

ARCTIC-YUKON-KUSKOKWIM CHINOOK SALMON RESEARCH ACTION PLAN

EVIDENCE OF DECLINE OF CHINOOK SALMON
POPULATIONS AND RECOMMENDATIONS FOR FUTURE
RESEARCH



ARCTIC-YUKON-KUSKOKWIM
SUSTAINABLE SALMON INITIATIVE
AYK SSI CHINOOK SALMON EXPERT PANEL

August 2013

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EVIDENCE OF DECLINE OF CHINOOK SALMON POPULATIONS AND
RECOMMENDATIONS FOR FUTURE RESEARCH

Prepared for

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This document should be cited as:

Schindler, D., C. Krueger, P. Bisson, M. Bradford, B. Clark, J. Conitz, K. Howard, M. Jones, J. Murphy, K. Myers, M. Scheuerell, E. Volk, and J. Winton. Arctic-Yukon-Kuskokwim Chinook Salmon Research Action Plan: Evidence of Decline of Chinook Salmon Populations and Recommendations for Future Research. Prepared for the AYK Sustainable Salmon Initiative (Anchorage, AK). v + 70 pp.



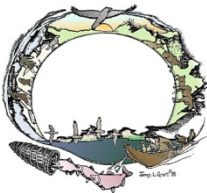
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1.0 Introduction and Overview

Since the late 1990s, Chinook salmon (*Oncorhynchus tshawytscha*) in the watersheds of the Arctic-Yukon-Kuskokwim (AYK) region have experienced sharp reductions in abundance. The decline in productivity of AYK Chinook salmon has resulted in widespread commercial fishing closures and restrictions in subsistence harvests (e.g., Evenson et al. 2009; Bue et al. 2009). Stock-recruitment analyses and models have failed to predict low adult returns in recent years. Reports of reduced body size of Chinook salmon and low numbers of females have increased (e.g., Evenson et al. 2009; JTC 2006). Low returns and changes in the characteristics of the adults prompted the Alaska Board of Fisheries to classify Yukon River Chinook salmon as a “stock of yield concern” from 2000 to the present. Kuskokwim River Chinook salmon stocks began a five-year period of sharp decline in 2007. Similarly, Norton Sound has experienced a sharp decline of Chinook salmon in the Unalakleet River notably during 2000, 2006, 2008, and 2010 (Menard et al. 2009; unpublished ADF&G).

As a result of the decline in adult run abundance in the region, restrictions and closures were implemented on the subsistence and small-scale commercial fisheries. These restrictions have caused nutritional, economic, and cultural hardship for thousands of people in the AYK region who depend upon salmon stocks. Critical questions that need to be addressed are as follows:

- 1) What are the variables or driving factors that have contributed most significantly to the patterns of declines observed in Chinook salmon and are those variables acting alone or in combination?
- 2) Are the major stressors responsible for the declines acting predominantly in the freshwater or the marine phase of the Chinook salmon life cycle?

In response to the need to focus on these critical issues, the Scientific and Technical Committee (STC) of the AYK Sustainable Salmon Initiative (SSI) decided to develop a Chinook salmon research action plan. The purpose of the research action plan is to identify:

Which variables and processes are the most likely causative factors of the AYK Chinook salmon declines and to produce a more detailed set of research priorities and questions to better understand the key drivers of salmon abundance in the region.

The approach used to accomplish this purpose was to establish an expert panel of fishery scientists and ecologists to review and synthesize information available from

published sources (e.g., Alaska Department of Fish and Game (ADFG) reports, peer reviewed literature, results of past AYK SSI research projects), and directly from salmon managers and local knowledge to identify the most likely critical variables and processes affecting Chinook salmon abundance. This research action plan is intended to be used to guide future research solicitations by the AYK SSI Steering Committee in consultation with the STC.

1.1 Goal and Objectives

The goal of the Chinook Salmon Research Action Plan is

To understand the trends and causes of variation in Chinook salmon abundance through the assembly of existing information and gaining new information through a collaborative and inclusive process.

In the context of this goal, the specific objectives of the Chinook Salmon Research Action Plan are to:

1) Review and Synthesize Existing Knowledge of Chinook Salmon

Survey the current state of knowledge regarding the observed patterns in abundance of AYK Chinook salmon stocks and identify the potential factors that could be driving those patterns.

2) Identify Key Variables and Processes that Affect Chinook Salmon Abundance

Identify and describe hypothesized causes for the recent declines, including the biological mechanisms at work, and present and evaluate the weight of evidence for and against each hypothesis.

3) Provide Recommendations for Future Research

Identify and describe specific research questions aimed at improving our understanding of the trends and causes of variation in the abundance of AYK Chinook salmon. Provide research questions for each hypothesis and develop a prioritized set of research hypotheses and questions.

1.2 Linkages to the Arctic-Yukon-Kuskokwim Salmon Research and Restoration Plan

Formed in 2001, the AYK SSI is an innovative partnership between public and private institutions that provides a forum for non-governmental organizations and state and federal agencies to cooperatively identify and address salmon research and restoration needs. The AYK region encompasses over 40% of the State of Alaska, including the watersheds of the Norton Sound region up to and including the village of Shishmaref, the Yukon River watershed within Alaska, the Kuskokwim River watershed (including the

coastal watersheds north of Cape Newenham), plus the Bering Sea marine ecosystem. The first step taken by the AYK SSI was to collaboratively develop and implement a comprehensive research plan to understand the causes for the decline of AYK salmon. The Research and Restoration Plan (RRP) (AYK SSI 2006) was prepared with guidance from a committee of the US National Research Council (NRC 2004).

The overall goal of the AYK SSI Research and Restoration Program is:

To understand the trends and causes of variation in salmon abundance and fisheries through the assembly of existing information, gaining new information, and improving management and restoration techniques through a collaborative and inclusive process.

The RRP in Sections 9.5 and 9.6 (page 59) specifies that the plan is to be reviewed and revised to establish new research priorities and hypotheses. This research action plan accomplishes this purpose for AYK Chinook salmon, and addresses and advances the goal of the AYK SSI RRP stated above.

1.3 Structure of this Report

The content and structure of this report is as follows.

Section 2 describes the process by which the research plan was developed, including details on the expert panel, hypotheses, review documents, and the synthesis workshop.

Section 3 explores the existing knowledge on the recent declines and variability of Chinook salmon stocks within the AYK region. The Yukon, Kuskokwim and Unalakleet rivers are examined in separate subsections. This section draws heavily upon the much more extensive report on the evidence of declines prepared by Spaeder and Catalano (2012).

Section 4 synthesizes some of the existing knowledge on the production dynamics of Alaska Chinook salmon populations outside of the AYK region, and contrasts them against the patterns observed within AYK Chinook salmon stocks.

Section 5 describes seven hypotheses identified by the expert panel that provide plausible explanations for the recent changes in AYK Chinook salmon abundance. The section provides for each hypothesis a description, discussion of the biological plausibility, a summary of the evidence available, and a set of research themes and questions to guide future research.

Section 6 provides the expert panel’s recommendations for research priorities based on the hypotheses, themes, and questions from Section 5.

1.4 Constraints, limitations and realistic expectations

Substantial constraints and limitations exist on the plan’s ability to guide research to provide definitive answers. Readers of this document should have realistic expectations in mind as they proceed through the plan. Specifically, three broad elements exist that readers should consider. First, the underlying ecosystems within which Chinook salmon live contain complex interactive elements operating over large ranges of spatial and temporal scale. This complexity makes the isolation of individual, well-defined relationships difficult. Second, the information base is incomplete and dynamic – substantial gaps exist in the data available to evaluate the hypotheses and questions. Third, this research plan must be placed within the context of the broader AYK SSI Research and Restoration Plan (AYK SSI 2006), which yields limitations on the capability of the program to address all hypotheses fully.

Ecosystem Complexity

The ecosystems that Chinook salmon use are highly dynamic, containing complex sets of interacting physical and biological components. Throughout their life history, Chinook salmon travel thousands of kilometers, through multiple freshwater and marine environments, while being exposed to natural and human stressors during each life stage. The mechanisms through which these stressors affect salmon biology are complex, varying both across space and time. Responses by the salmon to certain stressors may occur immediately or after considerable time lags. Mechanisms may operate independently or interactions may occur among multiple stressors. Individual Chinook salmon stocks show substantial variability, including differences in migration distances, genetics, life history characteristics, and use of specific habitats. The relationships between environmental stressors and their effects on Chinook salmon may vary within a single brood year, across multiple brood years, and among stocks. Most likely, the observed patterns of decline will not be attributed to single causes – the causes are more likely the result of interactions among multiple variables.

Data and Information

The available AYK Chinook salmon data are incomplete across stocks, across years, and across life stages. The spatial coverage of stocks with sufficiently detailed productivity data to explore is limited. This plan focuses on four stock groups with adequate data: the Canadian-origin Yukon River, the Kuskokwim River, the Chena and Salcha rivers, and the Unalakleet River. The entire U.S. portion of the Yukon River is represented by data

from only two stocks, Chena and Salcha rivers. Within these four stock groups, the period of record is limited to a few decades of data or shorter. Life-stage specific estimates of productivity within these stocks do not exist. Ideally, the data for potential explanatory variables (i.e., natural or human stressors) would be available for each stock over time, including the period prior to the observed declines. However, such data usually do not exist. The data on particular variables may be limited in space, time, or quality, or were not even collected. Our ability to explain the observed patterns may also be limited by fundamental gaps in our basic knowledge. For example, we generally do not observe actual mortalities, therefore our knowledge of how salmon die is usually inferred from survival rather than known by direct observation (McKinnell et al. 2011).

The knowledge base itself is highly dynamic over time. New information may strengthen our understanding of certain processes or add new knowledge, but it may also change or replace previous interpretations of existing data. New information may lead to a redirection of priorities or even an introduction of new hypotheses or new ways of thinking about Chinook salmon population dynamics.

Research process

This research plan must also be considered within the context of the broader constraints that operate on research programs such as the AYK SSI. Ultimately, as outlined above and detailed throughout this research plan, the information needs to address this issue are large; however, the funding available to fulfill those information needs remains limited and the long-term time frame of the entire program is not known. Consequently, constraints exist on the level of resources that can be applied to gain better information, both in terms of their amount and duration. The recommendations within this plan provide guidance on the research questions that are expected to be most beneficial to answer within a flexible framework that can be adapted to changes in priorities and constraints each year.

2.0 Approach and Methods

The process used to develop this research plan included appointment of a panel of experts on Chinook salmon by the AYK SSI STC, and the review and synthesis by the panel of the existing knowledge on Chinook salmon in the AYK region. The panel formulated a set of hypothesized mechanisms that most plausibly could have contributed to the observed declines in Chinook salmon. A synthesis workshop was held in May 2012 to evaluate existing and new information on the patterns of decline within Chinook salmon stocks in the AYK region and the hypotheses on factors that may have contributed to the observed declines. The workshop included summary papers, presentations, and integrative discussion on the strength of evidence and relative likelihood associated with various hypotheses. During the workshop, participants generated recommendations for future research to increase our understanding of the key variables potentially affecting Chinook salmon. Based on the proceedings of the workshop, a new summary was prepared for each of the hypotheses (Section 5). These hypotheses and recommendations were subsequently compiled and prioritized to guide critical future research (Section 6).

2.1 Establishment of the AYK SSI Chinook Salmon Expert Panel

The Action Plan was developed by a specially commissioned, 13 member AYK SSI Chinook Salmon Expert Panel, appointed by the AYK SSI STC. This panel is comprised of a group of salmon scientists, including four STC members, who collectively have expertise over the entire freshwater and marine life cycle phases of the salmon. Critical disciplinary areas represented within the panel include:

- juvenile and estuarine salmon ecology
- stock-recruitment analyses
- high-seas salmon population dynamics (including marine by-catch and other sources of mortality)
- pathology
- harvest management
- genetic stock identification
- research plan development

The members of the AYK SSI Chinook Salmon Expert Panel include:

Daniel Schindler (co-chair), University of Washington, School of Aquatic and Fishery Sciences

Charles Krueger (co-chair), Great Lakes Fishery Commission

Pete Bisson, US Forest Service, Pacific Northwest Research Station

Mike Bradford, Fisheries and Oceans Canada and Simon Fraser University, School of Resource and Environmental Management

Bob Clark, Alaska Department of Fish and Game, Sport Fish Division

Jan Conitz, Alaska Department of Fish and Game, Commercial Fisheries Division

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Mike Jones, Michigan State University, Quantitative Fisheries Center

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Kate Myers, University of Washington, School of Aquatic and Fishery Sciences (retired)

Mark Scheuerell, NOAA-Fisheries, Northwest Fisheries Science Center

Eric Volk, Alaska Department of Fish and Game, Commercial Fisheries Division

James Winton, US Geological Survey, Western Fisheries Research Center

The AYK SSI research coordinator, Joseph Spaeder, provided staff support to the panel.

2.2 Review and Synthesis of Existing Knowledge

The panel surveyed the current state of knowledge of AYK Chinook salmon by reviewing published and unpublished information. While the focus was specifically on Chinook salmon in the AYK region, information from other Chinook salmon stocks was also valuable to help inform and interpret AYK specific information (see Section 4). Inclusion of the additional information from elsewhere had the benefit of placing AYK region Chinook salmon declines within the larger context of North Pacific Chinook salmon declines. Where available and beneficial, unpublished information was sought from partners such as ADFG to help identify key variables and processes affecting AYK Chinook salmon abundance. Research funded by AYK SSI, and other research conducted by agencies, universities, NGOs, and other organizations was reviewed.

2.3 Development of Hypotheses to Explain the Changes in Production Dynamics

During the process of reviewing and synthesizing the existing knowledge, the panel identified an initial set of ten hypotheses, each describing a major driver, or a set of associated drivers that could plausibly have contributed to the observed declines in Chinook salmon stocks in the AYK region. The chosen set of hypotheses was not intended to be an exhaustive list of all possible mechanisms, but rather a focused set that covered the breadth of the most likely contributors to the observed declines. These hypotheses provided the focal points for summary papers, presentations and discussions conducted during a synthesis workshop held in May 2012. During the workshop (described below), each of the hypotheses was presented and then evaluated by the workshop participants. After the workshop, the panel consolidated some hypotheses and reduced the total number to the seven hypotheses presented in Section 5 of this plan.

Scientific hypotheses are conventionally written in the form of a declarative statement, as if the hypothesis is true, which is then tested to determine whether the available evidence supports (or fails to support) the hypothesized relationship or mechanism. However, to avoid potential misinterpretation, the hypotheses described in this research plan also are illustrated below through questions to emphasize explicitly their uncertainty.

The seven hypotheses and their restatements as questions are as follows.

1. Density-dependent Effects and Overcompensation

Hypothesis: Recent declines in AYK Chinook salmon stocks are caused by strong density-dependent feedbacks in population dynamics that cause decadal-scale changes in abundance.

Have density-dependent feedbacks in population dynamics caused the long-term variation and recent declines in AYK Chinook salmon stocks?

2. Freshwater Mortality

Hypothesis: Change in the suitability or productivity of freshwater habitats used for spawning, rearing and migration has contributed to declines in AYK Chinook salmon stocks.

Has change in the suitability or productivity of freshwater habitat used for spawning, rearing and migration contributed to declines in AYK Chinook salmon stocks?

3. Ocean Mortality

Hypothesis: Ocean conditions (physical and biological) have changed in the Bering Sea, causing an increase in mortality of Chinook salmon during the early marine portion of their life cycle and contributing to declines of AYK Chinook salmon stocks.

Have changing ocean conditions (physical and biological) in the Bering Sea caused an increase in mortality that has contributed to declines of AYK Chinook salmon stocks?

4. Anthropogenic Changes to Marine Ecological Processes

Hypothesis: Human-caused changes in the ocean have reduced growth and survival of AYK Chinook salmon contributing to the declines of these stocks.

Has an increase in anthropogenic forcing of density-dependent marine ecological processes that support ocean growth and survival of Chinook

salmon populations contributed to declines of AYK Chinook salmon stocks?

5. Marine Bycatch

Hypothesis: Mortality from non-salmon fisheries in the ocean has contributed to the decline of AYK Chinook salmon stocks.

Has marine fishery-caused mortality contributed to declines of AYK Chinook salmon stocks?

6. Escapement Quality

Hypothesis: Selective fishing and natural mortality have altered the genetic character of the stocks so that the expression of size, sex ratio, and composition of life history types have been altered and have contributed to declines in egg deposition to reduce recruitment in AYK Chinook salmon stocks.

Have selective fishing and natural mortality altered the size, sex ratio, and composition of life history types and therefore contributed to declines of AYK Chinook salmon stocks?

7. Pathogens

Hypothesis: Pathogens have increased mortality rates of adult Chinook salmon during upstream migration and have contributed to the decline of AYK salmon stocks.

Has adult mortality from pathogens during upstream migration contributed to declines of AYK Chinook salmon stocks?

2.4 Synthesis Workshop

In May 2012, the Chinook Salmon Expert Panel convened a synthesis workshop featuring presentations and discussions by panel members and other invited participants on selected topics related to understanding of the trends and causes of variation in the abundance of AYK region Chinook salmon throughout their life cycle. Participants included panel members as well as scientists and managers from ADFG and additional fisheries scientists from universities and federal agencies (refer to Appendix 1 for a list of participants). Several presentations were given on recent analyses of the underlying patterns observed in the Yukon and Kuskokwim rivers, including an assessment comparing AYK Chinook salmon stocks to non-AYK Chinook salmon stocks. The majority of the presentations addressed the hypotheses on the major factors that may have contributed to the observed declines in AYK Chinook salmon stocks.

Collectively, these presentations contributed to the first objective (review and synthesis) and addressed the second objective of identifying key variables and processes.

The presenters prepared written synthesis papers associated with each of the presentations. These reports, their presentation, and the discussion surrounding them during the workshop formed the basis for accomplishing the second objective.

