INDEPENDENT SCIENTIFIC ADVISORY BOARD

Density Dependence and its Implications for Fish Management and Restoration Programs in the Columbia River Basin

Also see July 2016 ISAB response to questions and concerns

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ISAB

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

ISAB Contributors

- **J. Richard Alldredge, Ph.D.,** Emeritus Professor of Statistics at Washington State University
- **Kurt D. Fausch, Ph.D.,** Professor of Fisheries and Aquatic Sciences, Department of Fish, Wildlife, and Conservation Biology at Colorado State University
- **Alec G. Maule, Ph.D.,** Fisheries Consultant and former head of the Ecology and Environmental Physiology Section, United States Geological Survey, Columbia River Research Laboratory
- **Katherine W. Myers, Ph.D.,** Research Scientist, Aquatic and Fishery Sciences, University of Washington (Retired)
- **Robert J. Naiman, Ph.D.,** (ISAB Chair) Emeritus Professor of Aquatic and Fishery Sciences at University of Washington
- **Gregory T. Ruggerone, Ph.D.,** (ISAB Vice-chair) Fisheries Scientist for Natural Resources Consultants
- **Laurel Saito, Ph.D., P.E.,** Director of the Graduate Program of Hydrologic Sciences at the University of Nevada Reno
- **Dennis L. Scarnecchia, Ph.D.,** Professor of Fish and Wildlife Resources at University of Idaho
- **Steve L. Schroder, Ph.D.,** Fisheries Consultant and former Fisheries Research Scientist at the Washington Department of Fish and Wildlife
- **Carl J. Schwarz, Ph.D.,** Professor of Statistics and Actuarial Science at Simon Fraser University, Canada
- **Chris C. Wood, Ph.D.,** Scientist Emeritus at the Pacific Biological Station, Department of Fisheries and Oceans, Nanaimo, British Columbia, Canada

ISAB Ex Officios and Coordinator

- **Michael Ford, Ph.D.,** Director of the Conservation Biology Program at the Northwest Fisheries Science Center
- **Jim Ruff, M.S., P.H.,** Manager, Mainstem Passage and River Operations, Northwest Power and Conservation Council
- **Phil Roger, Ph.D.,** Fisheries Science Manager (retired) at the Columbia River Inter-Tribal Fish Commission
- **Erik Merrill, J.D.,** Manager, Independent Scientific Review, Northwest Power and Conservation Council

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Acknowledgements

"If only density-independent causes of mortality exist, the stock can vary without limit, and must eventually by chance decrease to zero"

W.E. Ricker 1954

"Compensatory density dependence must exist for naturally stable populations to persist under harvesting"

Rose et al. 2001

"Consecutive years of large numbers of spawners can severely depress macrozooplankton populations leading to a collapse of subsequent broods of sockeye"

Edmundson et al. 2003

"Due to overflow of the spawning grounds almost the whole generation of pink salmon of the Western Kamchatka of 1983 died" [greater than 100 million spawners]

Bugaev 2002

"Nobody goes there anymore. It's too crowded."

Y. Berra 1998

Key Words with Multiple Meanings

The following three key words used in this report warrant careful definition as they have different meanings depending on context. Additional history and clarification of terms related to density dependence are provided by Herrando-Perez et al. (2012b).

Productivity: In general economic terms, productivity is the amount of output produced per unit of input. In fisheries biology, the productivity of a population can be defined as the amount of recruitment (R; i.e., progeny) produced per unit of spawner abundance (S). A population's productivity determines its growth rate, and typically declines as population density increases. "Intrinsic productivity" defines maximum productivity when the effects of density are negligible (as when S is very low). For this reason, the Northwest Power and Conservation Council's Fish and Wildlife Program (NPCC 2014) defines productivity as a measure of a population's ability to sustain itself or its ability to rebound from low numbers. In ecology, however, the terms productivity (a potential) or production (an actual real world performance) refer to the rate of biomass generation in an ecosystem (Warren 1971). Both terms are usually expressed in units of mass per unit surface (or volume) per unit time; for instance grams per square meter per day (g m^{-2} d^{-1}), and is related to the generation of food for metabolism and growth. In this report, the terms "population productivity" and "habitat productivity" are used to distinguish these two contrasting meanings unless the context is obvious.

Carrying Capacity: The carrying capacity parameter in population models—like the logistic equation, the Ricker model, and the Beverton-Holt model—defines an upper limit to population growth as density increases, and thus, determines a maximum equilibrium population size. Population size is expected to fluctuate around the maximum equilibrium population size because of variability in vital rates that is unrelated to density. Moreover, the carrying capacity parameter itself may change over time, tracking changes in habitat conditions. More generally in ecology, carrying capacity refers to the maximal load an environment can sustain—or more precisely, the maximum number of individuals of a species that a given habitat can support without being permanently damaged (Odum 1989). The two senses (maximum equilibrium population size and maximal environmental load) are related, but not identical and should not be confused (Hui 2006). In this report, the terms "population capacity" and "habitat capacity" are used to distinguish the meanings unless the context is obvious.

Resilience: The term resilience is used in two very different ways (Holling 1996). "Engineering resilience" refers to stability near an equilibrium steady state, as measured by resistance to disturbance and speed of return to equilibrium. It emphasizes efficiency, constancy, and predictability. In contrast, "ecological resilience" refers to an ecosystem's capacity to absorb and adapt to disturbance or change while maintaining essential functions (Walker and Salt 2006). It emphasizes persistence, change, and unpredictability. Resilience in the context of population viability implies engineering resilience whereas resilience of an ecosystem implies ecological resilience. Both senses are used in this report depending on the context.

Executive Summary

In response to an assignment from the Northwest Power and Conservation Council, NOAA Fisheries, and Columbia River Indian tribes, the Independent Scientific Advisory Board (ISAB) reviewed the implications of density dependence in fish populations in the Columbia River Basin. The ISAB's key findings include:

- Many salmon populations throughout the interior of the Columbia River Basin are experiencing reduced productivity associated with recent increases in natural spawning abundance, even though current abundance remains far below historical levels. Density dependence is now evident in most of the ESA-listed populations examined and appears strong enough to constrain their recovery. This fact raises the question: *Why is density dependence more evident than expected at low abundances?*
- The ISAB reanalyzed the admittedly limited historical data to better evaluate the potential capacity for salmon and steelhead in the Columbia Basin before hydrosystem development. The ISAB concludes that historical all-species capacity was likely in the range of 5 to 9 million adult fish per year, which is less than previously published estimates (e.g., 7.5 to 16 million adults per year) but still much higher than current abundance levels (~2.3 million fish per year during 2000-2012).
- Evidence for strong density dependence at current abundance suggests that habitat capacity has been greatly diminished. Roughly one-third of the Basin is no longer accessible to anadromous salmon, and continuing changes to environmental conditions stemming from climate change, chemicals, and intensified land use appear to have further diminished the capacity of habitat that remains accessible. Density dependence was also observed in some less altered watersheds.
- Hatchery releases account for a large proportion of current salmon abundance. Total smolt densities may be higher now than historically. By creating unintended density effects on natural populations, supplementation may fail to boost natural origin returns despite its effectiveness at increasing total spawning abundance.
- Identifying mechanisms that contribute to density dependence in particular habitats and life stages—such as limitations in spawning habitat, rearing habitat or food supply, or predator-prey interactions—can help to guide habitat restoration and population recovery actions.
- Understanding density dependence (e.g., stock-recruitment relationships) in salmon populations is central to evaluating responses to recovery actions and for setting spawning escapement goals that will sustain fisheries and a resilient ecosystem.

The ISAB's key recommendations include:

Anadromous salmonids

- Account for density effects when planning and evaluating habitat restoration actions.
- Establish biological spawning escapement objectives that account for density dependence.

- Balance hatchery supplementation with the Basin's capacity to support existing natural populations by considering density effects on the abundance and productivity of natural origin salmon.
- Improve capabilities to evaluate density dependent growth, dispersal, and survival by addressing primary data gaps.

Non-anadromous salmonids

- Recognize that carrying capacity for non-anadromous salmonids can be increased by restoring in-stream structure and riparian vegetation.
- Recognize that carrying capacity for non-anadromous salmonids can be reduced through competitive interactions with stocked hatchery trout or invasive non-native trout.
- Consider the probable effects of density on survival, emigration, growth, and size/age at maturity when developing angling regulations to achieve conservation and recreational goals.

Sturgeon

- Consider habitat capacity and the probable effects of density on growth and survival when developing stocking programs to conserve white sturgeon.

Lamprey

- Initiate studies to gather information about current densities of Pacific lamprey in the Basin and to learn about density dependent processes that might thwart efforts to promote their recovery.
- Consider lessons learned about supplementation and density dependence in anadromous salmonids when planning future actions to propagate and translocate (i.e., supplement) lamprey within the Basin.

Summary

Preface

Understanding density dependence—the relationship between population density and population growth rate—is important for effective implementation of the Columbia River Basin Fish and Wildlife Program, biological opinions, recovery plans, and tribal programs. Information on how density dependence limits fish population growth and habitat carrying capacity is vital for setting appropriate biological goals to aid in population recovery, sustain fisheries, and maintain a resilient ecosystem. Habitat restoration and population recovery actions can be planned and implemented more effectively by understanding mechanisms that cause density dependence in particular cases, such as limited food supply, limited rearing or spawning habitat, or altered predator-prey interactions.

In March 2014, representatives from the Northwest Power and Conservation Council (NPCC), NOAA Fisheries, and Columbia Basin tribes approved the Independent Scientific Advisory Board (ISAB) to review the implications of density dependence in fish populations in the Columbia River Basin. This report consists of two parts. Part 1 focuses on issues that are most relevant to restoring anadromous populations of Pacific salmon (*Oncorhynchus* species), particularly Chinook salmon and steelhead. It addresses the following questions:

1) *What is density dependence and why is it important?*
2) *Why is density dependence more evident than expected at current relatively low abundances of anadromous salmonids?*
3) *Where has density dependence been detected in the Basin?*
4) *How can we detect and diagnose density dependent limiting factors?*
5) *How can density dependent limitations be ameliorated to promote population rebuilding and recovery?*

Part 2 addresses issues that are more relevant to density dependence in other species groups including resident trout (rainbow, cutthroat and bull trout), kokanee, white sturgeon, and Pacific lamprey.

PART 1: Anadromous Salmonids

Chapter I. Introduction

Productivity (measured as adult returns per spawner) has been declining in many spring/summer Chinook salmon populations in the Upper Columbia and Snake river basins, and in steelhead populations in the interior Columbia region since approximately 2001. Surprisingly, this recent widespread decline in productivity seems to be caused primarily by increased spawning densities, even though current abundances are low compared to historical estimates.

Density effects on productivity are particularly evident in spring/summer Chinook salmon populations throughout the Snake River Basin where increasing spawners from 20,000 to 50,000 adult females has not resulted in additional smolt production. Additional evidence that increased abundance of juvenile Chinook is associated with reduced smolt size strongly suggests that food availability in freshwater habitat is limiting growth at current densities. In short, the capacity of some watersheds to support salmon or steelhead appears to have been exceeded at spawning abundances that are low relative to historical levels.

Chapter II. What is density dependence and why is it important?

Density dependence occurs when a population's density affects its growth rate by changing one or more vital rates—birth, death, immigration, or emigration. Density dependence can be of two types. Most common is compensatory density dependence (also termed *compensation*) in which a population's growth rate is highest at low density and decreases as density increases. Compensation is typically caused by competition for limiting resources, such as food or habitat. Less common is depensatory density dependence (*depensation*) in which a population's growth rate *decreases* at low densities, opposite to what is typically expected. Depensatory mortality occurs when predators tend to kill a fixed *number* of prey, so that the death rate becomes higher as fewer prey are present. Depensatory reproduction might occur when a population becomes so rare (e.g., mature endangered sturgeon) that individuals have difficulty finding suitable mates, driving down the birth rate at low densities.

As the name implies, compensatory density dependence can stabilize population abundance because it tends to restore the population to some equilibrium level. The stabilizing influence of compensation *must* occur at some times and places or populations would not persist. Compensation is also fundamental to the concept of sustainable yield in fisheries and wildlife management in that it explains how harvesting an abundant population can increase rather than decrease total production in the next generation.

Stock-recruitment models are commonly used to describe and quantify compensation in a managed fish population, to develop biologically based spawning and harvest rate goals, and to estimate the maximum equilibrium abundance that the habitat can support. These models typically describe the relationship between parent spawners (stock) and the subsequent returns of progeny as maturing adults (recruitment). In practice, there is considerable variability in recruitment from a given parent spawning population due to fluctuations in factors such as climate that are unrelated to density. For this reason, statistical procedures are needed to fit an appropriate model (see Appendix I to the main report). It is also important to recognize that stock-recruitment models typically reflect ecosystem conditions in the recent past and may not adequately account for longer-term effects of spawning abundance on ecosystem characteristics; for example, by sorting streambed gravels and delivering nutrients. Consequently, the ecosystem may not be able to sustain indefinitely the "maximum sustainable yield" estimated from a stock-recruitment model based on historical spawning abundances.

Chapter III. Pre-development capacity of the Columbia River Basin

The total annual abundance of adult salmon and steelhead in the Columbia River Basin during the pre-development period (~mid 1800s) has been estimated to range from 7.5 to 8.9 million fish (Chapman 1986) and 10 to 16 million fish (NPPC 1986).[1] However, the ISAB's re-analysis of the admittedly limited data suggests that the potential capacity for all species combined in the pre-development period was likely in the range of 5 to 9 million adult fish per year, with the primary evidence (i.e., probable harvest rates) supporting an estimate of around 6 million fish per year. This revised estimate of all-species capacity probably overestimates the historical long-term average annual abundance because it is based on harvests during a period of favorable ocean conditions (late 1800s-early 1900s).

Even so, there is little doubt that the average annual abundance of adult salmon returning to the Basin during the pre-development period was much greater than today (~2.3 million fish per year during 2000-2012). Accepting this fact raises the second question posed in the Preface: "*Why is density dependence more evident than expected at low abundances?*" As a first step in addressing this question, the ISAB compared the percentage change in accessible habitat to the percentage change in adult salmon abundance from the pre-development period to the present. Only approximately two-thirds of the habitat available in the pre-development period is currently accessible to anadromous salmonids, yet current adult abundances of spring Chinook, fall Chinook, coho, and steelhead (natural and hatchery fish combined) often exceed two-thirds of their historical abundances. These simple comparisons provide initial evidence that overall density (natural and hatchery origin salmonids combined) may now be greater for spring and fall Chinook, coho, and steelhead; similar for sockeye salmon; and much less for summer Chinook and chum salmon. Furthermore, the total abundance of salmon smolts (natural and hatchery combined) may also be greater now than historically. The overall implication is that total adult returns of naturally spawning and hatchery fish may now be exceeding the carrying capacity of some areas of the Columbia Basin and its estuary.

Chapter IV. Novel Ecosystem Effects on Capacity, Productivity, and Resilience

The contemporary Columbia River is a novel ecosystem: a river and an estuary substantially altered from historical conditions. Novel ecosystems (also called hybrid or no-analogue ecosystems) are those in which species composition and ecological processes are unprecedented in the ecosystem's history. The contemporary Columbia River, its tributaries and the adjacent ocean provide significant challenges for the long-term vitality of native species. Although a few native species—e.g., northern pikeminnow—may have benefitted from increased habitat (hydrosystem reservoirs) and prey (hatchery salmon smolts), the intrinsic

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[1] Chapman, D.W. 1986. Salmon and Steelhead Abundance in the Columbia River in the Nineteenth Century. Transactions of the American Fisheries Society 115:662-670.

NPPC (Northwest Power Planning Council) 1986. Compilation of information on salmon and steelhead losses in the Columbia River Basin. Northwest Power and Conservation Council (formerly named Northwest Power Planning Council) Portland, OR.

productivity of most populations has declined, and most habitats now have significantly reduced carrying capacity, resulting in less resilience to natural and human-induced environmental stresses.

Chapter IV of the main report summarizes important environmental changes in the Columbia River Basin and the adjacent ocean. It examines linkages among carrying capacity, productivity, resilience, and life history characteristics in response to the changed environmental conditions, the resulting density dependent responses of native fishes, and the consequences of reduced life history diversity.

Ecosystem properties affecting density dependence - Broad environmental changes have taken place over the last two centuries. Historic watercourses have been changed by extensive physical alterations to the water supply and stream channels, as well as by anthropogenic land use. Continuing changes include ecosystem-scale alterations from urban development, widespread use of artificial chemicals, the proliferation of non-native species, range expansions and contractions by native species, pervasive alterations to riparian zones and food supplies, and climate change.

Changing oceans - The Columbia River is intimately linked to the Pacific Ocean by the regular movement of energy, materials, and organisms. Ocean conditions for salmon are changing steadily due to climate change, acidification, hatchery releases of juvenile salmon, and pollution. These changes affect density dependent rates of growth, maturation, and survival of anadromous fishes, altering their productivity, as well as the carrying capacity and resilience of marine habitats.

Life history diversity effects on carrying capacity, productivity, and resilience - Novel ecosystems pose threats to the life history diversity of previously well-adapted populations. Life history adaptations within and among salmon populations effectively increase a watershed's capacity to produce salmon because diverse life histories use a variety of habitats during each life stage, thereby reducing competition among individuals. In addition, the diversity of species, populations, genes, and life history traits within biological communities contributes to ecological resilience in the face of disturbance and environmental variability by providing a greater range of options to absorb or respond to change.

Although it is not possible to make quantitative comparisons with historical conditions, the collective evidence overwhelmingly suggests that the carrying capacity, productivity, and resilience of the Columbia River for native species have been diminished by widespread changes to environmental conditions. Collectively, these environmental changes likely contribute to the widespread (and unexpected) evidence of density effects on salmon productivity even though current spawning abundance is low relative to historical levels. Ongoing changes to environmental conditions stemming from climate change, chemicals, and intensified land use may further diminish the carrying capacity, productivity, and resilience of habitats, thus reducing the productivity of fish populations at any given density.

Chapter V. Evidence for Density Dependence among Anadromous Salmonids by Life Stage

The ISAB concludes, based on a comprehensive overview of existing studies within the Basin (see Chapter V in the main report and Appendix III), that strong density effects are evident in many natural populations despite current spawning abundance being much lower than historical abundance. We focused initially on detecting density dependence over the entire life cycles of salmon and steelhead (spawners to recruits) and then looked for evidence of density effects during particular stages from freshwater spawning and rearing, to estuarine rearing, to ocean residence.

Density dependence over the full life cycle - Recent studies provide compelling evidence for compensatory density dependence over the full life cycles of salmon and steelhead in most populations examined, even though abundances of natural spawners remain well below historical levels (Appendix III). No evidence of depensation was evident in these studies. Depensatory mortality is thought to occur at some stages, but its influence must be masked by stronger compensatory mortality in other life stages. Similarly, the widespread evidence of density dependence indicates that factors independent of density, such as variable stream flow and temperature, have not been sufficiently variable to obscure compensatory relationships that define carrying capacity. Most of the populations studied are Chinook salmon (28 populations) and steelhead (24 populations) in the Upper Columbia and Snake river basins. Few studies have examined density effects in coho salmon populations in the Columbia River, and few studies have been conducted on any species in the lower Basin where numerous subyearling Chinook are released. Density dependence observed during the life cycle might occur, depending on the particular case, because of competition among salmonids for key resources on the spawning grounds, in natal rivers or downstream reaches, in the estuary, or in the ocean.

Freshwater spawning and rearing - Strong compensation in survival and growth between spawning and smolt migration has been detected in 33 spring/summer Chinook populations in the Snake River Basin, two fall Chinook populations (Snake River and Hanford Reach), and six steelhead populations in the interior Columbia River Basin. None of the available studies except Okanogan River sockeye suggests little or no density dependence. These studies indicate that freshwater habitat capacity is often limiting growth and survival even though current spawning abundances are low relative to historical levels. For example, approximately 1.5 million spring/summer Chinook reportedly returned to the Snake River Basin each year during the late 1800s compared with only approximately 110,000 spring/summer Chinook during 2000-2013 (hatchery and natural combined). In some cases, spawning or juvenile densities in recent years appear to be meeting or exceeding the current capacity of rivers to support sustainable natural populations. Few of these studies examined density dependence separately during the spawning versus juvenile rearing stages, so it was seldom possible to demonstrate density effects during spawning.

Estuary rearing - All anadromous salmonids in the Basin pass through the Columbia River estuary, so it is clearly important to know whether current densities in the estuary are contributing to density dependence detected in the full life cycle analyses. Unfortunately, few studies have tested for density dependence in the Columbia River estuary, and the evidence is too scant to draw conclusions. This information gap is of concern because an important goal of habitat restoration in the Columbia River estuary is to reduce density effects by increasing population capacity and productivity—especially for natural-origin sub-yearling Chinook salmon that use the estuary as rearing habitat before entering the ocean.

Ocean rearing - Carrying capacity of salmon in the North Pacific Ocean was once thought to be unlimited—a concept that encouraged industrial-scale production of hatchery salmon. That concept is being challenged by growing evidence that survival, growth, and maturation of salmon during ocean residence are affected by aggregate salmon densities in the ocean. However, very few studies have yet considered how the aggregate density of salmon from the Columbia River might affect their growth and survival during the ocean stage. The ISAB concludes that the lack of information about density dependence of Columbia River salmonids during their time in the ocean is a critical gap that hinders an understanding of factors affecting growth and survival of the Basin's anadromous salmon.

Chapter VI. Hatchery Effects on Density Dependence

The Council's 2014 Fish and Wildlife Program implicitly recognizes the need to balance artificial propagation of salmonids with the Columbia River's capacity to support existing natural populations. After reviewing available evidence (see main report), the ISAB concludes that hatchery supplementation (for the primary purpose of rebuilding natural populations of salmon and steelhead) and large-scale hatchery releases to support fisheries may both have unintended density dependent effects on natural populations. Key findings:

- Supplementation typically increases total spawning abundance, but may not boost natural origin returns as intended.
- Hatchery fish have become abundant in many spawning and rearing habitats, and often represent a large percentage of naturally spawning Chinook and steelhead in the Basin.
- By increasing overall density, hatchery fish lower the productivity of natural spawners, and most importantly, of natural origin spawners, which may have been reduced to a low proportion of the population.
- As salmon densities increase beyond habitat capacity, salmon productivity will fall below replacement (i.e., adult returns per natural spawner < 1).
- Continued hatchery releases can maintain or increase total spawning density even though the productivity of natural spawners has fallen below replacement.
- Most supplemented and non-supplemented interior Chinook and steelhead populations are not naturally sustainable at recent high levels of total spawners; lower densities might allow them to become sustainable, albeit at lower abundance.
- Hatchery supplementation of natural populations should be scaled back when the demographic benefits no longer outweigh the genetic and ecological risks. Studies have

shown that productivity and abundance of natural winter steelhead increase following the removal of hatchery summer steelhead, and that the abundance and productivity of natural coho salmon increase following removal of hatchery coho salmon.

Chapter VII. Predation Effects on Density Dependence

Predators can have a significant impact on the survival of salmonids at all life stages. Their overall impact on a salmon population depends on the feeding rate of individual predators, the number of predators, and the length of time the salmon are vulnerable. Mortality caused by individual predators is typically depensatory. That is, the impact on a prey population from individual predators is highest when fewer prey are present, but the impact decreases when more prey are available because the predators become satiated and reduce their feeding rate. However, the typical depensatory functional response of individual predators can be offset by an increase in the number of predators due to aggregation in the short term or increased predator reproduction and abundance in the long term. Thus, large releases of hatchery fish can affect predation of natural-origin fish indirectly, by influencing the behavior and dynamics of predator populations.

Predation on adults during upstream migration (e.g., by sea lions) is of particular concern because it may reduce the potential spawning population more than an equivalent rate of predation at earlier life stages. Losses to predators early in the salmonid life history (e.g., from bird and fish predation) are often mitigated by compensatory mortality during later life stages, especially if predators selectively remove the most vulnerable individuals. By the time adult salmon enter the Columbia River estuary, they have already survived numerous threats in both freshwater and marine environments, and all are potentially valuable for harvest or spawning. The escapement goal of spring Chinook counted at Bonneville Dam (115,000 fish) has been met or exceeded since 2008 despite recent indications that predation of salmon by pinnipeds is increasing. Moreover, the life cycle recruitment relationships for Columbia River salmon and steelhead populations examined in Chapter V indicate that density dependence over the entire life cycle remains strongly compensatory even though depensatory mortality likely occurs at some life stages.

Chapter VIII. Management of Anadromous Salmonids in the Columbia Basin

A better understanding of density dependence could help to develop quantitative goals and objectives as part of the Council's Fish and Wildlife Program, to manage and evaluate the status of anadromous salmon populations, and to guide and evaluate habitat restoration activities in the Basin.

Escapement goals - Spawning escapement goals are reference points set by management agencies to maintain the potential for abundant salmon returns in the future. *Biological* escapement goals are typically developed by fitting Ricker or Beverton-Holt models to empirical spawner and recruitment data, thereby taking density dependence into account. Typically, biological escapement goals are established to maximize the potential for future harvests in

fisheries, but other reference points could be developed to maximize adult returns with a view to supporting wildlife, such as mink or bear, or the ecosystem (e.g., riparian tree growth).

Most escapement goals or management objectives in the Basin do not appear to be based on quantitative recruitment models that account for density dependence. Instead, management of fisheries is largely based on harvest rates in relation to stock abundances as described in the U.S. versus Oregon Management Agreement. Biological escapement goals that take density dependence into account are needed for salmonids in the Columbia Basin not just to manage fishery harvests but also to (1) indicate the carrying capacity of watersheds, (2) guide restoration actions, and (3) explicitly consider ecosystem benefits beyond sustainable harvests.

Supplementation and hatchery efforts - Supplementation actions often appear to be initiated without fully considering the probable density effects on natural-origin salmonid populations. Hatchery fish often account for an exceptionally high proportion of naturally spawning fish in populations in which strong density dependence has been detected. High spawning densities have frequently produced adult returns that were less than the parent spawning population. A successful integrated hatchery program is dependent on a sustainable natural population; total fish densities must be within the capacity of the watershed to support them. The ISAB concludes that biological escapement goals are needed to identify the maximum number of spawners (including supplementation fish) that can be sustained by existing habitat, so that the influence of supplementation on the natural population can be evaluated and adjusted as necessary.

Habitat restoration actions - Knowledge about density dependent mechanisms can help in planning restoration activities. Research to measure density dependent relationships is needed to 1) identify life stages requiring habitat restoration, 2) set the baseline for current capacity and productivity of the streams, and 3) evaluate fish responses to restoration actions. Studies within Intensively Monitored Watersheds provide a unique opportunity to monitor and evaluate density dependence within salmon populations. There is also a need to develop explicit hypotheses for how restoration actions might reduce density dependence during each life stage, or be designed to ameliorate mortality that is unrelated to density (such as high water temperature and extreme water flows), or provide other benefits to the ecosystem.

Ecosystem-scale benefits may accrue from having fish abundances fluctuate above the population carrying capacity. The "excess" fish can be ecologically important in maintaining the long-term vitality of the ecosystem, and can enhance habitat restoration actions in a number of ways. For example, a high abundance of adult spawners is needed to clean stream gravel of fine materials that impede subsurface flow, to contribute nourishment to large predators, scavengers, and downstream communities, and to enhance the growth of riparian trees. However, these long-term benefits to the ecosystem must be balanced against short-term costs to fishing communities or to the fish population if there is overcompensation (less recruitment from larger spawning abundances).

<u>Evaluation of population status and program effectiveness</u> - The status of salmon populations or success of restoration actions cannot be fully evaluated without considering the effects of fish density. Many supplemented salmon populations have recently increased in abundance, suggesting that their status is improving. However, because of density dependence, the increased abundance of naturally spawning fish has often reduced productivity in the next generation such that natural spawners cannot maintain their hatchery-supplemented abundance.

Simply documenting a change in body growth, survival, or abundance is inadequate for evaluating success of restoration projects because density can have a strong effect on each metric. Instead, improvements in the response variable (growth, dispersal from the natal stream, survival, or recruitment) should be compared relative to changes in fish density. Ideally, relationships between the response variable and density would be developed for a baseline period prior to habitat restoration and then compared to post-treatment values and reference streams to determine the success of the restoration actions.

Chapter IX. ISAB Recommendations, Part 1

The following recommendations list ways to consider and account for density dependence when planning and evaluating habitat restoration actions, developing quantitative objectives for the Basin's anadromous salmon populations, and improving the research plan of the Council's Fish and Wildlife Program. These recommendations also apply generally to other efforts (e.g., the FCRPS Biological Opinion, NOAA recovery plans and life cycle modeling, and tribal programs) to mitigate impacts from the 4Hs (hydro, habitat, harvest, and hatcheries).

1. Account for density effects when planning and evaluating habitat restoration actions. The pre-development capacity of the Basin to support salmonids is likely less than previously believed; a re-analysis suggests that the capacity for all salmon species combined was 5 to 9 million adults. Additionally, there are significant environmental contraints imposed by the Basin as a dynamic but highly altered novel ecosystem. Therefore, it is important to consider the following in developing restoration actions for the Fish and Wildlife Program and other regional efforts:

- Use knowledge of mechanisms influencing density dependent growth, dispersal, and survival of anadromous salmonids to choose restoration actions that will most effectively increase habitat capacity and fish population productivity and abundance.

- In restoration planning, identify actions capable of reducing density dependence during each life stage, and integrate with actions designed to reduce mortality caused by density independent factors (e.g., water temperatures and flows).

- Consider density dependence when evaluating the success of restoration actions; fish response variables (growth, dispersal from the natal stream, survival, recruits) are typically influenced by fish density.

2. Establish biological spawning escapement objectives (reference points) based on recruitment models that account for density dependence, including population productivity and habitat carrying capacity. Accounting for density dependence helps determine realistic wild (i.e., natural origin) salmon abundance objectives for the Fish and Wildlife Program's wild fish strategy. Specifically:

- Establish biologically based reference points to guide the need for management actions (via harvests, supplementation, and removal of surplus hatchery fish entering the spawning areas) and to quantify when too few or too many spawners are present to sustain natural populations.

- In setting harvest rates, account for current population productivity and habitat capacity, and adjust harvest through Adaptive Management as environmental conditions change.

- Recognize that large spawning escapements can provide ecosystem benefits and promote long-term sustainability but might also impose short-term costs to fishing communities or to the fish population if there is overcompensation (less recruitment with larger spawning abundances).

- Acknowledge that ecosystem-based fishery management may prove to be the best strategy over the long term given existing uncertainty about density dependent and ecosystem-scale processes.

3. Balance hatchery supplementation with the Basin's capacity to support existing natural populations by considering density effects on the abundance and productivity of natural origin salmon. In particular:

- Clearly articulate anticipated benefits of supplementation actions and base these actions on established scientific principles.

- Estimate the abundance and proportion of hatchery and natural origin adults on spawning grounds, whenever possible, to target appropriate spawning densities that prevent the loss of productivity in natural populations, especially through overcompensation in the short term or domestication in the long term.

- Recognize that an integrated hatchery supplementation approach requires a self-sustaining natural salmon population, which in turn requires spawning densities that can be supported by the environment.

4. Improve capabilities to evaluate density dependent growth, dispersal, and survival by addressing primary data gaps. This relates directly to having monitoring strategies that quantify the success of Fish and Wildlife Program activities, as well as gather information that allows adjustments for ongoing human-driven environmental changes. The primary data gaps involve:

- Density effects in salmon populations that spawn in the lower Basin and in coho salmon populations throughout the Basin.

- Density effects on the growth and survival of juvenile salmonids emigrating downriver and rearing in the estuary and ocean.

- Predation on adult salmon by pinnipeds (seals and sea lions). Since depensatory mortality may pose a threat to ESA-listed populations, the ISAB recommends further quantification of mortality and evaluation of life cycle recruitment in salmon populations targeted by pinnipeds.

PART 2: Non-anadromous salmonids, sturgeon, and Pacific Lamprey

Part 2 addresses key issues of management interest for sturgeon, Pacific lamprey, and non-anadromous or "resident" salmonids including non-anadromous trout, charr, and kokanee. Questions about density dependence are different for these species groups than for anadromous salmonids, owing to differences in their life history and ecology, and the focus on conservation and increasing sport fishing opportunities rather than increasing harvest in commercial fisheries. Moreover, direct measurement or manipulation of densities or limiting resources is often more feasible for resident salmonids and sturgeon than for anadromous salmonids, so that different approaches can be used to address questions of management interest. Important management questions related to density dependence in resident trout include:

1) *Does habitat restoration decrease density dependent limiting factors and thereby increase carrying capacity?*
2) *Does stocking of hatchery trout reduce carrying capacity for natural origin trout, and thereby reduce their density?*
3) *Do invasions by non-native trout or other non-native species reduce the carrying capacity for native trout, and thereby reduce their density?*
4) *Can overexploited trout populations rebound when angling mortality is reduced to sustain higher densities for conservation or sport fishing?*

Chapter X. Non-Anadromous or "Resident" Trout

Rainbow, cutthroat, and bull trout (actually a charr) are termed "resident" because they do not migrate to the ocean. However, many populations make substantial migrations within fresh water to complete their life cycles, including adfluvial populations that migrate from lakes to streams to spawn and fluvial populations that live in large rivers and spawn in tributaries. Unlike anadromous Pacific salmon that spawn only once and die, resident trout may spawn repeatedly (some only in alternate years), mature late (e.g., age 3-7), and be long lived. These life history differences complicate the task of relating adult recruitment to parental spawning density. Only a few trout populations have been monitored long enough and in sufficient detail to fit recruitment models.

Populations of resident trout can be difficult to delineate because they often disperse throughout riverscapes to find suitable habitat for spawning, rearing, and refuge from extreme conditions. Hence, immigration and emigration (in addition to fecundity and survival) are potentially important considerations in managing trout populations. Moreover, adult and juvenile trout often use the same general habitats, allowing for more interactions among age classes than anadromous salmon and trout.

Resident trout are typically smaller and less fecund than anadromous salmonids, so they are less likely to saturate all available spawning habitat with eggs, a common cause of compensation in anadromous salmonids. Consequently, compensation in resident trout populations is more likely to occur at other life stages, such as among adults. In addition, recruitment of juvenile trout during their first summer in mountain streams and rivers is often more strongly limited by density independent effects of snowmelt runoff flows than density dependent competition.

Does habitat restoration decrease density dependent limiting factors and thereby increase carrying capacity?

Adding in-stream habitat for either juvenile or adult trout is expected to increase carrying capacity primarily via two mechanisms: decreasing mortality and/or decreasing emigration from the study reach. Fecundity reflects body growth, which is usually limited by habitat productivity, and annual immigration is typically substantial and relatively constant; therefore, these two rates are unlikely to change with in-stream habitat restoration. Even so, effects of habitat restoration or expansion are controversial, with recent comprehensive reviews arguing for and against positive effects. Expected benefits of restoration might not be detected because of uncontrolled confounding variables, or problems with the design and analysis of field experiments. In particular, measuring the long-term and large-scale effects of restoration for mobile trout in riverscapes is challenging, and requires appropriate hypotheses and methods to be effective. In comparison to adding in-stream habitat, restoration of riparian vegetation can increase the input of terrestrial invertebrates, which some studies have shown can increase growth and abundance, and reduce emigration.

Does stocking of hatchery trout reduce carrying capacity for natural origin trout, and thereby reduce their density?

One might expect hatchery trout to be "analogs" of natural-origin trout, and that they would compete for similar resources, thereby reducing the habitat's carrying capacity for natural-origin trout. However, whether they do in any specific case depends on the species, life stage, density stocked, carrying capacity of the environment, whether the hatchery trout are highly domesticated or progeny of natural-origin parents, and their competitive ability relative to natural-origin fish. Studies conducted at small scales in the laboratory or artificial streams have often shown that fish reared in hatcheries are more aggressive, waste energy, feed inefficiently, and are more susceptible to predation than their natural-origin counterparts. Direct observations of juvenile fish in natural streams have also shown that hatchery fish can

dominate profitable feeding positions and displace natural-origin fish, often owing to the larger size of hatchery fish. However, controlled experiments to test for effects of hatchery fish on growth or survival of natural-origin fish in natural streams are less common.

Overall, available evidence indicates that introducing hatchery-reared trout of the same species can have density dependent effects on growth—although a recent comprehensive study of stocking catchable sterile adult rainbow trout in the interior Columbia River Basin did not detect this effect. Likewise, effects on survival of natural-origin trout have not been demonstrated in any studies, probably because survival of hatchery-reared catchable trout is usually low. Hatchery-reared trout can also cause hybridization and introduce disease, but these effects were not reviewed.

Do invasions by non-native trout or other non-native species reduce the carrying capacity for native trout, and thereby reduce their density?

Reduction of carrying capacity can be inferred by measuring how much the native trout population expands when the non-native species is removed. Native cutthroat trout and bull trout abundance each increased about 10-fold when non-native brook trout were removed. Other research shows that when brook trout replace native cutthroat trout, they can achieve densities, biomass, and production 1.5 to 1.9 times that of the native trout, even after accounting for primary differences in habitat. Even when brook trout occur at the same density as cutthroat trout, brook trout can produce an increased "load" on the ecosystem by reducing adult aquatic insects emerging from streams that feed riparian animals like bats, birds, and spiders.

Can overexploited trout populations rebound when angling mortality is reduced to sustain higher densities for conservation or sport fishing?

Populations of bull, cutthroat, and rainbow trout in cold unproductive mountain streams, rivers, and lakes are particularly susceptible to angling mortality and overfishing. Recent federal listings and conservation plans have prompted restrictive angling regulations or closures, assuming that natural mortality and angling mortality are largely additive, as often inferred from subsequent increases in abundance. However, if natural mortality is compensatory and simply replaces angling mortality, then such regulations might be ineffective.

Studies of bull trout populations demonstrate that natural-origin populations can rebuild with reduced angling mortality, but that they eventually reach a carrying capacity because of density effects on growth, maturation, and life history characteristics. Stage-specific [recruitment models for one adfluvial population](#) suggest that density dependence is strongest in early life (egg to age-1) and is best described by the Ricker model. One management implication is that minimum length limits might need to be increased at low density when fish grow faster, to avoid angling mortality before they mature. Managers can determine when rebuilding has reached the habitat's existing carrying capacity by monitoring indices of density dependence such as growth, age and size at maturity, and reproductive periodicity.

Chapter XI. Kokanee

Kokanee is a resident form of sockeye salmon that is widely stocked into lakes or reservoirs of low to moderate productivity in an effort to create robust fisheries. Kokanee (and sockeye salmon) have several life history characteristics that promote strong density dependence through wide population fluctuations and intense competition for food. They are short-lived (typically 5 years or less), spawn only once and die, and typically feed on zooplankton in the limnetic zone of lakes. Whether intraspecific competition is an issue in any given situation depends on fish density, size or age, the food supply, and the density of predators.

Kokanee typically grow more slowly at higher density because of scramble competition for food. In many populations, the length of kokanee spawners (an indication of growth rate for a particular year class) can be used as a reliable index of year class strength (i.e., juvenile abundance) or spawner counts, and vice versa. The proportion of older age spawners can also be used to detect density dependence because slower growth typically delays age at maturity (e.g., from age 3 to age 4). Overstocking with kokanee fry can cause a population to collapse when the food base is overgrazed, a phenomenon analogous to overcompensation observed in natural populations of sockeye salmon.

Density dependent effects are typically taken into account when managing kokanee fisheries. Intermediate levels of fish density have been shown to produce the highest fishing effort and catch rate (in both numbers and biomass). Fast growth at very low population densities can produce trophy-size kokanee, but fluctuations in recruitment at such low densities may lead to population collapse. Slow growth at very high densities reduces the availability of desirable-sized fish to anglers as a high fraction of fish may spawn and die before reaching a desirable size. In most cases, the optimal harvest management approach is to maintain intermediate densities, resulting in intermediate growth rates, survival, age at maturity and yield, and the sort of stability that often characterizes successful long-term fisheries.

Chapter XII. Sturgeon

Both green and white sturgeon occur in the Columbia River Basin. Green sturgeon have historically been much less abundant than white sturgeon and are rarely found more than 60 km up-river from the estuary. They may not spawn in the Columbia River, and little information is available to assess the role of density in their population dynamics.

White sturgeon historically moved great distances up and down the Columbia River and into major tributaries, and they still occur upstream as far as Idaho and Canada. However, dams have fragmented sturgeon habitat into semi-isolated segments where conditions are no longer optimal and anadromy is difficult. White sturgeon abundance has declined basin-wide because reproductive success is inconsistent, and juvenile recruitment has been inadequate for population growth. Although the sub-population downstream of Bonneville Dam is far more abundant, productive, and reproductively robust than the impounded sub-populations

upstream, it too has declined, and harvest regulations have become more restrictive in recent years.

Density dependence has been detected in the geographically isolated, endangered Kootenai River white sturgeon population (Kootenai management unit). Libby Dam, constructed in 1972, altered discharge, downriver water temperature, suspended sediment and nutrient delivery, and habitat productivity. Subsequent recruitment failure prompted a conservation aquaculture program that started in 1990. Fish that were larger at release survived better in the river than smaller fish, and this size effect became stronger with continued stocking, which suggests that increasing the density in the river had reduced both growth and survival.

Seasonal density dependence can also occur in pre-adult and adult white sturgeon inhabiting reservoirs with limited rearing habitat. For example, the number of sturgeon that can be accommodated in Brownlee Reservoir, a mainstem Snake River impoundment on the Idaho-Oregon border, depends strongly on the amount of available habitat, a function of water temperature and dissolved oxygen concentrations. The carrying capacity for sturgeon varies greatly among years, such that fish unable to leave the confinement of dam-created pools might die in some years.

These study results underscore the importance of assessing the productivity and carrying capacity of habitats where sturgeon are stocked. Such assessment is particularly important for sturgeon now that dams have blocked or greatly impeded anadromy and dispersal. Before impoundment, fish often ranged widely throughout the river and into the ocean, reducing the likelihood of density effects, and increasing overall capacity. Density effects are more likely to arise under current conditions, especially as hatchery programs are expanded in fragmented habitats.

Chapter XIII. Pacific Lamprey

Pacific lamprey are native to the Columbia River Basin and are culturally important as food for Native Americans. The abundance of Pacific lamprey in the Basin and along the Pacific coast has declined greatly since 1970, creating important gaps in food webs. Pacific lamprey are both prey and predators, and they are a source of marine-derived nutrients. Little is known about the role that density plays in their population dynamics, but one laboratory study showed that the growth of larval Pacific lamprey declines with density of conspecifics when food is held constant. Moreover, an observed relationship between larval density and redd density suggests density dependent survival or dispersal in tributaries to the Willamette River.

The life history of the Pacific lamprey is very similar to that of the sea lamprey, which caused significant declines to commercial fisheries when it invaded the Great Lakes. Understanding density dependent factors that control sea lamprey abundance has been widely studied, and investigations have demonstrated compensation in both growth and survival. An age-structured model was recently developed with data from 75 areas in the Great Lakes during 1993 to 2011 to investigate stock-recruitment, spatial recruitment patterns, natural mortality, mortality from

chemical control treatments, and larval metamorphosis. This and other models could perhaps be adapted to explore density dependence in Pacific lamprey given their similar life history.

Chapter XIV. ISAB Recommendations, Part 2

The Council's Fish and Wildlife Program recognizes the importance of all native resident fish and other freshwater species in maintaining ecosystem diversity and function, as well as contributing to the Basin's culture. The following recommendations list ways to consider and account for density dependence when planning and evaluating habitat restoration actions, developing quantitative objectives for the Basin's non-anadromous salmonids (trout, charr and kokanee), sturgeon, and lamprey, and improving the research plan of the Council's Program. These recommendations also generally apply to other efforts (e.g., biological opinions and tribal programs) attempting to mitigate impacts from the 4Hs (hydro, habitat, harvest, and hatcheries). Due to differences in life history and ecology, sampling constraints, and a focus on conservation and/or sport fishing for non-anadromous salmonids, sturgeon, and lamprey as compared to anadromous salmonids (Part I), there are different issues related to density dependence for these species. Overall, there is a dearth of information on density dependence effects for nearly all resident (non-anadromous) fishes in the Basin. **The ISAB encourages the Council to continue to support a basic understanding of factors affecting the productivity and carrying capacity for these ecologically and culturally important species.**

Non-anadromous salmonids

Density dependent issues for non-anadromous salmonids include effects of habitat restoration, stocking of hatchery trout, and invasions by non-native species on carrying capacity, and whether restricting angling can allow populations to rebound and reach recovery or sport fishing goals. Accounting for density dependence helps determine realistic abundance objectives for the Fish and Wildlife Program's non-anadromous salmonid strategy. Therefore, it is important to consider the following in developing restoration actions for the Program as well as for other regional efforts:

- **Consider that in-stream habitat restoration is most likely to increase carrying capacity by reducing compensatory mortality and emigration**. The postulated mechanisms are related to increasing survival and decreasing emigration, rather than by affecting growth, fecundity, or immigration. Evidence from across many regions shows that increases can occur, but the true effects on survival and emigration occur at the riverscape scale and remain difficult to quantify.

- **Restore riparian vegetation to increase the input of terrestrial invertebrates**, which can improve growth and abundance and decrease emigration of salmonids.

- **Consider carefully the stocking of hatchery trout to avoid reducing carrying capacity for wild non-anadromous salmonids.** An investigation of stocking sterile hatchery rainbow trout did not detect effects on growth, survival, or recruitment, but this

depends on characteristics of the hatchery fish (e.g., degree of domestication), as well as when, where, and how many are stocked. Hatchery fish can also transfer diseases or parasites, and non-sterile ones can hybridize with natural-origin fish, so precautions against these effects are also warranted.

- **Take steps to prevent invasions by non-native trout**, which can often replace native salmonids quickly (i.e., usurping carrying capacity), achieve higher density and biomass when they do replace them, and have ecosystem-scale effects on emerging insects that are key food resources for other wildlife. Removing non-native trout above barriers allows native salmonid populations to rebound to their former carrying capacity, and in relatively undisturbed watersheds without barriers, maintaining stronghold populations of native salmonids at high density may help to prevent invasions by non-native trout.

- **Consider the use of angling regulations and fishery closures to achieve conservation and sport fishing goals.** Studies of bull trout populations show populations rebounding from low abundance to achieve density goals for conservation, indicating that they were far below carrying capacity and that angling mortality was partly additive to natural mortality. Many populations of cutthroat and rainbow trout throughout the Rocky Mountains also have rebounded when restrictive angling regulations were applied, indicating that fishery management can be effective at increasing the density of resident trout.

- **Ensure that fishery managers consider the probable effects of density on survival, emigration, growth, and size/age at maturity**. For example, kokanee populations can crash due to food limitation following overstocking with kokanee fry. In the absence of detailed data for stock assessment, managers should use their knowledge of limiting factors and fishery management principles to target intermediate densities, rather than seeking the ecologically unrealistic goal of a higher abundance of larger fish.

Sturgeon

The Council recognizes that sturgeon migration, distribution, abundance and productivity are severely limited by habitat changes, particularly those associated with hydropower system construction and operation. Further, habitat carrying capacities for impounded white sturgeon sub-populations are currently much lower than for the unimpounded, anadromous population downstream of Bonneville Dam. Specifically:

- **Ensure that white sturgeon stocking programs do not cause significant reductions in growth and survival of sturgeon during each life stage.** New sturgeon hatchery programs are being planned and built in the Basin. Hatchery production should be consistent with the capacity of the habitat to support sturgeon at all life stages.

Lamprey

Pacific lamprey populations in the Columbia Basin have declined sharply in the past 40 years. Despite the fact that this species is a key component of the Columbia Basin food web as both prey (e.g., for pinnipeds) and predator, virtually nothing is known about density effects on their abundance and growth. Therefore, the ISAB recommends:

- **Initiate a concerted effort to gather information that would help the recovery of this species.** Toward that end, research in the Great Lakes has documented significant density dependent effects for populations of sea lamprey, which is related to the Pacific lamprey. These sea lamprey studies might provide a template for developing a similar understanding of Pacific lamprey.

- **Consider lessons learned about supplementation and density dependence in anadromous salmonids when planning future actions to propagate and translocate (i.e., supplement) lamprey within the Basin.** While the ecological lessons might not be directly transferrable, they can be used to guide management and restoration actions.

Appendix I. How to Measure Density Dependence: Study Design and Analysis

Appendix I to the main report briefly describes a variety of statistical approaches developed to detect and evaluate density dependence. It also compares two commonly used recruitment models, and examines how errors in measuring the spawning population and/or the number of recruits can have important consequences for evaluating compensation and for setting biological targets and harvest policy. This appendix is provided to help salmon managers and restoration teams incorporate density dependence into their evaluations of population status and restoration effectiveness.

The Ricker model and the Beverton-Holt recruitment models differ importantly in their predictions about maximum equilibrium abundance. In the Beverton-Holt curve, recruitment reaches a plateau at high spawning abundances. In the Ricker curve, recruitment increases to a maximum but then declines as the number of parent spawners increases beyond the carrying capacity, a property called overcompensation.

This difference between the two models at high spawner abundances has important implications for managing salmon populations, especially when the populations are being supplemented with hatchery fish. For a population best described by the Beverton-Holt curve, excessive spawning density has no adverse consequences other than lost harvest opportunities during the year of return. However, for a population best described by the Ricker curve, excessive spawning density will, on average, reduce recruitment in the next generation, in addition to the lost opportunity for harvest in the year of the large return.

Appendix II. Density Effects during Spawning and Incubation

Appendix II to the main report provides a detailed review of the ways that spawning site selection is constrained by physical habitat, homing behavior, and seasonal temperature requirements such that competition for spawning locations and mates can be intense even at seemingly low population abundances. Compensation can occur when high spawning densities cause fish to disperse into other areas with less favorable spawning habitat, or lead to increased rates of egg retention due to incomplete spawning, or increased redd superimposition and subsequent destruction of previously deposited eggs. Even when redd superimposition does not destroy eggs directly, it can lead to intense scramble competition for dissolved oxygen during incubation. Depensation might also occur at very low spawning densities in cases where intermediate spawning densities help to "condition the environment" by digging and cleaning the gravel which improves hyporheic flow and dissolved oxygen levels.

Experimental investigation of factors affecting egg-to-fry survival in spawning channels indicates that Chinook salmon are more sensitive to density effects than chum salmon. Chum salmon often spawn in dense aggregations and may be better adapted to high spawning densities. This observation helps explain why strong density effects are evident in some Chinook populations despite their relatively low abundance and suggests that density dependence in Chinook may occur throughout spawning and incubation as well as during juvenile rearing.

Appendix III. Summary Table of Density Effects in the Columbia River Basin for Anadromous Salmonids

Appendix III identifies each of the anadromous salmonid density studies described in the main report. The table shows the salmonid population or group of populations that were investigated, life stage, years of investigation, the density effect, and whether or not the capacity was met or exceeded in some years.

PART I: Anadromous Salmonids

I. Introduction

Natural origin salmon and steelhead are much less abundant in the Columbia River Basin today than prior to Euro-American expansion in the mid-1800s (Chapman 1986, NPCC 2014). The low numbers and other factors led to concerns about population viability of most natural populations, many of which are now protected under the Endangered Species Act (ESA).[2] Biologists investigating the status of these populations in the 1990s and earlier considered abundance to be so low that concerns about competition for limited resources such as food, rearing habitat, and spawning habitat were a low priority (PFMC 1979; Cuenco et al. 1993; Cuenco 1994; Kareiva et al. 2000; Achord et al. 2003; McClure et al. 2003; Walters et al. 2013a)—despite the severely degraded quality of habitat. Based on that view, population recovery of the ESA-listed populations would not be constrained by density dependent interactions influencing survival, growth, and other population characteristics.

The reality, however, may be quite different. For example, biologists are observing unexpectedly strong evidence of density dependent reduction in productivity of spring/summer Chinook salmon populations in the Snake River Basin even at low abundances (Figure I.1). In this case, productivity measured as smolts produced per spawner is high (300 to 400 smolts per female) at low parent spawning abundances (~3,000 females), but lower than expected (only 75-150 smolts per female) at modestly higher spawner abundances (~10,000 females; Zabel et al. 2006, Kennedy et al. 2013). These spawner abundances are much lower than the reported 1.5 million adult spring/summer Chinook returning to this region during the late 1800s or 100,000 Chinook in the 1950s (Matthews and Waples 1991, Walters et al. 2013a). This productivity response to Chinook abundance could reflect, for instance, competition for limited space on the spawning grounds, for rearing habitat, or for food. However, the additional evidence that Chinook smolt size declines with greater juvenile abundance strongly suggests that food availability is limiting growth even at these low abundances (Crozier et al. 2010, Walters et al. 2013a). In this example, increasing natural spawners from 20,000 to 50,000 adult females in the Snake River Basin has not produced additional smolts, which indicates that the current average capacity or upper limit of juvenile abundance is approximately 1.6 million smolts—considerably lower than the 2-4 million smolts produced in the 1960s (Raymond 1979; Figure I.1A). In short, density effects on smolt production are now strongly evident at spawning abundances that are low relative to historical levels, implying that existing freshwater habitat is constraining the maximum sustainable size of the population.

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[2] www.nmfs.noaa.gov/pr/species/esa/

The importance of density dependence in the Columbia Basin is further highlighted in the 2014 supplemental Biological Opinion (BiOp) for the operation of the Federal Columbia River Power System (FCRPS; NOAA Fisheries 2014). The BiOp states that while abundances of Chinook and steelhead had increased in recent years, their productivity (adult return per spawner) had declined. Analysis of 27 spring/summer Chinook populations in the Upper Columbia and Snake River basins and 20 interior Columbia steelhead populations indicated that the productivity of most populations was inversely related to parent spawning abundances and consistent with the hypothesis of density dependence. The relatively low productivity estimates for some recent years can be largely explained by the increase in parent spawning densities. Furthermore, the capacity of some watersheds to support salmon or steelhead was exceeded at relatively low abundances, as indicated by recruitment that, in most years, was less than the parent spawning abundance. Zabel and Cooney (2013 *in* NOAA Fisheries 2014) concluded that there is no reason to infer that *intrinsic* productivity (measured at very low abundance) is continuing to decline. Collectively, these and other lines of evidence led the ISAB and several regional scientists and managers to raise concerns that density effects may be stronger and more widespread than previously thought.

Understanding density dependence is vitally important for estimating the carrying capacity of populations and for effective implementation of the NPPC's Fish and Wildlife Program. Evidence of strong density dependence at abundances lower than historical levels suggests that carrying capacity has been reduced. Density dependence, as shown in Figure I.1, is also critical for enhancing the stability of natural populations. Understanding the mechanisms causing density dependence—such as limited food supply, rearing habitat or spawning habitat, or predator-prey interactions—can help to guide habitat restoration and population recovery actions (ISAB 2011-1, ISRP 2011-14, ISRP 2013-11). Density dependent relationships are central to the development of spawning escapement goals that contribute to sustainable populations and fisheries (Hilborn and Walters 1992).
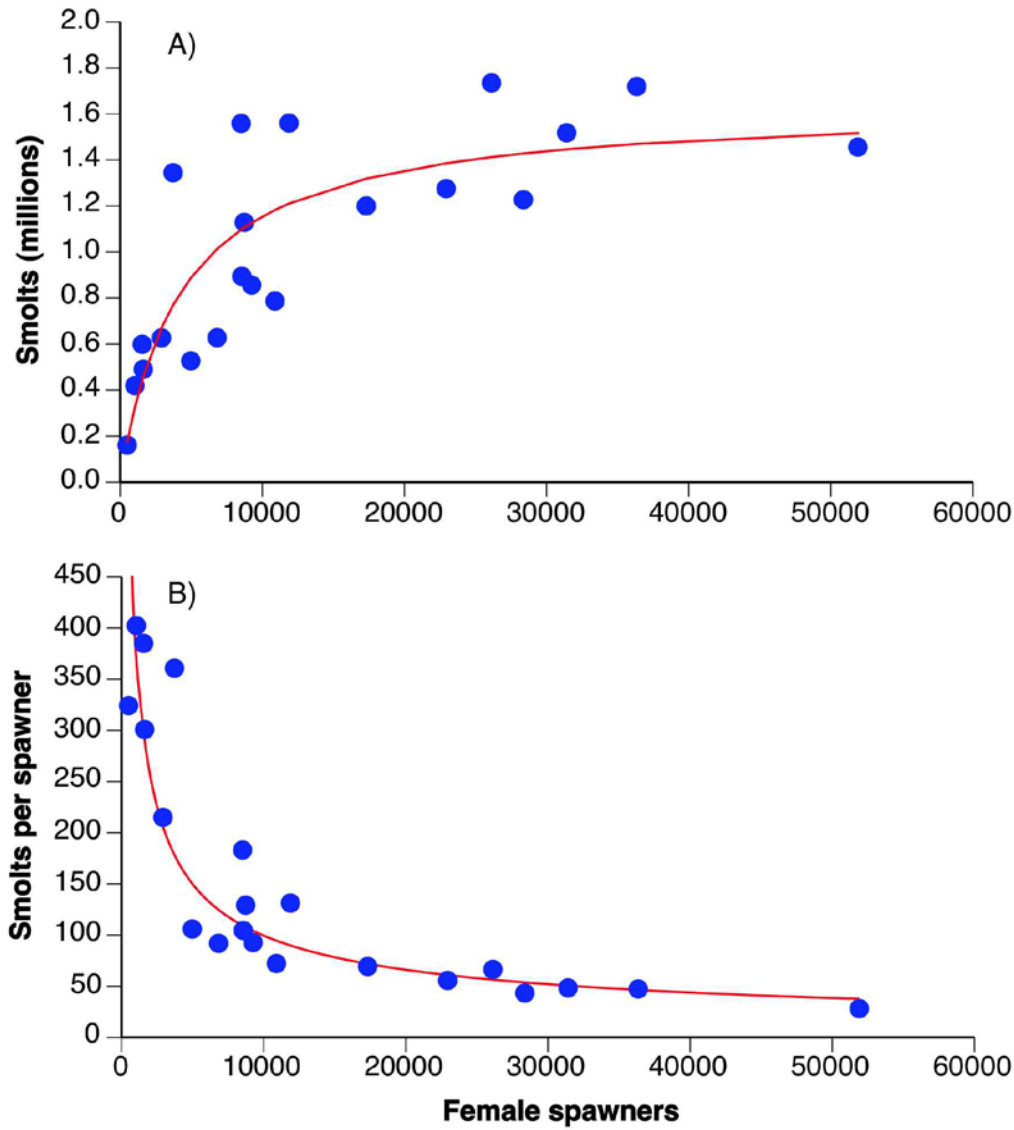
Figure I.1. Example of density dependence among spring/summer Chinook salmon in the Snake River Basin, brood years 1990-2010. A) Numbers of natural smolts produced by female spawners increased with greater parent spawners when spawners are less than 10,000 females, but reached maximum abundance of approximately 1.6 million smolts when spawners exceeded ~20,000 females. Additional spawners beyond ~20,000 females did not lead to greater smolt production. B) Productivity (smolts per spawner) declined rapidly as spawners increased from 500 to 10,000 females. Smolts were enumerated at Lower Granite Dam and a Beverton-Holt stock recruitment model was fit to data, as shown by the curved line in panel A. This stock recruitment model was used to estimate maximum smolt production (~1.6 million smolts) and intrinsic productivity at low spawner abundance (~389 smolts per spawner). Annual variability in productivity not associated with density is reflected by the scatter of values about the fitted curve. Smolt production in the 1960s was approximately 2-4 million. Source: Raymond (1979), Petrosky et al. (2001), Zabel et al. (2006), Kennedy et al. (2013), T. Copeland, IDFG, personal communication.

In March 2014, representatives from the Northwest Power and Conservation Council (NPCC), NOAA Fisheries, and Columbia Basin tribes approved the Independent Scientific Advisory Board (ISAB) to review the implications of density dependence in fish populations in the Columbia River Basin. The ISAB was asked to address the following questions related to density dependence:

- What is density dependence and why is it important?
- Why is density dependence more evident than expected at current relatively low abundances?
- Where—and at what life stages—has density dependence been detected in the Basin?
- How can density dependent limitations be ameliorated as a means to enhance population rebuilding and recovery?
- How can we detect and diagnose density dependent limiting factors?

We examine how population densities within the overall fish community influence the ability of watersheds to support key fish species in the Basin (Figure I.2) including anadromous salmonids (Part I) and non-anadromous salmonids, sturgeon and lamprey (Part II). The report is organized around the following topics:

- The importance of density dependence in regulating and managing fish populations.

- Pre-development (~mid-1800s) estimates of salmonid abundance in the Columbia Basin as an indicator of the Basin's potential capacity.
- Novel ecosystem and life history diversity effects on the productivity and capacity of the Basin to support existing and future salmonid populations.
- Evidence of density dependent and density independent effects on life stages of anadromous and resident salmonids, lamprey, and sturgeon.
- Use of density dependence information for enhancing population management and recovery efforts, and improving restoration efficiency.

It is important to recognize that current ecosystem conditions determine the strength of density dependence experienced by a population. Changes in ecosystem-scale characteristics and processes can alter a population's intrinsic productivity and carrying capacity. Similarly, a stock recruitment model reflects current ecosystem conditions from the perspective of the modeled population—it does not however reflect the vitally important, longer-term roles of populations in shaping ecosystem characteristics through various activities (e.g., sorting streambed gravels, delivering nutrients). Population abundance, whether too low or too high from a fisheries management perspective, has long-term ecosystem-scale consequences that cannot be fully appreciated when only short-term population-scale actions are implemented.
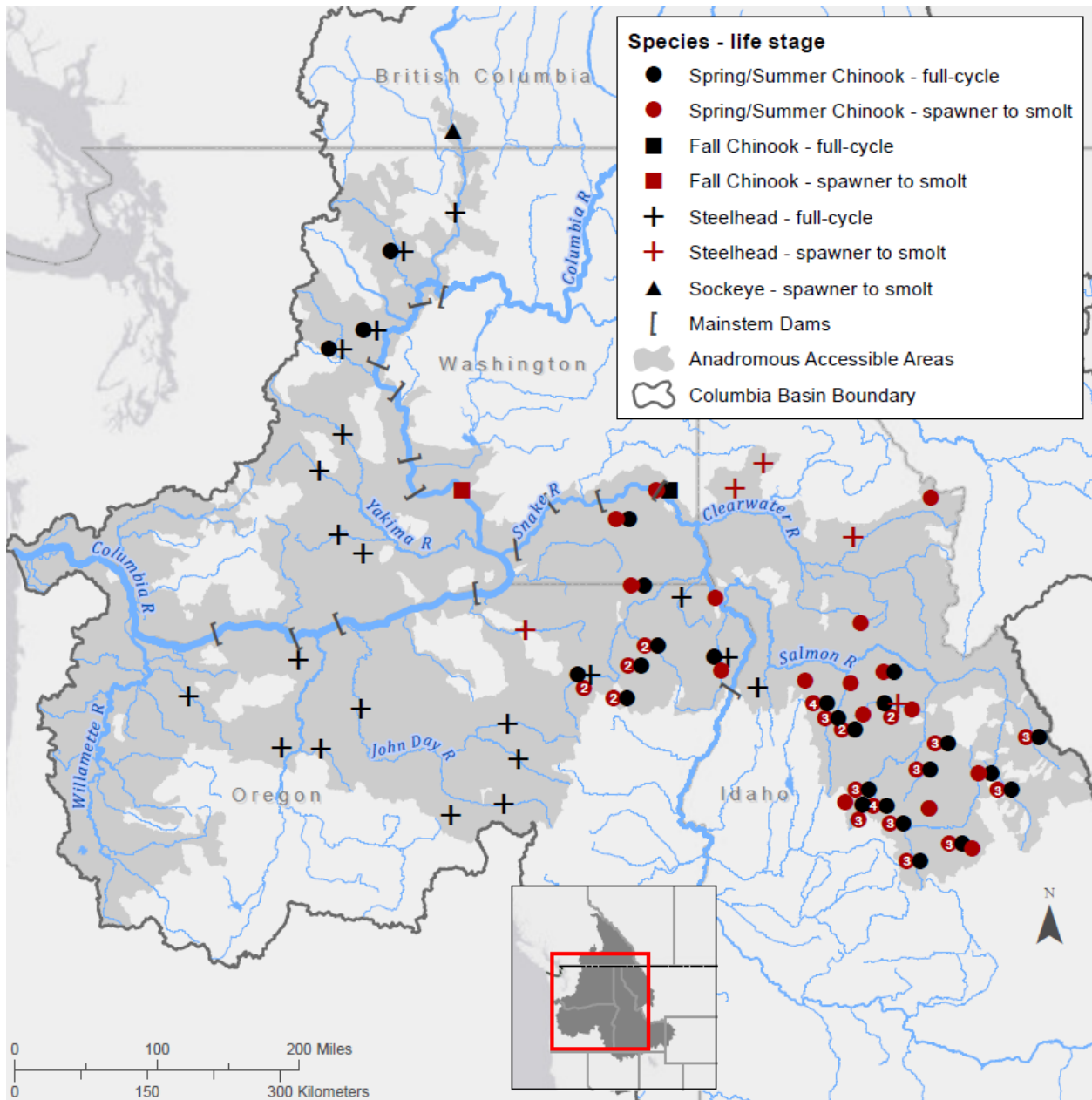
Figure I.2. Columbia River Basin locations of within-population studies of density dependence examined in this report. These studies describe intraspecific competition by life stage. The numeric values show the number of unique studies at that location. See Chapter V for description of these and related studies of density dependence. Map produced by Brett Holycross and Van C. Hare, Pacific States Marine Fisheries Commission.

II. What is density dependence and why is it important?

Density dependence occurs when a change in fish density causes a change in the growth rate of a population by affecting one or more of the vital rates (birth rate, death rate, immigration, or emigration; Turchin 2003; Hixon and Johnson 2009). Density dependence can also cause changes in the growth, survival, or fecundity of individual fish, which in turn affect vital rates. Populations are regulated by density dependence if population growth slows as density increases, and, in turn, increases at lower densities.

Density dependence can be of two types. The most common is direct density dependence (also termed *compensatory*, used hereafter in this document) where birth rate declines and death rate increases as density increases, driving population growth rate down (Hixon and Johnson 2009, see Herrando-Pérez et al. 2012b for more on terminology). Compensatory density dependence is most often caused by limitations in resources, principally food or habitat, which determine the carrying capacity. For example, if the density of age-0 coho salmon in the fall exceeds the carrying capacity set by overwinter habitat, survival will be lower than it would have been at lower densities. Overall, a relatively fixed number of fish will survive until spring, regardless of initial high density, owing to limited habitat.

Less common is inverse density dependence (*depensatory* hereafter; Neave 1953), where birth rates *decrease* and death rates *increase* at low densities instead of the opposite effects that are expected. For example, depensatory density dependence can occur when avian predators kill a fixed

number of out-migrating smolts, so that the mortality rate is higher when fewer fish are present. If predators can kill 1,000 smolts, then the mortality rate will be only 1% if 100,000 smolts migrate but will climb to 50% if only 2,000 smolts migrate. In another case, if fish are rare (e.g., mature endangered sturgeon), then they may have difficulty finding suitable mates, driving the birth rate down at low densities.

If population or individual vital rates are primarily affected by factors other than density, at least over a certain range of densities, then this is termed *density independence*. Density independence can occur over a range of intermediate densities where fish are not significantly limited by available resources. It can also be prevalent in harsh environments where survival is limited by physical constraints such as extreme flows or unsuitable temperatures rather than resources such as food or habitat. Constant "recruitment" of juvenile fish as adult spawner density increases is sometimes mistakenly referred to as density independence. However, constant recruitment can occur only if survival decreases as more young fish are produced, which is a compensatory response (Hilborn and Walters 1992).

A. Mechanisms causing density dependence

In a "closed" fish population with little immigration or emigration, such as in a lake with no inlet tributaries or outlet, compensatory density dependence that tends to regulate the population can occur because either birth rate declines as density

increases, death rate increases, or both. However, most populations are open to immigration and emigration, so an increase in emigration from habitats with high density and a consequent increase in immigration into habitats with lower density are also compensatory responses. Overall, changes in these population vital rates are the ultimate mechanisms by which density dependence occurs.

Proximate mechanisms causing birth rates to decrease and death rates to increase at high density include competition for limited resources such as food, and space for rearing, overwintering, refuge from predation, or spawning. In some cases death rates from predation, parasitism and disease also increase at higher density, and so these factors also can be proximate mechanisms causing compensatory density dependence. Investigators found evidence of compensation in nearly 80% of density-manipulation experiments involving a broad range of vertebrates and invertebrates (Harrison and Cappuccino 1995). Evidence for compensation was found in 80-90% of studies that tested for either scramble (exploitative) or contest (interference) competition, versus only about 40% in studies examining effects from predators, parasites, or diseases. In fishes as a group, competition for resources may often be the most prevalent mechanism driving density dependence.

In most situations, a combination of density dependent and density independent factors may be needed to fully explain population dynamics (Hixon et al. 2002). For example, even though birth and death rates may compensate for changing density, strong density independent factors like floods or droughts may overwhelm compensatory

responses and drive populations extinct. In addition, density dependent and density independent factors may interact. For example, harsh flooding, a density independent factor, can lower population abundance, thereby reducing competition for resources and subsequent density dependent effects (McFadden 1969, Einum 2005).

The current consensus among population ecologists is that both density dependent and density independent mechanisms operate, but that density dependence is necessary at some times and places for populations to persist (Hixon and Johnson 2009). For example, Brook and Bradshaw (2006) analyzed time series of population data for 1,198 species of plants and animals, and found that density dependence is a pervasive feature of population dynamics for most species and across taxonomic groups, including fish. Evidence for density dependence also increased with more years of data, which increased the chance that high and low densities occurred; such contrast is needed to detect density dependent changes in vital rates.

