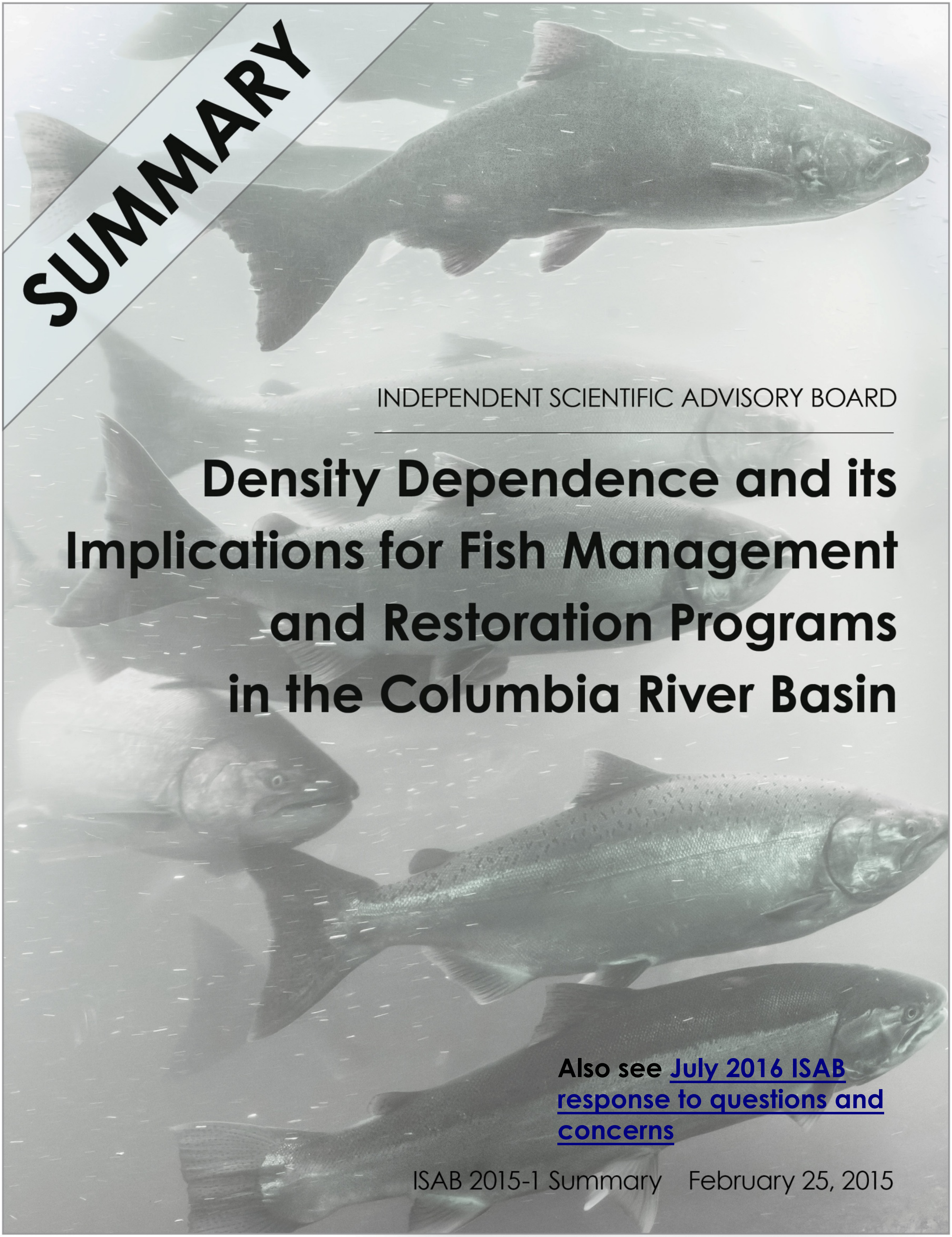

SUMMARY

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

ISAB 2015-1 Summary   February 25, 2015

Cover photo of Bonneville Dam fish ladder 2014 by Tony Grover; cover design by Eric Schrepel

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

Contents

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 (Figure 1). 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 (Figure 2). 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.

