



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*

Memorandum - ISAB 2015-1A

July 19, 2016

To: ISAB Administrative Oversight Panel
Paul Lumley, Executive Director, Columbia River Inter-Tribal Fish Commission
Henry Lorenzen, Chair, Northwest Power and Conservation Council
John Stein, Science Director, NOAA-Fisheries Northwest Fisheries Science Center

From: ISAB; Greg Ruggerone, Chair

Subject: ISAB response to questions and concerns about the ISAB Density Dependence Report

We appreciate the opportunity to address comments and questions from the Columbia River Inter-Tribal Fish Commission (CRITFC), Council, and other entities about the ISAB's report on density dependence in the Columbia Basin ([ISAB 2015-1](#)). In this letter, we address [comments received on July 22, 2015](#) from CRITFC; [April 20, 2016](#) from CRITFC on the ISAB's evaluation of historical salmon abundance; and, [additional questions received on May 5, 2015](#) from Council members and other entities during the Council's Fish and Wildlife Committee meeting.

To provide context, the need to produce an ISAB report addressing density dependence was identified through discussions among ISAB and ISRP members who had seen growing evidence for density dependence in the Basin. After formal consideration and approval by the ISAB Administrative Oversight Panel, with representatives from the Council, NOAA Fisheries, and CRITFC, the ISAB began working on this review topic. The approved review included the topics of historical salmon abundance and novel ecosystems. We also want to acknowledge the important contribution to the ISAB's report made by the Columbia Basins' excellent research and monitoring that has occurred over recent decades. This research and monitoring was the foundation of the ISAB report.

The main goal of the ISAB report was to encourage managers, stakeholders, and scientists in the Basin to recognize the importance of density dependence and to utilize this information when appropriate. The ISAB report summarized that 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. The widespread occurrence of density dependence suggests that habitat capacity has been greatly diminished during the past 150 years. Identifying mechanisms that contribute to density dependence in particular habitats and life stages—such as limitations in spawning habitat, rearing habitat, food supply, or predator-prey interactions—assists in guiding

habitat restoration and population recovery actions. Understanding density dependence (e.g., stock-recruitment relationships) is fundamental for evaluating responses to recovery actions and for setting spawning escapement goals that sustain fisheries and a resilient ecosystem.

The discussions and comments received about the ISAB report suggest that the importance of density dependence is gaining recognition. Consideration of density dependence could benefit both people and fish. For example, by identifying opportunities to harvest additional hatchery salmon while also reducing the percentage of hatchery fish on the spawning grounds (pHOS) and promoting productivity and adaptation of natural salmonid populations to their environment. Effective monitoring for density dependence and appropriate responses by agencies, tribes, and others can result in improved efficiencies and cost effectiveness in research, restoration, and monitoring.

Our responses to comments, concerns, and questions received from CRITFC, the Council, and other entities are provided in this letter. Specifically, the ISAB directly addresses the eight comments by CRITFC on the ISAB Density Dependence Report, including our response to CRITFC comments on the ISAB review of historical salmon abundance. This section is followed by questions raised by other entities in the Basin and ISAB responses to these queries. New references are at the end of this memo; previously cited references are available in the full [report](http://www.nwcouncil.org/fw/isab/isab2015-1), pages 219-246 (www.nwcouncil.org/fw/isab/isab2015-1). Each comment or question is in bold text. We provide a table of contents below to help navigate our response.

We look forward to further discussions of these issues with CRITFC and other managers and stakeholders in the Basin.

ISAB 2015-1 Addendum: Response to Questions and Concerns about the ISAB Density Dependence Report

Contents

Questions from CRITFC	1
Novel Ecosystems and Restoration Opportunities	1
Density Independent Effects.....	6
Hatchery Production and Harvest of Hatchery-origin Fish.....	8
Hatchery Supplementation in a Novel Ecosystem.....	11
Stock-recruitment Relationship: Beverton-Holt and Ricker Curves	13
Density Dependence Effects for Lamprey	14
Historical Abundance Estimates	15
Density Dependence Effects of Hatchery Fish in Freshwater Habitat.....	22
Questions from the Council and Others	23
Density Dependence: Why Use the Label at All?	23
Sweet Spot between Too Few and Too Many Fish.....	24
Is Density Dependence Self-correcting?.....	26
Comparison of Freshwater Carrying Capacity to Delisting Goals	27
Density Dependence in Pristine Habitat: Marine Derived Nutrients	27
Smolts per Spawner and Smolt to Adult Return Rate	28
Spawning Areas: Clumping and Egg Superimposition	30
Adequacy of Current Fishery Escapement Targets.....	31
Predation Concerns for Weak Populations.....	31
Lessons from Populations Not Showing Density Dependence.....	32
Hatchery Fish Contribution to Abundance	33
Density Dependence Effects of Hatchery Fish Compared to Natural-origin Fish.....	33
New References	34

Questions from CRITFC

Novel Ecosystems and Restoration Opportunities

- 1. Overall assumptions should be explicitly stated at the beginning of the document. The Report appears to operate under the assumption that the Columbia River system exists in a highly altered, irreversible state. The Report should clearly state which aspects of the “novel ecosystem” the authors assume to be irreversibly altered and which aspects can be managed towards a more natural and productive state. By clearly stating these assumptions, the Report’s recommendations would less likely be taken as evidence that the only way forward is to treat currently degraded conditions as the new normal, and would be more inclusive of solutions that account for the reversal of some aspects of system degradation.**

The ISAB response to Question 1 incorporates several related questions raised by other entities as listed below in italics.