Density dependence is a necessary condition for population regulation but may not be sufficient if strong effects on some vital rates are counteracted by weak effects on others. Population regulation results only when the net effect of density on all vital rates causes compensation. Herrando-Perez et al. (2012a) found that density dependence in vital rates like fecundity and survival was common in long-term data sets for 109 bird and mammal populations but explained little variation in the strength of density dependence for the overall (ensemble) population growth rate. Hence,

models that consider the entire life cycle, such as the stock-recruitment models described below, and also include dispersal, will be required to include important tradeoffs among vital rates and assess the overall importance of density dependence on population growth rate.

B. Implications of Compensation for Fisheries Management

Compensatory density dependence helps to stabilize populations affected by anthropogenic actions that remove some portion of the population. Stabilization occurs because a decline in population abundance is offset by an increase in productivity at lower abundance that tends to restore the population to some higher equilibrium level. Compensatory density dependence is highly important to fisheries management and sustainability (Rose et al. 2001). This process underpins the concept of sustainable yield in fisheries because growth and survival are reduced at higher densities, such that removal of fish in fisheries is compensated by faster growth and higher survival. Thus, removing fish from an abundant population can increase rather than decrease total production in the next generation.

1. Recruitment Curves

Recruitment (or reproduction) curves are commonly used to describe and quantify compensation in a managed fish population and to develop biologically based spawning goals. Salmon recruitment curves typically describe the relationship between parent spawners and the expected number of progeny successfully returning to spawn. Recruitment curves may also be developed for each life stage, as shown in Figure I.1.

For species with a more complex life history, such as Chinook salmon, a "brood table" is typically maintained and used to develop the recruitment curve. A brood table shows the annual abundance of the parent spawning population (escapement from the fishery) and the number and sex of returning progeny at each age class. To obtain this information, salmon in the annual run must be enumerated by age (e.g., with scales or otoliths), then assigned to the proper parent spawning year (i.e., brood year). This fishery management activity is fundamental for developing recruitment curves, which can then be used to determine intrinsic productivity and the maximum equilibrium abundance (population carrying capacity) in existing habitat.

Two common recruitment models for salmon are the Ricker model and Beverton-Holt model (Figure II.1), which are named after the fishery scientists that developed them (Ricker 1954, Beverton and Holt 1957). In both models, salmon recruitment increases as the number of parent spawners increases (Figure II.1a) but the rate of population growth (i.e., productivity, measured as recruits per spawner) declines (Figure II.1b). The Beverton-Holt (BH) and Ricker (R) models are described by the following relationships:

Beverton-Holt: $\quad R = \dfrac{S}{\alpha + \beta S} = \dfrac{\alpha^*}{1 + \beta^* S}$

Ricker: $\qquad\quad R = S e^{\alpha - \beta S}$

where, R is the number of recruits produced (on average) from S spawners. In both models, the α parameter refers to the maximum (intrinsic) productivity at low spawner numbers (i.e., survival

undiminished by the effect of density), and the β parameter determines how large the population would be at equilibrium in the absence of fishing. Maximum sustainable return is determined by β in the BH model, but by both α and β in the Ricker model. Appendix I provides information on fitting these two models to population data.
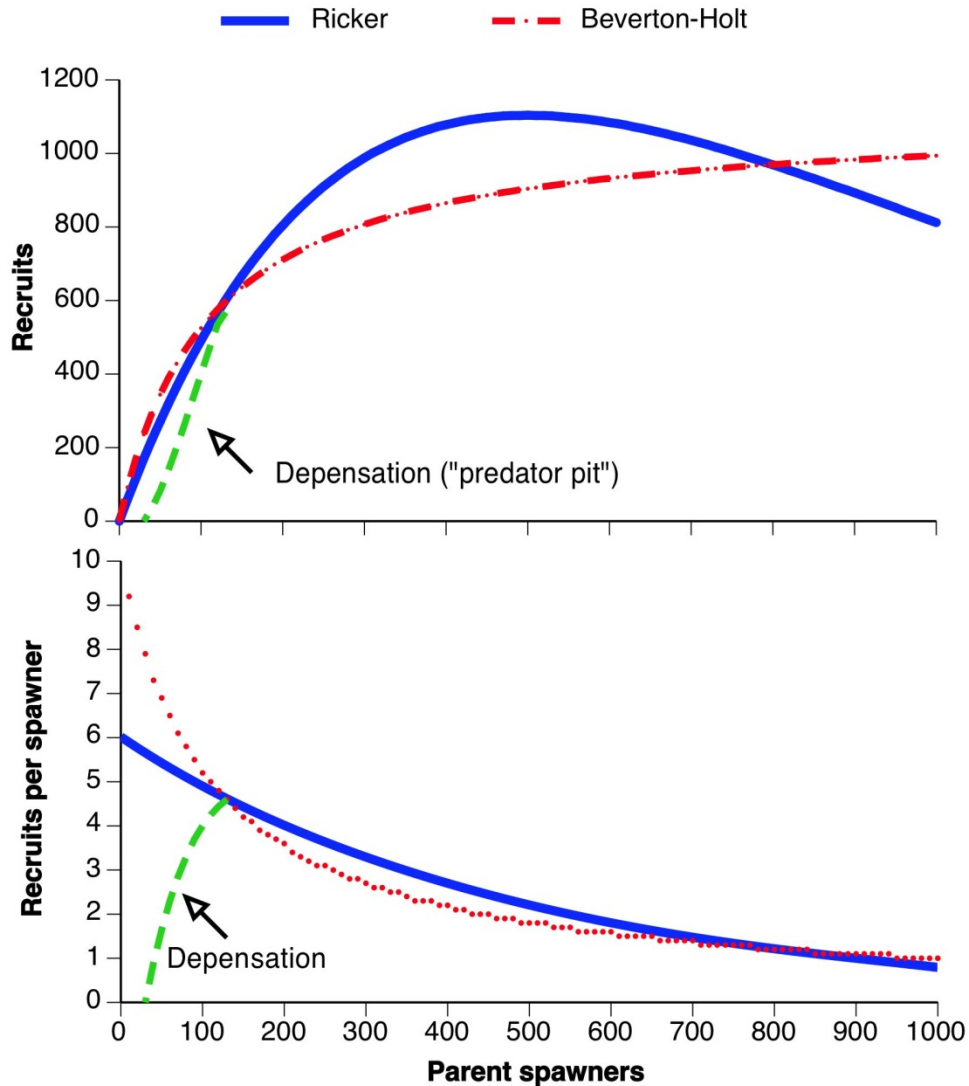
Figure II.1. Beverton-Holt and Ricker recruitment functions plotted as A) recruits versus parent spawners, and B) the corresponding productivity in recruits per spawner (R/S) versus spawners. Populations described by these models have the highest productivity (R/S) at small population size, thereby promoting population stability and resilience. Depensation, in which productivity decreases rather than increases as spawners decrease, is also shown. Depensation can inhibit stability in a declining population.

In practice, there is considerable variability in the number of recruits from a given parent spawning population due to density independent environmental factors. Errors in measuring both the spawning population and the number of recruits have important consequences for evaluating the magnitude of density dependence and for setting harvest policy (escapement goals or harvest rates). Measurement error may inhibit detection of density dependence, leading to overestimation of productivity and unsustainable harvest rates (Hilborn and Walters 1992). Potential bias caused by measurement error is reduced if the data span a wide range in spawning levels.

Stock-recruitment relationships for a salmon stock, whether with Ricker or Beverton-Holt models fit to the data, are often used by harvest managers to quantify salmon spawning levels leading to *maximum sustainable yield (MSY)*, i.e., biologically based escapement goals. We provide a graphic representation of how these goals are set using the Ricker model, which has mathematical qualities that facilitate quantification of important metrics such as MSY escapement (S_{msy}) (Hilborn and Walters 1992). The difference between the number of recruits (point A on Figure II.2) and the *"replacement line,"* where the number of recruits equals the number of parent spawners (point B), identifies the surplus production available for harvest by a fishery or for consumption by other predators while maintaining spawning abundance at B. MSY occurs at the parent spawning abundance (point C) that maximizes the difference between point A and point B. *Maximum recruitment* that might be targeted—if the policy is to maximize food and nutrient production (including spent carcasses) for the

freshwater ecosystem, riparian trees, and wildlife—occurs at a slightly greater parent spawning abundance (point D). *Intrinsic productivity*[3] (α) occurs near the origin where few parent spawners are present. *Overcompensation*, in which recruits decline with greater parent spawning abundance in the Ricker model (but not the BH model), begins immediately beyond the spawning level leading to maximum return. *Equilibrium of the population* (in the absence of fishing) occurs at the intersection of the recruitment curve and the replacement line, where the number of recruits (in this case adult salmon produced from the original spawners) equals the number of adults that produced them.

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[3] Hilborn and Walters (1992) note that when there is no density dependence, intrinsic productivity equals eggs per spawner times the survival rate through all life stages.
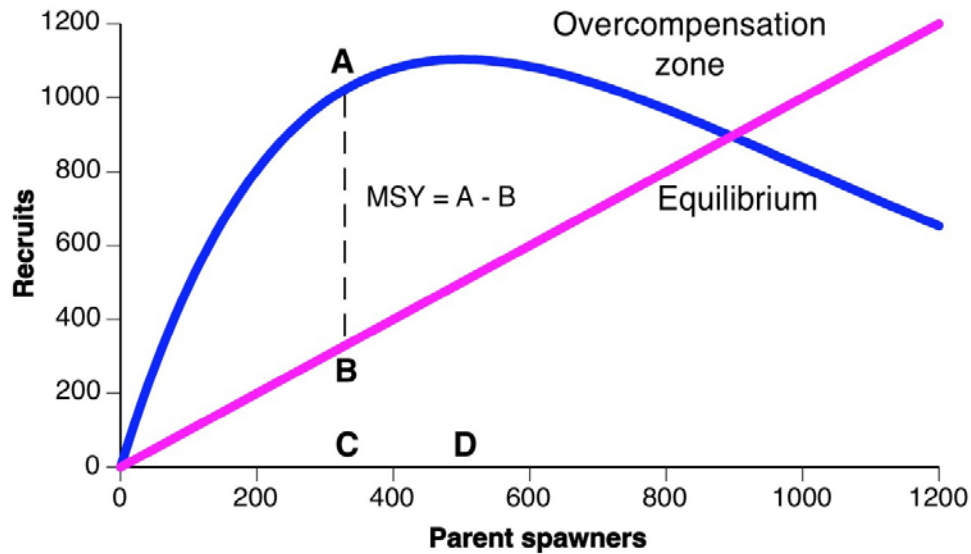
Figure II.2. Ricker recruitment curve showing the principal characteristics used to manage salmon fisheries. Maximum sustained yield (MSY) occurs at the parent spawner level (C) that maximizes the difference between adult recruits (A) and the replacement line where recruits equal parent spawners (B). Maximum adult return occurs at slightly higher spawning levels (D), but recruits may decline thereafter with greater number of spawners (overcompensation). Similar curves may be developed for recruitment of juveniles such as smolts (Figure I.1).

2. Ricker versus Beverton-Holt Recruitment

The Ricker (R) and Beverton-Holt (BH) models have important differences at high population abundances. The BH curve reaches a plateau at high spawning abundances such that recruits do not markedly increase or decline with greater abundance of spawners (i.e., the carrying capacity has been reached). In contrast, the Ricker curve is dome-shaped and recruits decline as the number of parent spawners increase beyond the level producing maximum return.

This difference between the two models at high spawner abundances has important implications for managing salmon populations, especially when the

populations are being supplemented with hatchery fish. If the dynamics of a population follows the BH curve, then excessive spawning density has no adverse consequences other than lost harvest opportunities during the year of return. Furthermore, it might be beneficial to err on the side of more abundance if there is uncertainty in the level of spawning escapement that leads to maximum return or harvest or if there is a desire to provide ecosystem benefits. However, excessive spawning density in a population best described by a Ricker curve will reduce recruitment, on average, in the next generation, and will also result in lost harvest opportunity in the year of the large return. A natural-origin salmon population would eventually recover from

overcompensation, as defined by the Ricker recruitment curve. However, programs working with supplemented populations should be careful not to reach the overcompensation zone because future abundances and productivity of the natural spawning stock would remain depressed until the total population was managed within the capacity of the watershed.

Overcompensation is not frequently observed in natural-origin salmon populations because fisheries typically prevent large escapements of spawning salmon (Walters et al. 2004). Furthermore, other factors not associated with density cause considerable annual variability in the recruitment of progeny from the parent population, so it is often difficult to judge whether the population exhibits overcompensation at high spawning levels or simply reaches a plateau in recruits. Even so, significant overcompensation has been observed in some populations. In Bristol Bay Alaska, restricted fishing to protect the weak Kvichak sockeye stock in 2004 and 2005 led to a ~10-fold increase in sockeye spawning escapement in the adjacent Alagnak River (4.2 to 5.4 million spawners), which resulted in a 23-44% decrease in potential egg deposition and 25% decline in adult progeny relative to the previous 10 years (Quinn et al. 2007; Ruggerone unpublished analysis of adult returns). In Southeast Alaska, large spawning escapements of natural-origin pink salmon have periodically caused significant pre-spawning mortality of adult pink, chum, and coho salmon, and juvenile coho salmon (Figure II.3; Shaul et al. 2014). In western Kamchatka Russia, a spawning escapement of 110 million pink salmon in 1983 led to the collapse of the odd-year line of pink salmon (Ruggerone and Nielsen 2009).

Walters et al. (2004) concluded that there was no evidence that high spawning escapements of sockeye salmon in the Fraser River watershed would cause a population collapse, but they did provide evidence of overcompensation.

Overcompensation is most likely to be observed in large populations of pink, sockeye, and chum salmon that aggregate in spawning habitats that are spatially limited relative to rearing habitats (lakes or the ocean; Quinn 2005). Less abundant species—such as Chinook, coho and steelhead—typically exhibit much lower spawning densities. Competition within less abundant species is more likely during juvenile residence in freshwater rather than on the spawning grounds (Chapman 1966). Even so, Chapman (1986) reported overcompensation when examining recruitment of Chinook salmon in the Columbia Basin, but the life stage of this effect was not identified. Most recruitment curves developed for Chinook populations in North America, including the Columbia, have relied upon the Ricker model that incorporates overcompensation rather than Beverton-Holt model (Chinook Technical Committee 1999).

The Ricker and Beverton-Holt models also have important differences at low spawning levels. The BH model tends to estimate a higher intrinsic productivity (α) than the Ricker model, leading to higher estimates of optimal harvest rate, which depends solely on the productivity parameter (Hilborn and Walters 1992). Thus, some fishery scientists have recommended the use of the Ricker model when setting conservative harvest policies even if the dome-shaped curve is not apparent (Walters and Martell 2004). Harvest policies may also consider whether

or not overcompensation is likely to be present in the population.

The theoretical derivations of the Ricker and Beverton-Holt models are compared in Appendix 1 and described in greater detail elsewhere (e.g., Hilborn and Walters 1992). These derivations make very simplistic assumptions about the base causes of density dependence that are unlikely to be true in complex ecosystems. Walters and Korman (1999) have shown that a wide range of different behavioral ecologies at very fine scales can give rise to a BH relationship at many different scales. Consequently, the BH or Ricker curves should be considered as empirical relationships that provide a convenient summary of density dependence.

Figure II.3. Prespawning mortality of pink salmon in a Southeast Alaska stream following the record harvest in 2013 (95 million pink salmon). Dead juvenile coho are also shown. Mortality was caused by high pink salmon density and the resulting low oxygen level, which was exacerbated by low river flow and high water temperature (Shaul et al. 2014). Massive prespawning mortality can cause overcompensation as described by the Ricker curve. Photos provided by A. Hemenway and L. Shaul, Alaska Dept. Fish and Game, Juneau.

3. Mechanisms Leading to Overcompensation

Several mechanisms may lead to declining recruitment at high parent stock density, and produce the overcompensation portion of the Ricker curve. Cannibalism, disease, and physical disturbance by later-spawning salmon are often cited as mechanisms. Cannibalism is not common in semelparous salmon, but iteroparous trout may cannibalize their eggs and young, potentially leading to overcompensation (Ricker 1954). Disease associated with high spawning densities and redd

superimposition (later-spawning salmon digging up eggs laid by earlier spawners) are likely sources of mortality that can impact a large percentage of the progeny. Likewise numerous eggs in the gravel or spawners in the river may lead to high consumption of oxygen and insufficient oxygen for all eggs or fish (Heard 1978, Quinn et al. 2007, Shaul et al. 2014). Most mechanisms leading to overcompensation involve the parent spawning population. However, it is conceivable that depletion of prey resources by high abundances of juvenile salmon could cause overcompensation if a large fraction of the population was unable to reach some size threshold necessary to survive over winter (Edmundson et al. 2003).

4. Brood Interaction

Recruitment curves involve the relationship between recruits and parent abundance, but interactions between cohorts are often not considered among Pacific salmonids because they are anadromous and semelparous (except steelhead). Nevertheless, there is some evidence of "brood interaction" also known as "delayed density dependence." Brood interaction can be adverse. For example, a large year-class of juvenile sockeye salmon may deplete zooplankton prey so severely that it takes several years to recover, during which time the growth and survival of subsequent salmon broods will be adversely affected; or conversely, the large year-class may generate a lingering predator population. Alternatively, brood interaction might be beneficial, resulting from a long-lasting addition of salmon-derived nutrients produced by a large number of parent spawners.

Evidence from Alaskan sockeye populations suggests overgrazing of zooplankton prey by a large brood can adversely affect growth and survival of subsequent broods (Eggers and Rogers 1987, Ruggerone and Rogers 2003, Edmundson et al. 2003), whereas Myers et al. (1997) concluded that this interaction was mild for a number of sockeye populations. Detection of brood interaction is dependent on periodic high abundances of salmon. We are not aware of brood interaction involving other species of salmon, although it has been implicated in the maintenance of the odd/even-year lines of pink salmon, and it has been observed in resident trout (White and Hunt 1969, Latterell et al. 1998).

5. Climate and Recruitment Stationarity

Climate shifts (and other habitat-related shifts) can cause a significant change in the intrinsic productivity of salmon populations spanning a broad area and it is important to account for major environmental disturbances or shifts when evaluating stock-recruitment relationships (Buhle et al. 2009, Dorner et al. 2013). An example of Ricker recruitment curves fit to the same sockeye population during two different periods of production reveals how density dependent relationships can change (Figure II.4). Standardized productivity since 1922 (measured here as the residual from the long-term recruitment relationship) was typically high during warm phases of the Pacific Decadal Oscillation (PDO)[4] but low during the mid-1900s when the PDO was typically negative, leading to the development of two distinct recruitment

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[4] http://jisao.washington.edu/pdo/

relationships. The data suggest a change in both intrinsic productivity and capacity of this sockeye population, likely in response to large-scale climate factors, which in turn influenced levels of sustainable harvest.

These data also show how annual variability in recruitment tends to obscure the effect of density, yet despite the variability, overcompensation is evident at high spawner abundance (Figure II.4).
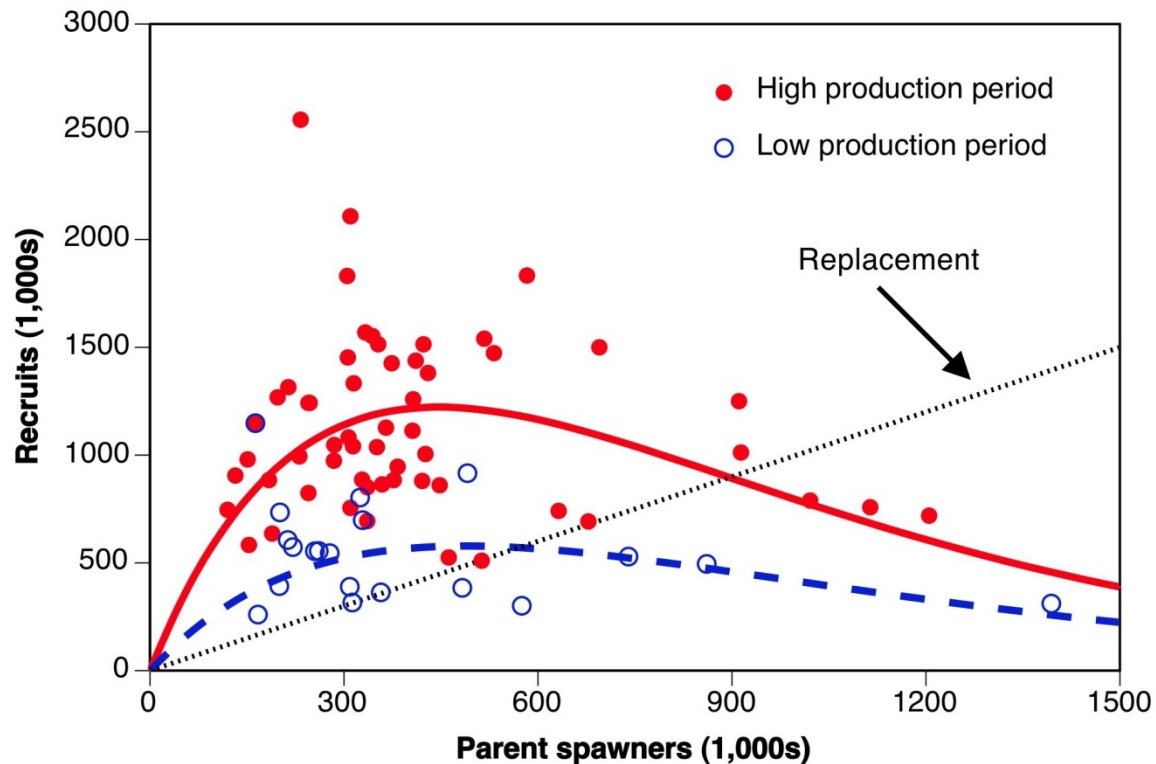
Figure II.4. An example of two Ricker recruitment relationships characterizing a single sockeye salmon population (Chignik Lake, Alaska) in two different periods of productivity during the past 74 years. Long periods of similar productivity were determined by examining the residuals from the recruitment curve spanning the entire period (not shown), brood years 1922-1996. Two extended periods of high production and one extended period of low production generally corresponded with shifts in the Pacific Decadal Oscillation. The recruitment relationships suggest that both intrinsic productivity and capacity changed in response to climate shifts. Values based on age-specific catch (fish scale evaluations) and spawning escapement (weir counts). Source: Ruggerone (2003).

C. Implications of Depensation

Depensatory density dependence, in which the percentage of a population lost to mortality increases as population size decreases, is less commonly observed in fish populations than compensatory density dependence (Myers et al. 1995, Liermann and Hilborn 2001, Hilborn et al. 2014). There are relatively few observations of

depensation because populations typically do not decline to unusually low levels and because environmental and demographic stochasticity inhibit detection of underlying population dynamics over time (Liermann and Hilborn 2001). Predators often cause depensatory mortality at some life stages, but this effect tends to be overwhelmed by compensatory processes during other life stages. Nevertheless, Liermann and Hilborn (2001) conclude that depensatory mortality can have a profound influence on fish populations and should be considered in fisheries assessments.

Depensatory mortality is destabilizing and can lead to extinction when low population size is coupled with high environmental variability (Peterman 1977). Declining populations such as endangered salmonids are especially vulnerable to depensatory mortality because it may further accelerate population decline and inhibit recovery. Conversely, a recovering population may grow more rapidly when subject to depensatory versus compensatory mortality, at least until compensation becomes stronger at higher densities.

Among salmon, depensatory mortality is sometimes caused by predators (Liermann and Hilborn 2001), including fishermen (Myers et al. 1995). In Bristol Bay, Alaska, strong depensatory mortality was observed in the mixed-stock fishery in which a relatively high percentage of the Kvichak sockeye run was harvested in mixed-stock fisheries during years when the run was weak (Eggers and Rogers 1987). Conceivably, depleted salmon populations may experience depensatory mortality in a mixed-stock fishery that targets abundant stocks while also removing a high proportion of the depleted stock.

Depensatory fishing mortality was proposed as an important contributor to the cyclic nature of many sockeye populations in the Fraser River (Walters and Staley 1987). However, subsequent research revealed that much of the apparent depensation was measurement error associated with the bias in overestimating catches of minor stocks and supports the original hypothesis that depensatory predation by rainbow trout was the crucial factor (Cass and Wood 1994, Ricker 1997). Additionally, inbreeding depression and loss of life history diversity at very low population size can reduce intrinsic productivity, thereby creating a depensatory effect that may erode and eventually overwhelm normal compensatory potential (McElhany et al. 2000).

III. Pre-development Capacity of the Columbia River Basin

A fundamental question when attempting to manage and restore the Basin's salmon runs is *"How many salmon and steelhead can the Basin support now and in the future, assuming restoration actions are effective?"* Contemporary abundances of adult salmonids returning to the Columbia Basin (hatchery plus natural fish) are known (Figure III.1), and there is information on the current capacity and productivity of salmon and steelhead in some watersheds (e.g., Zabel and Cooney 2013; and Chapter V). Current capacity for producing natural salmon has been greatly reduced by dams, other migration barriers, and broadly degraded habitat (see Chapter IV). In general, expectations for restored salmon populations stem, in part, from pre-development estimates of salmon abundance and capacity (NPPC 1986).

This chapter reviews and refines estimates of anadromous salmon and steelhead abundance during the pre-development period (prior to 1850). Current and widely quoted estimates of pre-development abundance of salmonids are only rough approximations based on several major assumptions. Approaches previously used to approximate pre-development abundances of salmon include 1) expanded commercial landings, 2) daily salmon consumption by the Native American population prior to 1800, 3) consideration of ocean harvests of Chinook and coho salmon, and 4) habitat-based estimates of potential salmon production. Most pre-development estimates of abundance reportedly represent the period prior to 1850 when there was relatively little habitat degradation (NPPC 1986), even though the harvest-based values reflect the period of

large catch during 1880 to 1928. In this Chapter, as a means to initially evaluate the question posed in the Introduction, "*Why is density dependence more evident than expected at low abundances?*," we approximate and compare historical versus contemporary estimates of adult salmon abundance, extent of accessible river habitat, and total smolt abundance.

A. Harvest-based Estimates of Abundance

Most pre-development estimates are based on early records of commercial harvests, which began around 1861 (Thompson 1951) and expanded rapidly thereafter (Figure III.1), and estimates of tribal consumption per capita (Hewes 1947). Commercial catch evaluation of the early developing fishery is complicated because the fishery primarily targeted highly prized and initially abundant summer Chinook in June and July. Sockeye salmon would have been captured with the summer Chinook, but sockeye catch records prior to 1889 are incomplete. The early fishery (circa 1877) was initially closed by regulation during March, April, and August, the months when many of the spring and fall Chinook returned (Wendler 1966). Fisheries for fall and spring Chinook and other species of salmon developed following the overharvest and decline of summer Chinook (Thompson 1951). Spawning escapement estimates of upriver populations became available in 1938 with the construction of Bonneville Dam, which facilitated estimates of minimum abundances entering the Basin thereafter (Figure III.1). Prior to this, total abundance (i.e., the sum of fish caught in the fishery

plus those that escaped to spawn) was typically estimated from commercial catch and assumed harvest rates (i.e., the proportion of the run entering the Columbia River that was taken in the fishery).
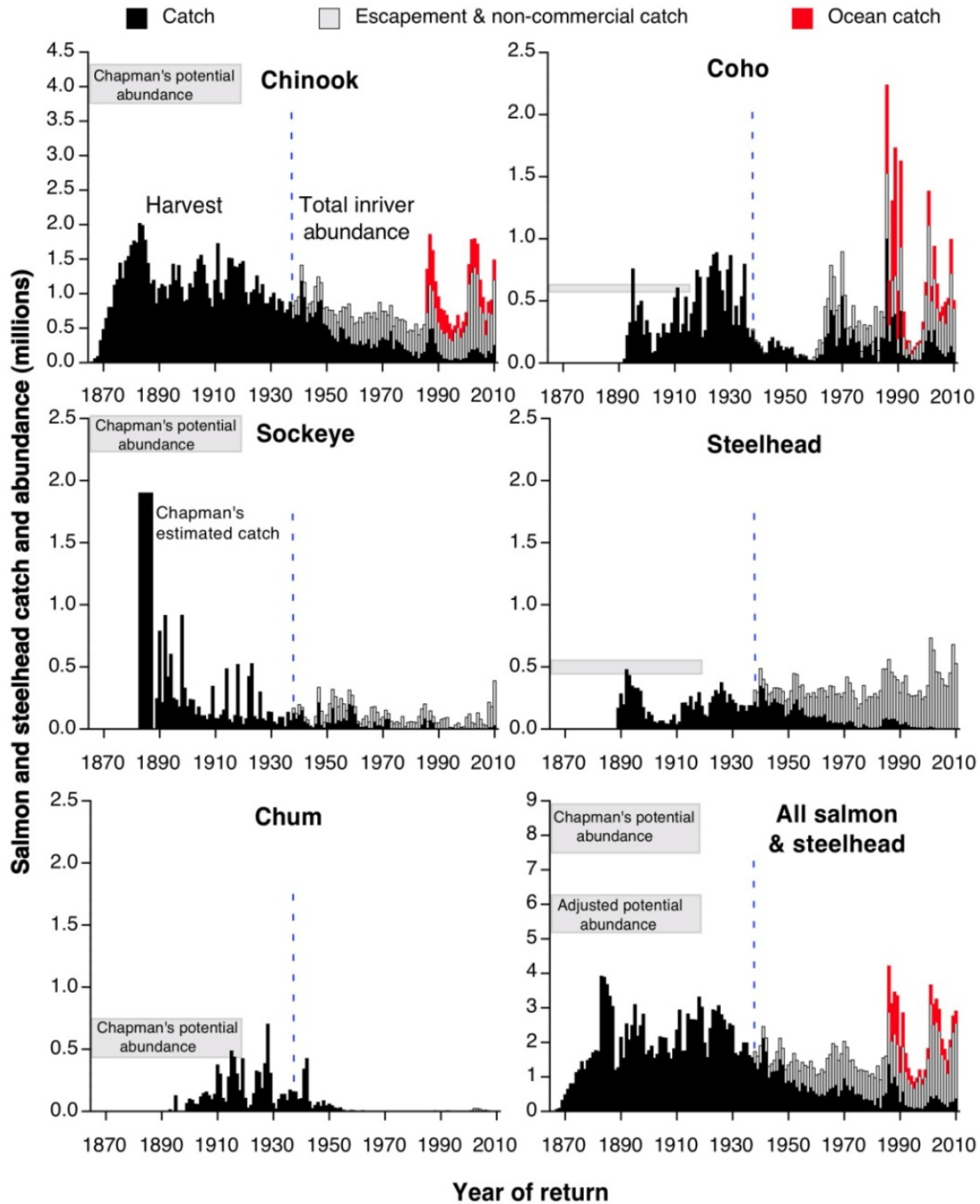
Figure III.1. Reported commercial catch of salmon and steelhead from 1866 to 1937 (no escapement values) and total abundance (catch and escapement) of each species entering the

Columbia River since 1938. Chapman's (1986) estimated ranges for potential abundances during the pre-development period are shown as gray boxes in each panel. The ISAB's adjusted range for all-species potential abundance is also shown (see text). Escapement was not estimated prior to 1938 (vertical dash line). Values prior to 1938 were based on landed weight and Chapman's (1986) average fish size (Table III.1). Values include both hatchery and natural-origin fish, which are not separately estimated in most years; see Figure III.2 for releases of juvenile hatchery salmon since 1877. Values are unavailable for some species such as sockeye prior to 1890, but Chapman's (1986) extrapolation of peak sockeye catch in fish wheels during 1883-1887 is shown. Ocean harvests of Columbia-bound Chinook and coho include fisheries from Alaska to California, based on coded-wire-tag recoveries from 1986-2010. Significant ocean harvests of Chinook and coho have occurred from about 1910 to the present. In-river abundances beginning in 1938 are considered minimum estimates because some spawning escapements below Bonneville Dam and some sport harvests were not available. Primary sources: Chapman (1986), WDFW/ODFW (2002), and A. Hagen-Breaux, WDFW, personal communication regarding ocean harvests.
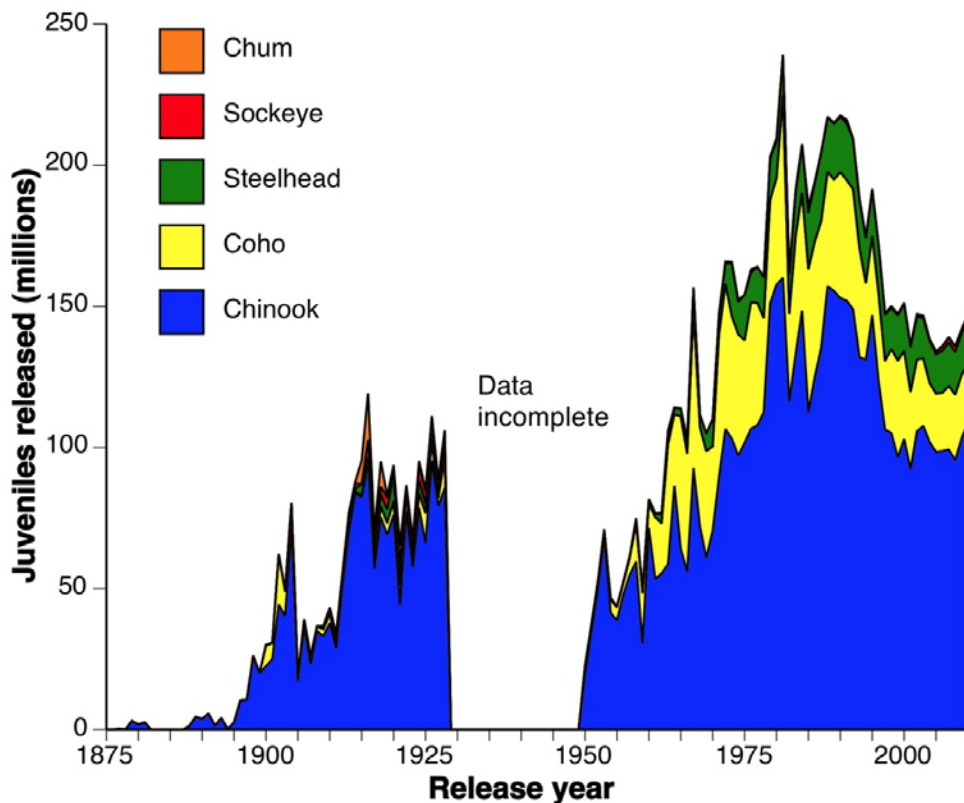
Figure III.2. Annual releases of hatchery salmon and steelhead into the Columbia River Basin from 1877 to 2010. Values include both subyearling and yearling releases, whose proportions vary among species and from year to year within each species. Fish quality improved over time as hatchery technology improved, especially after 1950. Data sources: Cobb 1931, Mahnken et al. 1998, Fish Passage Center (http://www.fpc.org/).

Chapman (1986) provides a detailed analysis based on fishery science concepts and approximates "potential" salmon abundance in the Basin prior to significant development. Chapman (1986) recognized that salmon abundances fluctuated widely over time, and his potential salmon abundance estimates, which were based on peak catches, were stated to overestimate average abundances. His approach was to select five-year periods that yielded the largest commercial harvest for each species, divide by 5 to obtain the average annual catch during the peak five-year period (hereafter called "*peak five-year average catch*") and then assume two harvest rates to estimate "probable" and "high" values of potential abundance (Table III.1). The peak five-year average catches for individual species summed to a total of 6.3 million salmon and steelhead per year. It is important to note, however, that the years selected varied among species—a fact that was not considered when estimating total pre-development abundance for all species combined. In contrast, the peak five-year average for the reported catch of all species during the same five-year period (1915-1919) was only 2.9 million fish per year (Figure III.1). This value is much lower than the sum of peak five-year average catches for individual species from various five-year periods (6.3 million). Chapman (1986) estimated the peak five-year average catch of sockeye during 1883-1887 from fish wheel catch data, and that value greatly exceeded any subsequent catch. If the peak five-year average catch of sockeye is combined with the peak five-year average catch of Chinook during 1883-1887, then the peak five-year average catch of both species combined increases to 3.6 million fish. Catches of other species were not reported during 1883-1887. If we assume

that these unreported catches were similar to those reported in subsequent years and add in the mean annual catch of the other salmon species, then the peak five-year average catch of all species increases to 4.4 million[5], still only 70% of the 6.3 million value obtained by summing peak five-year average catches for individual species in various five-year periods. The key point here is that the five-year period of peak catch varies among species, therefore the sum of the peak five-year average catches for individual species derived from different five-year periods greatly overestimates the average catch of all salmon that can be expected in any given five-year period.

Chapman (1986) argued that the large harvest of fall Chinook salmon during 1915-1919 (the largest harvest to date) was not significantly influenced by habitat degradation because fall Chinook typically spawn in large rivers that had not yet been degraded as had some tributaries. However, we note that Swan Falls Dam was built in the middle Snake River in 1901 with poorly performing fish passage facilities, leading to an estimated loss of 253 km of Chinook spawning and rearing habitat

[5] Peak five-year average catch of all species occurred during 1883-1887 due to the large Chinook catch and Chapman's (1986) approximation of sockeye catch (1.9 million per year). Harvests of other species, if any, were not reported at this time. To account for these other species, we included the average reported catch during the most recent five-year period of each species with the 1883-1887 reported catch. This adjustment increased average catch from 3 million to 4.4 million fish. After this early period, the maximum one-year catch was only 3.1 million (1918) and the peak five-year average catch was only 2.7 million fish (1915-1919) (see Figure III.1). These harvests corresponded with World War I when demand was high.

below Shoshone Falls (Dauble et al. 2003, Schuck 2014). Harvests prior to the mid-1920s were largely driven by market conditions in addition to abundance (C. Smith, Oregon State University, personal communication). For example, the high catch of fall Chinook and chum during 1915-1919 reflected high government market demand for salmon during World War I.

Table III.1. Estimates of salmon and steelhead peak five-year average catch and total abundance prior to development in the Basin (millions of fish). Chapman (1986) considered his values to represent potential annual run size whereas NPPC (1986) considered its estimates to represent average annual run size. Years of peak five-year or maximum one-year catch are shown. Weights shown are those used by Chapman (1986), who obtained estimates of early fish size. Chapman (1986) reportedly used a coho weight of 3.18 kg but his coho values indicate he actually used 4 kg. NPPC (1986) fish weights were typically smaller, yielding greater fish abundances: summer Chinook 7.4 kg, sockeye 1.6 kg, coho 4 kg, steelhead 3.3 kg, chum 5.5 kg. Sources: Chapman (1986), PFMC (1979), NPPC (1986).

Species	Chapman[1]			NPPC[2]			PFMC[3]
	Peak 5-yr catch	Years	Peak 5-yr run	Max 1-yr catch	Year	Max run	(habitat approach)
Chinook salmon	3.20		3.75-4.34	4.60		5.4-9.2	3.44
Spring (10.45 kg)	0.40	1890-1895	0.5-0.59	1.15	--	1.35-2.3	--
Summer (10.45 kg)	1.70	1881-1885	2.0-2.5	2.30	1883	2.7-4.6	--
Fall (8.24 kg)	1.10	1915-1919	1.25-1.25	1.15	--	1.3-2.3	--
Sockeye (2.25 kg)	1.92	1883-1887	2.25-2.62	1.3	1898	1.53-2.6	0.65
Coho (4.05 kg)	0.48	1894-1898	0.56-0.62	0.89	1925	1.05-1.78	1.20
Chum (5.5 kg)	0.36	1915-1919	0.45-0.75	0.70	1928	0.82-1.04	0.95
Steelhead (4.68 kg)	0.38	1892-1896	0.45-0.55	0.67	1892	0.79-1.35	2.04
Total	6.33	Various	7.5-8.9	8.2	Various	9.6-16.3	8.28

1 Run size range based on assumed optimal (variable) and probable (80-88%) harvest rates.
2 Maximum catch of spring and fall run Chinook assumed to be 50% of summer run.
   Run size range based on assumed harvest rates 50-85%.
3 Steelhead estimated by NPPC (1986). Steelhead abundance = 1.7x coho abundance.

Chapman's (1986) estimate of total potential salmon abundance (harvest plus spawning escapement), based on peak five-year average catches of each species, ranged from 7.5 million to 8.9 million fish (Table III.1). The upper-end abundance estimate was calculated by assuming a well-managed fishery with "optimal" harvest rates for each species, even though it was widely recognized that the Columbia River fishery was not well-managed and harvest rates were much higher than optimum (Thompson 1951). The lower value (i.e., 7.5 million fish) was considered more probable by Chapman (1986) because it was based on higher harvest rates that contributed to the observed decline in abundance over time. The most abundant species, based on the more probable harvest rates, were Chinook (3.75 million) and sockeye (2.25 million), followed by coho, chum, and steelhead (approximately 0.5 million each).

These abundance values were based on the landed weight of each species (derived from records of canned, frozen, and mild-cured salmon, adjusted for percentage of the fish carcass utilized) and average weight of each species in the late 1800s (Craig and Hacker 1940).

Non-commercial harvests were not included in these estimates. Chapman (1986) thought non-commercial harvests were relatively small compared with commercial harvests, in part because the Native American population had been decimated by disease. Accounting for an 83% decline in the Native American population (from about 50,000 to 8,300 people), Chapman (1986) estimated 200,000 to 450,000 additional fish would have been harvested and could be added to the aforementioned estimates of abundance. Chapman (1986) noted that European settlers would have also taken some salmon but estimated these harvests would have been much less than about 10% of the reported commercial catch.

Chapman (1986) considered density dependent effects in his analysis. He reported that salmon and steelhead recruitment in the Columbia Basin exhibited overcompensation at high spawner abundances, such that relatively large spawning escapements would produce less recruitment (as shown in the Ricker recruitment curve in Figure II.2). Accordingly, he speculated that reduced fishing by Native Americans during 1825 to 1850, a period of exceptionally rapid decline in the Native American population, would have led to overcompensation and a decline in salmon abundance. Chapman (1986) also suggested that salmon

abundance initially increased as the early years of commercial fishing around 1861 reduced spawner escapements to the highly productive range, then decreased as fishing expanded and began to exceed optimum harvest rates. This observation differs from that of Craig and Hacker (1940) and Hewes (1973), who simply assumed salmon abundance would have increased following reduced fishing pressure by Native Americans, then decreased with intense commercial fishing (i.e., would have been represented by the ascending limb of a recruitment curve).

NPPC (1986) developed estimates of *"average annual salmon runs before development of the basin."* The NPPC estimate was based on the one-year maximum reported catch of each species during 1883 to 1928 and *assumed* harvest rates (Table III.1). Maximum catch of summer Chinook occurred in 1883 (2.3 million fish). Maximum catch of fall and spring Chinook were each *assumed* to be 1.15 million fish or 50% of the maximum summer Chinook catch. Lower and upper bounds on harvest rates were *assumed* to be 50% and 85% for all species, resulting in an estimated average annual run size for all species ranging from 10 to 16 million (Table III.1). NPPC (1986) based its salmon abundances on Beiningen's (1976) average fish weights, which were derived from more contemporary, smaller fish than those used by Chapman. The use of smaller fish leads to greater abundances when back-calculated from pounds of fish processed (Table III.1). The NPPC (1986) range for "average annual run size" (10 to 16 million fish) was considerably larger than the "potential run size" estimated by Chapman (1986) (7.5 to 8.9 million fish).

B. Ocean Catch of Columbia Basin Salmon

Ocean troll fisheries in Alaska, British Columbia and the lower west coast of the United States intercept Chinook (primarily fall runs) destined for the Columbia River. These harvests should be considered in total abundance estimates of Columbia River salmon. Between 12.5% and 60% of adult Chinook salmon tagged and released off British Columbia during 1929 and 1930 were subsequently recovered in the Columbia River (Craig and Hacker 1940), providing some of the first data showing that salmon taken in northern areas had originated from many regions, including the Columbia Basin. Columbia River coho are also harvested in British Columbia and the lower west coast but few are taken in Southeast Alaska. Other salmon gear types harvest south-bound salmon, but to a lesser extent.

Ocean harvests in Alaska and British Columbia were small before 1910 and would have had negligible effect on the pre-development estimates of salmon abundance (Shepard et al. 1985). After 1910, troll fisheries in British Columbia and Southeast Alaska increased steadily, with annual harvests of approximately 160,000 Chinook and 150,000 coho salmon between 1910 and 1919 that were reportedly destined for the lower United States (based on tagging experiments), including the Columbia River (Shepard et al. 1985). By 1970-1979, annual harvests of salmon destined for the lower states had increased to approximately 825,000 Chinook and one million coho salmon (Shepard et al. 1985; also see Figure III.1).

The troll fishery off Oregon and Washington, including the Columbia River District, developed rapidly after 1912 (Craig and Hacker 1940) and may have contributed to a slight positive bias in pre-development estimates of abundance in the Columbia Basin. Harvests in the Columbia River District (up to about 25 miles offshore and 50 miles to the north and south) were landed in the Columbia River and counted in Columbia River statistics even though some of the captured salmon were destined for other coastal areas. Average annual catch during 1926-1934 was approximately 42,000 Chinook and 254,000 coho; catches were presumably higher in 1919 when fishing effort was greater but troll-specific catch was not reported. Trolling for coho began after the peak catch estimates reported by Chapman (1894-1898), but troll fisheries did influence the maximum catch of coho in 1925 used by NPPC (1986) (Table III.1). Chapman (1986) used 1915-1919 as the peak period for fall Chinook harvests. This period likely included relatively small numbers of non-Columbia River Chinook taken in the troll fishery, which were offset to some extent by Columbia River Chinook taken in troll fisheries beyond the Columbia District.

C. Tribal Harvests Prior to 1800

Several estimates of salmon harvests by Native American tribes prior to the 1800s have been developed based on a variety of assumptions, including population size (~50,000 to 62,000 people), per capita utilization rates (up to 1.8 lbs of salmon per day), and constant salmon availability for harvest each year regardless of how the environment affected salmon abundance. Estimates of the number of salmon harvested range from 1.9-2.4 million fish

(Craig and Hacker 1940) to 2.3-3.0 million fish (Hewes 1947, 1973) to 4.5-5.6 million fish (NPPC 1986, Schalk 1986), based on the weight of fish harvested and NPPC (1986) estimates of average fish weight.

The tribal harvest estimates tend to be lower than the five-year peak average annual commercial harvest value (6.3 million) reported by Chapman (1986) and the maximum one-year commercial harvest value (8.2 million) reported by NPPC (1986), both of which likely led to smaller runs via over-exploitation. This might suggest that Native Americans did not over-exploit the salmon runs (Butler and Campbell 2004, Campbell and Butler 2010). However, periodic overexploitation of salmon runs would be possible if large numbers of fish continued to be harvested during years when relatively few fish returned (i.e., if Native Americans did not switch to other food sources when salmon were scarce; Walker 1967, Suttles 1968). Tribes may have exerted some depensatory mortality when salmon abundances were low, but this adverse effect was likely moderated by the difficulty in catching salmon when they were less abundant and by other opportunities to meet dietary needs.

D. Habitat-based Estimates of Abundance

The Pacific Fishery Management Council (PFMC 1979) estimated pre-development abundance of salmon based on *assumed* salmon production from habitat area occupied by each species. These estimates did not explicitly consider density dependence; rather, they apparently assumed maximum salmon production from available habitat. The goal of the Pacific Fishery Management Council (PFMC)

analysis, which included all of the west coast United States, was to compare historical versus current habitat as a means to evaluate the potential from improving natural salmon production in freshwater habitat versus increasing production with hatchery programs. No distinction was made between spawning and rearing habitat. Regarding spawning escapement in the 1970s, PFMC (1979) concluded that most salmon populations in the Columbia Basin were below capacity, such that considerably greater adult returns could be achieved by increasing spawning escapement.

PFMC (1979) estimated 3.4 million Chinook, 1.2 million coho, 650,000 sockeye, and 950,000 chum salmon in the pre-developed Columbia Basin (Table III.1). PFMC (1979) did not estimate steelhead abundance but NPPC (1986) assumed steelhead abundance was 1.7 times coho abundance, or 2 million steelhead. Total abundance based on the habitat approach was 8.3 million salmon and steelhead (Table III.1).

E. How Accurate Are the Abundance Estimates?

Several factors suggest that the salmon and steelhead abundance estimates may be too high if they are meant to represent average annual estimates. Chapman (1986) noted that his estimates of 7.5 to 8.9 million, which were the lowest of all abundance estimates, represented *potential,* not average abundance. In other words, Chapman (1986) considered his values to represent maximum abundance or the capacity of the Basin to produce salmon. This seems to be a reasonable conclusion, although it is worth noting that Chapman's (1986) total abundance values (all species

combined) assumed an unusual situation whereby the peak catch of each species occurred in the same five-year period. In contrast, the NPPC (1986) estimates of 10-16 million salmon were reported to represent average annual abundances prior to development even though 1) maximum observed one-year catch for each species was assumed to occur during the same year, 2) abundances that support maximum catch cannot be expected to occur every year given environmental variability, 3) market conditions strongly influenced the early harvest rates, and 4) the *assumed* lower bound for harvest rate (50%) was probably too low (leading to excessively high upper limits on abundance) based on observations of over-harvesting of the salmon runs (e.g., Thompson 1951 and others). Habitat-based estimates of abundance (pre-dam) were about 75% to 87% of Chapman's (1986) salmon estimates, but four times higher for steelhead (Table III.1). The habitat-based estimate of 2 million steelhead is larger than the entire annual average abundance of steelhead (hatchery plus natural-origin) estimated to have returned to North America during the years 1970-1986 (i.e., 1.6 million steelhead; Light 1987).

Both Chapman (1986) and NPPC (1986) assumed that all Chinook harvested in 1881-1885 were summer Chinook, which were highly prized fish. However, Wendler (1966) reported that commercial fishing was open during April, May, June, and July beginning in 1879. Fishing during September was open in Washington beginning in 1881. These regulations indicate some Chinook harvested from 1881 to 1885 were spring and fall Chinook salmon, leading to overly high estimates of summer Chinook abundance by both

Chapman (1986) and NPPC (1986). The high summer Chinook estimate affects the NPPC estimates of spring and fall Chinook, which were each assumed to be 50% of the maximum one-year summer Chinook abundance in 1883 (Table III.1).

Peak catches were probably sometimes higher than reported. Some fish were not sold and processed when cannery capacity was exceeded (Cobb 1917, www.nwcouncil.org/history/CommercialFishing), or they were transported to other coastal areas for processing. Some canneries may not have reported the fish they processed. Catch by Native Americans and non-commercial fishermen were not included in the commercial catch estimates. As noted above, some Chinook and coho were harvested in ocean fisheries extending north to Southeast Alaska, but harvests during this early period likely had a relatively small effect on the peak harvest estimates.

Environmental conditions likely influenced abundances of salmon from which the pre-development estimates were based. The abundance estimates were based on harvests prior to most mainstem dam construction, but habitat had already been degraded during this early period in some areas due to mining, agriculture, logging and other human activities (see Figure IV.1 for timeline). In contrast, climate evidence suggests conditions may have been more favorable for salmon during the late 1800s and early 1900s. Columbia River salmon abundance tends to be higher during cool phases of the Pacific Decadal Oscillation (PDO; Jacobsen et al. 2012). Cool phases of the PDO prevailed during 1890-1924 and again during 1947-1976, whereas the warm phase dominated from 1925-1946 and from

1977 through the late 1990s (Mantua et al. 1997; http://jisao.washington.edu/pdo/; Jacobsen et al. 2012). This suggests that some pre-development abundance estimates pertain to the cool phase of the PDO when climate conditions were likely more favorable for Columbia River salmonids than they are now.

Production of hatchery salmon in the Columbia Basin began in 1877, but hatcheries likely contributed relatively little to the pre-development estimates of abundance because the quality of fish released then was much lower than it is today. Chinook have been the principal species released from hatcheries in the Basin. In 1900, nearly 30 million Chinook, 7 million coho, and 0.3 million steelhead were released from hatcheries (Figure III.2). At this time, nearly all releases were fry; production of yearling Chinook increased in 1918 and thereafter.

Chapman (1986) compared his estimates of potential Chinook and coho abundances with recent abundances produced in the Fraser River, as a means to evaluate his abundance estimates against a large nearby watershed with relatively few dams. He found the comparison provided some grounds for confidence that his estimates for predevelopment runs were not extreme.

The composition of salmon species produced in the Columbia Basin has a large influence on the total abundance of adult salmonids that it can produce because some species have a higher potential maximum abundance than other species. Pink, chum, and sockeye salmon are much more abundant than Chinook, coho, and steelhead across the North Pacific (Light 1987, Ruggerone et al 2010, Irvine et al.

2012), presumably because the abundant species depend less on stream rearing habitats. However, since the 1950s, the Columbia Basin has produced only modest numbers of sockeye[6] which typically rear in lakes, very few pink salmon (e.g., 3,828 and 508 pink salmon counted at Bonneville Dam in 2011 and 2013, respectively), and only small numbers of chum salmon (less than about 25,000 chum per year; Figure III.1). The Columbia Basin is at or near the southern-most range of these abundant salmon species. Nevertheless, the Columbia Basin is the third largest salmon-bearing watershed flowing into the North Pacific Ocean (behind the Amur and Yukon rivers), and its capacity to support numerous natural-origin salmon was undoubtedly large in the pre-development period. Compared with other watersheds, the pre-developed Columbia probably produced more Chinook and steelhead than any other watershed, along with relatively large numbers of coho salmon.

F. Historical Versus Contemporary Salmon Production per Accessible Habitat

A significant percentage of habitat formerly available to anadromous salmonids is no longer accessible, leading to the question: *How much has salmon density changed given that both habitat area and total salmon abundance have declined?* Historical and contemporary densities

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[6] The rankings of salmon abundances in the Columbia is based on the average annual natural-origin abundances of 75 million sockeye, 150 million pink, and 28 million chum returning to North America, 1980-2005 (Ruggerone et al. 2010).

cannot be accurately calculated, but we can ask the simpler question: Has the *ratio* of adult salmon abundance to accessible river habitat changed since the early development period?

We compared the percentage change of adult salmon abundance with percentage change in accessible river length (or lake area for sockeye) during the early development period (1881-1919) and contemporary period (1986-2010) as an initial step to evaluate why density dependence has been detected in the Basin when salmonid abundances are much lower than they once were. Historical and contemporary estimates of habitat supporting each species are based on the cumulative in-river distance each species traversed to reach their spawning areas (river kilometers; Lavier 1976a,b; PFMC 1979), or lake surface area in the case of sockeye salmon (Fryer 1995). For fall Chinook, we relied upon more detailed information on spawning habitat in mainstem areas provided by Dauble et al. (2003). River distances are imprecise proxies of salmon rearing and spawning habitat area, but they represent the best habitat metric obtainable for both time periods. The adult salmon abundance estimates used for the early period are Chapman's (1986) "probable" peak five-year average annual estimates for each species (assuming likely harvest rates; Table III.1). The abundance estimates representing the contemporary period are peak five-year average annual fish abundances during 1986-2010 (Figure III.1). The contemporary estimates include harvests in the ocean, whereas ocean harvests beyond the Columbia District in the early period were unavailable but were thought to be minimal (see Section B

above). Both early and contemporary estimates include hatchery salmon, but the hatchery component during the contemporary period is a much larger proportion of returning Chinook, coho, and steelhead (Figure III.2). It should be noted that salmon returning to hatcheries do not compete with natural-origin salmon during spawning and juvenile rearing prior to release, and that the current distribution of hatchery fish differs from the historical distribution of salmonids. Therefore, the comparison of adult abundance (both natural-origin and hatchery) to accessible habitat in the contemporary period likely over-estimates the potential for density dependent interactions during some life stages relative to historical conditions.

Total kilometers of river habitat accessible to all anadromous salmonids declined by 31% from 1850 to 1976, but the extent of decline differed widely among species (Table III.2). River kilometers available to spring and summer Chinook declined about 50%, while mainstem spawning areas of fall Chinook declined 83%. A 31% and 40% decline in river kilometers occurred for steelhead and chum salmon, respectively. Conversely, river kilometers for coho reportedly *increased* 26-36% in response to passage improvements at Willamette Falls. Sockeye lake surface area declined 96% following dam construction that prevented sockeye from accessing a number of large lake systems (Fryer 1995).

Peak five-year average annual abundance of all salmonid species combined (including both hatchery and natural-origin fish) declined by approximately 38% from 1881-1919 to 1986-2010 (Table III.2). However, the decline in fish abundance relative to the decline in accessible habitat varied by

species, and in some cases, accessible habitat declined more than species abundance. For example, the percentage change in accessible habitat for spring Chinook, fall Chinook, and steelhead was greater than the percentage change in the abundance of these species (Figure III.3). For sockeye, the percentage losses of accessible habitat and abundance were of similar magnitude, whereas for coho, the percentage gain in abundance exceeded the percentage gain in habitat associated with improved passage at Willamette Falls.

These simple comparisons provide initial evidence that the density of adults in accessible freshwater habitat may be greater in the contemporary period for spring Chinook, fall Chinook, coho, and steelhead, and similar for sockeye salmon as compared to the historical period. In contrast, the abundance of summer Chinook and chum salmon has declined much more than accessible habitat, suggesting that the current density of these two species in freshwater habitat is less than it was in the historical period.

Additional testing of the density dependence hypothesis is described in Chapters V, VI, and VII.

Table III.2. Changes in adult salmon and steelhead abundance and accessible river length, spawning habitat, or lake surface area in the Columbia River Basin following mainstem dam construction. Contemporary abundance values include hatchery adult salmonids, many of which only spend a brief portion of their lives in rivers where they may compete with natural salmonids. Percentage change in habitat and species abundance is shown in bold. See text for caveats.

Parameter	River kilometers (km)			Peak 5-year abundance (millions of fish)		
	Period: 1850	Period: 1976	% Change	1881-1919	1986-2010	% Change
River kilometers (Total)	29,438	29,438	0			
Km Available to Anadromous Fish	23,598	16,207	-31%	5.20	3.20	-38%
Km Blocked to Anadromous Fish	5,841	13,231	127%			
Potential river habitat [km] based on Lavier (1976a,b):						
Chinook (Spring)	17,084	8,716	-49%	0.50	0.444	-11%
Chinook (Summer)	8,000	3,649	-54%	2.00	0.164	-92%
Chinook (Fall)	2,936	2,668	-9%	1.25	1.137	-9%
Coho	4,109	5,162	26%	0.56	1.300	132%
Chum	497	312	-37%	0.45	0.016	-96%
Steelhead	20,812	14,344	-31%	0.45	0.536	19%
Chinook (Fall) mainstem spawning habitat (km) based on Dauble et al. (2003):						
Chinook (Fall)	1,466	248	-83%	1.25	1.14	-9%
Sockeye lake surface area [ha] (Fryer 1995):						
Sockeye	84,000	3,700	-96%	2.25	0.169	-92%
Potential river habitat [km] based on PFMC (1979):						
Chinook	19,221	10,240	-47%	3.75	1.75	-53%
Coho	4,034	5,483	36%	0.56	1.300	132%
Chum	402	232	-42%	0.45	0.016	-96%

1. 1881-1919 peak abundance from Chapman's (1986) "most probable values." Table III-1.
2. Contemporary peak abundance based on Chapman's method & includes ocean catch (see Fig. III-1).
3. All-species abundances based on the adjustments described in text.
4. Reported estimates of sockeye habitat based on river kilometers excluded from table (most sockeye rear in lakes).
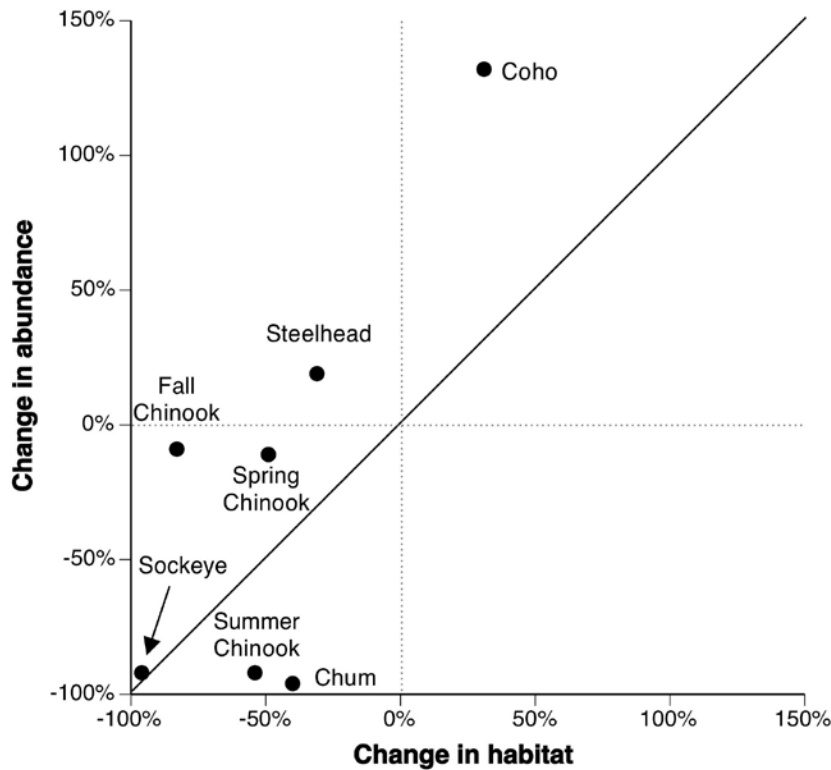
Figure III.3. Percentage change in accessible habitat (river kilometers or lake area) and salmon abundance (natural-origin and hatchery combined) from the pre-development period (late 1800s) to 1986-2010 in the Columbia River Basin. Values above the 1:1 line indicate that the ratio of total abundance relative to accessible habitat is greater now than in the pre-development period, which suggests that density dependence is potentially greater in the current period. See text for caveats. Values based on data in Table III.2.

G. Historical Versus Contemporary Smolt Production

Pre-development and recent estimates of smolt production from the Columbia Basin do not exist, but the ISAB (2011-1) examined the question of whether current total smolt production, including salmonids released from hatcheries, might equal or exceed that prior to dam construction in the Columbia mainstem. If so, this would suggest that density dependence in the Basin could be strong, especially in mainstem and estuarine habitats. The ISAB

(2011-1) cautioned readers that the reconstructed smolt estimates are very imprecise. The pre-development estimates of smolts were based on abundances of 3.1 to 3.9 million adult salmon and steelhead (sum of each species based on 10-year peak abundance rather than the five-year estimate by Chapman) and species-specific *assumptions* about smolt to adult survival rates (ISAB 2011-1).

Reconstruction of smolt abundances suggested that considerably more smolts (hatchery and natural-origin combined) are

migrating down the Columbia River now than before mainstem hydropower development, but the pattern varied across species (ISAB 2011-1). Current smolt abundances increased most for steelhead (by about four to eight times higher than estimated from historical data) and fall Chinook (about three to seven times higher), followed by coho (about two to three times higher), and spring/summer Chinook (up to two times higher; ISAB 2011-1). Trends in sockeye smolt abundance were especially uncertain.

H. Conclusions

The arguments presented in this chapter suggest that *long-term average abundances* of salmonids in the Columbia River during the pre-development period were lower than estimated by Chapman (1986) and NPPC (1986). Chapman's (1986) lower potential abundance estimates *for each species*, however, can be considered as reasonable estimates of the *pre-development capacity* of each species (Table III.1). These values were used in the comparison of declines in habitat versus abundance. Our differentiation between long-term average abundance and capacity reflects the influence of ocean and climate conditions on salmon returns and the observation that the pre-development estimates of abundance may have occurred during a period of favorable survival conditions (i.e., during the cool phase of the PDO).

Previous assessments of the overall abundance of Columbia River salmonids likely over-estimated their long-term average annual abundance and the capacity of the Basin to support these species. It seems unrealistic to expect that all species

could achieve their maximum annual abundance in the same five-year or one-year period, as assumed for the all-species estimates of 7.5 to 8.9 million fish (Chapman 1986) or 10 to 16 million fish (NPPC 1986). The peak five-year average annual catch of all species combined (about 4.4 million fish in 1883-1887)[7] was only about 70% of the sum of peak five-year average annual catches of each species considered separately (6.3 million fish per year over a range of five-year periods). Likewise, the maximum annual catch of all species combined (~4.7 million fish in 1883)[8] was only about 57% of the sum of maximum annual catches of each species considered separately (8.2 million fish over a range of years). Applying these ratios of all-species peak catches to the sum of individual peak catches (70% for peak five-year periods, 57% for maximum years) to adjust the Chapman (1986) and NPPC

[7] Peak five-year average annual catch of all species occurred during 1883-1887 due solely to the large Chinook catch and Chapman's (1986) approximation of sockeye catch (1.9 million per year). Harvests of other species, if any, were not reported at this time. To account for these other species, the average reported annual catch during the most recent five-year period of each species was added to the 1883-1887 reported annual catch. This adjustment increased peak five-year average annual catch from 3 million to 4.4 million fish. After this early period, peak five-year average annual catch was only 2.7 million fish (1915-1919; see Figure III.1), a number much smaller than the expanded peak catch values. These peak harvests corresponded with World War I when demand was high.

[8] Using the same approach described above to account for species that were not harvested in 1883, the maximum one-year catch increased from 3.9 million to 4.7 million fish in 1883. After this early period, maximum one-year catch was only 3.1 million (1918).

(1986) all-species estimates of total abundance for both catch and escapement yields a cumulative abundance range of 5.2-6.2 million and 5.5-9.3 million salmon and steelhead, respectively (Figure III.1). After analyzing the available, albeit limited, data and early estimates by Chapman (1986) and NPPC (1986), the ISAB believes the potential capacity for all species combined in the pre-development period was likely in the range of 5 to 9 million fish per year, with the primary evidence (i.e., probable harvest rates) supporting an estimate of around 6 million fish per year. The all-species capacity estimate likely over-estimates long-term average annual abundance because ocean conditions can become less favorable such as during the warm phase of the PDO.

Although this evaluation suggests that salmon abundance in the Columbia Basin during the pre-development period may have been lower than previously thought, our revised estimates of pre-development abundance are still considerably higher than current abundances (see adjusted potential abundance in Figure III.1, and Table III.2). This leads to the question posed in the Introduction: "*Why is density dependence more evident than expected at low abundances?*" As a first step in addressing this question, we compared the percentage change in accessible habitat versus percentage change in adult salmon abundance from the pre-development period to present. These simple

comparisons provide initial evidence that overall density (natural-origin and hatchery origin salmonids combined) may be greater in the contemporary period for spring Chinook, fall Chinook, coho, and steelhead; similar for sockeye salmon; and much less for summer Chinook and chum salmon. Furthermore, more smolts (both hatchery and natural origin) may be emigrating from the Columbia Basin now than in the pre-development period. The implication of these approximate comparisons is that current production from natural spawners and hatchery fish may be exceeding the current capacity of the Columbia Basin and estuary to support anadromous salmonids (ISAB 2011-1, Naiman et al. 2012). This hypothesis is especially relevant given the major alteration of the Columbia Basin ecosystem that has reduced the capacity and productivity of the Basin to support salmonid populations.

In the next Chapter (IV), we provide additional information on factors that have likely contributed to reducing the capacity and productivity of salmonids in the Columbia Basin. The corresponding evidence for density dependent reductions in growth and survival is presented generally for salmonid populations in the Columbia Basin in Chapter V, and with a special focus on the consequences of hatchery production in Chapter VI.

IV. Novel Ecosystem Effects on Capacity, Productivity and Resilience

Environmental changes to the Columbia River Basin have been pervasive and well-recognized for several decades (e.g., Columbia Basin Fish and Wildlife Authority 1990, Williams 2006). Alterations to flow regimes and habitats, as well as the proliferation of non-native species and hatchery-bred salmonids, the widespread use of artificial chemicals, substantial land use, and other ubiquitous environmental alterations, characterize today's Columbia River. In addition, the ocean is changing in fundamental ways that affect the vitality of anadromous fishes. This "new version" of the Columbia River, its tributaries, and the adjacent ocean creates significant challenges for most native species.

In effect, the new Columbia River is a prime example of a *novel ecosystem;* a river and an estuary representing vestiges of historical conditions. And the ocean is moving steadily toward becoming a novel ecosystem. In this chapter we summarize important environmental changes in the Columbia River Basin and the adjacent ocean. We examine linkages among carrying capacity, productivity, resilience, and life history characteristics in response to the changed environmental conditions, the resulting density dependent responses of native fishes, and the consequences of weakened life history diversity. Although a few native species may have benefitted, most habitats have significantly reduced *carrying capacity* and the overall *intrinsic productivity* of most populations have declined, resulting in less *resilience* to natural and human-induced environmental stresses.

A. Ecosystem Properties Affecting Density Dependence

Novel ecosystems (also called hybrid or no-analogue ecosystems; Hobbs et al. 2013) are those whose species composition and ecological processes are unprecedented in the history of specific locations. The distribution, abundances and life history diversity of native species persisting in novel ecosystems are profoundly affected by changes to the carrying capacity, productivity and resilience of habitats, and by the presence of new species. A major challenge confronting managers in the Columbia Basin is determining the extent to which the ecosystem is irreversibly changed and how best to evaluate and manage novel ecosystems.

Changing the carrying capacity of specific habitats influences density dependent characteristics for native fishes. This may result from altering food supplies, community composition, chemicals, or physical habitat features, or from modification of habitat-to-habitat linkages. In turn, a reduced habitat carrying capacity alters life history and population parameters such as migration, growth, fecundity, mortality, and overall population productivity. For instance, it is doubtful that the contemporary Columbia River, or its tributaries, can provide sufficient food or rearing and spawning habitat to simultaneously support large populations of artificially raised fishes and abundant non-native species, as well as substantial abundances of the native aquatic and

terrestrial biota for the long term (Williams 2006, Naiman et al. 2012).

Ecological resilience is enhanced by protecting diversity and redundancy of species, populations, life histories, and habitats; that is, by maintaining biological options, by maintaining intrinsic population productivity, and by avoiding management actions that reduce natural genetic and phenotypic variability. Population resilience depends in part on the nature of density dependence—the steepness and shape of the recruitment curve (e.g., whether asymptotic like the Beverton-Holt curve or dome-shaped like the Ricker curve, see discussion of overcompensation in Chapter II.B: Implications of Compensation for Fisheries Management).