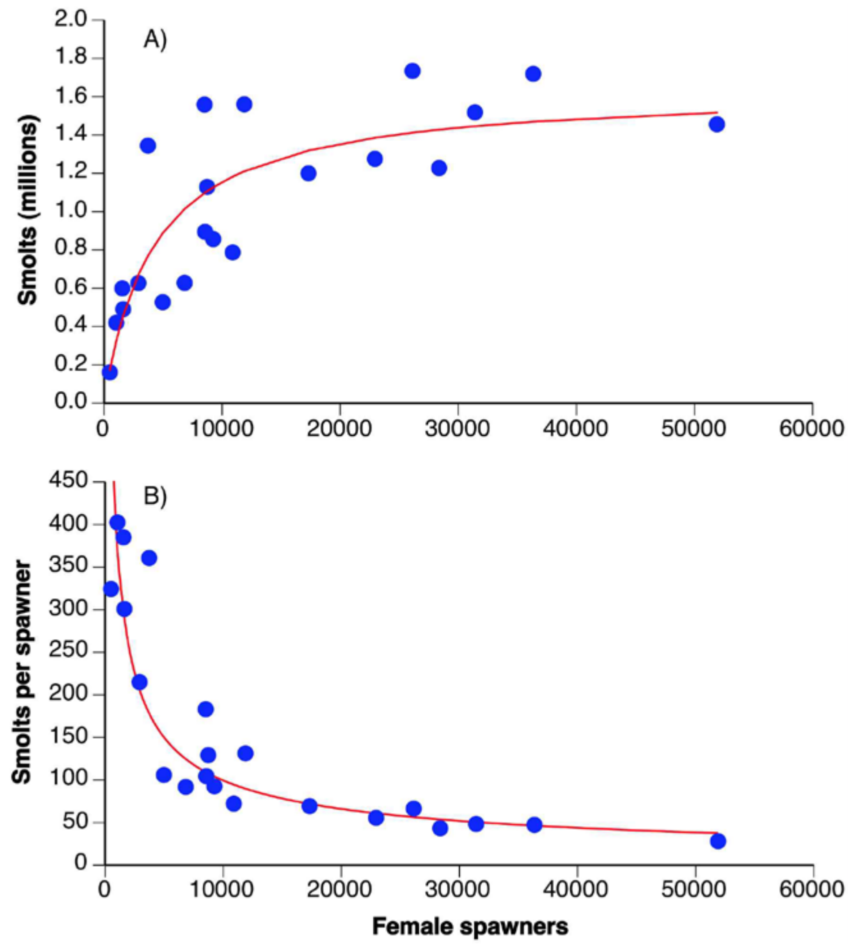

Figure 1. Example of density dependence among spring/summer Chinook salmon in the Snake River Basin, brood years 1990-2010. A) Numbers of natural-origin smolts produced by female spawners increased with greater parent spawners when spawners are less than 10,000 females, but reached maximum abundance 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, indicating the capacity of the watershed to support spring/summer Chinook salmon had been reached. 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. 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. Sources: Raymond (1979), Petrosky et al. (2001), Zabel et al. (2006), Kennedy et al. (2013), T. Copeland, IDFG, personal communication. (Figure I.1 in the full ISAB Report)

