (to prevent the imminent extirpation of river populations).

The reviewer followed and appreciated the working paper and its progression of logic, and found no major problems with the approach, methods, or analyses. His main comment was that there is increasing reason to suspect that *some* (not all) of the loss of fitness between early generation hatchery and wild-origin salmon reported in the literature may be due to non-genetic factors, including environmentally-induced epigenetic effects that may be passed from generation to generation. The relevance here is that these epigenetic effects may have impacted estimates of selection and heritability of fitness estimates obtained from the literature, and used in the model

The reviewer mentioned that although there is not currently a lot of information available to allow for the incorporation of possible epigenetic effects into model, perhaps the authors could briefly speculate (in one or two sentences) on what the effects of possible undetected epigenetic influences might have been on estimates of heritability and selection produced in the literature, and used in the model, and how this might have impacted the modelling results.

Main Considerations

1. Some of the model parameters are extremely difficult to estimate e.g. heritability and selection, and that research indicates that these values can vary significantly from study to study and across environments in which they are assessed.
2. There is a risk of interpreting epigenetic change as genetic change. It is important that the advice include a broader discussion of the implications of genetic vs epigenetic impacts of enhancement.

AUTHORS RESPONSE TO REVIEWERS

- Authors response on epigenetic issues continued the academic theme of the discussion. It is acknowledged likely that epigenetics play a much stronger role than previously understood relative to reductions in fitness observed with enhanced fish. New research is emerging all the time on these topics.

-
- There was further discussion of the components and contributions of epigenetic effects including short term methylation versus long term stressors, transgenerational effects, plasticity and its adaptive importance and reversal of epigenetic effects.
 - Discussion of epigenetics is important, and it is too simple to assume that everything reverses, the long term accumulation of change needs to be considered. Also, changes to the phenotype as a result of hatchery breeding could prevent the flow of potential fitness enhancing genes to the wild population.
 - Authors acknowledge that the paper likely doesn't give enough attention to demographic related genetic diversity effects, and will include more discussion on loss in general genetic diversity.
 - Authors acknowledged that RRS was used in the model as more of a correction factor, combining multiple different fitness effects, rather than changes in RRS alone.
 - Authors identified that the sensitivity analyses had demonstrated the relative robustness of the model, and noted that the three parameters related to phenotypic optima are all inter related. More parameters could potentially be included.
 - Authors were uncertain that directional versus stabilizing selection would have a strong effect on the results, but agreed that they may need to be considered more carefully in future work.
 - Authors thanked the reviewers for their positive comments, and noted that due to some of the general questions raised and the rapidly evolving nature of the knowledge around this topic, the recommendations of this paper should be revisited soon.

GENERAL DISCUSSION

EPIGENETICS

- It is clear from the literature that hatcheries cause a reduction in fitness, sometimes quite strongly. Sometimes the observed strength and speed of these effects cannot be attributed solely to genetic factors. Epigenetic effects are a plausible contributor.
- Forthcoming research shows increased methylation of genes in hatchery fish, which is associated with down-regulation of genes without a change in the base genetic structure.
- It is unclear how this might impact the results of this advice. Genetic and Epigenetic effects have different long term fitness outcomes.
- Genetic change is always occurring, but epigenetic change is superimposed over this, and epigenetic change occurs most strongly in the first generation, but the transgenerational effects of these changes are debatable and it's not clear how and if reversal of these changes occur.
- Epigenetics are one mechanism for plasticity, and plasticity itself may be heritable.
- It is too easy to assume that plastic changes are reversible, however, the cumulative genetic effects of fish not contributing genetically because of epigenetic effects are unknown.
- It is important to acknowledge that not all changes in fitness are genetic.
- There was uncertainty regarding whether or not the discounting effect for hatchery fish in the model, can account for potential epigenetic effects.

RELATIVE REPRODUCTIVE SUCCESS (RRS)

- The use of the term RRS in the research doc is likely not appropriate. It is more of a “fudge factor” used in the model to account for an amalgam of different factors, and therefore is not strictly “RRS” as it has been applied in previous studies.
- It is accepted that hatchery fish have less reproduction success in the wild, regardless of the mechanism. A model correction factor is necessary to capture this.
- The correction factor does not influence the model strongly, and as such serves more as a placeholder. It is applied in the spawning phase, however there are other discounting effects in other stages of the model.
- There was some discussion about the difficulty in determining the values and mechanisms underlying RRS in the wild. There is need for more research to evaluate this, however it is beyond the scope of this process.

PHOS (EFFECTIVE VS CENSUS)

- The use of pHOscen (a measure of total number of individuals) versus pHOseff (a measure incorporating a correction factor for reproductive success) was discussed briefly.
- The US Hatchery Science Reform Group recommends use of pHOseff to account for non-genetic factors effecting RRS.
- There was confusion about the use of RRS correction factor in the model and PHOseff; the authors provided clarification that the application of RRS in the context of their working paper was as a general correction factor, as noted above (RRS section). General consensus was to continue using PHOseff in the model, and rename RRS to a more generic term like ‘correction factor’.

SELECTION AND OTHER MODEL PARAMETERS

- Sensitivity testing of many of the model parameters was conducted, including selection strength, and the model was relatively insensitive to most of the factors. The most significant factor is relatively hatchery size.
- It was noted that based on figures presented in the working paper it appears that the most effective tool available to hatchery managers is to reduce hatchery size. Participants asked if there were other potential management tool options available that had not been modelled. Through discussion no further management tool options were identified.

CLARIFICATION OF PNI

- There was some discussion about the use of PNI, with general agreement that it is a relatively “blunt” tool (metric), however it was agreed that at this time the PNI is the best tool available to meet the objectives of this request for science advice.
- Participants noted that it is important to clarify that PNI is not a measure of fitness which is difficult to obtain; rather, it is a measure of the contribution of hatchery selection versus natural selection, and it is unlikely to capture or quantify all the potential genetic risk associated with hatchery influences in wild Chinook Salmon populations.
- Participants agreed that it was important to emphasize the HSRG recommendation that PNI should be calculated over a minimum of 5 years, and to note that PNI is not to be used tactically, but, rather is intended to be used to inform strategic decisions.

MODEL STOCHASTICITY

- There was some discussion about the length of the model run and choice of a deterministic versus a stochastic model. A stochastic model could include varying selection parameters over time to mimic the variability in real world selection pressures.
- There was general agreement that a long term stochastic model would be beneficial but not necessary for the objectives of this process. The deterministic model was sufficient for the current questions.

DEFINITION OF WILD AND IMPACTS OF STRAYING

- There was some discussion of the definition of “wild” used in the working paper as per the wild salmon policy, however this advice is not dependent on that definition and can be applied regardless of how managers decide to define wild.
- Participants agreed that the use of integrated and segregated hatchery definitions in the working paper is consistent with their use by the HSRG.
- The impacts of straying, particularly on the west coast of Vancouver Island were discussed at length. It is understood that straying is occurring, potentially to significant impact, however it is very difficult to account for or incorporate in the current decision making framework.

FUTURE WORK CONSIDERATIONS

- Potential future work options were discussed, including:
 - Improve model with stochasticity
 - Investigate cumulative effects of multiple traits
 - Underlying mechanisms of reduced RRS in hatchery fish and relationships with other life history characteristics
 - Develop finer metric than PNI eventually
 - Investigate three way interaction of straying, hatchery and natural

Additionally, several participants requested that PNI values be calculated for BC hatchery programs, or that the research needed to acquire the information to be able to calculate PNI values be identified.

OTHER CONSIDERATIONS

- Implementation concerns of these categories being applied to BC discussed at length. Multiple proposals to include wording of how the recommendations should be implemented, however these were deemed out of scope of the objectives for the process.
- Participants stressed the importance of acknowledging, in the SAR and in the working paper, that hatcheries and hatchery planning do not exist in isolation. There was interest in how current hatcheries fit within the proposed categories.
- Develop guidelines for hatchery programs with a conservation purpose.

CONCLUSIONS

- The working paper was accepted with the minor revisions listed in the next section.

-
- The general consensus was that while PNI and the chosen modelling methodology had identifiable shortcomings, they were the best choice among the alternatives and appropriate to meet the objectives laid out in the terms of reference.