B. Alterations to the Columbia River Basin: An Overview

Broad changes have taken place over the last two centuries (Williams 2006, ISAB 2011-4, Lichatowich 2013, Rieman et al. 2015). Historic changes to watercourses have resulted from extensive alterations of water supplies and stream channels, as well as from intensive land use (Figure IV.1). Current and ongoing changes include ecosystem-scale alterations from the extensive use of artificial chemicals, the arrival of numerous non-native species, range expansions and contractions by native species, alterations to riparian zones and food supplies, and climate change (Table IV.1). An extensive planning process in the 1980s identified hundreds of restoration actions needed at the subbasin scale and estimated costs for their implementation with a goal of doubling the number of anadromous salmonids over 50 years (Columbia Basin Fish and Wildlife

Authority 1990). While progress has been made, the goal remains elusive.

General Physical Conditions. Altered channel structure, hydrology, and sediment delivery have resulted from numerous human actions (Gregory and Bisson 1996). These include beaver trapping, the construction of numerous dams and reservoirs, forest harvest, wood removal, dredging, agriculture, grazing, road construction, urbanization, and climate change (Figure IV.1). Additionally, significant biotic changes have resulted from the proliferation of chemical contaminants, widespread use of hatcheries, and the prevalence of non-native species (ISAB 2007-2, 2011-1, 2011-4). Collectively, these alterations have significantly reduced habitat-specific carrying capacity and productivity, as well as the overall resilience of the ecosystem to respond to unanticipated alterations.

The evolution of anadromous, adfluvial, and fluvial migratory life histories within the Basin provides the most convincing evidence for the limited carrying capacity of headwater streams alone to support a high abundance of native fishes (Gross et al. 1988, Finstad and Hein 2012). With low productivity comes a strong potential for density dependence within natal habitats. Counteracting that low productivity, mainstem and tributary habitats downriver of spawning and early rearing areas have historically fostered greater abundance and life history diversity, especially for coldwater anadromous salmonids. As salmonids in unproductive streams spawn and the young fish begin to grow, the severe carrying capacity and productivity limitations in the colder, less productive spawning waters are often circumvented as

fish emigrate into tributary and main channel habitats for rearing before migration to the estuary and Pacific Ocean or to inland lakes (e.g., Petrosky 1990, Downs et al. 2006). Returning salmon in abundances far exceeding the carrying capacity of the natal streams provide nutrients to increase productivity and

carrying capacity in a positive feedback loop (Cedarholm et al. 1999, Gresh et al. 2000, Naiman et al. 2009). The net result is a wide diversity of life histories, many of them migratory, which serve to not only disperse individual fish to various habitats, but also serve to lessen density dependence.
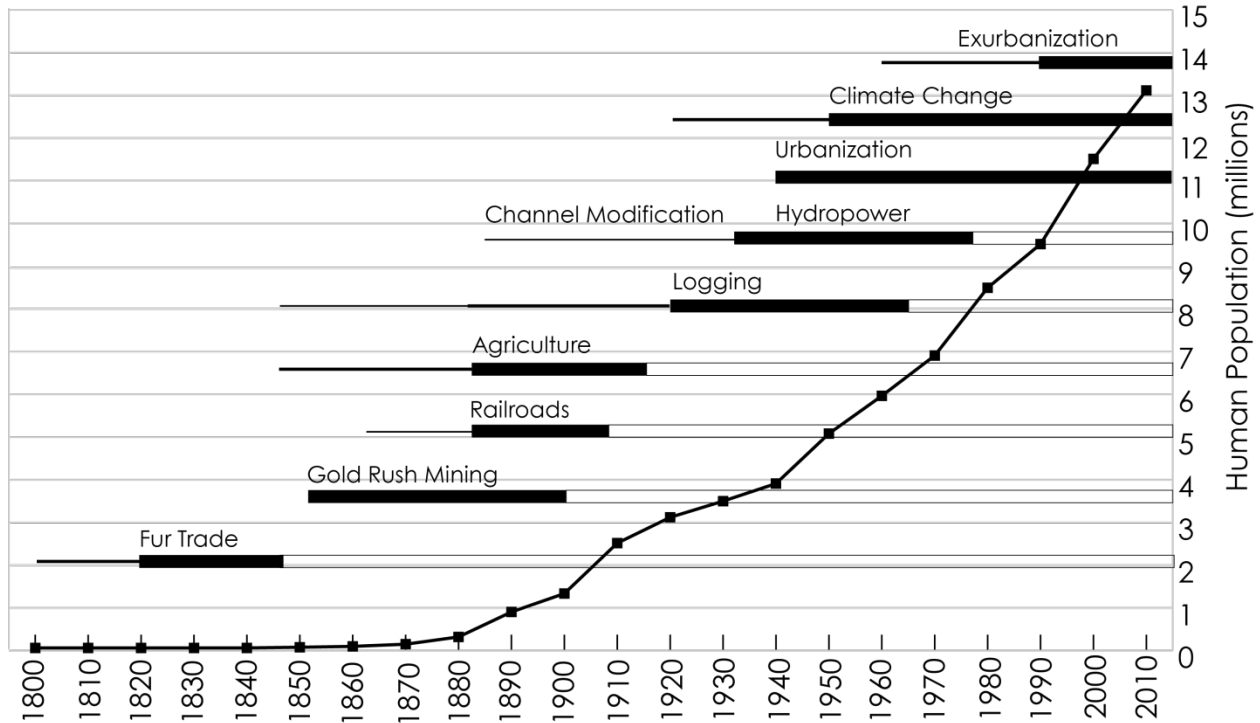
Figure IV.1. Sequential development driving landscape change in the U.S. portion of the Columbia River Basin and concurrent changes in human population size. Wide dark bars indicate the period of peak development and rapid habitat conversion. Wide light bars indicate continued effects following the initial period of rapid change (from ISAB 2011b, Rieman et al. 2015).

The Basin's numerous dams, reservoirs, and artificial ponds have exerted profound effects on the carrying capacity, productivity, and resilience of native species. Dams and reservoirs block many movements that evolved in response to density dependence and limited carrying capacity (see Figure IV.2 and Table III.2). Just as importantly, many downriver rearing areas suitable for coldwater species have

been converted into reservoirs better suited to coolwater and warmwater species, most of which are non-natives. Additionally, recovery of ESA-listed populations requires quality habitat downstream of the pristine natal rivers because of density dependent emigration prior to winter (e.g., Chapman 2014).

Within the contemporary Columbia River hydrosystem, salmonids may meet density dependent limitations much sooner and at much lower total abundance than in the past. This is because impoundments contain non-native predators and provide less suitable rearing conditions for juveniles escaping density dependent growth associated with limited habitat capacity upstream. Although great emphasis has been placed on providing passage for juveniles through the hydrosystem, much less has been done to address detrimental changes in rearing conditions in mainstem habitats (Sidebar IV.1).

Sidebar IV.1. Effects of dams and non-native species on bull trout carrying capacity

An example where dams have impacted carrying capacity is Noxon and Cabinet Gorge reservoirs on the Clark Fork River, Montana. These are locations where adfluvial bull trout historically spawned in very unproductive tributaries, but the bull trout used the Clark Fork River as a migratory corridor and seasonal rearing area before emigrating to more productive habitat in Lake Pend Oreille, Idaho. Returning adfluvial fish reached a much greater abundance and larger size in the lake than they would have as resident fish remaining in tributaries and the mainstem. Concurrently, introductions of non-native species in reservoirs, including predatory walleye, northern pike, smallmouth bass and largemouth bass, produced populations that now occupy mainstem reservoir habitats—the bull trout migratory corridor (Scarnecchia et al. 2014). Several non-harvested native species have declined in abundance (suggesting a decline in carrying capacity of the system for those native species) and recently documented increases in abundance of non-native species present challenges for restoration of bull trout since the habitat is now occupied by a novel fish community. Similar problems exist in lakes, such as Flathead, where high abundance of non-native, piscivorous lake trout are a concern for restoration of adfluvial bull trout that spawned in streams around the lake but historically emigrated to rear in the lake (Ellis et al. 2011). In restoration efforts where migratory characteristics have been abbreviated or rendered obsolete by dams or invasions by non-native piscivores, bull trout restoration is more likely to reach carrying capacity sooner and undergo density dependent limitations earlier in the restoration process.

The lack of fish passage in many historical dams undoubtedly increased the likelihood that non-native species, once introduced, would become established in former salmon habitat. Some dams were built with no way for salmon to travel either downstream or upstream (e.g., Grand Coulee, Hells Canyon; Figure IV.2). In addition to changing flow regimes, extensively dammed ecosystems also experience reduced sediment delivery (Collier et al. 1996), changes in channel geomorphology (Magilligan and Nislow 2005, Waples et al. 2009, Malcolm et al. 2012), altered thermal regimes (Saito and Koski 2006, Olden and Naiman 2010) and are often subject to extensive water withdrawals. Even dams with fish passage facilities can act as barriers to fish passage (Waples et al. 2008), reducing and isolating habitat for longer time periods (decades to centuries) than natural blockages such as landslides (hours to days; Waples et al. 2009). Reservoirs, by inundating former lotic habitat, create ecosystem characteristics that encourage non-native

species, and may lead to juvenile salmon overwintering in reservoirs, delaying migration to the ocean (Connor et al. 2005). Widespread diversion of water for agriculture, mining, or power generation also contributes to changed surface and hyporheic flows (Stanford et al. 2005).
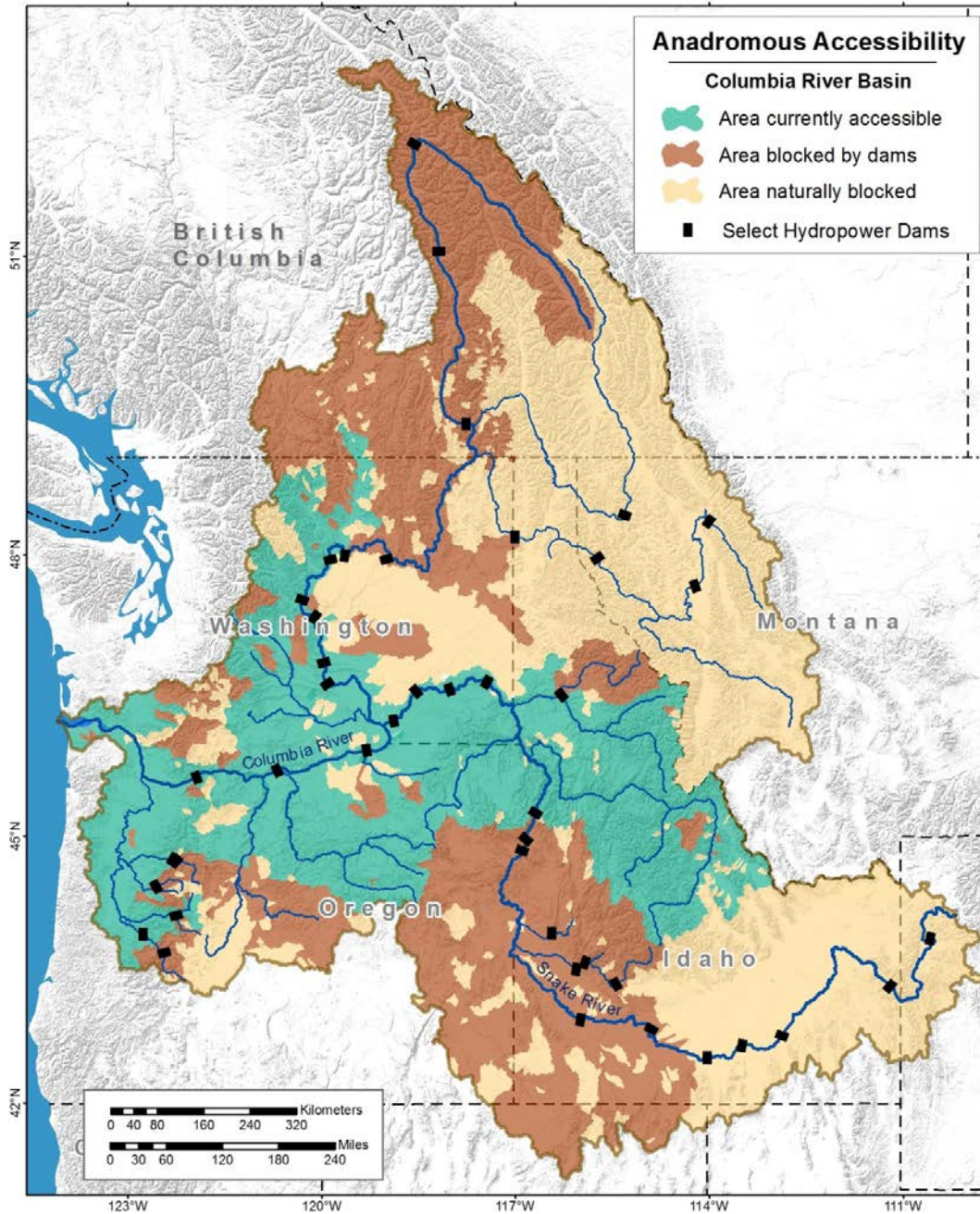
Figure IV.2. Area blocked to anadromous fish in the Columbia River Basin. Streams blocked by dams or other barriers leads to lower population abundance of migratory fishes. Source: Pacific States Marine Fisheries Commission. Source details: NOAA TRT Salmon Population Boundaries

(July, 2011); beyond the extent of NOAA's TRT data, accessibility status was informed by professional judgment of staff at the Northwest Power and Conservation Council (NPCC), the Columbia River Inter-tribal Fisheries Commission (CRITFC), the Canadian Columbia River Inter-tribal Fisheries Commission (CCRIFC) and the Pacific States Marine Fisheries Commission (PSMFC); please help improve this map layer by directing feedback to gis@psmfc.org. Compiled: April 28, 2014 by Van C. Hare, PSMFC (prj 276).

Alterations to Riparian Zones and Food Supplies. Riparian forests along thousands of kilometers of the Basin's streams also have been severely modified (Fullerton et al. 2006; Table IV.1; Sidebar IV.2). Riparian forests provide large wood to rivers and streams, stabilize streambanks, buffer streams from pollutants, provide habitat for fish, aquatic and terrestrial invertebrates and wildlife (Steel et al. 2003, Wipfli and Baxter 2010, Wahl et al. 2013) and furnish shade that moderates water temperatures (Naiman et al. 2005). It is common that about half the food energy that sustains fish in small streams enters in the form of terrestrial invertebrates that fall into streams from riparian vegetation (Nakano and Murakami 2001, Baxter et al. 2005). Collectively, these attributes enhance habitat carrying capacity and productivity and ecological resilience for native species. Unfortunately, these "subsidies" are significantly compromised by human actions (Baxter et al. 2004, Naiman et al. 2005, Saunders and Fausch 2007, 2012).

Sidebar IV.2. Riparian modifications to the Willamette River, Oregon.

While modifications to riparian areas have been severe throughout the Basin (Fullerton et al. 2006), extensive quantitative data on changes are available for only a handful of locations. Nevertheless, the data consistently show the broad extent of riparian changes. For example, early visitors to the Willamette River Valley documented multiple channels and dense woodlands covering a broad floodplain (Sedell and Froggatt 1984). Snags and fallen trees were systematically removed between 1870 and 1950 to enable navigation. Over a distance of 273 km, the total area of river channels decreased by 22% and the total length of all channels decreased by 26% from 1850 to 1995 (Gregory 2008). More than 30% of high quality fish habitat in alcoves and sloughs disappeared and the area of islands declined by 63%. Between Albany and Eugene the total length of all channels decreased from 340 to 185 km, and more than 70% of the side channels, 40% of the alcoves, and 80% of the islands were either eliminated or converted to floodplain banks (Gregory 2008).

Proliferation of Chemicals and Contaminants. While control of point-source contaminants and regulations designed for waste discharges have reduced incidents of fish kills, these actions do not adequately protect migratory fish like salmon that encounter many different contaminants in many different habitats (Table IV.1; Ross et al. 2013). Bioaccumulation and biomagnification of chemical contaminants affect fish metabolism as well as critical components of the food web (e.g., microbes, sensitive invertebrates, and top consumers).

Herbicides cause direct loss of food sources such as aquatic plants and algae (leading to food shortages for higher trophic levels). Exotic chemicals reduce the ability of species and individuals to cope with normal predation risk and environmental stresses due to altered behaviors, slower somatic growth, and increased disease susceptibility (ISAB 2011-1). Contaminants affect the sensitive early life history stages of fish and the basal layers of food webs (Relyea and Hoverman 2006, Fleishman 2011). The use of artificial chemicals and contaminants continues to expand, threatening the productivity and carrying capacity of habitats, the life history diversity of species, and ecological resilience.

Investigations on the ecotoxic potential of chemical mixtures on fish metabolism and food webs are just beginning. For instance, the Columbia River Contaminants and Habitat Characterization (ConHab) Project, an interdisciplinary study, is making headway by investigating transport pathways, chemical fates and effects of polybrominated diphenyl ether (PBDE) flame retardants and other endocrine disrupting chemicals (EDCs) in water, sediments, and the food web in the lower Columbia River (Nilsen and Morace 2013). Fortunately, the need to quantify spatial patterns of chemical use and discharge, assess their transfer and accumulation rates, and document the vulnerabilities of species and food webs to them are broadly recognized (EPA 2014).

Non-natives and Species Expansion. Even though biodiversity (i.e., the number and relative abundance of different species) is declining globally, it is sometimes increasing locally through the rapid turnover of species (Dornelas et al. 2014, Pandolfi and Lovelock

2014). In the Noxon Reservoir on the Clark Fork River, Montana, non-native additions to a depauperate fauna (Frissell 1993) resulted in a higher total number of fish species, consisting mostly of non-natives (Scarnecchia et al. 2014), which is typical of many locales throughout the Basin. In general, the trend appears to be one of gaining species through the addition of non-natives, with concomitant impacts on the utilization and division of available resources (Table IV.1). The increase in non-native species impacts native species and may lead to observable density dependent responses as resources become increasingly limited.

Preventive measures against invasions of economic importance (e.g., zebra and quagga mussels; *Dreissena polymorpha and D. bugensis*) such as border inspections, cleaning stations and invasive species tags for boats, have increased in recent years. Nevertheless, basin-wide monitoring to address the temporal pace and spatial extent of non-native invasion and establishment, and to identify impending problems while they are still manageable, is not occurring (ISAB 2011-1, ISAB 2013-1).

Additionally, there is the continued threat of additional new species that drastically alter ecosystem characteristics (e.g., aquatic weeds, mussels, diseases), and thereby further impact carrying capacity, productivity and ecosystem resilience (for example, see Catford et al. 2013). The ecological threats posed by quagga and zebra mussels, aquatic plants such as milfoil (*Myriophyllum spp.*), and other invaders are real—they have fundamentally altered ecosystem properties elsewhere. For instance, in highly polluted Lake Erie (USA and Canada), it has been determined that

invasive mussels have had a greater impact on the zooplankton community in the last 25 years than extensive pollution (Burlakova et al. 2014).

Climate Change. While there are numerous mechanisms through which climate change affects organisms and habitat, one pervasive example may be sufficient: Climate change influences most aquatic organisms via temperature effects on metabolism, which in turn affects growth, survival and distribution (Steel et al. 2012). The greatest exposure to high stream temperatures appears to be occurring in the Basin's low elevation and low latitude streams under climate change (Wade et al. 2013). As the Basin continues to warm, streams with flat slopes (0.1-1%) are expected to experience greater isotherm shifts upstream than steeper streams, with shifts as fast as 25 km/decade (Isaak and Rieman 2012), allowing warm-water species to expand their ranges. Elevated water

temperatures also cause fish emergence times to become mismatched with flows and food resources, alter migration times, and increase susceptibility to disease and mortality (ISAB 2007-2).

Besides harming native species, projected climate change shifts in water temperature and flow regimes favor many non-native species, resulting in continuously changing novel food webs, predator-prey interactions and spawning and rearing conditions (Fausch et al. 2001, Rahel and Olden 2008, Lawrence et al. 2012, Goode et al. 2013). In adjacent uplands, continuing climate change will also likely increase wildfire frequencies, insect infestations, and drought-induced tree mortality, all of which result in increased erosion and flooding, in addition to numerous other ecosystem-scale changes (Vose et al. 2012).

Table IV.1. A brief overview of biophysical alterations to the Columbia River Basin.		
Alteration	**Impacts on Biotic Carrying Capacity and Productivity**	**Key References**
Beaver Removal	Historically, the Basin had widespread beaver activity on many alluvial floodplains; trapping in the late 1800s greatly reduced or extirpated most beaver populations. Beaver dams and other biogenic structures increase channel aggradation rates, energy dissipation, and attenuation of peak flows; improve groundwater recharge; and provide important rearing and wintering habitat for salmonids.	Naiman et al. 1988, Stanford et al. 2005; Pollock et al. 2003, 2014
Dams and Reservoirs	The construction of numerous dams has changed the free-flowing system to a fragmented network of regulated flows and lentic reservoirs and ponds, and blocked many immigrations and emigrations—evolved adaptations that reduce density dependence and increase carrying capacity. Just as importantly, many downriver rearing areas, either highly or marginally suitable for coldwater species, have been converted into reservoir habitat better suited to coolwater and warmwater species that are often non-natives. In total, ~30 - 55% of the habitat originally available to salmon has been lost. Further, an estimated 30 - 50% of the original anadromous	www.psmfc.org/habitat/salmondam.html; www.nwcouncil.org/history; www.internationalrivers.org/dams-and-migratory-fish

	spawning habitat in the Columbia Basin is either submerged under reservoirs or blocked by dams without adequate bypass facilities.	
Forest Harvest, Wood Removal and Dredging	Logging began in the early 1800s and removed forest cover at rates exceeding natural wildfire, disease and wind-throw. Early logging involved transporting logs in stream channels, with detrimental impacts on riparian zones and aquatic communities. Road networks constructed to support silviculture further altered hydrology and thermal regimes by increasing surface runoff and hillslope erosion. Widespread dredging for navigation continues to be an important activity with potentially severe ecological consequences.	Gregory and Bisson 1996, Stanford et al. 2005, Waples et al. 2009
Mining	Historically, mining occurred in many parts of the Basin. While the effects are still widely evident, mining is not as extensive today as other activities such as logging, grazing, urbanization, and agriculture. Mining substantially increases erosion and sediment delivery to streams while drainage and leaching of toxic contaminants impair or eliminate stream ecosystems for decades after mining activities have ceased (e.g., Upper Clark Fork and Coeur d'Alene River basins).	Stanford et al. 2005
Agriculture and Grazing	Irrigated agriculture has been present in the Basin since the mid-1800s, and today covers about 5 million acres (~3% of the Basin). As of 1993, agricultural land use constituted about 20% of the Basin's land area, and rangelands about 30%. Irrigation return flow often is warm with high nutrient, sediment, and pesticide concentrations. Poorly managed grazing can degrade instream habitat while simultaneously drastically reducing inputs of terrestrial invertebrates that supply about half the energy requirements of stream fish.	Gregory and Bisson 1996, Stanford et al. 2005; Saunders and Fausch 2007, 2012
Hatcheries	There are approximately 130-150 million hatchery-bred salmon and steelhead added to the river annually from > 200 hatcheries. The very large annual releases of juvenile fish from the Basin's hatcheries impact food webs and the vitality of natural-origin fish. It is not clear whether the Columbia River, or any of its tributaries, can provide sufficient food to support large populations of artificially raised fishes for the long term. Evidence suggests that more salmon smolts (mostly hatchery) are produced in the Basin today than were present during the period prior to major hatchery and dam construction.	Paquet et al. 2011, ISAB 2011-1, Naiman et al. 2012
Roads	Most of the Basin's many thousands of kilometers of roads are situated near streams or cross streams, and significantly influence sedimentation and the volume of dead wood in the channel. For instance, streams < 30 m from roads have fewer pieces of total wood, fewer pieces of coarse wood, fewer pieces of pool-forming wood, and less wood volume per kilometer than sites > 60 m from roads.	Reid 1998, Meredith et al. 2014
Urbanization	Urban land area in the Basin increased from 26,000 km^2 in 1977 to 61,000 km^2 in 2000. Urbanization and population growth increase sewage effluent, storm runoff, and industrial discharge to rivers and streams. For instance, annual oil and grease loads to the ocean due to urban runoff were estimated to increase by more than 100% between 1977 and 2000. Urban areas are often located on historic wetland sites, which eliminate these sites as productive habitat. The increased	Gregory and Bisson 1996, Stanford et al. 2005, ISAB 2007b , Saito et al. 2010

	desire for exurban development (low density-semi-rural residential) near water is a dominant trend that can result in degraded and fragmented aquatic habitat.	
Climate Change	Significant climate change has been detected throughout the Basin. Over the last century, warming has occurred in the Northwest US by about 0.7°C, with higher nighttime minimum temperatures. Although a consistent trend in precipitation has not been observed over this period, larger fluctuations have been observed since 1970 when compared with the previous 75 years. Predictions suggest that a continued warming of ~1 to 5°C, with variable forecasts of increased or decreased precipitation by 2070. Because of the increased temperatures, changes in the form of precipitation are likely, with proportionately more rain than snow, especially in mid-elevation areas. Streamflow hydrology in snowmelt and rain-snow mixtures is expected to change greatly in timing and quantity, with some watersheds completely losing snowmelt in April by 2080. By 2070-2099 the only snowmelt-driven region of the Basin is projected to be the Canadian Rockies. Models suggest that formerly snowmelt-driven streams will see significantly reduced summer stream flows and warmer temperatures throughout the Pacific Northwest by the 2080s, which may result in less summer but greater winter hydropower generation and increased susceptibility of salmonids and other species to disease and mortality. Alterations in streamflow quantity and timing may also impact channel structure. Recent updated projections indicate warmer air temperatures and greater runoff on the Columbia River than previous projections.	Hamlet and Lettenmaier 1999, Battin et al. 2007, ISAB 2007a, Elsner et al. 2010, Beechie et al. 2012, Wu et al. 2012, Dalton et al. 2013, Brekke et al. 2013
Chemicals and Contaminants	The widespread use of artificial chemicals in the Basin provides cause for concern. The most recent tally of pesticide use (average for 1999-2004) lists 182 chemicals, with an aggregate application rate of ~46,000 mt of active ingredients annually; these are concentrated mostly in agricultural lands along water courses. In addition, there are yet-to-be-quantified but apparently abundant organic compounds such as pharmaceuticals, steroids, surfactants, flame retardants, fragrances, and plasticizers detected, especially in waters in the vicinity of municipal wastewater discharges and livestock agricultural facilities.	ISAB 2011a, Morace 2012, Naiman et al. 2012, Nilsen and Morace 2013, EPA 2014
Non-natives and Species Expansion	A total of about 1,000 non-native species of plants and animals, of which 326 are documented aquatic species, inhabit the Columbia Basin. Many others are expected to arrive in future years as the ranges of native species adjust to new environmental conditions. The stark reality is that hybrid food webs will persist; non-native species are widely established, and eradication is virtually impossible. A positive step has been taken by the Willamette Habitat team to develop a website to track and map changes to fish communities in the river, one that could be expanded to other parts of the Basin.	Sanderson et al. 2009, Carey et al. 2012, Mims and Olden 2013 http://ocid.nacse.org/wrfish_test/

C. Changing Oceans

The Columbia River and the Pacific Ocean are intimately linked by the regular movement of energy, materials and organisms - and ocean conditions are steadily changing. In the California Current, multiple threats from human activities occur everywhere, and coastal ecosystems near centers of high human population density and the continental shelves off Oregon and Washington are the most severely affected by human activities (Halpern et al. 2009). Important biophysical alterations to the ocean include climate regime shifts, acidification, excessive hatchery production and pollution (Table IV.2), all of which could impact density dependent growth, maturation, and survival of anadromous fish through changes to carrying capacity, productivity, and resilience of marine habitats (ISAB 2007-2, ISAB 2011-1, ISAB 2011-4, NPCC 2014-12). At present, the timing of future regime shifts cannot be predicted (Overland et al. 2010), and the effects of global climate change on the frequency, duration, and intensity of these events remain highly uncertain.

There is much speculation about the potential effects of ocean acidification and hypoxia on salmonid food webs in the ocean. Focused process studies that directly address this question are needed to reduce scientific uncertainty. The ISAB has suggested that marine pollution is an emerging issue for the Columbia Basin (ISAB 2011-1). However, the recent EPA Columbia River Chemicals of Emerging Concern (CEC) Research and Monitoring Strategy (EPA 2014) and the Columbia River Toxics Reduction Working Group Action Plan (EPA 2010) do not specifically address marine pollution issues. Hatcheries introduce a relatively constant and large number of fish regardless of ocean conditions and, as well, the assumption of unlimited carrying capacity for the ocean may be unrealistic (e.g., Holt et al. 2008; see Section V.E). Confidence in projections of the potential impacts of both natural and human-caused alterations to marine ecosystems would improve if density dependent effects and interactions among species and between hatchery and natural-origin salmon were better known (Irvine and Fukuwaka 2011). As recommended by ISAB in past reports (e.g., ISAB 2003-3, ISAB 2007-2, ISAB 2011-1, ISAB 2013-1), an adaptive management approach involving carefully-designed experimental releases of hatchery salmon to address specific hypotheses would help reduce scientific uncertainty about the potential density dependent effects and interactions of hatchery salmon on ESA-listed species in both the Columbia Basin and in marine ecosystems.

Table IV.2. A brief overview of biophysical alterations to the ocean.		
Alteration	**Impacts on biotic carrying capacity & productivity**	**Key references**
Regime shifts	A "regime shift" is a rapid (1-2 yr) climate-driven change from one persistent state (decadal scale) to another. Natural regime shifts are associated with broad reorganization of marine communities and food webs, as observed during a multi-decadal state of the Pacific Decadal Oscillation (PDO). Ecosystem effects in the Northern California Current (NCC) during positive (warm) PDO phases are an analog for potential effects of global warming due to greenhouse gas emissions. A warm (cool) PDO phase in the NCC is associated with low (high) abundance and survival of Columbia River salmon, warm (cool) sea surface temperature, low (high) biomass of lipid-rich northern copepods, low (high) abundance of forage fish, and high (low) abundance of predators such as hake. Ecologically important cool PDO regimes occurred during 1890-1924 and 1947-1976 and warm regimes occurred during 1925-1946 and 1977 through, at least, the mid 2000s. A shift to a cooler PDO period starting in winter 2007/2008 also may be ecologically important. In the NCC ecosystem, natural regional mechanisms (atmospheric forcing and reduced sea-level pressure) may explain an apparent century-long warming trend (~0.5-1.0 °C, 1900-2012) in sea surface temperature. In the open ocean, the International Panel on Climate Change (IPCC) projected warming of sea surface temperatures due to global warming suggests a substantial shrinking of the amount of preferred thermal habitat available to salmon and steelhead during this century.	Mantua et al. 1997, Anderson and Piatt 1999, Hare et al. 1999, Hoof and Peterson 2006, ISAB 2007-2, http://jisao.washington.edu/pdo/PDO.latest; King 2005, Alexander et al. 2008; Overland et al. 2008, 2010; Peterson 2009, Abdul-Aziz et al. 2011, Bi et al. 2011, Johnstone and Mantua 2014, Litzow and Mueter 2014
Ocean acidification	Ocean acidification is caused by a long-term increase in carbonic acid, which forms when atmospheric carbon dioxide dissolves in seawater. Ocean acidification is amplified by human activities; for example, ocean uptake of atmospheric carbon dioxide from burning of fossil fuels. Nitrogen oxides, sulfur oxide gases, and nutrients and organic carbon from wastewater discharge and runoff from land-based human activities also contribute to ocean acidification. The changes to seawater chemistry as carbonic acid breaks down include an increase in hydrogen and bicarbonate ion concentrations and a decrease in carbonate ion concentration and pH. Ocean acidification reduces concentrations of aragonite, a biogenic calcium carbonate that is used by many marine taxa to build skeletons, tests, and shells. Ocean acidification is likely to have a large impact on oceanic food webs of Columbia River salmon and steelhead, particularly in regions where shelled zooplankton (e.g., pteropods) and squid are preferred prey. Squid are very sensitive to acidic (low pH) conditions, which interferes with oxygen binding at the gills, reducing oxygen consumption and scope for activity.	Kaeriyama et al. 2004, Armstrong et al. 2008, Fabry et al. 2008, Guinotte and Fabry 2008, Atcheson et al. 2012a, Feely et al. 2012, WSBRPOA 2012, Lachkar 2014

Hypoxia	Along the Washington and Oregon coast, seasonal upwelling of naturally acidic water from deep ocean layers intensifies the acidifying effects of global carbon dioxide emissions. Marine dead zones or low-oxygen (hypoxic) conditions indicate areas where high rates of decomposition of organic matter, which produces carbon dioxide, are contributing to ocean acidification. The Northern California Current (NCC) ecosystem exhibits a natural history of seasonal hypoxia. While it is not known if hypoxic events in the NCC are becoming more severe due to ocean acidification, an extreme hypoxia event (associated with increased upwelling) occurred over a large area (~5,000 km^2) of the Washington continental shelf in 2006 with dissolved oxygen concentrations below 0.5 mL/L at the inner shelf. Interannual variability in hypoxia is associated with upwelling of water with low dissolved oxygen concentrations and changes in source water. Hypoxic events are most likely to affect Columbia River salmon through bottom-up food web effects.	Feely et al. 2012; Connolly et al. 2010; WSBRPOA 2012, Lachkar 2014
Hatcheries	At present, ~5 billion juvenile hatchery salmon are released into the North Pacific Ocean and adjacent seas from hatcheries in Asia and North America. Hatcheries introduce a relatively constant and large number of fish regardless of freshwater and ocean conditions. From the 1990s to present, ocean conditions favorable to pink and chum salmon, as well as increased hatchery releases, have contributed to increasing abundances of these species in both the eastern and western subarctic North Pacific, while abundances of coho and Chinook salmon in the eastern North Pacific Ocean have declined. Artificial production strategies using hatcheries (ocean ranching) to increase in-river harvests in the Columbia River, as well as industrial-scale ocean ranching operations in Asia and Alaska, might limit the recovery of ESA-listed Columbia River salmon due to density dependent ecological (trophic) interactions in marine habitats.	ISAB 2003-3, 2007-2, 2011-1, 2013-1; Holt et al. 2008, Ruggerone et al. 2010; Irvine and Fukuwaka 2011
Marine Pollution	All anadromous Columbia River Basin fish that have been tested (spring/fall Chinook, coho, steelhead, lamprey, smelt) have some levels of toxic chemicals in their tissues, as well as in the eggs of Chinook, coho, and steelhead. Little is known about the sources of the toxic chemicals. Organic chemicals of environmental concern (OCEC) in the marine environment include persistent organic pollutants (POPs), polycyclic aromatic hydrocarbons (PAHs), and plastics. Decomposing plastic debris can leach and absorb OCECs, and some are known to cause endocrine disruption and reproductive defects in aquatic organisms. In some North Pacific regions, a decadal-scale increase (several orders of magnitude) in concentrations of micro-plastic debris has created a new hard-substrate ecosystem for marine organisms, dubbed the plastisphere. These problems might be of particular concern for steelhead in the open ocean because they consume more plastic than other species of salmon, particularly when availability of preferred prey (squid and fish) is low.	EPA 2002, 2009, 2010, 2014; Kang et al. 2007, Teuten et al. 2009, ISAB 2011-1, Atcheson et al. 2012b, Goldstein et al. 2012, Myers and Mantua 2013, Myers et al. 2013, Zettler et al. 2013, Farrington and Takada 2014

D. Life History Diversity Effects on Carrying Capacity, Productivity, and Resilience

A diversity of life histories for salmon increases their ability to utilize a variety of habitats, potentially increasing population carrying capacity (Lichatowich and Mobrand 1995). In addition, the diversity of species, populations, genes, and life history traits within biological communities contributes to ecological resilience by providing a greater range of options to absorb, or respond to disturbance and environmental variability (ISAB 2013-1, Thorson et al. 2014). Species or populations with a diverse set of life histories use more types of habitats during each life stage (e.g., Bottom et al. 2005a,b; 2011; Secor and Rooker 2005, Jones et al. 2014), thereby reducing competition and potentially increasing overall capacity of the habitat to support the population (Figure IV.3). Life history diversity stems from the diversity of habitat conditions and genetic/behavioral adaptations of species to them (Waples et al. 2009, ISAB 2011-4, 2013-5; Rieman et al. 2015). Life history diversity has been diminished in the Columbia River Basin owing to broad environmental alterations and genetic changes in previously well-adapted populations (ISAB 2013-1). The crux of the issue is whether reduced life history diversity imposes a type of reduced carrying capacity, whereby the remaining, more homogenized, population uses fewer habitat types and hence can achieve only a lower abundance.

The diversity of life histories typically reflects a species' physical or behavioral responses to the variety of habitat types and environmental conditions encountered across the landscape or catchment (ISAB 2013-1, Rieman et al. 2015). For example, key life histories of spring Chinook in the Snake River Basin that may enhance population carrying capacity include 1) fry that emigrate from the natal river in March-June and rear downstream, 2) age-0 smolt that emigrate from natal streams in May-June and enter the ocean in the same year, 3) parr that emigrate from natal streams in July-November and overwinter in the mainstem Snake River, and 4) smolts that overwinter in the natal stream before emigrating to sea as yearlings (Copeland and Venditti 2009). Life history diversity typically involves adaptations that have a genetic basis, but density dependence may still influence the expression, productivity, and relative abundance of different life history traits (Copeland et al. 2014). The loss of specific life history adaptations through habitat degradation, dams, or mismanagement reduces options that could confer resilience within a novel ecosystem.

Important drivers of reduced life history diversity are habitat alterations and hatchery programs. The diverse set of habitats and populations that supported native fish production has been simplified by habitat loss and alteration. Further, large-scale hatchery releases inhibit the natural rebound in the productivity of the natural-origin population, especially when its abundance is low (Kostow et al. 2003). Interbreeding of natural-origin and hatchery fish, especially those from segregated hatcheries, can reduce the genetic diversity and associated life history traits that support the fitness of natural-origin populations (Araki et al. 2008, Fraser et al. 2011, Paquet et al. 2011, Christie et al. 2014)—thereby altering intrinsic productivity and possibly population

carrying capacity (see Chapter VI). The effects of hatcheries on the environmental conditions for natural-origin populations, such as through concentration of predators, disruption of food webs critical to habitat carrying capacity, and influences on density dependence, remain largely unknown (Naiman et al. 2012).
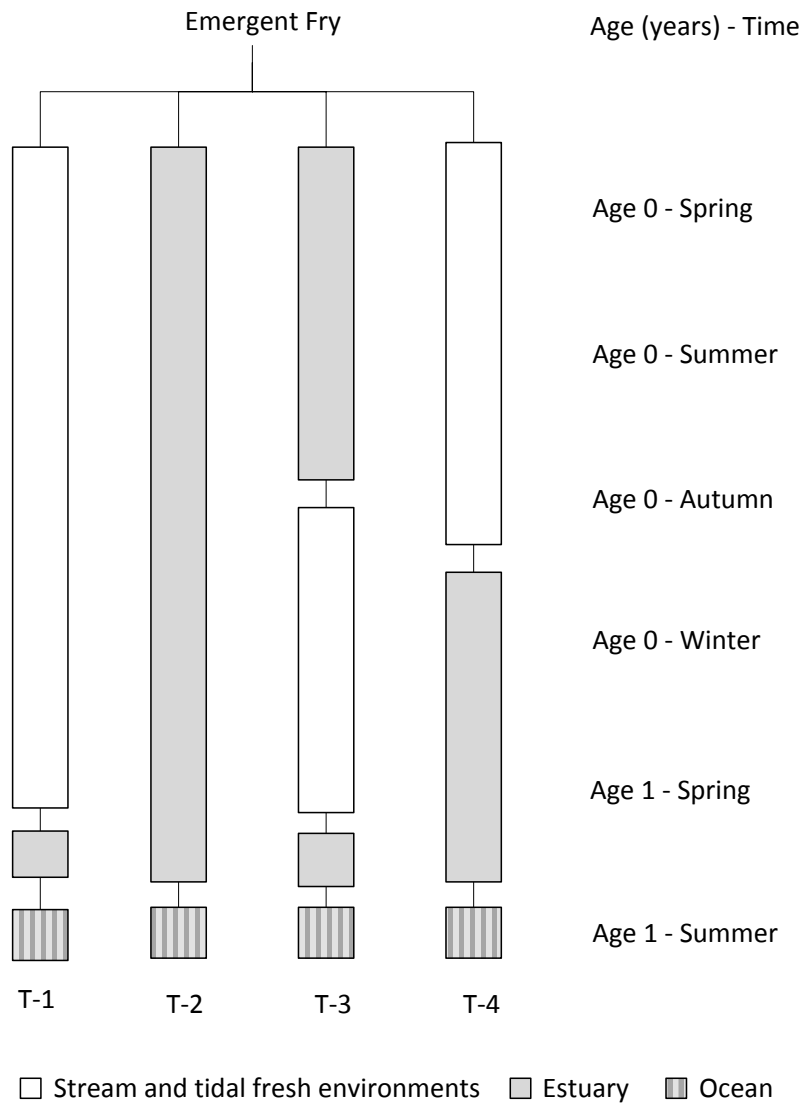
Figure IV.3. Life history diversity as expressed by the potential life-history pathways of juvenile *Oncorhynchus kisutch* in the Salmon River from emergence to ocean entrance. (From Jones et al. 2014).

Locally Adapted Traits. The ability of Pacific salmon to return home to natal streams is facilitated by sequential imprinting during juvenile rearing and outmigration (Quinn 2005). Precise homing contributes to reproductive isolation, which in turn enables natural selection for unique, locally adapted traits that confer a fitness advantage to individuals and increases productivity of the overall population.

Locally adapted traits that evolved in isolated populations (i.e., occupying different habitats) created the life history diversity within each species. Traits that may differ among salmonid populations can influence morphology, meristics, behavior (e.g., timing of runs), development, physiology, biochemistry, disease resistance, and life history characteristics (Taylor 1991, Garcia de Leaniz et al. 2007). Expression of these characteristics is complicated and depends on environment-genetic interactions so that heritability varies among traits (Fraser et al. 2011). A review of quantitative genetic components of fitness indicates that heritability in salmonine fishes is highest for morphological traits, intermediate for behavioral and physiological traits, and lowest for life history traits (Carlson and Seamons 2008). Thus, the emergence of novel ecosystems will have strong influences on the expression and fitness of life history traits.

There are many examples of local adaptations of Pacific salmon that confer some survival advantage (Sidebar IV.3; Taylor 1991, Ramstad et al. 2010, McGlauflin et al. 2011, Grant 2012, Thorson et al. 2014), though the level of benefit is sometimes difficult to evaluate without controlled experiments. However, a meta-analysis involving all salmonid fishes reported some level of local adaptation in 70% of the investigations (100/143 comparisons) with local populations having an average fitness benefit 1.2 times that of non-local populations (Fraser et al. 2011). The upshot is that loss of local adaptations reduces the fitness, life history diversity and future adaptability of the remaining population, hence effectively reducing the intrinsic productivity and carrying capacity of the population and altering the density dependent recruitment relationship (e.g., lower growth and survival at higher density). The heritability and maintenance of these traits are key reasons why high levels of straying and interbreeding of non-local hatchery salmon with local salmon populations may lead to lower fitness (Christie et al. 2014).

Sidebar IV.3. Locally adaptive traits are common and diverse.

Spawning sockeye body shape and ocean-age are linked to characteristics of the spawning habitat: younger salmon with less body depth occur in shallower streams, whereas older and/or deeper-bodied salmon occur in larger rivers or spawning beaches (Quinn 2005). These traits enable salmon to prosper in more habitats than they might otherwise use, thereby increasing population capacity. Juvenile salmon produced from parents spawning in a lake outlet stream migrate upriver to reach the rearing habitat, whereas juveniles produced in inlet streams migrate downstream to reach rearing habitat. Timing of adult spawning migrations (e.g., spring, summer, fall, winter) and smolt emigrations to sea vary among populations even within a single watershed (Bottom et al. 2005a,b; Jones et al. 2014). Some salmon populations are resistant to specific diseases or parasites, whereas others are not, as shown by high mortality when certain populations are introduced into areas with a pathogen. Overwinter water temperature affects the development rates of embryos incubating in gravel, and spawning time varies adaptively among populations in response to water temperatures typically experienced by the population

in its specific habitat, leading to synchronized emergence timing that facilitates juvenile feeding in the spring (Brannon 1987). The physiology of Fraser River sockeye salmon during upstream migration varies among populations consistent with historic river temperatures, to which each population has evolved adaptations that provide a survival advantage (Eliason et al. 2011). Finally, a clear example of the survival benefit of locally adaptive traits is shown by the failure of most transplanted salmon experiments within their native range, including those with pink salmon (Reisenbichler 1988, Quinn 2005).

Straying of adult salmon to non-natal streams allows for colonization of new habitats, thereby potentially increasing population capacity (Quinn 2005). Straying tends to be higher among older individuals within most species. Straying tends to be lowest among natural-origin sockeye, steelhead, and Chinook salmon, and higher among natural-origin pink and chum salmon. Straying rates tends to be lower among species that spend considerable time in freshwater (e.g., sockeye, steelhead) than species that emigrate to sea soon after emergence (e.g., pink salmon). Genetic differences in relation to distance between populations therefore tend to be greater for sockeye, steelhead, and Chinook salmon than pink and chum salmon (Wood 1995, Hendry et al. 2004, Quinn 2005, Wood et al. 2008). This suggests that genetic control of locally adapted traits is likely higher in species such as sockeye, steelhead, and Chinook salmon versus pink and chum salmon. Furthermore, life history diversity of populations is greater for sockeye, steelhead, and Chinook salmon than pink and chum salmon (e.g., Wood 1995, Seeb et al. 2004, 2011).

Population life-history diversity is an important characteristic for maintaining abundant and relatively stable populations that can support fisheries. Population diversity effectively maximizes the capacity of a region to support many populations

(e.g., Thorson et al. 2014). The analogy of population diversity has been drawn to the portfolio effect in financial markets in which diversity in assets leads to greater financial stability. An example of the stabilizing effect of diverse populations is shown by natural-origin sockeye salmon returning to Bristol Bay, Alaska during the past 50 years. Standardized variability (coefficient of variation) in annual Bristol Bay salmon returns was estimated to be ~55% lower than it would have been if the system consisted of a single homogenous population rather than the existing several hundred discrete populations with diverse life history traits (Hilborn et al. 2003, Schindler et al. 2010). Furthermore, if it were a single homogeneous population, such increased variability would lead to ten times more frequent fisheries closures.

Consequences for life history diversity and population resilience. Loss of locally adapted populations through extirpation or introgression with non-adapted sources lessens phenotypic and life history diversity, overall productivity, and ecological resilience. For example, the current narrow temporal period of estuarine use by juveniles and upstream spawners (Figure IV.4; Thompson 1951, Bottom et al. 2005a,b) concentrates the feeding, predation and social interactions of hatchery and natural-origin fish. The net result is density dependent effects on

growth and survivorship. Likewise, strongholds for native salmonids and sturgeon are often small and isolated (Wild Salmon Center 2015), significantly constricting the diversity and resilience of remaining populations. Genetic diversity and the associated adaptive traits within populations, plus the diversity among populations across the landscape, are central to maintaining robust and relatively stable populations that can support fisheries.

Novel ecosystem characteristics and life history diversity have direct relevance to density dependence. However, what is the evidence that density dependence is strong and widespread enough to be a serious concern for management?
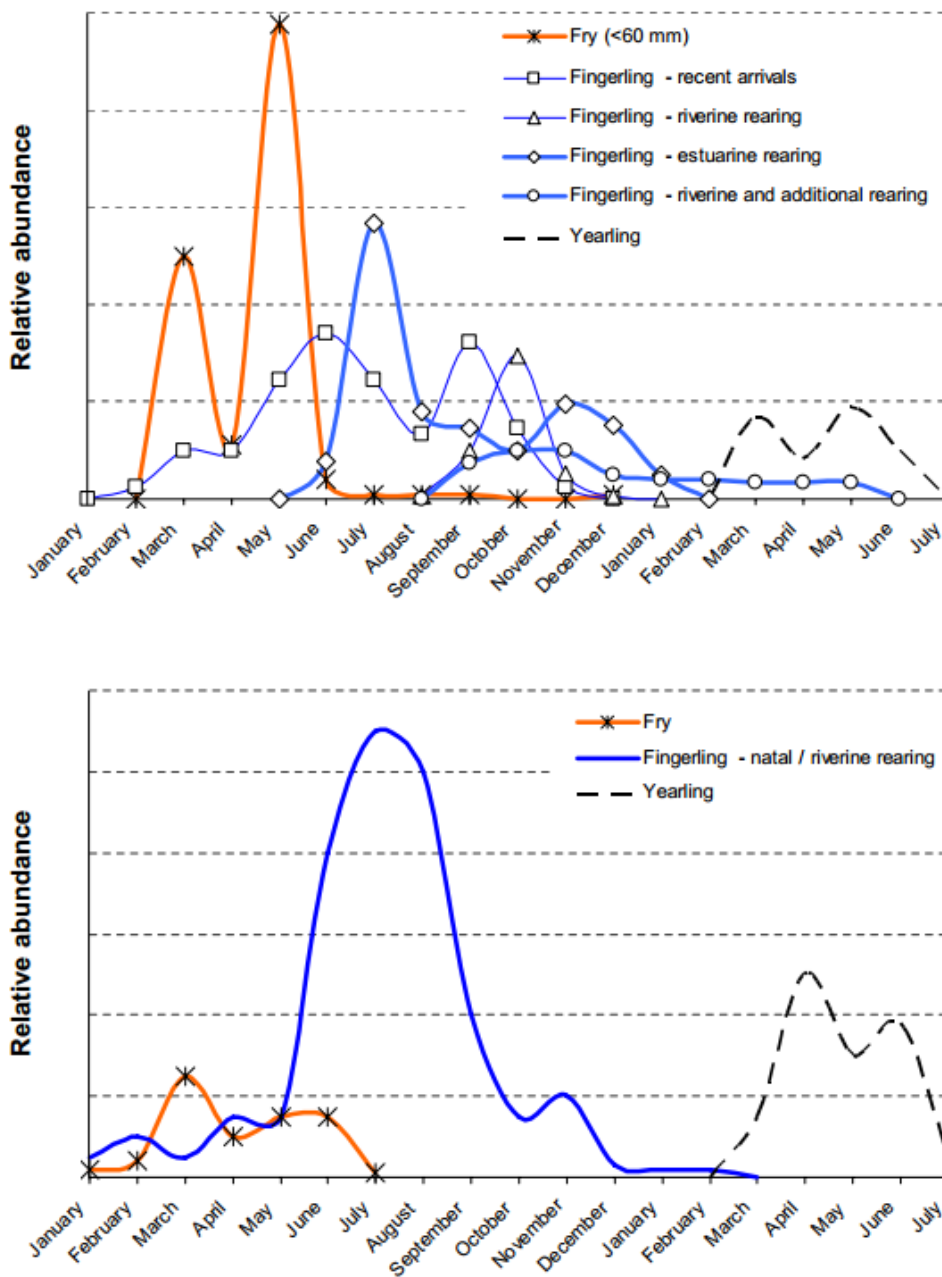
Figure IV.4. Historical and contemporary early life history types for one brood-year of Chinook salmon in the Columbia River estuary. Historical timing and relative abundance (top) based on historical sampling throughout the lower estuary (Rich 1920). Contemporary timing and relative abundance (bottom) derived from Dawley et al. (1986) sampling at Jones Beach. Data were smoothed for appearance (from Bottom et al. 2005b, Fresh et al. 2005)

V. Evidence for Density Dependence among Anadromous Salmonids by Life Stage

The importance of density dependence in the regulation of natural salmon populations is well recognized in the broader scientific literature. In this chapter, we provide emerging evidence that contemporary densities are reducing productivity of salmon populations in the Columbia Basin, implying that habitat capacity is lower now than historically. The issue here is not whether density dependence occurs, but whether strong density effects are being observed in natural populations despite current spawning abundances being much lower than historical abundances.

We begin by presenting evidence of density effects on productivity measured over the entire life cycle of salmon and steelhead (spawners to recruits), followed by evidence during the spawning and freshwater rearing stages, estuarine rearing, and during residence in the ocean (see map of study locations: Figure I.2). This information is supplemented with experimental studies and information from other watersheds for life stages where information is lacking in the Basin (e.g., spawning, estuarine rearing, and the ocean). Many of the examples provided in this chapter include a mixture of natural and hatchery salmonids, but testing for density dependent effects of hatchery fish was not an objective of most of these investigations. The ISAB did not conduct an exhaustive survey of studies within the Basin, but we are confident that most well-developed studies were considered in writing this chapter.

In the next chapter (VI), we provide evidence that competition involving supplementation and large-scale hatchery production may affect density dependent relationships of natural salmonids. In Chapter VII, we examine how predation might affect these density dependent relationships.

A. Life-cycle Density Dependence

Substantial recent evidence demonstrates density dependence within many populations of Chinook and steelhead in the interior Columbia Basin (e.g., Zabel et al. 2006, Zabel and Cooney 2013, Walters et al. 2013a, Cooney 2014; Figure I.2). This evidence stems from recruitment curves relating adult recruits (R) to the number of parent spawners (S), which are central to evaluating status and managing salmon populations (reviewed in Chapter II). The slope of the recruitment curve indicates productivity (R/S) at a specified density of spawners. As noted in the 2014 supplemental Biological Opinion (NOAA Fisheries 2014), high salmon densities can greatly reduce productivity and should be considered when examining population recovery metrics such as productivity or survival (NOAA Fisheries 2014). When carrying capacity is exceeded, productivity falls below 1 (or equivalently, log[R/S] < 0), and recruitment will not be adequate to maintain the high level of abundance. Unfortunately, historical stock-recruitment data from the late 1800s and early 1900s are not available for comparison with contemporary relationships.

1. Spring/summer Chinook

Density dependence was examined in 27 interior Columbia River spring and summer Chinook populations representing the Upper Columbia River Spring-Run Evolutionarily Significant Unit (ESU) and the Snake River Spring/Summer-Run ESU, brood years 1980 to 2005 (Zabel and Cooney 2013). Of these 27 populations, 25 exhibited strong density dependence, as shown by a steep decline in productivity (adult returns per spawner)[9] at moderate spawning abundances (Figure V.1). For example, in the Tucannon River, predicted productivity declined from ~1.7 adults per spawner when 100 parents spawned to only ~0.2 adults per spawner when 900 parents spawned. Thus, at very moderate spawning abundances the population failed to replace itself. As well, in the Lemhi River, predicted productivity declined from ~2.3 adults per spawner when 50 parents spawned to only ~0.1 adults per spawner when 600 parents spawned.

The data in Figure V.1 show that many populations are currently unable to replace themselves at higher parent spawner abundances. The investigators (Zabel and Cooney 2013) did not provide estimates of hatchery salmon on the spawning grounds, but some populations include many hatchery fish (see Chapter VI). The degree to which overcompensation in the Ricker model fits the data should be examined to evaluate the likelihood of fewer adult

returns at the highest observed spawning levels, especially in populations that are being supplemented with hatchery fish. Variability about the predicted regression relationship (line) reflects density independent factors and measurement error.

2. Fall Chinook

Fall Chinook salmon returning to the Snake River Basin (Snake River Fall-Run ESU) exhibited density dependence during brood years 1991-2009 (Figure V.2; T. Cooney, NMFS, presentation to ISAB). Brood year natural recruits increased with greater spawning abundances up to ~6,000 fish and then leveled off except for two large returns from larger spawning escapements (brood years 2007 and 2009). The parent escapement levels in this analysis include natural and hatchery returns to the spawning grounds after harvest and hatchery broodstock removals. Five of the more recent years in the series had spawning escapements (natural origin plus hatchery origin) exceeding approximately 10,000 spawners. Natural production was less than replacement for four of the five brood years (Figure V.2, lower panel). Evidence of overcompensation was equivocal.

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[9] All adult recruitment values in this report include estimates of fish harvested in fisheries so that productivity (R/S) is estimated before the onset of the fishery. Thus, recruitment reflects productivity in the absence of fisheries.

Spring/Summer Chinook Populations
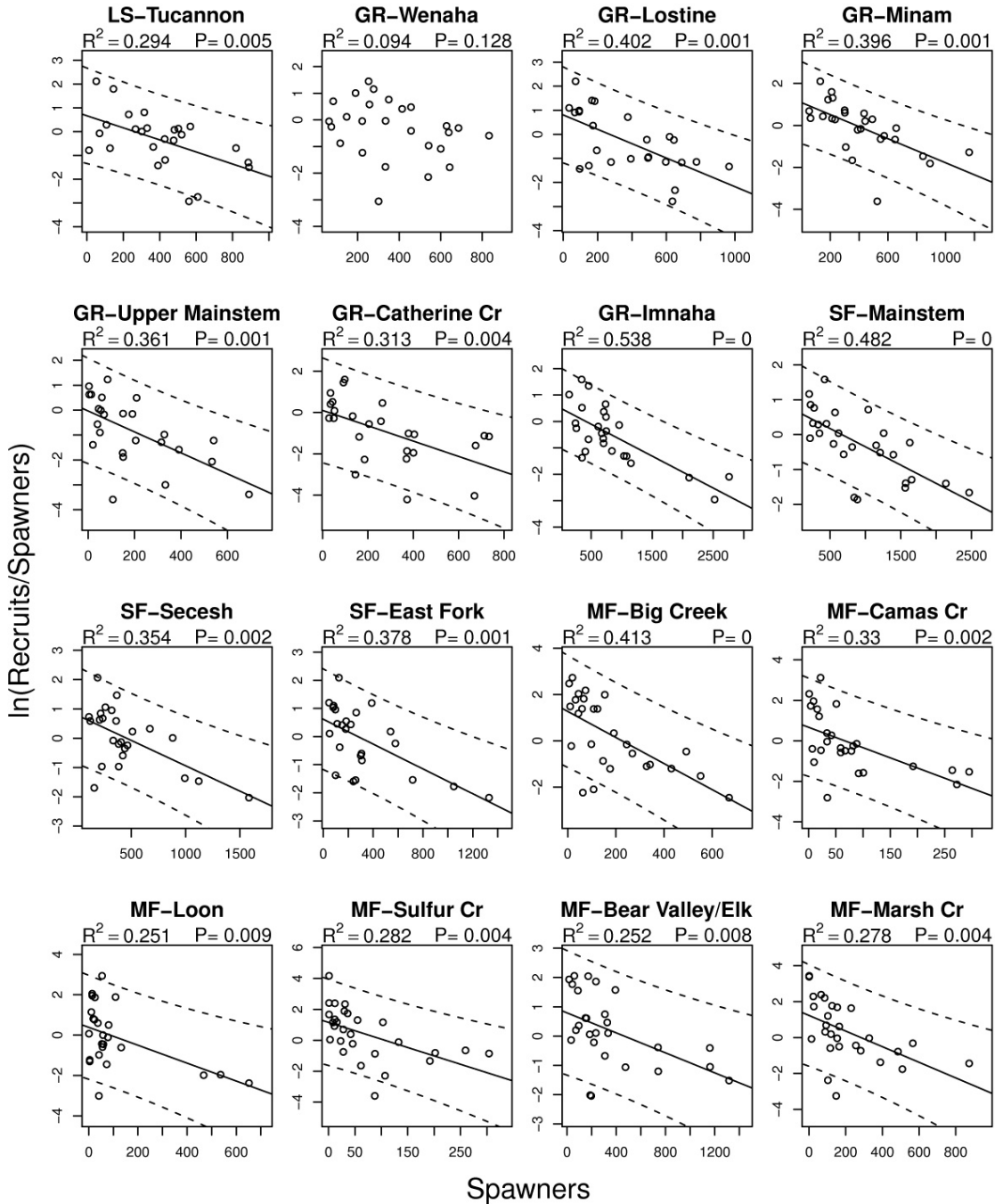
Figure V.1. Evidence for density dependence in 27 Interior Columbia River spring and summer Chinook populations, brood years 1980 to ~2005. Relationships based on the linearized form of the Ricker model. Recruitment includes ocean and in-river harvests. Dashed lines represent 95% prediction intervals for a specified number of spawners when regression was statistically significant (P < 0.05). Values less than log[R/S] < 0 indicate R/S is less than 1. LS = Lower Snake River, SF = South Fork Salmon River, MF = Middle Fork Salmon River, GR = Grande Ronde. Source: Zabel and Cooney (2013).
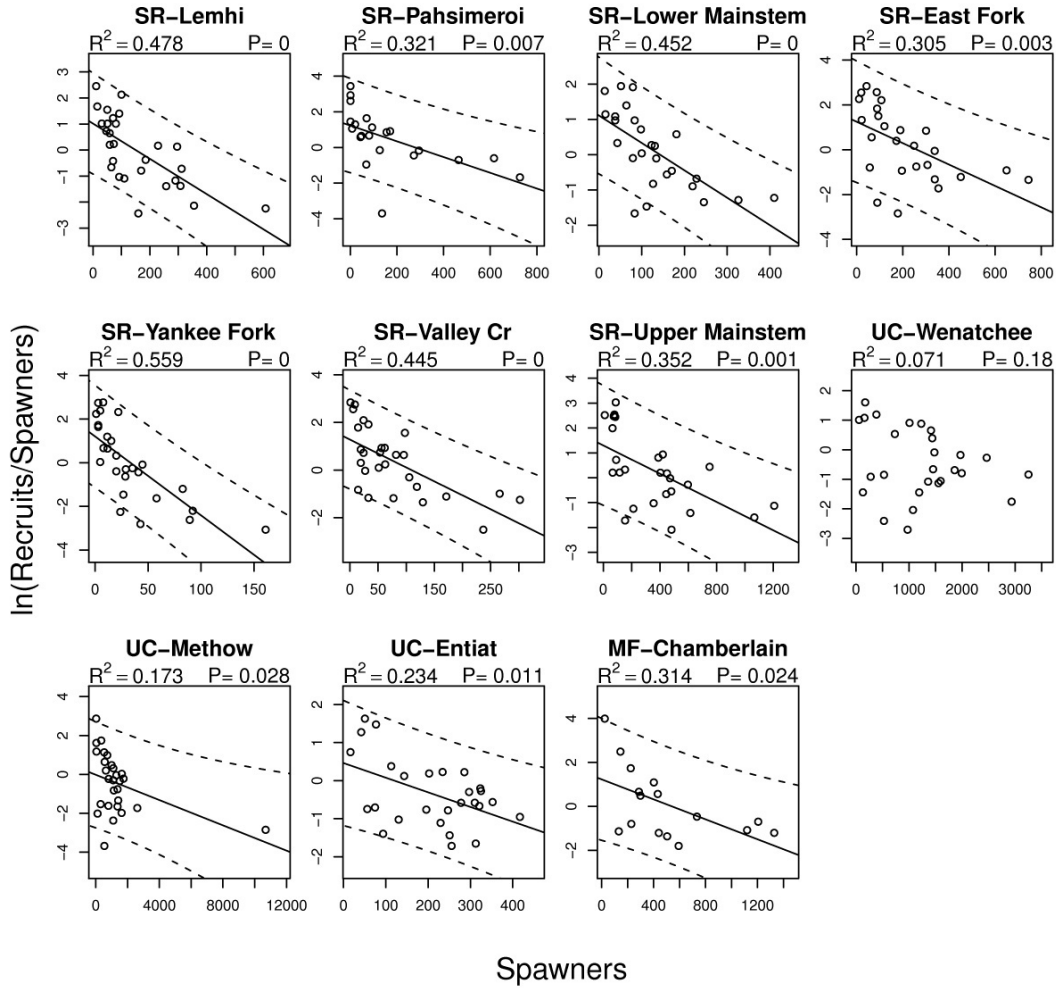
Figure V.1 continued. Evidence for density dependence in 27 Interior Columbia River spring and summer Chinook populations, brood years 1980 to ~2005. Relationships based on the linearized form of the Ricker model. Recruitment includes ocean and in-river harvests. Dashed lines represent 95% prediction intervals for a specified number of spawners. Values less than log[R/S] < 0 indicate R/S is less than 1. SR = Salmon River, UC = Upper Columbia River. Source: Zabel and Cooney (2013).
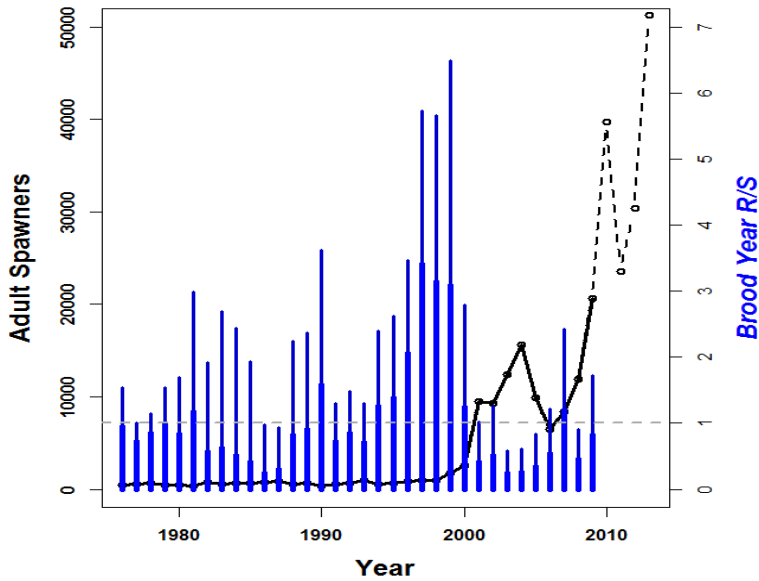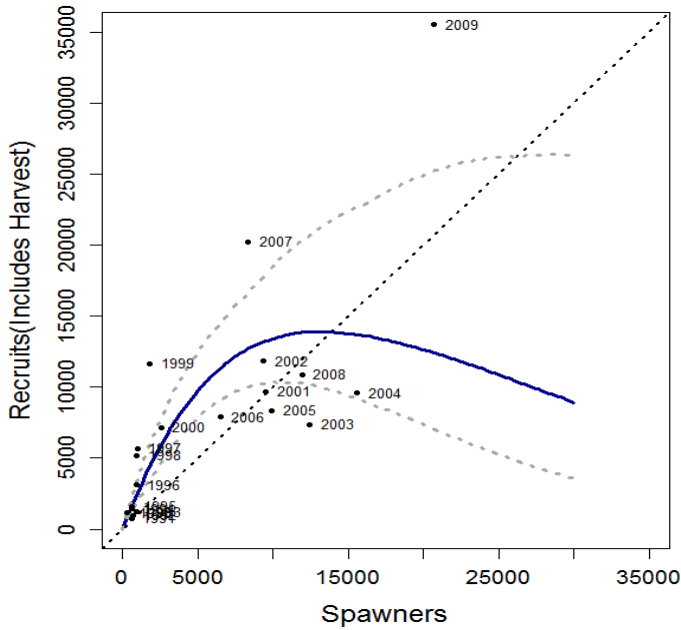
Figure V.2. Ricker recruitment relationship between adult recruits of fall Chinook salmon to the Snake River and the abundance of spawners, brood years 1991-2009 (solid line, upper panel), and the time series of recruitment data used to generate the recruitment relationship (lower panel, 1976-2009). Recruitment in the upper panel includes fish harvested in the ocean and river. The linear dashed line in both panels is the replacement line where recruits equal parent spawners. Adult returns to the Snake River per spawner (R/S) is shown in the lower panel (thick vertical bars; excluding harvests); R/S that incorporates ocean and river harvests (adult-equivalent) is shown by thin vertical bars. Spawning abundance shown through 2013. Source: T. Cooney, NOAA Fisheries, personal communication.

3. Steelhead

Density dependence was observed in all 20 interior Columbia River steelhead populations, brood years 1980 to 2008 (Figure V.3; Zabel and Cooney 2013). These populations encompass three distinct population segments (DPS): Upper Columbia River, Snake River, and Mid Columbia River. In the Wenatchee River (Upper Columbia River DPS), the predicted productivity declined from ~0.4 adults per spawner when 500 parents spawned to only ~0.2 adults per spawner when 5,000 spawned. Adult returns per spawner in the Wenatchee River and in three other Upper Columbia River populations (Entiat, Methow, Okanogan) typically did not exceed replacement (i.e., R/S was < 1), even at the lowest spawning levels, suggesting that the current capacity of the rivers was consistently exceeded or that intrinsic productivity was too low, possibly in response to degraded habitat and hatchery supplementation (see hatchery supplementation discussion in Chapter VI).

 In the unsupplemented North Fork John Day River (~5% hatchery strays; Mid Columbia River DPS), predicted productivity declined from ~3 adults per spawner when 500 parents spawned in the river to only ~0.2 adults per spawner when 5000 parents spawned (Figure V.3). Investigations involving steelhead in the Clackamas River (Lower Columbia River DPS) also indicate strong density dependent recruitment of natural spawning winter-run steelhead, including the influence of hatchery supplementation with summer-run steelhead on the natural-origin winter run (Kostow et al. 2003, Kostow and Zhou

2006). The degree to which overcompensation may or may not be occurring in these and related populations should be examined to determine whether larger spawning populations are producing fewer and fewer adult returns.

Furthermore, direct evidence of density dependence to date does not account for the number of adult steelhead produced by resident rainbow trout spawners. For example, pedigree analyses of Hood River, Oregon steelhead returns indicates that 23% of anadromous steelhead genes come from matings between two resident parents (Christie et al. 2011). Thus, evaluations of density dependence that include only anadromous spawners may underestimate the total number of adult spawners.