During the workshop, participants completed a survey for each hypothesis after the presentation(s) and discussion associated with that hypothesis. Each participant provided their assessment of the biological plausibility of the hypothesis, its relative likelihood of being a substantial contributor to the observed declines, and the key evidence supporting that conclusion. In addition, participants provided recommendations for research that could shed further light on the hypothesis and uncertainties associated with it, and whether any management actions existed that could provide opportunities for further learning. The results were compiled for each hypothesis and made available to the panel members to review and draw upon while writing the hypothesis sub-sections of Section 5.

2.5 Recommendations for Future Research

A key deliverable from this project is a detailed set of recommendations for future research (Sections 5 and 6) that will advance the AYK SSI program goal of gaining an improved understanding of the causes of the declines of AYK region Chinook salmon and improving tools and approaches for management of those stocks. Based on the synthesis of the current information and identification of gaps in knowledge, the panel has:

- Identified emerging hypotheses or revised existing hypotheses contained in the RPP in light of new information.
- Determined the highest priority hypotheses to focus future projects.
- Identified, under high priority hypotheses, questions specific to the AYK region Chinook salmon.

Recommendations for future research actions and priorities were generated and reviewed in an iterative, multi-stage approach. After the workshop presentations, participants were asked in a survey form to provide their individual recommendations for the five research topics that they believed to be the highest priority. The participants were asked to provide a rationale for their recommendations and to indicate the approximate time frame that would be necessary to achieve informative results. After providing this information, a round-table discussion was facilitated to discuss each participant's highest priority recommendations. Participants were then given more time

after the workshop to refine the recommendations in their survey based on the round-table discussion of research priorities. The panel was able to draw upon summary materials generated through the workshop process when writing the hypothesis summaries in Section 5 and recommending the highest priority research themes and questions for each hypothesis (Section 6).

3.0 Decline and Variability of AYK Region Chinook Salmon Stocks

This section explores the existing knowledge on the recent declines and variability of Chinook salmon stocks within the AYK region, identifying the fundamental patterns that research should seek to explain. The Yukon, Kuskokwim, and Unalakleet rivers are examined in separate subsections. The material in this section is drawn predominantly from the more extensive report prepared by Spaeder and Catalano (2012) in response to the expert panel's request for a compilation of evidence for long-term declines and periodic low returns of AYK region Chinook salmon populations. The data on Chinook salmon returns to this region are incomplete and likely have considerable uncertainties that derive from the limited sampling and enumeration that has occurred in these vast watersheds. However, the expert panel felt it was critical to produce a current synthesis of the existing data upon which subsequent discussions of the status of AYK Chinook salmon could be based. Subsistence and commercial harvest trends, abundance measures, and long-term productivity trends are presented for the Yukon River and Kuskokwim River watersheds. For the Unalakleet River watershed, where data are particularly limited, only harvest levels, escapement, and test-fishery CPUE data are presented. Spaeder and Catalano (2012) provide further details not presented here on these data sources, describe additional analyses of trends in age and size composition, and summarize the importance of the harvest of Chinook salmon to subsistence-dependent communities.

Measures of Abundance and Productivity

Measures of abundance (mainly from sonar enumeration, harvest data, and test-fishery CPUE) provide an approximation of the strength and timing of spawning runs. While subsistence and commercial harvest levels provide important information, they can be affected by variables independent of abundance, such as changes in harvest regulations (e.g., closed seasons, gear restrictions), river conditions, and variability in commercial fish markets (e.g., low or high prices for salmon).

Productivity (typically expressed as the recruits-per-spawner) is measured as the total number of returning adult salmon from a given brood-year cohort (recruits = harvest + escapement) divided by the escapement that produced that brood year (number of spawners that produced that cohort). The measures of productivity presented here require a data set on the order of 20 years or more and cannot be assessed for a given brood year until all the members produced from that brood year have returned to spawn (often over a 3-7 year period) and their abundance has been estimated.

Productivity must be greater than 1.0 for the population to replace itself and remain stable in the face of harvesting. That is, over the long term and in the absence of fishing, each spawner must give rise to at least one future spawner on average, or the abundance of the population will decrease.

The interpretation of changes in recruits-per-spawner ratios is obscured by a number of variables including the extended time lag in adult returns from a brood year. For example, Chinook salmon generally do not return to spawn until age 3 or 4 but most mature at ages 5 or 6. Whereas the recruits-per-spawner ratio may be declining, run abundance within a year is a composite of recruits of ages 3-7 from several brood years, and a recent change in recruits-per-spawner ratio may be masked. Thus, depending on year-class strength, a lag of up to 5 or 6 years can occur between a downturn in productivity and the downturn in run abundance.

Density-dependent processes provide feedbacks from population abundance to the reproductive success of Chinook salmon. The number of recruits-per-spawner is a measure of the per capita reproductive success and survival to the next generation that depends not only on density-independent (i.e., environmental) variables, but also on salmon abundance. Density-dependent processes produce compensatory dynamics in fish populations because intensified competition for limiting resources such as juvenile food, predation refuges, and adult spawning habitat typically leads to declines in the per capita reproductive success of a population as abundance increases. Density-dependent effects potentially mask or interact with the environmental processes.

3.1 Trends in Yukon River Chinook Salmon Populations

During the 37-year period from 1961 to 1997, the Chinook salmon populations of the Yukon River watershed sustained substantial harvest levels, with a mean annual harvest of approximately 143,000 fish (**Figure 1**). For the period of 1982 to 1997, the average estimated total run was approximately 300,000 fish (**Figure 2**). Alaskan and Canadian commercial harvests during these years accounted for approximately 77% of the average total harvest. The Canadian portion of the run sustained an exploitation rate that averaged 68% during the 16-year period from 1982 to 1997 (**Figure 3**). From 1980 to 2010, estimates of annual subsistence harvest levels (U.S. subsistence and Canadian aboriginal combined) were fairly stable, varying from 36,000 to 69,000 Chinook salmon. Commercial harvests decreased over 70% in the period 1998-2010 when compared to 1961-1997 (**Figure 1**).

Beginning in 1998, the Yukon River stocks entered a five-year period of low abundance (Evenson et. al. 2009). For the four-year period 2003-2006, Chinook salmon runs

showed improvement and escapement goals and treaty obligations were generally met or exceeded. Subsistence harvest needs were generally met and harvestable surpluses permitted limited commercial harvests averaging approximately 49,000 salmon. From 2007 to 2010, the Yukon River Chinook salmon populations entered a new multiyear period of low abundance (**Figures 1 - 3**). Escapement goals to Canada were not met in 2007, 2008, or 2010. This period of decline was accompanied by the imposition of subsistence harvest restrictions each year. Subsistence harvests remain below the “amounts necessary for subsistence” levels established by the Alaska Board of Fisheries from 2008 to 2010 (the last three years for which data are available). Mean run size of Canadian-origin Chinook for the period 1998-2010 declined 45% relative to 1982-1997 (**Figure 3**).

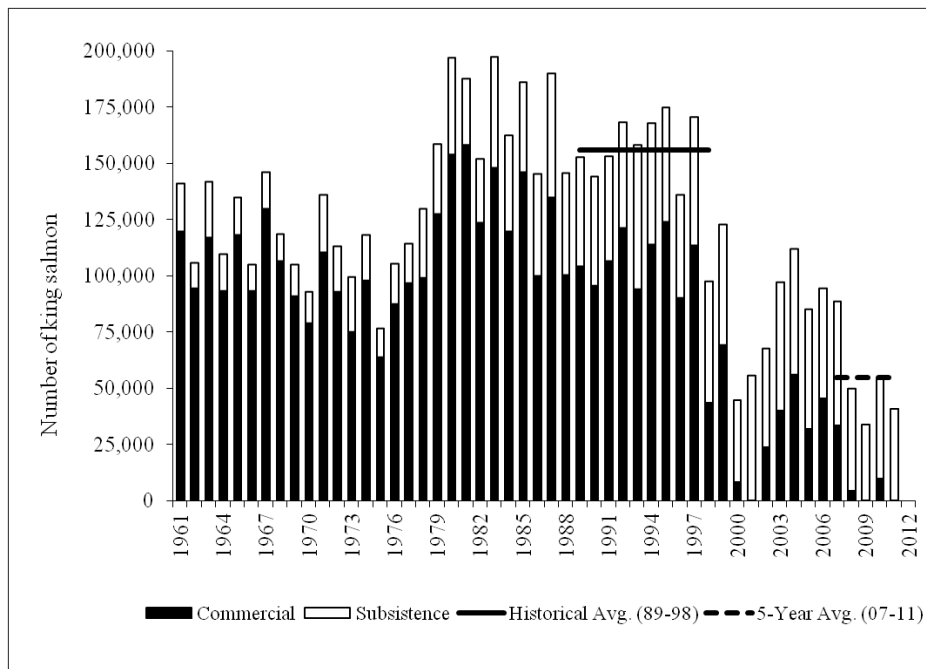


Figure 1. Yukon River king salmon subsistence and commercial harvests from 1961 to 2011, illustrating the historical average (1989–1998; 156,092 salmon) and the recent average (2007–2011; 54,665 salmon). Source: Schmidt and Newland, 2012

Yukon River Chinook salmon were designated as a stock of yield concern by the Alaska Board of Fisheries in 2000 after three years of poor runs. A stock of yield concern is defined as “a concern arising from a chronic inability, despite the use of specific management measures, to maintain expected yields, or harvestable surpluses, above a stock’s escapement needs; a yield concern is less severe than a management concern” (5 AAC 39.222(f)(42)). Based on these poor runs of Chinook salmon, plus concurrent declines of chum salmon, state and federal agencies declared either fishery or economic disasters in the following years: 1997, 1998, 2000, 2001, 2002, 2009, 2010, 2011, and 2012.

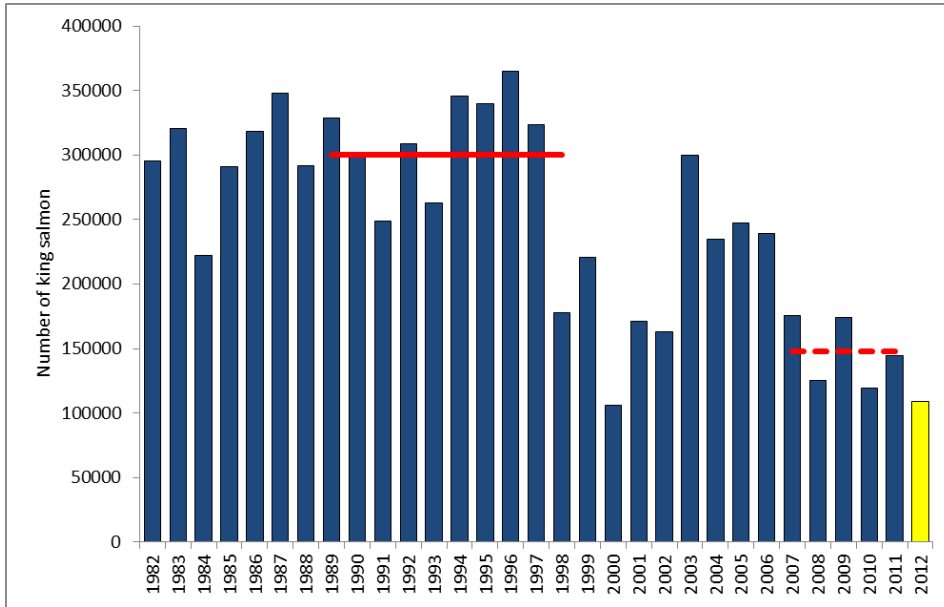


Figure 2. Yukon River estimated total Chinook salmon run, 1982-2012, showing average abundance for the period 1989-98 and the period 2007-2011. Estimation based on expansion from estimated Canadian-origin Chinook salmon run sizes. Source: JTC 2012.

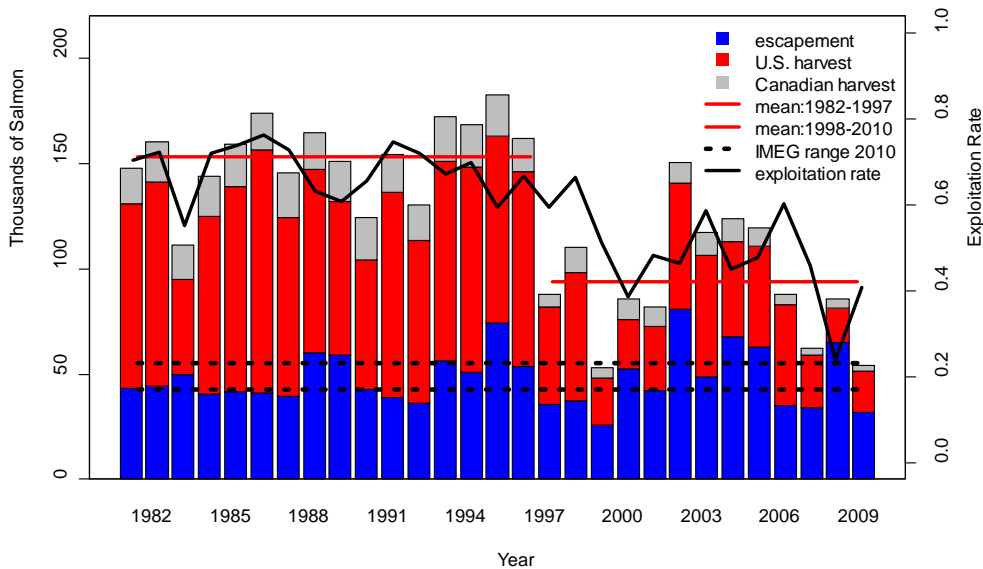


Figure 3. Estimated run sizes, escapement and US harvest of Canadian-origin Chinook salmon in relation to 2010-2011 Interim Management Escapement Goal (IMEG), and exploitation rate (dashed line). Canadian-origin Chinook salmon typically comprise approximately 50% of the total Yukon River Chinook salmon run. Total run size = escapement + U.S. harvest + Canadian harvest. Source: adapted from JTC 2011 and Howard 2011.

The Pilot Station sonar project can be used to provide a relative run abundance index, though this index does not account for harvest taken below the sonar, years when the index is strongly affected by environmental conditions in (e.g., particularly 2009), and known apportionment biases. Preliminary estimates through July 26, 2012 suggest that

the size of the 2012 Chinook salmon run is similar to the previous two years, which were the second and fourth lowest abundances estimated in the past 13 years (**Figure 4**). The preliminary 2012 index of low numbers of fish suggests that the run is a continuation of the recent trend of low abundance that began in 2007.

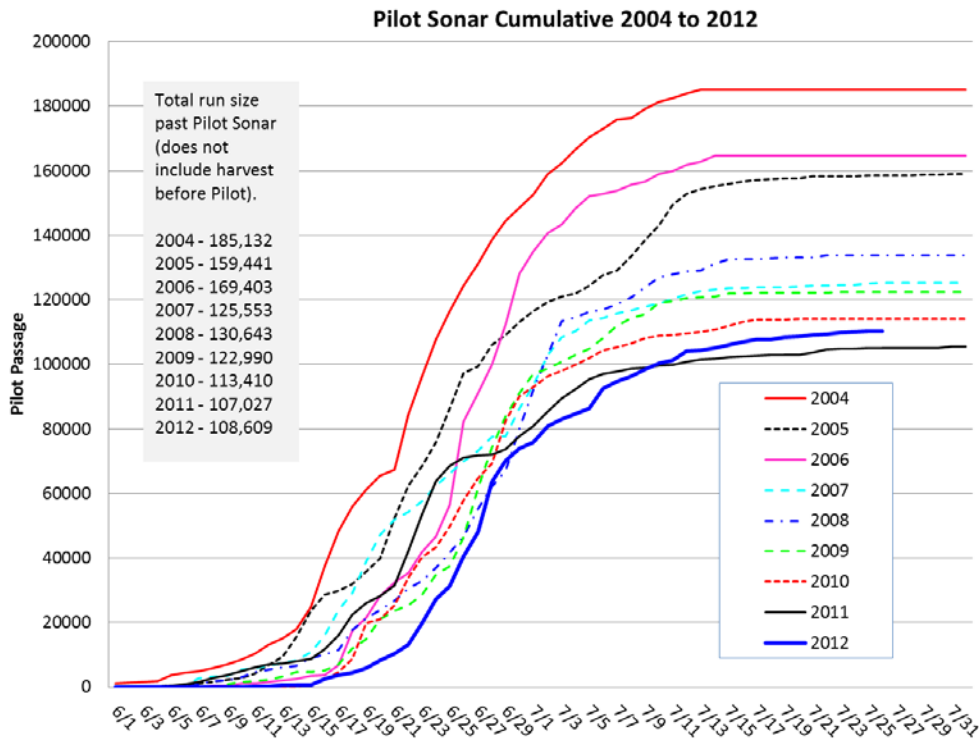


Figure 4. Cumulative estimates of total Chinook salmon passage at Pilot Station by date, 2004-2012, based on Pilot Station sonar and species apportionment via test-fishery. The 2012 estimate is preliminary. *Source:* ADFG 2012 In-season updates and JTC 2011.

Productivity, as measured by recruits-per-spawner by brood year, is presented for the Canadian-origin Yukon River Chinook salmon stocks (**Figure 5**) and for the Chena and Salcha rivers, which are tributaries to the Yukon River located in the Fairbanks area (**Figure 6**). Full run reconstruction and an associated spawner-recruit analysis for the full Yukon River Chinook salmon run were not yet available. The productivity data indicate that the most recent period of low abundance (**Figure 2** and **Figure 3**), which began in 2007, resulted from the low productivity of the 2002-2005 brood years (**Figure 5**). Estimated productivity from the 2002-2005 brood years varied close to one return per spawner, the ratio required for the population to replace itself in the absence of any harvest. Productivity (recruits-per-spawner) was negatively related to spawner abundance; with the highest spawner abundances producing the lowest productivities (see Spaeder and Catalano 2012).