The purpose of ISAB Chapter IV on the environmental characteristics of the Columbia River Basin was to describe briefly major alterations that have occurred over the past century and more. This information is necessary because density dependence is the response of species to current habitat conditions. As noted here and in the Density Dependence Report, the evaluation of density dependence can help identify limiting factors and refine restoration efforts.

The Columbia River system is a significantly altered ecosystem. Abundant evidence shows it has changed substantially from historical conditions, such as resulting from the construction and operation of mainstem dams, addition of chemicals, invasive species, and land use changes. As noted in the Density Dependence report, as well as in the ISAB’s Food Web, Landscape and 2009 Fish and Wildlife Program Review reports ([ISAB 2011-1](#), [2011-4](#), [2013-1](#)), widespread alterations to ecosystem structure and processes have resulted in a novel or hybrid ecosystem and collectively constrain the recovery of many naturally reproducing native species. While the alterations are widespread, these are especially extensive and disruptive to fish and wildlife in mainstem habitats, and can strongly affect outcomes of many otherwise well-designed and executed restoration actions upstream. Nevertheless, the ISAB believes that good outcomes are possible from restoration of habitats and populations, as long as density dependence responses are evaluated to inform decisions about the actions needed for recovery.

The ISAB did not assume, or state, in its Density Dependence report that the Columbia River ecosystem is irreversibly altered. It is, however, reasonable to assume that certain large human-made changes, such as the mainstem dams, are irreversible under current and foreseeable policies. The ISAB did discuss the Columbia River ecosystem as a novel ecosystem. The novel ecosystem has reduced and constrained life history diversity of salmonids that is necessary for lessening density effects and promoting resilient populations. However, this constraint can be partially ameliorated by establishing and managing habitats that support a

broad portfolio of fish life histories (see [ISAB 2011-4](#)). Restoration actions with positive outcomes—provided they are spatially extensive—include improving degraded riparian areas and floodplains, removing barriers that fragment habitat, addressing fish passage issues in the mainstem, and limiting the widespread use of artificial toxic chemicals. However, some properties of the novel system are irreversible in a practical sense. These include the proliferation of non-native species, persistence of harmful chemicals, extensive land cover changes and uses, altered water flow regimes (including dams, water extraction, artificial ponds), modified estuarine/plume characteristics, and directional climate change. These properties have changed in the past and are continuing to change. Whether or not these changes are truly irreversible is not a subject of this report, although some might be partially reversible given adequate time and substantial resources.

The phrase “new normal” in the comment above implies that a new set of static properties has been established in the Columbia Basin, but that is not the case. In reality, the Columbia River continues to change in many ways that may not be favorable for many native species, especially anadromous species or species that move over significant distances for feeding, spawning, and rearing. The River is exhibiting “non-stationarity” which means that, in a practical sense, the past is not a good model for the future, although the past does provide a reference point. Many trends in ecosystem scale properties (e.g., non-native species, chemicals) show no signs of reverting to historical conditions.

Overall, the spatial extent of the documented changes on the mainstem, tributaries, estuary, and ocean is massive. The public investment (e.g., roads, dams, facilities that demand power, and other infrastructures) in creating and maintaining the new (novel) ecosystem properties is also massive. The ISAB believes changes will be relatively small and incremental unless contemporary cultural values and behavior come into closer alignment with restoration goals and activities ([ISAB 2011-4](#), Rieman et al. 2015).

Despite the widespread changes that have taken place in the Columbia River Basin, is it possible to overcome limitations imposed by the existing novel ecosystems? What can be done to improve or expand life history and habitat diversity?

The ISAB believes there are a variety of approaches—most of which are intimately linked with social-cultural institutions and knowledge—that can be used to improve or expand life history and habitat diversity (see [ISAB 2011-4](#)). Diversity encompasses a variety of basic elements such as habitats, species, life histories, genes, and populations (e.g., Healey 2009, Bisson et al. 2009 *in* [ISAB 2011-4](#)) and, as such, provides biological options for both natural adaptation and human efforts at restoration. The following “rule-of-thumb” is useful for improving or expanding life history diversity: maintain many populations, species, and habitats; tolerate the perspectives of diverse socioeconomic groups and individuals; and recognize and embrace variability across the landscape (which is a form of and a support for diversity) rather than trying to control it.

Pragmatically, the landscape must contain “complementary” patches of habitat that are extensive, persistent, productive, and interconnected enough to allow completion of the

species' full life cycle ([ISAB 2011-4](#)). As well, the spatial array and connectivity of habitats, especially thermal refugia, are vitally important for conserving and restoring the diversity of species' movement patterns and life histories in the face of climate change. Finally, as variation in life histories among streams and local populations has declined, so has asynchrony in spawning abundances (Isaak et al. 2003, Moore et al. 2010 in [ISAB 2011-4](#)), reducing the overall stability of populations and metapopulations. Asynchrony in spawning abundance among specific populations appears to be a fundamental characteristic of healthy and sustainable metapopulations. Diversity in the age at maturation can also enhance stability and sustainability (see Sidebar 1, below). Clearly, planning for the conservation and restoration of biological diversity in an unpredictable future will require innovative and flexible strategies to adapt to changing conditions. Here are a few practical suggestions to consider:

Develop and maintain a diversified “portfolio” of populations. Doing so provides benefits such as extending seasonal availability of salmon to food webs and fisheries, stabilizing aggregate ecological benefits, and providing insurance against fluctuating conditions. Populations with different local adaptations have distinct responses to changing environmental conditions, such that productivity increases for some and decreases for others. This “response diversity” reduces variation in the overall abundance and productivity of a species in the landscape. For instance, Schindler et al. (2010 in [ISAB 2011-4](#)) summarized the diversity of run timing among 30 sockeye salmon populations of the Wood River Lakes system in Alaska and demonstrated how diversity contributed to the long-term stability of the composite salmon run.