4. Life-cycle summary

These examples of salmon and steelhead recruitment in the *interior* Columbia Basin demonstrate that strong compensatory density dependence has been observed in most rivers where data have been examined (26 of 28 Chinook and 20 of 20 steelhead populations), even though natural spawners are much less abundant now than historically. Few recruitment relationships were available for the lower Columbia Basin, such as the region below Bonneville Dam. None of the life-cycle recruitment relationships (Figs. V.1-3) exhibits signs of depensation, suggesting that if depensatory mortality does occur at some life stages, it must be masked by stronger compensatory mortality elsewhere in the life cycle. The presence of overcompensation was not evaluated in most recruitment relationships. The

widespread evidence of density dependence among Chinook and steelhead in the Upper Columbia and Snake River basins indicates that density *independent* factors, such as variable streamflow and temperature, have not been sufficiently strong to mask density dependent relationships. These observations raise several inter-related questions as to when and where density dependence is occurring:

- What life stage(s) are responsible for the density dependence shown in the life-cycle recruitment relationships?
- Is the density dependent response related to the spawning stage where adults compete for suitable habitat to deposit their eggs?
- Or, do juveniles compete for rearing habitat or prey in streams?
- Or, do they compete during both spawning and juvenile stages?

Competition among salmonids for resources may occur in natal rivers, downstream reaches, the estuary, or the ocean. Competition within natal rivers for spawning or rearing resources primarily involves individuals from within those natal areas, including both hatchery fish and other species. The recruitment relationships described above likely involve competition within natal rivers, but they may also reflect dispersal and within-population competition for downstream habitats, to the extent that fish emigrate downstream together. As juveniles emigrate downstream from natal rivers, they encounter additional juveniles from other populations of the same or different species that potentially compete for the same resources. These potential interactions, which are often elusive to untangle, are not specifically estimated in the stock-recruitment relationships described above, but they are still important to the production and resilience of each population and to understanding habitat-specific carrying capacity. Density dependent interactions involving other species can be examined using "extended" recruitment models that attempt to use additional variables to further explain variability in the single-species recruitment relationships (see Appendix I: How to Measure Density Dependence).
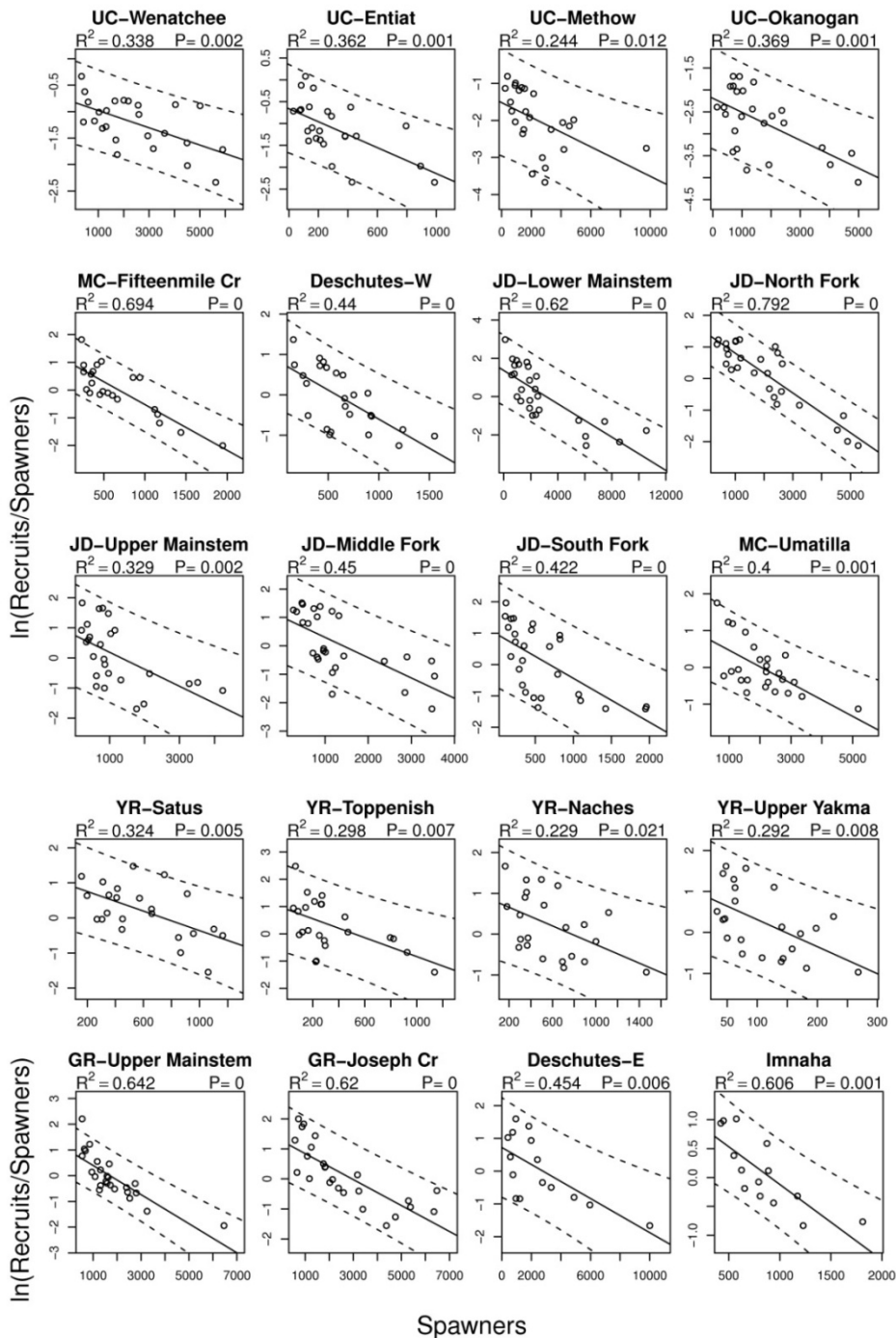
Figure V.3. Evidence for density dependence in 20 Interior Columbia River steelhead populations, brood years 1980 to 2008. Relationships based on the linearized form of the Ricker model. Recruitment includes harvests. Dashed lines represent 95% prediction intervals for a specified number of spawners. Values less than log[R/S] < 0 indicate R/S is less than 1. UC = Upper Columbia River, MC = Middle Columbia, JD = John Day, YR = Yakima River, GR = Grande Ronde. Source: Zabel and Cooney (2013).

B. Density Dependence during the Spawning Stage

Competition for resources can lead to density dependent effects during spawning and incubation. Several behavioral tendencies, including responses to geological and hydrological features in streams, tend to limit where spawning will occur within a watershed. For instance, a number of factors, such as stream geomorphology, water temperatures, and flow regimes influence which stream locations are utilized for spawning (Beechie et al. 2008; Appendix II). Within these stream segments, females respond to many cues–including water velocity, depth, substrate composition, channel gradient, proximity to cover, and river, hyporheic, and groundwater currents—to help identify preferred spawning locations (Bjornn and Reiser 1991). Also, the propensity to return to natal spawning areas can further restrict the portions of a watershed that fish examine for potential spawning locations (Quinn 2005). The end result is that only relatively small portions of a stream may be used for spawning and incubation.

Temporal restrictions on when spawning takes place also exist. Embryonic development in salmonids is largely temperature-driven, and numerous studies have shown that adult maturation timing is strongly linked to the thermal regimes their embryos are expected to experience during incubation (Sheridan 1962, Brannon 1987, Quinn et al. 2002, Beechie et al. 2006). When optimal conditions for newly emerged juveniles occur over a short period of time, adult maturation and subsequent spawning periods are temporally compressed. Conversely, adult maturation and spawning periods may become protracted when optimal conditions for juveniles occur over a broad period of time or are variable (Brannon 1987, Webb and McLay 1996). Thus, spawning site criteria, homing, and juvenile temperature requirements may constrain where and when spawning occurs. Such limitations are likely to create areas where numerous females compete for spawning locations and males compete for mates over a narrow temporal timeframe, even with seemingly low population abundances. Under such circumstances, density dependent factors are expected to affect offspring survival and production (*see* Appendix II for further details).

Few studies in the Columbia Basin have examined density dependence of salmon during the spawning and incubation periods (but see Cooney et al. 2013 and 2014 in section V.C below). Most information presented here is based on experiments conducted on spring Chinook salmon in the Cle Elum Supplementation Research Facility's observation stream (Schroder et al. 2008) and on Puget Sound chum salmon placed into the University of Washington's Big Beef Creek spawning channel (Schroder 1973, Schroder 1977, S Schroder unpublished data).

1. Separating Density Dependent from Density Independent Effects

Sedimentation, streamflow, water temperatures, freezing, and desiccation can be responsible for significant mortality during spawning and incubation. The effects of such density independent factors on a spawning population need to be quantified or controlled before it is possible to assess the impacts of density dependent factors. This can be difficult to accomplish because

both types of influences operate simultaneously on a population. One way to distinguish the effects is by observing fish reproducing in a controlled environment such as a spawning channel or controlled-flow stream. In such a setting, water flows, gravel composition, and spawner densities can be manipulated to expose the effects of density dependent and density independent factors. Artificial streams have been used to examine how differing levels of competition for spawning locations affect spawning behavior and fry production in chum and Chinook salmon. Results from this work, described below, have shown that under some circumstances adult spawning behavior and offspring survival and production can be impaired by compensatory density effects. A question posed when controlled environments are used in this manner is whether the results obtained are applicable to fish spawning under natural conditions. Fish movements may be constrained and environmental conditions are typically less variable than in nature. Additionally, fish could be anesthetized, tagged, and transported to such sites, all of which may affect their reproductive behavior. Despite these possible effects, the ability to manipulate environmental and social conditions and avoid the consequences of confounding factors allows insights to be gained that might otherwise be overwhelmed by natural variation.

2. Compensatory Density Effects

Compensatory density effects are likely in spawning aggregations where resident females compete for egg burial locations.

They may also take place if a spawning location is sequentially used by different females, regardless of species, over the course of a spawning season (*see* Appendix II). Field work performed in nature and in artificial streams indicates that under high instantaneous densities ($\geq$ 1 female/m^2) mean redd sizes decrease (Figure V.4) and the occurrence of agonistic or aggressive interactions, particularly among neighboring territorial females, escalates (Figure V.5). The fact that females vigorously defend redd locations and are not easily evicted often means that some females will be forced to seek new spawning locations, perhaps in less optimal areas. Conversely, some may remain and attempt to reuse spawning areas that become available after a previous resident dies or is too weak to defend her location. In the latter case, significant increases in egg retention rates, pre-spawn mortality (Figure V.6) and redd superimposition (the repeated use of the same spawning location by multiple females) may occur (Figure V.7).

Of all of these effects, redd superimposition accounts for the greatest mortality. For example, Fukushima et al. (1998) estimated that hundreds of thousands of eggs were dislodged per day when 1,000 pink salmon spawned in a 125-m long segment of a southeastern Alaskan stream. Most eggs dislodged by superimposition perish due to mechanical shock or consumption by predators and scavengers. In aggregate, the use of spawning areas by multiple females, either at the same time or over the course of a spawning season decreases the number of offspring that each individual female can produce (Figure V.8).
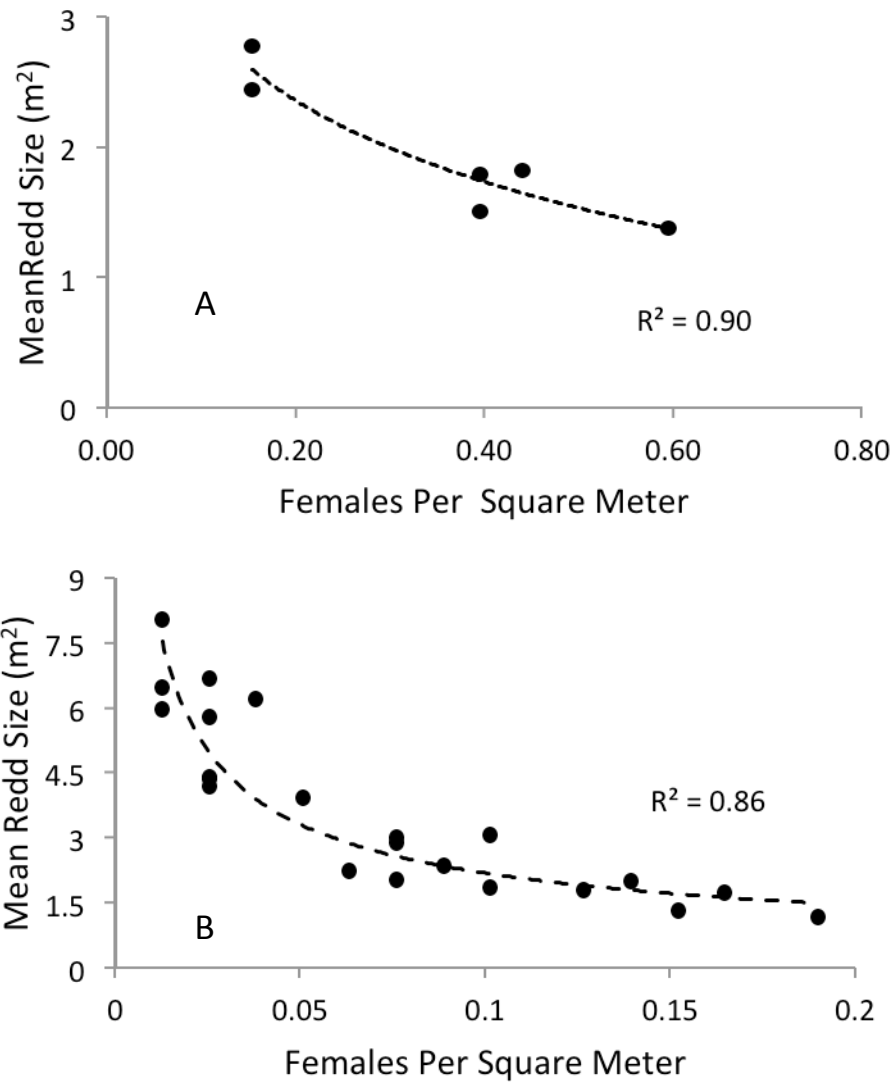
Figure V.4. The effects of spawner densities on redd sizes in chum (A) and spring Chinook salmon (B). Each point represents a mean value taken from fish spawning in discrete sections of the Big Beef Creek spawning channel (chum), Puget Sound (Hood Canal), Washington, or a controlled-flow stream located at the Cle Elum Supplementation Research Facility (spring Chinook), Yakima River, Washington. Grid systems and the cross section paper method (Welch 1948) were used to determine the surface area of redds for 98 chum salmon and 127 spring Chinook salmon. Chum salmon data came from Schroder (1977) while spring Chinook data were provided by S Schroder (unpublished data).
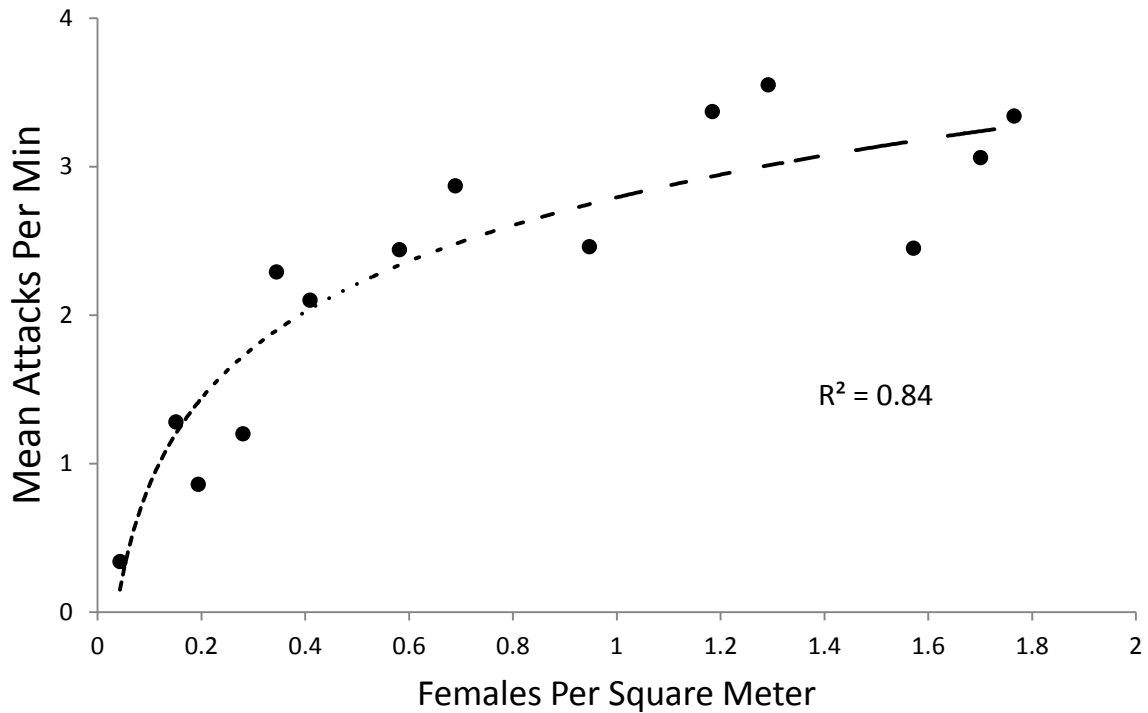
Figure V.5. The average number of attacks per minute experienced by chum salmon spawning under different densities in sections of the Big Beef Creek spawning channel, Puget Sound (Hood Canal), Washington. Each data point represents the mean number of agonistic interactions courting pairs experienced when preparing to spawn. The activities of 141 females and 123 males were recorded for 2,842 minutes. Source: Schroder (1973) and S Schroder (unpublished data).
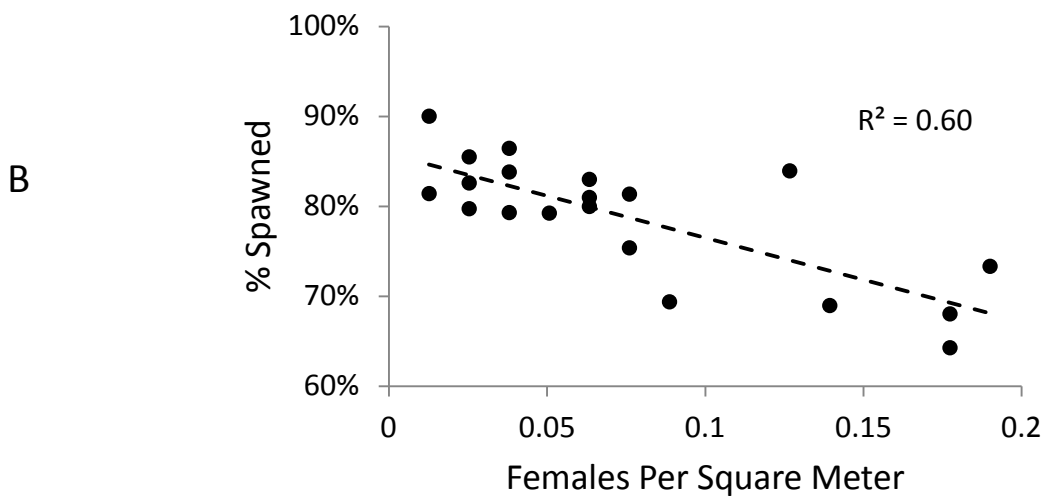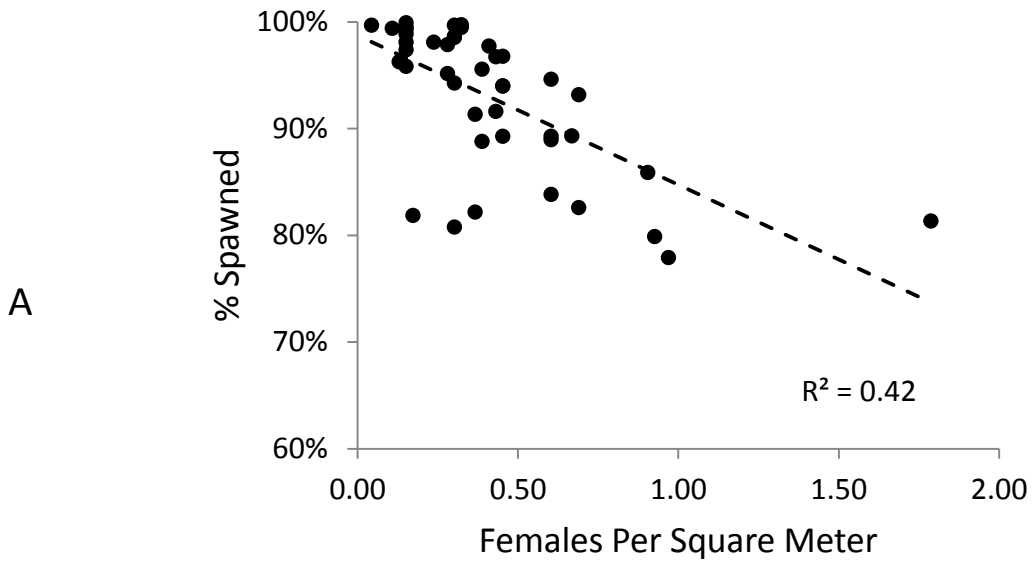
Figure V.6. Relationship between egg retention and spawning densities in chum (A) and spring Chinook salmon (B) spawning in controlled-flow streams. Data points are mean values obtained from 43 separate groups of chum and 20 distinct groups of spring Chinook salmon. Egg retention values were obtained from 840 chum and 119 spring Chinook. The chum salmon relationship came from Schroder (1973) and information from Schroder et al. (2008) was used to create the spring Chinook figure.
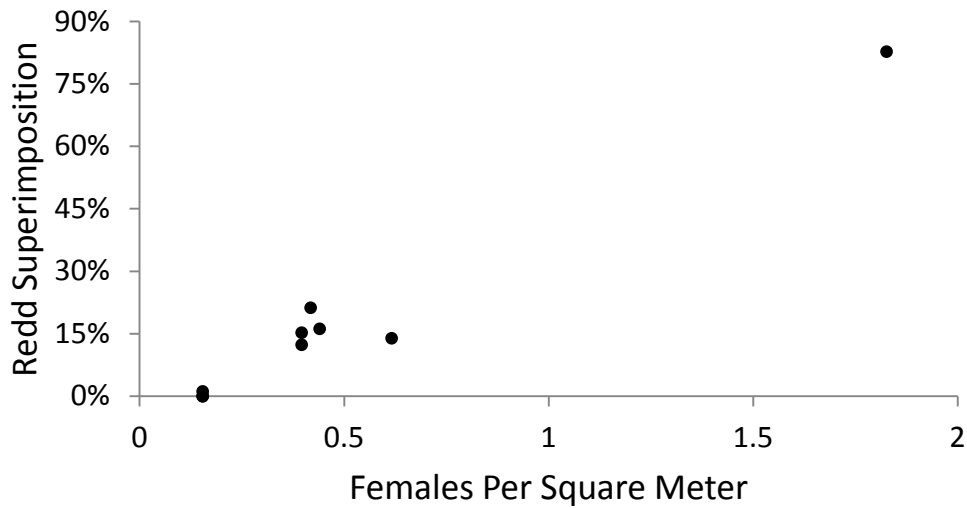
Figure V.7. The occurrence of redd superimposition at different instantaneous spawning densities in chum salmon placed into sections of the Big Beef Creek spawning channel, Puget Sound (Hood Canal), Washington. Each dot represents the percentage of a spawning area that was used by more than one female as determined by using grid systems placed over nine sections of the Big Beef Creek spawning channel. Source: Schroder (1973, 1977).
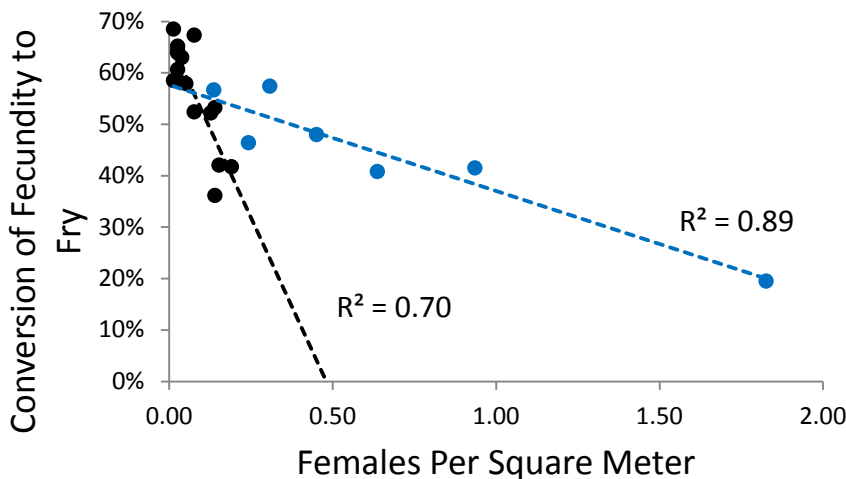
Figure V.8. The effect of spawning densities on fecundity-to-fry survival in chum (blue/grey dots and line) and spring Chinook salmon (black dots and line). Data collected on 480 females placed into sections of the Big Beef Creek spawning channel, Puget Sound (Hood Canal), Washington, were used to create the chum salmon relationship while similar data obtained from 90 females spawning in the Cle Elum observation stream, Yakima River, Washington, were used to generate the spring Chinook association. The steeper slope of the Chinook relationship suggests that this species may not be as tolerant to high spawning densities as chum salmon. Source: Schroder (1974) for chum salmon and Schroder et al. (2008) for spring Chinook.

Data collected on upper Yakima River spring Chinook and Puget Sound chum salmon were used to create Figs. V.4-V.8. Chum salmon along with pink and sockeye often reproduce in dense aggregations and are likely to possess adaptations that accommodate high instantaneous spawning densities. Chinook, coho, and steelhead on the other hand, spawn under lower densities and thus may not be similarly adapted. Figs. V.4, V.6, and V.8 tend to support this contention. For example, as shown here, redds in Chinook salmon start to decrease in size when densities are greater than or equal to 0.025 females per m^2 (1 female per 40 m^2). A comparable compression in chum salmon redd size does not occur until densities exceed 0.10 females per m^2 (1 female per 10 m^2)—a fourfold difference. Similarly, egg retention rates start to increase at densities an order of magnitude lower in Chinook salmon than in chum. In combination, these and other behavioral differences allow chum salmon females to convert more of their eggs to fry when instantaneous densities exceed 0.10 females per m^2 (Figure V.8), suggesting that they are more tolerant to high spawning densities than Chinook. Thus compensatory density dependence during spawning appears to occur at much lower densities for Chinook salmon than in species adapted to higher densities such as chum salmon. This relationship may contribute to the strong density dependence observed in a number of Chinook populations in addition to competition for resources during rearing (Figs. V.1, V.2). For example, there is evidence of crowding on the spawning grounds by Snake River fall Chinook during recent years of high spawning escapement (T. Cooney, NOAA Fisheries, personal communication).

Less is known about the effects of compensatory density dependence during incubation. Heard (1978) examined the disappearance of millions of pink salmon eggs and alevins in a small southeastern Alaskan stream and implicated a form of compensatory density dependence referred to as scramble competition.[10] He found that oxygen levels in the stream were adequate to support millions of pink salmon eggs during early development. However, as the oxygen demands of the developing eggs increased, many died due to oxygen deprivation. Their deaths increased the biological oxygen demand in the intra-gravel environment and created a run-away process that led to the destruction of over 70% of the 11 million eyed eggs that were alive at the beginning of the last half of the incubation period. How important scramble competition for oxygen might be in other spawning locations is unknown. However, as suggested above, a number of factors tend to restrict where salmon spawn which could lead to high concentrations of eggs that might be susceptible to scramble competition for oxygen. Scramble competition for oxygen has also been implicated in significant pink and sockeye salmon pre-spawning mortality events

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[10] Two basic forms of compensatory dependence occur: contest (or interference) and scramble (or exploitation) competition (Chesson 2001). In contest competition there are winners and losers as individuals compete for defensible resources. During spawning this may occur among females for egg burial locations or among males for potential mates. Scramble competition occurs when individuals compete for non-defensible resources. For example, adults and developing eggs may compete for dissolved oxygen—a non-defendable commodity. In this case, all individuals may lose to some extent.

(Figure II.3; Quinn et al. 2007, Shaul et al. 2014).

3. Depensatory Density Effects

The effects of depensatory density dependence become serious when the abundance of a spawning population falls below a critical level and is unable to maintain itself. One depensatory effect at spawning would be the inability to find mates due to a scarcity of fish. Other forms of depensation effects, including a reduced ability to improve stream spawning conditions, impaired group dynamics, and disproportionate losses to predators have also been identified (Liermann and Hilborn 2001). Salmon redds are often found in clusters, and it has been suggested that such aggregations may enhance egg-to-fry survival rates. Montgomery et al. (1996) noticed that the digging actions of spawning chum salmon reduced grain mobility and therefore susceptibility to scouring. They stated that this benefit would only occur if "mass" spawning took place and hypothesized that survival would decrease, possibly leading to extirpation, if spawning densities fell below certain levels. Additionally, a fluid dynamics model produced by Tonina and Buffington (2009) predicted that areas with multiple redds would have high permeabilities and intense hyporheic flows and therefore have better intra-gravel conditions for incubating eggs and embryos than sites with few, scattered redds. Further investigations are needed to determine how important environmental conditions created by spawning salmon might be in enhancing offspring production. Indeed, the prevalence, types, and possible importance of depensatory effects during spawning have not received much attention and could benefit from further research.

Determining how important density dependent effects are during the spawning period on a population basis is a challenging problem. Collecting information on egg retention, pre-spawning mortality, and the degree of redd superimposition that occurred during spawning would help identify whether density dependent factors acting during spawning and incubation were adversely affecting spawning aggregations. Published accounts of such research on Columbia Basin salmonids is not extensive and further work in this area, particularly for Snake River fall Chinook, could be useful for managers. Further details on the possible effects of compensatory and depensatory density during spawning and incubation are discussed in Appendix II.

C. Density Dependent Growth, Emigration and Survival of Juvenile Salmonids

Considerable evidence has been reported for density dependent survival and growth of juvenile salmonids and survival from spawners to smolts in the *interior* Columbia Basin (Achord et al. 2003, 2007; Zabel et al. 2006, Copeland and Venditti 2009, Cooney et al. 2013, 2014; Walters et al. 2013a, Copeland et al. 2014). The following section includes examples involving juvenile spring/summer Chinook salmon from the interior Columbia Basin, followed by Snake River fall Chinook, Snake River steelhead, and Okanogan sockeye salmon (Figure I.2). Some of the studies described below utilize data from the same populations, but the analyses differ. Less density dependence information is available for juvenile coho salmon throughout the Columbia Basin, and for all juvenile salmonids in the lower Basin.

We note that growth of salmonids is often a strong predictor of their survival, age at smoltification, and age at maturation (Evans et al. 2014). However, density dependent changes in growth can be masked by high mortality of slower growing fish and early dispersal of faster growing fish. The implication is that the effects of density on growth measured in the field may be underestimated to the extent that slower growing fish are more likely to die than faster growing fish. Alternatively, density dependent growth may be overestimated to the extent that emigration of faster growing fish has occurred.

1. Spring/summer Chinook

Strong density dependent survival of juveniles within populations of spring/summer Chinook salmon in the Snake River Basin was observed even though adult abundances were only at ~5% of historical levels (Achord et al. 2003, 2007, Zabel et al. 2006). Density dependent recruitment of juvenile spring/summer Chinook salmon was consistently found to be one of the top two variables explaining population viability, indicating that density dependence was more important than many ocean and climate variables (Zabel et al. 2006). Survival of juvenile Chinook cohorts was positively associated with their mean body length (Zabel and Achord 2004), which is often related to density. The stock-recruitment relationship for natural spring/summer Chinook smolts emigrating from Lower Granite Dam (Snake River) indicates the current capacity of this large river is approximately 1.6 million smolts, which is achieved from ~20,000 female spawners (see Figure I.1). Additional spawners beyond ~20,000 females have not produced additional smolts based on data

collected during brood years 1990-2010, highlighting the importance of density dependence to the recovery of ESA-listed salmon populations.

Walters et al. (2013a) expanded upon these early analyses by examining density dependent growth and survival in nine Chinook populations in the Snake River Basin. Beverton-Holt recruitment functions were developed for each population, providing quantitative estimates of intrinsic productivity (smolts per redd) and capacity expressed as maximum smolt production. On average, the intrinsic productivity of each population was 275 smolts per redd and maximum smolt production was 25,710 smolts passing Lower Granite Dam. The Lemhi, East Fork and Crooked Fork populations had the highest level of density dependence and also the highest level of anthropogenic disturbance. Recruitment to the subyearling parr stage was also found to be density dependent, and there was no evidence of overcompensation (Thorson et al. 2014). Density dependence during the spawner to juvenile stage explains some, if not most, of the density dependence described in the life cycle recruitment relationships of these populations (Figure V.1).

Density dependent growth and survival was observed in the migratory parr and smolt life history strategies of these nine Chinook populations (Walters et al. 2013a). Parr represent subyearlings that emigrate from the natal reach during June through November, and overwinter in the mainstem above Lower Granite Dam before migrating to sea during the next spring. Age-1 smolts overwinter in the natal area, and then migrate to sea during March to June. The age-0 smolt and fry migrant life history

types were not considered here because they currently produce few adults. Both migratory parr and age-1 smolt survival from the natal river to Lower Granite Dam decreased with increasing parent abundance, but density dependence was stronger for parr (Figure V.9; Walters et al. 2013a). Density dependent survival appeared to be related to growth, which was reduced at high fish densities (Figure V.10).

Copeland et al. (2014) examined many of the same populations examined by Walters et al. (2013a) and report that dispersal of juveniles to downstream habitats is density dependent. Their conclusion is based on the observation that the proportion of downstream migrants observed in the adult returns increased with total adult abundance, suggesting that more of them had emigrated from the natal river as parr than as smolts as habitat capacity was reached. This pattern highlights the importance of dispersal from limited rearing habitat in the natal stream when the population abundance is increasing. The migratory parr strategy likely evolved as a means for individuals to reduce competition in the natal river, thereby reducing density dependence and increasing population capacity. Thus, the migratory parr life strategy is likely very important for population recovery. Adults that smolt at age-1 (natal reach rearing strategy) are relatively abundant at low adult returns, suggesting the importance of rearing in the natal river for maintaining population stability. In contrast, Walters et al. (2013a) found no statistically significant evidence that movements of juvenile Chinook were related to the density of redds, although each population exhibited density dependent tendencies.

Overwinter survival and suitable habitat affects the abundance of age-1 smolts that emigrate from their natal rivers (Walters et al. 2013a). Juvenile salmonids often inhabit interstitial spaces of rubble while overwintering in streams. In experimental channels, fewer parr emigrated in fall when the rearing substrate was rubble rather than gravel, showing the importance of habitat characteristics in maintaining high population capacity of fish preparing to overwinter (Bjornn 1971). Walters et al. (2013a) hypothesized that density dependent survival occurred primarily during the winter, a period when habitat is limited.

It is hypothesized that density dependence is common in these populations because spawning adults, although less numerous now than historically, are crowded into small areas, leading to high local densities of juveniles (Walters et al. 2013a). Spawning salmon tend to return to the same locations each generation. Consequently, the spawning distribution expands or contracts from a limited number of core areas in response to abundance—as observed in the Middle Fork Salmon River (Isaak and Thurow 2006). The distribution of young salmonids often reflects the distribution of redds, suggesting somewhat limited dispersal into other potential rearing habitats. Walters et al. (2013a) noted the likely influence of marine derived nutrients from salmon carcasses on juvenile growth in these nutrient-limited streams, but noted that studies to date have not demonstrated population increases in response to carcass augmentation (see Ecosystem Benefits of Excess Fish in Chapter VIII). Both nutrient addition and high quality rearing habitat may be needed to support larger populations.

In the Pahsimeroi River, Idaho, spawning density influenced juvenile growth, age at emigration, and survival of spring/summer Chinook salmon during 1992 to 2004 (Copeland and Venditti 2009). Low parent spawning abundances led to greater body growth of all three juvenile life history types examined (age-0 smolt, fall parr migrants, and age-1 smolt) and to greater numbers of age-0 smolts. Lower juvenile densities were associated with faster growing fish, leading to earlier age at emigration. Survival of juveniles migrating from the Pahsimeroi River to Lower Granite Dam was lower at high parent spawning densities, but this density effect was more evident in fall parr (R^2 = 0.55) than age-0 smolts (R^2 = 0.27). However, despite more age-0 smolts being produced when growth conditions were favorable, very few age-0 smolts were detected among returning adults. This might be explained by late emigration of age-0 smolts through the hydrosystem (June and July) compared with fall parr and age-1 smolts (April, early May) and lower survival of late migrating Chinook (Haeseker et al. 2012). Copeland and Venditti (2009) hypothesize that age-0 smolts were historically a productive component of the Pahsimeroi and some other Chinook populations. Given the currently large production of age-0 smolts (i.e., similar abundance to fall parr migrants and much greater than age-1 smolts), they conclude that a small increase in the survival of age-0 smolts to adults would have a large impact on the production and resilience of Snake River spring/summer Chinook salmon, especially the Pahsimeroi and Lemhi populations.

The findings described above are consistent with more recent findings for juvenile summer Chinook salmon in four tributaries of the Grande Ronde watershed where length and survival are negatively correlated with parr density during summer (Cooney et al. 2013, 2014). Streams having degraded habitat had lower capacities compared with less degraded streams, indicating the need for restoration. The analyses indicated that density dependence was greater within the summer parr to spring migrant stage compared with the spawner to summer parr stage, suggesting relatively little density dependence during the spawning stage (T. Cooney, NOAA Fisheries, personal communication). Differences in density dependent relationships by life stages (spawning versus rearing) may be used to guide restoration efforts in the Basin, as described in Chapter VIII. In this example, restoration activities might target the summer and winter rearing of summer Chinook (Walters et al. 2013a), or improvements in the hydrosystem could focus on survival of downstream migrants (Petrosky et al. 2001, Copeland and Venditti 2009, Copeland et al. 2014).

Temperature Intensifies Density Dependent Growth

Crozier et al. (2010) examined the question: *Does Chinook density affect the relationship between juvenile growth and water temperature?* Their 15-year study in the Salmon River Basin provides strong evidence for a negative interaction between mean summer temperature and density even though water temperatures in the high elevation habitats were relatively cool. At low fish densities, mean body length of salmon in August increased with greater temperature; predicted mean length of Chinook salmon increased from 65 mm at 10°C to 90 mm at 15 °C (Figure V.11). However, at relatively high densities, mean

Chinook body length in August decreased with greater temperature; predicted mean length decreased from ~63 mm at 10°C to ~57 mm at 14°C. The relationships were similar among all 13 populations despite heterogeneity in habitat conditions (Paulsen and Fisher 2001).

This study indicates that warmer temperature may intensify density dependent processes. Crozier et al. (2010) suggest that this interaction might be caused by the disproportionate effect of Chinook density on reduced food ration and growth at high temperatures, increased activity due to intraspecific interactions, or habitat shifts to avoid these costs. The density dependent interaction may also be influenced by flow, which is inversely correlated with water temperature (T. Copeland, IDFG, personal communication).

Non-native Brook Trout Can Reduce Compensation

The presence of non-native brook trout (*Salvelinus fontinalis*) appears to alter the density dependent relationship of spring/summer Chinook salmon in the Snake River Basin (Levin et al. 2002, Achord et al. 2003). Survival of Chinook salmon is more strongly density dependent in tributaries without brook trout than in tributaries with brook trout where Chinook density is 30% lower. Low Chinook density is apparently caused by consumption of juvenile Chinook by brook trout. The presence of non-native brook trout reportedly inhibits the compensatory rebound in survival of juvenile Chinook that at low Chinook densities when no brook trout are present. This example suggests that a non-native species can interfere with compensatory density dependence that might otherwise contribute to population stability.

In contrast to these findings, an ecosystem-based model for the summer rearing period of Chinook salmon found little effect of removing brook trout on production of juvenile Chinook salmon (Warren et al. 2014). Instead, adding salmon carcasses to the stream and reducing supplementation with hatchery Chinook appear to provide greater benefits for natural-origin Chinook. Both actions would reduce the influence of density dependence caused by competition for resources.
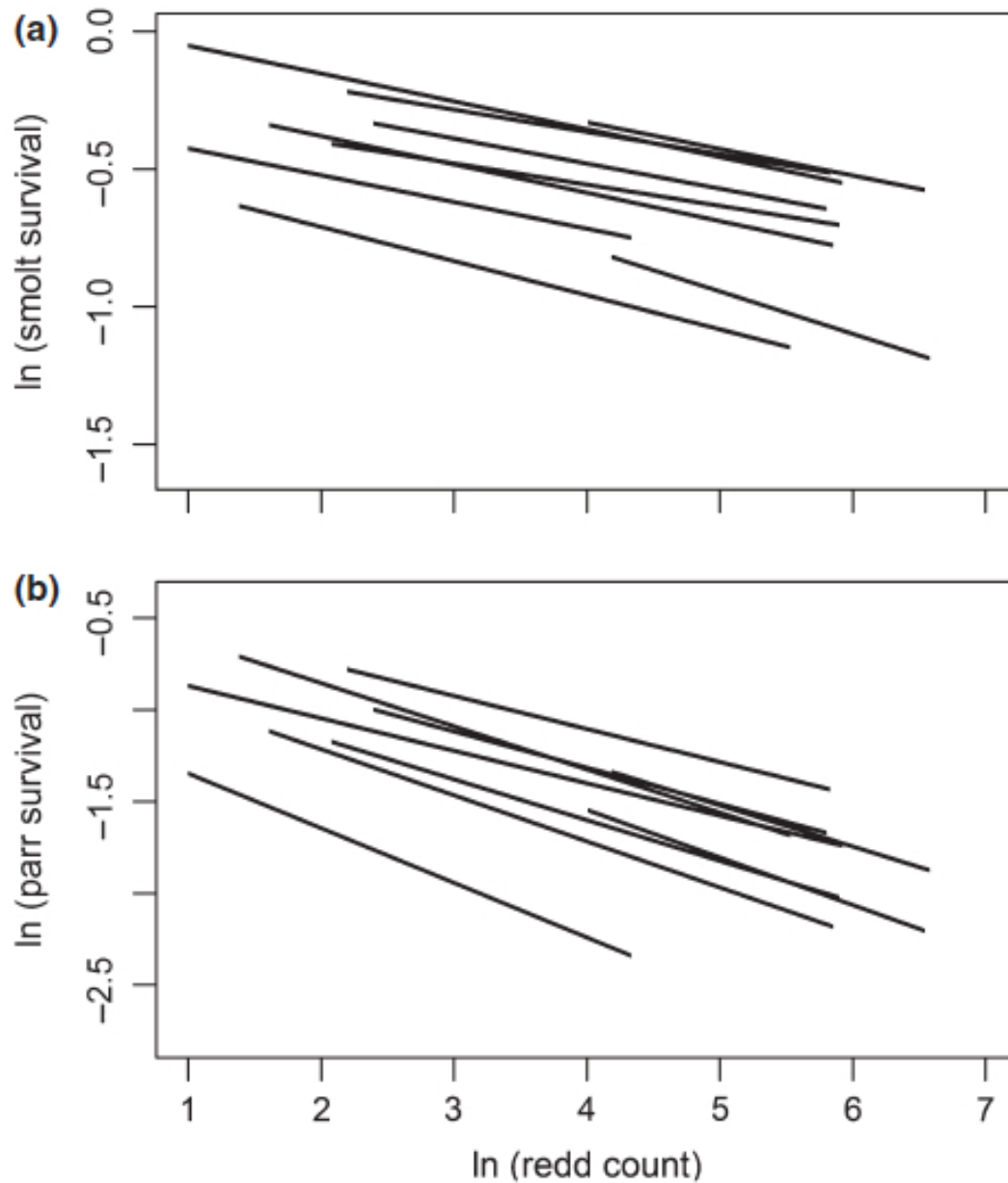
Figure V.9. Population-specific predicted relationships between smolt survival (a) and parr survival (b) of spring/summer Chinook versus an index of parent spawners (redd counts). Survival is estimated from PIT tag data for the period from collection at the traps on the natal river to detection at the Lower Granite Dam (Snake River, Washington). A significant negative relationship (P < 0.05) is evident in all nine populations. The investigators suggest that the steeper slopes for parr reflect higher density dependent mortality during winter. More numerous spawners lead to reduced growth (Figure V.10) and lower survival. Source: Walters et al. (2013a).
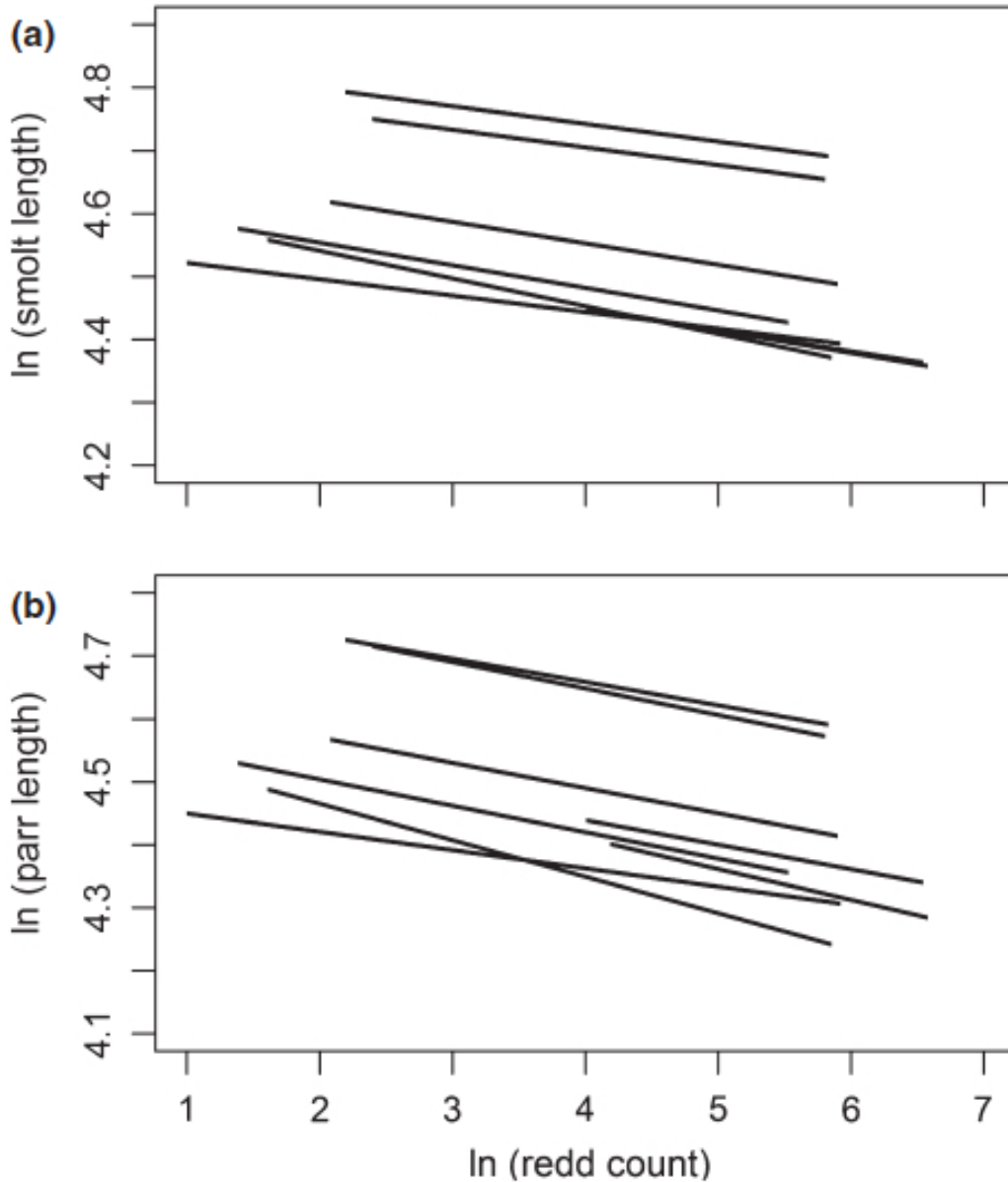
Figure V.10. Population-specific predicted relationships between average smolt length (a) and average parr length (b) of spring/summer Chinook versus an index of parent spawners (redd counts) in the Snake River Basin. Average length values are estimated at traps on the natal river during fall (parr) and spring (smolts). A significant negative relationship (P < 0.05) is evident in all nine populations. Source: Walters et al. (2013a).
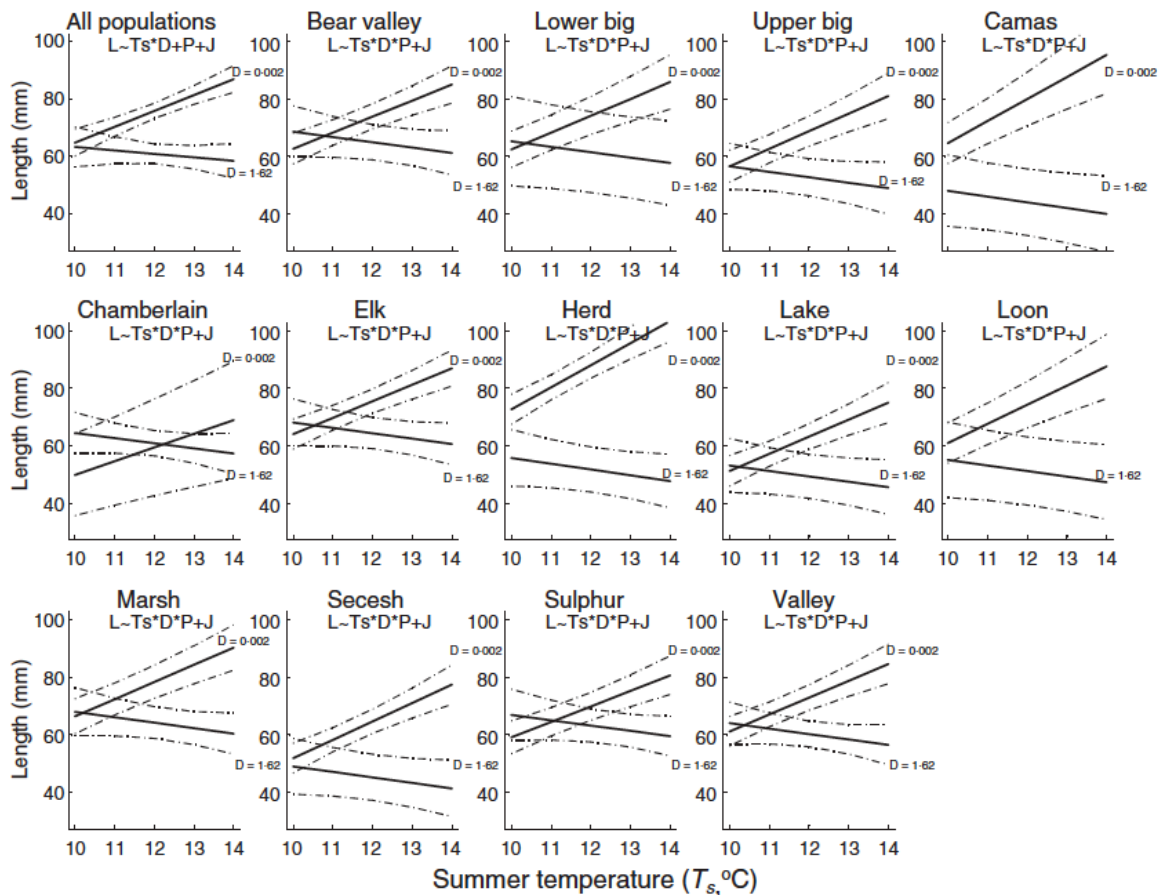
Figure V.11. Model-predicted mean length of juvenile Chinook as a function of temperature at the lowest (0.002 fish per m^2) and highest (1.62 fish per m^2) densities observed in each of 13 Salmon River populations (Snake River Basin, Idaho) during a 15-year period. The upper left plot shows the model prediction without population-specific interaction terms for comparison with the remaining plots that include interaction terms for each population. L = length, T_s = mean March-August air temperature, D = fish density, P = population, and J = Julian date of the sample. Source: Crozier et al. (2010).

2. Fall Chinook

Recruitment of adult fall Chinook salmon to the Snake River Basin shows strong density dependence (Figure V.2). Connor et al. (2013) tested the hypothesis that high abundances in recent years (2000-2011 versus 1992-1999) reduced growth of natural parr in river habitat, hastened their time of dispersal from the river to Lower Granite Dam reservoir, and also reduced growth and altered the emigration timing of smolts through the reservoir and Lower Granite Dam. They found that, when abundance was high, daily growth rate of natural parr in the Snake River did not change, but timing of dispersal from the river to the reservoir was on average 17 days earlier and the length of Chinook at the time of dispersal was on average 10 mm

(1.8 g) less. In Lower Granite reservoir, mean growth rate declined from 0.6 to 0.2 g/day at higher abundance. Abundant non-native prey, which have lower energy content than native prey, contributed to reduced growth in the reservoir versus riverine habitats (Tiffan et al. 2014). The median date of passage through the reservoir was 14 days earlier, and smolts were on average 38 mm (22 g) smaller when emigrating from Lower Granite Dam during the period of high abundance. These density dependent responses were detected while also accounting for temperature and flow in the river and reservoir.

Connor et al. (2013) suggest that the failure to detect density dependent growth of Chinook in the Snake River (riverine habitat above the reservoir) is an artifact of fish sampling and fish behavior. They suggest that PIT-tagged Chinook recaptured in the river may include more competitively dominant fish that held territories in the river habitats, whereas smaller, less dominant PIT-tagged fish may disperse earlier into the reservoir and avoid capture in beach seines. They also suggest that Chinook may switch from territorial behavior in the more complex river habitat to schooling behavior in the homogeneous reservoir habitat. They hypothesize that schooling behavior and the "Pied-Piper effect" (natural fish induced to migrate by hatchery fish) in response to numerous hatchery Chinook may contribute to earlier emigration from the reservoir during periods of high abundance. Earlier emigration reduces exposure to unfavorable warmer water in the reservoir. Migration timing during the high abundance period is more similar to the migration timing prior to construction of the dams.

Early migrating fall Chinook experience higher survival from parr-to-smolt (Connor and Tiffan 2012).

Recruitment of juvenile fall Chinook in the Hanford Reach of the mainstem Columbia River was examined relative to Chinook density and recent constraints on flow fluctuations below Priest Rapids Dam for brood years 1975-2004 (Harnish et al. 2012, 2014). This population is one of the most productive natural Chinook populations in the Columbia Basin. Productivity (presmolts per egg) declined with greater deposition of eggs in the free-flowing mainstem river, indicating density dependence between the spawning and presmolt[11] stages. Productivity of the population improved following management actions to improve flows, especially at the stage of intragravel development. However, the capacity of the population remained relatively unchanged in response to management actions.

3. Steelhead

Steelhead populations in the Upper Columbia River and in the Snake River Basin show strong density dependent recruitment of adults (Figure V.3). Nevertheless, relatively few studies have examined whether density dependence stems from limitations in spawning versus rearing habitat, especially for steelhead (e.g., ISRP 2013-3; see Density Dependence During Spawning Stage). Although density dependence in steelhead is expected to stem from interactions during rearing more than spawning stages (see Chapter II), studies are needed to confirm this

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[11] Presmolts in this study were subyearling juvenile fall Chinook captured along the natal river reach.

expectation. Available studies in the Columbia Basin are summarized below; findings related to supplementation of steelhead populations with hatchery fish are discussed in Chapter VI. Steelhead also interact with resident trout, but these interactions are not addressed in this report.

The number of steelhead emigrants produced in relation to parent spawner abundance has been measured in five tributaries in the Snake River Basin, and density dependence has been detected in each tributary (Figure V.12). For example, in Fish Creek, a mean of approximately 1,500 steelhead emigrants were produced per female spawner when the spawning population was small (~20 females), decreasing to a mean of 200 emigrants per female when the spawning population was high (~240 females). The capacity of Fish Creek to support juvenile steelhead was considerably greater than that of other tributaries, such as Big Bear Creek, where restoration actions are underway to increase productivity and capacity (Figure V.12; Bowersox and Biggs 2012). Density dependence shown for the freshwater rearing stage (Figure V.12, upper panel) was also apparent in adult recruitment (Figure V.12, lower panel), suggesting that density dependence during the freshwater stage could account for most if not all of the density dependence evident in the whole life cycle.
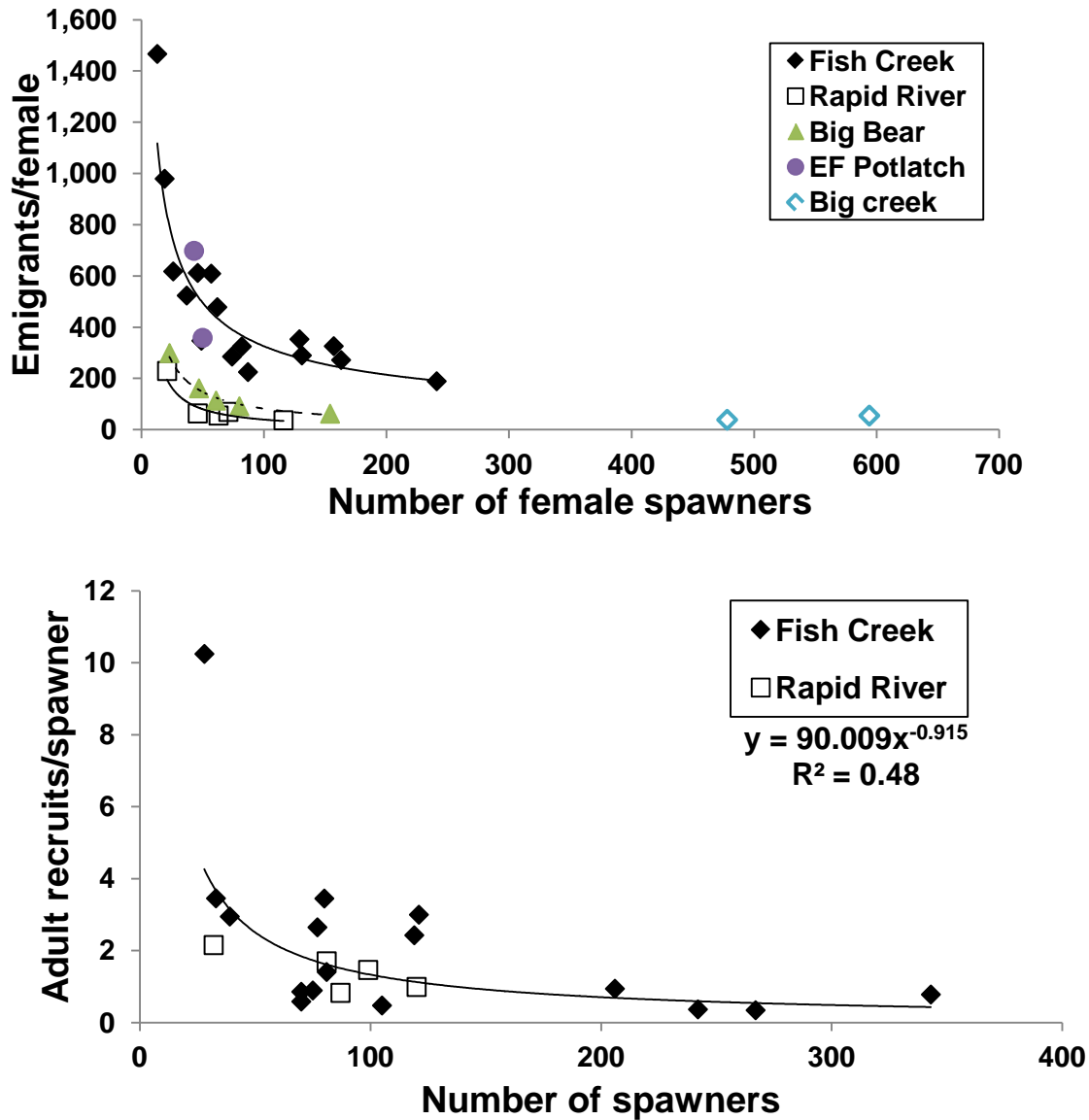
Figure V.12. Relationship between parent spawners and (A: upper panel) juvenile steelhead emigrants per female spawner and (B: lower panel) adult steelhead per spawner in selected watersheds of the Snake River Basin. These examples are in addition to those described in Figure V.3. Source: T. Copeland, IDFG, personal communication.

4. Sockeye

The majority of adult sockeye salmon returning to the Columbia River spawn in Canada in the Okanagan River and rear as juveniles in Osoyoos Lake. In 2004, the Canadian Okanagan Basin Technical Working initiated a detailed experimental and monitoring program to explore the possibility of restoring anadromous sockeye salmon to their former range in the Okanagan watershed, including Skaha and Okanagan lakes. Among other things, this program has assessed the carrying capacity

for naturally spawning sockeye in Osoyoos Lake (and artificially stocked age-0 juveniles in Skaha Lake) by measuring zooplankton production and sockeye growth and survival over eight years in which spawning densities have varied by more than an order of magnitude (<20,000 to >200,000 fish). Age-0 sockeye ("presmolt") density in Osoyoos Lake in the fall has been linearly related to the number of spawners recorded in the previous fall, with no significant relationship between survival or growth rate and presmolt density over a range of 1000-9000 fish per hectare of lake surface (Kim Hyatt, Fisheries and Oceans Canada, unpublished data). Bioenergetic modeling based on zooplankton production, predator densities, and grazing rates, suggests that the pelagic food web in Osyoos Lake could support a maximum of about 15,000 age-0 sockeye per hectare of lake (McQueen et al. 2013). Hyatt and Stockwell (2013) have shown that natural-origin age-0 sockeye production is ultimately limited not by lake rearing conditions, but by the availability of spawning sites in the Okanagan River and down-stream management of harvests and escapement.

5. Interspecific Competition

Density dependent effects on stream-dwelling Pacific salmon may also involve other species of fish (Everest and Chapman 1972, Stein et al. 1972, Sabo and Pauley 1997). Examination of published studies indicates additional rigorous investigations are needed to further evaluate and quantify interspecific competition (Fausch 1998a,b). Few studies of interspecific competition have been conducted in the Columbia Basin (Levin and Williams 2002, Pearsons and

Temple 2010). Additional research on interspecific competition is needed.

6. Summary

In summary, evidence suggests that the higher juvenile densities observed in recent years are sometimes exceeding the current capacity of watersheds to support sustainable natural populations. Most evidence for density dependence during the spawning to juvenile stages comes from studies of Chinook and steelhead populations in the interior Columbia Basin and/or the Snake River Basin. Density of sockeye does not appear to be limiting their current production in the Okanogan River. Few studies have involved coho salmon, and few studies have been conducted in the lower Basin, where numerous subyearling Chinook are released. This information highlights the importance of density effects on population dynamics of many natural populations even at current spawning abundances, which are low relative to historical levels.

The findings of strong density dependence within populations of spring Chinook, fall Chinook, and steelhead (see Sections A and C) generally support our initial findings in Chapter III in which the percentage change in abundance (hatchery and natural-origin combined) versus the available habitat for these species is currently higher than historical values (Figure III.3, Table III.2). However, much of the evidence for density dependence also involves summer Chinook salmon, whose abundance/habitat relationship is much lower today than historically (i.e., current density dependence is expected to be weak). Although strong density dependence might be expected in coho salmon, based on the

relatively high abundance/habitat relationship seen today (Figure III.3). However, we are not aware of studies that tested for density dependence of coho salmon, and we note that most coho production is from hatcheries (i.e., less interaction with coho spawning and rearing in streams). Sockeye rearing habitat and abundance have both declined significantly over time (Figure III.3, Table III.2), and no evidence of density dependence was detected in the Okanogan River population.

D. Estuary Rearing Stage

Whether or not density dependent processes in the estuary contribute to overall regulation of Columbia Basin salmon populations is clearly an important question because all anadromous salmonids pass through the estuary. However, until recently few studies have directly addressed this issue. Early research (1914-1916) to determine juvenile Chinook salmon life histories in the Columbia River estuary (Rich 1920) was followed by a long gap in such research, essentially until the mid-1960s. This research gap may have been due in large part to the then widely held belief that research on density dependence in estuarine and ocean life history stages was unimportant (Fresh et al. 2003).

A food habits study, ancillary to the first long-term (1966-1983) research program on salmonids in the Columbia River estuary, was the first to show limited evidence of density dependence (Dawley et al. 1986). In all four years examined (1980-1983), mean daily stomach fullness of yearling Chinook salmon during the peak period of outmigration (May and June) was negatively correlated with salmonid

abundance (accumulated catch per unit effort of all yearling Chinook, coho salmon and steelhead migrants passing Jones Beach). Overlaps in diet composition of yearling Chinook, coho, and steelhead were significant. In contrast, no density dependent foraging relationships were evident for subyearling Chinook, coho, or steelhead.

Since the 1980s, the prevailing conceptual framework for Columbia River estuary research has been that salmonid species comprise populations that vary in spatiotemporal use of habitats (e.g., Fresh et al. 2003, Bottom et al. 2005b, 2011). Thus, Columbia River estuary research has focused primarily on investigations of estuarine habitats needed to support the diverse life histories of juvenile salmon. Within this conceptual framework, habitat capacity is defined as the *"…qualities that promote salmon production within estuarine habitats, including conditions for feeding, growth, assimilation efficiency, and predator avoidance,"* and is *"…often determined by density dependent biological interactions or bioenergetic relationships"* (Bottom et al. 2011). Therefore, temporary or permanent loss of habitat capacity and diversity in the Columbia River estuary would likely intensify density dependent ecological interactions such as competition, predation, disease and migration, depending on abundances of life history types passing through the estuary.

Total abundances of smolts (hatchery and natural) entering the Columbia estuary might be greater now than in the pre-development period prior to construction of dams in the mainstem river (see Chapter III: Historical Smolt Production), suggesting that the capacity of the Columbia River

estuary to support anadromous salmonid smolts might be exceeded by current smolt production. Levin and Williams (2002) investigated the relation between smolt-to-adult survival of natural-origin Snake River Basin spring/summer Chinook salmon and steelhead and abundance of hatchery steelhead smolts released in the Snake River Basin during the 1977-1994 outmigration years. No relationship between natural-origin steelhead survival and abundance of hatchery steelhead smolt releases was found. The survival of natural-origin Chinook salmon, however, was negatively related to numbers of hatchery steelhead smolts released. The authors speculated that density dependent effects on smolt-to-adult survival probably occurred in fresh water or in the estuary because the early ocean distribution and migration patterns of steelhead and spring/summer Chinook salmon differ greatly. Levin and Williams (2002) speculated that potential mechanisms underlying decreased survival of Chinook salmon smolts included increased feeding competition, stress-related mortality, and increased predation by birds and pinnipeds at high densities of hatchery steelhead smolts.

The ISAB suggests an update of this study since there are now over ten additional years of data, as well as perhaps a better understanding of appropriate ocean co-variables. Concurrent and later studies showed that avian predators seem to be attracted to large concentrations of juvenile steelhead, and large numbers of juvenile hatchery and natural-origin salmonids are consumed by avian predators in the Columbia River estuary (Collis et al. 2001, 2002; Ryan et al. 2001, 2003; Roby et al. 2003, Anderson et al. 2005, 2007). At

present, however, there is little direct evidence of density dependent interactions between hatchery and natural-origin salmonids in the Columbia River estuary (Bottom et al. 2011).

Natural-origin salmonids exhibit temporal, spatial, and trophic partitioning behaviors that reduce interspecific competition in the Columbia River estuary. For example, Eaton (2010) manipulated a tidal channel by adding juvenile hatchery coho salmon, and the smaller juvenile natural-origin chum and Chinook salmon emigrated from the channel; however, altering salmon density did not cause a shift in diets. Bottom et al. (2011) compared current Columbia River estuary use by juvenile Chinook salmon to that in 1916 (Rich 1920). The loss of habitat appears to have reduced the rearing capacity of the estuary for smaller fish after mid-summer. These smaller fish tend to be of natural-origin (natural spawner). The results of a field manipulation (enclosure) in the Chinook River estuary, a tributary of the lower Columbia River, indicated that in April when abundance of drifting terrestrial invertebrate prey is low, threespine stickleback (*Gasterosteus aculeatus*) displaced juvenile Chinook salmon foraging on epibenthic prey by interference competition, resulting in reduced salmon growth rates (Bottom et al. 2011). However, comparison between consumption rates and estimated invertebrate production indicated that exploitative competition between sticklebacks and juvenile Chinook salmon was unlikely (Spilseth and Simenstad 2011), suggesting that displacement caused the reduced growth rates cited above.

The ISAB concludes that there is little direct evidence of density dependent interactions

between hatchery and natural-origin juvenile salmonids in the Columbia River estuary, due to the lack of carefully designed experimental studies. Density dependence is not included as a limiting factor in the Columbia River estuary ESA recovery plan module for salmon and steelhead because of uncertainty about the mechanisms and effects of density dependence in the estuary (NMFS 2011). Instead, the estuary module "*assumes that density-dependent mortality that may be occurring in the estuary is manifested in part through limiting factors related to habitat availability, competition for food and space, disease, and predation*" (NMFS 2011). The estuary module also does not include the effects of hatchery fish as a limiting factor, while stating "*it is likely that hatchery fish influence the estuarine survival of naturally produced fish (possibly through mechanisms of competition, predation, and disease transfer*)."

Due to lack of data on density dependence, competition between hatchery and natural-origin fish for food and space in the Columbia River estuary has been identified in other estuary recovery plans as either a critical uncertainty (LCFRB 2010) or as a secondary limiting factor (ODFW 2010) for juvenile salmonids (NMFS 2013). Nevertheless, multi-state life history models of Columbia River estuary salmonid survival often assume density independence during the estuary rearing stage due to lack of direct data (e.g., NOAA 2010) or lump estuary and early ocean survival (1st ocean summer and fall) into one annual estimate representing both stages (e.g., NOAA 2013). Preliminary life-cycle models with separate steps for estuary and early ocean rearing stages include only the effects of avian predation on survival (NOAA 2013).