Ricker and Beverton-Holt stock-recruitment relationships were estimated within a Bayesian age-structured stock recruitment model (Fleischman and Borba 2009, Fleischman et al 2013) that was fit to harvest and reconstructed spawner abundance data from 1982-2010 (S. Fleischman, ADFG, unpublished data). The Ricker model allows for the possibility of a dome-shaped “overcompensatory” relationship between recruitment and spawner abundance, where recruitment can decrease at high spawner abundance. In contrast, the Beverton-Holt model assumes an asymptotic relationship. The analysis found that neither model had significantly higher support for one or the other, suggesting that based on the current data, the analysis cannot differentiate between the two production models (Catalano 2012).

Chena and Salcha Rivers

The Chinook salmon stocks using the Chena and Salcha rivers are the only US stocks for which productivity estimates are available based on a long time-series of data (**Figure 6**). Runs into these rivers closely track each other and appear to be sustained by some episodic years of high productivity, interspersed with periods of low productivity. For this analysis, the two stocks were treated as a single aggregate population. Productivity for the Chena/Salcha stocks was low for the brood years from 1994 to 1997 and from 2001 to 2006, suggesting that at least portions of the US component of the run had productivity levels similar to those shown by the Canadian stocks during similar periods. An analysis of the relative empirical support for the Ricker or Beverton-Holt stock-recruitment models indicated that the Ricker model has slightly more support (58% vs. 42%; Catalano 2012).

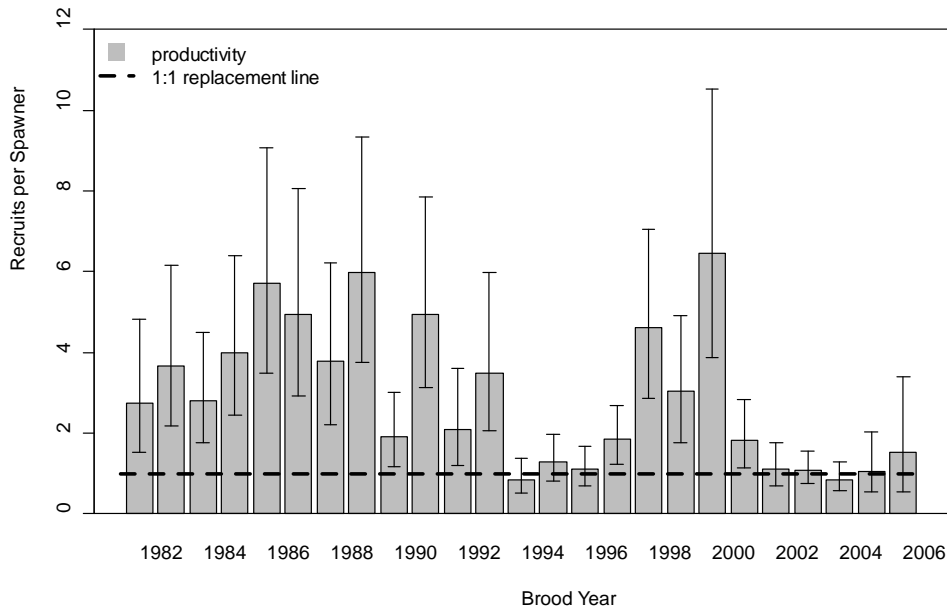


Figure 5. Estimated brood-year productivity (recruits-per-spawner; bars $\pm 95\%$ CI) for Yukon River Canadian-Origin Chinook salmon, 1982-2006. Productivity was estimated by dividing the sum of returns from a given brood year by the escapement that produced them. Brood year is defined as the year of the escapement that gave rise to the subsequent returns. For example, the 1982 brood-year productivity estimate was the sum of age 3-7 salmon that returned from 1985-1989, respectively, divided by the escapement in 1982. Productivity from the 2007-2010 brood years was not estimable because those cohorts have not yet returned to the river. The horizontal dashed line depicts the productivity required for the population to replace itself. The estimates were obtained from a preliminary Bayesian run reconstruction and stock-recruitment analysis. Thus, the estimates should be interpreted as preliminary and potentially subject to revision. *Source:* Steve Fleischman, ADFG, unpublished data, 2011.

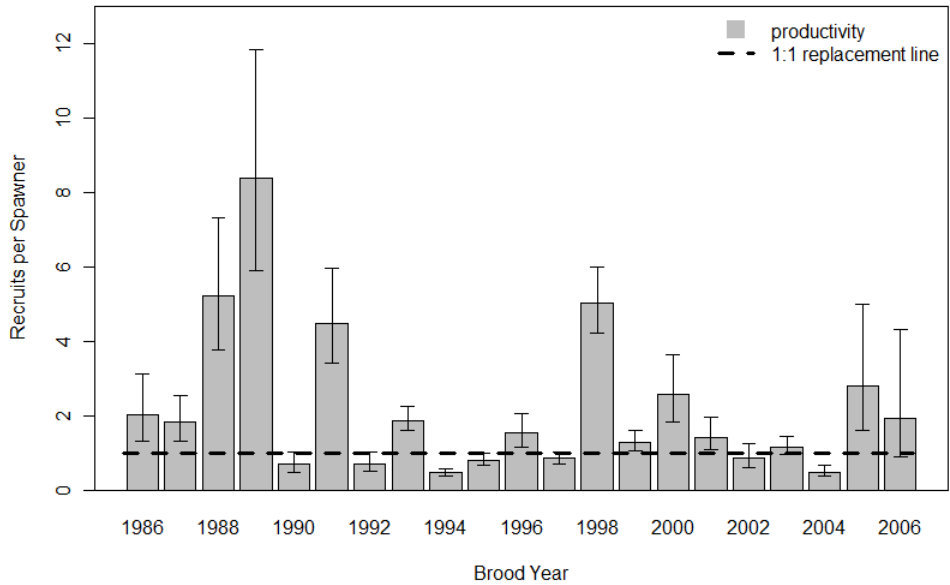


Figure 6. Estimated brood-year productivity (recruits-per-spawner; bars) of the aggregate Chena/Salcha River Chinook salmon stock, 1986-2006. Productivity was estimated by dividing the sum of returns from a given brood year by the escapement that produced them. Brood year is defined as the year of the escapement that gave rise to the subsequent returns. The horizontal dashed line depicts the productivity required for the population to replace itself. Source: Matthew Evenson, ADF&G, unpublished data.

Summary of Yukon River

Available harvest data during the 37 years from 1961 to 1997 show that abundance had been sustained at higher levels, but then significant declines occurred during the next 15 years that followed. During the early period from 1961 to 1997, the Yukon River Chinook salmon populations sustained an average combined subsistence and commercial harvest level of approximately 155,000 fish per year. The data available show periods of above-average abundance (1982-1997) and periods of below-average abundance (1998 onwards), as well as periods of generally higher productivity (brood years 1993 and earlier) mixed with years of low productivity (brood years 1994-1996 and 2002-2005). The problem currently facing Yukon River Chinook salmon stocks is that the analyses indicate that the stocks in the watershed appear to be in the 6th year of a multi-year period of low productivity. The resulting low abundance of Chinook salmon is insufficient to meet mandated escapement levels or treaty obligations, and provide subsistence users with a reasonable opportunity to harvest “amounts necessary for subsistence” as established by the Alaska Board of Fisheries. The current trend of weak runs has extended into the 2011 and 2012 run and has resulted from low recruits-per-spawner ratios from the 2002-2006 brood years. This multi-year decline has critical implications for the 40 rural communities in the watershed that have a high reliance on

the subsistence harvest of Chinook salmon and have among the lowest household incomes in the state.

3.2 Trends in Kuskokwim River Chinook Salmon Populations

The Kuskokwim River has the largest Chinook salmon subsistence fishery in the state, harvesting about 70,000 fish per year over the past decade (**Figure 7**) (Linderman and Bergstrom 2009). These salmon runs supported modest commercial fisheries for several decades until the directed Chinook salmon commercial fishery was formally closed in 1987. Subsequent Kuskokwim River commercial harvests are the result of incidental catch in the chum and sockeye salmon commercial fishery.

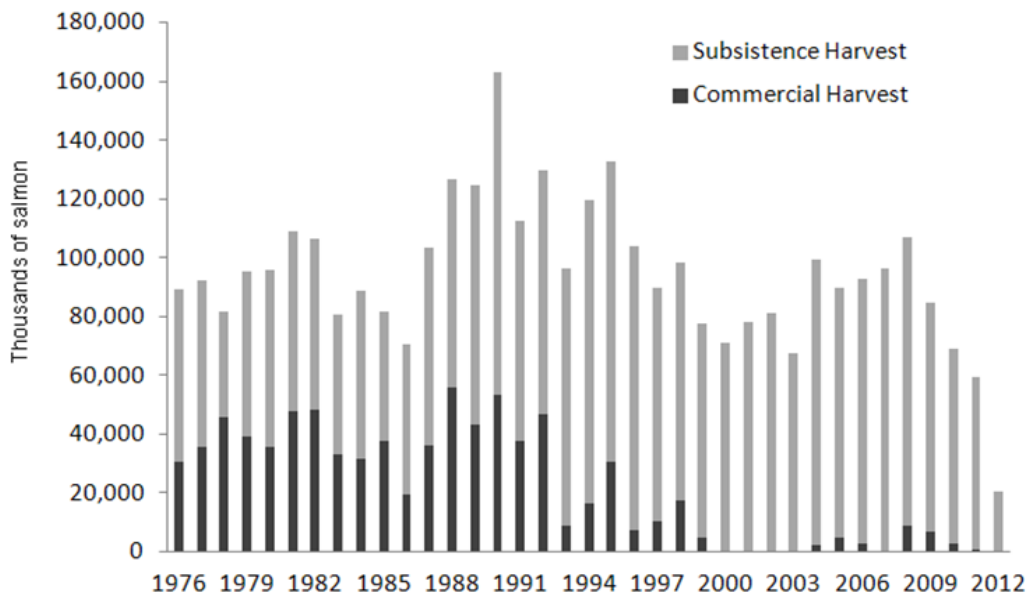


Figure 7. Estimated Kuskokwim River subsistence and commercial harvests of Chinook salmon 1976-2012. Estimate for 2012 should be interpreted as preliminary and potentially subject to revision. *Source:* Ellison et al 2012, Kevin Schaberg, ADFG, personal communication.

Chinook salmon abundance in the Kuskokwim River system has been highly variable based on estimates of drainage-wide reconstructed total abundance (**Figure 8**). The stock has undergone three periods of low abundance during which stock abundance dropped substantially. Each of these periods of low abundance was preceded by a period of high abundance during which sustainable escapement goals (SEGs) were exceeded in nearly all systems. Beginning in 2007, the Kuskokwim River Chinook salmon stocks began a five-year period of sharp, but not unprecedented, decline (**Figure 8**). The 2010 run, the lowest recorded in 35 years, did not meet escapement goals in the region, despite some restrictions to the subsistence fishery. The cumulative CPUE from the Bethel test fishery (most recent data at time of writing) currently shows the 2012 run

abundance to be lower than the 2010 run, and therefore unlikely to meet the low end of escapement targets throughout the watershed (**Figure 9**).

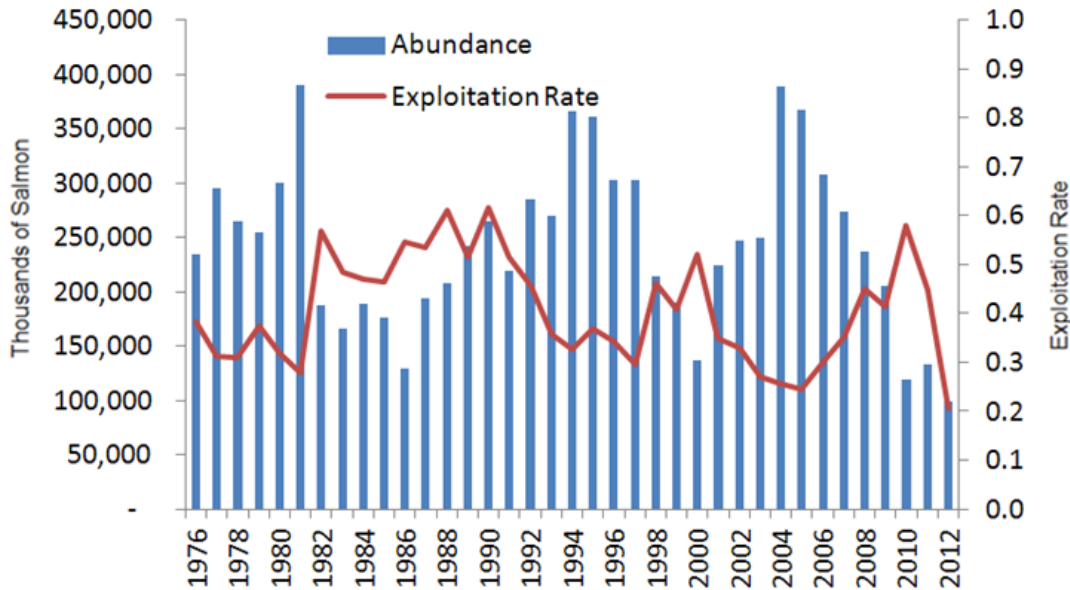


Figure 8. Estimated Kuskokwim River Chinook salmon drainage-wide total abundance (bars) and exploitation rate (solid line), 1976-2012. Estimate for 2012 should be interpreted as preliminary and potentially subject to revision. *Source:* Ellison et al 2012, Kevin Schaberg, ADFG, personal communication.

Chinook Salmon Cumulative CPUE Index, Bethel Test Fishery

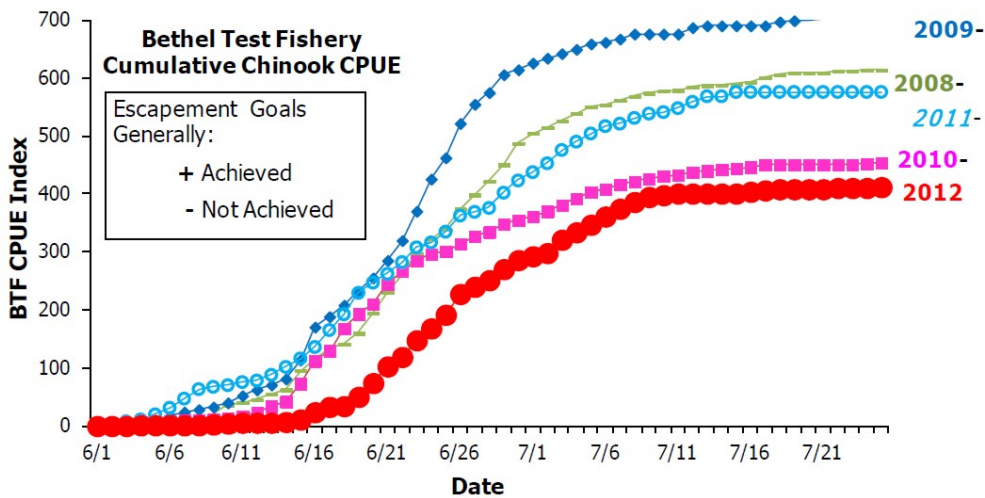


Figure 9. Cumulative CPUE from the Bethel test fishery for 2012 (red solid circles) in relation to CPUE from recent runs (2008-2011). Escapement goal achievement refers to tributaries to the Kuskokwim River. *Source:* ADFG, Comm. Fish Div., Kuskokwim River Salmon Management Working Group Information Packet, August 21, 2012.

Over the past 16 years, the productivity of Kuskokwim River Chinook salmon typically has been low, with the exception of the high productivity of the 1989 and 2000 brood years (**Figure 10**). From 1992 to 2007, only three brood years had productivity levels greater than 2:1 and seven brood years had productivity levels less than or equal to one recruit-per-spawner. The productivity of the 2004, 2005, and 2006 brood years was well below the minimum replacement level of one recruit-per-spawner, which has resulted in the declining trend in run abundance over the past four years. Based on the assumptions and results of the Kuskokwim River run reconstruction and analysis of productivity, recruits-per-spawner was negatively related to spawner abundance across most of the time series, with the highest spawner abundances producing the lowest recruit numbers (Schaberg et al 2012, Bue et al 2012). In general, escapements that exceeded 200,000 salmon resulted in recruitments that were below replacement (Bue et al 2012).