REVISIONS FOR WORKING PAPER

- Change use of RRS to correction factor in model and include some more discussion about components of correction factor relative RRS
- Clarify use of $pHOS_{census}$ vs $pHOS_{eff}$ re: discounting effect of “RRS” correction factor
- Clarify use of PNI is at population level and recognize that this may not reconcile with CU level
- Expand the literature review to include more discussion on loss in general genetic diversity in regards to demographic effects, brood stock management as well as stabilizing versus directional selection
- Include new published data from HSRG in discussion
- Include 1-2 sentences speculating on genetic-based selection vs. epigenetic effects
- Clarify that hatchery size refers to hatchery population size, not physical size
- Include current hatchery sizes as histogram (or in future work)
- Clarify use of “visual” marking in the paper, develop marking recommendations more explicitly
- Model wider ranges of RRS, and heritability
- Modify recommendation #1 to align with table on pg 36 of working paper and WSP (rephrase “not effected by enhanced”)
- Recognize uncertainty with recommendation of time to re-evaluate given rapid research in field
- Clarify in recommendations that any changes must be handled in integrated way, not in isolation from habitat and harvest (this idea in body text but not explicit in recommendations)
- Clarify use of integrated management vs. integrated hatchery population terminology re: recommendation 6
- Avoid adaptive management language re: recommendation 10

ACKNOWLEDGEMENTS

CSAS would like to acknowledge the many significant contributors to this effort including external reviewers Patrick O'Reilly and Jeff Hard, authors and presenters Ruth Withler, Mike Bradford, David Willis and Carrie Holt, chair Lesley MacDougall and assistant Erika Anderson.

APPENDIX A: TERMS OF REFERENCE

EVALUATION AND UPDATE OF BIOLOGICALLY-BASED TARGETS FOR ENHANCED CONTRIBUTIONS TO CHINOOK POPULATIONS

Regional Peer Review Process – Pacific Region

August 31 - September 1, 2017
Nanaimo, British Columbia

Chairperson: Lesley MacDougall

Context

DFO's Salmonid Enhancement Program (SEP) has guidelines for hatchery program management that have been in place for many years in the Pacific Region, and have been used as part of an integrated enhancement planning process to address multiple biological and socioeconomic objectives. Whereas over-arching SEP objectives are commonly framed in broad socioeconomic terms; management of risk to natural populations requires a detailed assessment of the nature, degree and duration of enhancement on a species, population and site-specific basis .

Key advancements have been made since the implementation of the existing enhancement guidelines, including the development of Canada's *Policy for Conservation of Wild Pacific Salmon* (the Wild Salmon Policy or WSP), the development of SEP's Biological Risk Management Framework (SEP RMF), and collection of new scientific information on the level and nature of direct gene flow and genetic interactions (i.e. based on competition for resources or altered harvest regimes) between hatchery and wild fish. Additionally, the US hatchery reform process (HSRG) highlighted the distinction between 'integrated' and 'segregated' hatchery programs and the need to develop benchmarks consistent with the specific biological objectives set for hatchery programs. The HSRG process also led to the development of the Proportion Natural Influence (PNI) metric as an indicator of the genetic influence of enhancement on a natural population. Chinook Salmon enhancement guideline updates that can be applied at the population level are required to ensure that: (a) guidelines can be developed to manage risk to fitness of natural populations resulting from the genetic influences of co-existing hatchery-origin salmon, (b) hatchery Chinook Salmon programs are planned and managed in a manner to better acknowledge and quantify biological risk while achieving the socio-economic benefits of enhanced fish, and (c) the biological risks of hatchery enhancement can be more transparently evaluated against the intended socioeconomic benefits.

DFO's Salmonid Enhancement Program requested DFO Science provide advice on genetically based targets for enhanced contributions to Chinook Salmon populations. This advice will reflect new Canadian policy, new genetic information, assessment tools, and measurement metrics for the genetic effects of hatchery rearing and enhancement on wild fish. The advice will be used to support management of the genetic risks associated with the current types of enhancement programs in the context of Canadian policy, fisheries, and hatchery management, as well as provide a framework to better quantify the potential genetic risks of enhancement to wild populations and allow for explicit decision making regarding trade-offs between risk and socioeconomic benefit.

Objectives

The following working paper will be reviewed and provide the basis for discussion and advice on the specific objectives outlined below .

Withler, R., Bradford, M., Willis D., and Holt, C. 2017. Genetically Based Targets for Enhanced Contributions to Canadian Pacific Chinook Salmon Populations. CSAP Working Paper 2013SEP02.

1. Review the current scientific understanding of observed and potential genetic risks to wild populations associated with hatchery propagation .
2. Describe categories of biological status for enhanced Chinook Salmon populations measured in terms of proportion of wild fish as defined in the Canadian WSP. Describe how to assess hatchery influence on Chinook Salmon populations, using the Proportion Natural Influence (PNI) metric, including its rationale and its applicability to the Canadian context .
3. Provide advice on quantitative benchmarks for the PNI and/or other appropriate metrics for the biological categories of status, and management measures to achieve those benchmarks .
4. Summarize the information and analyses needed to implement the PNI-based genetic risk management guidelines.
5. Summarize advice and guidance for development of new enhancement guidelines .

Expected Publications

- Proceedings
- Science Advisory Report
- Research Document

Expected Participation

- Fisheries and Oceans Canada (DFO) (Science, Fisheries Management, and Salmonid Enhancement Program)

APPENDIX B: WORKING PAPER ABSTRACT

The Wild Salmon Policy (WSP) establishes conservation of wild Pacific salmon and their habitat as the highest priority for Pacific salmon resource management decision-making. Hatchery production in the Salmon Enhancement Program of DFO is used as a conservation tool for wild populations and can increase the availability of fish for harvest but is a risk factor to wild genetic diversity that requires management and mitigation to safeguard Pacific salmon biodiversity in Canada. We recommend use of the proportionate natural influence (*PNI*) and associated metrics developed by the U.S. Hatchery Scientific Review Group to evaluate and monitor the adaptive state of integrated hatchery populations and to identify hatchery-influenced populations that might be included in WSP assessments. We develop a classification system for Canadian Pacific salmon populations that reflects the adaptive state of the population based on constituent proportions of natural- and hatchery-origin fish. Among the biological categories, increased genetic risk is associated with increasing hatchery influence and a decreasing proportion of wild fish. We modelled the population dynamics of a Chinook Salmon population including the genetic impacts on fitness from hatcheries to evaluate the use of three management measures - hatchery size, proportion of hatchery fish marked, and proportion of marked fish selectively harvested - in managing to a target *PNI* level. Except for populations at risk of extirpation, limiting hatchery size by scaling the size of the hatchery to natural production is an effective way to minimize genetic risk of enhancement to wild populations. Limiting hatchery size also limits the production of fish for harvest, resulting in a trade-off between genetic risk and socioeconomic benefit in enhancement programs implemented for harvest augmentation. Genetic risk associated with higher levels of hatchery production can be minimized by reducing the proportions of hatchery-origin fish included in the hatchery broodstock and/or allowed to spawn in the natural environment. Manipulation of proportions of natural- and hatchery-origin fish is dependent upon some type and level of marking that allows pre-spawning differentiation of fish originating from the two spawning environments. In conservation programs, the risk of domestication occurring at low *PNI* values must be balanced against the genetic and demographic risks of small population size in the absence of high proportions of hatchery-origin fish. We provide recommendations for the classification and management of enhanced populations consistent with the principles of developing explicit biological goals for hatchery-influenced populations, implementing scientifically defensible hatchery programs and using adaptive management of hatchery programs to meet objectives in a risk averse manner.

APPENDIX C: AGENDA

Canadian Science Advisory Secretariat

Centre for Science Advice Pacific

Evaluation and update of biologically-based targets for enhanced contributions to Chinook populations

August 31 - September 1, 2017

Pacific Biological Station, Nanaimo BC

Chair: Lesley MacDougall

DAY 1 – August 31, 2017

Time	Subject	Presenter
0900	Introductions Review Agenda & Housekeeping CSAS Overview and Procedures	Chair
0915	Review Terms of Reference	Chair
0930	Presentation of Working Paper	Authors
1030	Break	
1050	Continue Working Paper presentation	Authors
12:00	Lunch Break	
1300	Review 1	Patrick O'Reilly / Authors
1330	Review 2	Jeff Hard / Authors
1445	Break	
1500	General discussion – Working Paper, Reviews, Major points	RPR Participants
1630	Continue discussion – identify major points	RPR Participants
1700	Adjourn for the Day	

DAY 2 - September 1, 2017

Time	Subject	Presenter
0900	Introductions Review Agenda & Housekeeping Review Status of Day 1	Chair
0945	Carry forward outstanding issues from Day 1	RPR Participants
1000	Develop Consensus on Paper Acceptability & Agreed-upon Revisions	RPR Participants
1030	Break	
1050	<i>Science Advisory Report (SAR)</i> Develop consensus on the following for inclusion: <ul style="list-style-type: none">• Sources of Uncertainty• Results & Conclusions Additional advice to Management (as warranted)	RPR Participants
1130	Lunch Break	
1300	<i>Science Advisory Report (SAR)</i> Develop consensus on the following for inclusion: <ul style="list-style-type: none">• Sources of Uncertainty• Results & Conclusions Additional advice to Management (as warranted)	RPR Participants
1445	Break	
1500	Next Steps – Chair to review <ul style="list-style-type: none">• SAR review/approval process and timelines• Research Document & Proceedings timelines• Other follow-up or commitments (<i>as necessary</i>)	Chair
1545	Other Business arising from the review	Chair & Participants
1600	Adjourn meeting	