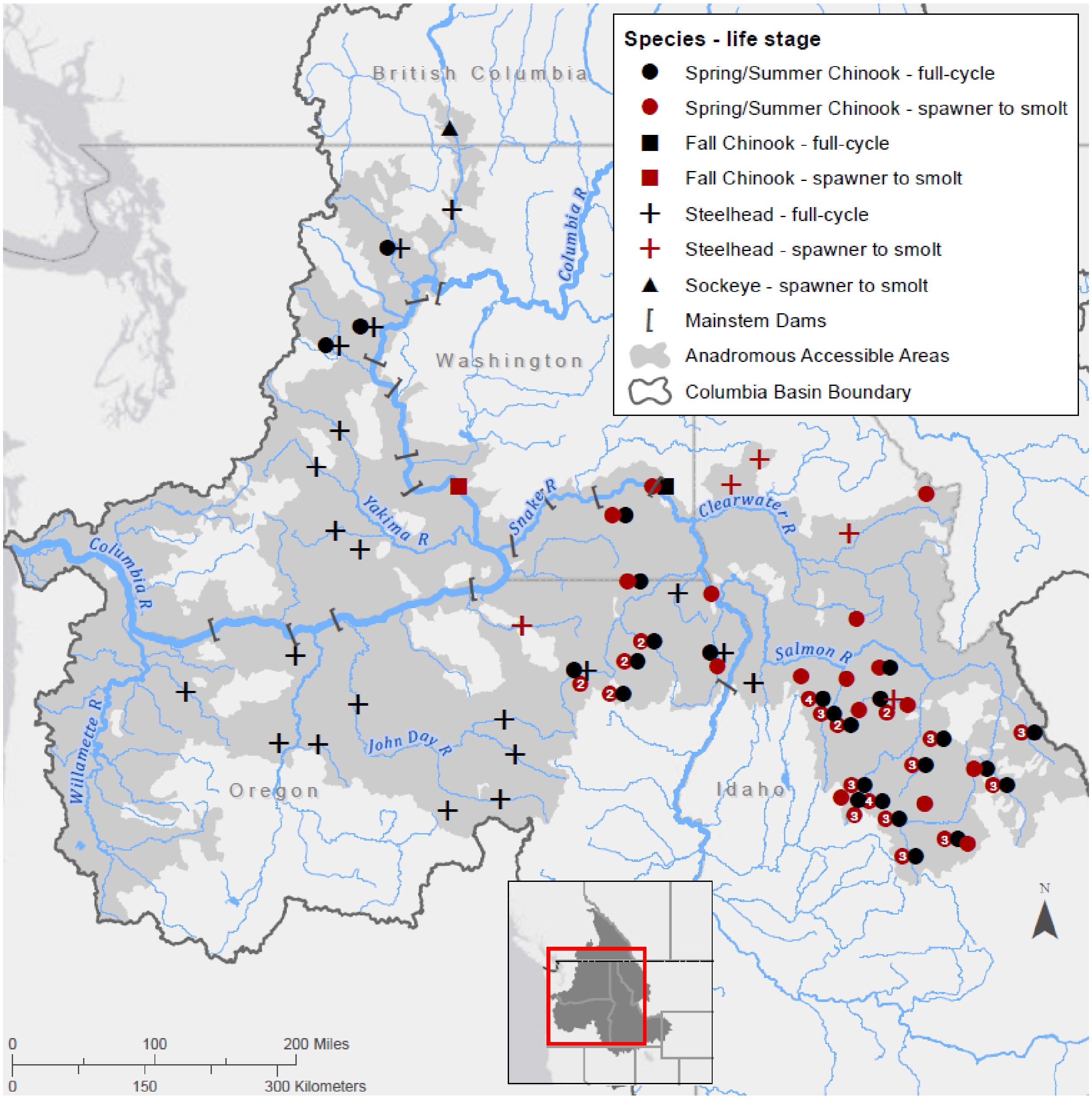

Figure 2. Columbia River Basin locations of within-population studies of density dependence examined in this report. These studies describe intraspecific competition by life stage. The numeric values show the number of unique studies at that location. See Chapter V for description of these and related studies of density dependence. Map produced by Brett Holycross and Van C. Hare, Pacific States Marine Fisheries Commission. (Figure I.2 in the full ISAB report)

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) (Figure 3). 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.