Research in other estuaries provides some strong evidence of density dependence and good examples of how density dependence influences natural-origin salmon populations. For example, research in the Puget Sound addressed the connectivity of the freshwater-estuary continuum in the Skagit River and the role of density dependence in movement of juvenile natural-origin Chinook salmon (age 0+) from habitats along that continuum (Sidebar V.1).

The ISAB suspects that density dependent processes in the Columbia River estuary contribute to the overall density dependent regulation of Columbia River Basin salmon populations, as has been demonstrated in other large estuaries like the Skagit River in Puget Sound (Beamer and Larsen 2004, Beamer et al. 2005; Sidebar V.1). Evidence from the Skagit River indicates that larger fish (which have higher survival) force smaller fish out of the prime habitat. However, evidence for the Columbia River estuary is weak because few studies have tested for density dependence. The ESA recovery plan estuary module suggests, "…*the degree of density-dependent mortality occurring in the estuary, the role of large releases of hatchery fish, and the cumulative impact of hatchery releases on density-dependent mechanisms are worth exploring through further research*" (NMFS 2011).

The ISAB considers this an important information gap because a key goal of Columbia River estuary habitat restoration is to reduce limitations caused by density dependence by increasing capacity and productivity—especially for natural-origin subyearling Chinook salmon. Evaluation of restoration activities against current

management goals, such as minimizing impacts of hatchery salmon on natural-origin fish, may be confounded if density dependence in the estuary is not considered.

Sidebar V.1. Density dependent dispersal of juvenile Chinook salmon in the Skagit River estuary and Puget Sound.

Beamer and Larsen (2004) and Beamer et al. (2005) classified Skagit River age-0 Chinook as early (fry) migrants that spent little time in fresh water and late (fingerling) migrants that reared in the fresh water for several weeks (Figure V.13). The capacity of the estuarine habitat to support rearing Chinook (fingerlings) was reached at intermediate juvenile abundances (Figure V.14); density did not increase with additional migrants. Therefore, the proportion of fry migrants bypassing rearing opportunities in the estuary increased with greater population size. Furthermore, size of rearing juveniles decreased with density, indicating a density dependent response among juveniles that reared in the estuary. Fry migrants entered Puget Sound soon after emergence and inhabited "pocket estuaries" along the Puget Sound shoreline until growing and dispersing offshore. This investigation supports the hypothesis that young-of-the-year salmonids move through an estuary and lower-river habitat searching for shallow habitat where they can feed efficiently, grow, and acclimate to increasing salinity while also avoiding predators. If suitable habitat is not available or if it is filled with other fishes, then the juveniles will keep searching for suitable habitat. Juveniles that fail to find suitable estuarine rearing habitat experience higher risk of mortality.
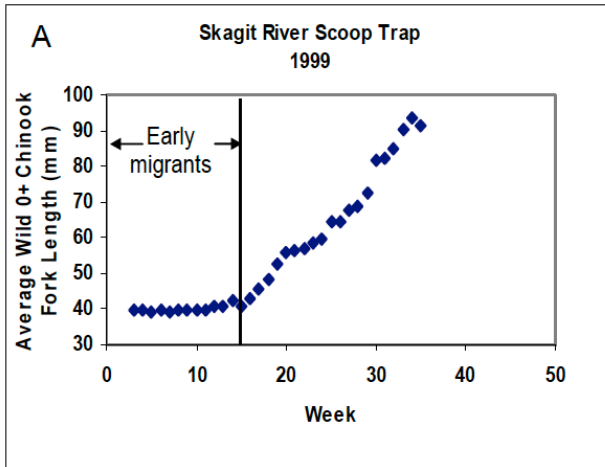
(A) Average length trend of subyearling Chinook salmon moving through the lower Skagit River in example year 1999. Fish captured before week 15 (mid-April) were similar sized reflecting a population that migrated relatively quickly following emergence. After week 15, the average length of juvenile Chinook salmon steadily increased reflecting a population that delayed in riverine habitat long enough to exhibit growth.
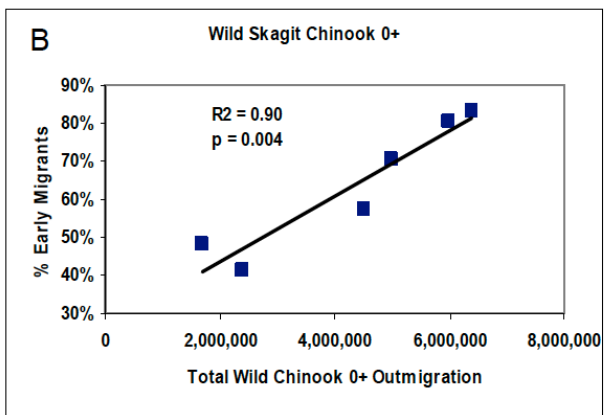
(B) The relationship between total freshwater wild Chinook salmon population size and the proportion of the population that are early migrants (those fish that don't exhibit significant growth in freshwater).
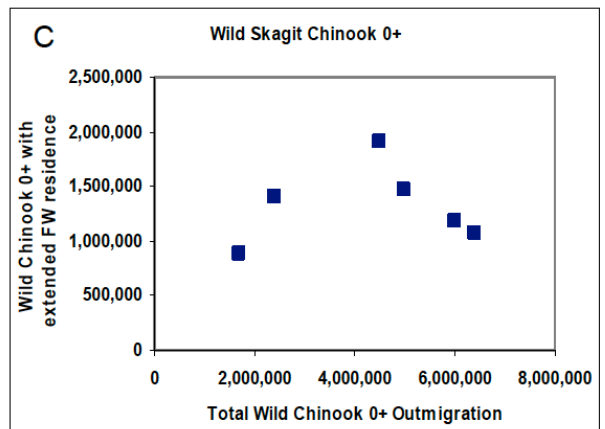
(C) The relationship between total freshwater wild Chinook salmon population size and the number of late migrants (those fish that do exhibit significant growth in freshwater).

Figure V.13. Freshwater outmigration data for subyearling Chinook salmon in the Skagit River, Puget Sound, Washington. Source: Beamer et al. (2005).
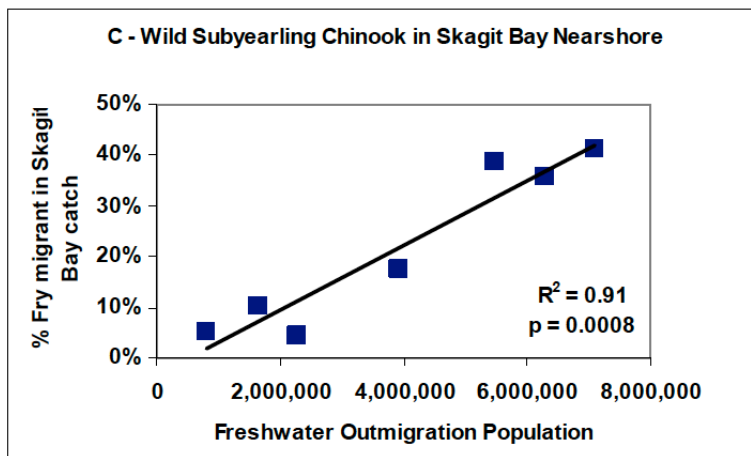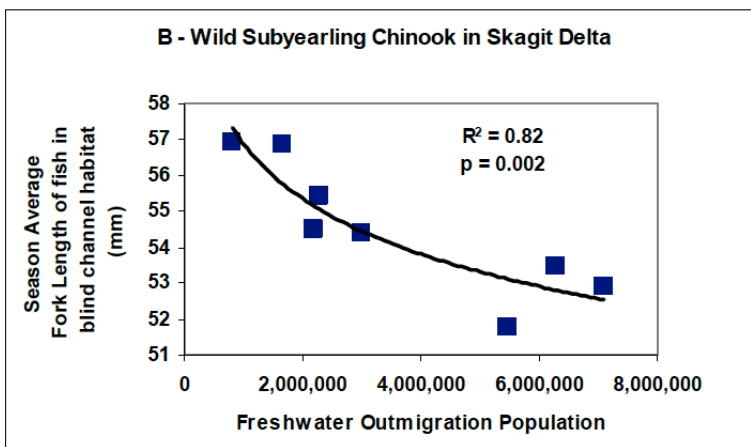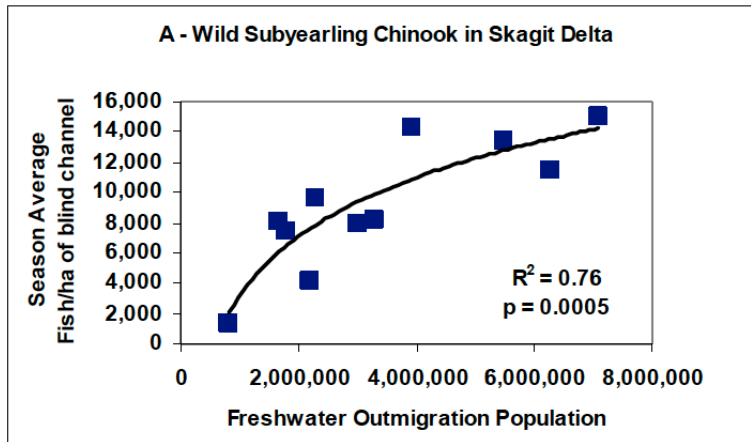
Figure V.14. Density dependence of subyearling Chinook salmon in the Skagit River Delta, Puget Sound, Washington. The charts indicate that Chinook density in the estuary reached its maximum when the outmigrant population was of intermediate size, Chinook length declined with population size, and the percentage of fry migrants in the population increased with population size, reflecting early dispersal of small fry through the estuary when estuarine rearing habitat was saturated. Source: Beamer et al. (2005).

E. Ocean Rearing Stage

Carrying capacity of salmon in the North Pacific Ocean was once thought to be unlimited—a concept that provided much of the original justification for industrial-scale production of hatchery salmon (Peterman 1978, Pearcy and McKinnell 2007). However, a growing body of evidence since the mid-1970s has established the importance of density dependent survival and growth of salmonids during the ocean stage (e.g., see reviews by Larkin 1975, Pearcy 1992, Ruggerone and Nielsen 2004, Quinn 2005, Pearcy and McKinnell 2007, Holt et al. 2008, Nielsen and Ruggerone 2008, NMFS 2014).

Important conclusions from past reviews are:

- The effects of "good ocean conditions" predominate over any density dependent effect (Pearcy 1992);
- The strongest evidence for density dependence pertains to highly abundant species and population complexes of sockeye, chum, and pink salmon (Quinn 2005).
- Pink salmon are the dominant competitor among salmon species in marine waters and can significantly affect population dynamics of other species by reducing prey abundance (zooplankton, squid), leading to reduced growth, delayed maturation, and reduced survival of other salmon (Ruggerone and Nielsen 2004, Ruggerone and Connors 2015)
- Both climate-change effects on salmon carrying capacity in the ocean and density dependent effects on salmon growth and survival are important; the effects vary by ocean life stage.

Relationships between the effects of climate change and density dependence need to be accounted for in salmon life-history models (Nielsen and Ruggerone 2008).

- Industrial-scale releases of juvenile hatchery salmon can result in competition for prey resources and reduced body size of both hatchery and natural-origin salmon populations that share common feeding grounds in international waters of the North Pacific Ocean, with associated reductions in benefits to all salmon-producing nations around the Pacific Rim (Holt et al. 2008).
- The large production of hatchery fish in the Columbia River is a potential source of competitors for the listed ESU's of the Snake River. The arrival of large numbers of fish in the estuary and Northern California Current within narrow time windows could create conditions whereby hatchery fish might compete with and reduce growth rates of listed populations (NMFS 2014).

Despite the importance of density dependence, very few studies have directly tested or even hypothesized density dependence during the ocean stage of Columbia River Basin salmonid populations (Table V.1). In a presentation to the Northwest Power and Conservation Council, Brodeur et al. (2013) summarized the limited evidence for density dependence of Columbia River juvenile salmonids in the Columbia River plume and coastal ocean (California Current ecosystem off the mouth of the Columbia River), and concluded: *"(1) salmon populations, rearing types, and species overlap in distribution and diet* [indicating the potential for density dependent interactions]*, (2) large releases of hatchery salmon may compete with*

natural-origin salmon, especially when ocean conditions are poor; (3) juvenile salmonids are minor constituents of shelf communities in the California Current and food web interactions must be considered to understand variation in salmon production and survival; and (4) predation rates on salmon [which are probably influenced by body size] are difficult to quantify but are likely important to survival and may be related to availability of alternative prey" (www.nwcouncil.org/media/4683221/brodeur.pdf). The ISAB concurs with the Brodeur et al. (2013) summary. More recently, the draft ESA recovery plan's ocean module has identified density dependent ocean growth and survival, especially as it relates to hatchery fish impacts on natural-origin fish, as a key information need for Snake River ESUs (NMFS 2014). The authors of the plan suggest, "*some additional analytical approaches could be taken with existing information (e.g., bioenergetic analyses) to help further refine under what conditions density dependent interactions are likely occurring and how management approaches in terms of release timing can help mitigate effects*" (NMFS 2014).

The ISAB concludes that the lack of scientific knowledge about density dependence of Columbia River salmonids during their time in the ocean is an important information gap that might help explain abundance patterns of natural salmonid resources in the Columbia River Basin. If Columbia River salmonids are limited by density dependence in the ocean, then we may need to take a harder look at the effects of large-scale hatchery

production, especially during periods of low ocean productivity. As stated in the module for the ocean environment (NMFS 2014): "*given the accumulation of evidence that density dependent interactions are occurring under some circumstances, it seems that managing to reduce risks associated with the occurrence of this interaction seems prudent. For example, it seems prudent to spread out hatchery releases to reduce the likelihood of density dependent effects on naturally reproducing fish. Clearly, while this might be effective in managing density dependence in the estuary and NCC* [Northern California Current]*, it may be less likely to work as the fish from the Snake River mix in the ocean with stocks from other regions.*"

Columbia Basin salmon and steelhead migrate thousands of miles into the North Pacific, depending on species and population, and they have the potential to interact with populations originating from distant regions (Myers et al. 2007, Atcheson et al. 2012). If Columbia River fish compete with salmon populations from other countries, then an international dialog is needed (Holt et al. 2008). Holt et al. (2008) recommended formation of a new international organization or amendment of an existing organization to "*encourage collective action to reduce competition among salmon from different nations by using side-payments to change the incentive structure, by establishing a multi-national scientific assessment team to create a common frame of reference for the problem, and by implementing policy prescriptions.*"

Table V.1. Evidence for density dependence (DD) of Columbia River salmon and steelhead during the ocean rearing stage. Evidence type/strength: studies either tested DD (T) or hypothesized DD (H); evidence in the studies was considered by ISAB to be weak or correlative (W) or strong (S).		
Evidence type/strength	**Major findings**	**Reference**
Coastal marine, hatchery-natural-origin competition, juvenile spring/summer Chinook (T) (W)	This study found a negative relationship between the number of spring/summer Chinook salmon released by hatcheries in the Columbia River Basin and smolt-to-adult survival of natural-origin Snake River Basin spring/summer Chinook salmon during years (six) when nearshore ocean productivity was low (1982-1983, 1990-1992, 1997). No apparent relationship was found between abundance of hatchery salmon and survival of natural-origin salmon during years of average ocean productivity near the mouth of the Columbia River.	Levin et al. 2001
Coastal marine, hatchery-natural-origin competition, juvenile Chinook (H) (W)	Research vessel (trawl) survey results indicated high overlap in spatial distribution of marked (hatchery) and unmarked (natural-origin) juvenile Chinook salmon in the coastal waters of Oregon and Washington from May to June (1999-2009), although abundance of natural-origin fish was low compared to hatchery fish. Hatchery fish were longer (fork length) than natural-origin fish, but body condition during peak catches in May was significantly greater in natural-origin fish. Diets, feeding intensity, and growth of both groups were similar and catch, length, body condition, feeding intensity, and growth of both groups responded similarly to ocean conditions. Daly et al. (2012) concluded that "varying the number of hatchery fish released in response to perceived ocean conditions could assist us in understanding potential density dependent growth suppression and competition between hatchery and endangered and threatened naturally-produced salmon."	Daly et al. 2012
Coastal marine, competition w/forage fish and predation, juvenile Chinook (T) (S)	The authors used statistical models to evaluate interacting effects of translocation, artificial propagation, and environmental conditions on the marine survival of Columbia River Chinook salmon in 1998-2006. Increases in both forage-fish and predator densities in coastal marine waters were strong predictors of large decreases in survival of hatchery and (especially transported) natural-origin fish. The authors found slightly more evidence for "apparent" competition between salmon and forage fish (through increased predation by mutual predators) than "direct" competition through shared prey resources.	Holsman et al. 2012
River, plume, coastal marine; competition, juvenile Chinook	This study investigated the hypothesis that variation in size, growth, and condition of juvenile (sub-yearling) upper Columbia River summer-fall run Chinook salmon is related	Miller et al. 2013

Evidence type/strength	Major findings	Reference
conspecifics (T) (W)	to the density of conspecifics in the river and coastal ocean during emigration and/or variation in river, plume, and/or ocean conditions. Results showed that >95% of the variation in adult returns was related to physical (river plume volume during emigration) and biological (condition) variables and their interaction. There was no evidence of density dependence in size, growth, and condition in the river or coastal ocean, but the authors cautioned that this may be due to (1) relatively low juvenile abundance, resulting in limited capacity for intraspecific competition or (2) inadequate spatial coverage of ocean sampling. The results also indicated that during years with good ocean conditions otolith growth and body condition of juveniles in September (but not in June) were relatively low compared to years with poor ocean conditions. The authors concluded that top-down effects (e.g., selective mortality) or competition are important during early marine residence.	
Estuary, plume, coastal marine; hatchery-natural-origin competition, juvenile steelhead (H) (W)	The study compared distribution, migration, feeding, and growth of hatchery (marked) and putative natural-origin (unmarked) juvenile steelhead in the Columbia River estuary, plume, and coastal ocean (1998-2011). In both the estuary and ocean, natural-origin steelhead had higher feeding intensities, fewer empty stomachs, better condition, and slightly higher growth than hatchery fish, and both hatchery and natural-origin steelhead smolts migrated westward and quickly (within ~ 10 days) offshore after ocean entrance.	Daly et al. 2014
High seas, competition, immature steelhead and pink salmon (H) (W)	Data from annual high seas surveys in the central North Pacific Ocean (CNP, June-July 1991-2009) and Gulf of Alaska (GOA, June-July 1993-2002) were used to identify potential trophodynamic and environmental drivers of steelhead productivity in international waters of the North Pacific Ocean. The authors found that indicators of good steelhead diets (high proportions of squid and high prey energy density) in the CNP were negatively correlated with the abundance of natural-origin populations of eastern Kamchatka pink salmon. The CNP survey transect along the international dateline (180°-longitude) is near the center of the known high seas distribution of Columbia River Basin steelhead, as indicated by high seas tag recovery data. There was no evidence for competition between steelhead and North American pink salmon in the GOA. Population-specific density dependence could not be evaluated due to the lack of a comprehensive genetic baseline for Asian and North American steelhead.	Atcheson et al. 2012

VI. Hatchery Effects on Density Dependence

Hatchery production in the Columbia Basin is designed to support fisheries, mitigate lost production due to hydrosystem development, rebuild depleted natural populations, and prevent extinction. Hatchery programs designed to support fisheries typically release numerous juvenile salmonids and often employ a segregated hatchery approach[12] whereby the returning adults are to be harvested and ideally contribute little to the natural spawning population (Paquet et al. 2011). Supplementation hatcheries attempt to use an integrated hatchery approach to help rescue populations that might otherwise become extinct. The intent of supplementation is to maintain the long-term fitness of the natural population while also staying within the capacity of the habitat to support the population (ISAB 2003-3; ISRP/ISAB 2005-15).

A decline in adult return per spawner in response to greater spawner abundance (hatchery and natural origin) is an expected outcome from supplementation but return per spawner should be maintained at or above replacement (R/S ≥ 1), i.e., the natural population level is within its capacity and is therefore viable. Supplementation beyond the capacity of

the watershed to support the hatchery and natural population may not produce additional adults in the near term, but excessive spawning might provide ecosystem benefits in the future. The Council's 2014 Fish and Wildlife Plan ([NPCC 2014-12](#)) implicitly recognizes the need to balance the level of supplementation with the capacity of the watershed and with the existing salmonid population.

There are four key questions addressed in this Chapter using several case studies primarily from the Basin:

1. How many hatchery-origin salmonids contribute to the natural spawning populations in the Columbia Basin?
2. Is the capacity of watersheds to support natural salmonids exceeded with the addition of supplementation and hatchery salmonids?
3. To what extent will an increased density of hatchery fish, released for the purpose of rebuilding natural populations or augmenting fishery harvests, inhibit a rebound in productivity of naturally spawning populations over that expected at low abundance?
4. What are the near-term consequences of exceeding the carrying capacity of the watersheds with supplementation and hatchery salmonids?

A. Hatchery Contributions to Natural Spawning

Many natural populations in the Basin are supplemented with hatchery spawners and juvenile releases from hatcheries, which

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[12] A segregated hatchery approach uses few natural origin fish in the hatchery broodstock and attempts to minimize straying of the genetically distinct hatchery fish to the spawning grounds. An integrated hatchery utilizes a large percentage of natural origin salmon in the hatchery broodstock and encourages a portion of returning adults to spawn in streams. A viable natural population is necessary for a successful integrated approach (see Paquet et al. 2011; ISRP 2010-44).

therefore contribute to density dependence in these natural populations. Hatchery fish on the spawning grounds stem from intentional supplementation to rebuild populations as well as the inability to effectively harvest or collect for broodstock all surplus hatchery salmon produced by some segregated production hatcheries. NOAA Fisheries[13] reports annual proportions of natural spawners in many watersheds that are of hatchery origin (pHOS), but this database does not distinguish between those released from supplementation versus major production hatcheries. In its status reviews, NOAA Fisheries does consider natural spawning of hatchery fish originating from supplementation versus production hatcheries (T. Cooney, NOAA Fisheries, personal communication).

The Hatchery Scientific Reform Group (HSRG) estimated the percentage of natural spawners originating from hatchery fish for each Chinook and steelhead population in the Columbia Basin (L. Mobrand, personal communication). All but one Chinook salmon ESU includes 30% or more hatchery-origin fish on the spawning grounds. One ESU (Snake River fall Chinook) included approximately 80% hatchery-origin spawners (Figure VI.1a). Only the Deschutes River summer/fall Chinook ESU contained less than 5% hatchery spawners. Each steelhead DPS contained >15% hatchery fish on the spawning grounds (Figure VI.1). Approximately 80% of the steelhead spawning in Upper Columbia River streams are of hatchery origin (Figure VI.1). Natural spawning of coho salmon in the lower

Columbia Basin appears to include numerous hatchery salmon (www.webapps.nwfsc.noaa.gov; Ruggerone 1999). In contrast, hatchery contributions to upper Columbia River sockeye salmon are likely low because few hatchery sockeye are released into this area relative to natural population size. Little information is available for the survival of approximately 250,000 hatchery chum salmon fry and their contribution to natural spawning chum salmon in the lower Columbia River Basin (Figure III.2).

In Chapter V, we presented evidence for strong density dependence among 48 interior Chinook and steelhead populations (Figs. V.1-3). Hatchery spawners contributed to the density dependence in some but not all of the populations (www.webapps.nwfsc.noaa.gov). For example, supplementation occurred in 14 of the 27 spring/summer Chinook populations examined and 12 of 20 steelhead populations (Appendix III). The current capacities of both natural-origin and supplemented populations were exceeded in approximately 50% of the years, as indicated by R/S < 1.

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[13] https://www.webapps.nwfsc.noaa.gov/apex/f?p=238:home:0
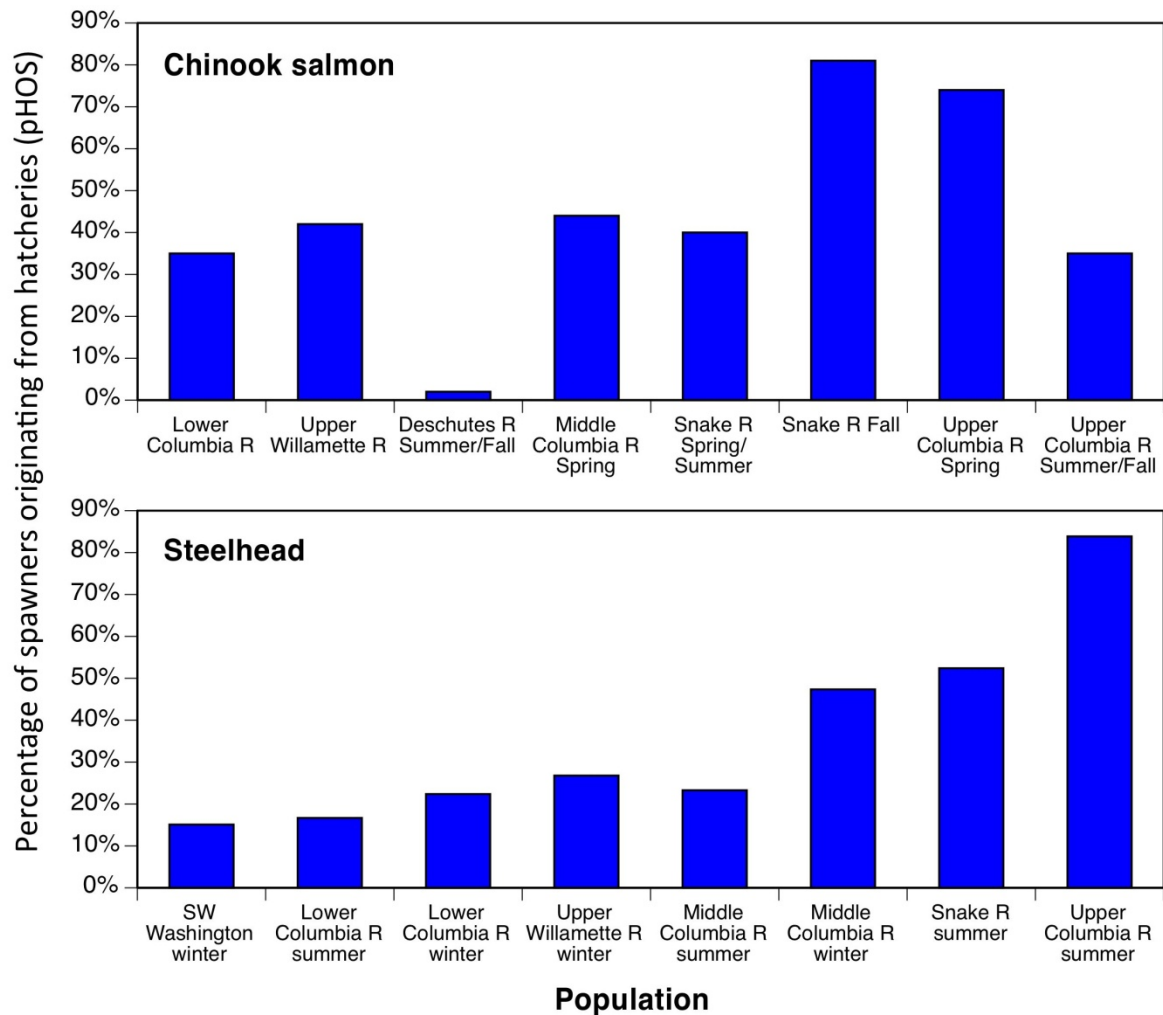
Figure VI.1. Estimated proportion of naturally spawning Chinook salmon and steelhead in each ESU or DPS that originated from hatcheries (pHOS). Modeled data provided to ISAB by L. Mobrand, Hatchery Scientific Reform Group, February 2013.

B. Hatchery Effects on Salmonids

1. Snake River Spring/Summer Chinook

Preliminary modeling indicates that hatchery supplementation of spring/summer Chinook populations in the Snake River Basin did not produce the intended boost of natural origin returns even though total spawning abundance had increased (Buhle et al. 2013, 2014). The investigators examined whether the addition of hatchery-derived spawners altered density dependent relationships for natural Chinook populations and whether supplementation led to increased smolt production in the Snake River spring/summer Chinook ESU. The analysis involved 24 populations, including 13 supplemented and 11 non-supplemented populations. Eight of the 13 supplemented populations used local broodstock, consistent with an integrated hatchery approach. Many populations are the same as those shown in Figure V.1, where strong density dependence was observed across the entire life cycle. The study period spanned 46 years (brood years 1962-2007), and the Beverton-Holt recruitment model was used (Buhle et al. 2013, 2014).

Strong evidence for density dependence was observed in all 24 Chinook populations in the Snake River Basin (i.e., supplemented and non-supplemented populations), consistent with life-cycle analyses of these populations presented in Chapter V (Figure V.1). However, preliminary analyses indicate that maximum smolt production per unit area (capacity) was more than doubled when no hatchery fish contributed to the spawning population, as compared to a modeled scenario when all spawners originated from hatcheries (Figure VI.2). Unexpectedly, intrinsic productivity was higher for hatchery versus natural origin recruit (NOR) parents (Figure VI.2a). The unexpected higher intrinsic productivity of hatchery spawners was attributed to too few data points at low spawning densities in this unplanned experiment. Further modeling of smolt recruitment indicated that smolts produced by hatchery spawners were offset by reduced smolt production of NOR spawners. Therefore, inclusion of additional hatchery spawners did not lead to greater total smolt production even though hatchery spawners contributed to a larger spawning population. Consequently, a shift toward a higher percentage of hatchery spawners may reduce per capita productivity enough to outweigh the numerical advantage of adding hatchery fish to the spawning population. The lack of a significant population boost in response to supplementation is shown for nine of the 13 supplemented populations examined by Buhle et al. (2013, 2014; Figure VI.3). Only four of the 13 populations tended to produce additional smolts due to supplementation with additional hatchery fish.

The capacity of subyearling parr was estimated to be 5,000 fish per hectare, on average, in 15 Snake River tributaries (based on data collected from 1984-2008; Thorson et al. 2014). The investigators concluded that hatchery supplementation efforts seeking to increase parr abundance above 500 parr per hectare will often not increase production in many of the populations.
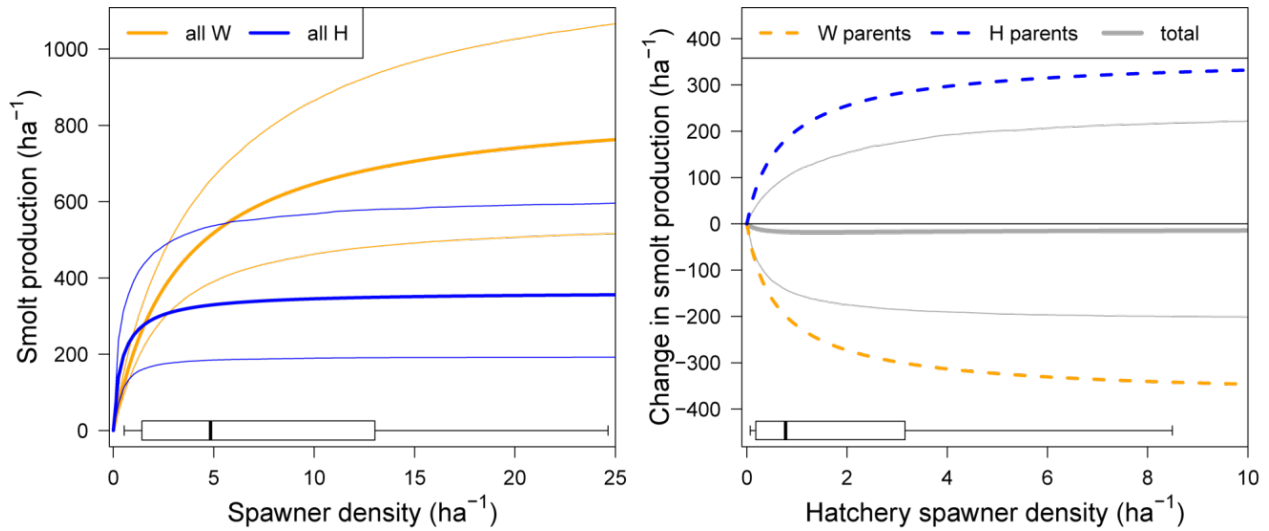
Figure VI.2. Left graph: Predicted production of spring/summer Chinook smolts in the Snake River Basin, assuming all NOR parents (W) or all hatchery-origin parents (H). Right graph: Change in smolt production as hatchery spawner density increases relative to the unsupplemented case. The boxplot (near graph bottom) shows the actual distribution of spawner density (left) or hatchery spawner density (right) where W spawner density is fixed at the median value. Left graph shows that the capacity to produce smolts is more than double for NOR parents than for hatchery parents, but intrinsic productivity of hatchery fish was higher, likely in response to low sample size at very low spawner densities in the unplanned experiment. Modeling indicated that gains from reproduction by hatchery fish are offset by losses in production by natural fish, so there is essentially no net change (see right graph). The balance of gains and losses depends on the parameter values for the specific population and on the absolute and relative densities of natural and hatchery fish. Source: Buhle et al. (2013, 2014).
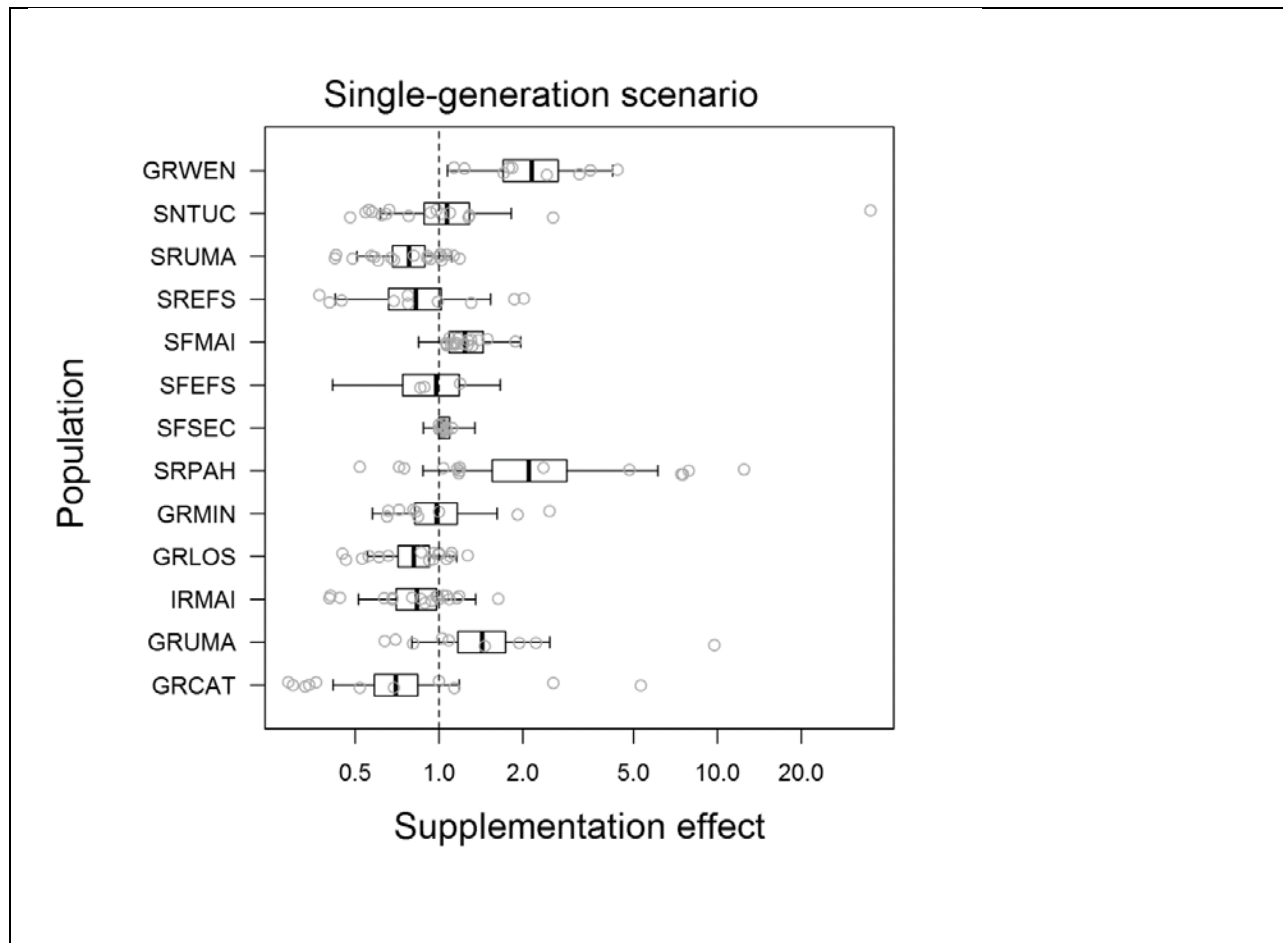
Figure VI.3. Effect of supplementation with adult hatchery spawners on smolt production of 13 spring/summer Chinook populations in the Snake River Basin. The simulation incorporated population trends of 11 unsupplemented populations as control populations. The supplementation effect is the ratio of smolt production with hatchery spawners to that without hatchery spawners; values above 1 indicate that supplementation increased smolt production, whereas values less than 1 indicate reduced smolt production; values near 1 indicate no effect on smolt production even though supplementation increased overall spawning abundance; note log scale. The boxplots show the effect averaged over all years, and the circles show median estimates for individual brood years. Source: Buhle et al. (2013, 2014). GRWEN: Wenaha R, SNTUC: Tucannon R, SRUMA: Upper Salmon R, SREFS: Salmon R East Fork, SFMAI: South Fork Salmon R, SFEFS: South Fork Salmon R East Fork, SFSEC: Secesh R, SRPAH: Pahsimeroi R, GRMIN: Minam R, GRLOS: Lostine R, IRMAI: Imnaha R, GRUMA: Upper Grande Ronde R, GRCAT: Catherine Cr.

2. Snake River Fall Chinook

Abundance of natural-origin fall Chinook salmon in the Snake River Basin has increased significantly since the early 2000s in response to intentional supplementation efforts to rebuild the population, and to improved environmental conditions, including those in the hydrosystem (Figure V.2). Strong density dependence has been observed when the spawning population exceeds approximately 10,000 fish, although two large returns have been produced from large spawner abundances (Figure V.2). According to *U.S. versus Oregon*, hatchery fall Chinook entering the Snake River should be allowed to spawn naturally, unless directed otherwise by the co-managers, when numbers exceed hatchery broodstock requirements. The management agreement, which encourages natural spawning of surplus hatchery fish, has led to large numbers of spawners in the river, of which ~73% are hatchery origin (Hesse 2014, ISRP 2014-4). Beginning in 2001, when spawning escapement substantially increased to approximately 10,000 fish or more, adult returns (excluding catch) per spawner in the Snake River was less than 1 (replacement) in 90% of the years, whereas returns per spawner prior to the removal of Chinook salmon in ocean and river fisheries exceeded replacement in 55% of the years (Figure V.2, lower panel). An important next step will be to evaluate the potential benefits of harvesting surplus hatchery fish (i.e., fish that contribute little to future production because the capacity has been reached), including the benefit of facilitating adaptation of the natural origin population to current conditions.

A basic question arising from supplementation of Snake River fall Chinook is: *"at what level of supplementation do genetic and ecological risks outweigh demographic benefits, indicating that hatchery supplementation should be scaled back (Cooney 2013)?"* Studies indicate that fitness of natural spawning salmon may be reduced by interbreeding with hatchery salmon (e.g., Araki et al. 2008, Christie et al. 2014). Density dependent growth and migration of juvenile Snake River fall Chinook salmon has been observed (Connor et al. 2013) in addition to density dependent recruitment when spawning abundance exceed approximately 6,000 to 10,000 fish. A key uncertainty is whether the natural population can sustain itself with reduced or no supplementation (Cooney 2013). Evaluation of this issue requires consideration of the effects of ocean and in-river harvests, the hydrosystem, and hatchery supplementation on the recruitment and viability of Snake River fall Chinook salmon.

3. Steelhead

A hatchery program for summer steelhead in the Clackamas River, Oregon (Lower Columbia River DPS), reduced the productivity and capacity of the wild winter steelhead population, but the wild population rebounded after removal of hatchery steelhead (Kostow et al. 2003, Kostow and Zhou 2006). Summer steelhead are not native to this watershed. Intrinsic productivity (recruits per spawner at very low density) of wild winter steelhead declined 50% and estimated capacity (maximum equilibrium abundance) declined 22% when high numbers of hatchery summer steelhead were present. Although adult hatchery summer steelhead

accounted for 60-82% of the natural spawning parents (all stocks), they produced only 36-53% of the smolts and only 13-18% of the returning adults (Kostow et al. 2003). The investigators concluded that over the duration of the hatchery program, the high number of hatchery steelhead in the upper Clackamas River basin regularly caused the total number of steelhead to exceed carrying capacity by approximately 300%, triggering a density dependent reduction in the productivity of the natural population. The effect was due primarily to progeny produced by natural spawning of hatchery summer steelhead, rather than the release of hatchery smolts. Juveniles produced by naturally spawning hatchery summer steelhead rear in the watershed for 2-3 years and compete for resources for several years; whereas steelhead smolts released from the hatchery emigrate to sea.

Competition with hatchery steelhead in the Clackamas River appears to have reduced the productivity of wild steelhead, so that they are unable to rebound as expected from low abundance following periods of low ocean survival. In other words, the presence of numerous hatchery summer steelhead inhibited a compensatory response by the wild steelhead population that would have promoted their recovery. These findings were attributed to ecological rather than genetic effects because few hatchery summer steelhead interbreed with wild winter steelhead (Kostow et al. 2003).

In response to such evidence of adverse interactions between hatchery summer steelhead and natural winter steelhead in the Clackamas River, the State of Oregon, since 2000, has culled hatchery salmonids (steelhead, coho, Chinook) when

transporting natural salmon above the dam on the Clackamas River and prohibited hatchery smolt releases into the upper basin. Subsequently, both the productivity (smolts per spawner) and total smolt production of natural winter steelhead has increased, and the abundance of natural adult steelhead has increased from less than 100 fish to an average of 1,500 adults per year (K. Kostow, ODFW, personal communication). Production of natural coho and spring Chinook has also improved.

Supplementation of steelhead in the Umatilla River, Oregon, has influenced at least three density dependent responses in the natural population (Hanson et al. 2010). This river receives supplements of adult hatchery fish that spawn in the river (~31% of total spawners) and hatchery juveniles that are released into the river. Steelhead productivity (smolts produced per female spawner) declined with greater abundance of total spawners. Smolt abundance did not increase with greater number of hatchery spawners, suggesting that the additional spawners did not boost smolt production as intended. Smolt length-at-age declined and the percentage of older smolts increased with additional spawners, indicating that the decline in productivity (smolts per spawner) was related to slower growth in the river. These findings suggest that food availability and rearing habitat are limiting the production of natural-origin steelhead in this watershed.

4. Coho Salmon

In coastal Oregon, stray hatchery spawners had a much stronger (5x) negative density dependent effect on coho productivity than do natural-origin spawners (Buhle et al. 2009). The investigators examined the

effect of a large scale reduction in hatchery releases on 15 natural coho populations along the Oregon coast, and found that the two most important variables in a statistical model predicting salmon productivity (R/S) were coho spawner density and sea surface temperature, followed next by hatchery smolt releases. Their models predict that at any given spawning density, a spawning population that includes hatchery fish will produce fewer recruits than one that is an entirely natural. For example, at the median density (7 spawners/km), an all-hatchery origin spawning population is predicted to produce only 45% as many recruits as an all-natural population. Even at critically low spawning densities (1.6 spawners/km), such as might occur when ocean conditions are unfavorable, an all-hatchery origin spawning population would produce only 87% as many recruits as an all-natural population. The presence of hatchery spawners is also predicted to reduce the carrying capacity (maximum abundance) of the natural population. The investigators used retrospective simulations to show that if hatchery production had not been terminated in 1997, productivity would be 27% lower in the recent period of higher coho abundance. The findings of this study are consistent with those of an earlier study involving 15 stocked versus 15 non-stocked coho streams in Oregon (Nickelson 1986).

5. Intrinsic Productivity of Chinook, Coho, and Steelhead

A population's intrinsic productivity (i.e., productivity at very low spawning densities) determines what proportion of the population can be harvested sustainably and is key to managing fisheries. Recent studies indicate that intrinsic productivity is affected by the proportion of hatchery fish

in naturally spawning salmon and steelhead populations (Chilcote et al. 2011, 2013). These investigators examined how intrinsic productivity was related to a variety of variables using data for 23 Chinook, 30 steelhead, and 18 coho populations over a 20-year period. Most of the Chinook and steelhead populations were from the Columbia Basin whereas the majority of the coho populations were from the Oregon coast. The best statistical model included the mean percentage of hatchery fish in the spawning population and explained 88% of the variability in intrinsic productivity of the populations. The percentage of hatchery fish on the spawning grounds was 13 times more influential than the next best variable in the model, suggesting that hatchery strays have an important effect on natural salmon productivity. Their modeling results predicted that intrinsic productivity would decline by 45%, on average for these 78 populations, if the percentage of hatchery fish was increased from 0% to 25% (Figure VI.4). The observed percentage of hatchery fish on the spawning grounds averaged 24%. Intrinsic productivity of spawning populations consisting of 50% hatchery fish was predicted to decline by 74% compared to a population consisting entirely of natural-origin salmon. Although the absolute value of intrinsic productivity varied among the species, the model predicted similar rates of decline as the percentage of hatchery fish increased (Figure VI.4). Unexpectedly, the investigators could not attribute any difference in outcome to the use of an integrated versus segregated approach in the hatchery, or to the length of time the hatchery had been operated, as might be expected if introgression led to a cumulative adverse effect over time. Insensitivity of the model to hatchery legacy

may stem from opportunistic use of available data rather than a planned and controlled experiment. The study approach used here cannot identify the mechanism (genetic or ecological) by which hatchery strays affect natural-origin salmon.
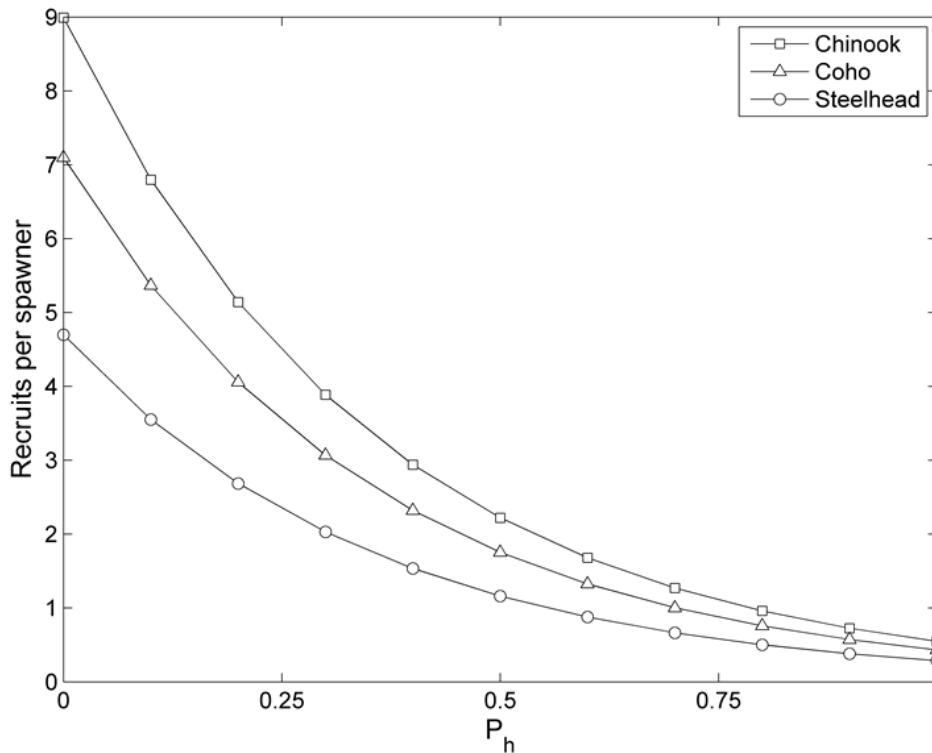
Figure VI.4. Modeled relationships between intrinsic productivity (recruits per spawner) of Chinook, coho, and steelhead and the proportion of hatchery fish on the spawning grounds (P_h). Model results are based on data spanning 20 years from 71 populations, primarily from the Columbia Basin. Source: Chilcote et al. (2013).

6. Interspecific Competition

Supplementation with yearling hatchery salmon also can reduce native rainbow trout abundance and biomass. In the Teanaway River, a tributary of the Yakima River, approximately 250,000 yearling spring Chinook and coho salmon were released into the test river in each of nine years; salmonid densities were considered low prior to the smolt release (1 fish per m²; Pearsons and Temple 2010). Specific mechanisms responsible for reduced trout abundance and biomass were believed to be large numbers of salmon released from the hatcheries, numerous non-migratory mini-jacks produced by the hatchery Chinook, and an increase in naturally

produced salmon parr. Consistent effects of supplementation on the body size of trout were not detected. This study updated previous findings by the investigators.

C. Summary

An important question regarding supplementation programs is *"at what level of supplementation do genetic and ecological risks outweigh demographic benefits, indicating that hatchery supplementation should be scaled back?"* The studies described in this Chapter indicate that supplementation of natural-origin salmon and steelhead populations, whether for the primary purpose of rebuilding natural populations or supporting fisheries, may have the following ecological effects:

- Supplementation may increase total spawning abundance, yet fail to produce the intended boost to natural origin returns, e.g., spring/summer Chinook (Buhle et al. 2013).
- Supplementation and hatchery production in the Basin has led to high proportions of hatchery fish in many spawning areas (Figure VI.1), and relatively high total spawning abundances, such that capacity is often exceeded and the return per spawner of the populations averages less than 1 (e.g., Figs. V.1-3; Zabel and Cooney 2013). Many interior Chinook and

steelhead populations, including some populations with little or no supplementation, are not self-sustaining at the higher levels of total spawners that are occurring.
- Increased natural spawning of hatchery fish lowers the productivity of the natural population and inhibits the rebound (resilience) of a natural population that would likely occur at low abundances (Kostow and Zhou 2006, Buhle et al. 2009, Chilcote et al. 2011, 2013).
- Supplementation may lead to greater natural origin returns even though returns per spawner may be less than 1 (replacement), e.g., Snake River fall Chinook (Cooney 2013). This occurs when an increasing number of natural spawning hatchery adults (produced by large releases of hatchery smolts) more than offset the declining productivity of the total natural population.
- Removal of hatchery fish may facilitate resilience of the natural population. Removal of hatchery summer steelhead led to increased productivity and abundance of natural-origin winter steelhead (Kostow and Zhou 2006). Capacity and productivity of natural-origin coho increased following removal of hatchery coho salmon in coastal rivers (Buhle et al. 2009).

VII. Predation Effects

Salmon are susceptible to predation at all life stages, and predators can impose significant density dependent mortality on salmon populations. In this chapter we consider how mortality imposed by predators is related to prey density and summarize recent findings about the overall impact of major predators on Columbia River salmon populations. Note that this chapter is not an exhaustive review of predation in the Basin.

We also consider how predation on natural ESA-listed salmonid populations might be affected directly or indirectly by hatchery releases that change the density of prey (hatchery and natural-origin fish) available to predators. Contemporary predator populations are in part supported by the relatively constant annual releases of ~150 million salmon and steelhead from hatcheries (Figure III.2).

A. Predation Mortality Can Be Depensatory

The total consumption of prey by predators depends on the feeding rate of individual predators (determined by the "functional response to prey density"), predator abundance (determined by the "numerical response to prey density"), and the length of time that prey remain vulnerable (Holling 1959, 1966). Mortality caused by individual predators is typically depensatory because they become satiated and reduce their feeding rate as prey density increases. However, the typical depensatory functional response of individual predators can be offset completely or partially by a compensatory increase in the number of

predators due to aggregation in the short term or increased reproduction in the long term.

B. Predation on Juveniles during Downstream Migration

Caspian terns *Hydroprogne caspia* and double-crested cormorants *Phalacrocorax auritus* are the major predators on salmonid smolts in the estuary and mainstem of the Columbia River (Collis et al. 2002, Evans et al. 2012, reviewed in ISAB 2011-1). Because of their larger size, steelhead smolts are particularly susceptible to predation by terns and cormorants. Over 15% of the tags from PIT-tagged steelhead detected at Bonneville Dam in 1998 were later found on estuarine bird colonies compared with only 2% of the tags from PIT-tagged yearling Chinook salmon (Collis et al. 2001). Similarly, the percentage of tagged smolts recovered from bird colonies upstream of McNary Dam was higher for steelhead than for Chinook (Faulkner et al. 2007). From 1998 through 2007, the percentage of PIT tags recovered from bird colonies near McNary pool has been negatively correlated with estimates of the total number of steelhead smolts remaining in the river downstream of Lower Monumental Dam, indicating that overall, predation by bird colonies was depensatory (Figure VII.1). This depensatory predation accounts in part for a reduction in steelhead mortality rate between 1998 and 2007 during which time the in-river abundance of steelhead smolts increased following reduced transportation and increased spill (Faulkner et al. 2008). Increasing spill percentage increases the

number of in-river migrants which could temporarily buffer all potential prey species inhabiting the river from predation risk, thereby decreasing the relative benefit of transporting smolts downstream in barges (ISAB 2008-5). The potential influence of migrant numbers on predation-related mortality, in-river survival and SARs remains an important concern (ISAB 2010-2).
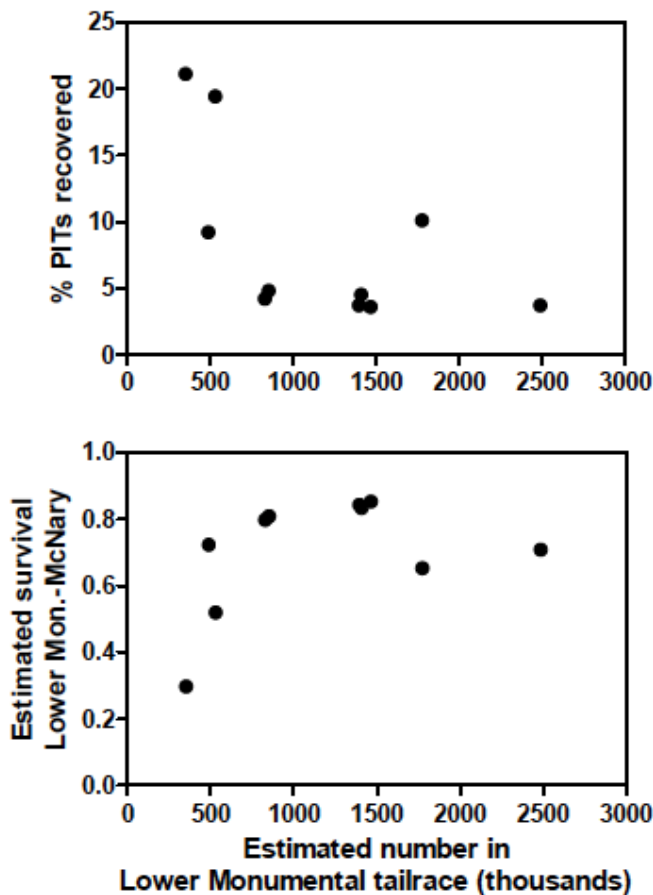
Figure VII.1. Evidence that avian predators imposed depensatory mortality on steelhead smolts migrating between Lower Monumental (Snake River, Washington) and McNary (Columbia River) dams, 1998-2007. Higher densities of steelhead in the tailrace of Lower Monumental Dam (x-axis of both frames) were associated with a lower percentage of PIT tags eaten by birds after passing Lower Monumental Dam (i.e., recovered on bird colonies, upper frame) and higher overall steelhead survival between Lower Monumental and McNary dam (lower frame). Source: Faulkner et al. (2008).

Several studies in the Columbia River estuary have also shown that hatchery-reared salmonids are more susceptible to avian predation than their natural-origin counterparts (Collis et al. 2001, Ryan et al. 2003, Kennedy et al. 2007). Hostetter et al. (2012) recently confirmed that hatchery steelhead were more susceptible than

natural-origin steelhead to double-crested cormorants (which pursue prey underwater) but not to Caspian terns (which plunge from the air). Both species disproportionately consumed steelhead that were in an externally degraded condition when PIT tagged at Lower Monumental Dam), suggesting that avian predators tend to consume smolts that are less likely to survive to adulthood (Hostetter et al. 2011, 2012). Even so, a substantial proportion of healthy smolts must also be killed by avian predation given the low prevalence of externally degraded steelhead smolts observed in the study (13%), and the recovery of PIT tags from non-degraded steelhead at bird colonies (Hostetter et al. 2012).

Predation of juvenile salmonids by piscivorous fishes is probably also depensatory, but no data are available for the Columbia River to confirm this speculation. The most important fish predators of juvenile salmon in the Basin are native northern pikeminnow, followed by non-native smallmouth bass and walleye (reviewed in ISAB 2011-1). It is estimated that prior to the control program, pikeminnow ate roughly 8% of the 200 million juvenile salmonids that migrated downstream in the Basin each year (Raymond et al. 1996); the control program appears to have reduced that rate to about 5% (CBFWA 2010).

C. Predation on Adults during Upstream Migration

Predation on adults during upstream migration is of particular concern because it may reduce the potential spawning population more than an equivalent rate of predation at earlier life stages. Losses to

predators early in the salmonid life history are often mitigated by compensatory mortality during later life stages, especially if predators selectively remove the most vulnerable individuals. By the time adult salmon enter the Columbia River estuary, they have already survived numerous threats in both freshwater and marine environments, and all are potentially valuable for harvest or spawning.

Pinnipeds (seals and sea lions) are top carnivores in lower Columbia River food webs and are capable of consuming large quantities of adult salmonids and other fishes (ISAB 2011-1). The minimum number of pinnipeds estimated from visual observations at Bonneville Dam increased from 31 in 2002 to 166 in 2010, with 137 observed during 2014 (Stansell et al. 2014). However, there are no reliable estimates of total pinniped abundances in the estuary, integrated over all seasons, and the impact of pinniped predation on salmonids in the Columbia River is still unknown or largely speculative.

A telemetry study of four runs (spring, summer, and fall Chinook salmon and steelhead, 1996-2004) showed decreasing percentages of pinniped-wounded Chinook and steelhead as run sizes increased, indicating depensation due to predator satiation. However, as discussed by Naughton et al. (2011), an earlier study by Fryer (1998) did not find significant relationships between the incidence of pinniped-caused wounds and salmon run sizes, possibly because abundance of pinnipeds in the Columbia River estuary was relatively low at that time (Wright et al. 2010).

More recent tagging studies by NOAA indicate that after accounting for fishing mortality and impacts from sampling gear, the weighted mean annual survival of spring Chinook migrating upstream from the Lower Columbia estuary past Bonneville Dam has declined steadily from 90% in 2010 to 69% in 2013 (Wargo Rub et al. 2014). Survival was consistently higher for Chinook arriving late in the run compared to those returning early or at the peak, when predation by pinnipeds would have been more intense (Wargo Rub et al. 2014). The declining survival rates also mirror the growing presence of sea lions and seals in the estuary. The number of sea lions identified at haul out sites near Astoria in 2013 was five times that observed during each of the previous three years, and a still larger number was observed in 2014 (Wargo Rub et al. 2014). Despite the recent indications that predation of salmon by pinnipeds is increasing, the escapement goal of spring Chinook counted at Bonneville Dam (115,000 fish) has essentially been met or exceeded each year since 2008 (www.pcouncil.org/salmon/stock-assessment-and-fishery-evaluation-safe-documents/; the preliminary count for 2014 was 214,000 spring Chinook, www.fpc.org). Further studies are needed to track pinniped abundance in the estuary, and to confirm that salmon mortality attributed to pinnipeds is depensatory, as expected, and as suggested by studies to date.

D. Hatchery Production and Predation of ESA-listed Salmonids

Salmon released from hatcheries might affect predation mortality of natural-origin ESA-listed salmonid populations both directly and indirectly. Existing evidence in the Columbia/Snake River system suggests that hatchery-released steelhead and Chinook will consume juvenile natural-origin Chinook, and possibly juvenile steelhead (Flagg et al. 2000). The impact on natural-origin populations in tributaries of the Columbia and Snake rivers is generally considered negligible (reviewed in USFWS 1992, Naman and Cameron 2011), but mortality may exceed 22% in some cases (Cannamella 1993).

Large releases of hatchery fish can also affect predation of natural-origin fish indirectly, by influencing the behavior and dynamics of predator populations. Because predation by individual predators is typically depensatory, mortality on natural-origin fish will likely be reduced ("buffered") by the presence of large numbers of hatchery-produced fish unless the local abundance of predators increases quickly and proportionately through aggregation. Although a proportional increase is not likely through aggregation in the short term (Wood 1985), continued hatchery production can lead to a long-term increase in predator populations through reproduction. For example, Kirn et al. (1986) and Beamesderfer and Rieman (1991) demonstrated that northern pikeminnow abundance in the lower Columbia River increased during the 1980s at the same time that hatchery releases increased. If predator populations were to grow in proportion to the increased availability of hatchery fish, then the buffering benefit of hatchery fish releases would be lost. Even so, predation mortality on natural-origin populations should not increase beyond levels experienced before the initiation of hatchery releases unless

the natural-origin fish become differentially vulnerable (see next paragraph). Flagg et al. (2000) conclude that releases of hatchery-reared fish do affect the behavior of predator populations in the Columbia River system, but no studies have demonstrated the effects of such changes on intermixed natural-origin populations.

One scenario warrants special consideration however. A long-term increase in the number of predators following increased availability of hatchery fish would pose a special problem for natural-origin populations if hatchery fish suddenly become less available to the expanded predator population. Such a situation could arise if hatchery production were deliberately curtailed as part of an experiment, for example, to measure the influence of density on growth or survival (Peterman 1978, 1991), or declined abruptly due to disease or catastrophic failures during artificial propagation. In such a scenario, predation mortality on the natural-origin population could increase dramatically over levels sustained before the hatchery releases began.

E. Component versus Ensemble Density Dependence

It is important to recognize that depensatory mortality from predation in particular life stages (i.e., in components of the life cycle) can be overwhelmed by compensatory mortality at other life stages, so that the ensemble effects of density over the entire life cycle remain compensatory. For example, in Alaska, brown bear predation on spawning sockeye salmon is strongly depensatory (80% of spawners killed at low densities), yet no evidence of depensation was observed in life-cycle recruitment, apparently because compensatory effects in the high-quality spawning habitat overwhelmed depensatory predation (Quinn et al. 2014). Similarly, none of the life-cycle recruitment relationships for Columbia River salmon populations examined in Chapter V (Figs. V.1-3) exhibit signs of depensation. Thus, ensemble density dependence over the entire life cycle remains strongly compensatory even though depensatory mortality likely occurs at some life stages.

Actions that increase population productivity by improving, for example, habitat quality for spawning, incubation and early juvenile rearing, or by alleviating hydrosystem impacts during migration, can help a population escape the potentially destabilizing effects of depensatory predation at low density. Understanding density dependence at particular life stages is useful for guiding actions to help increase population productivity. However, ensemble density dependence over the entire life cycle is what really matters for determining a population's overall productivity and resilience.

VIII. Management of Columbia Basin Salmon

This section briefly identifies ways by which density dependence might be used to more effectively manage and evaluate the status of anadromous salmon populations in the Basin. We also describe how this information can be used to guide and evaluate habitat restoration activities. Consideration of density effects will be important as regional quantitative goals and objectives are developed as part of the Council's Fish and Wildlife Program.

A. Spawning Escapement Goals

Spawning escapement goals are reference points set by management agencies and used to ensure the potential for sustained future abundances of salmon and steelhead. *Biological* escapement goals typically refer to reference points that are developed by fitting Ricker or Beverton-Holt models to empirical spawner and recruitment data, thereby accounting for density dependence (e.g., Figure II.4). Typically, biological escapement goals are established to maintain or maximize the potential for future harvests in fisheries (S_{MSY}), but other reference points could be developed to maximize adult returns if the goal is to support wildlife, such as mink or bears, or the ecosystem (e.g., Piccolo et al. 2009).

Data quality is an important consideration when developing biological escapement goals and some management agencies, such as the Pacific Salmon Commission, evaluate data quality before accepting and relying upon the goals for fisheries management (Chinook Technical Committee 1999). An important consideration is that measurement error typically causes population productivity to be overestimated, leading to estimates of spawning escapement (S_{MSY}) that are too low and harvest rates that are too high. Additionally, the length of the stock-recruitment data series relative to environmental conditions and the assumption of stationarity over time must be considered when developing biological escapement goals. This is especially important in the Columbia Basin where relatively long-term shifts in salmon survival at sea may violate the stationarity assumption.

Biological escapement goals have been estimated for some salmon populations in the Columbia Basin (Chinook Technical Committee 1999, *US versus Oregon*, www.pcouncil.org). The biological escapement goal developed for summer Chinook passing Rock Island Dam (12,143 fish) was recently adopted by the Pacific Fishery Management Council, representing one of the few populations in the Basin that has an escapement goal that is designed to support the potential for maximizing sustainable harvests. This biological escapement goal has been exceeded every year since 1998 (www.pcouncil.org; Joint Columbia River Management Staff 2014a). A biological escapement goal to support the potential for maximum sustainable yield (MSY) was adopted in 2011 for upriver bright (URB) fall Chinook (Yakima, Hanford, Priest Rapids Dam stocks). The MSY goal of 39,625 fish has been exceeded in 13 of the past 14 years. These biological escapement goals are typically exceeded because these stocks are more productive than other co-mingling stocks and managers attempt to

minimize over-harvesting of the weaker co-mingling stocks.

Most escapement goals or management objectives in the Columbia Basin are not directly calculated from quantitative stock-recruitment relationships (Joint Columbia River Management Staff 2014a, b). Instead, management of fisheries is largely based on harvest rates in relation to stock abundances as described in the *US versus Oregon* Management Agreement. This approach contributes to compensatory density dependence and the stability in spawning escapements. A detailed description of factors considered during the development of the harvest rate schedules was not readily available, but key goals are to maintain spawning escapements during periods of low survival and adult returns, and to ensure sufficient spawners to facilitate rebuilding of populations as habitat restoration efforts attempt to increase juvenile survival and habitat capacity (T. Cooney, NOAA Fisheries, personal communication). Although the harvest rate schedule provides a means for managing the fishery, development of stock-recruitment relationships and associated spawner reference points provides a biologically based approach for evaluating the current status of the salmon population.

Snake River fall Chinook is an example where the existing escapement goal (14,360 Chinook spawners) is high relative to the capacity of the watershed to support fall Chinook salmon (Figure V.2). This goal is not based on the stock-recruitment relationship, but rather reflects the desire to mitigate for past hydrosystem impacts and habitat loss (Dauble et al. 2003) and to facilitate rebuilding of the population. The

observed recruitment relationship for fall Chinook returning to the Snake River indicates that spawner abundances exceeding 6,000 to 10,000 fish typically do not produce additional recruits, although two of nine large spawning populations did produce a larger number of recruits. Hatchery origin fish account for approximately 73% of natural spawners. An important issue is the level of supplementation needed to support anticipated levels of harvest versus the level of supplementation needed to support population viability and rebuilding.

In summary, biological escapement goals are needed for salmon in the Columbia Basin for a number of reasons. First, development of biological escapement goals provides a biologically based approach for managing sustainable harvests and for protecting against short-term demographic risks. Second, biological escapement goals reflect the current productivity and capacity of the populations so that spawning escapements can be quantitatively compared with current capacity. This would facilitate an understanding of why the productivity (R/S) of some populations averages less than 1, suggesting that their carrying capacity has been exceeded. Intentionally exceeding the carrying capacity may be part of the strategy to rebuild the populations, but it would be worthwhile to estimate the level at which the capacity has been exceeded. Third, density dependence must be considered when evaluating population status. A population's response to restoration actions (e.g., its productivity and capacity) is best assessed while also considering density effects (its abundance) as a covariate. Simply measuring abundance or survival in isolation is insufficient to infer

population status, especially in supplemented populations. Finally, biological escapement goals would help to identify the level of hatchery supplementation needed to support natural populations when natural origin abundance is very low or when capacity is achieved or exceeded. Culling of surplus hatchery fish when the capacity is exceeded may promote development of adaptive traits in the natural origin population and help to achieve harvest goals.

B. Supplementation and Hatchery Efforts

Evidence from the Columbia River Basin (Chapters V and VI) clearly shows that the productivity of smolts typically declines with increasing juvenile or parent abundance. It is not clear to what extent the managers of supplementation actions actually consider density effects on the growth and survival of natural origin salmonids (ISRP 2011-14, 2013-3). In many Chinook ESUs and steelhead DPSs, hatchery fish account for an exceptionally high proportion of natural spawning populations (e.g., Figure VI.1), including watersheds where strong density dependence has been observed (e.g., Figs. V.1, V.2, V.3). High spawning densities have frequently led to adult returns less than the number of parent spawners (R/S < 1) under current conditions. Biological escapement goals are needed to identify the level of total spawners, including supplementation fish that can be supported by the existing habitat.

The HSRG developed a number of guidelines for implementing an integrated hatchery approach that attempt to conserve natural salmon and harvests

(HSRG 2009, Paquet et al. 2011), and density dependence is a critical component of a successful integrated hatchery. First, the naturally spawning populations must be self-sustaining in order for hatchery broodstock to be genetically integrated with the naturally spawning component. Therefore, the abundance of the natural spawning population, which includes supplemental hatchery fish, must not exceed the capacity of the habitat that supports the salmon population; average adult return per spawner must be greater than or equal to 1. Some populations described in Chapter V and VI may achieve greater sustainability if some surplus hatchery fish are removed from the spawning grounds. Second, HSRG guidelines recognize the need to balance the size of the integrated hatchery with the size and productivity of the natural population so that sufficient natural-origin fish can be used for hatchery broodstock while also regulating the contribution of hatchery fish spawning in the rivers. Clearly, the goals of an integrated hatchery approach, as defined by the HSRG, cannot be achieved without consideration of density dependence and the capacity of the habitat to support the natural supplemented population.