APPENDIX D: PARTICIPANTS

Last Name	First Name	Affiliation
Ackerman	Paige	SEP - RHQ
Anderson	Erika	Science
Ayers	Cheri	Cowichan Tribes
Bailey	Richard	Science - Salmon Fraser River
Bocking	Robert	LGL
Bradford	Mike	Science
Brown	Gayle	Science - Salmon Core
Campbell	Kelsey	Atlegay
Candy	John	Science
Churchland	Carolyn	SEP - RHQ
Desrochers	Dale	SEP - South Coast
Dobson	Diana	Science - Salmon South Coast
Dunlop	Roger	Nuu-chah-nulth Tribal Council
Fraser	Kathryn	Science - MRP
Gale	Rupert	SFAB
Godbout	Lyse	Science - QAM
Grant	Sue	Science - Salmon Fraser River
Grout	Jeff	Fisheries Management - RHQ
Hard	Jeff	NOAA Washington North Fisheries Science Centre
Holt	Carrie	Science - Salmon Core
Holt	Kendra	Science
Huang	Ann-Marie	Science - Salmon Team
Hyatt	Kim	Science - Salmon Core
Irvine	Jim	Science - Salmon Core
Jenewein	Brittany	Science
Kennedy	Eddy	Science
Luedke	Wilf	Science - Salmon South Coast
Lynch	Cheryl	EMB - SEP
MacDonald	Bronwyn	Science
MacDougall	Lesley	Science - CSAS
Mahoney	Jason	SEP - RHQ
Maxwell	Marla	Fisheries Management - Fraser River
McDuffee	Misty	Raincoast/Pacific Marine Conservation Caucus
McHugh	Diana	Science - Salmon South Coast
O'Reilly	Patrick	Atlantic DFO
Parken	Chuck	Science - Salmon Fraser River
Porszt	Erin	Science - Salmon South Coast
Riddell	Brian	PSF
Rosenberger	Andy	Pacific Marine Conservation Caucus/Lake Babine Nation Fisheries

Last Name	First Name	Affiliation
Schut	Steven	Science
Staley	Mike	FRAFS
Tadey	Joe	Science DFO
Taylor	Nathan	Science
Thiess	Mary	Science
Tompkins	Arlene	Science - Salmon Core
Townsend	Matthew	Science - Fraser
Willis	David	EMB - SEP
Winther	Ivan	Science - Salmon North Coast
Withler	Ruth	Science - Salmon Genetics

APPENDIX E: WRITTEN REVIEW BY JEFF HARD

Date: 18 August 2017

Reviewer: Jeffrey J. Hard, U.S. National Marine Fisheries Service, Northwest Fisheries Science Center CSAS Working Paper: 2013SEP02

Working Paper Title: Genetically Based Targets for Enhanced Contributions to Canadian Pacific Chinook Salmon Populations

General Comments:

First, I would like to express my appreciation to the organizers for the opportunity to review this report. It is an impressive piece of work—well organized and clearly written—and I believe it will be central to the efforts of the Department of Fisheries and Oceans and the Salmon Enhancement Program to carefully evaluate Chinook salmon enhancement and supplementation programs in Canada. The report clearly reflects a careful review of the current science and a considerable amount of thought by the authors as they attempted to adapt principles and concepts applied in the U.S. Pacific Northwest to the situation in Canada. Although the document is highly technical in places, it is presented in a way that the core ideas should be accessible to readers with diverse backgrounds and experience in evaluating salmon culture programs for potential effects on wild production.

The overarching objective of this report is to identify scientifically based guidelines for enhancement of Canadian Chinook salmon that minimize genetic risk to wild populations. In it the authors conduct a timely and rather comprehensive review of the current scientific understanding of genetic risks to wild salmon associated with hatchery propagation. They use guidelines from the Canadian Wild Salmonid Policy to describe the biological status of natural populations associated with different levels of hatchery production, as indexed by the proportion of wild fish among spawners. They recommend threshold criteria for this index and associated metrics, such as the proportion of hatchery fish on spawning grounds, and provide some management advice for how to meet these criteria and develop revised guidelines for integrated hatchery program operations in Canada. The report's recommendations are limited to genetic risk of hatchery propagation and do not directly address concomitant ecological risk, and the genetic risk evaluated in it does not address indirect or legacy effects of hatchery introgression. The report provides recommendations associated with the three major types of genetic risk to wild populations: loss of within-population diversity, loss of among-population diversity, and loss of fitness (typically measured as lifetime reproductive success).

I found this document to be a rather comprehensive approach to evaluating several key parameters that heavily affect the genetic influence of hatchery fish on associated natural populations and to characterizing the importance of the primary control measures at managers' disposal to mitigate this influence. The modeling that is at the heart of this document is, I believe, well thought out and clearly described and summarized. I have a number of specific comments about the approach and the discussion of the model and its results below, but overall I found this to be a thoughtful approach to addressing the overarching objective using a relatively simple, deterministic model based on that of Ford (2002). I also appreciated that the authors conducted some sensitivity analyses of several parameters that are thought to have large influences on genetic impacts of hatchery production, and that they were careful to recognize and clearly identify the most important limitations of their model. Ideally, a stochastic model with parameters drawn from distributions that are allowed to change realistically over the time frame considered here (100 generations) would be preferable, but this is an area of research that remains largely unexplored and would be challenging to implement quickly. The authors apparently recognize that the model is largely heuristic and not intended to be predictive

at specific time points; nevertheless, I'd recommend limiting the scenarios explored to 5-10 generations (25-50 years) unless temporal changes in the key parameters are permissible and monitored carefully over time.

The model is based heavily on that published by Mike Ford in *Conservation Biology* in 2002, which itself is an extension of Russ Lande's (1976) classical model of phenotypic evolution. The deterministic model simulates evolution in an effectively infinite population exposed to two distinct environments with natural and artificial selection operative but without any explicit genetics; it is based on the seminal work of Fisher (1918, 1958), who assumed very weak selection on a trait phenotype that is influenced both by environment and by a large number of unspecified loci of very small effect (the 'infinitesimal' model).

A primary focus of this document is on PNI (proportionate natural influence), a metric that reflects the influence via gene flow between natural fish (defined as fish that were born in the wild from naturally spawning parents) and a hatchery broodstock. PNI also tends to reflect the relative productivities of the two environments. The Hatchery Scientific Review Group (HSRG) also focused on PNI, for which they derived critical values based on the relationship between pNOB and pHOS. pHOS, the proportion of hatchery-origin fish spawning naturally, is a critically important component metric for an associated natural population and must be monitored independently to fully assess and minimize genetic risk. In many cases, pHOS is assumed or estimated based on rack counts or hatchery returns, but PNI recommendations are more realistic and effective if pHOS can be estimated more accurately through spawner surveys or, preferably, parentage studies. The combination of these two metrics determines the gene flow between the hatchery and natural components and thereby the potential for natural selection, for genetic and phenotypic divergence, and for overall diversity and productivity of each component.

I think this report will prove to be very useful in evaluating the potential effects of current salmon hatchery programs on natural populations in Canada—along the lines of the HSRG process in much of the U.S. Pacific Northwest—and in recommending specific changes to them in terms of scale and operation going forward. Personally, I would love to see a modification of this or a similar model made available on the web for ready exploration by managers and researchers. I urge the authors to refine their model code to provide a user-friendly web-based interface to allow managers and researchers to manipulate key model parameters using the 'Shiny' R package, so that these users could interactively manipulate key parameters such as pHOS, heritability, selection strength, and relative reproductive success, and examine their individual and collective effects on PNI, pNOB, spawner recruits, catch, and estimates of natural productivity in real time. A simple example of a [Shiny interface](#) for a plotting program; the code could easily be modified to generate 2D contour plots. There are other examples of contour plot/response surface applications with Shiny. A Shiny interface would allow a user to directly change one or more control inputs using programmer-constrained (i.e., realistic) values drawn from distributions and quickly see the plotted results.

A reader might infer from the report that the HSRG approaches are American approaches. A policy colleague of mine has reminded me that while the HSRG was federally funded (through influential Washington members of the U.S. Congress), acceptance of HSRG guidelines has been spotty. They are generally policy in the state of Washington; are applied or not applied locally in Oregon, and are widely accepted in Idaho. California is a mixed bag because of the more flexible approach taken there.

Acceptance of HSRG guidelines among groups with strong fishing interests has generally been low. The basic problem is that strict application of pHOS and PNI guidelines in Endangered

Species Act applications makes many harvest-oriented programs seem oversized. These issues are still being worked out.