Sidebar 1. Reducing Spawning Density Effects Can Increase Life History Diversity

Diversity in age-at-maturity can reduce the risk of catastrophic failure in annual salmon returns. Consider the following example as an approach that uses insights about density dependence to increase diversity in the age structure of maturing Chinook salmon. In the John Day River, Tattam et al. (2015) examined relationships among spawner abundance, yearling smolt size, and age-at-maturation of wild Chinook salmon over a period of 10 brood years. They reported that higher spawner abundances led to greater smolt abundances but reduced smolt size, which in turn delayed maturation in the ocean and increased the probability of maturing at age-5 (after 3 years at sea) compared with age-3 or age-4. They suggested that intraspecific competition in the river led to reduced smolt size and that smolt size was the key determinant in the number of years spent at sea. High stream temperatures confined the entire juvenile population to a small portion of the total stream network. A Ricker recruitment model of life cycle production in relation to spawner abundance showed signs of over-compensation, with the four largest spawning escapements producing the fewest adult returns. The authors suggested that managing spawning escapement to achieve stock recruitment equilibrium (see Figure 3 below) rather than maximum sustained yield could increase the number of older Chinook salmon and increase diversity in age structure.

Examine the approach used on the Skagit River, Washington. The approach of the Skagit Watershed Council has been to target restoration in specific areas guided by three principles: 1) restore processes that form and sustain habitats by focusing on underlying causes of

degradation, considering local potential, and matching the scale of restoration to the underlying problem; 2) protect processes and habitats that are currently functioning as sources for long-term recovery and represent the most cost-effective actions; and 3) focus protection and restoration on the most biologically important areas. These principles are consistent with the Council's Fish and Wildlife Program and the ISAB Landscape Report ([ISAB 2011-4](#)).

Evaluate the roles of hatcheries, non-natives, and existing conservation strategies in improving life history diversity. Hatchery programs developed to restore higher numbers of fish may inadvertently contribute to the loss of genetic and life-history diversity through artificial selection or homogenization of stocks and life-history patterns (Lindley et al. 2009). In some areas, the introduction of non-native species, often to create new sport fisheries, threatens native species (Sanderson et al. 2009). Conservation efforts should take into account that marginal or currently unproductive populations may represent an important part of total diversity or evolutionary potential, and these populations may become more productive in the future (e.g., Hilborn et al. 2003).

Density Dependence and Habitat Conditions

The ISAB received three closely related questions from other entities about the relation between density dependence and habitat conditions. Admittedly, providing straightforward answers to these questions is complicated by spatial variability in fish responses, by a general lack of quantitative measures in previous restoration actions, by the absence of a scientific landscape perspective until recent years, and by gaps in landscape-scale information and analyses about the collective effectiveness of restoration actions. Nevertheless, the following thoughts may be useful as initial responses to specific questions:

A. To demonstrate changes in habitat capacity, are there specific fish measurements that BPA-funded projects should collect and report on, for example, smolt age and size composition, size at emergence, adult escapement, etc? What key metrics should be measured and reported at each life stage? Are those data being collected on a broad scale in the Columbia River Basin?

The ISAB report acknowledges that valuable data are collected in many Basin areas and scientists are analyzing these data in some areas to evaluate questions about density dependence; see ISAB/ISRP ([2016](#)) for an update on research and monitoring in the basin. The recent publications and reports on density dependence would not have been possible without the monitoring that has been ongoing for many decades. Nevertheless, as highlighted in the ISAB report, additional monitoring and evaluation are needed (e.g., see Fig. 1.2 for a map showing the limited distribution of recent studies).

Key metrics for evaluating density dependence and habitat capacity to support salmonid populations include:

- spawner abundances (hatchery versus wild)
- smolt abundance and size by age
- pre-smolt emigrant abundance and size, and
- adult returns by age.

These metrics are important for developing density dependent recruitment relationships, as shown here and in the report.

B. To reduce density dependence, can we compensate for the increase in smolt abundances with habitat improvements?

A primary goal of habitat restoration in tributaries and the estuary is to enhance habitat quality and quantity (i.e., improve carrying capacity), which should improve productivity by reducing density dependence. Continued monitoring is needed to quantify these benefits. Nevertheless, for the mainstem river, the answer to this concern is not adequately known. The mainstem river is a strong candidate for focused research using food web analyses and bioenergetics modeling to improve understanding of the nutrient requirements and growth of migrating smolts. Even though most hatcheries release large, smolt-ready fish that emigrate relatively quickly, these smolts consume massive quantities of prey in a short period ([ISAB 2011-1](#)). The ecological consequences of this consumption are unknown, especially for native smolts and pre-smolts needing large amounts of food ([ISAB/ISRP 2016-1](#)). Likewise, the ability of mainstem and lower tributary habitats to support pre-smolts that disperse from natal rivers to overwinter in the mainstem is uncertain. In summary, it is critical to understand the limiting factors—in specific habitats and at precise times—that contribute to density dependence.