Snake River spring/summer Chinook salmon provide an example of high spawner abundances that cannot be sustained naturally because of long-term reductions in life-cycle productivity. There are two important questions to be addressed:

1. How many smolts per spawner would be needed to replace the parental spawning population given the current smolt-to-adult return (SAR), and

2. How many parent spawners can be maintained at this level of productivity given current smolt-to-adult returns?

The level of smolts per spawner productivity needed to achieve population replacement is readily calculated for any specified rate of smolt-to-adult return (SAR) (see Figure VIII.1a). For example, the geometric mean SAR of natural-origin Snake River spring/summer Chinook salmon is approximately 1.4%,[14] implying that approximately 72 smolts per spawner are typically needed just to achieve replacement and more smolts per spawner are needed to produce surplus for fishery harvests (see Figure VIII.1a). However, because of density dependence, this level of smolts per spawner productivity is typically not achieved except at very low spawning densities. Many adults (natural and hatchery origin) have been allowed to spawn in the Snake River Basin relative to its capacity such that smolts per spawner productivity is often well below 72 smolts (Figure VIII.1b). For example, approximately 15,000 to 100,000 spring/summer Chinook often spawn in the Snake River Basin and only ~50 or fewer smolts are produced per spawner (Figure VIII.1b).[15] The density

dependent relationship shows that approximately 11,300 or fewer spawners are needed to reach or exceed 72 smolts per spawner given current habitat conditions. This level of spawners and productivity would produce approximately 820,000 smolts.

In contrast, to achieve maximum smolt production (~1.3 million) for the Snake River Basin, the number of spawners would have to equal or exceed ~20,000 females or ~40,000 total spawners (see Figure I.1). Such a spawning population could not be sustained naturally because the predicted smolts per spawner from 40,000 spawners is only 33 smolts per spawner (Figure VIII.1). At this freshwater productivity, and assuming a SAR of 1.4%, the predicted adult return per spawner (R/S) is only 0.46, leading to an adult return of only 18,550 natural origin spring/summer Chinook. In other words, 40,000 spawners would produce only about 18,550 future adults. In fact, it is generally true for salmonid populations conforming to the Beverton-Holt model of density dependence that maximum smolt production cannot be sustained by returns from natural spawning. Maximum smolt production is therefore an unrealistic target for such populations if the goal is sustainability.

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[14] See Kennedy et al. (2013) for SAR methodology. For comparison, the Comparative Survival Study (CSS) geometric mean survival of natural-origin Chinook for the same smolt years is 0.8% (1996-2009). A SAR of 0.8% would require 125 smolts per spawner to achieve replacement, or approximately 5,100 spawners.

[15] The number of Chinook spawning naturally in the Snake River Basin and the production of natural-origin smolts produced by these spawners requires a number of calculations that may lead to error in the reported estimates, as noted by the investigators (Kennedy et al. 2013). For this analysis, we assumed

females represented 50% of the spawning population.
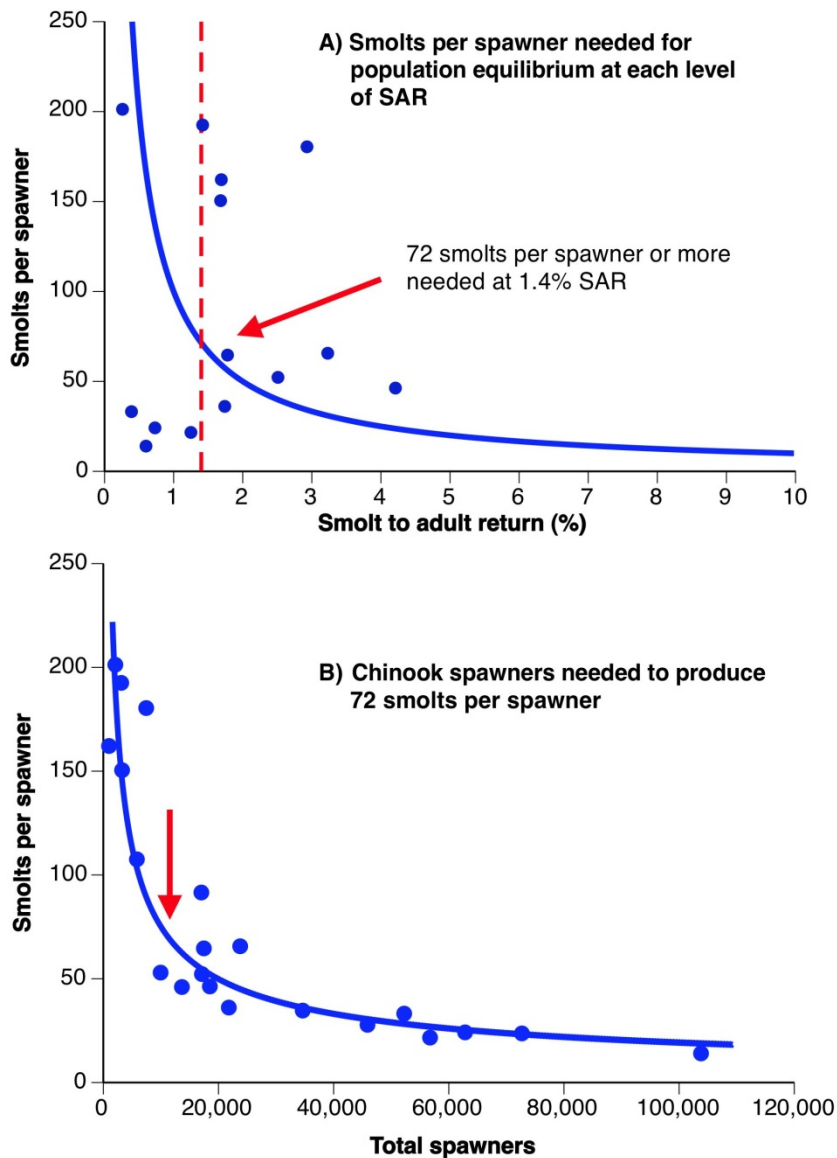
Figure VIII.1. Smolts per spawner needed to achieve replacement (equilibrium) in relation to the rate of smolt-to-adult return (SAR) (A), and the empirical relationship between smolts per spawner and total spawners of Snake River spring/summer Chinook (B). In panel (A), smolt per spawner values below the solid line represent smolt migrations that failed to replace themselves at the specified level of SAR. The geometric mean SAR of natural Snake River spring/summer Chinook was 1.4% (1996-2009; red dashed line in A), indicating that approximately 72 smolts per spawner are typically needed to reach equilibrium and many more are needed to produce surplus fish for harvests and other uses. Observed smolts per spawner and corresponding SAR are shown in Panel A. Panel B indicates ~11,300 or fewer spawners are needed to achieve a productivity of 72 or more smolts per spawner (red arrow)—a self-sustaining population at 1.4% SAR. This Snake River relationship assumes an equal ratio of females to males on spawning grounds (see Figure I.1). Approach in panel A developed by K. Kostow, ODFW. Data source: Kennedy et al. (2013).

This example of density dependence in Snake River Chinook demonstrates the important trade-off between abundance and productivity of a salmon population. The ISAB is not suggesting that spawning abundance in the Snake River Basin should be greatly reduced, as reducing abundance could increase the demographic risk to some small isolated populations. Rather, the message from this example is that major actions are necessary to increase the productivity of the population (SARs and smolts per spawner) in order to create a self-sustaining population at the current level of spawning salmon.

Potential actions include habitat restoration to improve survival to the smolt stage and hydrosystem improvements in the mainstem river as a means to increase SAR and thereby reduce the smolts per spawner needed to achieve replacement. Petrosky et al. (2001) show that dam construction in the Snake River Basin, rather than changing conditions in spawning and rearing habitats, was responsible for the decline in Chinook salmon productivity, suggesting that the greatest potential gains in productivity would stem from improvements in the hydrosystem. For example, if SAR improved to 2%, then only 50 smolts per spawner would be needed to reach replacement (Figure VIII.1a). A reduction in hatchery Chinook on the spawning grounds might also contribute to higher *intrinsic* productivity of the natural spawning population (Buhle et al. 2009, 2013; Chilcote et al. 2013). Alternatively, hatchery supplementation may be used to artificially maintain an abundant spawning population (e.g., >15,000 spawners) given that existing conditions cannot produce a self-sustaining run at the current level of abundance. This

latter approach, however, has potential ecological and genetic costs for the natural spawning population.

Supplementation (release of hatchery smolts) may temporarily increase the current total abundance of salmonids in a watershed (hatchery plus natural-origin), but it may also inhibit the resilience of the natural population. In a non-supplemented population, the growth and survival of individual salmonids typically improves at low densities. This natural compensatory response helps the natural population rebound to greater abundance and was necessary for its persistence to the present day. Increasing abundance through supplementation typically reduces the productivity of the natural population simply because fewer resources are available to each individual as the population density increases. The rate at which productivity (e.g., smolts per spawner) declines in response to greater abundance is illustrated by the rate at which the slope of the recruitment curve changes. Steep recruitment curves that bend over sharply imply a rapid decline in productivity as abundance increases.

Plans for supplementation should balance the desire for greater abundance against the impact that greater abundance will have on the productivity and resilience of the natural population. This balance can be evaluated and potentially achieved through the development of biological escapement goals based on quantitative relationships between smolts and parent spawning abundances (Figure VIII.1). Managers must also consider the risk of too few spawners in a non-supplemented population and

potential depensatory mortality at low spawning levels.

In contrast to the previous discussion, a supplementation advocate might reasonably argue that these ESA-listed populations have had trouble rebounding from low abundance due to the variety of factors described in Chapter IV. The primary goal of hatchery supplementation is, to some extent, to avoid the very low density situations that would require a population to bounce back from low abundance. In other words, hatchery supplementation is a strategy to address poor productivity, and high hatchery spawner ratios and associated low R/S are not due to hatchery supplementation per se but rather simply reflect the poor habitat conditions. This line of reasoning underscores why studies are needed, such as those by Buhle et al. (2013, 2014), to identify both beneficial and adverse effects of supplementation on natural salmon populations. An important remaining question is *"at what level of supplementation do genetic and ecological risks outweigh demographic benefits, such that hatchery supplementation should be scaled back?"* (T. Cooney, NOAA Fisheries, personal communication).

Supplementation of salmon populations with large numbers of hatchery-origin spawners (or natural-origin spawners) will not increase smolt production and adult returns once the population carrying capacity has been exceeded. Indeed, large spawning abundances may lead to a reduction in smolt and adult returns if overcompensation occurs (see next paragraph). Snake River spring/summer Chinook and fall Chinook provide examples of spawning abundances that have exceeded population capacity in recent

years, largely in response to numerous hatchery-origin salmon on the spawning grounds. The recruitment curves show that few additional progeny are produced when spawning abundances exceed ~15,000 female spring/summer Chinook (Figure I.1) or ~6,000 to 10,000 total spawners of fall Chinook (Figure V.2). Supplementation beyond these spawning levels has occurred frequently but typically has not provided additional future adult returns. However, as noted later in this chapter (Ecosystem Benefits of Excess Fish), spawner levels that exceed capacity would add nutrients and food that may benefit the broader biological community and potentially enhance the stock-recruitment relationship in the future. Furthermore, excess spawners might encourage some spawners to seek new, less utilized but likely less productive, habitats (See Appendix II).

The shape of the salmon recruitment relationship has special implications for supplementation of salmonid populations. If the recruitment curve is represented by a Beverton-Holt model, then recruits from exceedingly large spawner abundances will stabilize at a plateau. However, if the recruitment curve is represented by a Ricker model, then larger spawner abundances will produce fewer recruits depending on the degree of overcompensation. When overcompensation is present, supplementation with large numbers of spawners can cause a decline in abundance of the natural-origin smolts and adult returns (NOR) and a sharp decline in productivity. Therefore, when overcompensation is present, maximum future smolt and adult abundances occur at intermediate parent spawning levels and harvests are needed to sustain maximum

smolt or adult production. In practice, it can be difficult to determine whether recruitment data fit a Beverton-Holt or Ricker model because data are often highly variable in response to ever-changing environmental factors. Moreover, Milner et al. (2003) suggest that recruitment curves based on a mixture of populations, as is typical in salmon management, may mask the underlying overcompensation portion of the Ricker relationship. Monitoring of spawning populations and their progeny (smolts, adults) are needed to identify the shape of a recruitment curve and to develop biological escapement goals. Monitoring of subyearling Chinook salmon parr in relation to spawning abundance in 15 rivers in the Snake River Basin generated more support for a Beverton-Holt versus Ricker recruitment model, providing little or no support for overcompensation in these populations (Thorson et al. 2014).

One obvious goal of hatchery supplementation is to produce more fish for harvest. Consideration of density dependence and development of biological escapement goals for the natural populations could potentially lead to greater harvests while also maintaining the productivity of the natural population. However, fishery participants and managers must agree upon approaches to harvest surplus hatchery salmon while also minimizing overharvest and incidental mortality of the natural populations. These approaches require thoughtful discussions by all participants and potentially significant changes to current management. The benefits, in terms of harvested fish and minimizing loss of productivity of the natural populations, could be significant. One example of this approach is taking place in the upper Columbia Basin where

the Colville Tribe is using a purse seine to catch hatchery Chinook salmon while live-releasing unmarked natural Chinook (www.cbbulletin.com/411335.aspp, www.colvilletribes.com/september_2014_newsletter.php).

Scientists in the Basin are aware of the potential effects of supplementation on non-target native fishes. Protocols for evaluating these interactions have been developed and implemented in the Yakima River Basin (Pearsons and Hopely 1999, Pearsons and Temple 2007, 2010, Temple and Pearsons 2012). Nevertheless, widespread use of supplementation in the Columbia Basin indicates that further evaluations are warranted (Pearsons 2010). In the upper Columbia Basin, Pearsons et al. (2012) presented two approaches, largely based on expert opinion, which will be implemented to evaluate ecological effects of supplementation over the next 10 years. We encourage investigators to also implement field studies to scientifically test hypotheses about the effects of supplementation on native fishes.

In summary, supplementation can impact the density dependent relationship of natural salmon in several ways, and these factors should be considered when managing supplemented salmon populations. First, interbreeding of hatchery and natural salmon may affect the genetic fitness of the population, leading to a potentially long-term reduction in intrinsic productivity. Second, hatchery salmon may temporarily lower the productivity and/or capacity of the population because they have lower reproductive success when spawning in the wild (e.g., selection of less suitable spawning habitat; Cram et al. 2013). Third, there is some evidence that

the presence of numerous hatchery spawners reduces the overall capacity (maximum abundance) of the population, which might be related to selection of less suitable spawning habitat by hatchery fish or some other factor. Fourth, the addition of numerous juvenile and adult hatchery salmon reduces the availability of resources to each individual salmon, thereby reducing the productivity of natural-origin salmon. Therefore, supplementation with hatchery salmon can reduce natural compensation and inhibit the population's resilience at low abundance. Lastly, in contrast to the adverse effects described above, supplementation of severely depleted natural populations with hatchery fish produced by an *integrated* hatchery may prevent depensatory mortality and extinction. However, an integrated hatchery program requires a self-sustaining natural population (HSRG 2004, ISRP 2011-14), which is dependent on a spawning population that is within the capacity of the environment to support the population.

Ultimately, however, improvements in the life cycle survival of the naturally spawning population, such as from habitat and hydrosystem restoration actions, are needed to develop self-sustaining populations at densities and abundances desired by stakeholders. Consideration of density dependent relationships is critical to managing and evaluating sustainable natural populations.

C. Habitat Restoration Actions

Density dependence should be used to guide and evaluate habitat restoration activities (Greene and Beechie 2004). Density dependent relationships can 1) identify life stages requiring habitat

restoration, 2) set the baseline for current capacity and productivity of the rivers and estuary, and 3) evaluate fish responses to restoration actions.

Density dependence is often not considered in habitat restoration efforts in the Basin or even in other regions (Greene and Beechie 2004; P. Roni, NOAA Fisheries, personal communication). In part, this stems from the belief that density effects should be negligible for threatened populations whose populations are small. For example, some life cycle models in the Basin have assumed that population dynamics are density independent (Kareiva et al. 2000, Wilson 2003). However, this assumption of density independence is erroneous, especially when habitat quality and quantity has been degraded. When reviewing habitat proposals in the Basin, the ISRP (2013-11) noted that density dependence within specific life stages was rarely examined as a means to identify habitats and life stages that may be limiting salmon production. In restoration proposals, there is a need to identify hypotheses about how restoration actions might reduce density dependence during each life stage. These hypotheses should be integrated with actions designed to reduce density independent mortality such as high water temperature and extreme water flows. Currently, many Intensively Monitored Watersheds are planning to incorporate density dependence into their evaluations, but most have yet to formally do so (Gallagher et al. 2012; P. Roni, NOAA Fisheries, personal communication).

In the following sections, we discuss the benefits of 1) targeting specific life stages and habitats, 2) providing excess fish to enhance ecosystem function and capacity,

and 3) developing recruitment relationships as a means to evaluate the benefits of restoration actions.

1. Target Life-Stages and Specific Habitats

Density dependent relationships can be used as a tool to guide restoration actions (Greene and Beechie 2004, Gallagher et al. 2012). Restoration of spawning habitat is indicated when density effects are evident within the spawning stage whereas restoration of rearing habitat is indicated by density effects during the rearing stage (for example, if numerous fish are emigrating at too early an age, or if both growth and survival are reduced). Steelhead in the Umatilla River provide an example of how density effects can be used to target specific habitat (Chapter VI). Here, steelhead smolts per spawner declined with greater abundance of parent spawners, indicating a density effect between the spawning and smolting stages (Hanson et al. 2010). Furthermore, smolt length-at-age declined and age of smoltification increased with abundance. These analyses suggest that high density of juvenile steelhead reduced the availability of food per fish, leading to reduced growth and delayed age of smoltification. Ongoing work in this river suggests that water flow may also influence production of juvenile steelhead (J. Hanson, ODF&W, personal communication). Water flow (volume) and water diversion influence the capacity of streams to support salmonids (Walters et al. 2013b). Thus, restoration actions are needed that produce more rearing habitat and food in addition to favorable water flows.

Studies of density dependence among spring/summer Chinook in the Snake River Basin indicate the need for conservation actions to target specific life history stages and associated habitat (Copeland and Venditti 2009, Walters et al. 2013a, Copeland et al. 2014). Growth and survival of juvenile Chinook salmon were reduced, and numbers (and proportion of total) of subyearlings emigrating from the natal river increased at higher densities. Many subyearling emigrants overwinter upriver from Lower Granite Dam and the investigators concluded that small improvements in the survival of this relatively abundant life history type could have large positive impacts on adult returns and population recovery. Growth was important to the survival of these fish during winter. Fewer adults tended to be produced from fish overwintering in the natal reaches because rearing habitat was limited and fish dispersed downstream when densities increased. Availability of appropriate substrate is important for overwintering juvenile Chinook salmon (Bjornn 1971).

Some populations of Snake River spring/summer Chinook, such as those in the Pahsimeroi River, spawn in tributary habitats with extensive spring-fed areas where temperatures promote early emergence and rapid growth. In those cases, a proportion of the parr emigrate downstream as smolts during the early summer of their first year (Copeland and Venditti 2009). Restoration of the Columbia River mainstem and estuarine habitats could benefit fish with that life history.

Density dependent growth and survival has been observed in relatively pristine habitats supporting spring/summer Chinook in the Snake River Basin (Cuenco et al. 1993, Cuenco 1994, Achord et al. 2003, Walters et

al. 2013a). This finding initially surprised investigators because the density of fish was low during the study period compared with historical estimates and the stream habitats were largely intact. Achord et al. (2003) suggest that this finding might reflect the need for additional salmon carcasses in pristine areas to rebuild the food web. Experimental investigations to identify the mechanisms of strong density dependence in the relatively pristine habitats are needed (Bjornn 1971, Walters et al. 2013a).

2. Ecosystem Benefits of Excess Fish

Ecosystem-scale benefits may accrue from allowing spawning abundances to exceed levels expected to generate maximum sustainable yield or even the maximum equilibrium population size (carrying capacity). The "excess" fish can be ecologically important in a number of ways that can enhance habitat restoration actions and eventually lead to an upward shift in salmon recruitment. For example, an abundance of adult spawners is needed to clean stream gravels of fine materials impeding subsurface flow (Montgomery et al. 1996, Tonina and Buffington 2009), to contribute much needed nourishment to large predators, scavengers, and downstream communities (Naiman et al. 2002, 2009; Helfield and Naiman 2006), to enhance the growth of important riparian trees (Helfield and Naiman 2001, Bartz and Naiman 2005, Drake and Naiman 2007), and to ensure that the ecosystem underpinning the vitality of fish populations remains vital itself over the longer term (Naiman et al. 2009). It is paramount that these and other ecosystem-scale benefits be considered when managing—and attempting to

optimize—fish populations for density dependence.

These ecosystem benefits might be achieved, for example, by setting minimum spawning escapement reference points and by periodically allowing large numbers of fish to spawn in the river, as a result of high survival of natural origin fish, supplementation with hatchery returns, or both. Alternatively, carcasses of spent hatchery salmon may be strategically placed into streams to provide nutrients for the biological community. A number of studies suggest that the addition of salmon carcasses or carcass analogs has increased the growth of salmonids in addition to other components in the food web, and it is reasonable to expect that this action has contributed to greater numbers of juvenile salmon (Bilby et al. 1998, Sanderson and Kiffney 2003, Pearsons et al. 2007, Kohler et al. 2012, Warren et al. 2014).[16] Furthermore, in the Snake River Basin, net input of marine derived nutrients by

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[16] Periodic pulses of nutrients may not suffice to quickly restore the habitat capacity. For instance, in Idaho, several years of high escapement since 2000 have done little to increase ecosystem productivity. It is possible that, if nutrient reserves are indeed a limiting factor, they have been depleted by decades of low escapement. Therefore, a sustained, long-term approach to restoring nutrient reserves may be needed to increase total ecosystem capacity or productivity (T. Copeland, IDFG, personal communication). Further, Walters et al. (2013a) conclude that nutrient augmentations have not demonstrated a population level benefit to date. However, nutrient augmentation may be more successful if complemented by an increase in refugia in summer rearing reaches, which may allow juveniles to safely access resources currently too risky to use.

Chinook salmon is density dependent; at low spawning densities more nutrients are exported by emigrating smolts than brought in by adult salmon (Kohler et al. 2013). This relationship highlights the need to maintain spawning escapements above the threshold needed to achieve a net positive influx of nutrients.

3. Establish Baseline and Evaluate Improvements

The evidence for density dependence presented in Chapters V and VI demonstrates that the status of salmon populations cannot be fully evaluated without consideration of fish density. Zabel and Cooney (2013) show that abundances of many salmon populations have increased in recent years, suggesting that their status are improving. However, the relatively high abundances of these populations were associated with much lower productivity in response to density dependence. Often, the populations were unable to replace their initial high abundance, indicating that abundance would rapidly decline if not supported by hatchery supplementation.

The approach used by Zabel and Cooney (2013), which evaluates productivity of salmon populations in relation to abundance, is important for evaluating the response of fish populations to restoration actions. Simply documenting a change in juvenile body growth, survival, or abundance is not adequate for evaluating progress because density often has a strong effect on each metric. Instead, improvements in growth and survival should be compared relative to fish abundance. Additionally, dispersal of juveniles from natal rearing habitats must be considered because dispersal is a mechanism that ultimately enhances population capacity. Dispersal may reflect limited availability of habitat. Ideally, relationships between growth, dispersal, survival, and population abundance would be developed for a baseline period prior to habitat restoration, and then post-treatment values could be compared to determine whether improvements have occurred relative to the pre-treatment values. Comparison with reference streams should be part of this evaluation. A description of this approach is discussed in Appendix I.

IX. Key Findings, Conclusions and Recommendations of Part I

Scientists in the Columbia Basin initially thought that contemporary abundances of salmon and steelhead were so low that concerns about competition for limited resources such as food, rearing habitat and spawning habitat were a low priority. Density of salmon was thought to be too low to inhibit salmon recovery. The reality, however, is quite different. Scientists have discovered many cases where freshwater densities are constraining salmon recovery, which implies that habitat is more degraded or less accessible than previously thought. Less is known about density dependence in the estuary and ocean. Key findings are described below in response to the central questions identified in the Introduction.

What is density dependence and why is it important?

- Density dependence is the ubiquitous relationship between population density and vital rates of a population (survival, dispersal and reproduction) or individual traits (such as body growth). Populations cannot persist without the stability conferred by compensatory density dependence; a declining population is typically restored by improved survival or reproduction due to greater resources per individual at low density. Without compensatory density dependence, a population would eventually become extinct due to chance.

- Sustainable fisheries cannot persist in the absence of compensatory density dependence because it provides the stability needed by the population to rebound when the population is

harvested. Productivity (e.g., survival) is higher when density (abundance) is lower. Fisheries managers can use density dependent relationships (stock-recruitment curves) to guide management actions so that a fish population provides desirable benefits such as maximum sustainable harvests for fishermen or maximum returns for ecosystem processes and wildlife.

- Overcompensation may occur at high abundances (e.g., *Ricker recruitment*), whereby recruitment declines (rather than reaching a plateau) with increasing parent abundances. This potential outcome should be considered during hatchery supplementation efforts (or if natural origin returns become very large).

- Predation (and other factors) can destabilize populations when mortality increases at lower population levels. However, in Columbia River salmon, this potential destabilizing (*depensatory*) effect seems to be overwhelmed by compensatory density dependence elsewhere in the life cycle.

- Current ecosystem conditions determine the strength of density dependence experienced by a population. Changes in ecosystem-scale characteristics and processes can alter a population's intrinsic productivity and carrying capacity. Similarly, a stock-recruitment relationship reflects current ecosystem conditions from the perspective of the population—it does not however reflect the longer-term roles of populations in shaping

ecosystem characteristics through various activities (e.g., sorting streambed gravels, delivering nutrients). Consequently, maximum sustainable yield determined from a stock-recruitment relationship may not be sustainable by the ecosystem in the long term.

Why is density dependence more evident than expected at current relatively low abundances?

- Total annual adult salmon and steelhead abundance before hydrosystem development has been estimated at 7.5 to 8.9 million fish (Chapman 1986) or 10 to 16 million fish (NPPC 1986). These values likely overestimate the long-term average abundance because they were derived from peak abundances of each species occurring in different years, rather than in the same time period. The potential capacity for all species combined was likely in the range of 5 to 9 million fish per year, with the primary evidence (i.e., probable harvest rates) supporting an estimate of around 6 million fish per year for the entire Basin, of which only ~69% is accessible today.

- Only approximately two-thirds of the habitat available in the pre-development period is currently accessible to anadromous salmonids, yet current adult abundances of spring Chinook, fall Chinook, coho and steelhead (natural and hatchery fish combined) often exceed two-thirds of their historical abundances. Current spawning densities may be particularly high in some localized core areas, including less disturbed habitats. The

total abundance of salmon smolts (natural-origin *and* hatchery combined) may also be greater now than historically.

- Today's Columbia River Basin is a novel ecosystem. Changes in the quality and quantity of habitat for salmonids have likely altered density dependent relationships such that the carrying capacity of anadromous salmon and steelhead is reached at lower abundances, and productivity (return per spawner) is lower at each level of abundance. Reduced productivity in downstream habitats, including the ocean, may have eliminated and continues to threaten marginally productive populations and life history types that once contributed to overall capacity.

- Life history diversity of salmonids is likely an evolutionary response to density dependence, as it allows a population to utilize a wider range of habitats over time. Life history diversity of salmonids has declined, further reducing capacity, productivity, and resilience.

Where—and at what life stages—has density dependence been detected in the Basin?

- Strong density dependence is now evident in at least 25 of 27 spring/summer Chinook populations, the Snake River fall Chinook ESU, and all 20 steelhead populations examined upstream of Bonneville Dam. Larger population abundances are typically not self-sustaining (R/S < 1). All populations are ESA-listed.

- Density dependence during the spawning stage is not well studied in the Basin. However, experimental investigations with chum and Chinook salmon in controlled spawning channels indicate that density dependence during the spawning and incubation stages becomes evident at lower spawning densities in Chinook than chum salmon. Chum salmon often spawn in dense aggregations and may be better adapted to high density. This finding may help to explain why strong density dependence is being observed in some Chinook populations even when their abundance seems relatively low.

- Most studies of Chinook and steelhead, primarily in the interior of the Basin, suggest that density dependence occurs during the juvenile stage. Survival and mean growth of juveniles often decline with greater density; mean age of smoltification was delayed in one steelhead population in response to reduced growth. Density dependence in the interior Basin was sufficiently strong to be detected despite considerable environmental variability (e.g., temperature, flows).

- Juvenile Chinook salmon disperse (migrate) to downstream rearing habitats as their natal habitat becomes filled. This density dependent behavior is key to increasing abundance (carrying capacity) and the timing of the behavior varies among life history types. Investigators suggest that early migrating parr are particularly important to the recovery of spring/summer Chinook populations because early migrating Chinook become more prevalent and produce

more adults as spawning densities increase. Adults returning from juveniles that overwintered in natal rivers are relatively more common at low population levels suggesting that age-1 smolts are important to population persistence.

- Few studies of density dependence have taken place in tributaries below Bonneville Dam and in the estuary or examined outmigrating smolts in the mainstem river. Few studies have involved coho and chum salmon anywhere in the Basin. The lack of information on density dependence in the estuary is a critical gap because a key goal for habitat restoration is to reduce density dependent limitations by increasing capacity and productivity, especially for natural-origin subyearling Chinook salmon that are primarily produced by fall Chinook spawning in the lower Basin. Evaluation of restoration activities against current management goals, such as minimizing impacts of hatchery salmon on natural-origin fish, may be confounded if density dependence is not considered.

- A few studies of density dependence of Columbia River salmonids in the ocean provide limited evidence for potential competitive interactions between (1) hatchery and natural-origin salmon in coastal waters, especially when ocean conditions are poor, and (2) steelhead and highly abundant pink salmon in the central subarctic North Pacific (distant water rearing grounds of Columbia steelhead). In addition, increases in both forage-fish and predator densities in coastal waters are strong predictors of large decreases in survival of

hatchery and (especially transported) natural-origin Columbia River Chinook salmon. The lack of information about density dependence of Columbia River salmonids during their time in the ocean is a data gap that hinders our understanding of factors affecting growth and survival of Columbia River salmon.

Hatchery Effects on Density Dependence

- Hatchery salmon often represent a large percentage of naturally spawning Chinook (35-80% of spawners per ESU except in the Deschutes [<5%]) and steelhead (15-80% of spawners per DPS) in the Columbia River Basin.

- By increasing overall density and thereby reducing availability of resources per fish, hatchery fish lower the productivity of natural populations which could inhibit their natural resilience at low abundance. For instance, removal of hatchery summer steelhead led to increased productivity and abundance of the natural winter steelhead in the Clackamas River. Natural-origin coho capacity and productivity increased following removal of hatchery coho salmon in coastal rivers.

- Supplementation may not produce the intended boost of natural origin returns even when total spawning abundance has increased (e.g., Snake River spring/summer Chinook).

- Alternatively, supplementation may lead to greater natural origin returns even though adult returns per spawner may be less than 1 (replacement; e.g.,

Snake River fall Chinook). This increase occurs when the number of hatchery adults returning to spawn naturally (70-80% of all spawners) more than offsets the declining productivity of the total natural-origin population.

- Density effects were also observed in populations that received little or no hatchery supplementation.

Predation Effects

- Predation in the Columbia mainstem on juvenile salmon by birds and fishes, and adult salmon by pinnipeds, is typically depensatory such that the percentage of the population eaten by predators increases at small salmon population size. Depensatory predation can destabilize populations. However, because only compensation is evident over the full life cycle of Columbia River salmon, any depensatory effects due to predation appear to be overwhelmed by compensatory effects in other life stages.

How can density dependent limitations be ameliorated as a means to enhance population rebuilding and recovery?

- Habitat projects and restoration efforts will have a higher probability of success in improving the productivity and capacity of targeted populations if density dependence is considered when identifying limiting factors specific to each life stage and life history type, including the effect of density on juvenile dispersal. Density dependent dispersal from natal rivers indicates a need to restore downstream habitats in addition to habitats in the natal river.

Studies, such as those described here, help identify limiting factors affecting each salmon life stage that should be addressed by restoration actions.

- Evaluation of salmonid population responses to restoration may be confounded if density dependence is strong but not considered. Improvements in fish growth and survival should be compared relative to fish abundance.

- Monitoring programs must collect population data necessary to identify density dependent relationships so that factors limiting population growth at each life stage can be identified.

- Biological spawning escapement goals developed from recruitment relationships are needed to help identify spawning levels that enable the potential for maximum adult returns (benefit the ecosystem) or harvests (benefit fishermen), while also identifying minimum spawning levels needed to avoid demographic risks. The potential for overcompensation at large spawning levels should be evaluated.

- Biological spawning escapement goals could be used to manage the level of supplementation with adult hatchery fish relative to the current capacity of the stream/river. An integrated hatchery approach, as described by the HSRG, requires a sustainable natural-origin salmon population, which implies spawning escapements that can be supported by the habitat. Achievement of spawning goals may involve increased harvest of surplus hatchery fish, which would help achieve harvest goals.

Alternatively, excess spawners may be allowed on the spawning grounds to provide ecosystem-scale benefits. The management strategy and rationale should be described.

How can we detect and diagnose density dependent limiting factors?

- Statistical approaches for detecting and evaluating density dependence are discussed in Appendix I.

ISAB Recommendations

The following recommendations list ways to consider and account for density dependence when planning and evaluating habitat restoration actions, developing quantitative objectives for the Basin's anadromous salmon populations, and improving the research plan of the Council's Fish and Wildlife Program. These recommendations also apply generally to other efforts (e.g., the FCRPS Biological Opinion, NOAA recovery plans and life cycle modeling, and tribal programs) to mitigate impacts from the 4Hs (hydro, habitat, harvest, and hatcheries).

1. Account for density effects when planning and evaluating habitat restoration actions. The pre-development capacity of the Basin to support salmonids is likely less than previously believed; a re-analysis suggests that the capacity for all salmon species combined was 5 to 9 million adults. Additionally, there are significant environmental contraints imposed by the Basin as a dynamic but highly altered novel ecosystem. Therefore, it is important to consider the following in developing

restoration actions for the Fish and Wildlife Program and other regional efforts:

- Use knowledge of mechanisms influencing density dependent growth, dispersal, and survival of anadromous salmonids to choose restoration actions that will most effectively increase habitat capacity and fish population productivity and abundance.

- In restoration planning, identify actions capable of reducing density dependence during each life stage, and integrate with actions designed to reduce mortality caused by density independent factors (e.g., water temperatures and flows).

- Consider density dependence when evaluating the success of restoration actions; fish response variables (growth, dispersal from the natal stream, survival, recruits) are typically influenced by fish density.

2. Establish biological spawning escapement objectives (reference points) based on recruitment models that account for density dependence, including population productivity and habitat carrying capacity. Accounting for density dependence helps determine realistic wild (i.e., natural origin) salmon abundance objectives for the Fish and Wildlife Program's wild fish strategy. Specifically:

- Establish biologically based reference points to guide the need for management actions (via harvests, supplementation, and removal of surplus hatchery fish entering the spawning areas) and to quantify when

too few or too many spawners are present to sustain natural populations.

- In setting harvest rates, account for current population productivity and habitat capacity, and adjust harvest through Adaptive Management as environmental conditions change.

- Recognize that large spawning escapements can provide ecosystem benefits and promote long-term sustainability but might also impose short-term costs to fishing communities or to the fish population if there is overcompensation (less recruitment with larger spawning abundances).

- Acknowledge that ecosystem-based fishery management may prove to be the best strategy over the long term given existing uncertainty about density dependent and ecosystem-scale processes.

3. Balance hatchery supplementation with the Basin's capacity to support existing natural populations by considering density effects on the abundance and productivity of natural origin salmon. In particular:

- Clearly articulate anticipated benefits of supplementation actions and base these actions on established scientific principles.

- Estimate the abundance and proportion of hatchery and natural origin adults on spawning grounds, whenever possible, to target appropriate spawning densities that prevent the loss of productivity in natural populations, especially through overcompensation in

the short term or domestication in the long term.

- Recognize that an integrated hatchery supplementation approach requires a self-sustaining natural salmon population, which in turn requires spawning densities that can be supported by the environment.

4. Improve capabilities to evaluate density dependent growth, dispersal, and survival by addressing primary data gaps. This relates directly to having monitoring strategies that quantify the success of Fish and Wildlife Program activities, as well as gather information that allows adjustments for ongoing human-driven environmental changes. The primary data gaps involve:

- Density effects in salmon populations that spawn in the lower Basin and in coho salmon populations throughout the Basin.

- Density effects on the growth and survival of juvenile salmonids emigrating downriver and rearing in the estuary and ocean.

- Predation on adult salmon by pinnipeds (seals and sea lions). Since depensatory mortality may pose a threat to ESA-listed populations, the ISAB recommends further quantification of mortality and evaluation of life cycle recruitment in salmon populations targeted by pinnipeds.

PART II. Non-anadromous Salmonids, Sturgeon, and Lamprey

In Part II, we explore how management questions about density dependence, and approaches for addressing those questions, are different for non-anadromous salmonids, sturgeon, and lamprey than for anadromous salmonids. The differences arise primarily from different life histories and ecology, different constraints on sampling, and a focus on conservation or increasing sport fishing opportunity rather than increasing harvest in tribal, sport, and commercial fisheries. For example, stock recruitment curves are typically used to describe density dependence in anadromous salmonids (see Part I), but that approach is often impractical for non-anadromous salmonids, and few recruitment curves have been developed (with the exception of semelparous kokanee salmon). On the other hand, it is often feasible to directly measure or manipulate densities of non-anadromous salmonids, as well as the resources for which they compete, at multiple life stages so that large-scale field experiments can address management questions.

X. Non-anadromous Trout

Non-anadromous forms of rainbow (*O. mykiss*), cutthroat (*O. clarkii*), and bull trout (*Salvelinus confluentus*; actually a charr) are often called "resident" because they do not migrate to the ocean. However, many populations make substantial migrations within freshwater to fulfill their life history (Northcote 1997), including adfluvial populations that migrate from lakes to streams to spawn (Johnston et al. 2007; Gresswell 2011), and fluvial populations that live in large rivers and spawn in

tributaries (Henderson et al. 2000; DeRito et al. 2010). Other populations may be considered resident in streams and rivers, making much shorter movements to spawn. In relatively undisturbed habitats, many life history types can co-occur (e.g., Meka et al. 2003). However, unless specifically referring to adfluvial or fluvial life histories, for simplicity all non-anadromous trout and charr are referred to as "resident trout" here.

Differences in life history – Unlike anadromous salmon that are semelparous (spawn only once and die), resident trout are iteroparous (may spawn repeatedly). Populations in relatively unproductive lakes can mature late (e.g., 3-7 years) and be long lived, but many adults spawn only in alternate years (Benson and Bulkley 1963, Johnston et al. 2007, Gresswell 2011). This life history complicates the task of assembling data needed for stock-recruitment relationships. Moreover, few populations have been measured for a decade or more, which means that in only a few cases have data been collected that would allow fitting a stock-recruitment curve. One case found adjacent to the Columbia River Basin is for adfluvial bull trout in a southern Alberta reservoir (Johnston et al. 2007). In addition, Bulkley and Benson (1962) attempted to fit a model to a small data set for cutthroat trout in Yellowstone Lake.

Differences in population ecology – Anadromous salmon are known to home to specific rivers and to exist as reproductively isolated populations that can be sampled during their spawning migrations. In

contrast, populations of resident trout are often difficult to define. Resident trout often live in patches of habitat, and the different habitat patches needed to complete their life cycle are often dispersed throughout riverscapes (Fausch et al. 2002, Falke and Fausch 2010). This means that fish often must move to find suitable habitats for spawning, rearing, and refuging from harsh conditions—such as winter, and low or high flows. Hence, immigration and emigration across various spatial scales are often important processes driving resident trout populations, in addition to births and deaths, and all of these processes may be density dependent. And, at the scale of the local patch, adult and juvenile trout often use the same general habitat for rearing and refuging, allowing for more interactions among age classes compared to semelparous salmon where adults and juveniles use separate habitats and rarely interact.

Anadromy also allows salmon and steelhead to emigrate to the ocean and grow large, so the number of eggs they produce is not limited by conditions in their natal stream as it is for resident trout. As a result, anadromous salmonids often saturate all available spawning habitat with eggs, which may lead to strong and consistent density dependent mortality in early life (McFadden 1969, Elliott 2001). In contrast, resident trout populations typically produce fewer juveniles, and density dependent mortality may occur at several different life stages, including adults as they compete in dominance hierarchies for limited feeding positions and overwinter habitats in streams or in lakes (e.g., Elliott and Hurley 1998, Johnston et al. 2007, Urabe et al. 2010, Lobón-Cerviá 2012). Although no direct evidence is available for

the Columbia River Basin, density dependence may influence anadromy and residency in rainbow trout (see review by Kendall et al. 2015).

Recruitment of juvenile resident trout during their first summer in mountain streams and rivers often may be more strongly limited by density independent effects of snowmelt runoff flows than by density dependent competition. For instance, Bulkley and Benson (1962) found that early summer water levels accounted for 91% of the variation in year classes of first-time spawners of Yellowstone cutthroat trout (*O. c. bouvieri*) ascending the largest spawning tributary of Yellowstone Lake, leaving little more variation to be explained by parent stock density. A plot of the parent-progeny relationship suggested it might be fit by a Ricker model, but the data were too sparse (*n* = 9 years) and only one year had high parent density. They concluded that a wide range of spawner escapement could produce abundant year classes, but only if stream flows were favorable during spawning and early life. Other investigators have reported similar declines in juvenile recruitment with higher snowmelt runoff in the southern Rocky Mountains (Anderson and Nehring 1984), and in one case this was combined with density dependent effects from older trout (Latterell et al. 1998).

Sampling constraints – Sampling constraints often dictate what can be measured about fish populations, which in turn drives what questions can be addressed. Entire adult populations of anadromous salmon often can be sampled during their mass spawning migrations, allowing stock-recruitment relationships to be fit from time series data. In contrast,

only adfluvial and fluvial trout make such migrations among resident trout, although most of these are not sampled with the goal of developing stock-recruitment relationships. For resident trout that spawn and rear in dispersed locations throughout long stream or river segments, collecting the data to fit these relationships is more difficult and usually not attempted.

Differences in questions – Relevant management questions related to density dependence for anadromous salmon include the appropriate levels of harvest, the role of supplementation, and in some cases restoration of habitat for juveniles (see Part I). In contrast, management questions for resident trout are often whether habitat restoration can increase the carrying capacity so that native trout populations can be sustained for conservation or sport fishing or whether hatchery fish stocked to support recreational fisheries or invading non-native species can decrease carrying capacity for natural-origin native trout. A fourth major topic is whether angling mortality is at least partly additive or entirely compensatory (i.e., the form of density dependence). If it is at least partly additive, when angling mortality is reduced or eliminated, overexploited populations can rebound and sustain populations for conservation or produce larger fish of interest to sport anglers (e.g., Gresswell et al. 1994, Johnston et al. 2007, Erhardt and Scarnecchia 2014). In contrast, if natural mortality is high and simply replaces much of the angling mortality, then a higher abundance of large trout cannot be sustained for anglers (Hunt 1977).

A. Questions of Interest for Management of Resident Trout

Populations of resident trout are limited by resources that set carrying capacity, via density dependent mechanisms regulating populations (e.g., competition for food or habitat; see Part I, Chapter II). To the extent that hatchery trout or non-native trout are "analogs" of natural-origin trout, they may usurp these resources and cause density dependent reductions in growth or survival, or increased emigration, of the natural-origin trout. Other forces that are only weakly density dependent, or wholly density independent, may also limit these populations (e.g., harsh conditions like floods, droughts, unsuitable temperatures, and perhaps angling mortality). However, if these reduce fish abundance, compensatory increases in growth or survival, or decreased emigration, may result.

Densities of resident trout (and hatchery and non-native trout) at different life stages, and the resources for which they compete, can often be measured directly in freshwater systems. As a result, biologists have relied less on analyzing stock-recruitment curves to address questions of management interest. Overall, four main questions related to density dependence and carrying capacity have been the main focus of management-oriented research on native resident trout in the Columbia River Basin (Table X.1).

1. ***Does habitat restoration decrease density dependent limiting factors and thereby increase carrying capacity?*** That is, if managers add critical habitats for spawning, rearing, or refuge, or restore food producing habitats like

riparian vegetation, will this increase resources and lead to increased trout density?

2. ***Does stocking of hatchery trout reduce carrying capacity for natural-origin trout and thereby reduce their density?*** To what extent are hatchery trout analogs of natural-origin native trout?

3. ***Do invasions by non-native trout or other non-native species reduce the carrying capacity for native trout, and thereby reduce their density?*** To what extent are non-native trout stronger competitors than native trout?

4. ***Can overexploited trout populations rebound when angling mortality is reduced to sustain higher densities for conservation or sport fishing?*** Will numbers of larger older trout increase, or will natural mortality simply replace angling mortality?

1. Does habitat restoration decrease density dependent limiting factors and thereby increase carrying capacity?

Adding habitat for either juvenile or adult trout is expected to change one or more density dependent rates in resident trout populations (Table X.1). If all possibilities are considered, this includes the rate of births, deaths, immigration, and emigration.

Predicted responses could be:

- Increased birth rate, perhaps owing to greater growth that drives greater fecundity
- Decreased death rate (higher survival), at some life stage
- Decreased emigration of either resident fish (born in the study reach) or immigrants

Although it is possible that another response is increased immigration, if only habitat is added it seems unlikely that fish could detect the added habitat from some distance and be attracted. Instead, it is more likely that annual immigration is substantial and relatively constant (e.g., Gowan and Fausch 1996b), and that local abundance is adjusted by changing rates of death or emigration (Burgess and Bider 1980).

Habitat restoration includes adding in-stream habitat such as structures made from logs or boulders and restoring riparian vegetation and floodplains. Somewhat surprisingly, the effects of in-stream habitat restoration or addition are controversial, with two recent reviews arguing for positive effects (Roni et al. 2008, Whiteway et al. 2010) versus two others concluding that the evidence was equivocal or lacking (Thompson 2006, Stewart et al. 2009). Three of these reviews were comprehensive, and one supporting and one refuting positive effects were based on formal meta-analysis of a broad set of experiments and comparative studies. For example, several field experiments, some of which were at large spatial scales, have reported few or no effects of structures created to mimic natural logs or log jams, in both coldwater (e.g., Vehanen et al. 2010) and warmwater lowland streams (Brooks et al. 2006, Howson et al. 2009, Howell et al. 2012).

Why is in-stream habitat restoration sometimes apparently not successful in causing an increase in trout density? Managers often operate under the logical hypothesis that resident trout populations are limited by pool habitat with complex physical structure (logs, boulders, and

undercut banks) that provides refuge for adults or juveniles during harsh conditions (e.g., low flows during late summer through winter in Rocky Mountain streams, or high winter flows in Pacific Northwest rivers). However, many factors combine to control fish populations across different life stages, including not only habitat, but also food, predators, diseases and parasites, and other natural disturbances (McFadden 1969). These other uncontrolled variables may confound a study and prevent investigators from detecting the benefits of restoration. Several key aspects of the design and analysis of field experiments can also reduce the ability to detect effects, such as: a) ineffective treatments that fail to create a sufficient change in habitat area or volume at an appropriate spatial scale, b) inadequate numbers of treatment and control sites (replication) to provide adequate statistical power given high natural variation in fish populations, c) inadequate length of study given lags in population responses, or d) flawed analyses or interpretation (e.g., see Discussion sections in Whiteway et al. 2010 and White et al. 2011 for examples of studies with flawed analyses). Therefore, it is perhaps not surprising that studies with effective habitat "treatments," with sufficient sample sizes of treated sites carried out at a large enough spatial scale, measured for sufficiently long periods, and analyzed and interpreted accurately, are rare.

One study outside the Columbia Basin that sought to address these issues showed that density of resident brook, brown, and rainbow trout did increase after habitat restoration, but that the increase was driven more by fish movement rather than increased overwinter survival. Gowan and Fausch (1996a; see Sidebar X.1) conducted a relatively long-term controlled and replicated field experiment in six northern Colorado streams to add log structures that made pools, which mimicked the natural recruitment of large woody debris (Richmond and Fausch 1995). They found large and rapid increases in adult trout abundance, driven primarily by reduced emigration of trout that were immigrating into study reaches at a relatively constant rate. Increased overwinter survival was documented in only one of two streams where it was measured in detail, and then only the first year after logs were placed. Adults increased despite strong density independent effects of high snowmelt runoff flows, which created wide fluctuations in survival of fry and recruitment of age-1 trout (Latterell et al. 1998). In addition, 21 years after the treatment, the adult trout abundance was still as high as that measured for the first 6 years after logs were installed (White et al. 2011), indicating that the habitat restoration was effective for an extended period.

Sidebar X.1. A comprehensive study of habitat restoration for resident trout

Management biologists often install log structures in streams to create pools and increase overwinter survival of trout. For example, in mountain streams, extended periods of very low winter water temperatures followed by high snowmelt runoff in early summer are thought to reduce trout survival. How such habitat restoration actions can actually change density dependent processes was revealed by one study with an approved BACI (Before-After-Control-Impact) design (Gowan and Fausch 1996a). Abundance of brook or brown trout in six Colorado mountain streams (one had a combination of brook, brown, and rainbow trout) was measured two years before and six years after log structures were placed to create pools in 250-m treatment reaches, and compared to adjacent 250-m control reaches with no added logs.

The study confirmed that placing log structures can significantly increase the carrying capacity of treatment reaches. Abundance of adult trout in treatment reaches increased to a level 42% higher than in control reaches within a few years, and 21 years later was still 53% higher (Gowan and Fausch 1996a, White et al. 2011). However, the study also demonstrated that the increase resulted primarily from reduced emigration of immigrants that had entered the treated sites from outside the study area, rather than from increased survival or reproduction within the sites. Survival was significantly higher in the reaches with logs in only one of two streams in which it was measured in detail, and only during the first year after logs were installed (Gowan and Fausch 1996a). Fecundity was not measured, but no significant difference in growth of tagged fish was detected between treatment and control reaches during the first six years after logs were placed in these two streams. In contrast, the median rates of immigration into all the streams were high—45% of the fish captured each year in the four higher-elevation streams with primarily brook trout, and 12% of those captured in the two lower-elevation streams with brown trout (or a mixture of trout species) were immigrants (i.e., unmarked, despite efficient sampling that allowed capturing and marking nearly all trout every year; Gowan and Fausch 1996a). Detailed analysis revealed that emigration of marked fish from the treatment reach was significantly lower than immigration in one of the two streams studied. Thus, the primary mechanism for the rapid increase in density was apparently high natural rates of immigration coupled with a density dependent decrease in the rate of emigration following treatment. Increased over-winter survival was a lesser and transient response.

The prevalence of movement in stream trout populations (Gowan et al. 1994, Fausch and Young 1995) suggests that this response could also occur in other streams, although it should not be assumed to be universal (Rodríguez 2002). For example, brown trout populations at low density in unproductive streams in Finland apparently respond much more slowly to added habitat, suggesting that immigrants may not be available to colonize the new habitats (Vehanen et al. 2010). The broader question of whether increasing habitat at the local scale can increase stream-wide trout abundance and production is a difficult one to answer and would require marking and recapturing fish over a larger spatial extent to measure movement and survival of immigrants to treatment reaches and emigrants from them. This is possible with PIT technology and better sampling designs and analysis methods, but it is a complex issue for which no one

has sufficient data yet. However, until such data are amassed, it seems logical to assume that immigrants that colonize the added habitat survive better than those that never find vacant locations (i.e., in streams without added habitat), and hence increase stream-wide density and production of trout.

The effects of restoration of riparian habitats and floodplains on trout populations have been examined much less than in-stream habitat, but several studies show the importance of terrestrial insects falling from riparian vegetation as food resources for trout. Cutting off inputs of these terrestrial insects using mesh greenhouses caused reductions in growth when fish were enclosed (Baxter et al. 2007) and emigration when they were not enclosed (Kawaguchi et al. 2003; reviewed in Fausch et al. 2010). Improved management of cattle grazing that increased riparian vegetation also led to higher inputs of terrestrial insects, greater amounts in trout diets, and higher trout biomass than at poorly managed sites (Saunders and Fausch 2007, 2012).

2. Does stocking of hatchery trout[17] reduce carrying capacity for natural-origin trout, and thereby reduce their density?

It seems logical that hatchery trout could be sufficient "analogs" of natural-origin native trout to compete for similar resources and thereby reduce their carrying capacity (Table X.1). However, whether they do in any specific case depends on many variables, including whether hatchery trout are highly domesticated or progeny of

largely natural-origin parents, and the species, life stage, and density stocked. Most of the discussion here addresses cases where hatchery trout are stocked in streams already inhabited by natural-origin trout of the same species. The worst case scenario would be if hatchery fish reduced survival or growth of natural-origin fish, but then died themselves, thereby reducing trout abundance overall (Weber and Fausch 2003).

Most studies of effects of hatchery fish have been conducted at small scales in laboratory tanks, hatcheries, or artificial streams. These often showed that fish reared in hatcheries are more aggressive than their natural-origin counterparts, waste energy, feed inefficiently, and are more susceptible to predation (reviewed in Weber and Fausch 2003). Few of these studies were conducted in natural streams (but see Bachman 1984, McMichael et al. 1999), and characteristics like aggression are often accentuated when fish are held at unnaturally high densities in small tanks or enclosures.

Direct observations of fish in natural streams show that hatchery fish have equal or greater ability to dominate profitable feeding positions and displace natural-origin fish from them, at least as juveniles, often owing to the larger size of hatchery fish (Weber and Fausch 2003). However, controlled experiments on the effects of hatchery fish on natural-origin fish growth or survival in wild streams are less common.

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[17] The ISAB describes the effect of stocking anadromous salmonids on non-anadromous trout in Part I: *Section* VI.B.6 *Interspecific competition.*

These are of two types: Experiments adding hatchery fish as a perturbation or invader to streams with natural-origin fish (additive design) test whether hatchery fish compete and reduce fitness of natural-origin fish but ignore the effects of the increased density. In contrast, experiments substituting some hatchery fish for natural-origin fish but maintaining equal density (or adding hatchery vs. additional natural-origin fish in separate treatments, compared to a control), can detect whether the relative effect of hatchery fish is greater or less than natural-origin fish (substitutive design; see Fausch 1988, 1998; Weber and Fausch 2003). The effects of hatchery fish depend on the density of each group, the carrying capacity of the environment, and the relative competitive ability of hatchery versus natural-origin fish. Which design is better depends on the question of interest.

Most studies in natural streams used the additive design and either failed to detect effects of stocking hatchery trout or detected effects only in some circumstances. Most were not conducted in the Columbia River Basin. For example, stocking of age-1 brown trout reared in hatcheries from natural-origin fluvial or adfluvial parents (i.e., with little domestication) into European streams with natural-origin brown trout had no detectable effect on growth (Baer and Brinker 2008, an additive design that tripled and quintupled density; Vehanen et al. 2009, a substitutive design that maintained constant density), or there was no evidence that the effect was different than adding the same density of natural-origin trout (Bohlin et al. 2002). These studies were generally not designed to rigorously assess effects on survival, or separate it from emigration.

A common management practice is to stock adult catchable trout to support angler harvest, especially in habitats where natural reproduction or overwinter survival is low. In four of five replicated field experiments, investigators could detect either no effects or only modest effects of stocking catchable trout, and results of the fifth may have been confounded by less favorable flows and higher angler harvest of both natural-origin and hatchery fish in years when trout were stocked (Schill 2014). For example, Petrosky and Bjornn (1988) found short-term effects of stocking adult hatchery rainbow trout on natural-origin rainbow and cutthroat trout in Idaho streams during summer, and only at the highest stocking density (>9 times the density of natural-origin trout). There was no evidence that total mortality of natural-origin fish subject to hatchery fish stocking differed from that of control groups later in the year, because of either compensatory survival or small-sample error. In a recent well-designed and comprehensive study, Meyer et al. (2012) found no evidence of an effect of stocking sterile adult catchable rainbow trout on natural-origin (native or naturalized) rainbow trout density, survival, recruitment, or growth in 12 reaches of 11 Idaho streams studied for 5 years (before, during, and after 3 years of stocking that increased densities nearly 80% on average). This study mimicked closely the stocking practices of the state fisheries agency. In contrast, Weiss and Schmutz (1999) reported that mean growth of adult natural-origin brown trout was reduced when density was doubled or tripled by stocking hatchery brown trout in an unproductive (soft-water) stream in Germany, although there was no evidence of a change in a productive (hard-water) one. There was also no evidence that the

trout recapture rate (which they used as a proxy for survival) differed in either stream.

Overall, introducing trout of the same species that are reared in hatcheries can have density dependent effects on growth (e.g., Weiss and Schmutz 1999, Bohlin et al. 2002), but effects on survival have not been reported. A general hypothesis is that hatchery trout are unprepared for foraging and avoiding predators in the wild, waste energy, are easily caught by anglers, and suffer high mortality during the first summer (see Weber and Fausch 2003, Schill 2014 for reviews).

It is important to note that hatchery fish may have other effects on natural-origin fish that are not addressed here, including transferring diseases or parasites, or interbreeding and producing hybrids. These can have important effects on survival and genetic integrity that cannot be ignored when considering effects of stocking fish raised in hatcheries.

3. Do invasions by non-native trout or other non-native species reduce the carrying capacity for native trout, and thereby reduce their density?

Non-native species also may be sufficient analogs of native species and use similar food or space resources, thereby reducing the carrying capacity for native species (Table X.1). When the non-native species usurp scarce resources, it is possible that they could cause density dependent reductions in growth, fecundity, or survival of the native species, or increase emigration. These effects may also depend on the ecological context, including both the physical conditions of habitat as well as the density of native species.

Most studies of competition among stream-resident trout have been conducted in the laboratory in tanks, as head-to-head trials among groups of adults or large juveniles, lasting up to a few weeks duration. Although these experiments can provide useful information about competitive interactions, invasions by non-native species play out over the entire life cycles of fish populations (Parker 2000), and across entire riverine landscapes. Therefore, the most comprehensive approach would be to measure births, deaths, immigration, and emigration (and ideally growth and fecundity) at this large spatial scale over several generations of the fish studied, and in replicate whole streams. Unfortunately, no such complete experiment has been done, to our knowledge.

The expansion of native trout to fill habitat left when non-natives are removed from a stream is the simplest and in some ways the best measure of how much carrying capacity is reduced by non-natives, assuming there are appropriate controls where non-natives were not removed. Populations of juvenile and adult native westslope cutthroat trout (*O. c. lewisi*) in a small Montana stream (Shepard et al. 2002) and bull trout in a small Oregon stream (Buktenica et al. 2014) both increased about 10 times after complete removal of non-native brook trout. In the first case, the population of cutthroat trout in a reach downstream of the barrier continued to be suppressed by brook trout throughout the study period, providing a suitable control. Neither experiment was replicated in more than one stream. Nevertheless, these studies suggest that non-native brook trout can have strong negative effects on carrying capacity for native trout.

A fundamental question is whether non-native species, such as non-native trout, are analogs of native species, producing the same density and biomass, and hence having the same effects on carrying capacity and serving the same function in ecosystems. For example, native cutthroat trout and non-native brook trout in the inland West are thought to be quite similar, functioning primarily as insectivores in streams (Quist and Hubert 2004). However, Benjamin and Baxter (2010, 2012) found from extensive analysis that when brook trout replace native cutthroat trout they achieve densities, biomass, and production 1.5-1.9 times that of the native trout, even after accounting for primary differences in habitat (e.g., elevation, gradient). Even before the invasion is complete, when the two species are together (sympatric), density of brook trout averaged more than three times that of cutthroat trout, which likely has strong effects on carrying capacity for cutthroat trout and their density dependent survival, fecundity, and growth. Additional research showed that differences in brook trout foraging and life history produced an increased "load" on the ecosystem, even when they were at the same density as cutthroat trout (Benjamin et al. 2011, 2013). For example, brook trout reduced the biomass of adult aquatic insects emerging from streams by a third to more than half in the two studies (one was comparative, the other a field experiment), which in turn reduced riparian spiders, and eliminated the food supply for an estimated 2/3 of riparian summer migrant birds.

Although a complete and replicated experiment of all the mechanisms by which a non-native trout invasion affects the life cycle of native trout throughout a watershed has not been accomplished, one large-scale field experiment of the effects of non-native brook trout on native Colorado River cutthroat trout (*O. c. pleuriticus*) in Colorado mountain streams shows the complexity of responses and how they interact with habitat. Peterson et al. (2004) removed brook trout for four years from ca. 1-km segments of two streams where they were sympatric with native cutthroat trout and left two others as controls. The streams were arranged in pairs at mid-elevation (warmer) and high elevation (colder), and each pair had a treatment and control stream.

During their first year of life (at age-0), the survival rate of cutthroat trout in the warmer mid-elevation stream where brook trout had been removed was 13 times higher than their counterparts in the control stream with brook trout, and the survival rate of age-1 cutthroat was 1.9 times higher, clearly showing the effects of the non-native trout on reducing carrying capacity for native trout. For their part, age-0 brook trout in the control streams survived at a rate 10 times higher than the cutthroat trout there. Nevertheless, the survival rates for adult cutthroat trout of age-2 and older were very similar whether brook trout were present or not, in each pair of streams, and there was no evidence for a difference. The experiment showed that in mid-elevation streams brook trout decimated cutthroat trout during their first two years of life, and other research showed that this could be due to both competition and predation, including predation by the larger age-0 brook trout on newly emerged cutthroat trout fry (Novinger 2000). Fry of the fall-spawning brook trout emerge earlier than those of the spring-spawning cutthroat trout and

hence are always larger during their first year of life.

In contrast, in the colder high-elevation stream pair, fry of the spring-spawning cutthroat trout failed to survive at all (Peterson et al. 2004) owing to cold temperatures that delay incubation and emergence, and limit first-summer growth, thereby causing subsequent high overwinter mortality (Harig and Fausch 2002, Coleman and Fausch 2007). As a result, cutthroat trout populations isolated in such high-elevation headwater streams by invading brook trout gradually disappear as the remaining adults die out. In comparison to cutthroat trout, fry of the fall-spawning brook trout emerge earlier and some can grow enough to survive at colder temperatures. More important is that rapid rates of immigration of adult brook trout from downstream source populations ensure that invaders are constantly pressing upstream to increase their densities and replace cutthroat trout there (Peterson and Fausch 2003), making them a highly flexible and successful invader (Kennedy et al. 2003). For the cutthroat trout, however, there was no evidence that more emigrated from the study segments in control streams with brook trout than treatment streams without brook trout, based on direct measurements with weirs, so the effects of brook trout were primarily on survival rather than movement.

Managers often want to know whether certain factors help native species resist invasions, and new research shows that the relative density of natives versus invaders can play a role here too. A general hypothesis has been advanced that in strongholds for native trout, the invasion

success of non-natives is limited, especially in the early stages of invasions (e.g., Benjamin et al. 2007, Peterson et al. 2008). Saunders and Budy (unpublished MS) tested this idea for Bonneville cutthroat trout (*O. c. utah*) interacting with non-native brown trout in two experiments at different scales. In mesocosm tanks (4.5 m^2) and stream enclosures (50-100 m^2) they found evidence that survival and growth of the cutthroat trout was higher in treatments where their density was about 3-6 times that of the brown trout versus those where it was only about twice as high.

Based on the mesocosm study, the mechanism appeared to be that significantly more aggressive interactions per capita were initiated by brown trout at lower cutthroat densities, causing higher stress-related columnaris disease. This disease accounted for 75% of the mortality in the experiment, whereas brown trout predation accounted for only 20%. Overall, maintaining robust densities in native trout populations may improve prospects for their persistence more than isolating them with barriers (Peterson et al. 2008, Fausch et al. 2009). Barriers can compromise the resilience of the isolated population, although they are often the only option for smaller populations that have already lost resilience.

Long-term field experiments from outside the region may also provide useful information on the effects of introducing fish above barriers. For example, Nuhfer et al. (2014) reported that an experiment moving adult spawning steelhead above a barrier on a tributary to Lake Michigan reduced age-0 brown trout overwinter survival by nearly 40%, on average, showing clear density dependent effects. In turn, this

reduced age-1 brown trout abundance by nearly half for year classes that interacted with the juvenile steelhead progeny, based on a 14-year study before, during, and after the transplants. In this case, neither species is native although both have been naturalized in that region for a century or more. It is also worth noting that various factors that operate independently of density may limit invasions and provide refuges for native fishes. Habitat factors such as specific flow regimes can hamper survival and recruitment of non-native fish and hence favor native fish that have evolved under these regimes. For example, the widely introduced rainbow trout are more likely to invade in "winter rain" flow regimes that match those in their native range compared to summer snowmelt regimes that do not (Fausch et al. 2001), a prediction borne out for Hokkaido Island, northern Japan (Inoue et al. 2009). Understanding such "environmental resistance" could help managers predict where invasions are more likely and hence require more attention (Fausch 2008).

4. Can overexploited trout populations rebound when angling mortality is reduced to sustain larger populations for conservation or sport fishing?

A fourth question of management interest is whether density dependent growth, survival, fecundity, or maturation can help populations rebound from overfishing or hamper efforts to produce large fish for anglers (Table X.1). Populations of bull, cutthroat, and rainbow trout in cold unproductive mountain streams, rivers, and lakes often grow slowly and mature late. They are also relatively easy to catch by angling and hence are susceptible to angling mortality and overfishing. Recent federal

listings of bull trout and conservation plans for cutthroat and rainbow trout have resulted in restrictive angling regulations including catch-and-release angling or closures altogether.

Fluvial bull trout in a north Idaho river and adfluvial bull trout in a southeast Alberta reservoir and its main tributary both responded positively to closures that virtually eliminated angling mortality (Johnston et al. 2007, Erhardt and Scarnecchia 2014). Erhardt and Scarnecchia (2014) reported increased numbers of larger and older fluvial bull trout in the North Fork Clearwater River, Idaho, which they attributed to increased survival rather than growth. After a decade, population growth rate had begun to slow as it reached carrying capacity, and the density estimate exceeded the recovery goals for the drainage (Sidebar X.2).

Johnston et al. (2007) found a similar result for adfluvial bull trout in Lower Kananaskis Lake, Alberta. Adfluvial bull trout there rebounded from a very low abundance (60 spawning adults) and mounted a 28-fold increase over 10 years after angling mortality was reduced by closures in the spawning tributary and catch-and-release fishing in portions of the reservoir. Analysis of stage-specific stock-recruitment models showed that density dependence was strongest in early life (egg to age-1) and was best explained by a Ricker model, although the Beverton-Holt model fit better for the overall stock-recruitment relationship from egg to first spawning (Figure X.1). A second density dependent survival bottleneck occurred for adult spawning bull trout (which mature at age 6-9 years), with lower survival at higher densities. Further analysis showed that as the population recovered

growth of individual fish slowed, maturation was delayed, and the frequency of skipped spawning events increased (Johnston and Post 2009; Sidebar X.2). One management implication is that minimum length limits may need to be increased at low density when fish grow faster, to avoid angling mortality before they mature.

Although compensatory processes could help populations rebound from low abundance, strong density dependence could also hamper efforts to sustain large fish for angling, even under catch-and-release regulations. This could occur in small habitats or harsh conditions where natural mortality is high, so that fish released in good condition by anglers nevertheless die of natural causes (e.g., overwinter mortality). For example, Hunt (1977) measured angling and natural

mortality of brook trout in a small Wisconsin spring stream under liberal versus restrictive regulations, the latter with a larger minimum size limit and smaller bag limit, and the effects of each regulation were measured for three years. He found that when angling mortality was reduced from 52% to 4%, natural mortality doubled from 23% to 52% to largely replace it (i.e., was compensatory). However, in many other cases for rainbow and cutthroat trout in the Rocky Mountain region angling mortality has been found to be more additive than compensatory. In these cases, catch-and-release angling allows increased survival of fish to older and larger sizes, thereby "stockpiling" these fish for repeated catch-and-release by anglers (e.g., Bjornn et al. 1977, Anderson and Nehring 1984, Schill et al. 1986, Gresswell 1995).
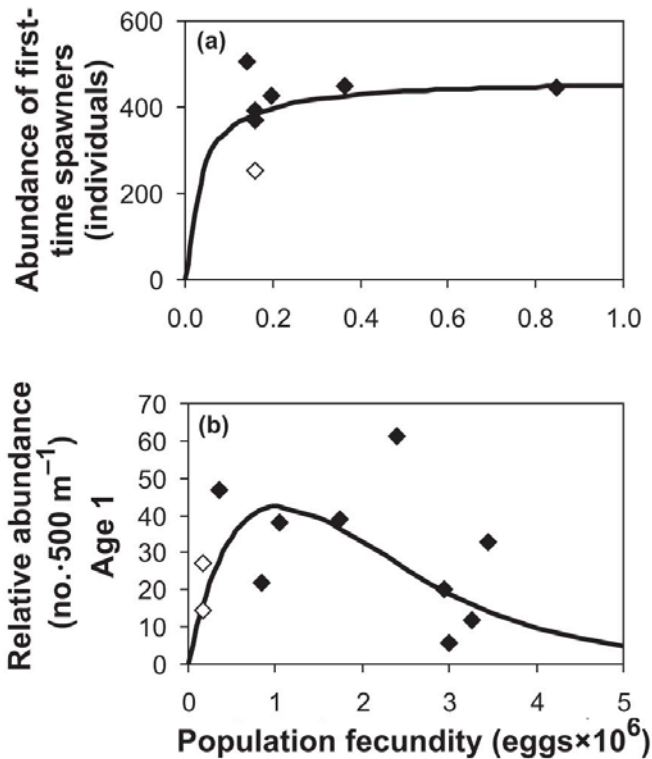
Figure X.1. Stock-recruitment relationships for two life-history stages of bull trout in Lower Kananaskis Lake, Alberta: (a) recruitment from eggs to first-time spawners, fit with a Beverton-Holt curve; (b) recruitment from eggs to age-1 juveniles fit a Ricker curve. Open diamonds in (a) are a conservative estimate of spawners, since this first year-class measured after fishery closure was vulnerable to angler harvest as juveniles in the spawning stream. Open diamonds in (b) represent an additional year when juveniles were captured in two different stream reaches, but these were not used in fitting the model. Source: Johnston et al. (2007).