In response to the guiding questions for the review, I found that

- the objectives of this report are clearly outlined, concise, and closely aligned to the Terms of Reference for this CSAS review;
- in general, the approach taken in the report to identify biologically based genetic targets for enhancement of Chinook salmon in Canada is thoughtful, comprehensive, and a sensible extension of the Hatchery Scientific Review Group (HSRG) guidelines for management of hatchery salmon populations in the U.S. Pacific Northwest;
- the data, methods, and results are explained in sufficient detail to provide a means to assess the report's conclusions and their limitations;
- the recommendations provided at the end of the report are aligned well with the objectives described in the Terms of Reference, and—while overall they are quite general—the recommendations describe a concise set of clear actions to take in initiating, monitoring, or managing hatchery propagation. I would have like to have seen more detailed recommendations in some instances, but I recognize that these would typically need to be made on a case-by-case basis after evaluating the information for a specific program through, for example, an HSRG-like Hatchery Genetic Management Plan (HSRG 2009);
- the advice provided does incorporate uncertainty associated with several aspects of the model to a reasonable degree, and it is influenced by the sensitivity analyses of several key parameters. I have some recommendations about further developing the model in terms of timeline and structure (i.e., stochastic rather than deterministic; see the detailed comments below), but these would require considerable additional work; I have some suggestions for future research in my detailed comments below. Foremost among these are to 1) explore selection on multiple, correlated traits that are known to be influenced by hatchery domestication: e.g., adult salmon age, size, fertility, and phenology (run and spawn timing), in addition to stage-specific survival (freshwater, marine); and 2) allow for direct evaluation of relative reproductive success (RRS) on genetic risk through manipulation of an RRS parameter in the model. There are a couple of reasons for this: 1) indirect assessment of the effects of RRS through its influence on PHOS and, thereby, PNI can be problematic through inflation of PNI (see detailed comments below); and 2) I'd recommend that the model output be evaluated as a function of a range of RRS values as well (e.g., 0.2-0.7 vs 0.8 only), based on what we now know from studies of Chinook salmon.

My detailed comments on the report, referencing specific passages in order, are provided below. Although they are rather lengthy, most of them relate to details that do not detract from the general findings of the report, and many focus on minor modifications suggested for the modeling or suggestions for further model development. Most of them are provided simply for the authors' consideration.

Detailed Comments:

The growing scientific literature on relative reproductive success (RRS) of hatchery and wild salmonids is key to understanding the consequences of hatchery production for natural populations. This literature, which has burgeoned with the growing accessibility of tools to assess parentage and other close relationships among individuals in the wild, has focused primarily on steelhead (*O. mykiss*), Chinook salmon (*O. tshawytscha*), coho salmon (*O. kisutch*), and Atlantic salmon (*Salmo salar*). It is important to recognize that there may be considerable variation in RRS among species, populations, and habitats, as well as temporal variability owing

to environmental change. The literature suggests that strong and rapid declines in fitness due to hatchery propagation are possible, and that environmental (e.g., habitat selection) as well as genetic effects may be responsible for these declines.

I see no mention of the Ryman-Laikre (R-L) effect. In the salmon hatchery context, this is a correlate of PNI that is relevant to the issue of maintaining diversity in a naturally spawning aggregate where genetic contributions of parents in the components can differ considerably. [Edit: I see that this concept is touched upon at the top of p. 21 (but not identified as R-L), where Christie et al. (2012) is cited.]

p. 12: “This approach allows for gene flow between the hatchery and the natural population components as a means of mitigating potentially negative effects of genetic divergence (DFO 2013b).” This and the findings of Waters et al. (2015) are consistent with the idea that gene flow between the hatchery and natural populations may limit the rate of domestication selection. However, I think it is important to note that integrated hatchery production does not by itself adequately account for the loss of fitness due to eroded local adaptation that can stem from domestication in the hatchery. Furthermore, the methods applied in that paper may detect genetic signals that are consistent with selective change but they are not directly indicative of selection.

p. 14: As stated in the report, enhancement for harvest objectives can result in hatchery programs that are closer to segregated than integrated, although there is no formal intent to prevent hatchery-origin spawners from remaining in the natural environment. This issue centers on one of my primary concerns about the current status of guidelines for pHOS for production or transitional hatchery programs.

Existing general guidelines from A Compilation of Operational and Planning Guidelines for the Salmonid Enhancement Program: pHOS \leq 50% (to limit potential for interbreeding between hatchery and natural spawners), \leq 30% of river return taken into hatchery broodstock (to limit “mining” of natural broodstock). For conservation programs, the latter metric could be up to 50%. If natural productivity is not likely to be compromised, in general for integrated hatchery programs pNOB should be as large or larger than (1-pHOS) or p(NN). The modeling in the report addresses how variability in these metrics can be influenced by fitness of naturally spawning fish, through the pHOSeff metric, but I would like to see a more direct assessment of how knowledge of RRS would be used to identify demonstrable PNI and pHOS criteria.

As stated, there is also currently no specific guidance on the appropriate duration of enhancement, on biologically based thresholds to trigger transition from conservation to rebuilding programs, or for management of risk tolerance. These are issues I hope will also be addressed soon, as they are all important tools that can limit the effects of hatchery propagation on natural production.

p. 15: “Large scale ecological interactions between hatchery and natural salmon have been identified as a concern in Prince William Sound (Amoroso et al. 2017), as has straying of hatchery Chinook Salmon into non-natal streams, but hatchery guidance based on the risks of gene flow between hatchery- and natural-origin fish has not been developed, thus providing little of use in the Canadian context.” This is not strictly true; the Alaska Department of Fish & Game has had a longstanding finfish genetic policy in place to regulate aspects of hatchery salmon production (maintenance of genetic variability in hatchery and wild stocks and protection of wild stocks from hatchery strays and broodstock mining) and fish transport among regions and watersheds (ADF&G 1985). The policy provides general guidance to reduce risks of gene flow between hatchery and wild fish in the state. ADF&G, in conjunction with processors and salmon producers, is also currently supporting a [large-scale research](#) effort to estimate RRS in pink and

chum salmon in Prince William Sound and southeastern Alaska to address concerns about the impacts of hatchery salmon production on wild salmon productivity in the state.

p. 16 (Sec. 2.2): I should note that "supplementation" has a more specific meaning here in the U.S.; it is used only for programs where the intent is to use hatchery technology to increase natural production.

p. 17: The point is made that in Canada salmon hatchery programs are typically operated as integrated programs because facilities in most watersheds are incapable of limiting hatchery fish from spawning naturally due to lack of weirs, etc., even when complete marking could be achieved. In this case one needs to consider carefully, on a case by case basis, the likely trade-offs between reducing opportunities for interbreeding (keeping hatchery-produced fish and wild fish as separate as possible to reduce adverse genetic and ecological interactions, as intended for some segregated hatchery programs) and reducing the consequences of interbreeding when it does occur (attempting to keep hatchery and wild fish as similar as possible to minimize the adverse effects of introgression of "maladapted" hatchery genes into wild genomes, as intended for integrated hatchery supplementation programs).

p. 18-20 (Sec. 2.3): This is a concise summary of the factors that can influence the fitness of naturally spawning hatchery fish. The literature it is drawn from is based heavily on steelhead and Chinook salmon studies from the Columbia River basin. A prominent and widely cited example: researchers examining RRS in steelhead from the Hood River in the basin have found that RRS of hatchery fish in the natural environment is typically considerably less than natural fish in that environment, and that such declines in fitness can occur within one or two generations of propagation in the hatchery, presumably due to adaptation to the hatchery environment (domestication selection via genetic or epigenetic mechanisms). I am not convinced this is a general result for salmonids, but it might be common for a species like steelhead.

This section is key to how the guidelines reflect the available science on this topic. That said, there is a focus on potential genotype-phenotype mismatch, which—while I find this a tantalizing and reasonable hypothesis—I also find it somewhat speculative. What nearly all RRS studies to date that I am aware of are not identifying rigorously is how natural selection is actually operating in the two environments. This seems to me to be an important information gap that needs to be more fully addressed, ideally incorporated directly into hatchery monitoring programs. Characterizing the form and intensity of selection, based on lifetime reproductive success as a proxy for fitness, will be critical to evaluating alternative hypotheses for the mechanisms of reduced RRS in hatchery-produced fish. I agree with the authors that there are several features of most hatchery programs that are likely to reduce RRS but also obscure the actual mechanism(s) responsible, including high pHOS on the spawning grounds, ecological interactions between juvenile or adult hatchery and wild fish (especially at high densities due to high hatchery production), and legacy introgression effects, exacerbated by a limited ability to discriminate hatchery and wild adults (e.g., due to low marking rates) in nature.

p. 19: "Two control factors available for management to avoid or reduce the loss of fitness, and possibly the capacity for self-sustainability, in an integrated hatchery program consist of 1) the maintenance of a certain proportion of naturally-spawned adult fish in the natural environment and 2) the maintenance of a certain proportion of naturally-spawned fish in hatchery broodstock." These factors are pNOS (1- pHOS) and PNI, respectively. Of course, they are not independent of one another; PNI depends on pHOS (and therefore pNOS) as well as pNOB:

"An understanding of the above process has led to the overarching conclusion that in situations in which integrated hatchery supplementation is intended to coexist with (rather than replace) the network of genetically connected but diverse natural spawning populations such as those

comprising a Canadian CU, a primary requirement is limitation of the number of hatchery-origin fish that spawn in the supplemented and surrounding watersheds (McClure et al. 2008, Paquet et al. 2011, Flagg 2015, HSRG 2014, Trushenski et al. 2015).” I completely agree with this statement. Developing guidelines that consider the interaction between PNI and pHOS in determining effective gene flow between hatchery and wild fish is critical to long-term sustainability of natural salmon production.