C. Have you seen evidence that the addition of nutrients to a stream will improve juvenile growth?

Naiman et al. (2009) and Wipfli and Baxter (2010) provide reviews of this topic, and Marcarelli et al. (2014) address the recent literature. It is widely known that many stream-resident salmonids grow much faster and larger in southeastern Alaska streams enriched with salmon carcasses and eggs. Similarly, juvenile salmonid growth in selected Washington streams increases in response to artificially added salmon carcasses. Overall, however, responses to marine subsidies can vary, with some stream communities showing no effects or even negative effects, possibly due to the lack of nutrient limitation in some streams or localized physical disturbance. As well, increases in salmonid growth in response to nutrient additions to large rivers has been equivocal (e.g., Kootenai River). Nonetheless, the amount of adult salmon biomass actually available for ingestion by fish (directly via salmon eggs or fragmenting tissue, or indirectly through ingesting invertebrates that assimilate carcass tissue) is probably a very small fraction (est. 0.1–1%) of what enters freshwater systems, after accounting for removal by vertebrates and other “losses” from flushing, fragmentation, physical adsorption, or burial. Design of biologically and cost-effective strategies for nutrient addition will require understanding the rates at which stream microbes take up nutrients and how far exported nutrients travel downstream.

Density Independent Effects

- 2. The Report presents itself as a general review of the ecology of density-related effects on abundance and productivity of Columbia basin fish populations, with an emphasis specifically on density dependent limitations in recruitment and survival. The central tenet of the Report is that despite abundances being below historical levels, some populations are producing adult recruitment below replacement. The Report delves into the realm of population recovery and management, but does so without first comparing the magnitude of these density dependent effects relative to the magnitude of density independent sources of mortality (e.g., mortality in the hydrosystem, elevated water temperature, and diversion of water). While CRITFC understands the ISAB cannot address every problem in a single report, we think clarification is needed to help readers understand the relative magnitudes of different sources of mortality.**

The ISAB was surprised at the prevalence and strength of evidence for density dependence in Columbia River salmon and steelhead populations, both over the full life cycle and during the spawner-to-smolt stage, especially since density independent factors (e.g., mortality in the hydrosystem, elevated water temperature, and diversion of water) are known to be important in the Basin. Highly variable water temperature and river flows can mask detection of density dependence or reduce density to levels where density has little effect on salmonids.

The magnitude of density independent effects is indicated in some figures in the ISAB report, although we did not specifically compare the magnitude of density dependent and density independent mortality. In Fig. I.1 (Page 24), the ISAB notes that the scatter in values around the recruitment curve for Snake River spring/summer Chinook is a reflection of density independent factors as well as measurement error. Variability about recruitment curves is shown in Figures V.1, V.2, V.3, and this reflects variability in density independent survival related to environmental variability and measurement error.

A key ISAB recommendation was *“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)”* (see Page 11). The primary focus of the report is density dependence, but the ISAB certainly recognizes the importance of density independent factors, including mortality of salmonids passing through the hydrosystem (e.g., pages 91, 116, 125, 131, 134).

In Chapter VIII, while addressing the issue of achieving sufficient smolts per spawner or SARs to enable a self-sustaining population, the ISAB stated the need to increase productivity during the spawner to smolt life stage by improving habitat and hydrosystem conditions. Degradation of habitat has undoubtedly reduced survival of salmonids and the number of natural salmonids that can be sustained in the Basin. Regarding the hydrosystem (e.g., see pages 125, 131, 134), we note that enhancing survival through the hydrosystem (thereby increasing SAR and lifetime intrinsic productivity) would push the equilibrium point on a recruitment curve to the right (see 20% productivity increase in Fig. 1 below) allowing higher harvest rates and larger spawning

populations to be sustained. Likewise, increasing habitat capacity by 20% (e.g., by increasing access to new habitat or by creating/restoring habitat in accessible areas) would also lead to larger sustainable populations. As shown in Fig. 1, an increase in a population’s intrinsic productivity implies greater recruitment at smaller parent spawner abundances, whereas an increase in a population’s capacity implies greater recruitment at higher spawner abundances.

Following the release of the ISAB report, CSS (2015) used a life cycle model to examine increases in spring/summer Chinook salmon abundance associated with improving density independent survival through the hydrosystem compared with increasing productivity and capacity in the Grande Ronde and the Imnaha watersheds. CSS (2015) concluded that improvements in the hydrosystem could have a more immediate benefit on salmon abundance but that simultaneous restoration actions in both the hydrosystem and the watersheds are needed. The degree of density dependence varied among the watersheds. The CSS modeling effort is ongoing.