Sidebar X.2. Density dependence in two bull trout populations

In the Columbia River Basin, Erhardt and Scarnecchia (2014) documented changes in bull trout in the North Fork of the Clearwater River following 14 years of harvest closure, a management action designed to rebuild the stock. Redd counts increased over the duration of the sampling (1994-2008), but a logistic model fitted to the data indicated that the recovery is slowing. The population is expected to slowly approach a carrying capacity, estimated to be 138 redds within the monitored portion of the Basin, by 2018, 24 years after the closure. In terms of population size, an estimated 112 spawning adults in 1994 will slowly increase to a maximum equilibrium abundance of 3,911 spawning adults. In terms of total adults and present levels of spawning frequency (75-80%), it would surpass the recovery goal for this stock (Figure X.2).
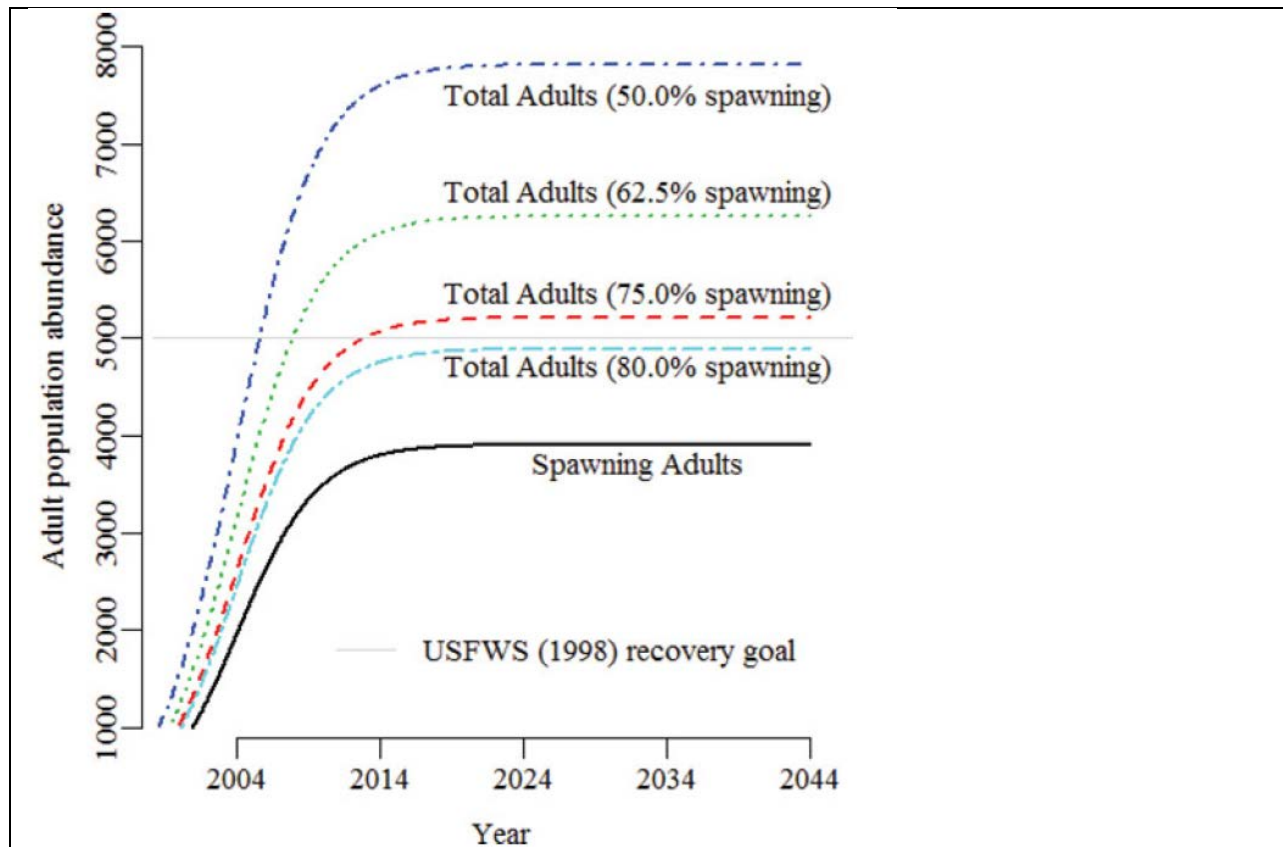
Figure X.2. Logistic model projections of the adult population of North Fork migratory bull trout compared with the U.S. Fish and Wildlife Service recovery goal of 5,000 adults. The intrinsic rate of growth was derived from redd counts from 1994 to 2008. The population estimate in 2004 was based on estimates from Hanson et al. (2006). Total adult abundances were estimated from the spawning frequency (80%) reported by Hanson et al. (2006), and additional frequencies were added for comparison. Source: Erhardt and Scarnecchia (2014).

Density dependent responses of bull trout were also observed in Lower Lake Kananaskis, Alberta after a no-harvest regulation had rebuilt the stock 28-fold from a seriously depleted state (Johnston et al. 2007, Johnston and Post 2009). In addition to the density dependent recruitment described above, density dependent growth was reported. Individual growth in length declined with adult abundance and fish length. Density also affected size at maturation, age of maturation, and the reproductive periodicity (i.e., period of gonadal recrudescence). Mean size at maturation differed by sex; it increased with density in males (by 19 mm) but decreased in females (by 11 mm) when the population increased by 1,500 fish. Large females were 29% more fecund at low densities than at high densities. Mean age at maturation increased with density for both sexes, as did the period of time between successive spawning for individual fish. After maturation, fish of both sexes, and especially males, were more likely to skip a spawning year as fish densities increased because their growth rates in the prior year were lower (Figure X.3; Johnston et al. 2007, Johnston and Post 2009). These studies indicate that if natural-origin stocks such as bull trout in limited habitats are protected from angling mortality, they will eventually reach a carrying capacity and encounter density dependent

recruitment, growth, and maturation. They will also show altered life history characteristics as densities change.
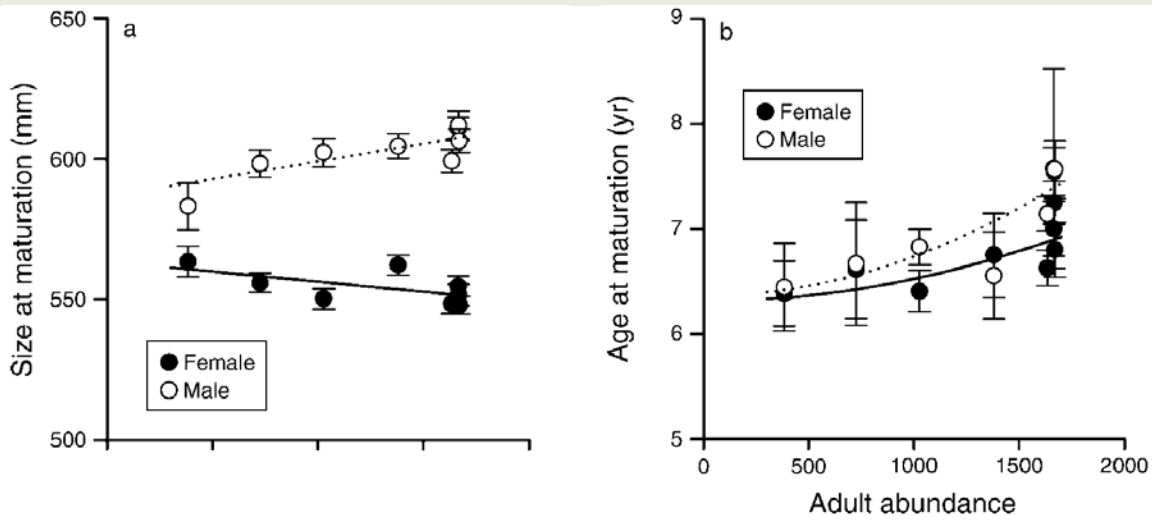
Figure X.3. (a) Size at maturation and (b) age of maturation (mean $\pm$ 95% CL) in relation to total adult abundance and gender for adult bull trout in Lower Kananaskis Lake, Alberta, Canada. Solid lines indicate linear model predictions; n = 3,111 and 305 for size and age, respectively. Source: Johnston and Post (2009).

Table X.1. Questions of management interest about density dependence for resident trout, and a synopsis of information from previous studies that addresses them.

Question of management interest	Synopsis of information from previous studies
1. Does habitat restoration decrease density dependent limiting factors and thereby increase carrying capacity?	Restoring in-stream habitat can increase carrying capacity and thereby increase numbers of resident trout, but the density dependent mechanisms are not clear and probably vary among ecosystems. In one comprehensive long-term study, reduced emigration was a stronger response than increased survival or fecundity, and sufficient to explain most of the increase in density.

Restoring riparian vegetation can increase the input of terrestrial invertebrates, which can increase growth and abundance and decrease emigration of resident trout. |
2. Does stocking of hatchery trout reduce carrying capacity for natural-origin trout, and thereby reduce their density?	Overall, introducing trout of the same species that are reared in hatcheries can have density dependent effects on growth (e.g., Weiss and Schmutz 1999, Bohlin et al. 2002), but effects on survival have not been reported. A general hypothesis is that hatchery fish have low survival, reducing the opportunity for long-term density dependent effects on natural-origin trout.
3. Do invasions by non-native trout or other non-native species reduce the carrying capacity for native trout, and thereby reduce their density?	Non-native species can have strong effects on native species, reducing the carrying capacity remaining for the natives, but these effects depend strongly on density of the native species and the environmental conditions. Favorable environmental conditions may favor the native over the invader, whereas unfavorable ones can hamper the native species and favor tolerant invaders.
4. Can overexploited trout populations rebound when angling mortality is reduced to sustain higher densities for conservation or sport fishing?	Populations of resident trout often rebound after angling mortality is reduced, and thereby sustain larger numbers of large fish that can contribute to conservation goals or be caught and released by anglers. This indicates that angling mortality is more often closer to additive than compensatory for older fish, which suggests that most natural mortality has occurred at earlier life stages, before angling mortality occurs.

XI. Kokanee

The kokanee, a landlocked form of sockeye salmon, *O. nerka,* is native to the northwest where it supports valuable recreational fisheries. It also has been stocked widely outside of its native range into waters of low to moderate productivity in an effort to create robust harvest fisheries. However, its life history, which consists of semelparity (i.e., spawns once and dies), a short lifespan (typically 5 years or less), variable spawning success affected by habitat fluctuations (Fraley and Decker-Hess 1987), and zooplanktivorous or sometimes benthivorous food habits (Scott and Crossman 1973), leads to wide population fluctuations and intense competition for food (Holton and Johnson 2003).

Whether intraspecific competition becomes an issue for kokanee in a given situation may depend on the density of fish, fish size or age, the productivity of the habitat (Rieman and Myers 1992), and density of predator species (Maiolie and Fredericks 2014). For instance, Beauchamp et al. (1995) estimated that competition was unlikely to be limiting in Lake Ozette, Washington because of a high

concentration of *Daphnia* related to projected consumption by kokanee. Rieman and Myers (1992) found that density dependence in kokanee occurred commonly in oligotrophic lakes of northern Idaho but only in older age classes of fish. They suggested that "*density dependent growth should be less important for young kokanee because shifts in forage size with selective predation will not create the same change in foraging efficiency for small fish as for large fish*" (p. 188). That is, as kokanee become larger relative to their zooplankton prey, their efficiency in finding adequate forage would decline, creating more opportunity for density dependent growth to occur at high fish densities and in unproductive waters. Strong density dependence has also been shown in Lake Pend Oreille kokanee, consistent with a dome-shaped Ricker recruitment curve when numbers at each age are plotted against numbers at the same age in the previous generation (Figure XI.1). Fredericks et al. (1995b) concluded that "*density-dependent mortality of kokanee in Lake Pend Oreille is a factor regulating the population*" (p. 16).
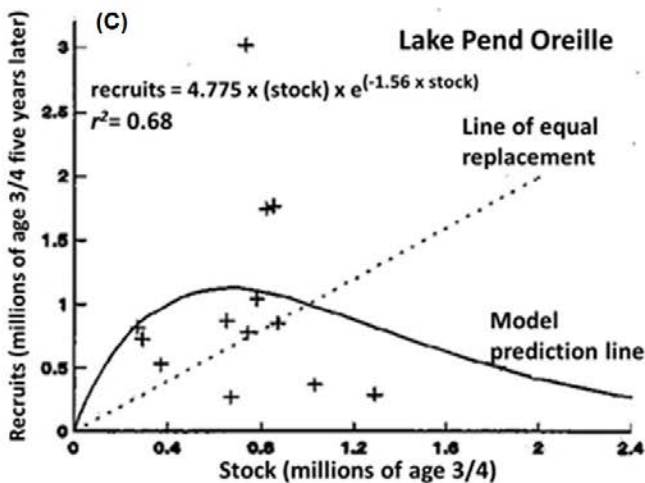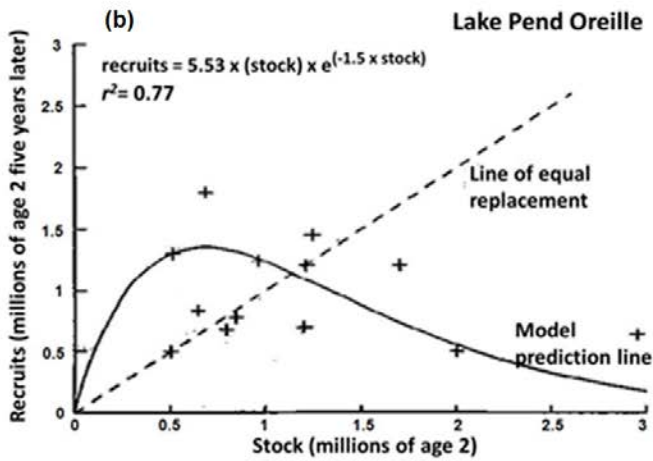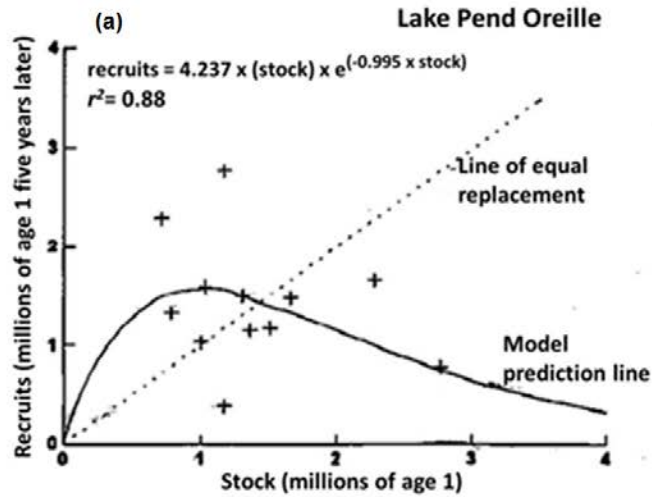
Figure XI.1. (a) Abundance of age1+ kokanee (recruits) as a function of age1+ kokanee five years prior (stock). (b) Abundance of age2+ kokanee (recruits) as a function of age2+kokanee five years prior (stock). (c) Abundance of age3+/4+ kokanee (recruits) as a function of age3+/4+ kokanee five years prior (stock). Source: Fredericks et al. (1995b).

Variable size at age in kokanee is often caused by density dependent changes in growth rate following wide fluctuations in kokanee abundance. For example, Fraley and Decker-Hess (1987) investigated kokanee in the regulated Flathead Lake and river system, Montana and found a strong relationship between the mean total length of kokanee spawners in the system in a given year and the flow levels during their brood years for the years 1966 to 1984. In periods (three-year running averages) when lake levels were high and river gauge heights were high, the result was less variable conditions during incubation. Greater water level fluctuations led to increased incubation mortality (i.e., reduced spawning success) due to embryo desiccation and freezing (sites influenced by springs were an exception). During favorable flows and lake levels, female kokanee spawners were more abundant but were, on average, shorter in length (299.5 mm TL) at spawning than in less favorable lake and flow levels, when the fish were fewer in number but longer (345 mm TL; R^2 = 0.93; p < 0.001). From a habitat standpoint, the lake and reservoir levels were directly affected by operation of Kerr Dam (constructed 1938) on the Flathead River below Flathead Lake and Hungry Horse Dam (constructed 1948-1953) on the South Fork of the Flathead River above Flathead Lake. This example depicts how habitat factors and operation decisions can have major effects on year class strengths and fish size at age (i.e., growth rate) through mechanisms of density dependence.

Based on a range of studies, the importance of year class strength in affecting growth of kokanee is sufficiently well established that in a given year the mean length of kokanee

spawners (an indication of growth rate in that year class) can be used as a reliable indicator of the year class strength (Rieman and Bowler 1980) and of spawner abundance (Figure XI.2a; Fredericks et al. 1995a,b), and vice versa. For example, in Dworshak Reservoir, Idaho, Fredericks et al. (1995a) found that higher spawner counts in three creeks flowing into the reservoir explained variation in mean total length of spawners over a range of up to 100 mm in length (Figure XI.2b). Rather than fish necessarily delaying maturity, many kokanee matured at a smaller size. In some instances, slower growth trajectories can delay age at maturity (e.g., from age-3 to age-4; Grover 2005), so that a higher fraction of older age spawners on spawning grounds can indicate a density effect on growth. Such delayed maturation can obscure the expected decrease in mean fish size on the spawning grounds, as older fish become larger in the year following their maturation delay. Because of the complex and confounding effects of growth, size, and age at maturity, the effect of density is best observed by following both the growth or size and the maturation trends of an individual cohort through its lifespan (Patterson et al. 2008).

Overstocking of kokanee fry has also been implicated as a cause of density dependent effects leading to intraspecific competition, zooplankton overgrazing, and population declines. Martinez and Wiltzius (1991) reported that high levels of stocking in a Colorado reservoir led to strong year classes in the short term but ultimate population collapse as the *Daphnia* food base was overgrazed.
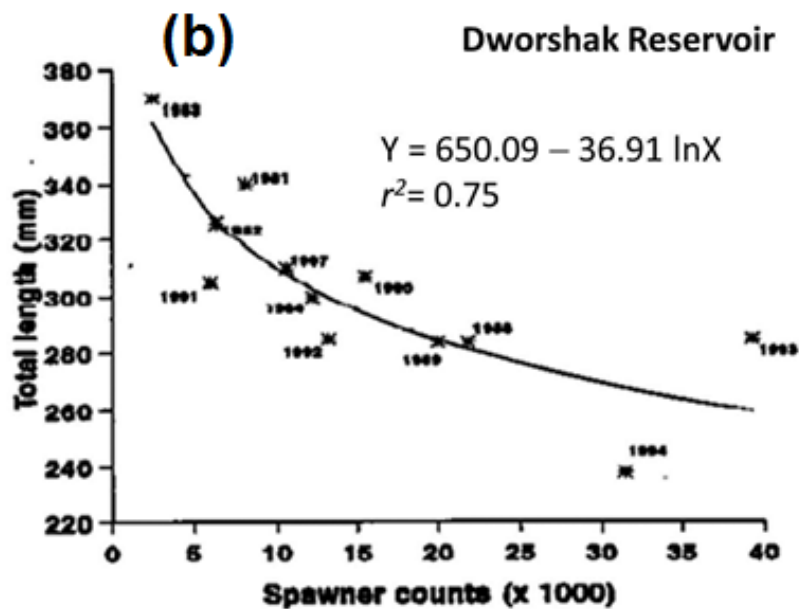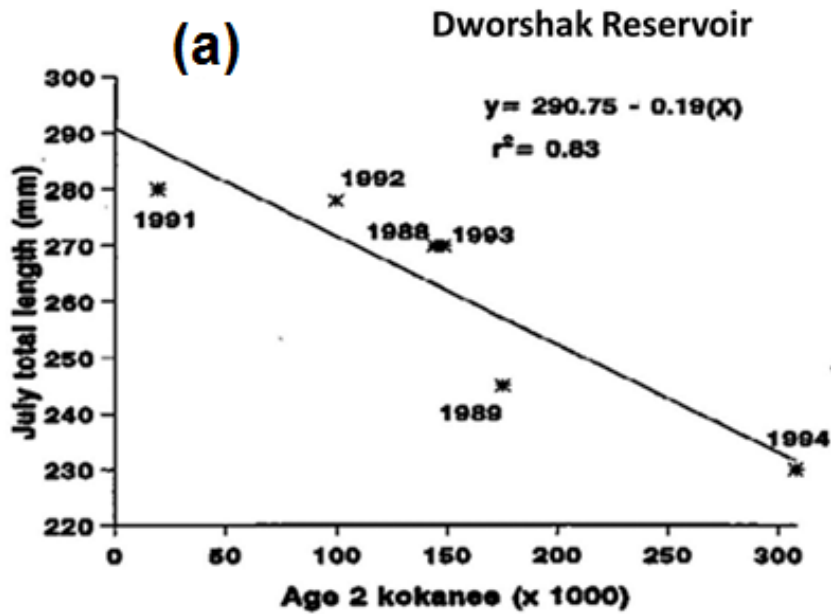
Figure XI.2. (a) Abundance of age 2+ and 3+ kokanee and their modal length estimated from the July trawling effort. (b) The number of spawning kokanee in Isabella, Quartz, and Skull creeks since 1981 and their modal length. Source: Fredericks et al. (1995a).

As a result of population fluctuations and angler responses to kokanee density, optimal fishery management for the species typically needs to be conducted with regard to potential density dependent effects. For example, Rieman and Maiolie (1995) found strong density dependent responses between fish density and fishing effort, fish density and catch rate, and fish density and yield of fish (kg/hour; Figure XI.3). In all cases, relationships were dome-shaped, indicating that intermediate levels of fish density led to the highest effort, catch rate, and yield. In years when density of fish is very low, large trophy-size kokanee can result, but the low spawner densities may lead to strong population fluctuations and collapse. At excessively low densities, growth can be faster and sizes of fish caught larger, but there are fewer fish and fewer spawners, potentially resulting in unstable year classes. At excessively high densities, growth can be slowed, reducing availability of desirable-sized fish to anglers as a high fraction of fish may spawn and die before reaching a desirable size (Patterson et al. 2008). In some cases, however, where population fluctuations are especially extreme, the population may be regulated more by extrinsic conditions than by harvest. For example, Askey and Johnston (2013) investigated the Lake Okanagan recreational fishery and found that the wide population fluctuations experienced by kokanee were more a result of lake productivity or fluctuations in abundance of competitors such as opossum shrimp (*Mysis relicta*) than by fishing. In that case, as the kokanee population abundance declined to

low levels, the fishery became self-regulating as anglers greatly reduced their effort as catches dropped to fewer than two fish per day.

In most cases, especially in less productive waters where density effects tend to be more apparent, managers are advised to use their knowledge of limiting factors to seek intermediate densities and to avoid the ecologically unrealistic goals of trying to produce either trophy fish or larger and larger year classes of large fish. The optimal harvest management approach is to maintain intermediate densities, resulting in intermediate growth rates, intermediate survival, intermediate age at maturity, intermediate yield, and the sort of stability that often characterizes successful long-term fisheries. This approach is currently applied in Lake Coeur d'Alene, Idaho (Maiolie and Fredericks 2014), where intermediate densities of kokanee are the management goal and predator tule fall Chinook salmon have been stocked, providing two popular fisheries while "keeping kokanee (the prey) and Chinook salmon (the predator) populations in balance" (p. 1; Maiolie and Fredericks 2014). Kokanee abundance (density) is assessed through trawling and hydroacoustics and Chinook salmon abundance through redd counts; adjustments can be made if densities of predators or prey species become too high or too low. Evidence suggests that this approach has been effective for balancing numbers and densities of each species (Figure XI.4).
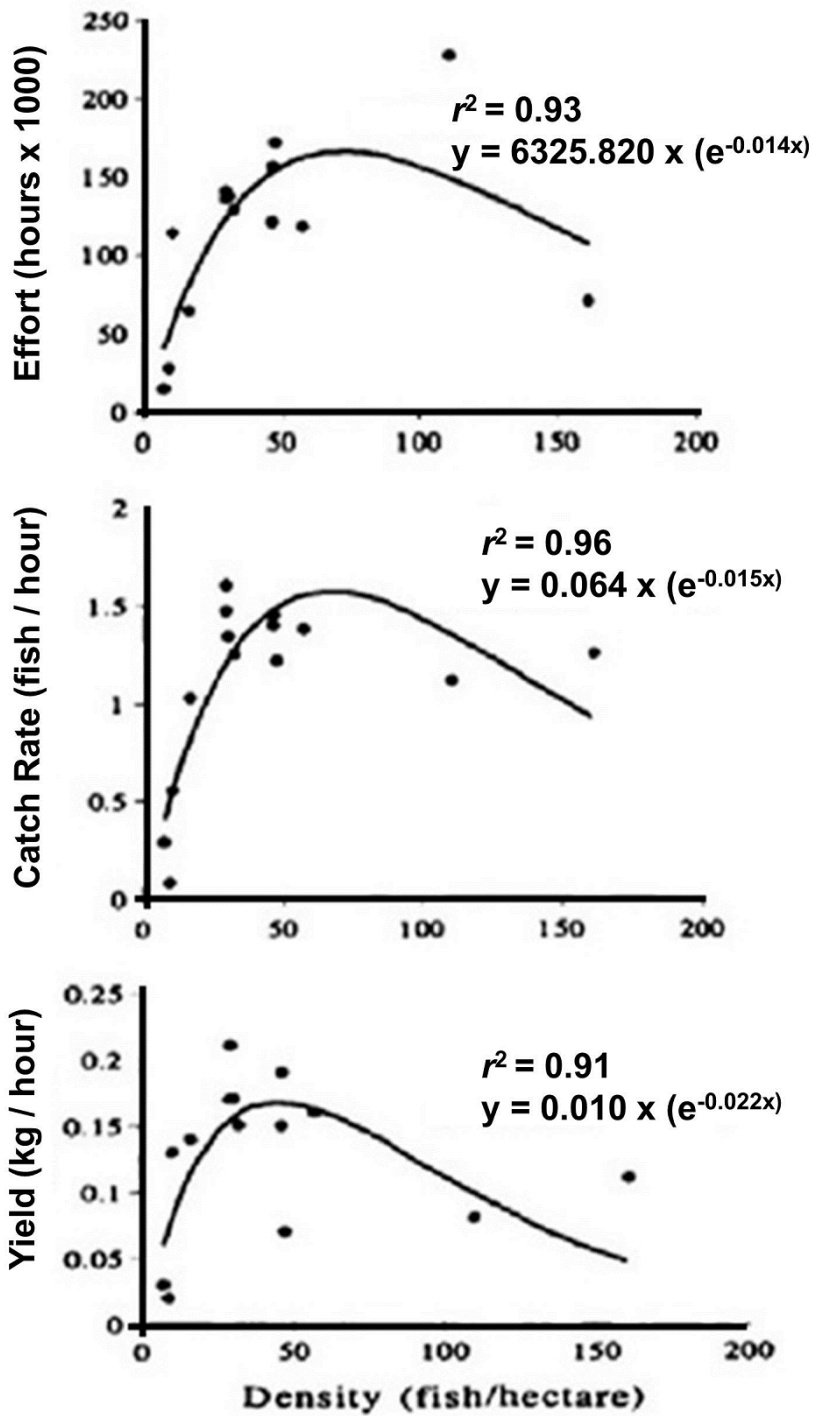
Figure XI.3. Relationships of estimated angler effort (thousands of hours), catch rate, and yield against kokanee density for fisheries in Idaho and Oregon. Source: Rieman and Maiolie (1995).

Figure XI.4. Mean total length of mature male and female Kokanee in Coeur d'Alene Lake, Idaho, from 1954 to 2013. Years where mean lengths were identical between sexes were a result of averaging male and female lengths together. The horizontal line depicts a desired range between 250 mm and 280 mm. Source: Fishery Management Annual Report (IDFG 14-102), Idaho Dept. of Fish and Game (2014).

XII. Sturgeon

Density dependence has also been observed in the Columbia Basin in long-lived fish such as the sturgeons. The Columbia Basin is inhabited by two sturgeon species, the white sturgeon (*Acipenser transmontanus*) and the green sturgeon (*A. medirostris*)*.* The green sturgeon has historically been much less abundant than the white sturgeon; they are rarely found more than 60 km up the river (King and Norman 1991) and little information is available to suggest that they spawn in the Columbia River Basin. Insufficient data are available to assess the role of density in their population dynamics. In contrast, the white sturgeon distribution extends into Idaho and Canada, as historically they were able to move great distances up and down the river. Dams have now fragmented sturgeon habitat into "*… semi-isolated segments where conditions are no longer optimal for completion of the sturgeon life cycle. Productivity of impounded sturgeon sub-populations is currently much lower than that of the unimpounded population downstream of Bonneville Dam*" (p. 20, Beamesderfer 2011). This lower productivity may be an important issue for sturgeon that were formerly anadromous but are now landlocked. Lower food availability may be manifested as smaller adult fish with fewer eggs.

The fish have been classified into nine distinct management units: Lower Columbia, Lower Mid-Columbia, Upper mid-Columbia, Transboundary Upper Columbia, Far Upper Columbia, Kootenai, Lower Snake, Mid-Snake, and Upper Snake (Beamesderfer et al. 2011). The species has declined in abundance basin-wide. Reproductive success (inconsistent) and

recruitment past the first one or two years (inadequate) are limiting factors. The Lower Columbia management unit, below Bonneville Dam, is by far the most abundant, productive, and reproductively robust of the management units but has nevertheless declined to where harvest regulations have become progressively more restrictive, emphasizing catch-and-release and short harvest windows with a harvest slot limit based on fish length (www.dfw.state.or.us/resources/fishing).

Density effects on growth or survival in natural-origin populations are more difficult to detect now than they would have been historically because of inadequate contrast in densities (high and low density data points are typically lacking). Under current conditions, therefore, density effects are most easily detected via growth and survival information from hatchery programs aimed at population restoration in portions of the Basin where stock size has declined.

One case where density dependence has been observed in white sturgeon in the Columbia Basin is the geographically isolated, endangered Kootenai River population (Kootenai management unit). Recruitment declines documented as early as 1960, and the subsequent total recruitment failure coincided with loss of river function and reduced riverine productivity for fish. Factors associated with the long-term recruitment failure have included channel confinement and loss of river-floodplain connectivity. The construction of Libby Dam in 1972 led to changes in discharge, downriver water temperature, suspended sediment and

nutrient delivery, and productivity for fish (Snyder and Minshall 2005), including sturgeon. The recruitment failure led to the initiation of a conservation aquaculture program in 1990 (reviewed in Justice et al. 2009). In the program, natural-origin broodstock is captured each year, artificially spawned and reared in two hatcheries. Fish are released into the Kootenai River after one or two years. This program has increased the number of young fish in the river (Figure XII.1; Kootenai Tribe of Idaho 2010).
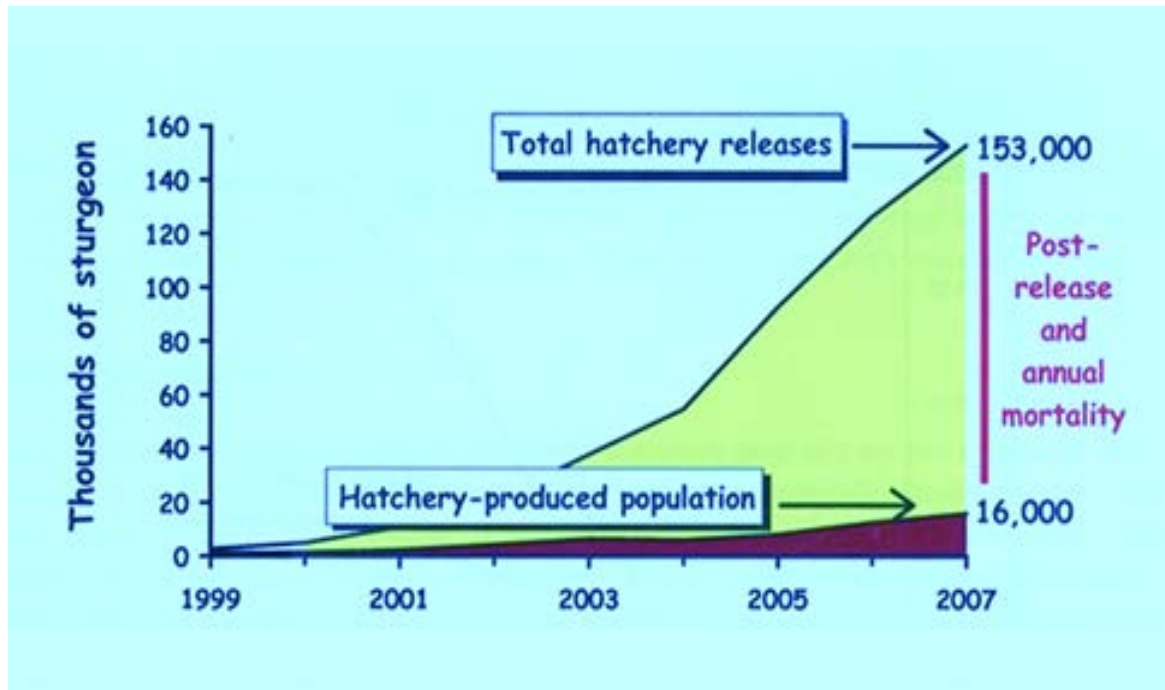
Figure XII.1. Estimated population of hatchery-reared sturgeon one year following release into the Kootenai River from 1997-2007. Source: Kootenai Tribe of Idaho (2010).

Justice et al. (2009) reported that survival of hatchery-reared juvenile white sturgeon released into the Kootenai River was negatively correlated with fish fork length at release in 1992, the first year of release, and not correlated with fork length at release in 1994. In subsequent years, however, as numbers and densities of young pre-recruited fish in the river increased, larger size at release conferred an advantage in survival (Figs. XII.2, XII.3). At higher densities, slower growth resulted in a lower survival rate (Figs. XII.3, XII.4; Justice et al. 2009). This response to higher densities has changed the tradeoff between numbers stocked and survival rate (Figure XII.5). The observed density dependent response might have occurred soon after stocking in the Kootenai River. Productivity of the river section has declined greatly as a result of lower temperatures and less delivery of nutrients (i.e., reduced autotrophic and detrital contributions) below Libby Dam (Snyder and Minshall 2005). Low productivity habitats would be most likely to show the effects of density, even at low stocking numbers.

Seasonal changes in water quality in river reservoirs with limited rearing habitat

create the potential for density effects on survival of pre-adult and adult fish. Sullivan et al. (2003) modeled potential distribution and survival of white sturgeon in Brownlee Reservoir, a mainstem Snake River impoundment on the Idaho-Oregon border. In this situation, reduced nutrient inputs into the reservoir resulted in better water quality (including temperature and dissolved oxygen) for the sturgeon. The model indicated that the number of sturgeon that could be accommodated depended strongly on the amount of available habitat, a function of water temperature and dissolved oxygen concentrations. The carrying capacity for sturgeon varied greatly among years; in years with little suitable habitat, fish unable to leave the confinement of dam-created pools could suffer mortality.

The results of Justice et al. (2009) and Sullivan et al. (2003) underscore the importance of realistically assessing the potential productivity of release areas for white sturgeon as stocking programs expand. Understanding potential productivity of Columbia Basin pools and riverine reaches for sturgeon is particularly important now that dams have blocked or greatly impeded movements throughout the basin, often limiting sturgeon movements to a single river reach or reservoir pool. Prior to impoundment, fish often ranged widely throughout the river, into the ocean, and into other West Coast rivers, resulting in increased overall production and a lower likelihood of being limited by local density effects on food availability or water quality. Density effects are more likely to arise under current conditions and with increasing interest in expanding hatchery programs to restore sturgeon into fragmented habitats.
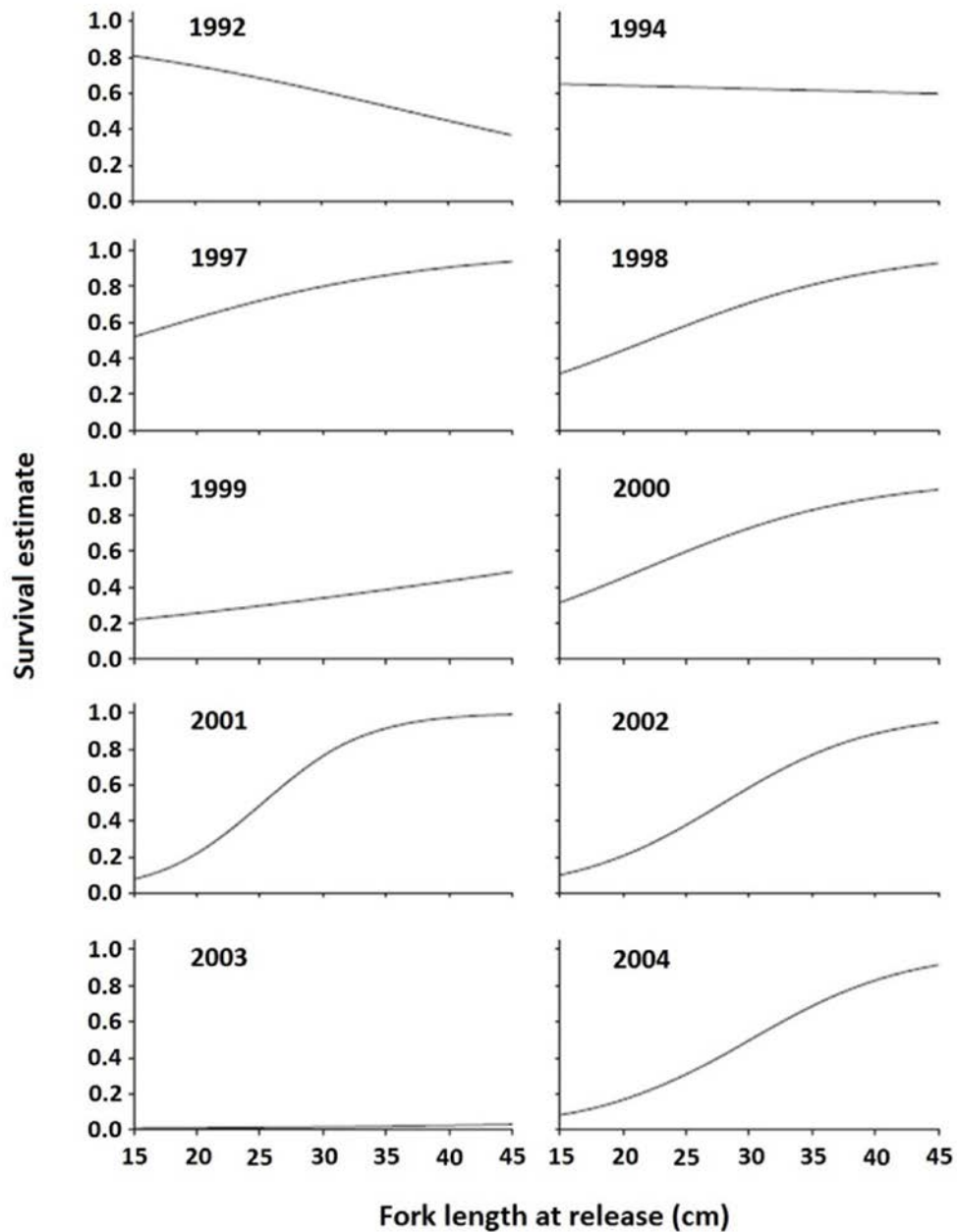
Figure XII.2. Relationships between fork length-at-release (cm) and age-1 survival of hatchery-reared white sturgeon released into the Kootenai River as estimated from the best-fitting covariate model (Model 11). No fish were released in 1993, 1995, and 1996. Source: Justice et al. (2009).
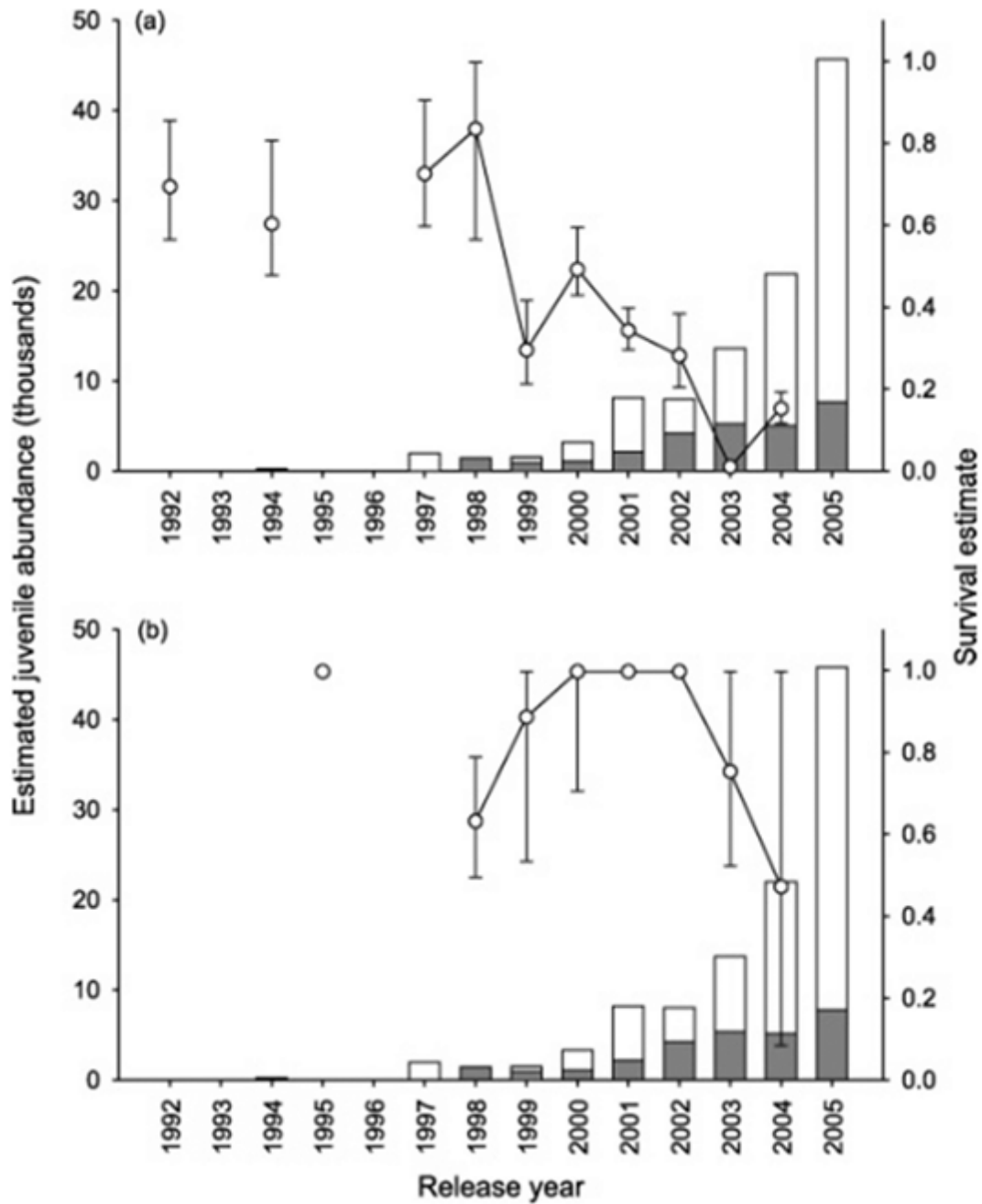
Figure XII.3. Estimated abundance (total releases + residual population) of hatchery-reared juvenile white sturgeon released into the Kootenai River compared with (a) age-1 survival rates and (b) age-2 survival rates for release years 1992-2005. New releases, residual population, and survival rates are denoted by open bars, solid bars, and circles, respectively. Survival estimates were derived from the best-fitting non-covariate model (Model 6). Source: Justice et al. (2009).
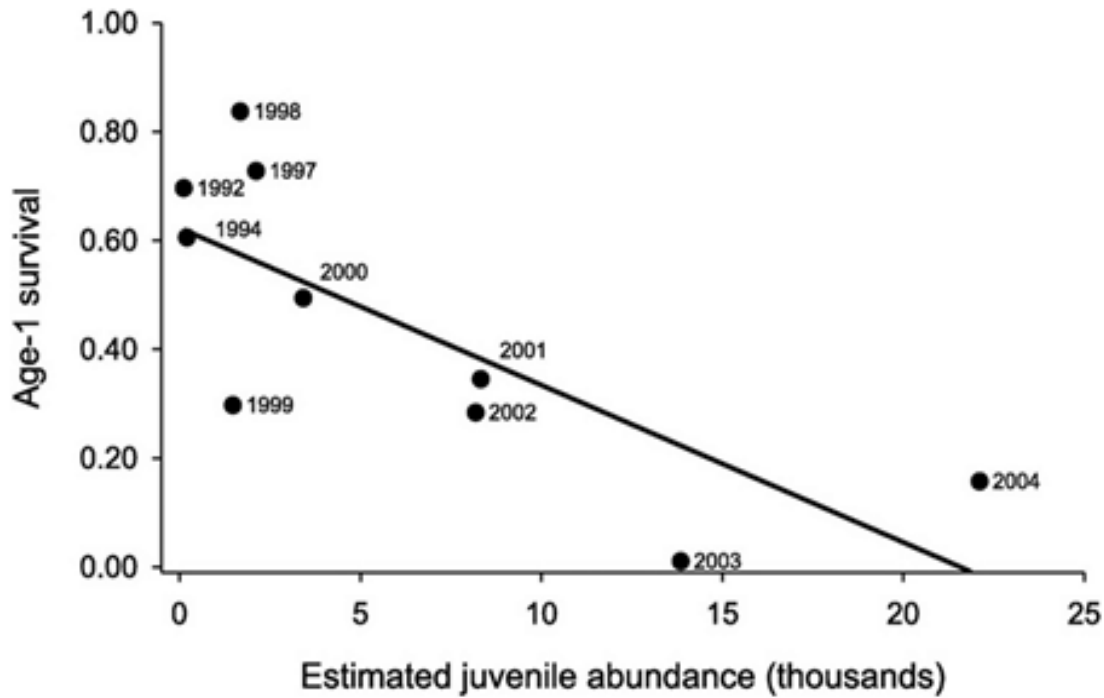
Figure XII.4. Relationship between annual estimates of juvenile white sturgeon abundance and age-1 survival rates in the Kootenai River. Survival estimates were derived from the best-fitting non-covariate model (Model 6). Source: Justice et al. (2009).
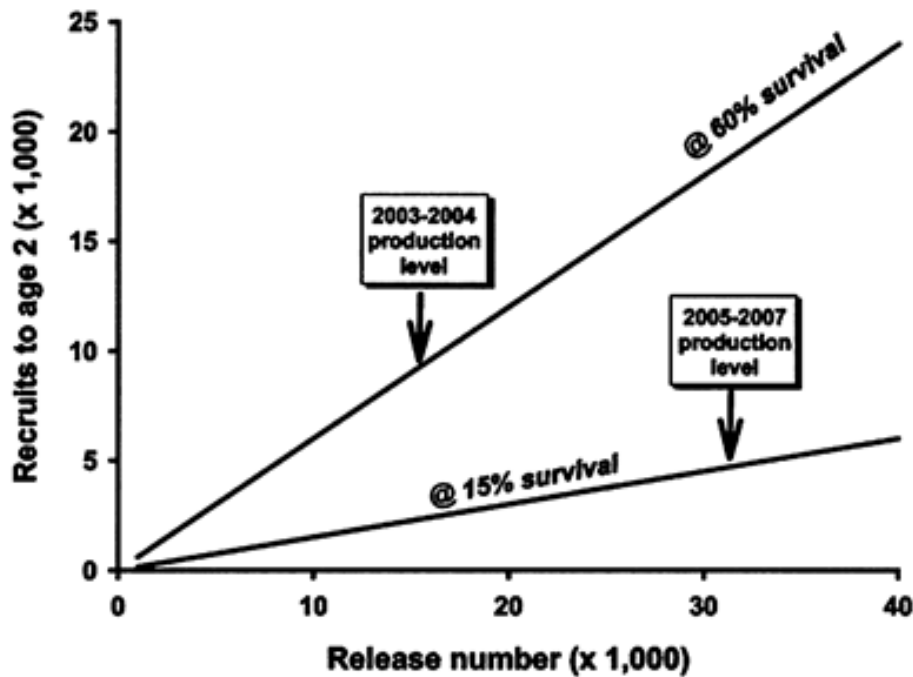
Figure XII.5. Tradeoff in recruitment between release number and survival. Source: Kootenai Tribe of Idaho (2010).

XIII. Lamprey

Pacific lamprey (*Entosphenus tridentatus*) is a native fish of the Columbia River Basin that was a historically important food for Native Americans (Close et al. 2002, Petersen Lewis 2009). Since 1970, Pacific lamprey abundances in the Basin and along the west coast have been greatly reduced (Close 2002). For instance, based on traditional ecological knowledge (TEK) of the Yurok and Karuk tribes, adult lamprey returning to the Klamath River basin in California and Oregon have been reduced by > 99% in the last 50 years (Petersen Lewis 2009).

The decline of Pacific lamprey in northwest ecosystems has created gaps in foodwebs as they are prey as well as predators (Roffe and Mate 1984, Close et al. 2002, 2010) and are a source of marine-derived nutrients (MDN; Wipfli et al. 1998). Pacific lamprey are semelparous, anadromous fish that require a variety of marine and freshwater habitats to complete their life cycles (Luzier et al. 2011, Starcevich et al. 2014). After several years in the ocean, adult lampreys enter fresh water and spawn in gravel, similar to salmon. After hatching, larval lamprey (Figure XIII.1) drift downstream to silted areas where they spend up to 10

years filter-feeding and growing before metamorphosing and migrating to the ocean as macrophthalmia (Mesa and Copeland 2009; Figure XIII.2). Based on traditional knowledge of tribal "*eelers,*" the density of larvae increases with decreased substrate particle size (Petersen Lewis, 2009). There is little information available on the distribution and abundance of Pacific lamprey (Mesa and Copeland 2009), thus it is impossible to describe definitively the role that density dependent factors play in their population dynamics. Preferred habitat types of the various Pacific lamprey life stages have been described (Robinson and Bayer 2005, Luzier et al. 2011, Starcevich et al. 2014). A single laboratory study correlated the growth of larval Pacific lamprey to the density of conspecifics and food availability (Mallatt 1983); if food was held constant, growth rate varied inversely with density. Close et al. (2009) documented an almost two orders of magnitude increase in larval density from 0.08 larvae/m^2 to 6.56 larvae/m^2 after adult Pacific lamprey were reintroduced into the Umatilla River, Oregon; however, whether or not the change in density affected growth or survival was not determined.

Figure XIII.1. Pacific lamprey larva. Photo courtesy of USGS.

Figure XIII.2. Pacific lamprey macrophthalmia. Photo courtesy of Luke Schultz, Oregon State University.

Recent research on Pacific lamprey spawning in tributaries of the Willamette River examined the number of lamprey redds versus the abundance of larval lamprey (Mayfield et al. 2014). The resulting graph (Figure XIII.3) has the appearance of a density dependent stock-recruitment curve, but the authors acknowledge that this is speculation given so few data and they encourage further study (Carl Schreck and Luke Schultz, Oregon State University, personal communication).

Murauskas et al. (2013) have shown that between 1997 and 2010 the abundance of adult Pacific lamprey counted at Bonneville Dam (i.e., migrating upstream) is correlated strongly with the abundance of potential hosts including Pacific hake *Merluccius productus*, walleye pollock *Theragra chalcogramma*, Pacific cod *Gadus macrocephalus*, Pacific herring *Clupea pallasii* and adult Chinook salmon (Figure XIII.4) in the northeast Pacific Ocean as evidenced by commercial landings. Abundances of the host species and lamprey were also correlated to PDO and measures of upwelling (these were not auto-correlated; Murauskas et al. 2013). The authors also point out that between the periods 1950-1969 and 1997-2010 the combined landings of cod, herring, and Chinook decreased by 68% and Pacific lamprey returns to the Columbia River declined by 65%. Thus, it seems that the productivity of Columbia River Pacific lamprey is positively correlated with the density of their potential hosts in the ocean.
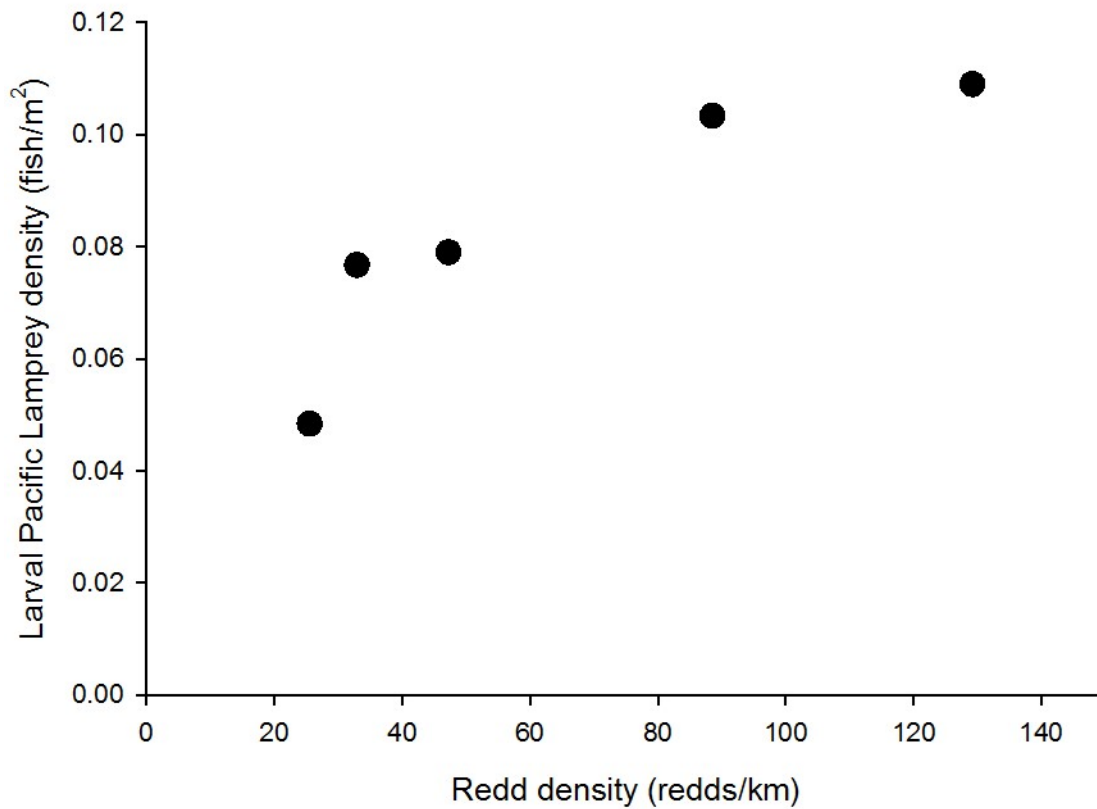
Figure XIII.3. Relationship between adult Pacific lamprey spawning (mean redd density; redds/km) and larval production (overall mean larval Pacific lamprey density from the same year of sampling; individuals/m2) in tributaries to the Willamette River. Larval data are from Schultz et al. (2014). This graph may also be interpreted as the relationship between larvae attracting adult spawners via pheromone responses (e.g., Yun et al. 2011). Source: Mayfield et al. (2014).
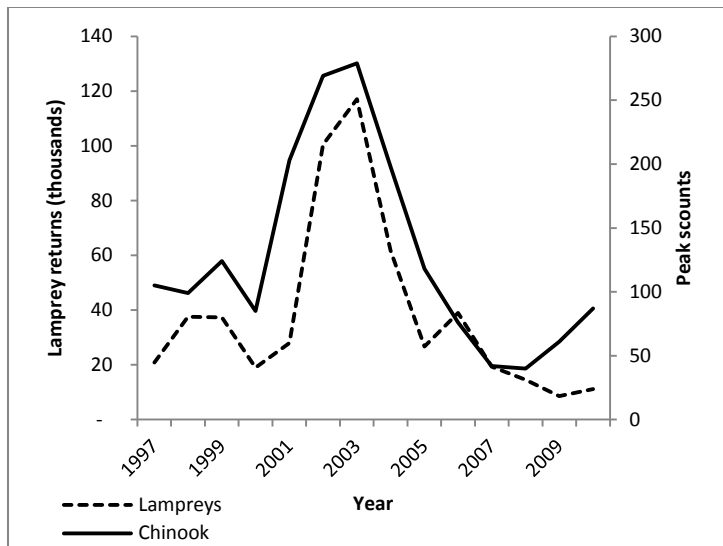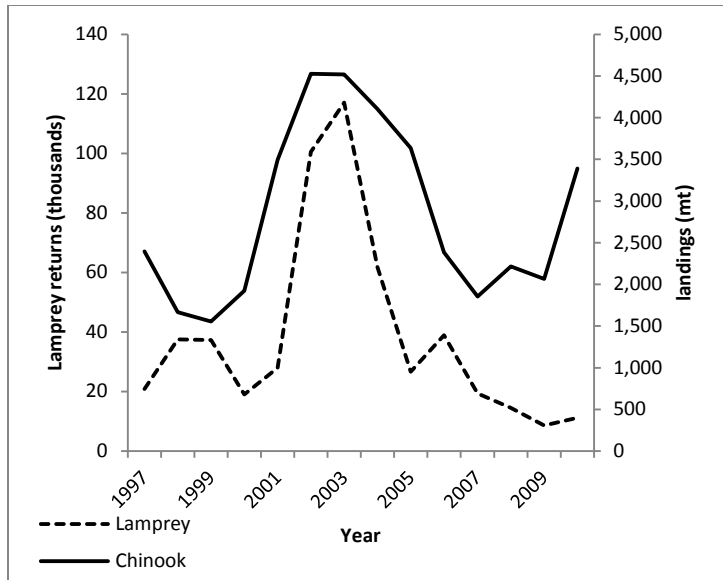
Figure XIII.4. Correlations between adult Pacific lamprey counted at Bonneville Dam and the abundance of adult Chinook salmon based on commercial landings (p = 0.005, r = 0.70) and counts at Bonneville Dam (p < 0.001, r = 0.88). Source: Murauskas et al. (2013).

The life history of the sea lamprey (*Petromyzon marinus*) is very similar to that of the Pacific lamprey. A significant research effort has been aimed at reducing the sea lamprey populations in the Great Lakes where they are an invasive species that has caused significant economic loss to commercial fishers (Lawrie 1970). Understanding density dependent factors affecting sea lamprey has been a focus of research that may be relevant to understanding these factors in Pacific lamprey. Jones et al. (2003) reviewed the evidence for compensation in sea lamprey populations and reported large shifts in sex ratios from 54-70% males to 21-44% males after lamprey control actions in the three upper Great Lakes (Superior, Huron and

Michigan) began in the 1960s. Jones et al. (2003) also conducted a meta-analysis of 26 data sets and used a Ricker stock-recruitment model to relate the density of age-1 recruits (larvae/m^2) to the size of the female sea lamprey spawning population. They reported significant compensation (negative slope to the linearized Ricker model) when spawners exceeded 10 females/100 m^2. Weise and Pajos (1998) examined the recolonization of a stream treated with a lampricide and measured larval growth, mortality, biomass, and the rate of metamorphosis. While total density of larvae did not change during the four-year study (83-73 larvae/m^2), biomass in the stream increased 28 g/m^2 each year. Most interestingly, both the numbers and biomass of larvae were dominated by the first year class to recolonize the stream. In addition, while density of the first year class was 37 larvae/m^2 at age 1 and had experienced virtually no mortality, the second year class started with a higher density (47 larvae/m^2) but experienced 63% mortality, which the authors attributed to intraspecific competition (Weise and Pajos 1998). In a similar study, Griffiths et al. (2001) looked at seven streams treated with lampricide and found no evidence of density dependent growth; however, the densities in six of those streams where < 1.0 larvae/m^2.

Weise and Pajos (1998) also reported that in the third and fourth years of their study, all of the metamorphosing larvae (i.e., emigrating macrophthalmia) were from the first year class. A possible mechanism for the results of the field study comes from a laboratory study by Rodriguez-Muñoz et al. (2003) who explored the effect of three different population densities on the growth rates of sea lamprey. They found that increasing larval density had a negative effect on growth and also that when lamprey at very low densities were exposed to water taken from the three density treatments, those fish also experienced reduced growth rates. Rodriguez-Muñoz et al. (2003) concluded that a biological agent released from the sea lamprey could control the growth of their conspecifics. Zerrenner and Marsden (2005) examined the sex ratios, size and age at metamorphosis in two comparisons of larval lamprey: (1) a low lamprey density stream reach separated by an impassable barrier from a high density reach and (2) pre- and post-lampricide treatment. They found that the streams with high-density lamprey populations produced smaller fish going through metamorphosis and had a lower proportion of females as compared to the low density streams.

In an effort to predict the effects of lamprey control programs, several researchers have examined sea lamprey population dynamics with stock-recruitment models to help identify density dependent and density independent factors. Expanding on earlier work (Jones et al. 2003), Dawson and Jones (2009) fit data from 37 Great Lakes streams to a linearized Ricker model and found a significant negative slope, indicating density dependent population dynamics. General linear modeling identified effects of stock size, lake and competitor density. The authors, however, also point out that the high variability in lamprey recruitment points to the effect of density independent abiotic factors (e.g., temperature, flow). Robinson et al. (2013) developed an age-structured model with data from 75 areas in the Great Lakes during the years of 1993 to 2011. Their model included stock-recruitment, spatial recruitment patterns,

natural mortality, treatment mortality and larval metamorphosis. During this time recruitment, larval abundance, and the abundance of metamorphosing individuals all declined by > 80%. Their model identified areas of high larval abundance and showed that areas of low larval density contribute significantly to the population. It is possible that these models could be adapted to explore density dependence in the similar life history of Pacific lamprey.

XIV. Non-anadromous Salmonids, Sturgeon, and Lamprey - Key Points and Recommendations

Differences in life history and ecology, sampling constraints, and a focus on conservation and/or sport fishing versus commercial fishing for non-anadromous salmonids (including trout, charr, and kokanee), sturgeon, and lamprey compared to anadromous salmonids result in different key questions about density dependence for these populations. Key points to be considered in restoring and managing these fishes are:

Resident trout

- Questions for resident trout include effects of habitat restoration, stocking of hatchery trout, and invasions by non-native species on carrying capacity, and whether restricting angling can allow populations to rebound and reach recovery or sport fishing goals

- In-stream habitat restoration is most likely to increase carrying capacity for resident trout, and hence increase density, by increasing survival and decreasing emigration rather than affecting growth, fecundity or immigration. Evidence from across many regions shows that increases can occur, but the true effects on survival and emigration occur at riverscape scales and are difficult to study.

- Restoration of riparian vegetation can increase input of terrestrial invertebrates, which can increase growth and abundance and decrease emigration of natural-origin trout.

- If hatchery trout are analogs of natural-origin trout they could reduce carrying capacity, but this depends on characteristics of the hatchery fish (e.g., degree of domestication), as well as when, where, and how many are stocked. In field studies from other regions, differences in growth have been detected, but none on survival. Neither effect was found in the most comprehensive study conducted in the Columbia River Basin, the stocking of sterile catchable rainbow trout into Idaho streams.

- Non-native trout that invade are often not analogs of native trout and can often replace them rapidly, mount higher density and biomass when they do replace them, and have ecosystem-scale effects on emerging insects that are key food resources for riparian insectivores (e.g., bats, birds). Removing non-native trout above barriers can allow natives to rebound, and in relatively undisturbed watersheds without barriers maintaining robust populations of native trout at high density may resist invasions at early stages.

- Regulating angling of overexploited bull trout, and various cutthroat and rainbow trout populations, allowed populations to reach higher abundances when angling mortality was reduced or eliminated. These results show that angling mortality is closer to additive than compensatory, indicating strong

potential for this type of management to increase density.

Kokanee salmon

- Kokanee, a landlocked form of sockeye salmon, have been documented as exhibiting density dependent growth, age at maturity, and size of fish. The outcome is often expressed as wide variation in abundance and variable size at age.

- Based on multiple studies, the mean length of kokanee spawners (an indication of growth) of a year class can be used as a reliable indicator of year class strength and spawner counts, and vice versa.

- Overstocking of kokanee fry has been implicated as a cause of density dependent effects, leading to intraspecific competition, zooplankton overgrazing, and population declines.

- As a result of population fluctuations and angler responses to kokanee density, optimal fishery management typically needs to consider density dependent effects.

- In most cases, especially in the less productive waters where density effects can be most apparent, managers can use their knowledge of limiting factors and some finesse in both habitat and harvest management in seeking intermediate densities rather than trying to either produce trophy fish or seeking the ecologically unrealistic goal of larger and larger abundances of large fish.

Sturgeon

- Productivity of impounded white sturgeon sub-populations is currently much lower than that of the unimpounded population downstream of Bonneville Dam. This lower productivity may be an important issue in terms of reduced carrying capacity for sturgeon that were formerly anadromous but are now landlocked.

- Lower food availability may be manifested in density dependent responses such as smaller adult fish with fewer eggs, but this hypothesis has yet to be examined.

- Density effects are most readily observed from growth and survival information from hatchery programs aimed at population restoration in portions of the Basin where stock size has declined.

- As the numbers and densities of young pre-recruited white sturgeon increase in rivers, hatchery-reared fish released at a longer fork length appear to survive better than smaller fish. Under conditions of higher density, release of yearlings rather than age-0 fish suggest better survival of released fish as the larger fish circumvent a survival bottleneck, evidently density-related, at a small size.

- In river-reservoir reaches where rearing habitat is limited, the potential also exists for seasonal density dependence to occur on pre-adult and adult fish.

- Results of Justice et al. (2009) and Sullivan et al. (2003) underscore the importance of assessing habitat capacity (i.e., productivity) of release areas for white sturgeon as stocking programs expand.

Lamprey

- Pacific lamprey populations in the Columbia Basin have declined sharply in the past 40 years, but virtually nothing is known about the role of density dependence in their abundance— information that would help managers recover this species.

- Research in the Great Lakes has documented significant density dependent effects for populations of sea lamprey, which is related to the Pacific lamprey. The sea lamprey studies might provide a template for developing a similar understanding of Pacific lamprey.

ISAB Recommendations

The Council's Fish and Wildlife Program recognizes the importance of all native resident fish and other freshwater species in maintaining ecosystem diversity and function, as well as contributing to the Basin's culture. The following recommendations list ways to consider and account for density dependence when planning and evaluating habitat restoration actions, developing quantitative objectives for the Basin's non-anadromous salmonids (trout, charr and kokanee), sturgeon, and lamprey, and improving the research plan of the Council's Program. These

recommendations also generally apply to other efforts (e.g., biological opinions and tribal programs) attempting to mitigate impacts from the 4Hs (hydro, habitat, harvest, and hatcheries).

Due to differences in life history and ecology, sampling constraints, and a focus on conservation and/or sport fishing for non-anadromous salmonids, sturgeon, and lamprey as compared to anadromous salmonids (Part I), there are different issues related to density dependence for these species. Overall, there is a dearth of information on density dependence effects for nearly all resident (non-anadromous) fishes in the Basin. **The ISAB encourages the Council to continue to support a basic understanding of factors affecting the productivity and carrying capacity for these ecologically and culturally important species.**

Non-anadromous salmonids

Density dependent issues for non-anadromous salmonids include effects of habitat restoration, stocking of hatchery trout, and invasions by non-native species on carrying capacity, and whether restricting angling can allow populations to rebound and reach recovery or sport fishing goals. Accounting for density dependence helps determine realistic abundance objectives for the Fish and Wildlife Program's non-anadromous salmonid strategy. Therefore, it is important to consider the following in developing restoration actions for the Program as well as for other regional efforts:

- **Consider that in-stream habitat restoration is most likely to increase carrying capacity by reducing**

compensatory mortality and emigration. The postulated mechanisms are related to increasing survival and decreasing emigration, rather than by affecting growth, fecundity, or immigration. Evidence from across many regions shows that increases can occur, but the true effects on survival and emigration occur at the riverscape scale and remain difficult to quantify.

- **Restore riparian vegetation to increase the input of terrestrial invertebrates**, which can improve growth and abundance and decrease emigration of salmonids.

- **Consider carefully the stocking of hatchery trout to avoid reducing carrying capacity for wild non-anadromous salmonids.** An investigation of stocking sterile hatchery rainbow trout did not detect effects on growth, survival, or recruitment, but this depends on characteristics of the hatchery fish (e.g., degree of domestication), as well as when, where, and how many are stocked. Hatchery fish can also transfer diseases or parasites, and non-sterile ones can hybridize with natural-origin fish, so precautions against these effects are also warranted.

- **Take steps to prevent invasions by non-native trout**, which can often replace native salmonids quickly (i.e., usurping carrying capacity), achieve higher density and biomass when they do replace them, and have ecosystem-scale effects on emerging insects that are key food resources for other wildlife. Removing non-native trout above barriers allows native salmonid

populations to rebound to their former carrying capacity, and in relatively undisturbed watersheds without barriers, maintaining stronghold populations of native salmonids at high density may help to prevent invasions by non-native trout.