Ricker and Beverton-Holt stock-recruitment relationships were estimated within a Bayesian age-structured stock recruitment model (Fleischman et al 2013, Fleischman and Borba 2009). Visual inspection of model fits suggested that the Beverton-Holt model was inappropriate due to a pattern of declining residuals with increasing spawner abundance. Formal statistical analysis confirmed that the Beverton Holt model had considerably less support than the Ricker model, indicating that the Beverton-Holt model was less appropriate than the Ricker model for the basin-wide Kuskokwim River Chinook salmon stock. Further details on the model-fitting analysis are provided by Spaeder and Catalano (2012)

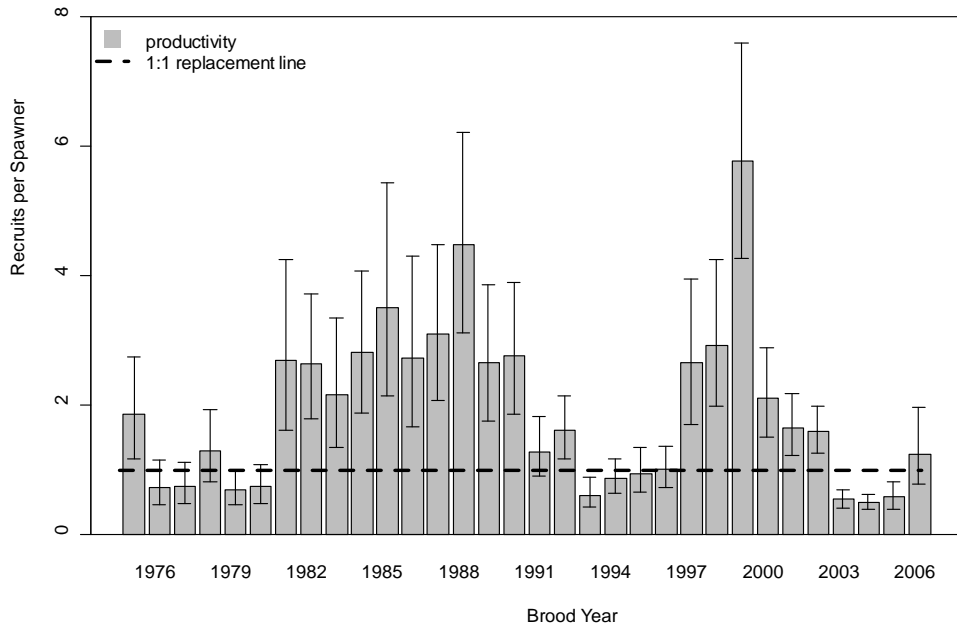


Figure 10. Estimated brood-year productivity (recruits-per-spawner; bars±95%CI) of Kuskokwim River Chinook salmon, 1976-2007. Productivity was estimated by dividing the sum of returns from a given brood year by the escapement that produced them. Brood year is defined as the escapement year of the parents that gave rise to the subsequent returns (progeny of the parents) and is also known as year class. Productivity from the 2008-2010 brood years was not estimable because those cohorts have not yet returned to the river. The horizontal dashed line depicts the productivity required for the population to replace itself. The estimates were obtained from a preliminary run reconstruction and Bayesian stock-recruitment analysis. Thus the estimates should be interpreted as preliminary and potentially subject to revision. *Source:* Kevin Schaberg, ADFG, personal communication.

Summary of Kuskokwim River

Over the 32 years from 1976 to 2007, productivity trends of Kuskokwim River Chinook salmon population dynamics have been marked by periods of high productivity (> 2:1 recruits-per-spawner ratio 1982-1991 and the 2000 brood years), but the majority of the years showed lower productivity (<2:1 recruits-per-spawner; 20 out of 30 years below) with returns in 11 years less than the replacement threshold of 1 recruit per spawner. The problem currently facing Kuskokwim River Chinook salmon stocks is that, based on analyses of recruits-per-spawner, observed runs sizes, and escapements, the salmon stocks appear to be in a multi-year period of low productivity and abundance, insufficient to meet necessary escapement levels, and to provide subsistence users with the opportunity to harvest “amounts necessary for subsistence” as established by the Alaska Board of Fisheries. This period of declining abundance, which began in 2007 has extended into at least the 2011 run and has resulted from the remarkably low recruits-per-spawner ratios of the 2004-2006 brood years. These recruits-per-spawner ratios fell below the minimum replacement level of one recruit-per-spawner required to sustain the population in the absence of any harvest. The current multi-year decline in the

Kuskokwim River has critical implications for the rural communities within the watershed that have a high reliance on the subsistence harvest of Chinook salmon and have among the lowest household incomes in the state.

3.3 Trends in Unalakleet River Chinook Salmon Populations

The Unalakleet River Chinook salmon population is a fairly small stock (4,000-25,000 fish) and is located near the northern edge of the coastal range of Chinook salmon. Combined subsistence and commercial harvest in the Unalakleet Subdistrict was estimated to be highest in 1985 (16,034 fish) and in 1997 (14,100 fish) and lowest in 2010 (1,234 fish) (**Figure 11**). Catches of Chinook salmon decreased sharply from 1998 to 2000 and since has remained stable ranging from 2,000 to 3,000 fish. Since the 2000s, little or no commercial fishing for Chinook salmon has been allowed because of low run abundance and an absence of a harvestable surplus. The variation in Chinook salmon catches in the Unalakleet River generally follows the same pattern of variation observed for escapement in the North River, a major tributary.

The largest escapements of Chinook salmon in the North River occurred over a three-year period, from 1997 to 1999, when the average was 2,849 fish, nearly double the long-term average of 1,475 fish (**Figure 12**) (Menard et al. 2009). However, since 1999 Chinook salmon escapement counts have been approximately 50% of this three-year average and at, or below, the long-term average.

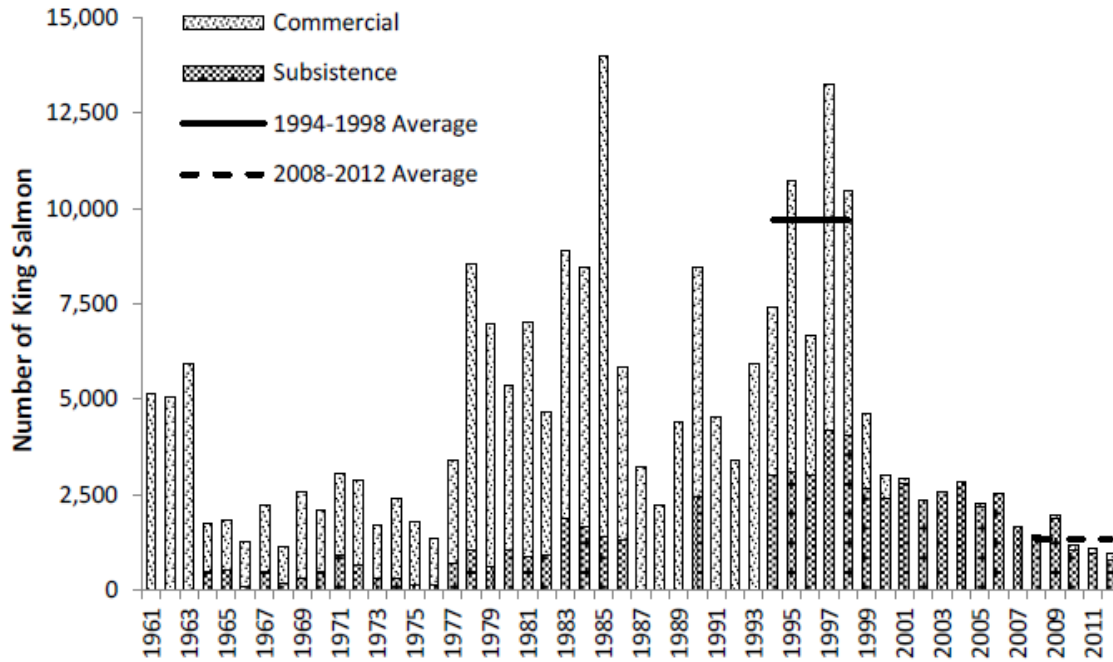


Figure 11. Subsistence and commercial harvests of Chinook salmon from the Unalakleet River fishing subdistrict (Norton Sound subdistrict 6) 1961-2012, compared to the recent 5-year (2008-2012) and historic (1994-1998) averages. *Source:* Kent and Bergstrom 2012.

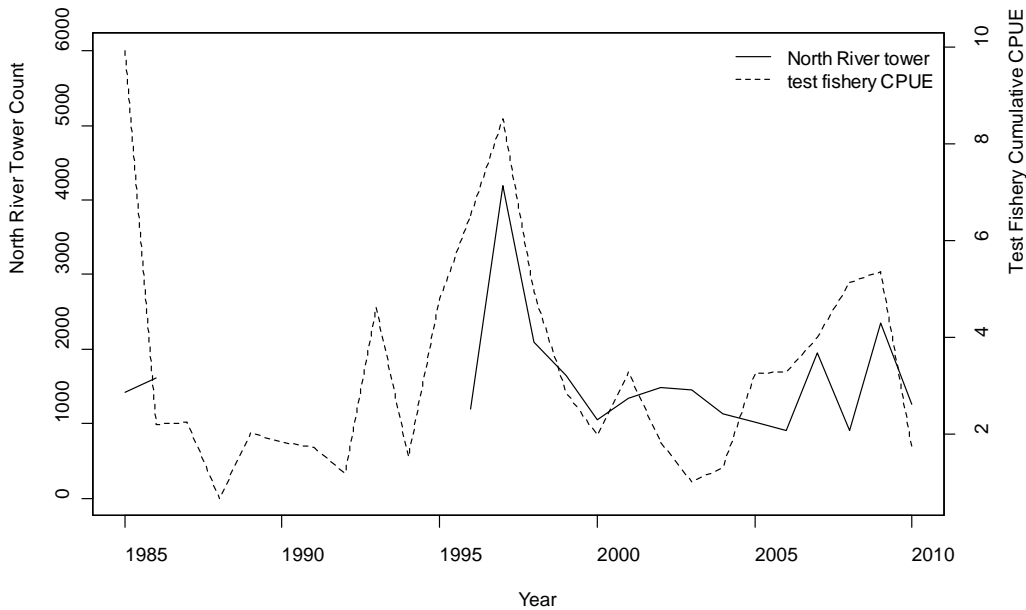


Figure 12. Indices of Unalakleet River Chinook salmon escapement from the North River counting tower and Unalakleet River test fishery CPUE. *Source:* Kent and Bergstrom 2009, Kent 2010, Scott Kent, personal communication.

Productivity of the Unalakleet River Chinook salmon stock has generally been lower since 1994 when compared to the 1985-1993 time period (**Figure 13**). Productivity (recruits-per-spawner) is weakly related to spawner abundance, but a large amount of

uncertainty exists in productivity and escapement estimates (Spaeder and Catalano, 2012).

Ricker and Beverton-Holt stock-recruitment relationships were estimated within a Bayesian age-structured stock-recruitment model with an integrated run reconstruction model (Fleischman and Borba 2009). The model made use of all available data (1985-2010) from weirs, counting towers, telemetry studies, harvest, age composition, and air surveys to estimate abundance and stock recruitment patterns. Both the Beverton-Holt and Ricker model provided plausible fits to the recruitment estimates (Catalano 2012). The run reconstruction component of the model indicated that few large escapements occurred, which substantially reduced contrast in the spawning stock estimates. Thus, the equilibrium stock size and the magnitude of compensation were weakly informed by the data.

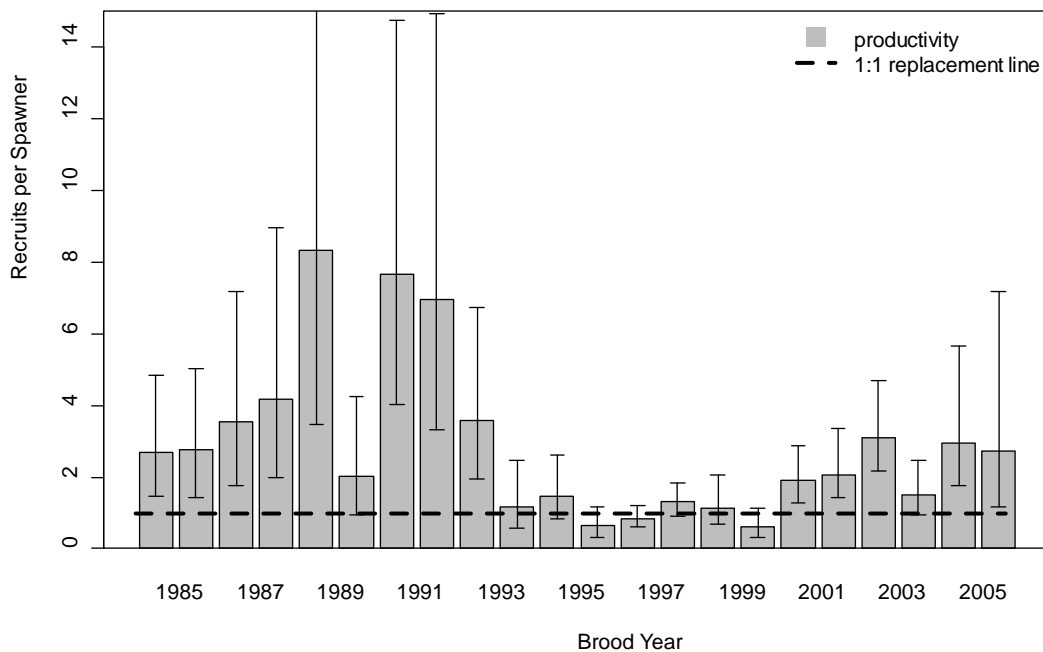


Figure 13. Brood-year productivity (recruits-per-spawner; bars, $\pm 95\%$ CI) of Unalakleet River Chinook salmon, 1985-2006. Productivity was estimated by dividing the sum of returns from a given brood year by the escapement that produced them. Brood year is defined as the escapement year of the parents that gave rise to the subsequent returns (progeny of the parents) and is also known as year class. The horizontal dashed line depicts the productivity required for the population to replace itself. The estimates were obtained from a preliminary run reconstruction and Bayesian stock-recruitment analysis. Thus the estimates should be interpreted as preliminary and potentially subject to revision. Source: Scott Kent, ADFG, personal communication.

Summary of Unalakleet River

The Unalakleet River Chinook salmon stock abundance has declined and is no longer sufficient to support a commercial fishery, nor customary subsistence levels that it supported for many years. Some evidence exists of coherency in run abundance between the Yukon River and Unalakleet River Chinook salmon stocks, both having generally weak returns since the late 1990s. However, the Unalakleet River stock did not show increases in productivity in the late 1990s to early 2000s followed by increases in abundance in the mid-2000s as was observed for the Yukon and Kuskokwim river stocks. Although the Unalakleet River Chinook salmon stock is relatively small compared to the Yukon River and Kuskokwim River stocks, it is important to include it in this broader analysis. As the most northern Chinook salmon stock for which stock-recruitment analyses have been conducted, it also provides a valuable reference point for Chinook salmon stock dynamics at the margins of the distribution of the species.

4.0 Summary of Production Dynamics of Non-AYK Region Chinook Salmon Populations

The influence of environmental variables that could affect salmon survival is addressed in three (Hypotheses 2-4) of the seven hypotheses put forth to explain declines in AYK Chinook salmon (Section 5). The prominence of potential environmental influences on salmon population dynamics begs the question “does evidence already exist within the available data that these variables play an important role?” To better understand the extent to which environmental mechanisms may explain the variability of AYK Chinook salmon stock abundance, Catalano (2012) examined trends in salmon productivity of non-AYK Chinook salmon stocks and compared these trends to those of AYK stocks. Are abundance patterns for non-AYK stocks similar to AYK stocks? For example, positive correlation (similar variation in abundance over the same time periods) across stocks over a broader geographic area would lend support for the existence of large-scale, influential environmental mechanisms affecting salmon abundance across a larger region.

The extent to which AYK stocks share productivity trends with non-AYK stocks could point to potential drivers of variation in productivity. Temporal trends in Chinook salmon recruitment and spawner abundance (total life cycle productivity) were compared between 11 non-AYK stocks from Alaska and the five AYK stocks - Unalakleet River, Yukon River (mainstem Canadian portion), Chena/Salcha rivers, Kuskokwim River (described in Section 3), and Goodnews River.

Although the overall abundance trends differed between AYK and most of the non-AYK stocks, many of the stocks across the four regions (AYK, Bristol Bay, Cook Inlet, Southeast) shared a period of very low abundance starting in the mid to late 2000s (**Figure 14**). The most recent abundance estimates for thirteen of the fifteen stocks were at or near the lowest on record (**Figure 14**). This correspondence in overall trends suggests that broad scale environmental variables (e.g., marine) have likely had a significant role in affecting the variability of Chinook salmon abundance.

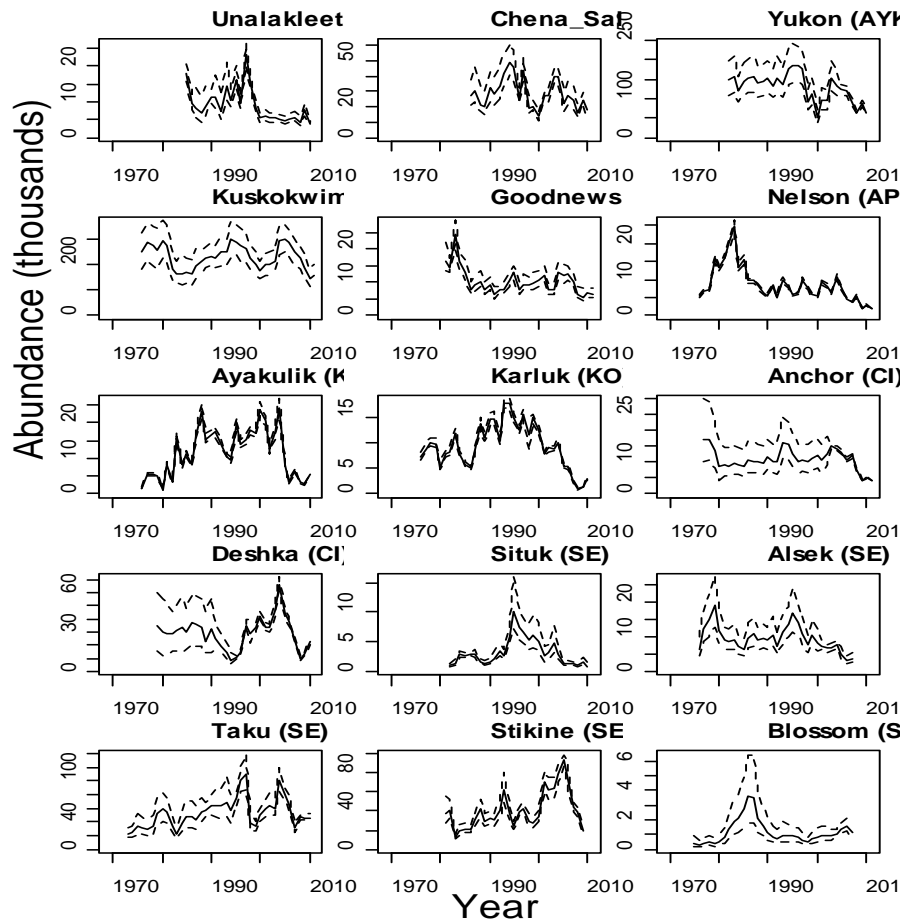


Figure 14. Total abundance estimates (solid line) and 95% credible intervals (dashed lines) for five AYK and 10 non-AYK Chinook salmon stocks. Estimates were obtained from Bayesian state-space Ricker stock recruitment models. AYK = Arctic-Yukon-Kuskokwim Region, AP = Alaska Peninsula Region, KO = Kodiak Island Region, CI = Cook Inlet Region, SE = South East Region.