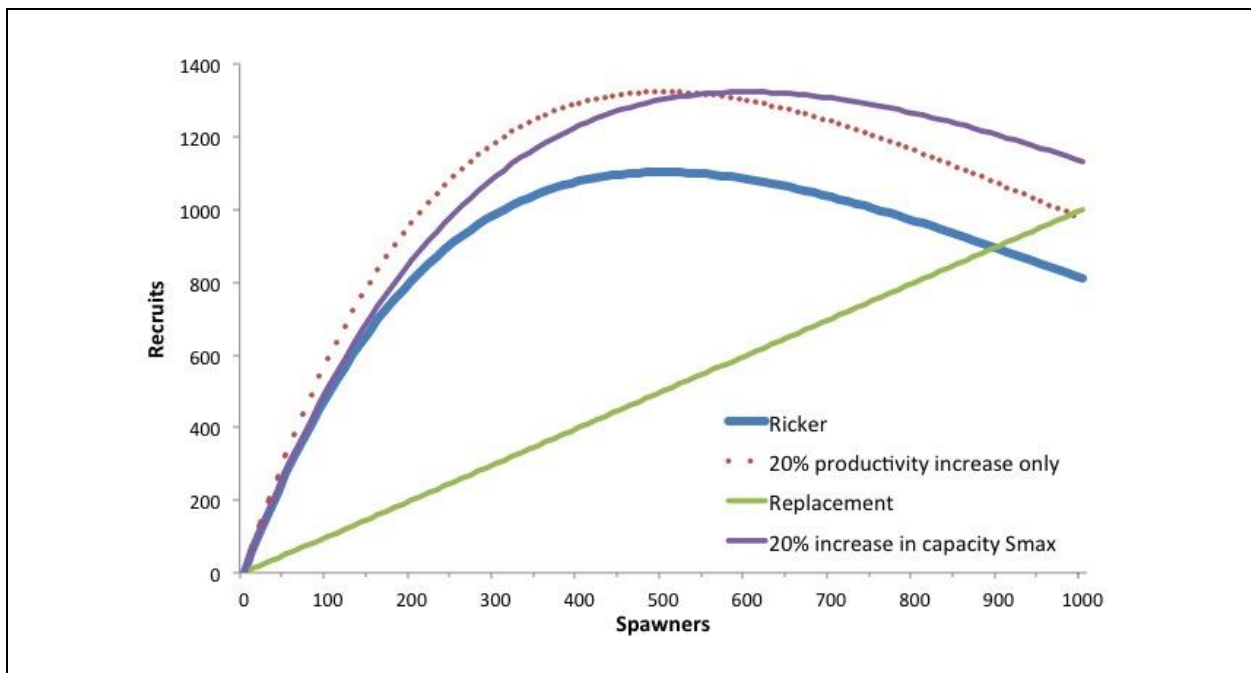


Fig. 1. The effect on adult recruitment of increasing intrinsic productivity by 20% (red dotted line) or population capacity by 20% (purple line; maximum recruitment occurs at higher spawner abundance) compared with base values shown in the Ricker recruitment curve (thick blue line). The replacement line (linear green line) is where recruitment equals parent spawner abundance. A 20% increase in intrinsic productivity enables faster population recovery, greater yield, and pushes the unfished equilibrium point to a higher spawning abundance (shown as the intersection with the green line). Thus, even with current spawning and rearing habitat conditions, a 20% increase in productivity would support a larger population. Also, see Table A.2 on page 197 of the density dependence report.

Hatchery Production and Harvest of Hatchery-origin Fish

- 3. The second and third key recommendations for anadromous salmonids focus on reducing hatchery production and *[increasing]* harvest of hatchery-origin fish, as a means to reduce purported negative effects on natural productivity associated with over-escapement of hatchery- origin fish. However, the hatchery programs were instituted as mitigation for lost production and lost harvest opportunities due to the largely density independent effects of hydrosystem development and other human activities (e.g., agriculture, mining, and forestry). The Report's general conclusion that managers need to be more cautious about over-production of hatchery fish, (i.e., hatchery production needs to be scaled back) due to density dependent decreases in recruitment, assumes tributary carrying capacities are static and also completely ignores the hydrosystem's mitigation obligations driving much of this production. Tribes are taking a two-pronged approach to restoration—investing in habitat improvements while simultaneously supplementing salmon populations with biologically appropriate hatchery fish to rebuild and maintain escapement. The CRITFC member tribes do not accept a static view of carrying capacity, and also continue to support further improvements in hydrosystem management. Does the ISAB have quantitative estimates of the relative benefits of reducing supplementation and *[increasing]* harvest compared to the benefits of actions that would yield truly significant improvements in freshwater habitat and migration conditions in the mainstem Snake and Columbia Rivers?**

The ISRP and ISAB have consistently recommended greater collaboration and integration of hatchery and habitat restoration efforts so that the habitat can support larger, more productive populations. This collaboration is needed to increase both productivity and capacity. Abundant, self-sustaining natural populations that support robust fisheries are the ultimate goal of the Fish and Wildlife Program. Improvements are needed in the hydrosystem, tributary habitats, and estuarine habitats, as noted above, as well as in the ISAB Density Dependence Report.

Supplementing natural salmon populations with biologically appropriate hatchery fish requires monitoring and controlling both the percentage of hatchery fish on the spawning grounds (pHOS) and the percentage of natural fish in the hatchery broodstock (pNOB). The benefits of this approach are described by the Hatchery Scientific Review Group (HSRG) and noted in the ISAB Density Dependence Report. A high percentage of hatchery fish on the spawning grounds is not consistent with the production of biologically appropriate hatchery fish. Please see Sidebar 2 for an approach that quantifies the benefit of managing supplemental hatchery spawners to both Tribal members and the natural salmon population.

The ISAB agrees that carrying capacity is not static; rather, it is dynamic as stated in Response 1 above and in the report (e.g., Figure II.4). Carrying capacity is much lower today than historically as evident in the observed strong density dependence at lower abundances of salmon. In many watersheds, the fish are telling us via density dependent reductions in survival or growth that the habitat quality and quantity is not sufficient to support the spawning and progeny of growing numbers of natural origin adults plus hatchery origin adults. For example,

Figure I.1 of the report suggests that relatively few additional spring/summer Chinook smolts can be produced when the number of spawners in the Snake River Basin exceeds approximately 20,000 females. The current capacity of the Snake River spring/summer Chinook population to produce smolts is about 1.6 million smolts. Approximately 40% of the natural spawners are hatchery origin fish (see references in the report). The ISAB report recommends that managers in the Basin use relationships such as this to identify opportunities to benefit both people and the fish.