- **Consider the use of angling regulations and fishery closures to achieve conservation and sport fishing goals.** Studies of bull trout populations show populations rebounding from low abundance to achieve density goals for conservation, indicating that they were far below carrying capacity and that angling mortality was partly additive to natural mortality. Many populations of cutthroat and rainbow trout throughout the Rocky Mountains also have rebounded when restrictive angling regulations were applied, indicating that fishery management can be effective at increasing the density of resident trout.

- **Ensure that fishery managers consider the probable effects of density on survival, emigration, growth, and size/age at maturity**. For example, kokanee populations can crash due to food limitation following overstocking with kokanee fry. In the absence of detailed data for stock assessment, managers should use their knowledge of limiting factors and fishery management principles to target intermediate densities, rather than seeking the ecologically unrealistic goal of a higher abundance of larger fish.

Sturgeon

The Council recognizes that sturgeon migration, distribution, abundance and

productivity are severely limited by habitat changes, particularly those associated with hydropower system construction and operation. Further, habitat carrying capacities for impounded white sturgeon sub-populations are currently much lower than for the unimpounded, anadromous population downstream of Bonneville Dam. Specifically:

- **Ensure that white sturgeon stocking programs do not cause significant reductions in growth and survival of sturgeon during each life stage.** New sturgeon hatchery programs are being planned and built in the Basin. Hatchery production should be consistent with the capacity of the habitat to support sturgeon at all life stages.

Lamprey

Pacific lamprey populations in the Columbia Basin have declined sharply in the past 40 years. Despite the fact that this species is a key component of the Columbia Basin food web as both prey (e.g., for pinnipeds) and predator, virtually nothing is known about

density effects on their abundance and growth. Therefore, the ISAB recommends:

- **Initiate a concerted effort to gather information that would help the recovery of this species.** Toward that end, research in the Great Lakes has documented significant density dependent effects for populations of sea lamprey, which is related to the Pacific lamprey. These sea lamprey studies might provide a template for developing a similar understanding of Pacific lamprey.

- **Consider lessons learned about supplementation and density dependence in anadromous salmonids when planning future actions to propagate and translocate (i.e., supplement) lamprey within the Basin.** While the ecological lessons might not be directly transferrable, they can be used to guide management and restoration actions.

Appendix I. How to Measure Density Dependence: Study Design and Analysis

Other parts of this document have outlined how density dependence can affect response variables such as recruitment, survival, growth, age of maturation, habitat selection, and such. Conceptually, a density dependence study is straightforward—vary the density and see if the response measure varies in some systematic fashion. There are several standard types of density dependent relationships that appear in the literature (Figure A.1)

However, there are potential pitfalls associated with both planning the study and analyzing the results that need to be accounted for in the planning stage to ensure that the study is successful (Table A.1).
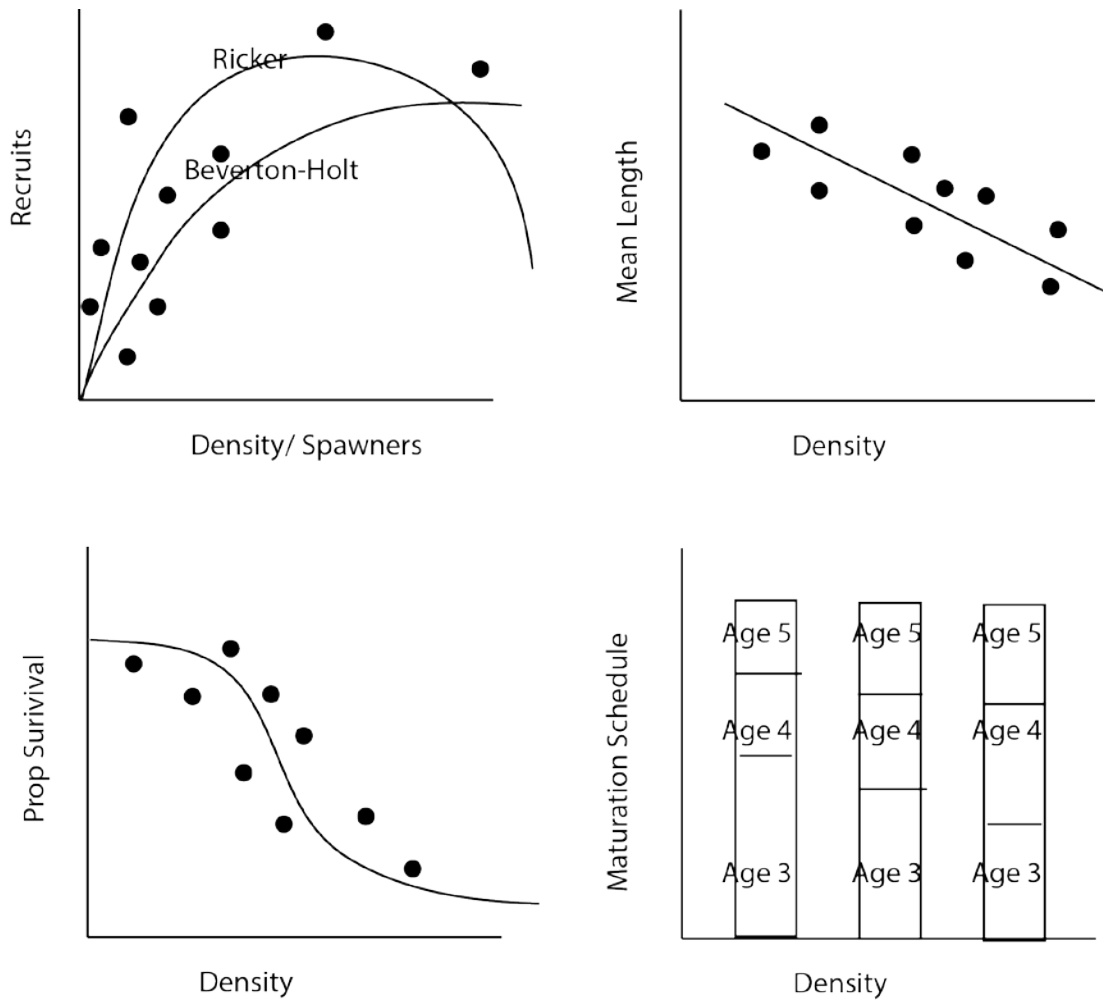
Figure A.1. Typical forms of density dependent relationships.

Table A.1. Summary of pitfalls for common density dependence study design.			
Type of response	Typical statistical analyses	Common pitfalls in design	Common pitfalls in analysis
Recruitment	Ricker or Beverton-Holt curves	Poor contrast	Uncertainty in number of spawners Autocorrelation Time-series bias Choice of error structure
Mass, length, condition	Regression	Sampling biases	Pseudo-replication Uncertainty in number of spawners
Survival	Logistic regression	Non-detection of survivors	Pseudo-replication Uncertainty in number of spawners
Maturation schedule Habitat selection	Polytomous regression	Sampling biases	Uncertainty in number of spawners Uncertainty in classification of response.

A. Issues in Planning Density Dependence Studies

1. Stationarity

Studies of density dependence often take several years because density can typically only be varied on a yearly scale (see next section). Consequently, it is implicitly assumed that the system is stationary (i.e., the relationship between the response variable and density is not changing over time). For short time periods (e.g., a few years) this may be a reasonable assumption, but for decadal-long studies, there are many long-term slowly varying effects such as climate-change, land-use change, and changing ocean conditions that make this assumption tenuous. Similarly, novel ecosystems may not yet have stabilized to where a stationary relationship between density and the response variable has occurred. For example, it may take several years after a dam removal for the ecosystem to stabilize and the density dependence relationship to become stable.

Non-stationarity can be hidden. For example, using a stock-recruitment curve with the number of spawners on the X-axis can hide changes in the area used by the spawners (i.e., the spawner density), which then can affect the relationship.

2. What are the experimental and observational units?

In some types of studies, the experimental unit and observational unit can differ leading to a common problem of pseudo-replication (Hurlbert 1984). Consider for example, studies of density dependence of fry in a lake over many different years and subsequent smolt production and mean mass of smolts (e.g., similar to Hyatt et al. 2011). The experimental unit is the lake-year combination. The observational unit refers to the unit on which the response is measured. The response variables measured could be total smolt production for the lake (observational unit is the lake-year) or the size of smolts (the observational unit is now a fish). An appropriate analysis in the former would be a regression analysis of total smolt production or average smolt size versus density, but a regression analysis using the individual fish sizes versus density is not appropriate. In the latter case, the measurements on the observational units need to be aggregated to match the experimental unit (i.e., only the total number of smolts or the average size of smolts for that lake should be used in the regression against density and each year provides a single datum, regardless of how many fish are measured in a year). Consequently, the number of years of measurement is the limiting factor in the ability to detect density dependence and not the number of fish measured.

3. Contrast

If density does not vary, it is impossible to measure density dependence. For example, it is quite common to fix the number of fish released from hatcheries, which makes it difficult to detect density dependence after release. Even though density dependence studies are usually observational studies, the same general principles about contrast from experimental studies are also applicable. Good studies have a wide range of densities (a high contrast). In cases of straight-line responses (e.g., regression analyses), optimal experimental design says that half of the data should be collected at low densities and half the data at high densities to give the highest power to detect an effect. Observations in the middle of the density range give very little information about the effect of density dependence. However, this would be a very dangerous study plan, as collecting data only at the two extremes gives no information about the shape of the response—it is implicitly assumed that the relationship is linear, but a prudent investigator would want some measurements in the middle of the curve to assess the assumption of linearity. A good compromise in these cases is to collect three quarters of the data on the extremes of density and expend the remaining one quarter of the observations over the range of densities in the middle.

In the case of Beverton-Holt and Ricker curves, the issue is more complex. In both the Beverton-Holt and Ricker relationships, measurements at high densities are required to estimate the asymptote of the Beverton-Holt relationship or the declining arm of the Ricker curve. Measurements at low densities are required to measure the

maximum productivity of the stock. Measurements at medium densities are needed to estimate the peak of the Ricker curve, or the inflection point of the Beverton-Holt curve. Both curves can be well approximated by a simple quadratic curve, and the optimal experimental design is to collect about a quarter of points at the two extremes and half of the data points in the middle. This latter design also provides good power to differentiate between the two forms of density dependence using this close approximation by simple quadratic curves (Stigler 1971, McClelland 2007)

The need for contrast may imply that some experimental manipulation be applied in observational studies. For example, spawners may be culled to reduce the density on the spawning grounds or additional spawners may be introduced to increase the density on the spawning grounds. The latter may introduce more complications if the new spawners are, for example, hatchery-origin fish that are added to a natural population. In this case, additional analyses are needed to determine whether hatchery-origin fish alters the intrinsic productivity and/or capacity of the population (see studies discussed in main report).

4. Biases from Sampling

In theory, studying density dependence is simple—just collect density and response information. However, unlike laboratory studies, both the density and response are often estimated under field conditions which will often be challenging.

Take for example density, the ratio of population numbers and "area." What is the appropriate unit for the denominator?

In studies of the effects of spawning density, is it spawners/river-km or spawners/river-km^2? This issue can be side-stepped by using only the number of spawners in an analysis, but this makes the implicit assumption that "area" is fixed over time, and so the definition of "area" is moot. This latter assumption may not be valid if, for example, habitat restoration is taking place over the same time frame as the study or if climate change is altering the natural habitat.

If the number of fish is to be used as a surrogate for density, how will it be determined? In some cases, exact counts are available (e.g., weir counts), but in many cases abundance must be estimated using, for example, a mark-recapture study. Now all of the problems in planning a good study to estimate abundance also come into play such as accounting for imperfect detection (leads to a positive bias), heterogeneity in catchability (leads to a negative bias), lost tags (leads to a positive bias), and so on (Seber 2002).

In some cases, density is estimated directly via sampling (e.g., based on electrofishing or redd counts of selected segments of a stream) rather than trying to first estimate abundance. Here issues about the appropriateness of the sampling plan are important. For starters, what is the "population" of sample units? Is it the entire river? Is it just areas with spawning gravel? This has implications when deciding which units are selected with which probability and how to extrapolate the measured units to the entire population. A poorly executed sampling plan will lead to biases in the estimate of density.

Similar concerns occur for the response variable. If the response measure is the number of smolts produced, how will smolts be enumerated? Rotary-screw trap designs are often used, but these are variants of capture-recapture studies so all the attendant problems of capture-recapture methods (e.g., biases from heterogeneity in catchability) need to be resolved. If the response measure is an individual fish attribute (e.g., length, growth, mass), how will the fish be sampled from the population? Here the major problems are non-representative sampling where unintended sampling biases (e.g., gear selectivity) are introduced. If the response variable is survival, how will issues of non-detection at the second time point (which looks like mortality) in monitoring the initial cohort be dealt with? If the response measure is categorical, can the category (e.g., age) be assigned unambiguously or are more complex methods needed (e.g., otolith examination)?

5. Cross-sectional or Longitudinal?

In cross-sectional studies, different experimental units are measured simultaneously whereas in longitudinal studies, the same experimental unit is measured repeatedly over time. For example, different lakes with different densities of fry and subsequent average size of smolt can be measured (cross-sectional study), or the same lake can be repeatedly measured over time (longitudinal study). All else being equal, longitudinal studies are more powerful for detection of density dependent effects because experimental unit effects are held constant over time (e.g., evaluate permanent versus temporary plots for measuring trends over time and

the results are expected to be similar for measuring density effects; Roper et al. 2003). However, longitudinal studies introduce potential problems of autocorrelation over time and lack of stationarity in the relationship (e.g., will the relationship remain the same in the face of climate change?). In many cases, longitudinal studies also have a limited number of observations. Cross-sectional studies are more flexible as (conceptually) there are no limits to the number of experimental units that can be found (thereby increasing sample size), the studies take place over a short period of time (stationarity more likely to hold), and units can be randomly selected within separate strata spanning a range of densities (improving contrast). However, cross-sectional studies introduce additional variation in the response from the experimental unit effects. It is possible to combine cross-sectional and longitudinal data to gain the benefits of both, but care is needed to properly account for the two aspects of the study in the analysis (e.g., Buhle et al. 2009).

6. Number of Data Points

How many data are sufficient to detect a density dependent effect? There is no easy answer to this as it depends on the contrast in the data (a larger contrast requires fewer data points), the size of the density effect (larger effects require fewer data points), and the sampling/process error (larger errors require more data points). As part of the study design, a power analysis should be undertaken to investigate these issues (e.g., Myers et al. 1997). After the analysis is complete, it should be remembered that failure to detect a density effect does not necessarily imply that there was no effect

because the study may have had insufficient power to detect the effect of interest. It is tempting to conduct a power analysis after the study is complete to confirm a lack of power to detect effects, but this retrospective power analysis actually provides no new information and should be avoided (Gerard et al. 1998).

As an aside, density dependence relationships often form part of a larger age-structured matrix population model where populations of fish are followed over time (e.g., the SLAM models for the Willamette Basin; Zabel et al. 2014). In many cases, the only data available are the inputs and outputs from the entire model rather than information about the individual stages. Sable and Rose (2014) indicate that at least 40 years of data are needed to reliably detect and model the density dependence in the earliest life stages. This is consistent with Solow and Steele (1990) and Dennis and Taper (1994) who conclude that even for moderately strong density dependence, it is necessary to observe up to 30 generations before density dependence can be detected with good power. This implies that the effects of density dependence should be measured as close as possible to when it occurs rather than relying on measuring it indirectly through its influence on subsequent life stages (i.e., measure the number of smolts produced as a function of the number of spawners rather than the number of adults returning as a function of the number of spawners to measure density dependence at the earliest life stages).

7. Additional Covariates

The simple relationships shown in Figure A.1 seem to assume that only two variables are in play. However, some of the variation in the data may be related to other variables (especially the process error which is usually related to environmental variables that operate at large spatial and temporal scales such as decadal oscillations) and relevant covariates need to be considered. Rather than using a shotgun approach and measuring everything poorly, it is better to concentrate on a few hypotheses about covariates and use quality data. For example, if both fry density and food availability affect subsequent smolt survival and mass, some measures of food availability would be prudent.

B. Issues in Fitting a Curve to the Data

It is unlikely that the points in a density dependent relationship will lie exactly on the fitted curve. For this reason, the curve that best fits the data must be determined. For Ricker or Beverton-Holt relationships, Hilborn and Walters (1992) provide details on the fitting procedures using a variety of methods. Millar and Meyer (2000) and Walters and Korman (2001) recommend a maximum likelihood or Bayesian approach (including state-space models) rather than using standard least squares on a linearized version of the curve. For relationships that are linear in the parameter (such as straight lines or quadratic curves) with continuous responses (e.g., mass vs. density) standard regression methods can be used. For relationships with categorical responses (e.g., survival, habitat selection), standard generalized linear models (e.g., logistic regression) can be used. Standard references (e.g., Dobson and Barnett 2008) should be consulted for details.

While the curve fitting appears to be a simple statistical exercise, there are a number of issues that need to be considered in the fit and, not surprisingly, a naïve analysis that ignores these issues may lead to spurious conclusions.

1. The Variation in the Vertical Direction

The observed response varies vertically above and below the fitted line at a particular density. This variation has two components—sampling error and process error. Sampling error arises because the recruitment is seldom exactly known (e.g., how are the number of smolts estimated) and survival is never known exactly (e.g., survival is often estimated using mark-recapture or similar methods). The sampling error should always be quantified using a measure of precision, such as a standard error. However, if the estimates of the response and confidence intervals for the estimate are plotted, the resulting intervals seldom cover the curve—there is additional variation in the response over and above sampling uncertainty. This is known as process error and is caused by (unknown) year-specific (experimental-unit specific) effects that affect the response (e.g., the weather in a particular year may lead to higher than expected number of recruits or a higher than expected survival rate at a particular density). Presumably, sampling error is independent among data points (errors in estimation of the response in different years are independent), but process error may be dependent among data points because of longer term climatic effects (e.g., El Nino or La Nina that cause the process errors to be related for years close together). This will introduce autocorrelation in the residuals (the

difference between the observed value and the fitted line) over time. The effect of autocorrelation in the residuals typically causes the fitted relationship to look better than it actually is (i.e., reported standard errors of the estimates are too small) and statistical measures to assess the evidence of a relationship (e.g., reported p-values) lead to too many false positives (Praetz 1981).

Process error effects are also applicable if there are multiple data points from the same year (e.g., several stocks having a density and response in the same year). The process error (yearly effects) may likely affect all of the responses simultaneously, again leading to a problem similar to autocorrelation with similar consequences.

If cross-sectional and longitudinal studies are combined, the process error from the experimental units will again induce a correlation among the repeated measurements on the same unit over time, over and above any autocorrelation induced over time. This will require a sophisticated modeling approach (e.g., Hansen 2007).

The modeled form of the vertical error (along the Y-axis) is also important. Classical statistical methods typically assume a normal distribution about the fitted curve so that values are equally likely to be above or below the curve, and the distribution of fitted values below the curve is symmetric to those above the curve. This may be suitable when the response variable is an average (e.g., an average growth rate or a survival rate), but if the response variable is recruitment, experience has shown that a log-normal error structure is more suitable (Hilborn and Walters1992). The log-normal

distribution is not symmetric but has a short lower tail and a (much) longer upper tail. Consequently, values high above the fitted curve are more common than values far below the fitted curve. Failure to use the correct distribution to describe the vertical error will again typically lead to estimated density dependent effects that look too large (i.e., false positives).

2. Pseudo-replication

By definition, density must act on groups of fish, but the response unit may be measureable on individual fish (e.g., individual growth rates). Pseudo-replication (Hurlbert 1984) must be considered during the design and analysis phases. The effects of pseudo-replication also cause the fitted relationship to look better than it actually is. The solution is to use an aggregated response to match the experimental unit on which the density was applied (e.g., use the average growth rate as the response value for a particular density). This is a particular problem when the response variable is survival; there will be a tendency to use standard generalized linear models (e.g., logistic regression) on the individual fish, but this is incorrect. This is seldom a problem for stock-recruitment relationships when the total recruitment for a stock is used as the response measure.

3. Uncertainty in the X Direction

A fundamental assumption in virtually all of the fitting methods is that the X (density) values are known exactly. As noted earlier, this is seldom true as the X variable is also often estimated.

Uncertainty in the X (density) values is known as an "error-in-variables" problem

and has a long statistical pedigree. If the uncertainty in density can be quantified, then a Bayesian analysis (e.g., Millar and Meyer 2000) can be used to account for this problem. The impact of unaccounted error-in-variables is typically attenuation where the density dependence is pulled toward no effect. Hilborn and Walters (1992) give an example where a small amount of uncertainty in the spawning stock completely masked density dependence.

Note that process error in the X variable is irrelevant because the actual density in the year, regardless of the cause, is the ultimate predictor and the theoretical number of spawners that would have returned under average conditions is not relevant.

4. Time-series Bias

Density dependent relationships are seldom the result of designed experiments, and are often collected from a time-series on a particular unit (e.g., spawners and their recruits over a number of years on single stream). In some cases, the response (number of returning spawners) become the "density" variable for the next year's data. This feedback loop can lead to substantial bias in the estimated density dependence relationship (Walters 1985), especially if the time series is rather short. An important conclusion from Walters (1985) is that this time series bias can be insidiously misleading for management, especially for overfished stocks because: "*the stock will appear too productive when it is low, and too unproductive when it is large.*" There is no simple way to correct for this source of bias, but refer to Walters (1990) and Walters and Korman (2001) for some approximate corrections.

5. Non-parametric Methods

It is very tempting in face of the difficulties enumerated above to use a classical non-parametric method (e.g., Spearman's rho; Kendall's tau) to examine if a density dependent effect exists. This temptation arises because of the mistaken belief that non-parametric methods make no assumptions about the data and are suitable for smaller sample sizes when outliers may be present. This is incorrect—non-parametric methods relax only one of the many assumptions necessary for a proper analysis but still require independence (i.e., no autocorrelation; no process error effects) and correct ranking of the density and response (i.e., no or small errors in the X direction). Only the assumption about the form of the vertical error distribution can be relaxed. Furthermore, while non-parametric methods can detect density dependence, it is more difficult to actually estimate the effect size. Modern statistical methods (Bayesian, bootstrapping, and resampling methods) can deal with many of the issue that prompt the use of classical non-parametric methods and may be more suitable alternatives (e.g., Munch et al. 2005).

6. Ricker vs. Beverton-Holt?

The form of these two curves (Figure A.1, top left panel) has important implications for management. The Beverton-Holt curve implies that while the benefits of increasing density decline, there is no penalty for increased density. However, the Ricker curve indicates that a severe penalty can accrue with excess density. Can the data differentiate between these two models?

Standard statistical methods such as likelihood ratio test or model-selection criteria (e.g., Akaike information criterion or Deviance Information Criteria; Burnham and Anderson 2002) can be used (Wang and Liu 2006, Zhou 2007). However, it is unlikely that these methods can differentiate between these two models if few data points are collected at high densities (refer to advice on contrast above). This is particularly true when a log-normal error structure (which is recommended by Hilborn and Walters 1992) is used so that a single high recruitment at high densities could simply be a large residual in the Ricker curve, or indicates an asymptote for the Beverton-Holt model.

7. Evaluating Effects of Restoration Activities

Restoration activities are intended to eliminate or alleviate bottlenecks where density dependence is occurring. For example, habitat restoration activities seek to add additional habitat, which will reduce density and decrease density dependent effects. Restoration projects also attempt to improve habitat quality as a means to increase productivity (survival). How can the benefits of such activities be assessed?

It is important that a proper experimental design be used. It is not sufficient to measure the response before and after restoration activities because any changes observed are completely confounded with temporal effects. For example, natural weather patterns may change simultaneously with the restoration activities and so any effect could be due to changes in weather patterns and not the restoration activity. A standard experimental design is the Before-After-

Control-Impact (BACI; Manly 2002) design where stream(s) that have restoration activities (impacted) and stream(s) without restoration activities (controls) are measured both before and after the restoration activity. Evidence of the effectiveness of the restoration activity is found in a non-parallel response between the two types of streams. The analysis of these designs is straightforward for simple responses such as survival or abundance. As noted previously, it is also advisable to measure the response as close as possible to the restoration action. For example, measure the production of smolts before and after habitat restoration that targets smolt production, rather than relying on measuring the number of returning adults before and after habitat restoration.

It is also possible to detect the impact of the restoration (or other activities) by looking at changes to Beverton-Holt or Ricker curves such that restoration activities result in an upwards shift of the curves (if the X variable is the number of spawners). If the Beverton-Holt or Ricker curve from prior to restoration is used as the baseline, the data points after restoration should have positive residuals from the pre-restoration curve if the restoration project is having a beneficial effect. Because a log-normal error structure is used with Beverton-Holt or Ricker curves, a simple "sign test" looking at the number of positive residuals after restoration[18] will not be

appropriate; however, residuals from the log(recruits/spawner) vs. the number of spawners should have an approximate normal distribution and a "sign test" on these residuals will be appropriate. Unfortunately, power to detect changes is unlikely to be large without at least 10 years post-restoration data and large effects of restoration on the population. A better strategy is to fit two separate Beverton-Holt or Ricker curves (one for each of pre- and post-restoration) and do a formal test that the curves are equal, but again the log-normal error structure implies that small shifts upward will be extremely difficult to detect without a long subsequent time series and sufficient contrast in the new dataset. Once again, it is desirable to measure changes as close to the action as possible. Additionally, extended recruitment models which incorporate other explanatory variables into the baseline and restoration periods are useful to account for some of the unexplained variation from a simple stock-recruitment curve and may increase the power to detect an effect.

One possible weakness of the BACI design is that treatments must be implemented in the streams simultaneously. However, many restoration activities are implemented in a staggered fashion. An alternative experimental design is the "staircase" design (Walter et al. 1988,

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[18] In a "sign test", you would expect to see about ½ of the residuals having a positive sign if there was no effect because about ½ of the data points are above and ½ of the data points are below the fitted curve. So if restoration activities were beneficial, you would tend to see substantially more than ½ of the new points above the appropriate curve pre-restoration. This implicitly assumes that the error structure is symmetric around zero which is not true for a log-normal distribution.

Loughin 2006, Loughin et al. 2007). In this design, restoration activities are staggered in time within the treatment area. Streams serve as their own "controls" until restoration activities are implemented. The staggering of restoration activities also protects against the possibility that the "before" period data are the result of random events (e.g., a Pacific Decadal Oscillation) and not reflective of the true level before restoration. The analysis of this design is more complex than the standard BACI design—an example of which is presented in Bennett and Bouwes (2008).

C. Additional Details: Ricker vs. Beverton Holt?

There are many different stock-recruitment relationships that have been proposed (Quinn and Deriso 1999, Chapter 3). The two-most commonly used relationships are the Beverton-Holt (Beverton and Holt 1957; BH) and Ricker (Ricker 1954; R) models.

Both models start by assuming that the change in population numbers at time t is a function of the mortality rate (Z_t) and the current population size:

$$\frac{dN}{dt} = -Z_t N$$

i.e., the decline in the population size at time t ($\frac{dN}{dt}$) is a fraction of the current population size (N) multiplied by an instantaneous mortality rate Z_t.

The two models then differ in how the instantaneous mortality rate, Z_t, varies with population size. In the BH model, the

mortality rate is a function of the current population size

$$\frac{dN}{dt}_{BH} = -\left(a_{BH} + b_{BH} N\right) N$$

whereas in the Ricker model, the mortality rate is a function of the number of spawners (S)

$$\frac{dN}{dt}_{R} = -\left(a_R + b_R S\right) N$$

In the BH model, the young fish themselves inhibit their numbers through mechanisms such as competition for food, whereas in the Ricker model, the number of spawners inhibit the population of young before recruitment through mechanisms such as cannibalism.

Solving the above differential equations, gives the two relationships

$$(BH)\ R = \frac{S}{\alpha + \beta S} = \frac{\alpha^*}{1 + \beta' S}$$

$$(R)\quad R = S e^{\alpha - \beta S}$$

where *Ricker* is the number of recruits produced (on average) from S spawners. In both models, the α parameter measures the productivity at low spawner numbers, and the β parameter is a measure of density dependence.

The two models have different functional forms as shown in Figure A.1 (top right panel). The BH model assumes that recruitment always increases with the number of spawners, but there is an asymptote that cannot be exceeded regardless of the number of spawners. For example, there may be an absolute

limitation in rearing habitat regardless of the number of young produced. The Ricker model has a dome-shaped relationship where the number of recruits has a maximum but then declines as the number of spawners increase. For example, the spawners may degrade the habitat so that too many spawners effectively destroy the habitat so that no recruits survive.

Ricker (1975, Appendix III) summarizes how to find various points of interest on the two curves as a function of the parameters. Three points of interest are shown in Table A.2. As noted previously, the maximum number of recruits in a Beverton-Holt model is never obtained in contrast to the definite maximum in the Ricker model. Both curves have an equilibrium point where the number of recruits matches the number of spawners. Finally, the distance between the curve and the replacement line X=Y represents "surplus" production, i.e., recruits not needed to replace the original number of spawners. The maximum distance between the curve and replacement line (the maximum sustainable yield, MSY) also can be found. Modern fisheries management treats the MSY with extreme caution (Larkin 1977b).

Table A.2. Three interesting points on the Beverton-Holt and Ricker curves in terms of the parameters of the curve. See Figure II.2.		
	Beverton-Holt	Ricker
Spawners needed for maximum recruits	Infinite Spawners	$1/\beta$
Spawners needed for maximum sustained yield	Solve for S in $$(1-\beta S)e^{\alpha-\beta S}=1$$	$\left(\sqrt{\alpha}-\alpha\right)\!/\beta$
Spawners at equilibrium	$(1-\alpha)\big/\beta$	α/β

Appendix II: Density Dependent Effects during Spawning and Incubation

A. Introduction

During spawning and incubation, salmonid populations may exhibit compensatory or depensatory dependence (Greene and Guilbault 2008). Compensatory or direct-density dependence can occur as two general types called "contest" and "scramble" competition (Chesson 2001). In contest competition, there are winners and losers as individuals compete against one another for defensible resources. During spawning, this type of competition may occur among females for egg burial sites and among males for spawning females. Scramble competition, on the other hand, happens when individuals compete for resources that are not defensible (Greene and Guilbault 2008). In this situation, all individuals may lose to some extent. An example of this type of competition is shown in Figure II.3 which depicts a large die-off of adult pink and juvenile coho salmon in a southeastern Alaska stream. In this instance, fish were competing for dissolved oxygen, a non-defensible resource. Depensatory or inverse-density dependence may be occurring in populations that experience a decrease in per-capita growth at low abundance levels. Liermann and Hilborn (2001) identified reduced fertilization success, impaired group dynamics, decreased capacity to change environmental conditions, and disproportionate losses to predators as four general examples of depensation effects. All of these depensatory or Allee effects may potentially impact spawning adults and incubating embryos and alevins.

B. Factors Affecting the Density of Salmon on Spawning Grounds

1. Factors Influencing the Location of Spawning Sites

Plainly, the absolute numbers of fish returning to a stream will affect local spawner densities. However, other factors may also influence the abundance of spawning fish at specific sites. Gottesfeld et al. (2004), for instance, examined the spawning ground distributions of Chinook and sockeye salmon in the Skeena River, British Columbia. They discovered that even though Chinook salmon spawned in more than 57 tributary streams, the majority (87%) of the fish spawned in seven reaches that comprised less than 0.4% of the higher order stream lengths available to them. Also, sockeye salmon were found spawning in about 90 streams in the Basin, but 90% of the spawning occurred in just 13 spawning reaches. Similar, but less extreme concentrations of spawning coho and steelhead were seen as well (Gottesfeld et al. 2004).

These observations bring with them some obvious questions. What factors cause aggregations of spawning fish to occur and how might the number of fish on a spawning ground affect the productivity of a salmon population? In this Appendix we review the effects of valley forms, stream discharge, water temperature, and homing (philopatry) on spawning ground distribution patterns. Next the role that phenological relationships have on when spawning occurs is briefly examined. It is

important to understand how these elements interact because in combination they control the likelihood that spawning aggregations will experience compensatory or depensatory density effects. The biological consequences of these density dependent effects during spawning and incubation are then reviewed.

Geomorphology, Stream Discharge and Water Temperature. The spatial distribution of spawning locations within a watershed appears to be largely driven by geomorphic features (Beechie et al. 2008). For example landscape features like valley width (Coulombe-Pontbriand and Lapointe 2004, Isaak and Thurow 2006), stream gradient (Moir et al. 1998, 2004; Beechie et al. 2008), stability of lower order tributaries, presence of knickpoints[19], and in-river structures like side channels or anabranches and islands (Burger et al. 1985) generally influence where salmonids will spawn. Other physical parameters like stream discharge, up-welling, and water temperature also shape the distribution of spawning locations. For example, annual stream flows in a Scottish stream affected the spawning distribution of Atlantic salmon. In this situation, there was a positive relationship between streamflow and the longitudinal placement of redds (Moir et al. 1998). A similar positive relationship between flow and upstream spawning locations was seen in Chinook salmon spawning in the Stillaguamish River

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[19] A knickpoint describes a location in a river or channel where there is a sharp change in channel slope, such as a waterfall or lake and consequently such sites create areas where water velocities and depths change and hyporheic exchanges occur.

(Washington State). Here, mean daily flows during September changed where peak spawning locations occurred (Beechie et al. 2008). Water temperatures may also influence where salmon spawn. Chinook salmon spawning in the John Day River located redds in sites with water temperatures that ranged from 19°C-23°C; other apparently suitable areas were avoided because of higher water temperatures (Beechie et al. 2008). Observations made in the Stillaguamish River also indicated that water temperatures could modify where Chinook salmon established redds. G. Pess (unpublished data, cited by Beechie et al. 2008) found that redd densities of Chinook salmon were five times higher in river sections with preferred spawning and holding temperatures (6-14°C) than in comparable river sections with different temperature regimes.

Redd Site Selection Criteria. An extensive literature exists on the factors that affect where female salmonids establish egg burial sites within a stream segment. These studies indicate that redd site selection likely involves the simultaneous assessment of many cues (Essington et al. 1998). Among the factors identified with redd site selection were water depth (Geist et al. 2000), velocity (Bjornn and Reiser 1991, Geist et al. 2000), substrate composition (Bjornn and Reiser 1991, Coulombe-Ponbriand and Lapointe 2004, Mull and Wilzbach 2007), channel gradient (Geist et al. 2000, Beechie et al. 2008), occurrence of down-welling flows (Geist et al. 2002, Mull and Wilzbach 2007, Mouw et al. 2014), up-welling groundwater(Curry and Noakes 1995, Blanchfield and Ridgway 1997, Baxter and Hauer 2000), up-welling hyporheic flows (Geist et al. 2000, Mouw et al. 2014),

proximity to cover (e.g., pools, cut banks, submerged vegetation, boulders, accumulations of woody debris and areas with turbulence; Hoopes 1972, Bjornn and Reiser 1991, Montgomery et al. 1996, Braun and Reynolds 2011), and localized topological features such as riffle crests or transition zones between pools and riffles (Vronskiy 1972, Bjornn and Reiser 1991, Coulombe-Ponbriand and Lapointe 2004, Beechie et al. 2008).

These preferences were not species-specific and can vary by population within a species. Parameters affecting nest site selection in chum salmon in an Alaskan River, for instance, varied by spawning location (Mouw et al. 2014). Chum salmon choosing to spawn in the river's primary channel sought out areas with down-welling flows while those spawning in off-channel sites selected areas with up-welling flows. Similar site-specific preferences exist in Columbia River Chinook salmon. Fall Chinook spawning near Ives Island just below Bonneville Dam established redds in areas with down-welling flows (Geist et al. 2002). Conversely, fall Chinook spawning in the Hanford Reach chose areas with up-welling hyporheic flows (Geist et al. 2000). It is likely that a key factor in redd site selection is proximity to areas with vertical, lateral, and longitudinal exchanges of river and hyporheic water (Mouw et al. 2013) or in some instances similar exchanges with ground water.

Philopatry, or the propensity to spawn in natal areas, may also cause concentrations of spawning fish. Several studies (one using thermal marks on otoliths (Quinn et al. 2006) and two others employing molecular genetics (Bentzen et al. 2001, Neville et al. 2006) showed that salmon have the

capacity to home to specific areas in watersheds. Homing to a location does not dictate where spawning will actually occur, however. Instead females may seek new spawning locations if conditions at the natal site are not suitable for spawning either due to poor environmental conditions (Dittman et al. 2010, Cram et al. 2013) or the presence of high densities of competing females (Isaak and Thurow 2006). In the latter case, Isaak et al. (2007) found that Chinook salmon persistently used spawning areas in the Middle Fork of the Salmon River that were geographically close to other suitable spawning locations. When densities were high, fish would move from an apparent natal area to an adjacent location. At low spawning densities the fish preferred to spawn in the largest of several connected patches of suitable natal habitat.

How far salmon may disperse from a natal spawning area to other locations has not been extensively studied, but maximal dispersal distances for spring Chinook salmon appear to range 10-30 km (Neville et al. 2006, Dittman et al. 2010, Cram et al. 2013). Thus, in some circumstances the connectivity of spawning habitats is another factor that can define redd-distribution patterns. However, Isaak and Thurow (2005) note that even at the highest escapements they observed, redds remained clustered within a limited portion of the Middle Fork of the Salmon River.

2. Factors that Affect Spawning Dates

Phenology. The biological goal of every spawning fish is to produce offspring that have a high probability of reaching maturation. To reach that outcome, fry must emerge at times that maximize their opportunities for survival. The ontogeny of

salmonids is largely controlled by water temperatures. Sheridan (1962) was one of the first investigators to link annual stream temperature profiles with adult maturation timing and subsequent fry emergence dates. Data he analyzed on pink salmon in southeast Alaska showed that fish spawning in mainland streams supplied with relatively cool water (snow and glacier melt) had earlier peak spawning dates than those that spawned in coastal streams with warmer waters. He hypothesized that there was likely an optimal period of time for fry to enter saltwater due to food availability, salinities, or other unidentified factors. By altering their maturation timing, pink salmon spawning in cool and warm water streams produced fry that emerged and entered saltwater rearing areas at comparable times. Similar phenological relationships between salmonid maturation dates and subsequent fry emergence timing have been found in numerous salmonid populations (e.g., Burger et al. 1985, Heggberget 1988, Brannon 1987, Webb and McLay 1996, Quinn et al. 2001, 2002; Beechie et al. 2006).

Adult maturation dates appear to be strongly linked to the thermal regimes that embryos are expected to experience during the incubation period. Thus, when spawning begins, its duration is strongly linked to conditions fry are expected to encounter upon emergence. If optimal conditions for juveniles occur over a short time span, spawning dates for adults will be compressed. Alternatively, if peak conditions for juveniles vary temporally or are acceptable over a broad period of time, adult spawning dates may be protracted (Brannon 1987). Atlantic salmon spawning in the upper portions of the River Dee in Scotland, for example, had a shorter

spawning period than those that spawned lower in the river (Webb and McLay 1996). This difference was attributed to the greater environmental variation in the lower portions of the stream that likely favored a longer emergence period (Webb and McLay 1996). How long adult fish may be present at a spawning location depends upon their longevity and the maturation schedules of fish using the site. The longevity of individual salmon while they reside on spawning grounds typically varies from one to three weeks (Groot and Margolis 1991). If the fish utilizing a location mature over a lengthy period of time, individuals could be present on a spawning ground for several months or longer.

The above discussion suggests that spawning site selection criteria, philopatry, and phenological temperature relationships between spawning and fry emergence can produce temporal and spatial constraints on where and when spawning takes place. Such constraints could create areas where numerous females compete for spawning locations and males compete for mates over a narrow temporal timeframe even at seemingly low population abundances.

C. Compensatory Density Effects

Compensatory density effects may occur within a spawning area if competition among females for egg burial sites takes place. They may also happen if a spawning area is serially used by females during the same spawning season. To better understand how compensatory effects may manifest themselves, the number of females per unit of spawning habitat or female density needs to be temporally partitioned into two phases: instantaneous and overall (Lister and Walker 1966).

Instantaneous densities represent the number of females present on a spawning ground at the same moment. Whereas overall density is equivalent to the total number of females, both con- and hetero-specific that have used a spawning area over the course of a single spawning season. High instantaneous densities will likely lead to the reuse of spawning locations or redd superimposition, increase the possibility that some females will die before depositing any or all of their eggs (egg retention and premature spawning mortality; *see* Figure V.6), and force other females to spawn in sub-optimal conditions. High overall densities increase the probabilities of redd superimposition and subsequent destruction of previously deposited eggs.

Redd Superimposition. Redd superimposition (the repeated use of the same location by multiple females during a spawning season) is an important mortality factor when instantaneous and overall spawning densities are high (McNeil 1964, McNeil 1969). Most of the observed effects of redd superimposition have been made on pink, chum and sockeye salmon (e.g., Gilbert and Rich 1927, Smirnov 1947, Burgner et al. 1969, Schroder 1973, Parenskiy 1990) that often spawn in dense aggregations (Quinn 2005). Semko (1954 as cited by McNeil 1969) found that 50% to 75% of the eggs deposited in a pink salmon population were lost due to superimposition when the instantaneous density equaled three females per square meter. This amount of egg loss was similar to that predicted by McNeil (1969) for pink salmon spawning at a similar instantaneous density in Sashin Creek, southeast Alaska. Fukushima et al. (1998) looked at the effects of superimposition on pink salmon

spawning in Auke Creek, another small southeast Alaskan stream. They estimated that approximately 400,000 eggs were dislodged per day due to redd superimposition when 1,000 females spawned in a 125-m long stream segment. Egg losses due to redd superimposition have also been reported for other salmonids. For instance, 20 to 28% of the coho redds in a small Washington State stream (Deer Creek Junior) were destroyed by later arriving females (van den Berge and Gross 1989).

The productivity of resident trout populations may be similarly impacted by redd superimposition. A study performed on brook trout by Blanchfield and Ridgway (1997) showed that spawning sites were limited and that substantial redd superimposition occurred during a 50-day spawning season. Additionally, egg losses due to superimposition may occur if multiple species sequentially use the same spawning sites. Hayes (1987) reported that rainbow and brown trout spawning in a lake tributary experienced poor spawning success due to severe redd superimposition caused by late spawning rainbow trout. He estimated that redd superimposition by rainbow trout caused a 94% reduction in the survival of eggs deposited in an experimental section of the stream. Work performed in a small Hokkaido stream showed that later spawning rainbow trout superimposed their redds onto 3-13% of the nest sites produced by earlier spawning Dolly Varden and white-spotted charr (Taniguchi et al. 2000). Analogous deleterious impacts of overall spawner densities were reported by Sorensen et al. (1995) and Witzel and MacCrimmon (1983) who observed brown trout constructing

redds over areas where brook trout had recently spawned.

The vulnerability of deposited eggs to redd superimposition depends on how redds are distributed within a spawning area. McNeil (1967, 1969) examined the spatial arrangement of pink salmon redds by using the Poisson distribution and found that they were distributed in a contagious fashion. That is, redds were clumped to a greater degree than by chance. A similar evaluation of chum salmon redd placement was performed in a controlled-flow stream (Schroder 1977). Grid systems were placed over several sections of the stream and were used to map and determine the surface area of redds under varying instantaneous densities. Measurements were also taken from each point of the grid to the streambed to determine how female digging changed the topography of the streambed. Redds were found to be uniformly distributed throughout each stream section. This spatial pattern was attributed to female aggression and was comparable to the uniform distribution of Chinook salmon redds observed by Neilson and Banford (1983). In general, chum salmon redd sizes decreased (see Figure V.4) and aggression (attacks/min) (see Figure V.5) and superimposition (see Figure V.7) increased as instantaneous densities rose. Additionally, a second group of fish was allowed to spawn in each stream section after all the fish in the first group had died. Females in the two groups preferred similar spawning sites and females in the second group often started redds in the upstream depression or "pot" (Crisp and Carling 1989) of a previously established redd. "Pot" areas were also found to be preferred starting points for redds by brown trout (Youngson et al.

2011). Measurements made in the stream sections with grids indicated that the digging actions of the fish created hummocks and that these rolling hills of gravel moved downstream when groups of fish spawned over the same streambed areas (Schroder 1977).

Egg destruction due to redd superimposition is mainly caused by three factors. One is death due to mechanical shock. Salmonid embryos are highly sensitive to mechanical agitation during early ontogeny, especially several hours after fertilization through epiboly, a developmental stage reached after an embryo surrounds its egg yolk (Jensen and Alderdice 1983, Jensen 2003). Depending on water temperatures, it may take 14 or more days for epiboly to be completed. Thus, superimposition soon after egg deposition can be quite destructive. Egg mortality due to superimposition can be high even when eggs are at embryonic stages where they can tolerate mechanical shock. van den Berge and Gross (1989), for instance, observed that coho eggs dislodged into the water column or onto the streambed surface by female digging were eaten within hours by birds and fishes. Finally, a three-dimensional fluid dynamics model by Tonina and Buffington (2009) showed that the topography of a completed redd increases water velocities, dissolved oxygen (DO) concentrations, and metabolite removal through egg pockets by enhancing down-welling flows. Gravel excavation and movement due to one or more females spawning over a previously established redd may disrupt its internal architecture, leading to possible decreases in water flow, DO and survival of earlier deposited eggs and alevins (but see Weeber et al. 2010).

The prevalence and consequences of redd superimposition are great enough that salmonid fishes appear to have developed tactics to minimize its impacts. In Pacific salmon, females quickly deposit all of their eggs, usually over a 1- to 3-day period (Schroder 1982, Peterson and Quinn 1996, McPhee and Quinn 1998, Hendry et al. 1999, Essington et al. 2000, Hruska et al. 2011). This allows a female to spend the rest of her reproductive life span depositing gravel on top of a redd site and on aggressively protecting it from re-use by other females. Nest guarding is an effective countermeasure to redd superimposition as once a female establishes a redd site, she is rarely evicted from it by other females (Schroder 1982, Foote 1990, McPhee and Quinn 1998).

To maximize post-spawning guarding, early arriving females invest less energy into egg production than those that arrive later. Substantial differences in spawning ground longevity, and gamete investments were, for example, found in female sockeye spawning in Pick Creek, Alaska (Hendry et al. 2004). In this stream the average longevity for early returning females was 26 days but was only 12 days for the latest arriving females. On the other hand, later returning females invested more energy into egg production. Their mean gonadal somatic index (GSI = gonad weight/body weight) values averaged 22%, whereas the earliest arriving females had mean GSI values that were significantly lower, averaging 18%. Early arriving females need to guard their eggs for as long as possible as later arriving fish are likely to superimpose redds on top of previously existing ones (Dickerson et al. 2002, Hendry et al. 2004). Results of the Hendry et al. (2004) study showed that changes in female longevity

were achieved when energy was differentially allocated into eggs or somatic stores that can be drawn upon during breeding. The tendency for early arriving females to live and guard redds longer than those using the same spawning area at later date has been observed for sockeye salmon (McPhee and Quinn 1998, Hendry et al. 1999, 2004; Hruska et al. 2011), kokanee (Morbey and Ydenberg 2003), pink salmon (Dickerson et al. 2002), and Chinook salmon (Neilson and Banford 1983).

Unlike semelparous salmonids that almost always construct a single redd, iteroparous species typically build numerous redds each with multiple nests that are separated from one another by hundreds or thousands of meters (Jones 1959, Jonsson and Fleming 1993, Lura et al. 1993, Barlaup et al. 1994). Females in these species spawn quickly, but do not guard their redd sites after egg deposition. The use of multiple spawning locations may provide some protection from redd superimposition as not all of them are likely to be destroyed by later spawning females. Another apparent tactic used by iteroparous and semelparous salmonids to ameliorate the effects of superimposition is the deposition of the majority of their eggs into the first several nests they construct. This phenomenon has been observed in Chinook (Hawke 1978) and chum salmon (Schroder 1981) as well as in brown trout (Hobbs 1937, Hardy 1963) and Atlantic salmon (Fleming 1996, de Gaudamar et al. 2000). Because the nests within a redd are constructed in an upstream fashion, gravel dislodged to create new nests and to bury completed ones tends to pile up over the first several egg pockets. Consequently, the absolute depth of eggs deposited in the first several nests can be substantially increased.

Chapman et al. (1986), for example, found egg pockets of Chinook salmon under 80 cm of gravel. Their initial burial depth was likely less than 30 cm. An increase in egg burial depth would provide protection from dislodgement by later arriving females.

Egg Retention. Egg retention, or incomplete spawning, is generally less than 5% at low to moderate instantaneous spawner densities (McNeil 1969). At excessive spawner densities ($\geq$ 1 female/m^2), however, it can be important. Mean egg retention rates exceeding 40% have been observed in sockeye (Mathisen 1962, Quinn et al. 2007), pink (Semko 1954, Hanavan and Skud 1954) and chum salmon (Helle et al. 1964, Schroder 1973) populations with high instantaneous densities. Such high rates occur because territorial females prevent newly arrived ones from establishing redds. In some cases, later arriving females will form aggregations below spawning areas, waiting for opportunities to spawn at later dates (Parenskiy 1990). Yet, in doing so, females are consuming energy that they cannot recover, making it less likely that they can spawn completely or guard their redds for lengthy periods of time. For example, chum salmon females that delayed spawning for more than 4 days when the instantaneous density equaled 1.8 females/m^2 retained about a third of their eggs. Conversely females spawning in this same population that had established a redd within a day or two after reaching maturation retained less than 1% of their eggs (Schroder 1973). A similar relationship between egg retention and time of redd establishment was observed in sockeye salmon where instantaneous densities ranged from 0.07 to 0.40 females/m^2 (Hruska et al. 2011). Females that established redds within 2

days after arriving on a spawning ground had a median egg retention value of 3%. In contrast, females that took longer than 2 days to establish redds had a median egg retention rate of 30% (Hruska et al. 2011).

The relative body size of a female appears to have no effect on egg retention. Relationships between the body sizes of sockeye (Quinn et al. 2007), chum (Schroder 1982) and Chinook salmon females (Schroder et al. 2008) and egg retention were not seen, for example. Positive relationships between spawning ground longevity and the ability to deposit eggs were, however, observed in sockeye (Hruska et al. 2011) and Chinook salmon (Schroder et al. 2008). Consequently, the ability to successfully deposit eggs was linked with the possession of adequate energy stores to complete spawning but was not associated with the relative size of a female. Additionally, McPhee and Quinn (1998) found that female size did not affect aggression or guarding behavior in the sockeye population they examined. Thus, the occurrence of high egg retentions in salmonid populations is largely caused by intrasexual competition among females for egg burial locations. In some circumstances, environmental conditions can interact with instantaneous densities and further increase egg retention rates. This was the case in two sockeye populations examined by Quinn et al. (2007). They found that high instantaneous densities plus warm water and low flows caused 23% and 44% of the potential egg deposition in these populations to be lost due to egg retention.

Movement into Sub-Optimal Spawning Locations. It was proposed by Larkin (1977a) that the first fish arriving on a spawning ground would choose the most

favorable sites. As more fish arrive, competition among females for ideal spawning sites may cause later arriving females to spawn in locations subject to scour, with fine sediment or other attributes that lead to poor embryo survival (Quinn et al. 2007). A number of field studies support this contention. For example, early arriving female Chinook salmon spawning in the Nechako River prepared redds in deep slow-moving water while those that came later spawned in shallower and faster moving waters (Neilson and Banford 1983). The sites chosen by the early spawning females had substrates with greater porosities than those used by females spawning in shallower locations as indicated by higher Fredle values (Lotspeich and Everest 1981). Additionally, the shallower locations used by the later maturing females were at greater risk of scouring, freezing, and desiccation (Neilson and Banford 1983). Similarly, the first Chinook salmon spawning on the Vernita bar in the Columbia River chose deep water sites (Chapman et al. 1986). Later arriving females were obliged to spawn at higher-elevation locations when spawner densities at the lower sites became high. Redds located at higher elevation positions were more vulnerable to dewatering due to periodic hydropower production.

Chum salmon spawning in Kennedy Creek prefer to establish redds in the pool riffle transition zone. Peterson and Quinn (1996) found that DO levels in egg pockets placed in this type of habitat were maintained at high levels throughout the incubation period. Redds were also constructed in glides and riffles and the DO levels found in egg pockets at these locations were generally lower and more variable. At the

time this study took place, some 22,000 chum salmon were spawning in the 4.4 km-long Puget Sound stream. It is surmised that intra-sexual competition forced some of the females to spawn in areas with sub-optimal incubation conditions (Peterson and Quinn 1996). The necessity of spawning in less than ideal circumstances due to high instantaneous spawner density also was observed in lake spawning sockeye (Adkison et al. 2014). During the early part of the spawning season, females preferred to spawn in shallow water areas that had high water circulation. As the spawning season progressed, a shift to deeper spawning areas was noticed and partially attributed to the high amount of aggression occurring in the shallower spawning location. The above studies suggest that high instantaneous densities can cause spawning females to disperse from natal spawning areas and utilize less than optimal spawning sites. This making the "best-of-a-bad-situation" or BBS strategy undertaken at high instantaneous densities undoubtedly reduces the breeding success and productivity of some spawning populations.

Incubation Period. Not much is known about how compensatory density may influence the survival of incubating eggs and alevins. An examination of the factors responsible for pink salmon egg and alevin mortality in Sashin Creek, however, does provide some insights (Heard 1978). In 1967, a run of 38,067 pink salmon returned to this 1.2 km-long southeastern Alaskan stream. Spawning began in mid-August and was completed by early October. Fifty-two percent of the fish were females and their potential egg deposition was estimated at 44.4 million eggs. Yet, only three million fry were produced. Even though instantaneous densities were high, losses due to egg

retention were low, averaging just 1.5%. A major source of egg loss was due to redd superimposition. Heard (1978) estimated that 55% or 24 million of the eggs deposited were dislodged and lost due to the digging actions of spawning females. In early October, at the end of the spawning period an estimated 19.9 million eggs remained in the gravel. About 7% of those were dead, most likely killed by mechanical shock caused by redd superimposition. Hydraulic sampling in the stream revealed that by the first day of December, there were approximately 11 million live eggs remaining in the streambed. From the first of day of December to March 25, an additional 8 million alevins died and disappeared. Predation by birds, fish, and invertebrates was ruled out as possible causes for this loss.

Instead, Heard (1978) presents a compelling argument that the considerable over-winter disappearance of alevins in Sashin Creek was due to scramble competition for oxygen—a compensatory density effect. His hypothesis was developed using the following observations. At early stages of development, salmon embryos can tolerate lower levels of DO than at later stages (Alderdice et al. 1958). Additionally, newly fertilized eggs consume less oxygen than those that are more developed (Brickell 1971, cited by Heard 1978). Consequently, during the early incubation period at Sashin Creek, dissolved oxygen levels in the intragravel environment were high enough to keep deposited eggs alive. However, as the oxygen needs of the embryos increased (e.g., at hatching), many died due to oxygen deprivation. Once this process began, egg and alevin mortality escalated because the presence of dead eggs and alevins further decreased the oxygen available for the

remaining live eggs and alevins (Brickell 1971, cited by Heard 1978). Heard (1978) postulated that this run-away process, driven by an initially high density of deposited eggs, substantially reduced egg-to-fry survival rates in Sashin Creek.

How important this type of compensatory mortality might be in other incubation situations is unknown. However, as indicated above, a number of factors tend to restrict where salmon spawn, which may lead to relatively high intragravel concentrations of eggs—locations where scramble competition for oxygen could occur.

D. Depensatory Effects

Salmon redds are often found in clusters (Geist et al. 2000, Geist et al. 2002, Mull and Wilzbach 2007), that may simply occur because females use similar cues to select spawning locations. Alternatively, such sites may be desirable because the digging actions of previous females have cleaned and loosened the substrate making it easier to create nests and redds (Essington et al. 1998, Quinn 2005). Spawning in these locations may also provide females with opportunities to destroy eggs deposited by previous fish and thereby enhance the survival of their own offspring by reducing competitive interactions during the juvenile rearing stage (Essington et al. 1998). Several investigators have also hypothesized that fish using these locations are "conditioning the environment" (Liermann and Hilborn 2001) in a manner that increases egg-to-fry survival rates. If true, this would mean that below certain abundance thresholds, survival could decrease and perhaps create a negative feedback loop that would lead to eventual extirpation.

Montgomery et al. (1996) noted that the digging activities of female chum salmon can substantially alter streambed topography as well as coarsen and sort gravels. They concluded that these changes reduced grain mobility and thus areas where mass spawning occurred would be less subject to egg losses due to scouring. Such a relationship may be particularly important in populations whose spawning period coincides with peak stream discharges (Montgomery et al. 1996). In this circumstance, low overall spawning densities would increase the jeopardy of deposited eggs to scouring. Montgomery et al. (1996) hypothesize that a decrease in embryo survival could lead to further population declines and start a cycle of ever greater vulnerability of eggs to scouring.

Another potential benefit associated with mass spawning was revealed by a fluid dynamics model produced by Tonina and Buffington (2009). Outputs from the model suggested that areas with multiple redds have high permeability and intense hyporheic flows and therefore provide intragravel conditions that are better suited for salmon incubation than sites with scattered or single redds. Further gains in egg-to-fry survival may also arise in mass spawning locations because the digging, swimming, and fighting actions of spawning fish dislodge surface algae (Moore et al. 2004, Greene and Guilbault 2008). Incubation environments are degraded by algae because it traps sediments, decreases intragravel water flows and lowers DO levels through metabolism.

Gottesfeld et al. (2004) and Hassan et al. (2008) studied bedload movement in British Columbian streams due to spawning activities. They found an annual shift in streambed topography. Prior to spawning, their study streams possessed streambeds with a streamlined flood morphology that was subsequently changed into a complex hilly one after spawning had been completed (Gottesfeld et al. 2004). The hummocks or rolling hills of gravel created by large numbers of spawning fish may persist in streams for nine months or longer. Exclusion and control plots were used by Moore et al. (2004) to explore the effects of this type of bio-disturbance on aquatic habitats. The spawning sockeye population studied by Moore et al. (2004) reduced surface algal biomass by 80% and also lessened invertebrate densities as spawning increased, which could have done two things: 1) decreased the abundance of potential invertebrate predators on newly deposited eggs, and 2) by coarsening the gravel, increased the streambed's capacity to produce insect food the following spring (Needham 1969). The potential benefits of both of these effects, if they occur, would be limited at low spawner densities.

Additionally, female salmonids make significant parental investments by producing nutrient rich eggs and constructing and defending egg deposition sites. As a result, evolutionary theory (Trivers 1972) predicts that females should be choosy about whom they spawn with. A female could ensure that she has an array of potential mates to choose from by spawning in areas already partially occupied by other females. The combined olfactory, auditory, and visual cues created by groups of spawning females are expected to be very attractive to males, for presumably past selection pressures have favored males that can quickly locate conspecific females (Schroder 1982). When spawning densities are low, such communal displays may be

rare. A decrease in possible mates could reduce genetic diversity and may eventually increase the likelihood of inbreeding. Both would reduce the viability of a population.

Greene and Guilbault (2008) have postulated that some of the above relationships create depensatory effects in salmon populations. In addition, they proposed that current abundance levels designed to recover depressed populations are probably too low and need to be increased because of these possible effects. It is clear that the importance of depensatory effects in salmon populations have not received much attention. What optimal spawning densities might be is still uncertain. It is very likely, as Heard (1978) points out, that optimal spawning densities are dynamic, changing under different density independent conditions such as streamflow and water temperature. It is also probable that species that depend upon substrate modifications to enhance survival like chum, sockeye, and pink salmon may be more susceptible than other salmonids to depensatory effects (Greene and Guilbault 2008).

Appendix III: Summary Table of Density Dependence Relationships for Anadromous Salmonids in the Columbia Basin by Population and Life Stage

This table includes summaries of density dependence relationships in the Columbia Basin by population and life stage, including the current density relative to capacity. Populations listed as Threatened or Endangered under the Endangered Species Act are shown in bold. Supplemented populations are those that had 5% or more hatchery fish on spawning grounds during the recent 10-year period. Initially, scientists thought the abundances of these ESA species to be so low that the strength of density dependence would be relatively weak, the population would be well below capacity, and density dependence would not constrain recovery.

Population Group	Habitat	Years studied	Response variable	Density effect?	Capacity met or exceeded?	Depen-sation?	Hatchery supplement	Comment	Reference
ENTIRE LIFE CYCLE									
Upper Columbia spring Chinook		1980-2005	R/S	Yes	Yes	No	Yes	3 populations	Zabel and Cooney 2013
Snake River spring/summer Chinook		1980-2005	R/S	Yes (11 of 13)	Yes	No	Yes	13 populations	Zabel and Cooney 2013
				Yes	Yes	No	No	11 populations	
Snake River fall Chinook		1999-2007	R/S	Yes	Yes	No	Yes	1 ESU; slight overcompensation	Cooney PPT
Upper Columbia steelhead		1980-2005	R/S	Yes	Yes	No	Yes	4 populations	Zabel and Cooney 2013
Middle CR steelhead		1980-2005	R/S	Yes	Yes	No	Yes	8 populations	Zabel and Cooney 2013
				Yes	Yes	No	No	5 populations	
Snake River steelhead		1980-2005	R/S	Yes	Yes	No	No	3 populations	Zabel and Cooney 2013

Population Group	Habitat	Years studied	Response variable	Density effect?	Capacity met or exceeded?	Depen-sation?	Hatchery supplement	Comment	Reference
Snake River steelhead	Natal river	NA	R/S	Yes	Yes	No	NA	2 populations	T. Copeland, IDFG, pers. comm.
Clackamas River winter steelhead		1958-2001	R/S	Yes	Yes	--	Yes	Hatchery spawners exceed capacity by 300%; improved survival after no hatchery fish.	Kostow and Zhou 2006, Kostow et al. 2003
Chinook salmon (23 populations)		variable	R/S $_{(low)}$	R/S declined as % hatchery spawners increased	--	--	Yes	Hatchery spawners may alter recruitment relationship. Most but not all populations from Columbia Basin.	Chilcote et al. 2011, 2013
Coho salmon (22 populations)		variable	R/S $_{(low)}$		--	--	Yes		Chilcote et al. 2011, 2013
Steelhead (30 populations)		variable	R/S $_{(low)}$		--	--	Yes		Chilcote et al. 2011, 2013
Yakima River rainbow trout	Natal river	1990-2007	trout abundance v. salmon stocking	Yes	--	--	Yes	Salmon supplementation reduced abundance and biomass of trout.	Pearsons and Temple 2010
			trout growth v. salmon stocking	Yes	--	--	Yes		

Population Group	Habitat	Years studied	Response variable	Density effect?	Capacity met or exceeded?	Depen-sation?	Hatchery supplement	Comment	Reference
SPAWNER TO SMOLT LIFE STAGE									
Snake River spring/summer Chinook	Natal river to LGD	1990-2010	smolts per spawner	Yes	Yes	No	Yes	all populations combined	Kennedy et al. 2013
Snake River spring/summer Chinook	Natal river	1991-2007	smolts per spawner		Yes	No	>50%	9 populations	Walters et al. 2013a
			parr length	Yes	--	--	>50%		Achord et al. 2003, 2007; Zabel et al. 2006
			smolt length	Yes	--	--	>50%		
			dispersal	No	--	--	>50%		
			parr survival	Yes	--	--	>50%		
			smolt survival	Yes	--	--	>50%		
Snake River spring/summer Chinook	Natal river	1997-2007	juvenile dispersal, age at migration	Yes	--	--	~50%	9 populations	Copeland et al. 2014
Snake River spring/summer Chinook	Natal river	1984-2008	parr density	Yes	5000 parr/ha	--	Yes	15 populations	Thorson et al. 2014
Snake River spring/summer Chinook	Natal river	1998-2008	nutrient import	Yes	--	--	--	Net nutrient loss caused by smolt emigration at low spawner levels	Kohler et al. 2013
Pahsimeroi River spring/summer Chinook	Natal river to Lower Granite Dam	1992-2004	age-0 smolt growth	Yes	--	--	Yes	1 population	Copeland and Venditti 2009

Population Group	Habitat	Years studied	Response variable	Density effect?	Capacity met or exceeded?	Depen-sation?	Hatchery supplement	Comment	Reference
			migrant parr growth	Yes	--	--	Yes		
			age-1 smolt growth	Yes	--	--	Yes		
			age-0 smolt abundance (dispersal)	Yes	--	Maybe	Yes	More age-0 smolts when few total juveniles & good growth but low survival to adults.	
			age-0 smolt survival to LGD	Equivocal	--	--	Yes		
			migrant parr survival to LGD	Yes	--	--	Yes		
			age-1 smolt survival to LGD	No	--	--	Yes		
Grande Ronde spring Chinook	Natal river	NA	summer parr length	Weak	--	--	Yes	4 populations	Cooney et al. 2013, 2014
			summer parr to spring migrant length	Strong	--	--	Yes	density dependence greater in degraded streams	
			egg to summer parr survival	Weak	--	--	Yes		
			summer parr to spring migrant survival	Strong	--	--	Yes		

Population Group	Habitat	Years studied	Response variable	Density effect?	Capacity met or exceeded?	Depen-sation?	Hatchery supplement	Comment	Reference
Salmon River spring/summer Chinook	Natal river	1992-2007	juvenile growth	Strong interaction with temperature	--	--	Mostly natural-origin	13 populations	Crozier et al. 2010
Snake River fall Chinook	Main-stem	2000-2011 &	parr growth in Snake River	No?	--	--	Yes	Behavior may confound growth and dispersal from river.	Connor et al. 2013
		1992-1999	parr dispersal (earlier w/ density)	Yes	--	--	Yes		
			growth in reservoir	Yes	--	--	Yes	low energy non-native prey	
			dispersal from reservoir (earlier w/ density)	Yes	--	Maybe	Yes	high density = earlier migration = greater survival	
			hatchery "pied-piper" effect	hypothesis	--	--	Yes		
Middle Columbia fall Chinook	Main-stem	1975-2004	presmolts per egg	Yes	--	No	Yes	Flow stabilization enhanced intrinsic productivity but not capacity.	Harnish et al. 2012, 2014
	Hanford Reach								

Population Group	Habitat	Years studied	Response variable	Density effect?	Capacity met or exceeded?	Depen-sation?	Hatchery supplement	Comment	Reference
Snake River steelhead	Natal river	2005-2009	smolts per spawner	Yes	--	No	No	5 populations	T. Copeland, IDFG, pers. comm.
Snake River spring/summer Chinook	Natal river	1962-2007	smolt density v. spawners	Yes	Yes	No	No	13 supplemented & 11 unsupplemented populations. Supplementation lowered capacity but increased intrinsic productivity. No population boost with supplementation.	Buhle et al. 2013, 2014
			smolt density v. spawners	Yes, stronger	Yes, stronger	No	Yes		
Okanagan River Sockeye	Natal river & lake	2005-2012	Age-0 presmolts per spawner	No	No	No	No	Some hatchery fry added in 2 years (as experiment)	K. Hyatt, DFO Canada pers. comm
Umatilla River steelhead	Natal river	1995-2009	smolts per spawner	Yes	Yes	--	Yes	Water flow influenced productivity	Hanson et al. 2010
			smolt length-at-age	Yes	--	--	Yes		
			age-at-smoltification (delayed)	Yes	--	--	Yes		

Population Group	Habitat	Years studied	Response variable	Density effect?	Capacity met or exceeded?	Depen-sation?	Hatchery supplement	Comment	Reference
SMOLTS: ESTUARY AND OCEAN									
Mixed-stock Columbia River yearling Chinook	Estuary	1980-1983	stomach fullness	Yes	--	--	Yes	Density is CPUE of all yearling Chinook, coho, steelhead in Columbia estuary	Dawley et al. 1986
Mixed-stock Columbia River subyearling Chinook, coho, steelhead	Estuary	1980-1983	stomach fullness	No	--	--	Yes		Dawley et al. 1986
Snake River spring/summer Chinook	River & estuary	1977-1994	smolt to adult survival v. hatchery steelhead release	Yes	--	--	Yes	Suggests interspecific competition in freshwater or estuary	Levin and Williams 2002
Snake River steelhead		1977-1994	smolt to adult survival v. hatchery steelhead release	No	--	--	Yes		Levin and Williams 2002
Lower Columbia tributary natural-origin Chinook & chum subyearlings	Estuary	2009	salmon density/diet v. coho density	Yes	--	--	Yes	Interspecific competition for space	Eaton 2010
Lower Columbia Chinook juveniles	Estuary	2007	growth v. stickleback density	Yes	--	--	--	Interspecific competition?	Bottom et al. 2011

Population Group	Habitat	Years studied	Response variable	Density effect?	Capacity met or exceeded?	Depen-sation?	Hatchery supplement	Comment	Reference
Juvenile Chinook	Estuary	2006	consumption rates v. stickleback density	No	--	--	--	No interspecific exploitative competition?	Spilseth and Simenstad 2011
Snake River spring/summer Chinook	Coastal ocean	1982-83, 1990-1992, 1997	smolt to adult survival v. hatchery release	Yes	--	--	Yes	Effect was evident only when ocean conditions were poor.	Levin et al. 2001
Snake River spring/summer Chinook	Coastal ocean	1998-2006	smolt to adult survival	Yes, w/ predator & forage fish density	--	--	--	Strong negative effects on both hatchery & natural-origin Chinook; suggests predation on salmon/forage fish by mutual predators	Holsman et al. 2012
Upper Columbia R summer/fall subyearling Chinook	Columbia R plume & coastal ocean	1998-2008	body condition index	Equivocal	--	--	--	Chinook abundance low & spatial coverage of samples inadequate	Miller et al. 2013
Mixed-stock steelhead	Open ocean (international waters)	1991-2009	Diet	Yes w/pink salmon	--	--	--	In central subarctic North Pacific where Columbia River steelhead intermingle w/Asian pinks	Atcheson et al. 2012

Population Group	Habitat	Years studied	Response variable	Density effect?	Capacity met or exceeded?	Depen-sation?	Hatchery supplement	Comment	Reference
Mixed-stock steelhead	Open ocean (international waters)	1993-2002	Diet	No w/pink salmon	--	--	--	In central Gulf of Alaska where Columbia River steelhead intermingle w/N American pinks	Atcheson et al. 2012

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