Ford et al. (2016, PLoS ONE and unpubl. data) and Williamson et al. (2010, CJFAS) have found that in the Wenatchee River, both Chinook salmon and steelhead often have low RRS, but RRS varies among brood years, especially for steelhead. They also found evidence for a strong broodstock effect—a “broad sense” genetic effect—in steelhead there, with RRS lowest when one or both parents were of hatchery origin. Again, temporal variability was strongly evident. There was no evidence of a broodstock effect in Chinook salmon in the Wenatchee River, but there was clearly a strong effect of spawning location, an environmental effect, on RRS in that species. Therefore, the species are responding differently to hatchery effects in the same drainage and a common cause of low RRS cannot be assumed.

What does the available evidence for natural selection on spawning salmon indicate? Unfortunately, there is still a dearth of studies that address this topic directly. The studies that do implicate body size or morphology or reproductive phenology (run or spawn timing), with some evidence for selection varying between adult males and females. Natural selection often appears to be relatively weak (standardized selection coefficients ranging from $<0.1 - 0.4$ phenotypic standard deviations, with adequate statistical power to detect selection coefficients as small as perhaps $0.2 - 0.3$ SD) but variable in form (stabilizing, directional) as well as intensity in different years.

p. 21-24 (Sec. 2.4): This section is a sensible summary of the features of hatchery propagation and broodstock selection/collection that need to be considered to weigh the benefits and risks of a program to a naturally spawning population. Consideration of phenotype (esp. those likely to influence RS on spawning grounds, such as spawn timing, age and size) in broodstock selection protocols is central to reducing undesirable changes in a population’s composition that can result from the joint forces of hatchery propagation (broodstock collection and rearing) and selective harvest. The trade-off between harvest and conservation goals in hatchery program management is not always explicitly acknowledged, which is a bit odd to me because one cannot always completely separate the effects of captive propagation and harvest on variation in survival and phenotypic composition.

I agree with the focus on two-way gene flow and on PNI as an appropriate index to help evaluate the potential effects of hatchery fish on natural populations they are associated with. I do not think, however, that PNI is the most direct way to assess the relative strengths of natural selection in the two environments. As mentioned above, this is more accurately assessed directly by estimating RRS from parentage work and associated phenotypic data. When that is not feasible to do, then PNI is an appropriate but potentially far less accurate proxy. My primary concern with relying on PNI as a primary measure of hatchery influence is that it is only indirectly related to phenotypic optima and fitness, two features of a population that determine the direction and rate of adaptive evolution. The relationship between these variables depend on how a model incorporating them is constructed—especially on the assumptions of form and strength of selection around the phenotypic optima associated with hatchery and natural environments. In effect, the choice of PNI amounts to tacitly accepting the fitness costs that it will entail, without a clear understanding of what the full consequences for variation in fitness and phenotype will be.

“Measurements of the RRS for hatchery Chinook Salmon tend to range between 0.8 and 1.0 (HSRG 2014), although lower values have been observed.” Indeed, I think there is growing evidence that lower values may be more common in Chinook salmon. Ford et al. (2016) found RRS values ranging from about 0.2-0.7 for Chinook salmon in the Wenatchee River (cf. 0.4-0.7 for the same system, from Williamson et al. 2010), so RRS can be quite low but as indicated above estimates can vary considerably between cohorts. Another study of Chinook salmon cited in the review paper by Christie et al. (2014) was that of Hess et al. (2012) for Johnson Creek, a tributary of the Salmon River in Idaho. Hess et al. (2012) found RSS estimates that ranged from 0.4-1.3. However, the way that RSS was estimated in that paper was seriously flawed, in my opinion: from the supplementary materials it is clear that the authors estimated RRS after removing potential parents that produced no offspring, which will tend to inflate RRS of hatchery fish. This is an inappropriate way to estimate RRS, in my view. It fails to address the questions: Did the hatchery fish mate successfully? If they did, were their offspring viable? At what stage(s) did they die? Did the characteristics of successfully reproducing hatchery fish differ from those that were unsuccessful? The answers to these questions get at the main features of natural/sexual selection on the spawning grounds, which are important because they determine the evolution of the natural spawning mixture over time. This information would also be essential to consider when comparing productivity of the two groups (e.g., recruits per spawner).

p. 22-5 (Sec. 2.4.3 and 2.5): This is a useful discussion of broodstock protocols and mating practices in the hatchery. The authors are prudent to highlight the importance of maximizing diversity in the hatchery population, especially for supplementation of natural production (as in conservation programs). The discussion of pedigree reconstruction and mean kinship approaches is especially germane to this topic. I would add that maximizing diversity and effective population size and minimizing rate of inbreeding through mating practices should entail some consideration of a Ryman-Laikre effect on the overall diversity in the hatchery-natural composite population, especially in an integrated program framework. By themselves, however, it should be recognized that these measures will not necessarily confer higher fitness in the wild. Achieving that goal will require improved understanding of the mechanisms that influence survival and reproductive fitness and, ultimately, restoring the dominant selective influence of the natural environment. I'd add to the authors' discussion of RRS here to argue that ultimately this will require focused study of the factors that influence selection and subsequent reproductive success in both the wild and hatchery environments. This means systematic monitoring of key phenotypic as well as genetic data at the individual level (e.g., sex, age, size, phenology), and assessment of fixed (or random) factors that could influence RRS (e.g., broodstock, cohort, spawning location, rearing or spawning density). I support the authors' recommendation for visual as well as genetic marking for monitoring diversity and adaptive responses to the environment because of its increased non-lethal capability in the natural environment.

p. 26 (Sec. 3.1): The second paragraph of this section seems a bit strong to me. PNI simply estimates the proportion of natural-origin fish among all spawners in a location; while it is expected to be positively correlated with the degree to which the adaptive influence of the natural environment is dominant, it is not a direct measure of that influence. (There is a reference to a “series of simplifying assumptions”, which are briefly touched on in Sec 3.1.1. Primarily, for the recursion equations in Ford's discrete-generation model, these are that fitness/phenotype is normally distributed with constant variance, that selection on the trait is stabilizing, that changes in the mean trait are due to selection only and that this is not affected by correlations with other traits.) It is more likely to reflect this influence in the case where the natural-origin fish have little or no history of hatchery introgression, which will seldom be known except in carefully monitored, long-term pedigreed populations. That said, the fourth paragraph succinctly captures some of the limitations of PNI as a tool for exploring hatchery influence. The

summary of the Ford model and its relation to Equation 1 in Sec. 3.1.1 is a useful description of their general relationship, although it should be noted that this relationship can break down when selection is not Gaussian or the population component mean phenotypes are far from equilibrium with respect to the optima. Moreover, the Ford model describes the heritability of “fitness” (i.e., lifetime reproductive success), which is modeled at a higher value than has generally been demonstrated for wild populations (e.g., Gustafsson 1986; Merilä and Sheldon 1999, 2000; Teplitsky et al. 2009, MacFarlane et al. 2014). That said, the low estimates of heritability of fitness appear to be due to elevated residual environmental variance rather than depressed genetic variance. (Note: this comment is also relevant to Sec. 4, paragraph 3, p. 39.)

p. 28 (Sec. 3.1.2): Note that relative reproductive success is usually denoted as RRS, not RSS (a typo?).