A key question raised by T. Cooney (NOAA Fisheries) is:

“At what level of supplementation do genetic and ecological risks outweigh demographic benefits, indicating that hatchery supplementation should be scaled back?”

Rather than reduce hatchery smolt production in the Columbia Basin where hatchery fish are used to mitigate reduced harvests, an alternative is to harvest adult hatchery fish that exceed the number of adults needed to achieve spawning capacity. This would help achieve the benefits of an integrated hatchery approach, which is often constrained by high pHOS. As stated in the ISAB report, we do not recommend this approach if there is significant demographic risk of extinction (e.g., the population abundance is too low). Rather, this approach could be implemented when adult hatchery fish exceed the capacity of the watershed to support the growing spawning population. This approach is supported by the Idaho Supplementation Studies that found that density dependence and spawning of non-local hatchery salmon constrained the productivity and abundance of spring/summer Chinook salmon in the Snake River Basin (Venditti et al. 2015).

We offer an example, based on Snake River spring/summer Chinook, of how knowledge of density dependence might be used to 1) increase harvests in terminal areas, 2) increase productivity of the natural population, and 3) enhance the quality of smolts produced by natural origin spawners (see Sidebar 2). This could be a win-win situation, though the approach requires changes in how the fish and fisheries are managed. Some of these changes may not be readily acceptable to some stakeholders and the approach may not be feasible in all areas. Nevertheless, the purpose of this example (Sidebar 2) is to highlight potential benefits and to encourage further discussion in the Basin to determine if such approaches are feasible.

Sidebar 2. Use of density dependence evaluations for the benefit of fish and the fishing community

A newspaper article painted a gloomy picture about the implications of the ISAB report ([“Report dampens salmon, steelhead hopes”](#) by Eric Barker, Lewiston Tribune, March 31, 2015). A key message overlooked in the news article was that information about density dependence can be used to improve management of salmon in the basin and to enhance the efficiency of habitat restoration. The example below shows how density information possibly could benefit fish as well as people. This approach may not be feasible in all areas, but the Colville Tribe has employed this approach in the upper Columbia River Basin.

Imagine 40,000 spring/summer Chinook salmon returning to the Snake River Basin, of which 40% are hatchery origin fish (HOR) (See Fig. 2). If 90% (14,400) of the hatchery fish were selectively harvested, potentially by tribal members in terminal areas, approximately 25,600 salmon (24,000 natural and 1,600 hatchery salmon) would reach the spawning grounds.

- Assuming 15 lbs. per salmon, this harvest would total 216,000 lbs.
- pHOS would decline from 40% to 6%, promoting adaptation of the Chinook salmon to the local environment and enhancing survival of progeny over time.
- Productivity, in terms of smolts produced per spawner, could increase 30% (see Fig. 2).
- This spawner level would produce ~17% fewer smolts, based on the empirical relationship between spawners and smolt production (Fig. 2). However, this decline may be offset by higher quality of smolts in terms of favorable genetic adaptations and increased size from reduced density dependence (Venditti et al. 2015). Larger smolt size and adaptation to the local environment could increase survival at sea and higher productivity of the population, e.g., Oregon coast coho (see Buhle et al. 2009).

The key challenge is to harvest surplus hatchery fish with minimal impact to natural salmonids. Catch and release mortality of natural salmon can be high, depending on fishing gear and release methods, especially if the fish are caught multiple times. Biological spawning escapement goals to identify the number of spawners that fully seed the watershed are needed, while recognizing that habitat improvements may lead to increased productivity and capacity. Discussions are needed to determine site-specific methods to harvest surplus hatchery fish while minimizing impacts on co-occurring natural salmonids. Presently, hatchery fish must be visually marked to enable selective harvest, but developing genetic tools may eventually eliminate this requirement. Marking is opposed by some Tribes in the Basin, partly because marking may increase selective fishing in non-tribal fisheries; discussion and actions are needed to address this concern and to enable fishing by Tribal members. The approach is consistent with recommendations by the HSRG (2015) and the Idaho Supplementation Studies (Venditti et al. 2015). Selective fishing techniques for targeting marked hatchery salmon or robust wild salmon species are well known and used in many other fisheries.