Temporal patterns in recruits-per-spawner (R/S) values and $\ln R/S$ residuals indicated considerable variability in productivity within and among regions but some general patterns existed (**Figure 15**). Correlation analysis of $\ln R/S$ residuals revealed positive (but in some cases weak) correlations among all of the AYK stocks as well as the Goodnews River stock, which is the next substantial Chinook salmon stock to the south of the Kuskokwim River (**Table 1**). The other four AYK stocks also showed some positive correlations with the Kodiak Island and Cook Inlet stocks of Karluk and Anchor rivers. Correlations among southeast stocks were variable and generally weak (**Table 1**).

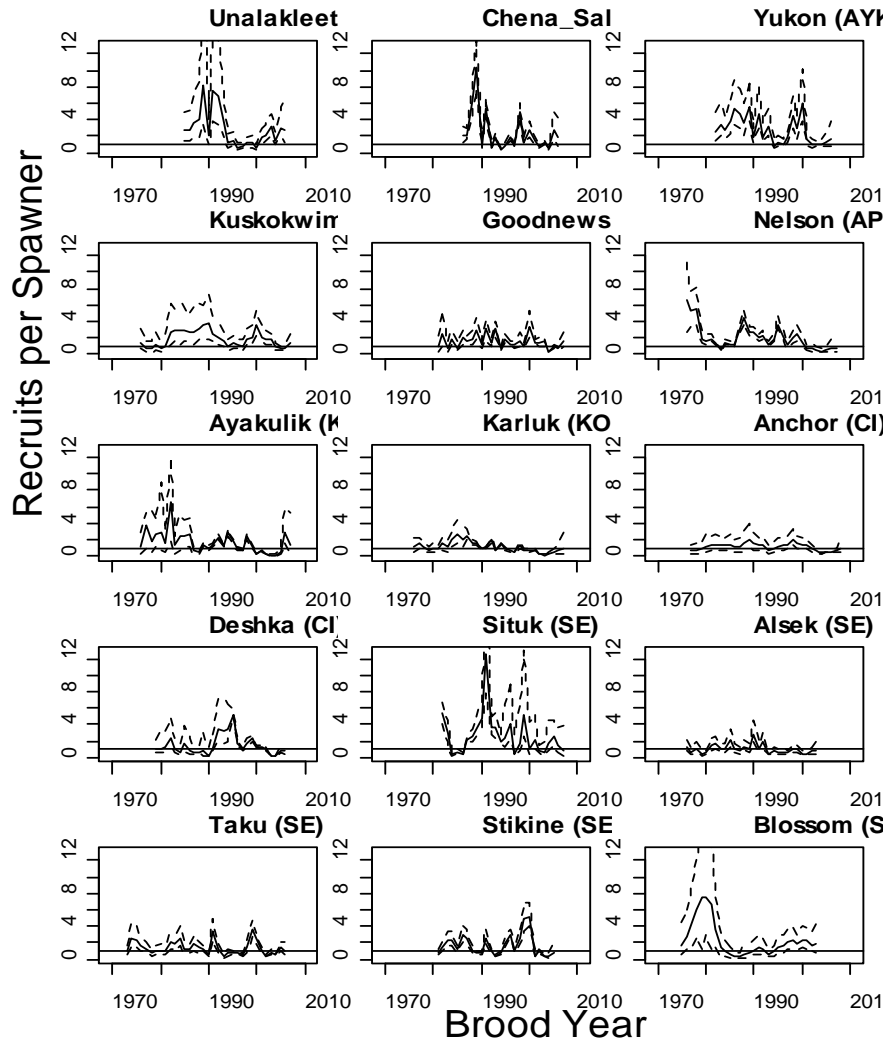


Figure 15. Estimated brood year total recruits-per-spawner (R/S; solid line) and 95% credible intervals (dashed lines) for five AYK and 10 non-AYK Chinook salmon stocks. Estimates were obtained from Bayesian state-space Ricker stock recruitment models. The solid horizontal line indicates the replacement level (1.0). AYK = Arctic-Yukon-Kuskokwim Region, AP = Alaska Peninsula Region, KO = Kodiak Region, CI = Cook Inlet Region, SE = South East Region.

Temporal trends in productivity were more similar for stocks that were geographically close together than for those that were far apart. Between-stock distance (i.e., between river ocean entry locations; km) and \ln R/S residual correlations were negatively related, and this relationship was statistically significant ($P = 0.003$). The expected correlation for adjacent stocks (distance = 1 km) was 0.29, and near zero at a distance of 2,100 km, which was the maximum between-river distance for the 15 stocks. However, the relationship was not predictive ($R^2 = 0.09$) due to a large amount of variability in correlations among different stock pairs that had similar between-river distances.

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Table 1. Pairwise Pearson’s correlations of stock-specific ln R/S residuals from Ricker stock recruitment models. Correlations that were significantly different from zero are indicated by ** ($\alpha = 0.05$) and * ($\alpha = 0.1$).

	Unala- kleet	Chena/ Salcha	Yukon	Kusko- kwim	Good- news	Nelson	Aya- kulik	Karluk	Anchor	Deshka	Situk	Alsek	Taku	Stikine
Chena/Salcha	0.26													
Yukon	0.33	0.71**												
Kuskokwim	0.16	0.30	0.48**											
Goodnews	0.12	0.53**	0.36*	0.42**										
Nelson	0.05	0.10	0.20	-0.03	0.15									
Ayakulik	0.17	0.17	0.16	-0.18	0.08	0.42**								
Karluk	0.28	0.13	0.28	0.03	0.06	0.64**	0.75**							
Anchor	0.00	0.30	0.33	0.38**	0.30	0.60**	0.43**	0.56**						
Deshka	-0.43**	-0.12	-0.39*	-0.19	0.17	0.08	0.23	-0.02	0.04					
Situk	0.08	-0.10	0.05	0.13	0.11	0.69**	0.47**	0.53**	0.43**	0.10				
Alsek	0.26	-0.30	0.01	-0.22	-0.50**	0.31	0.45**	0.57**	0.08	-0.30	0.44**			
Taku	-0.01	0.07	0.39*	0.26	0.16	0.05	0.18	0.26	0.15	0.09	0.24	0.05		
Stikine	-0.46**	-0.14	-0.12	0.10	0.25	0.11	-0.18	-0.19	0.04	0.41**	0.08	-0.46**	0.44**	
Blossom	-0.29	0.04	-0.02	-0.46**	0.02	0.18	0.03	-0.19	-0.36*	0.21	-0.53**	-0.05	-0.03	0.12

Summary

Correlation recruitment anomalies among stocks suggested that stocks in close geographic proximity to one another were more similar in their trends than widely separated stocks, possibly due to common environmental variables affecting stock dynamics. When looking broadly across all of the stocks, the significant negative relationship between correlations between recruitment anomalies and between-stock distance also suggested that regional environmental variables may explain at least some of the temporal variability in productivity. For Alaskan Chinook salmon stocks, it remains unclear whether these regional variables, to the extent that they exist, act in the freshwater or marine life stage, or both. Better understanding of these patterns and the extent to which the AYK stocks experience similar influences on productivity is needed.

5.0 Hypotheses to Explain the Changes in Production Dynamics

Below are descriptions of seven hypotheses addressing what are, in the opinion of the Chinook Salmon Expert Panel, the most likely causes of the long-term decline and periodic low returns of AYK region Chinook salmon.

The hypotheses presented below reflect statements describing how various processes **may** cause salmon abundance to vary. Hypotheses should not be interpreted as statements of fact or statements of belief of the AYK SSI, but instead are propositions about how the salmon system may work. The hypotheses are posed as positive statements for forthcoming studies to assess the strength of evidence supporting each potential cause of decline in AYK Chinook salmon populations. Understanding the plausibility of the hypotheses may be helped if the reader, while reading the hypothesis, inserts before each hypothesis, “To determine whether...[hypothesis]”. Please also note that the questions presented below are simply examples and are not intended to be the only questions of importance. The questions should serve to stimulate researchers to craft their own hypotheses and questions as they develop research proposals.

After the statement and description of the hypotheses, information is presented on the plausibility of the biological mechanism and summary of evidence supporting each hypothesis. Last, a set of research themes and example questions are presented for each hypothesis.

5.1 Hypothesis 1 – Density-dependent Effects and Overcompensation

Hypothesis: *Recent declines in AYK Chinook salmon stocks are caused by strong density-dependent feedbacks in population dynamics that cause decadal-scale changes in abundance.*

5.1.1 Description of the Hypothesis

In the salmon literature, high spawner abundances in some systems can cause declines in the recruitment of the next generation via strong density-dependent effects, a biological process referred to as “overcompensation”. Another term, “overescapement”, refers to exceeding a spawner escapement goal. Overescapement may result in overcompensation. At high spawner densities, which can be experienced when overescapement occurs, competition for critical resources (e.g., spawning habitat, food resources for overabundant juveniles) may become so intense as to substantially reduce recruitment to levels below what is needed for cohort replacement, thereby leading to temporary population declines.

5.1.2 Plausibility of the Biological Mechanism(s)

Density-dependent processes provide feedbacks from population abundance to the reproductive success of fishes, including Chinook salmon. The number of recruits produced per spawner (R/S) is a measure of the per-capita reproductive success and survival to the next generation that depends not only on density-independent (i.e., environmental) processes, but also on salmon abundance (density-dependent processes). At low population abundance, individual fish generally produce several successful recruits to the next generation, but this reproductive success declines as abundance increases and competition intensifies for limited resources such as food and space for juveniles, predation refuges, and adult spawning habitat. This intensification of competition at high densities slows population growth and prevents populations from building to infinite sizes. In some cases, competition can be sufficiently intense at high spawner abundances that overcompensation occurs, causing recruitment to drop below levels needed to replace the spawning population. Such feedbacks between population abundance and recruitment success can occur at different phases of the salmon life cycle and can produce highly complex population dynamics, even in the absence of any environmental effects on the population.

Density-dependent effects potentially mask or interact with the environmental processes addressed by other hypotheses described below. For example, average survival may be low at high spawner abundances, despite otherwise productive conditions in the environment. Thus, analyses to quantify effects of changing climatic conditions or ecosystem productivity on salmon populations (Hypotheses 2-4) must simultaneously account for changes in population abundance due to intrinsic, density-dependent processes.

Salmon management in Alaska seeks to manage fish stocks to achieve sustainable returns through establishment of escapement goals, of which several types are defined. The most rigorous of these is termed a biological escapement goal (BEG) and is based on spawner-recruitment analyses in systems where sufficient data are available to quantify stock-recruit relationships. These analyses are typically characterized with a Ricker stock-recruit function that quantifies the strength of density-dependence in individual stocks. The BEG is selected to maximize the probability that maximum sustainable yield (MSY) can be achieved, by regulating harvest rates on returning adults to produce spawning escapement levels thought to produce a sustainable maximum harvestable surplus over the long term. However, for most salmon stocks in Alaska a BEG cannot be determined because sufficient data do not exist to estimate the spawner-recruit relationship. Furthermore, many stocks cannot be managed according to MSY because fishing levels are inconsistent or inadequate to achieve harvest levels close to MSY.

Thus, according to the model, a wide range of less than maximum fishery yields exist that are sustainable over time.

Analysis of some salmon populations has revealed the phenomenon of overcompensation, an unusually strong density-dependent effect from competition among individuals that is sufficiently intense to drastically reduce population productivity at very high spawning abundance. Overcompensation is characterized by a hump-shaped relationship between spawner abundance and recruitment to the next generation, which can result in low recruitment (even below that needed for replacement) from broods that spawned at high abundances. These feedbacks, in turn, can produce abundance-scarcity cycles or chaotic dynamics in salmon populations. While statistical evidence of density-dependent effects (including overcompensation) exists for some AYK stocks, the specific mechanisms that could produce such effects remain poorly understood.

Many biological mechanisms could produce the recruitment feedbacks described above. The most commonly cited mechanism is competition for limited food resources for juvenile salmon (Hilborn and Walters 1992, Walters and Martell 2004). In some systems, competition among spawning adults for limited spawning habitat, and interactions with predators may also produce density-dependent population dynamics. Bradford et al. (2008) compiled evidence that suggests density-dependent survival in the juvenile stages does occur. While all of these mechanisms are biologically plausible and have been demonstrated in specific ecosystems, little information is available about their importance and prevalence in AYK ecosystems, and whether they are strong enough to produce overcompensation in population dynamics.

5.1.3 Summary of the Evidence for the Hypothesis

Statistical analyses of AYK Chinook salmon populations show mixed evidence for overcompensation in their dynamics. Evidence from the Kuskokwim River, based on a recent stock reconstruction by Bue et al. (2012), suggests strong density-dependent effects to the point of substantial overcompensation in this stock. Though Bue et al. (2012) did not include a full assessment of the uncertainty associated with the spawner-recruit relationship, the authors found that production of Chinook salmon in the Kuskokwim River dropped below 1.0 (the value needed for the population to replace itself in the next generation) at escapement levels above ~200,000 fish. Thus, given the assumptions of the run reconstruction and production model (Bue et al. 2012), the available evidence (1976-2006 brood years, Figure 10 above) tends to support the hypothesis that the observed dynamics of Chinook salmon in the Kuskokwim River are a reflection of strong density-dependent feedbacks in this stock. However, Scheuerell (2012) also finds evidence for environmentally driven changes in production. The

specific mechanisms that could produce such strong density-dependence in the Kuskokwim River Chinook salmon stock remain unknown.

Statistical evidence for overcompensation in Yukon River Chinook salmon is weak relative to evidence for strong environmentally driven changes in production based on a preliminary analysis of the relationship between spawning stock size and recruitment (Fleishman 2012; Catalano 2012). Analyses by Catalano (2012) of 12 Alaska stocks ranging from Southeast Alaska to the Yukon River, including the AYK stocks, show that statistical support for overcompensation in the stock-recruitment dynamics was generally weak across the 12 stocks, with the one exception of the Kuskokwim River stock. The anomalous result of the Kuskokwim River in comparison to other Alaska Chinook salmon stocks may be a product of a relatively low exploitation rate with high escapement in recent history that has produced data to characterize the stock-recruitment relationship at high spawner abundances. Uncertainty analysis of the Kuskokwim River stock would permit a direct comparison to the relationships observed in the other Alaska stocks and a determination of the confidence we can have in the evidence for overcompensation in Kuskokwim River Chinook salmon.

Recent coast-wide syntheses offer broad evidence that production dynamics of Chinook salmon along the North American coast are strongly density-dependent, including ‘Ricker’ dynamics that characterize overcompensation in population dynamics (Sharma and Liermann 2010, Liermann et al. 2010, M.D. Scheuerell, unpublished manuscript). However, these analyses also demonstrate that environmental covariates (including the strength of the Pacific Decadal Oscillation and sea surface temperatures) account for additional variation that is statistically significant in the Chinook salmon recruitment in all stocks, including some from the AYK region. Taken together, these results emphasize the expected universality of both density-dependent and environmental effects on Chinook salmon population dynamics, as preliminary analyses of Yukon River and Kuskokwim River stocks seem to indicate. The dominant influence of density-dependent factors on recruitment dynamics in Kuskokwim River Chinook salmon is anomalous when compared with the other stocks analyzed by Catalano (2012).

5.1.4 Priority Research Themes and Example Questions

Comparative Stock-Recruitment Analyses

1. How does the intensity of density-dependent effects (including overcompensation) in AYK stocks compare to those of other Chinook salmon stocks in Alaska and elsewhere? How does the uncertainty around the estimates of total run and stock-recruitment relationships for AYK stocks compare to those determined for other Alaska Chinook salmon stocks?

Comparison of Metrics to Produce Biological Reference Points in AYK Chinook Salmon

2. How do estimates of carrying capacity and specific escapement levels predicted by watershed habitat models compare to those produced by standard brood-table based stock-recruitment analyses? Metrics for AYK Chinook salmon escapement goals based on existing stock-recruit analyses should be compared to those predicted by the watershed habitat model in Liermann et al. (2010).

Density-dependent Processes

3. What processes are most likely to produce strong density-dependent effects in AYK Chinook salmon stocks? For example, based on studies of the ecology of salmon in their spawning and nursery habitats, does evidence of extreme crowding in the spawning areas exist? Are juvenile densities high relative to standard or expected densities? How sensitive is juvenile growth, body condition, and survival to their density in critical nursery habitats?

5.2 Hypothesis 2 – Freshwater Mortality

Hypothesis: *Change in the suitability or productivity of freshwater habitats used for spawning, rearing and migration has contributed to declines in AYK Chinook salmon stocks.*

5.2.1 Description of the Hypothesis

This hypothesis examines the way in which productivity and population dynamics of Chinook salmon populations are linked to environmental conditions that control growth and survival during the freshwater component of their life cycle. Adult, embryonic, and juvenile stages are all vulnerable to changes in freshwater environmental conditions. In adults, mortality associated with temperature and oxygen constraints during migration are likely variables that could be important. Incubating embryos could be affected by several variables including winter temperatures, oxygen regimes, flow-related gravel scouring, and entombment by fine sediment. In juvenile stages, food resources that affect growth rates and associated survival during smoltification, and mortality losses to freshwater predators are variables that could affect overall population dynamics. Additional research is needed to improve our understanding of the role of environmental variables on salmon population dynamics. The freshwater portion of the life cycle of Chinook salmon provides greater management opportunities because freshwater processes are more likely to be responsive to management actions than those processes relevant to the marine life stage. Thus, our ability to distinguish between freshwater and marine stressors on Chinook salmon population dynamics is important for management decisions.