My colleague Craig Busack at the NMFS West Coast Regional Office had this to say in a discussion about use of effective pHOS:

The method relies heavily on the use of effective pHOS rather than census pHOS. While pHOS is obviously a surrogate for gene flow, and thus it seems logical that any adjustment of pHOS to get closer to gene flow, this may not be the case. The NMFS West Coast Regional Office (WCRO) consulted with Mike Ford on this, and he clearly considers that this type of adjustment may be overly discounting the hatchery effect. As a result, at present, NMFS has limited use of effective pHOS in hatchery consultations. The following language currently appears in all NMFS biological opinions on hatchery programs:

“NMFS feels that adjustment of census pHOS by RRS should be done very cautiously, not nearly as freely as the HSRG document would suggest. The basic reason is quite simple: the Ford (2002) model, the foundation of the HSRG gene flow guidelines, implicitly includes a genetic component of RRS. In that model, hatchery fish are expected to have $RRS < 1$ (compared to natural fish) due to selection in the hatchery. A component of reduced RRS of hatchery fish is therefore already incorporated in the model and by extension the calculation of PNI. Therefore, reducing pHOS values by multiplying by RRS will result in underestimating the relevant pHOS and therefore overestimating PNI. Such adjustments would be particularly inappropriate for hatchery programs with low pNOB, as these programs may well have a substantial reduction in RRS due to genetic factors already incorporated in the model.

“In some cases, adjusting pHOS downward may be appropriate, however, particularly if there is strong evidence of a non-genetic component to RRS. An example of a case in which an adjustment by RRS might be justified is that of Wenatchee spring Chinook salmon (Williamson et al. 2010), where the spatial distribution of natural-origin and hatchery-origin spawners differs and the hatchery-origin fish tend to spawn in poorer habitat. However, even in a situation like this, it is unclear how much of an adjustment would be appropriate. By the same logic, it might also be appropriate to adjust pNOB in some circumstances. For example, if hatchery juveniles produced from natural-origin broodstock tend to mature early and residualize (due to non-genetic effects of rearing), as has been documented in some spring Chinook salmon and steelhead programs, the “effective” pNOB might be much lower than the census pNOB.”

p. 29 (Sec. 3.1.3): I’m a little confused about how selection strength is modeled here. Do the values given ($\omega = 10$ or 100) apply to σ or to σ^2 (as stated in the caption for Fig. 3.2)? The width of the fitness function, ω , is typically given in units of σ . In their reviews of empirical studies, Hoekstra et al. (2001) and Kingsolver et al. (2001) concluded that evidence from natural populations of a variety of taxa indicates that the strength of stabilizing/disruptive selection is typically weak, with a mean near 0, suggesting that stabilizing selection is not more common or

stronger in nature than disruptive selection. But their definition of “weak” appears to be different than the parameter here. Assuming that $1 + \omega^2/E = 20$, where E is the environmental variance (assumed to be 0.5, Turelli 1984), then ω is 3.1. The width of the fitness function ω is related to the quadratic selection gradient Y by approximately $Y = -1/\omega^2$ (Arnold et al. 2001), so that a value of $\omega = 4$ corresponds to a value of Y of about 0.06, close to the median value reported by Kingsolver et al. (2001).

To come to the point (as I realize the above is more detailed than probably warranted for the report), a range of ω from 1σ to 4σ should encompass most selection scenarios, with strong selection being represented by on the order of $1-2\sigma$ and weaker selection by perhaps $4-5\sigma$. This may not be too far off from what appears to be modeled here (strong selection: $10\sigma^2$ or $\sim 3\sigma$; weak selection: $100\sigma^2$ or 10σ), but it should be clarified that this is the case in the DFO model. The strong selection scenario might be somewhat weaker than intended. Anyway, this issue merits some consideration in the modeling.

p. 30 (Sec. 3.2): This section is very useful in describing options available for consideration by managers in manipulating PNI to manage risk of hatchery production to natural salmon populations. It is also a concise review of the HSRG standards in place in the U.S. Pacific Northwest, providing a convenient background for the proposed Canadian approach.

In reviewing the outcomes identified in the first paragraph, I think it’s also important to consider the duration of the hatchery program in terms of tolerating and managing risk to wild populations. All else being equal, a higher PNI might merit recommendation if the hatchery program is long term. It is usually very hard to terminate a program once started, unless that is the intent at the outset, but I believe that option should be on the table. It is difficult to tell whether hatchery supplementation has influenced (helped or harmed) natural productivity while the program is ongoing, unless systematic annual monitoring associated with a carefully reconstructed pedigree is undertaken.

“When more than 60-70% of the broodstock are hatchery-origin spawners increasing natural-origin spawners in the broodstock may be a particularly effective measure to increase PNI.” However, according to Fig. 3.3., the expected increase in PNI is will be more or less commensurate with the increased fraction of natural fish in the broodstock if RRS is ~ 0.8 ; if RRS is substantively lower than that, than improvement in PNI should increase more sharply. Fig. 3.4 shows the effectiveness of removing hatchery fish from natural spawners, which under most circumstances (but especially when pHOS is high) should have a greater influence on improving PNI than would increasing pNOB; however, it does require a reliable means of collecting and sorting adults before spawning.

p. 33 (Sec. 3.3): “Evolutionarily Significant Units (ESUs)”

p. 34 (“Proposed Canadian Approach”): The five designations proposed for salmon populations in terms of degree of hatchery influence and associated genetic management guidelines seem entirely sensible to me, as do the expected values of pHOS, pNOB, and PNI based on the equations provided. Adoption of a pHOS standard of < 0.05 is a prudent step. It is easy to show using Ford's (2002) recursion equations (Eqs. 5 and 6) that a pHOS of 0.05 does not necessarily afford the same limitation of genetic effects as a PNI of 0.67.

In examining the entries and the footnote in Table 3.2 on p. 37, it’s worth noting that the values of h^2 and ω used to estimate PNI when pNOB is 0 are central to the outcomes; my comments on Sec. 3.1.3 are relevant here. I’d strongly suggest expanding a sensitivity analysis of the results to variation in these and the other input variables (RRS, ΘH , ΘW , and σ).

In addition, the disparity between pHOS_{census} and pHOS_{eff} is greatest at intermediate values of pHOS_{census}, and this disparity becomes larger at lower values of RRS unless pHOS_{census}

is very low or very high. For example, at $pHOS_{census} = 0.50$, $pHOSeff = 0.44$ when $RRS = 0.8$, and $pHOSeff = 0.33$ when $RRS = 0.5$.

Because the lower value of RRS may be just as realistic for Chinook salmon based on recent studies, the values for $pHOSeff$ in Table 3.2 merit further reflection if a goal is to be more risk averse in such situations where hatchery fish are known to have lower fitness in nature.

p. 35: “Note that the definition of wild under the WSP requires that both parents of a wild fish also be born in natural environments.” This definition applied under the WSP is more stringent than that generally applied in the U.S., and it is difficult to overestimate its importance. Some in the U.S. have applied the term ‘natural’ for fish born in the wild regardless of parentage. But others can conflate the two terms. I think the WSP definition is a more appropriate use of the term ‘wild.’

p. 38-54 (Sec. 4): The modeling described in this section and in Appendix B is the heart of this document and it is comprehensive and thoughtful. It is also illustrative. I provide more detailed comments below, but I think the authors should consider—probably for a future exercise—using a stochastic rather than deterministic modeling approach, along the lines of a population viability analysis. My main rationale for this recommendation stems from the high levels of variation and/or uncertainty associated with measuring $pHOS$, selection, and reproductive fitness in the wild. Natural selection on phenotypes is notoriously variable in both time and space, lifetime fitness is difficult to estimate without careful, systematic pedigree information, and even $pHOS$ is challenging to ascertain without careful monitoring of spawners. I also have concerns with relying on the outputs of a deterministic model that does not incorporate variation in one or more parameters but evaluates results after an extended projection period (in this case, 100 generations).

Given the goals of many of the Canadian Chinook salmon hatchery programs, I appreciated the attention to trying to scale for analysis the candidate hatchery programs to the size of the natural spawning population and to attempt to maximize $pNOB$, to use external marks to remove hatchery fish from potential spawning through harvest or a weir, and to limit the potential for mining of natural spawners for hatchery broodstock. As the authors note, estimating natural origin abundance, either directly or through intrinsic potential or basin size, is important in scaling new hatchery programs and relying on PNI as an index of genetic risk posed by the hatchery fish.

I found the contour plots (Figs. 4.2-4.4) to be extremely helpful and intuitive in summarizing the sensitivities of PNI , $pNOB$, and $pHOSeff$ to key management control points representing hatchery size, marking rate, and selective removal of hatchery fish. These results demonstrate convincingly that scaling hatchery size to a small fraction of natural production in an associated watershed, especially if combined with a high selective marking rate, is the most effective single tool at the manager’s disposal in reducing short-term genetic impacts on wild fish by controlling PNI , $pNOB$, and $pHOSeff$.