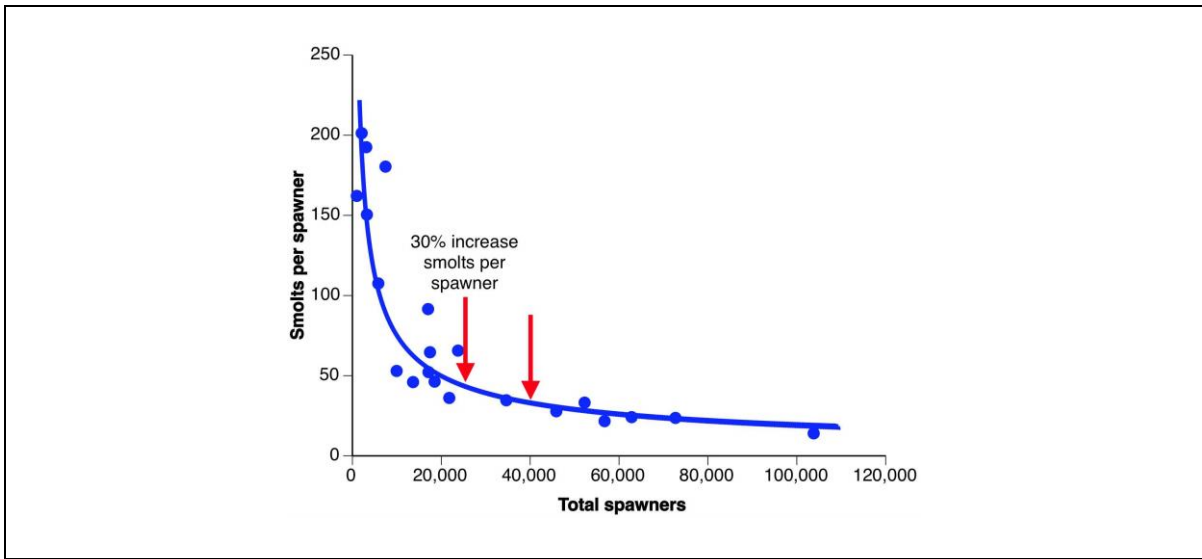


Fig. 2. Relationship between smolts per spawner (productivity) and parent spawner abundance of spring/summer Chinook returning to the Snake River Basin (adapted from ISAB Fig. I.1).

Hatchery Supplementation in a Novel Ecosystem

- The Report cautions against the high proportion of hatchery-origin Snake River fall Chinook on spawning grounds and opines that hatchery production risks causing density dependent reduction in natural productivity of the population. However, it is undeniable that the recent high returns are a direct response of the hatchery supplementation program and include current natural-origin escapement of Snake River fall Chinook at two orders of magnitude greater than before hatchery supplementation. Therefore, it would be beneficial if the ISAB could provide further insight on how supplementation should be balanced in a novel system, recognizing instances when supplementation has been key in rebuilding threatened and endangered populations.**

The supplementation program for fall Chinook salmon in the Snake River Basin coupled with favorable ocean and river conditions clearly increased returns of natural origin fall Chinook salmon (CSS 2015). However, these higher return levels will not be sustainable without improvements in habitat, including those associated with the hydrosystem. During the period of increasing spawner abundances since 2000, return per spawner has typically been at replacement or below replacement despite the recent favorable environmental conditions and accounting for ocean and river harvests in the return estimates (see Fig. V.2 in the ISAB report). Evidence indicates that density dependence, which reflects habitat condition, is constraining the sustainable abundance of the population.

As noted in the ISAB response to Question 3 and Sidebar 2, harvest of surplus hatchery fish could lead to a more productive, natural population that is capable of sustaining itself. The ISAB

has not analyzed the raw fall Chinook data, but visual examination of the graph provided by NOAA Fisheries (Fig. V.2 in the ISAB report) suggests that the unfished equilibrium point where total recruitment equals parent spawners is near 15,000 fish and maximum recruitment is slightly less than 15,000 fish for the data period. The minimum abundance threshold developed for this population by Interior Columbia Technical Recovery Team (ICTRT 2007) is 3,000 Chinook salmon, indicating the equilibrium point is well above the minimum abundance threshold.

We provide details on the benefits of harvesting surplus hatchery fall Chinook salmon, as previously described for spring/summer Chinook salmon, because fall Chinook salmon has become a high profile species. During 2009 to 2013, spawning escapement increased to about 20,000 to 50,000 fall Chinook salmon (i.e., consistently above the equilibrium point, where $R/S < 1$). However, the percentage of hatchery fish in the spawning escapement (pHOS) is typically ~70-80% (see Fig. VI.1 in the ISAB report; NOAA Fisheries 2015). These data indicate there are many hatchery fish in excess of the spawning abundance that, on average, would produce sustainable natural returns ($R/S > 1$). If the target spawning escapement had been 15,000 fish (the unfished equilibrium abundance for the natural spawning population), the harvest of surplus hatchery fish could have been 5,000 to 35,000 fall Chinook salmon per year. Assuming 15 lbs. per fish, this represents 75,000 to 525,000 lbs. of salmon harvested per year. A reduction in surplus hatchery salmon on the spawning grounds would increase productivity (R/S) simply by reducing density dependence.

Additionally, the natural fall Chinook population would benefit from the reduction in the percentage of hatchery fish in the spawning escapement (pHOS). The NOAA Fisheries recovery plan for fall Chinook salmon identifies a pHOS metric of <30% and a proportionate natural influence (PNI) metric of >67% (NOAA Fisheries 2015). Existing conditions are far from this desired state. The existing pHOS (>70%) and the very low percentage of natural origin Chinook salmon in the hatchery broodstock (<10%) has led to a very low PNI score of approximately 0.06 (NOAA Fisheries 2015). Harvesting surplus hatchery salmon has the potential to increase intrinsic productivity of the fall Chinook population by promoting local adaptation.

This information indicates significant potential benefits to tribal fishers (assuming additional harvests in terminal areas) and to the fish could be achieved by harvesting surplus hatchery Chinook salmon. This approach, if successfully implemented, would contribute to the recovery of a sustainable natural fall Chinook salmon population. The ISAB recognizes that the quality of fall Chinook in terminal areas is low compared with spring Chinook salmon. However, First Nations in the Skeena River watershed (British Columbia) have overcome challenges of harvesting lower quality spawning channel sockeye salmon in Babine Lake (<https://skeenawild.org/our-work/sustainable-fisheries/new-salmon-economy>). The terminal fishery approach in Babine Lake has reduced bycatch of non-target wild sockeye destined for other parts of the watershed while allowing harvest of the abundant sockeye salmon produced from spawning channels.