5.2.2 Plausibility of the Biological Mechanism(s)

For most salmon populations the freshwater stages sustain about half of the total egg-to-adult mortality (Bradford 1995). However, for stream-type Chinook salmon egg-to-smolt survival can be higher than other species, but marine survival can be lower due to their longer residence time in saltwater. Mortality can occur during the incubation stage as a result of environmental variables (e.g., spawning gravel, streamflow, ice, freezing), and during the rearing phase by environmental (e.g., streamflow, temperature, dissolved oxygen) or biological (e.g., food production, predation, competition, disease) variables. Fisheries interception of the marine-derived nutrients (MDN) transported from marine to freshwater ecosystems by migrating salmon has been widely proposed to reduce the capacity of freshwater habitats to support growth of juvenile salmon. Freshwater habitats are also vulnerable to anthropogenic and climate-related change. Mortality during the seaward migration in rivers could also be an important potential driver for population trends, especially for populations that have long riverine migratory routes (Quinn 2005). The central question underlying this hypothesis asks whether any specific variable in the freshwater environment, or some combination, could have contributed to the observed trends in AYK Chinook salmon.

5.2.3 Summary of the Evidence for the Hypothesis

Little evidence exists to support the hypothesis that large-scale environmental forcing produces coherence in abundance or survival only during the freshwater phase of salmon populations. Bradford (1999) found that coherence in the production of coho salmon smolts was limited to streams less than 30 km from each other, and even for adjacent streams the correlation in annual smolt abundance estimates was low ($r < 0.3$). A similar conclusion was reached by Rogers and Schindler (2008) for sockeye salmon in Bristol Bay. Bradford (1999) suggested that the effects of environmental variables would be “translated” to effects on stream biota by the nature of the catchment, and with the possible exception of extreme events, the effects of a single environmental forcing agent could be watershed-specific (e.g., as revealed by Crozier and Zabel 2006 for Snake River Chinook stocks). Furthermore, limited evidence suggests that the freshwater life history of AYK Chinook salmon is plastic, with juveniles undergoing a variety of migration and rearing strategies in their first year (Bradford et al. 2008) in response to environmental variation. This diversity in life history reduces the likelihood that a single environmental or biological forcing agent will be able to generate coherent trends in freshwater survival across a broad spatial scale.

While a lack of evidence of large-scale coherence produced by drivers acting solely within the freshwater phase of salmon populations exists, evidence for coherence among escapement indices occurs at broad watershed scales in the AYK region. For the

upper Yukon River stocks, the available escapement indices suggest that the trends in abundance fluctuate coherently across the basin (Fleischman 2012, Figure 2). A similar conclusion is reached in comparing the trend in recruits-per-spawner for Kuskokwim River and upper Yukon River stocks (Catalano 2012). For a mortality factor to be a driver of trends in abundance or productivity and produce coherence among returning adults among geographically distant stocks, that variable must operate at large spatial scales, or on a habitat that populations use in common such as in the ocean or major fresh water migratory routes (as adults between the ocean and freshwater spawning habitat or as juveniles between freshwater and the ocean).

Nonetheless, recent analyses of Neuswanger et al. (2012) indicated that some variation in adult returns rates was correlated with environmental variables affecting the productivity in freshwater habitats. However, this study took place in a single tributary system in the middle portion of the Yukon River, and whether its conclusions could apply throughout the AYK region is unknown. Anthropogenic effects on freshwater habitats in most portions of AYK region are relatively minor and are largely restricted to placer gold mining in a few basins (with the notable exceptions of many Nome subdistrict watersheds and the Tuluksak River watershed, a tributary to the Kuskokwim River). Placer mining has impacted a number of non-natal juvenile rearing streams in the Canadian portion of the basin. These effects would not provide coherent trends across a broad spatial scale but could be important at local scales. Last, the impacts of climate change on freshwater habitat conditions in the AYK region are expected to be substantial and a combination of retrospective analysis and focused field research may provide insights into the linkage between future climate change and freshwater habitats. These effects could provide broad spatial-scale coherence in the future.

5.2.4 Priority Research Themes and Example Questions

Role of Environmental Variables on Ecology of Chinook Salmon in Streams

1. Do environmental forcing variables such as flow extremes explain trends in Chinook salmon productivity in the AYK region? This analysis will extend and generalize the preliminary results for the Chena River (Neuswanger et al. 2012). Other drivers could be considered, including temperature and abundance of other species. Additional life stages should also be included, such as embryo incubation, juvenile overwintering habitat, and juvenile downstream migration. This analysis could guide further work on effects of climate change on freshwater habitats.
2. Are marine and freshwater habitat conditions linked by large-scale climate variation? Does co-variation exist across these habitats due to climate variation that could confound the analyses of one or the other? As an extension of #1, inter-annual and decadal variation in freshwater and marine environmental signals should be

compared to determine if co-variation exists across environments that could confound analyses.

Role of Downstream Smolt Survival to the Ocean

3. Does variation in smolt abundance and delivery to the ocean significantly explain later adult returns to rivers? Can inference about trends in freshwater and marine mortality be improved by an adult escapement/smolt assessment program? Partitioning mortality between freshwater and marine life stages is required as a step toward identifying the life stages that are influential in determining population trends. However, estimating smolt abundance in large-river systems is difficult and expensive. Possibly, other sources of information can be gathered to index smolt abundance such as nearshore marine sampling.

Marine-Derived Nutrients

4. Are marine-derived nutrients (MDN) an important contributor to production of juvenile Chinook salmon in freshwaters across the AYK basin? MDN is likely important in areas where high densities of pink, chum, and possibly sockeye salmon occur. Chinook salmon occur at substantially lower spawning abundances than these other species so the contribution of Chinook salmon to MDN in freshwater is probably minor compared to contributions from more abundant species. Interior regions have high densities of carcass predators and juveniles frequently disperse extensively; these variables can reduce the effects of MDN on juvenile production.

Climate Change and Adult Migration.

5. Are mid-summer temperatures in large rivers in western North America increasing as a result of changes in snowmelt, precipitation, land and water use, and air temperature? Warm temperatures can contribute to an increase in the incidence of migration mortality, either as a result of stress, energy depletion, or increased susceptibility to disease. Stress resulting from interactions with fishing gear can also increase due to high temperatures.

5.3 Hypothesis 3 – Ocean Mortality

Hypothesis: *Ocean conditions (physical and biological) have changed in the Bering Sea, causing an increase in mortality of Chinook salmon during their the early marine portion of their life cycle and contributing to declines of AYK Chinook salmon stocks.*

5.3.1 Description of the Hypothesis

Scientists have long recognized the importance of the ocean to salmon population dynamics via survival to maturity and return to the rivers as adults (e.g., Pearcy 1992, Beamish 1993). Indeed, Chinook salmon spend most of their life history and gain more than 95% of their weight while at sea. Changes in the physical environment (e.g.,

temperature) can affect salmon directly via physiological processes, with ultimate consequences for growth and reproduction. Changes in the physical environment can also affect salmon indirectly through changes in the food web. For example, increased upwelling can lead to better primary and secondary production, leading to increased food availability for juvenile salmon. Changes in the biological environment, such as food-web structure (i.e., prey, competitors, predators), can also affect feeding rates and ultimately survival. Importantly, both natural and human drivers play important roles in structuring the marine environment, though human drivers are addressed under Hypothesis 4. A potential exists for considerable sharing of ocean habitats among stocks, and therefore trends in survival during the early ocean phase of Chinook salmon can produce regionally synchronous changes in salmon abundance.

5.3.2 Plausibility of the Biological Mechanism(s)

Two time periods are believed to be especially important for salmon survival during their time at sea: the spring and summer months immediately after smolt out-migration, and the first winter at sea (Beamish and Mahnken 2001). An expanding body of literature links conditions in the marine environment to salmon survival. Some studies have been based on large-scale descriptors (e.g., Pacific Decadal Oscillation, Mantua et al. 1997) whereas others have relied more on direct measurements of regional physical conditions (e.g., sea surface temperature, Mueter et al. 2002).

Differences in migration timing can lead to matches or mismatches with important prey resources and predators that ultimately translate into varying growth opportunities and differences in survival (e.g., Scheuerell et al. 2009, Holsman et al. 2012). Chinook salmon endure long periods of low forage during winter and must rely on stored energy accumulated during the growing season for survival through the winter.

Changes to the marine environment experienced by AYK Chinook salmon upon entry to the marine environment and during the early period of the marine portion of their life cycle are certainly a plausible explanation for their decline in recent years.

5.3.3 Summary of the Evidence for the Hypothesis

Scheuerell (2012) presented an analysis of an extended Ricker model used to incorporate the possible effects of environmental covariates on four AYK stocks (i.e., Chena River, Salcha River, Kuskokwim River, and Canadian-origin Yukon River). After accounting for intrinsic productivity and density-dependence within a hierarchical Bayesian framework, Scheuerell found additional evidence that various “ocean indicators” offer additional power in explaining temporal trends in recruits-per-spawner. In particular, those indices associated with sea-level pressure (i.e., Arctic Oscillation Index, North Pacific Index, Bering Sea Pressure Index) and, to a lesser extent, sea

temperature (i.e., Pacific Decadal Oscillation) appeared most important. While these associations between survival and large-scale climate indices do not provide a mechanistic explanation for which specific processes are causing variation in survival, they do suggest that broad-scale changes in the environment are translating into a changing suitability of the ocean encountered by juvenile Chinook salmon during their early marine life phase. Perhaps more importantly, each of the four stocks showed different responses to the indicators, suggesting: 1) the different stocks do not use the same places in the ocean as either juveniles or adults, or 2) smolts from the different stocks out-migrate at different times, and thus experience different conditions upon ocean entry.

Murphy (2012) showed preliminary evidence based on a short time-series of data that the juvenile salmon abundance index for Canadian-origin Chinook salmon correlates with overall patterns in recruits-per-spawner, suggesting year-class strength is largely set during the first 2.5 years of life. However, a lack of data on intermediate stream-life stages (e.g., parr, smolts) precludes concluding that the hypothesized effects of a changing ocean environment on marine survival/mortality exclusively caused the connection to the patterns in recruits-per-spawner. That is, although several of the indicators discussed by Scheuerell (2012) (e.g., sea surface temperature) describe conditions within the Bering Sea *per se*, others (e.g., Pacific Decadal Oscillation) describe larger synoptic climate patterns that also manifest themselves over the continental land mass and may have affected the early life stages in freshwater or estuarine habitats.

Murphy (2012) also showed that the past spatial distribution of juvenile Chinook salmon in the Bering Sea indicated that few fish have been caught in southeastern areas since 2007. It is unclear why Chinook salmon are no longer caught in the southern Bering Sea; however, multiple factors are likely contributing, including changes in the distribution and abundance of Chinook salmon as well as changes to the survey design. Large differences in the distribution of juvenile Chinook salmon in the northeastern Bering Sea occurred between warm and cold years, which likely reflect changes in the migration patterns of juveniles. Large-scale changes in the migratory pattern of juveniles have the potential to alter marine survival, the apparent relationship between the number of juveniles and returns-per-spawner, and marine distribution patterns during their later marine life history stages. Last, Chinook salmon are piscivorous, and despite differences in diet content between warm and cold years, the diet data available suggest that they appear to maintain adequate food intake and energy levels.

5.3.4 Priority Research Themes and Example Questions

Forecasting Adult Salmon Returns to Rivers

1. When stocks other than those from the Chena River, Salcha River, Kuskokwim River, and Canadian-origin Yukon River are analyzed with a hierarchical Ricker model, do they show the same relationships with ocean indicators? Will adding additional covariates improve the explanatory power of such models? Add additional covariates and other populations/stocks, where possible, to the hierarchical Ricker model to empirically assess the potential effects of changes in the marine climate system on survival rates of AYK Chinook salmon.
2. What combination of freshwater and marine environmental variables, measured at different life history stages, and spawning stock size best predicts the next generation of salmon returns? Do these variables co-vary? Examine co-variation between freshwater (e.g., streamflow) and marine variables (e.g., sea surface temperature) at varying time lags (i.e., matching with life history, 0-5 years) to better understanding potential linkages between conditions in freshwater and in the nearshore ocean for determining recruitment success. Develop forecasting tools for returns.

Early Marine Survival

3. At what life stage is the strength of recruitment determined? When during the life cycle does most variation in mortality occur? Is mortality greatest during their first year at sea? Obtain abundance estimates of freshwater rearing stages (parr) and migrant/early ocean stages (smolts) to better pinpoint when in the migration timing and where in the life cycle mortality occurs.
4. What processes affect the survival of AYK Chinook salmon during their first year at sea? How do food availability, temperature, and other variables appear to affect survival? A better understanding is needed of the processes affecting survival of AYK Chinook salmon during their first year at sea.
5. Do migration timing and pathways vary by life stage among AYK stocks? Improvement of genetic tools to better identify origin/population of fish caught at sea would allow exploration of this question.

5.4 Hypothesis 4 – Anthropogenic Changes to Marine Ecological Processes

Hypothesis: Human-caused changes in the ocean have reduced growth and survival of AYK Chinook salmon contributing to the declines in these stocks.

5.4.1 Description of the Hypothesis

Marine ecological processes that affect interactions between Chinook salmon and other marine species through competition and predation can affect survival of Pacific salmon populations. These ecological processes vary across space and time, and are affected by internal biological processes (i.e., physiology) and by variation in the environment.

Environmental variation includes both natural (ocean and atmospheric conditions) and anthropogenic factors. This hypothesis addresses environmental variation that is produced through human activities, including but not limited to hatchery salmon production, global climate change, industrial-scale marine fisheries, and marine pollution, which may be contributing to declines in abundance of AYK Chinook salmon stocks.

5.4.2 Plausibility of the Biological Mechanism(s)

Anthropogenic stressors may have strong effects on adult returns and recruits-per-spawner of AYK Chinook salmon via competition and predation with other marine species. Competitive interactions influence predation (which is often size-selective) and growth. Ocean growth rate and adult body size of salmon are positively correlated with fecundity, reproductive potential, and abundance at initial freshwater life stages, and are closely linked to many freshwater processes that may also contribute to declines in salmon abundance (e.g., size-selective fishing mortality; physiological condition and associated susceptibility to pathogens and pre-spawning mortality; migratory traits such as changes in adult run timing; competitive interactions such as nest site selection; and productivity and quality of freshwater habitats through transport of marine-derived nutrients or pollutants).

Anthropogenic processes that could affect the growth and survival of salmon include competition with hatchery salmon, climate change, and industrial marine fisheries. Intraspecific or interspecific competition with abundant stocks of hatchery salmon for limited marine prey resources could result in reduced growth and increased size-selective predation mortality of AYK salmon. Competition with hatchery fish might also reduce body size and condition of adult AYK salmon returns, affecting their migratory and reproductive behavior and success. Climate change can alter marine community structure and dynamics affecting prey availability and influencing the magnitude of predation and competition with more abundant stocks of pink, chum, and sockeye salmon. Competitive interactions between AYK salmon and large-scale industrial marine fisheries targeting walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius*), both important prey species of AYK Chinook salmon, or direct consumption of at-sea fish processing wastes (pollock skin and bones) might lead to poor salmon growth or emerging diseases (e.g., *Ichthyophonus*).

5.4.3 Summary of the Evidence for the Hypothesis

Several potential anthropogenic stressors have increased substantially during the same period that AYK Chinook salmon have declined. Hatchery production of the most abundant salmon species (pink, chum, and sockeye) increased rapidly during the 1970s and 1980s, reaching approximately 4.5 billion juveniles per year during the 1990s and

2000s (Ruggerone et al. 2010a,b). The estimated current biomass of pink, chum, and sockeye salmon in the North Pacific Ocean (~4 million metric tons) is at historically high levels (~3.4 times higher than low levels in the early 1970s), in part (at least 38% of the total biomass) due to hatchery production (Eggers 2009). Data from tagging, scale pattern analysis, and genetic stock identification indicate extensive overlap in distribution of hatchery and wild populations of immature and maturing Asian and North American salmon in the Bering Sea (Myers et al. 2010). The overlap includes the most abundant populations of pink, chum, and sockeye salmon in the world (i.e., eastern Kamchatka pink salmon (wild), Japanese chum salmon (hatchery), and Bristol Bay sockeye salmon (wild); Ruggerone et al. 2010a,b), which are all distributed within foraging areas of AYK Chinook salmon in the western and central Bering Sea basin in summer through fall.

Ruggerone and Nielsen (2009) reviewed evidence that competition at sea can lead to reduced salmon growth and survival, and potentially to lower the reproductive potential of survivors. Myers et al. (2009) reviewed evidence from high-seas field research on interspecific diet overlap and interannual density-dependent shifts in diet composition of Chinook salmon in the Bering Sea. Scale-growth studies indicated that Norton Sound Chinook salmon growth and survival was influenced by competition with pink salmon (Ruggerone and Agler 2010). Alternating year patterns in Chinook salmon growth at sea were detected and may reflect direct or indirect interactions with maturing Russian (eastern Kamchatka) pink salmon that are most abundant in the Bering Sea during odd-numbered years. Yukon River and Kuskokwim River Chinook salmon scale patterns also showed alternating year patterns of growth, primarily during the second year at sea (Ruggerone et al. 2007, 2009a,b), which is the time when the distributions of Asian pink salmon and immature Yukon/Kuskokwim Chinook salmon overlap in the Aleutian Basin (Myers et al. 2009, 2010). Little is known about intra-specific interactions in the southeastern Bering Sea of AYK Chinook salmon with hatchery Chinook salmon from the US west coast and British Columbia.