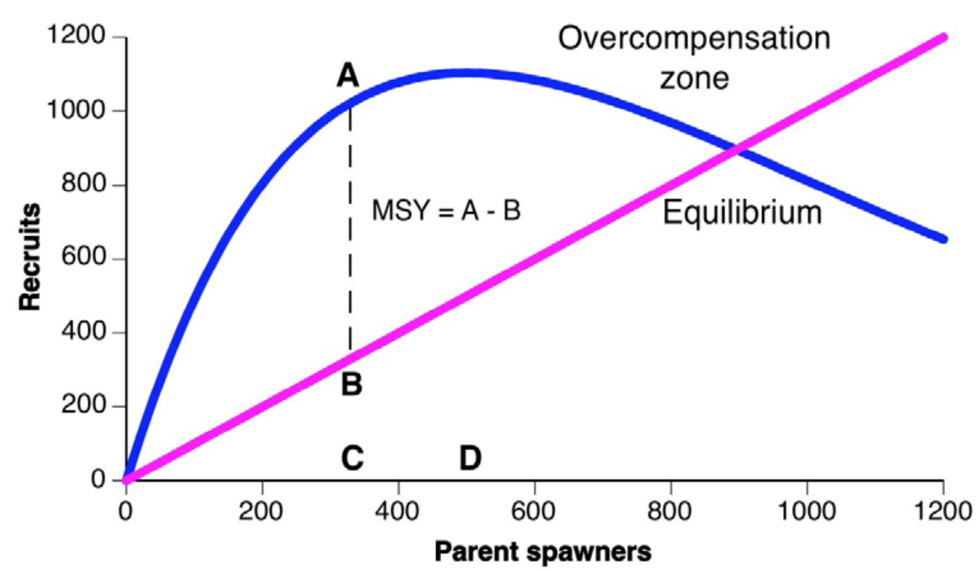

Figure 3. Ricker recruitment curve showing the principal characteristics used to manage salmon fisheries. Maximum sustained yield (MSY) occurs at the parent spawner level (C) that maximizes the difference between adult recruits (A) and the replacement line where recruits equal parent spawners (B). Maximum 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 1). (Figure II.2 in the full ISAB report)

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

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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.

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 (Figure 4). 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 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.

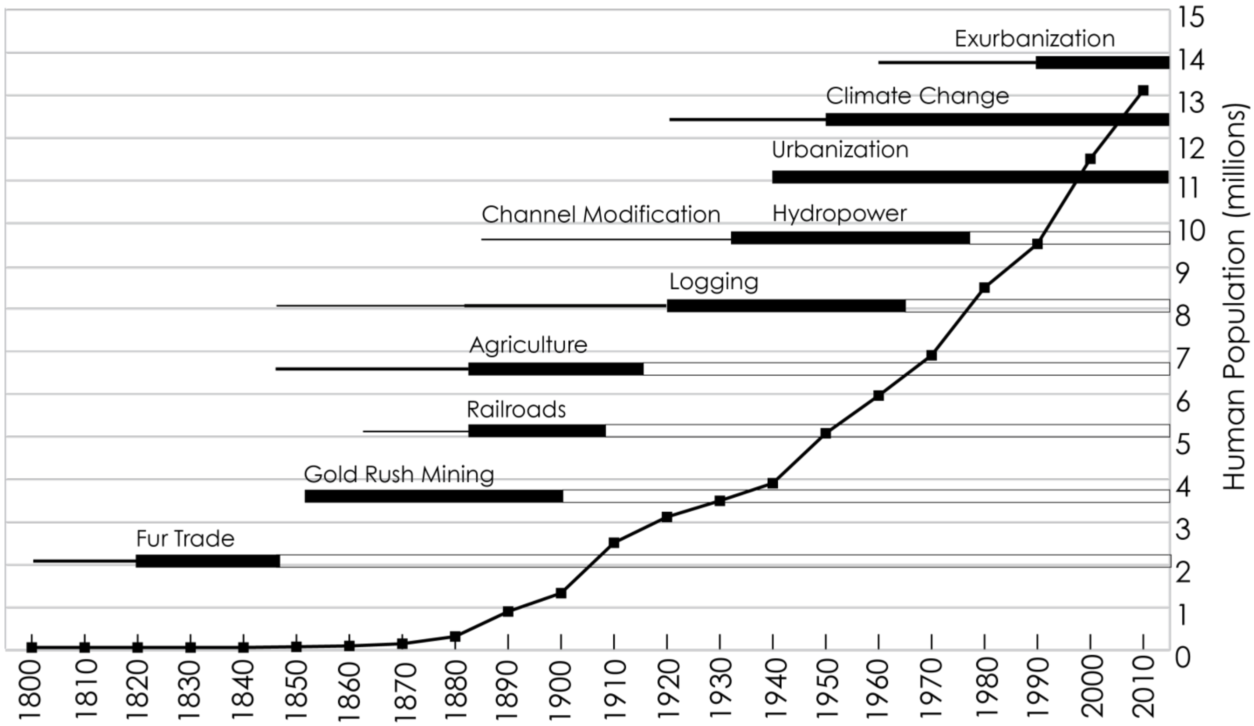

Figure 4. Sequential development driving landscape change in the U.S. portion of the Columbia River Basin and concurrent changes in human population size. These changes have altered the two parameters that influence density-dependent recruitment of salmonids: intrinsic productivity and capacity (maximum abundance). 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). (Figure IV.1 in the full ISAB report)

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 (Figure5).
- 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.