Similarly, Figs. 4.5-4.7 also plainly show the mostly intuitive results of the modeling. It might be illustrative to break down the recruits from river spawners and plot a corollary of Fig. 5 where recruits are limited to natural origin spawners (NOS). But even better, I think, would be to replot Fig. 5 at 3 levels of RRS : e.g., 0.4, 0.6, and 0.8. Given the variability in RRS for Chinook salmon, this seems an issue worth investigating, unless I am missing something.

p. 48-9 (Sec. 4.4): Although I would prefer to see a stochastic approach to simulation of these variables for the reasons stated above, especially over such a long time-frame for evaluation, the sensitivity analyses conducted in the report are helpful in evaluating the relative impacts of

the most prominent model parameters on genetic risk. The results are succinctly summarized in the associated text. Figs. 4.8-

4.11 show, for the management controls described in Figs. 4.2-4.7 (hatchery size, proportion marked, and selective removal of marked fish), the relatively weak sensitivity of PNI to increased heritability of the trait under selection ($h^2 = 0.5$ vs 0.25), reduced strength of selection on that trait ($\omega^2 = 100$ vs 1000), reduced RRS of hatchery fish spawning naturally (RRS = 0.5 vs 0.8), and lower marine survival for both hatchery (0.001 vs 0.0024 vs 0.005) and natural fish (0.01 , 0.02 , and 0.05).

I do wonder about some of the plots in Fig. 4.11. For example, I did not expect to see the contour pattern in panels (a), (d), (g), and (j), and further explanation may be helpful. The progression appears to demonstrate the strong dependence of PNI on natural marine survival—or, more precisely, the differential between hatchery and natural marine survival.

I've noticed from the values in Appendix Table B-1 that the phenotypic variance, optimal trait values in the two environments, and the strength of selection modeled indicate that the population optima are 6 SDs apart, or about 60% of the width of the fitness function under strong selection. Under weak selection, the optima are < 20% of the width of the fitness function. I think the range of values simulated in this section are reasonable, except perhaps that 1) both of the selection strengths modeled could be considered “weak” and it might be worth simulating a situation where the selection coefficient is stronger, on the order of 0.5 - 1.0 phenotypic SD (I realize that the values modeled in this document stem from those in Ford (2002), and 2) the range of heritability for “fitness” is too high, and is probably more realistic between 0.05 and 0.25 (other single-trait phenotypes, such as size and phenology, will likely have heritabilities in the range modeled here, 0.25 - 0.50). Another issue worth noting, specific to the Ford (2002) model, is that selection is always considered stabilizing in these scenarios. However, most of the work I am aware of on natural salmon populations where selection has been estimated has demonstrated that selection is often directional, sometimes more frequent than stabilizing. This probably reflects moving rather than stationary optima, especially in the wild. Domestication selection, at least in its initial phases, may be predominantly directional in character, and stabilizing selection around a temporally fluctuating optimum can invoke a fair amount of directional selection on a short time scale of perhaps a generation or two. This is a rich area for future investigation.

p. 54: “This model describes long-term, equilibrium impacts on fitness of integrated hatchery system (Ford 2002). As such, it can provide strategic guidance on choice of the management levers to reduce genetic impacts on naturally spawning populations, but not short-term or tactical advice that requires information on time-trends or inter-generational variability in population fitness, genetic impacts, and/or PNI.” This is an important qualification of the modeling results that I'm glad that the authors included here.

p. 58-9 (Sec. 5.3): This part of the report describes the HSRG 4-stage conservation program concept. While this concept seems logical and appealing, the document provides very little supporting information from the literature, and no real guidance for determining when a population has moved from one phase to another. Additionally, there is considerable debate within NMFS as to whether it is appropriate to delay adjusting pHOS and PNI until the local adaptation phase.

p. 60-1 (Sec. 6): I concur with these principles and goals. The first goal, in developing clear objectives for management of natural populations influenced by integrated hatchery production, is one that is often so obvious that it can be overlooked in a full and appropriate evaluation of a hatchery program, such as a Hatchery Genetic Management Plan under the HSRG. The last

goal, related to monitoring and evaluation, is one that is also often given little more than tacit support (i.e., carry out if feasible with existing resources).

With regard to the report's recommendations, these are generally a robust set of suggestions in line with the model results and authors' findings. Regarding Recommendation 4, it would be helpful to provide some basic guidance on how to evaluate tradeoffs between genetic risk from integrated hatchery propagation and increased natural abundance required to support harvest. What is the "currency" or other considerations that should be used to evaluate such tradeoffs? This is not strictly a technical issue but a policy one. In that case, perhaps some sort of decision theoretic framework such as a Bayes network or fuzzy logic could be employed to incorporate expert opinion or other metrics to conduct an analysis. At the least, identifying the considerations to effectively illuminate the consequences of such tradeoffs would be worth highlighting. A similar situation is associated with Recommendation 9.

p. 70-3 (Sec. 9, App. B): I couldn't detect any errors in Eqs. 1-16.

References

- Alaska Department of Fish & Game (ADF&G). 1985. [Alaska Department of Fish & Game Genetic Policy](#). Genetic Policy Review Team, Alaska Department of Fish & Game. Fisheries Rehabilitation, Enhancement and Development Division Special Report, Juneau, AK, June 1985, 25 p.
- Arnold, S. J., Pfrender, M.E., and Jones, A.G. 2001. The adaptive landscape as a conceptual bridge between micro-and macroevolution. *Genetica* 112:9-32.
- Fisher, R. A. 1918. The correlation between relatives on the supposition of Mendelian inheritance. *Transactions of the Royal Society of Edinburgh* 52:399-433.
- Fisher, R. A. 1958. *The Genetical Theory of Natural Selection*. Dover, New York, 291 p.
- Ford, M. J., Murdoch, A.R., Hughes, M.P., Seamons, T.R., and LaHood, E. 2016. Broodstock history strongly influences natural spawning success in hatchery steelhead (*Oncorhynchus mykiss*). *PLoS ONE* (doi.org/10.1371/journal.pone.0164801).
- Gustafsson, L. 1986. Lifetime reproductive success and heritability: empirical support for Fisher's fundamental theorem. *American Naturalist* 128:761-764.
- Hoekstra H. E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hoang, A., Hill, C.E., Beerli, P., and Kingsolver, J.G. 2001. Strength and tempo of directional selection in the wild. *Proceedings of the National Academy of Sciences USA* 98:9157-9160.
- Kingsolver, J. G., Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hill, C.E., Hoang, A., Gibert, P., and Beerli, P. 2001. The strength of phenotypic selection in natural populations. *American Naturalist* 157:245-261.
- Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. *Evolution* 30:314- 334.
- MacFarlane, S. E., Gorrell, J.C., Coltman, D.W., Humphries, M.M., Boutin, S., and McAdam, A.G. 2014. Very low levels of direct additive genetic variance in fitness and fitness components in a red squirrel population. *Ecology and Evolution* 4:1729-1738.
- Merilä, J., and Sheldon, B.C. 1999. Genetic architecture of fitness and non-fitness traits: empirical patterns and development of ideas. *Heredity* 83:103–109.
- Merilä, J., and Sheldon, B.C. 2000. Lifetime reproductive success and heritability in nature. *American Naturalist* 155:301–310.

Teplitsky, C., Mills, J.A., Yarrall, J.W., and Merila, J. 2009. Heritability of fitness components in a wild bird population. *Evolution* 63:716-726.

Turelli, M. 1984. Heritable genetic variation via mutation-selection balance: Lerch's zeta meets the abdominal bristle. *Theoretical Population Biology* 25:138-203.

APPENDIX F: WRITTEN REVIEW BY PATRICK O'REILLY

Date: 15 August 2017

Reviewer: Patrick O'Reilly

Science Center CSAS Working Paper: 2013SEP02

Working Paper Title: Genetically Based Targets for Enhanced Contributions to Canadian Pacific Chinook Salmon Populations

General comments:

The overall approach proposed by Withler et al. 2017 for establishing PNI-based benchmarks for categorizing Chinook Salmon populations appears to be both biologically appropriate (based on the best available science given stated objectives), and suitable in a 'Canadian' or 'Pacific region' context, with Conservation Units and Wild salmon defined as described in the Wild Pacific Salmon policy. Basing categorization (and management) of Chinook salmon populations on PNI makes sense because **(a)** enhancement on the West coast of Canada (as opposed to the typical situation on the East coast) is a big component of the overall management regime of these populations (and likely has a large effect on fitness and wild population persistence), and **(b)** PNI considers, simultaneously, i) impacts of hatchery-origin broodstock in the hatchery environment, ii) impacts of hatchery-origin spawners in the wild environment, and iii) gene flow in both directions (where appropriate), all in an evolutionary (adaptive) framework (reference). In addition to seeming to be very useful and scientifically credible to this reviewer, PNI (initially developed by the U.S. HSRG, appears to have been extensively reviewed and is used in the management of Pacific salmon populations in the US. The modified approach presented here also incorporates the definition of a wild salmon in the WSP; natural-origin salmon as used here include both Wild salmon and transition salmon as defined in WSP and enhanced salmon appear to be equivalent to hatchery salmon used here. The methods and associated formulae for estimating important parameters including pHO_{Seff} , $pNOB$, PNI and the proportion of offspring produced by different cross types (NN, NH and HH) are well explained (and all make sense); these are behind the proposed guidelines for categorizing Chinook populations, which are also well explained.