Both climate change and fisheries have substantially altered the Bering Sea ecosystem in the past, but their relative importance in shaping the current ecosystem state remains uncertain (Aydin and Meuter 2007). Numerous studies have addressed the impacts of climate change on Pacific salmon (e.g., Beamish et al. 2010). Royer and Grosch (2009) reviewed the physical mechanisms of changes in ocean conditions with respect to past and future climate change in the North Pacific and Bering Sea ecosystems. Climate change can affect prey availability, influencing the magnitude of competition (Ruggerone and Nielsen 2009). Salmon responses (growth and survival) to competition and climate shifts can vary with season and life stage of salmon. Estimated changes in

high-seas thermal habitat of salmon due to natural climatic variation in 20th century were relatively small compared to projected changes under anthropogenic climate-change scenarios by the mid to late 21st century (Abdul-Aziz et al. 2011). During the past decade climate and ocean conditions have become more erratic. For example, a shift from warmer (2000-2005) to colder (2006-2012) than average winters in the eastern Bering Sea was accompanied by large-scale shifts in the spatial distribution of marine populations during the warming trend in the 2000s (e.g., Mueter and Litzow 2008), as well as shifts in AYK juvenile salmon distribution during the cooling trend (Jim Murphy, NMFS-AFSC, personal communication).

Myers et al. (2010) speculated that overlap in the Bering Sea distribution of AYK Chinook salmon and southern populations of North American salmon fluctuates on decadal, inter-annual, and seasonal scales with ocean warming or cooling in the Gulf of Alaska. Future climate change scenarios predict that warming of the North Pacific Ocean may result in northward shifts the ocean ranges of southern populations of all salmon species into the Bering Sea. If prey resources in the Bering Sea are limiting to growth and survival of Chinook salmon, climate-induced increases in competitive interactions between AYK Chinook salmon and southern populations of hatchery salmon (Alaska and US west coast/British Columbia) could be increasingly important.

Industrial-scale marine fisheries act as both predators (e.g., salmon bycatch; Hypothesis 5) and competitors (e.g., reductions in prey densities) of AYK Chinook salmon, and they can alter the productivity, community structure and dynamics of the Bering Sea ecosystem through large removals of target species. Total catches of pollock in the eastern Bering Sea (including catches in the Aleutian Basin) decreased from a peak of 2.7 million tons in 1987 to 0.8 million tons in 2009 (Ianelli et al. 2011), with a recent estimate for 2012 of 1.21 million tons (http://www.fakr.noaa.gov/2012/car110_bsai_with_cdq.pdf). Although less is known about the Russian pollock fishery, catches in Russia's Exclusive Economic Zone also decreased in the 1980s and 1990s (Vaisman 2001). During the 1980s, overfishing by the foreign trawl fleet in the central Bering Sea (Aleutian Basin) resulted in the apparently permanent depletion of this pollock stock (Bailey 2011). Walleye pollock remain an important prey species for Steller sea lions (*Eumetopias jubatus*) and other salmon predators and competitors. The depletion of adult pollock that spawned in the Aleutian Basin might have had a large impact on AYK Chinook salmon. The Aleutian Basin is the primary summer feeding grounds of immature (>ocean age-0) and maturing AYK Chinook salmon (Myers et al. 2009, 2010), and juvenile pollock (age-0 to age-4) are a major prey of Chinook salmon (Davis et al. 2009). An unexpected result of the first study of winter food habits of Chinook salmon in the Bering Sea was that Chinook salmon consumed pollock offal (Davis et al. 2009). Groundfish fishery

vessels discharged approximately 1 billion pounds per year of fish processing waste (i.e., offal with a maximum 0.5 inch grind size) in the Bering Sea/Aleutian Islands area (US EPA 2009). Davis et al. (2009) reviewed information on piscine scavenging on offal generated from fish processing.

5.4.4 Priority Research Themes and Example Questions

Multiple Stressors and Cumulative Effects

1. How do abundance and productivity (recruits-per-spawner) of AYK Chinook salmon respond to the independent and interactive effects of multiple anthropogenic stressors in the marine environment?

Ocean Carrying Capacity

2. Does a threshold of maximum biomass (carrying capacity) of salmon exist in the ocean? Is a minimal marine prey (i.e., forage fish, squid, and euphausiid) biomass or density needed to sustain AYK Chinook salmon productivity over the long term (e.g., Cury et al. 2011)? What are these levels and is the ocean approaching these thresholds?

Climate Change

3. How will community structure and dynamics of AYK Chinook salmon, predators, and prey in the Bering Sea ecosystem be affected by the changes in species that are likely to result from climate change (including ocean acidification)?
4. Will competitive interactions between AYK Chinook salmon and northward-migrating southern populations of hatchery salmon (Alaska, British Columbia, and US west coast) stocks in the eastern Bering Sea increase?

Management of Marine Fisheries

5. Are there new, adaptive management strategies that could be used to reduce or minimize the potential impacts of industrial-scale marine fisheries on density-dependent ecological processes that support marine growth and survival of AYK Chinook salmon?

5.5 Hypothesis 5 – Marine Bycatch

Hypothesis: *Mortality from non-salmon fisheries in the ocean has contributed to the decline of AYK Chinook salmon stocks.*

5.5.1 Description of the Hypothesis

This hypothesis proposes that mortality of salmon resulting from marine bycatch has been large enough to produce detectable changes in Chinook salmon returns to AYK systems and accounts for the recent declines observed. Note that additional sources of

marine mortality and changes in the Bering Sea ecosystem are addressed via Hypothesis 3 (Ocean Mortality) and Hypothesis 4 (Anthropogenic Changes to Marine Processes).

5.5.2 Plausibility of the Biological Mechanism(s)

Bycatch (fish that cannot be retained by regulation, known as “prohibited species”) in foreign and domestic ocean fisheries causes mortality of pre-adult Chinook salmon prior to their return to rivers to spawn. Bycatch-induced mortality can be compensated by density-dependent mechanisms such as increased growth rates and improved survival rates. However, this mortality can be great enough that compensatory increases in survival are overcome, and in this case the return of adult salmon to rivers would decline. This rationale would predict that, if bycatch was the sole explanation for the decline, the reduction in returning fish to the rivers should be slightly less, than the bycatch numbers due to the compensatory mechanisms in addition to the fact that significant percentages of the bycatch comprise immature salmon.

5.5.3 Summary of the Evidence for the Hypothesis

Sources of marine mortality, including bycatch, all contribute to reduce the numbers of pre-adult Chinook salmon that return to rivers to spawn (see the Hypothesis 3 Ocean Mortality and 4 Anthropogenic Changes to Marine Processes). The question we address here is “what is the likelihood that this hypothesized driver has significantly contributed to the declines observed in the AYK region Chinook salmon populations?”. Can bycatch explain a large portion of the long-term Chinook salmon decline?

Evaluation of this hypothesis requires estimates of total bycatch of AYK Chinook salmon in domestic and foreign ocean fisheries apportioned by stock and estimated year-of-return that then would be compared to adult returns over time. Catch estimates such as these would help determine whether an increasingly large proportion of salmon were intercepted prior to their return to rivers over the last decade. Such catch estimates exist since the early 1990s for the domestic fisheries and the proportion of salmon intercepted prior to their return to rivers estimated through application of genetics data from 2005-2007. Unfortunately, estimated total catch of AYK Chinook salmon is unavailable for foreign fisheries (i.e., catches in the Russian zone) which limits a complete evaluation of this hypothesis.

Most data on this topic focus on the bycatch within the US domestic fishery for walleye pollock in the eastern Bering Sea (e.g., Stram and Ianelli 2009; Gisclair 2009). Chinook salmon bycatch in this fishery consistently increased from 2000 through 2007, peaked in 2007 at 121,770 fish but subsequently declined through 2012, ranging over this latter period from 9,692 (during 2010) to 25,499 fish (2011) (NOAA Fisheries, Alaska Regional Office, http://www.alaskafisheries.noaa.gov/sustainablefisheries/inseason/chinook_salmon_mortality.pdf). The

total number caught over this five-year period was estimated to be 78,038 Chinook salmon or an average of 15,608 fish per year.

The question is “of the approximately 10,000 to 26,000 fish per year (average of 15,608 per year) estimated to have been caught in the domestic walleye pollock fishery, how many of these were from coastal western Alaska (including the Arctic-Yukon-Kuskokwim region)?”. Some of the fish caught could be from elsewhere in North America or from Asia. Apportionment to stocks from coastal western Alaska from 2005 to 2007 based on genetic data ranged from 35 to 82%, based on mean catch-weighted stratified proportions (Seeb et al. 2008; NPFMC and NMFS 2009). If these stock proportions were constant over the most recent 5-year time period, then bycatch from the coastal western Alaska stocks could have ranged from a low of 3,392 fish in 2010 (at 35% of 9,962) to a high of 20,909 Chinook salmon in 2011 (at 82% of 25,499). As a comparison of mortality from other sources, the total subsistence and commercial harvest in the Yukon River has averaged slightly less than 50,000 fish since 2007 or at least twice as many fish as the estimated bycatch of coastal western Alaska salmon.

Another way to examine the potential role of bycatch in the walleye pollock fishery is to consider the peak years of the run and the recent new low in run abundance (2008 to 2012) and consider whether the difference between the two abundance levels could be caused by the bycatch in this domestic fishery. This difference can be determined from run reconstruction estimates for the Kuskokwim River and Yukon River systems. Estimated combined returns from both systems peaked at approximately 600,000 salmon and then declined to the new recent low average of approximately 300,000 fish (Howard 2011; Bue et al. unpublished). Thus, the level of bycatch required to explain a substantial proportion of the 300,000 Chinook salmon decline in the region could be considered to be on the order of 100,000 fish or more. As a worst case scenario, the bycatch from this part of the domestic fishery, at the most, could have been as high as about 15,000 fish and in most cases much less. Thus, this part of the domestic fishery cannot account for the striking decline in Chinook salmon abundance or even for a substantial proportion of the decline. Clearly, other sources of mortality must also have contributed to the decline. Whereas these bycatch estimates do not explain a substantial portion of the recent decline, mortality of Chinook salmon also occurs in marine fisheries other than the domestic pollock fishery.

Total Chinook salmon bycatch in all domestic groundfish fisheries (pollock and non-pollock) are considered well estimated since 1991. Some historical studies between 1977 and 1986 estimated incidental catches of western Alaskan Chinook salmon as less than 6% of the total commercial harvest from the region (Myers and Rogers 1988). From 1990 to 2001, Chinook salmon bycatch in Alaska groundfish fisheries was estimated to

have reduced the western Alaska Chinook salmon run by less than 2.7% (Witherell et al. 2002). The NMFS scientific observer program also continues to collect detailed sex, length, and age composition data on salmon bycatch. These data, combined with a variety of genetic sampling programs, allow estimation of bycatch impacts to different river systems. Studies were completed on the estimated impacts of Chinook salmon bycatch in the Bering Sea pollock fishery on returns to western Alaska river systems (NMFS/NPFMC 2009). From these studies the impact rates to the coastal western Alaska system is estimated to have peaked at around 44,000 Chinook salmon in 2007 (the 1994-2006 average run size for this region was approximately 712,000 Chinook salmon) (NMFS/NPFMC 2009). Average impact rates estimated to the coastal western Alaska system from 1994 to 2006 ranged from 1% to 4% (J. Ianelli, D. Stram, personal communication). Chinook salmon bycatch mortality also occurs in non-pollock fisheries in the Bering Sea. The relative amount of bycatch from the combined non-pollock fisheries is much lower, ranging from ~1100 to 10,600 from 1992-2012 (http://www.fakr.noaa.gov/sustainablefisheries/inseason/chinook_salmon_mortality.pdf). To date no additional analyses have been completed on the impact to river systems of the bycatch of these fisheries due to their bycatch being orders of magnitude less than that of the Bering Sea pollock fishery. Thus, if this mortality pattern for these other domestic fisheries still exists today then adding in the mortality from other domestic fisheries also would not explain a substantial proportion of the recent decline in Chinook salmon.

Bycatch of western Alaskan salmon also occurs in foreign fisheries. Estimates of catch of AYK Chinook salmon from these fisheries such as the Russian groundfish fisheries in their territorial waters is unknown and would be valuable to know to determine the effects of the total bycatch of Chinook salmon from all marine fisheries, domestic and foreign. To fully evaluate this hypothesis, total bycatch estimates, apportioned to the coastal western Alaska stocks, would be needed.

Based on available data, the bycatch within the domestic walleye pollock fisheries seems unlikely to have been the primary cause for the recent dramatic declines of Chinook salmon in the AYK region, because estimates of bycatch from this source are not high relative to the estimated declines in the total returns to the drainages. Unknown is the additional mortality to AYK Chinook salmon stocks caused by other domestic and foreign fisheries, and whether the combined sources of mortality from the total bycatch in all marine fisheries could have contributed significantly and produced the observed declines. If estimated, this source of total mortality from all bycatch sources then would need to be considered for its potential contribution cumulative with other sources of mortality as described in the other hypotheses.

5.5.4 *Priority Research Themes and Example Questions*

Ocean Catch of Chinook Salmon

1. What is the amount of bycatch and incidental catch of AYK Chinook salmon in all fisheries, domestic and foreign?

Relationship between Bycatch, Spawning Run Abundance, and Recruits/Spawner.

2. Does a relationship exist between AYK Chinook salmon annual mortality in domestic and foreign fisheries and subsequent spawning run abundance?
3. Has the proportion of AYK Chinook salmon catch in ocean fisheries increased over the past decade and produced detectable changes in stock productivity (recruits-per-spawner)?

Stock-specific Apportionment of Chinook Salmon Catch in Ocean Fisheries

4. How does the proportion of AYK stocks caught in the walleye pollock and other fisheries vary among years and are these variations due to fishery methods, time of year, and area fished? Does substantial inter-annual variability in bycatch proportions occur due to variation in fishing effort in different regions?
5. What is the potential weak stock vulnerability to ocean fisheries by time of year and fishery location? Are Canadian-origin Chinook salmon of the Yukon River more vulnerable to the bycatch in the walleye pollock fishery and other Bering Sea groundfish fisheries at certain times and locations in the Bering Sea?
6. Are some stocks (e.g., western Alaska vs. Canadian-origin Yukon River fish) more vulnerable in the non-pollock groundfish fisheries than in the pollock fishery?

5.6 Hypothesis 6 – Escapement Quality

Hypothesis: *Selective fishing and natural mortality have altered the genetic character of the stocks so that the expression of size, sex ratio, and composition of life history types have been altered and have contributed to declines in egg deposition to reduce recruitment in AYK Chinook salmon stocks.*

5.6.1 *Description of the Hypothesis*

This hypothesis focuses on the role of genetic selection by the fishery over multiple generations to change the components of age, size, growth, and time to maturity (phenotypic characters) that are genetically determined. Phenotypic characters are determined both by genetics and the environment. For example, genetics control the potential for growth and the environment provides food that controls the expression of that potential. The genetic changes hypothesized could affect the recruitment of subsequent generations of salmon.

5.6.2 Plausibility of the Biological Mechanism(s)

Fishing-induced evolution (FIE) in salmonids is challenging to demonstrate conclusively in the wild. However, declines in Chinook salmon abundance (Yukon and Kuskokwim rivers; JTC 2011; K. Schaberg, ADFG, personal communication), increasingly male-biased sex ratios (Yukon and Kogrugluk rivers; Hamazaki 2009; K. Harper, USFWS, personal communication), and decreased size of spawners (attributed to declines in size-at-age and declines in the return of the oldest age classes) (Yukon and Kuskokwim rivers; JTC 2011; K. Harper, USFWS, personal communication) are consistent with expected patterns that would result from selective harvest of the largest individuals, particularly when harvest rates increase (Bromaghin et al. 2008, 20011; Hard et al. 2009).

Disproportionate escapement of small fish causing genetic selection could produce lower than expected returns because fecundity and possibly egg quality are positively correlated with female size; male-biased sex ratios also reduce the overall egg production by a population. These effects in the short term can be caused simply by selective fishing affecting the immediate escapement quality and in the long term could be caused via changes in the genetic components that affect age, size, and time of maturity in salmon. Hence, the combined short- and long-term effects of selective fishing illustrate the complexity of this hypothesis. If size- and age-at-maturity are highly heritable, then the effects of selection would result in a propensity of stocks to propagate more small young mature fish in subsequent generations. This mechanism could cause a long-term decline in returns-per-spawner in the absence of other processes such as density-dependence and environmental forcing.

5.6.3 Summary of Evidence for Hypothesis

Declines in female composition of escapement and size- and age-at-maturity in both Yukon and Kogrugluk rivers is consistent with the hypothesis that FIE has driven declines in returns-per-spawner. Using realistic estimates of trait heritability (genetics), harvest selectivity, population productivity, and management strategies, recent modeling (Bromaghin et al. 2008, 2011) demonstrated that observed declines in size- and age-at-maturity fell within the range of modeled phenotypic changes attributable to FIE. This model also suggested that efforts to counteract declines would likely require reductions in size selectivity of gear and exploitation rates, and that improvements would be slow to materialize, requiring multiple generations under the new selection regime.

While declines in size- and age-at-maturity of returning adults provide compelling evidence of the potential for FIE to explain patterns in recruits-per-spawner, the available evidence cannot rule out other mechanisms as potential causes for changes in the age and size of returning adults. For instance, environmental variables could be the causal mechanism for the observed declines in age and size of returns, and subsequent

waning of recruits-per-spawner ratios in recent years in the AYK region. This alternative mechanism could be more likely if patterns of change occurred also in stocks that have low exploitation rates or where fishing gear is not selective for large, old individuals. Age-at-maturity data collected from projects estimating escapements and commercial harvests of Goodnews River Chinook salmon also show declines, despite the use of small mesh gillnet gear, which is presumably less selective for large individuals, throughout the history of that fishery (J. Linderman, ADFG, personal communication). While there is some synchrony in declines of size- and age-at-maturity and female proportion across the AYK region and across the entire US west coast, the cause and ecological consequences of these declines remain unclear.