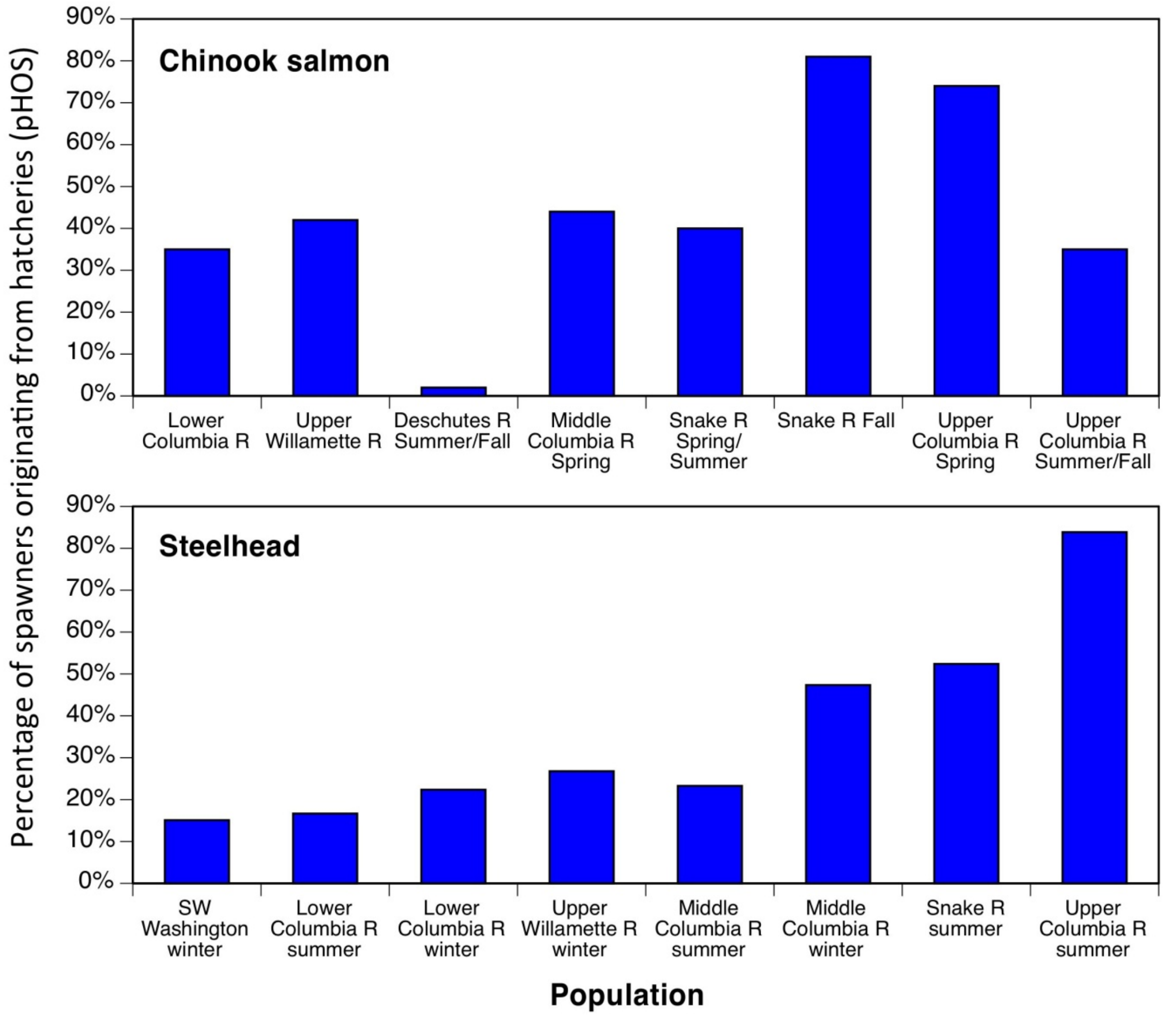

Figure 5. Estimated proportion of naturally spawning Chinook salmon and steelhead in each Evolutionarily Significant Unit (ESU) or Distinct Population Segment (DPS) that originated from hatcheries. Modeled data provided to ISAB by L. Mobrand, Hatchery Scientific Reform Group, February 2013. (Figure VI.1 in full ISAB report)

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).

Evaluation of population status and program effectiveness - 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.