Many parameters included in the model are difficult to estimate, including heritability of traits *in a particular environment* (heritability estimates are likely to vary from environment to environment) and selection coefficients, and information on other variables such as survival and relative reproductive success are likely going to be unavailable on a river specific basis. However, sensitivity analyses were carried out (section 4.4) to address all four; expected variation in three of the above was expected to have minimal impacts on conclusions, with only strength of selection being of potential concern. The authors do indicate that if selection is weak instead of strong, the impacts were greatly reduced resulting in a larger allowable hatchery program. In other words, the results provided are in a sense, conservative or precautionary.

Results from additional studies of RRS of hatchery versus wild salmon, estimates of heritability and selection, would be useful at some point, especially given possible confounding effects of epigenetic inheritance, which might be better understood and quantified in the future .

The authors mention possible epigenetic effects of the hatchery environment on offspring survival in the wild, including a) the degree of interest in this topic in terms of salmon management/conservation, and b) why this is of potential importance in the present context (e.g., it could be behind *some* of the very rapid hatchery-related loss of fitness often reported for salmonids). However, it might be useful to discuss the possible implication(s) of epigenetic transgenerational effects of the hatchery environment on results presented here.

Researchers are now beginning to think about the possible implications of epigenetic or non-genetic transgenerational effects on other studies of contemporary evolution, including reported rates of contemporary evolution. For example, Salinas and Munch (2012), in their study of the effects of parental temperature regimes on rates of growth in offspring note the following:

“The change in growth over a single generation (30%) exceeds the single-generation rate of adaptive evolution by an order of magnitude. If widespread, transgenerational effects on thermal performance may have important implications on physiology, ecology, and contemporary evolution...”

Salinas, S., and Munch, S.B. 2012. Thermal legacies: transgenerational effects of temperature on growth in a vertebrate. *Ecology Letters*, 15: 159-163 .

Although, clearly, insufficient (nearly zero) information exists to incorporate any non-genetic transgenerational effects in any of the modelling work done here, the authors could consider speculating on what kinds of impacts (direction?) a later finding that a portion (1/2?) of the intergenerational change (G0 to G1 or G1 to G2) in fitness reported in the literature is due to non-genetic transgeneration factors? Specifically, how might subsequent possible (?) findings of non-genetic transgenerational effects contributing to inter-generational hatchery-related loss of fitness reported by others effect (1) estimates of genetic heritability of the trait “fitness” used here, (2) estimates of rates of adaptive evolutionary change, (3) estimates of PNI, and (4) benchmarks proposed?

Possible negative effects of enhancement activities on wild or supplemented populations is often phrased in the context of “impacts on wild genetic diversity”. This appears to be a “catch all” approach meant to include possible loss of CUs, possible loss of local populations and among population diversity, loss of local adaptation, loss of wild lineages (within population diversity) and possibly loss of within population genetic variation (numbers of alleles, observed heterozygosity, etc). While this makes very good sense in a way, it also reduces the focus on fitness effects of enhancement on wild population, and the likely important effects of adaptation to captivity and relaxation of selection on the survival of descendants in the wild. Although fitness effects are discussed (and indeed, form much of basis of PNI management), they are often nested in discussions of hatchery influence and PNI and are not highlighted. Also, given the specific published effects of enhancement on variance in family size, effective population size, and expected rates of loss of genetic variation (e.g., Ryman-Laikre, 1991), the reader (at least initially) may be thinking the authors are talking about direct effects on effective population size and within population genetic variation.

Specific responses to TOR objectives 1 to 5.

1. Review the current scientific understanding of observed and potential genetic risks to wild populations associated with hatchery propagation.
2. In several sections in the manuscript, though mostly in section 2, most of the potential risks of hatchery supplementation that I am aware of were addressed (to some extent) in this report, including adaptation to captivity, relaxation of selection in the wild, environmentally induced phenotypic changes, environmentally induced epigenetic effects, initial sampling of gene variants and inadvertent changes in allele frequency distributions due to small sample size effects, representation of phenotypes and inadvertent selection, increased variance in family size and higher rates of loss of genetic variation and accumulation of inbreeding, etc. The focus of much of the discussion was centered around selection-mediated effects, which makes sense given the specific objectives 2-5 below, and the overall program objective of the minimizing domestication-associated impacts of hatchery activities (artificial spawning and captive rearing) on fitness in the wild.

-
3. Describe categories of biological status for enhanced Chinook Salmon populations measured in terms of proportion of wild fish as defined in the Canadian WSP. Describe how to assess hatchery influence on Chinook Salmon populations, using the Proportion Natural Influence (PNI) metric, including its rationale and its applicability to the Canadian context.
 4. The authors did an excellent job of defining and describing proposed designations or categories of enhanced Chinook salmon populations, based on the proportion of wild (or conversely, on effectively spawning hatchery-origin salmon) spawning in the river environment, where 'Wild' is defined as described in the WSP (see Table 3.2 and associated text in the report). The authors also discuss the amount of hatchery influence using the Proportion Natural Influence (PNI), which takes into account both the proportion of natural salmon in the brood stock group spawned in the hatchery, and the proportion of hatchery-origin salmon effectively spawning in the river environment (and gene flow between the two components of the population). Proportion Natural Influence is adapted to the Canadian context by using the WSP definition of wild salmon, and incorporating this into calculations of PNI. The actual Population designations, including "Wild", "Wild-stray influenced", "Integrated-wild", "Integrated-transition" and "Integrated-Hatchery", make intuitive sense. Associated values of pHOSeff, pNOB, PNI, and contributions of Natural (NN), hybrid (NH) vs Hatchery (HH) salmon (based on WSP) are all internally consistent, and makes sense based on both context and the available literature.
 5. Provide advice on quantitative benchmarks for the PNI and/or other appropriate metrics for the biological categories of status, and management measures to achieve those benchmarks.
 6. Benchmarks associated with different PNI-based designations of Chinook salmon populations are given in Table 3.2 (and in the associated text). Associated metrics include pHOSeff, pNOB (where appropriate), PNI, and the proportion of offspring contributed by NxN parents, NxH parents and HxH parents, where H is Hatchery origin and N is Natural origin. Also provided is the biological basis for each of the above metrics, and rationale for associations between metrics (e.g., pHOSeff and WSP NN, etc.). Furthermore, the benchmark values themselves (eg., pHOSeff < 0.02) both make intuitive sense and, where possible, are based on published findings. Finally, the designations themselves seem appropriate given the associated values and comments (e.g., Wild-stray influenced pHOSeff > 0.03, pNOB = n/a; Integrated wild < or = 0.28 and pNOB = 0.72).
 7. Summarize the information and analyses needed to implement the PNI-based genetic risk management guidelines.
 8. Information needed to implement PNI-based guidelines, as described in Withler et al. 2017, for both existing and new programs, has been provided (see section 5.2 and elsewhere). Examples of important information required to implement PNI-based management for new projects (given in the report) include average abundance of the natural-origin spawning population, hatchery production, survival rates of hatchery produced salmon in captivity, expected return rates of hatchery salmon, and for existing programs, estimates of pHOSeff and pNOB. Recommendations are also given regarding how estimates of the above can be obtained, what some of the problems likely to be encountered are, and how to mitigate each. Elsewhere in the report (including the sensitivity analyses) the authors also discuss additional information that can be collected or obtained from other sources (e.g., RRS of hatchery versus wild salmon, etc.) that can further improve PNI-based management.
 9. Summarize advice and guidance for development of new enhancement guidelines.

10. Advice and guidance for the development of new enhancement guidelines has been provided in section 5.2. First, the authors review relevant insights from the HSRG, including requirements for assessments of population status, habitat, harvest goals, the importance of an Ecosystem-based approach, adherence to the precautionary principles, and possible synergistic effects of hatchery supplementation, habitat quality/quantity, and harvest pressures on wild populations. All would seem to be important going forward. The authors then provide guidance that reflects existing Canadian (actually, Pacific region) conditions/policy. For example, it is recommended that implementing guidelines would be facilitated by first assigning populations within a CU to one of the 5 biological categories listed in Table 3.2 (Wild, Integrated hatchery, etc), and that the overall risk of the management regime (category) be considered in context of the status of the CU itself, including the number of populations. This makes sense, especially given the definition of the CU under WSP. More specific guidance, including required information, is provided for developing guidelines for existing and new programs, including the need for a specific portion (depending on local circumstances) of hatchery salmon to be marked in order to discriminate between Hatchery-origin and natural-origin in broodstock collections and on the spawning grounds. The authors also provide broader advice, including suggestions that annual adjustments do not need to be made, but that PNI should be monitored and adjusted from time to time.