5.6.4 Priority Research Themes and Example Questions

Causality of Genetic Changes/FIE vs. Environmental Variables

1. What proportion of changes in size- and age-at-maturity of returning Chinook salmon adults are determined by changes in genetics caused by selective fishing versus environmental variables?
2. How has size- and age-at-maturity of returning adults changed among stocks, and drainage areas (Yukon and Kuskokwim rivers) and has this occurred synchronously with stocks elsewhere such as in Bristol Bay populations and coastwide?
3. What is the relationship between size- and age-at-maturity of returning adults in stocks fished by gear selective for small fish versus gear selective for large fish?
4. Which explanation, genetic selection or changes in environmental parameters (e.g., ocean conditions), better accounts for the phenotypic changes in size- and age-at-maturity of returning adults in stocks? What is the relative contribution of anthropogenic and environmental variables as causal mechanisms for changes in size- and age-at-maturity?

Variables Affecting Spawning and Reproductive Fitness

5. Are fewer eggs being deposited than in the past because the size- and age-at-maturity of returning adults in stocks has changed? What is the relative role of different variables affecting fecundity and egg deposition?
6. Among those salmon that escape and have access to spawning grounds, does size-at-maturity and age-at-maturity of returning adults affect whether they spawn or not, or in the success of their spawning (i.e., successful hatch, juvenile recruitment)? The identification of parent-offspring/sibling relationships in regards to key phenotypes (age- and size-at-maturity, migration timing, and fecundity) and reproductive fitness would illuminate underlying assumptions and could be obtained through pedigree analyses.

7. Do stock-recruit relationships improve if they are expressed in units of eggs rather than as aggregate spawning population numbers?

5.7 Hypothesis 7 – Pathogens

Hypothesis: *Pathogens have increased mortality rates of adult Chinook salmon during upstream migration and have contributed to the decline of AYK salmon stocks.*

5.7.1 Description of the Hypothesis

This hypothesis proposes that infectious diseases, specifically ichthyophoniasis caused by infection with the protistan pathogen *Ichthyophonus sp.*, are responsible for an increase in pre-spawning mortality and a reduction in spawning effectiveness (sub-lethal effects) that has contributed to the decline of Chinook salmon in the Yukon River. As a result, the spawning effectiveness of escapement has been lower than estimated and juvenile recruitment per spawner has declined causing poor returns in subsequent generations.

5.7.2 Plausibility of the Biological Mechanism(s)

Infectious diseases have been shown to be associated with significant losses (Smith et al. 2006) or large-scale oscillations (Hudson et al. 1998) in animal populations; however, our understanding of disease impacts on populations of wild fish is limited to periodic case studies describing large-scale epizootics accompanied with massive fish kills. The first reports of ichthyophoniasis in Chinook salmon from the Yukon River occurred in the mid-1980s when characteristic lesions of the disease were observed in the skeletal muscle of affected individuals, and fillets were reported to have an off-odor and failed to dry properly using traditional techniques (Kocan et al. 2004a). The etiological agent associated with the condition was diagnosed as *Ichthyophonus*, and studies provided evidence indicating that *Ichthyophonus* affects the health and survival of infected Chinook salmon.

5.7.3 Summary of Evidence for Hypothesis

The strongest circumstantial evidence supporting the hypothesis that ichthyophoniasis causes pre-spawning mortality in adult Chinook salmon involves changes in the proportion of fish that are infected in adult populations migrating up the Yukon River. For example, in 2000, the prevalence of infected females entering the Yukon River was 29% (10/34); this infection prevalence remained fairly consistent (27-43%) at numerous sampling locations upstream as far as the US / Canada border; however, the infection prevalence then dropped as the fish approached their terminal spawning locations suggesting that mortality was occurring (11% in Whitehorse, Yukon Territory, and 18% in the upper Tanana River; Kocan et al. 2004b, Kocan and Hershberger 2006). More telling,

however, was the change in the prevalence of clinical manifestations of the disease increasing from 3% at RM 24 (Emmonak), 6% at RM 530 (Galena), 19% at RM 731 (Rapids), 34% at RM 1,081 (Circle), and 30% at RM 1230 (US / Canada border); the prevalence of clinical disease then decreased as the fish approached their terminal spawning locations (11% at Whitehorse and 18% in the Upper Tanana River). Increasing disease severity occurred consistently during the adult freshwater migration, followed by otherwise inexplicable loss of the diseased salmon near the spawning locations (Kocan et al. 2004a).

Information about the onset, severity, duration, mechanisms of action and effects of environmental variables on ichthyophoniasis-associated mortality is provided by experimental studies. Controlled laboratory exposures result in mortality to Yukon River Chinook salmon (Jones and Dawe 2002), where 20% mortality occurred 25-42 days after feeding on infected herring tissues. In addition to direct mortality, *Ichthyophonus* infections can affect other measures of overall health or performance in the host. On a physiological level, *Ichthyophonus* infections can cause anemia and leucopenia (Rand and Cone 1990). Other studies indicate that *Ichthyophonus* can be associated with decreased body condition, gonado-somatic index, and reduced lipid storage in other fishes (Kramer-Schadt et al. 2010; Vollenweider et al. 2011). Thus, *Ichthyophonus* can also result in compounding sub-lethal effects that indirectly impact the health, performance, and survival of infected fishes. For example, if reduced lipid storage occurs in Chinook salmon, this could result in inadequate energy supplies for the long-distance upriver migration for spawning.

Some of the most direct evidence that ichthyophoniasis may be an important cause of pre-spawning mortality in adult Chinook salmon in the Yukon River comes from laboratory studies on the mechanisms of disease and the effects of temperature on the loss of stamina in the infected fish. In experimental groups of rainbow trout, *Ichthyophonus* infections were shown to produce cardiac damage that led to decreased swimming performance, (Kocan et al. 2006). Further, the progression of disease was more rapid as ambient water temperatures increased to levels similar to those now observed during the adult Chinook salmon spawning migration in the Yukon River (Kocan et al. 2009). Diseased fish likely lack the stamina to maintain the migration or the energy to spawn. It is possible that increasing river temperatures are accelerating the progression and severity of disease as the fish migrate, thus resulting in elevated levels of pre-spawning mortality as these fish struggle to ascend steeper gradients in the upper regions of the river, or to dig and defend redds if they do reach the spawning grounds (Kocan et al. 2009).

5.7.4 Priority Research Themes and Example Questions

Past and Current Status of *Ichthyophonus* Infections

1. Have *Ichthyophonus* infections produced sufficient levels of disease to affect the health and survival of adult Yukon River Chinook salmon?
2. How do *Ichthyophonus* infection rates change within the spawning migration and among years? Continued surveillance at selected index sites located along the Yukon River to document inter- and intra-annual changes in *Ichthyophonus* prevalence and intensity should be monitored each year.
3. Do river conditions (e.g., flow and temperature) affect infection, disease, or mortality rates of adult Chinook salmon?

Lethal and Sub-lethal Effects of *Ichthyophonus* Infections

4. What is the fate of *Ichthyophonus*-infected individuals, placing particular emphasis on understanding the variables (e.g., temperature, corticosteroid levels, concurrent infections) that influence the progression of disease and salmon mortality?
5. How do *Ichthyophonus* infections affect the migration, survival, and spawning success of Chinook salmon having various degrees of infection?

Causes of *Ichthyophonus* Infections

6. What are the epizootiological variables leading to *Ichthyophonus* infections and disease progression in Yukon River Chinook salmon? Such studies should include: determination of the sources of infection; understanding the mechanisms of transmission; a more detailed description of the parasite life cycle; knowledge of the conditions that affect prevalence and intensity of infection in returning adult Chinook salmon; determination of the host and environmental variables that control the progression of low-level infection into overt disease; and, understanding the effect of overt disease on levels of adult pre-spawning mortality in Yukon River Chinook salmon.
7. Does a relationship exist between climate-driven ocean circulation patterns in the Bering Sea and disease prevalence in adult Chinook salmon returning to the Yukon River? Particular emphasis should be placed on climate-driven changes in biological assemblages (e.g., fish community, salmon prey) that may affect the probability of *Ichthyophonus* infection in the ocean.

6.0 Recommendations for Research

The AYK SSI Steering Committee will use these recommendations to select a set of hypotheses to promote through the AYK SSI's annual "invitation to submit research proposals". Over time, the integration and synthesis of new information will help to develop new hypotheses, revise existing hypotheses and questions, establish new priorities, and possibly discard old hypotheses. This process of incorporation of new information will guide the use of the recommendations below.

6.1 Linkages to the AYK SSI Research and Restoration Plan

The hypotheses and questions described within this Chinook Salmon Research Action Plan fit within the structure of the AYK SSI's overarching plan titled, **Arctic-Yukon-Kuskokwim Salmon Research & Restoration Plan** (RRP; AYK SSI 2006), but represent an updated focus specifically on Chinook salmon. The RRP further emphasized the need to prioritize hypotheses based on criteria, the first criteria of which was the potential for projects to contribute to achieving the program's goal. This same approach is used here. The goal of this Chinook Salmon Research Action Plan is:

To understand the trends and causes of variation in Chinook salmon abundance through the assembly of existing information and gaining new information through a collaborative and inclusive process.

6.2 Challenges in Setting Priorities

Research priorities are important to establish so that funds can be directed to those projects that have the highest probability for explaining the "*trends and causes of variation in Chinook salmon*". Several challenges exist in setting priorities for the Chinook salmon research plan. These challenges are as follows.

- **Diverse and large number of hypotheses, themes, and questions.** A total of seven hypotheses, 21 themes, and 38 example questions were identified in this plan. Every question cannot be fully addressed within every funding cycle.
- **Modest funding.** Funding is not available to adequately address all hypotheses. Some topics, especially some of those related to the marine ecology of Chinook salmon, could represent very expensive projects to fully pursue.
- **Changing information base.** Over time as the information base about Chinook salmon grows, some research priorities will have been met, others may be discarded as unimportant based on new knowledge.

- **Unknown future information needs.** New hypotheses that affect Chinook salmon population dynamics may arise from new information about currently unknown processes. As result, the priorities must be dynamic and adaptive over time.

6.3 Criteria Used to Set Research Priorities

The purpose of establishing criteria is to help focus research efforts on the most important hypotheses, themes, and questions concerning the variability of Chinook salmon returns to the AYK region. In addition, the criteria should promote the use of historic data where possible, encourage the formation of collaborative opportunities among agencies and organizations, and maximize the use of AYK SSI funds. The criteria listed below are not mutually exclusive but must be used in combination with each other. The criteria are as follows.

- **Program Goal** – Priorities must directly help to achieve the goal of *“To understand the trends and causes in variation in Chinook salmon abundance through the assembly of existing information and gaining new information through a collaborative and inclusive process”*.
- **Knowledge Gaps** – Priorities must fill clear gaps in knowledge, unaddressed by other research and management programs, and must complement but not duplicate past work by others nor provide substitute funding.
- **Time Efficient** – Priorities must encourage projects which will produce results within a reasonably short period of time. Retrospective analyses of existing time series data are especially valuable and time efficient.
- **Local Traditional Knowledge** – Priorities should encourage the incorporation and evaluation of LTK, where possible and appropriate, so as to better understand Chinook salmon and to contribute to capacity building
- **Ecological Processes** – Priorities must promote the linking of ecological processes across the spatial and temporal scales that characterize the Chinook salmon life cycle.
- **Stock-Recruitment Variation** – Priorities should promote understanding of the causes for variation in stock-recruit relationships, explore the use of environmental conditions as sources of variation, and develop process-based explanations for changes in Chinook salmon abundance and stock diversity.

- **Prediction** – Priorities must encourage the development of ways to forecast future abundance of Chinook salmon spawning runs and the responses of the fishery to regulatory changes.

6.4 Research Priorities

All of the research hypotheses, themes, and questions described in Section 5 qualify as important for funding. Proposed projects that do not address the highest priority hypotheses should still be considered for funding and judged against other proposed projects based on the criteria above. Especially important is to maintain the opportunity within each annual “invitation to submit research proposals” to permit the consideration of completely novel research proposals focused on new hypotheses not considered or articulated within this plan.

The hypotheses and questions listed below are those identified as being the highest priority. These priorities will assist the AYK SSI to wisely, efficiently, and economically untangle and answer some of the questions regarding why Chinook salmon populations have varied in abundance. A total of **six hypotheses, 11 themes, and 16 questions** were selected from the seven hypotheses, 21 themes, and 38 example questions described in Section 5.

Hypothesis 1 – Density-dependent Effects and Overcompensation

Hypothesis: *Recent declines in AYK Chinook salmon stocks are caused by strong density-dependent feedbacks in population dynamics that cause decadal-scale changes in abundance.*

Comparative Stock-Recruitment Analyses

- How does the intensity of density-dependent effects and overcompensation in AYK stocks compare to those of other Alaska Chinook salmon stocks? How does the uncertainty around the estimates of total run and stock-recruitment relationships for AYK stocks compare to those determined for other Alaska Chinook salmon stocks?

Comparison of metrics to produce biological reference points in AYK Chinook salmon

- How do estimates of carrying capacity and optimal escapement levels predicted by watershed habitat models compare to those produced by standard brood-table based stock-recruitment analysis

Density-dependent Processes

- What processes are most likely to produce strong density-dependent effects, including overcompensation, in AYK Chinook salmon stocks?

Hypothesis 2 – Freshwater Mortality

Hypothesis: *Change in the suitability or productivity of freshwater habitats used for spawning, rearing and migration has contributed to declines in AYK Chinook salmon stocks.*

Role of Environmental Variables in Streams

- Do environmental forcing variables such as hydrologic flow extremes explain trends in Chinook salmon productivity in the AYK region?
- Are marine and freshwater habitat conditions linked by large-scale climate variation? Does co-variation exist across these habitats due to climate variation that could confound the analysis of one or the other?

Hypothesis 3 – Ocean Mortality

Hypothesis: *Ocean conditions (physical and biological) have changed in the Bering Sea, causing an increase in mortality of Chinook salmon during the early marine portion of their life cycle and contributing to declines of AYK Chinook salmon stocks.*

Forecasting Adult Salmon Returns to Rivers

- When other stocks are analyzed with a hierarchical stock-recruit model, do they show the same relationships as Chena River, Salcha River, Kuskokwim River, and Canadian-origin Yukon River with ocean indicators?
- What combination of freshwater and marine environmental variables combined with spawning stock size, and juvenile freshwater and marine life phases best predict the next generation of salmon returns?

Early Marine Survival

- At what life stage is the strength of the recruitment of a brood year determined? When during the life cycle does most variation in mortality occur?
- What processes affect the survival of AYK Chinook salmon during their first year at sea? How do food availability, temperature, and other variables appear to affect survival?

Hypothesis 4 – Anthropogenic Changes to Marine Ecological Processes

Hypothesis: *Human-caused changes in the ocean have reduced growth and survival of AYK Chinook salmon contributing to the declines in these stocks.*

Multiple Stressors and Cumulative Effects

- How do abundance and productivity (recruits-per-spawner) of AYK Chinook salmon respond to the independent and interactive effects of multiple anthropogenic stressors in the marine environment?

Hypothesis 6 – Escapement Quality

Hypothesis: *Selective fishing and natural mortality have altered the genetic character of the stocks so that the expression of size, sex ratio, and composition of life history types have been altered and have contributed to declines in egg deposition to reduce recruitment in AYK Chinook salmon stocks.*

Causality of Genetic Changes (FIE) Versus Environmental Variables

- How has size- and age-at-maturity of returning adults changed among stocks, and drainage areas (Yukon and Kuskokwim rivers) and has this occurred synchronously with stocks elsewhere such as in Bristol Bay populations and coastwide?

Variables Affecting Spawning and Reproductive Fitness

- Are fewer eggs being deposited than in the past because the size- and age-at-maturity of returning adults in stocks has changed? What is the relative role of different variables affecting fecundity and egg deposition?
- Do stock-recruit relationships improve if they are expressed in units of eggs rather than as aggregate spawning population numbers?

Hypothesis 7 – Pathogens

Hypothesis: *Pathogens have increased mortality rates of adult Chinook salmon during upstream migration and have contributed to the decline of AYK salmon stocks.*

Past and Current Status of *Ichthyophonus* Infections

- How do *Ichthyophonus* infection rates change within the spawning migration and among years?
- Do river conditions (e.g., flow and temperature) affect infection, disease, or mortality rates of adult Chinook salmon?

Lethal and Sub-lethal Effects of *Ichthyophonus* Infections

- How do *Ichthyophonus* infections affect the migration, survival, and spawning success of Chinook salmon having various degrees of infection?

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Appendix 1: Participants- AYK SSI Chinook Salmon Synthesis Workshop, May 2-3, 2012

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Jan Conitz	Alaska Department of Fish and Game, Commercial Fisheries Division
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Steve Fleischman	Alaska Department of Fish and Game, Sport Fish Division
Alex Hall	ESSA Technologies, Ltd.
Jeff Hard	NOAA Northwest Fisheries Science Center, Conservation Biology Division
Paul Hershberger	US Geological Survey , Western Fisheries Research Center
Katie Howard	Alaska Department of Fish and Game, Commercial Fisheries Division
Mike Jones	Michigan State University, Quantitative Fisheries Center
Charles Krueger	Great Lakes Fishery Commission
John Linderman	Alaska Department of Fish and Game, Commercial Fisheries Division
Nate Mantua	University of Washington, School of Aquatic and Fishery Sciences
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Kate Myers	University of Washington, School of Aquatic and Fishery Sciences (retired)
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Randall Peterman	Simon Fraser University, School of Resource and Environmental Management (retired)
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