There are, however, many ecosystem-scale benefits of high spawning densities (e.g., nutrients, stream cleaning, food for wildlife), and these are noted in the Density Dependence Report. The

ecosystem-scale benefits of increased spawners and the concept of nutrient additions are also discussed in the ISAB report (see also reviews by Naiman et al. 2002, 2009; and nutrient analog review by Collins et al. 2015). The question that we raise here and in the report is whether hatchery fish should be used to produce the additional spawners needed to stimulate ecosystem benefits, or should the surplus hatchery fish be harvested for the benefit of people while also reducing pHOS and promoting local adaptation. If surplus hatchery fish are encouraged to spawn in rivers in excess of current capacity, then we suggest an experimental approach is needed to evaluate the trade-off between potential benefits of surplus hatchery fish for the ecosystem and future capacity versus deleterious genetic consequences for the natural salmon population.

Stock-recruitment Relationship: Beverton-Holt and Ricker Curves

- 5. The Report recognizes that identification of the appropriate stock-recruitment relationship has important management implications. As indicated in the Executive Summary - Appendix I (p.20), “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 reducing opportunity for harvest in the year of the large return.”**

Simply put, if the population follows the Ricker model, “too many” fish is bad, but if it follows a Beverton-Holt model, “too many” fish is not bad, and the “excess” adults have the beneficial effect of delivering additional valuable marine-derived nutrients to the freshwater ecosystem. The working assumption throughout the Report is that observation of compensatory density dependent effects means that the population will suffer from overcompensation at high escapement levels. That is, the Report assumes that Columbia Basin populations are represented by Ricker relationships, despite the fact that the very first illustration of a stock-recruitment relationship in the Report (Figure I.1, p. 24), which is of hatchery supplemented Snake River spring Chinook, clearly fits the Beverton-Holt model. The Report should be revised to address the Beverton-Holt relationship as at least equally probable if not more probable than to the Ricker relationship.

Although some of the recruitment relationships described in the Density Dependence Report and in this response involve Ricker curves, the ISAB report does not assume that salmon populations always follow a Ricker rather than Beverton-Holt recruitment curve. The Density Dependence Report does state that it is important for managers and scientists to plot their data and evaluate whether recruitment shows signs of overcompensation to ensure that large numbers of spawners do not lead to small returns (please see ISAB report pages 32-34, 126-128, 132-133, 138). The ISAB report states (P. 33) that harvest managers often prefer a Ricker relationship, primarily because fitting a Ricker rather than Beverton-Holt curve helps to prevent

overestimation of intrinsic productivity, which determines the maximum sustainable harvest rate (i.e., the Ricker curve leads to more conservative harvest policies). There are statistical tests to determine which curve is a better fit to the data, but these tests are likely to have low power unless the dataset includes large spawning escapements. Nevertheless, even under assumptions of Beverton-Holt recruitment, high numbers of hatchery fish on the spawning grounds leads to high pHOS and potentially deleterious genetic effects for the natural population.

Investigations since the ISAB report on density dependence have modeled salmon recruitment relationships. Tattam et al. (2015) modeled recruitment of wild Chinook salmon in the John Day River using a Ricker curve (see Sidebar 1). The data exhibited overcompensation whereby fewer adults returned from the largest parent spawning escapements. NOAA Fisheries (2015) modeled recruitment of fall Chinook using three density dependent models (Beverton-Holt, Ricker, and Shepard) and a density independent model. All three models incorporating density dependence terms fit the data significantly better than the density independent model. The Beverton-Holt and Shepard models produced the lowest AIC scores, indicating better fits than the Ricker model.

Density Dependence Effects for Lamprey

6. The Report recommends consideration of possible density dependent effects for lamprey, particularly in relation to tribal programs for translocation and supplementation. Given that most interior Columbia populations of lamprey are teetering on the brink of extinction, this recommendation borders on nonsensical. As one CRITFC member mentioned during our April 22 meeting, “the only problem with lamprey is that there aren’t enough of them.” Should the ISAB instead have focused its evaluation on possible Allee effects - positive density dependence with increasing density of a population at very low abundance? Such an evaluation could help guide the tribes in their Pacific lamprey translocation/reintroduction efforts in the basin. Unfortunately, this aspect of density dependence was not addressed in the Report.

The ISAB report fully acknowledges the lack of scientific information about the life history, habitat requirements, and factors limiting Pacific lamprey populations. Questions and comments provided by CRITFC seem to focus on the recommendation that it would be prudent to learn from documented experiences with salmonid hatcheries and supplementation. This was the basis of the ISAB’s cautionary recommendation. Despite what salmonid biologists and managers once thought, the data presented and discussed in the ISAB report describe observations that salmonid hatchery fish in spawning, rearing and/or migratory habitats are contributing to density dependent responses. Having accepted this position, the ISAB considers it reasonable that the “lessons learned” be considered when managing and restoring other threatened species, such as Pacific lamprey. For example, managers might think about how lamprey should be stocked to maximize their recovery.

In the report the ISAB discussed depensatory density dependence (i.e., Allee effects) especially as it pertains to reduced population growth and possible extinction when population numbers are below a certain threshold as the result of predation, reduced reproduction by individuals failing to find mates, inbreeding depression, and loss of life history diversity (see pages 36-37, 88, 121-125 and 198-209 of Appendix II). There is an indication that adult Pacific lamprey rely on chemical pheromones released by juvenile conspecifics to guide them to optimal spawning habitat. Thus, reproductive success of individual Pacific lamprey may be reduced at low population size if there are inadequate numbers of juveniles releasing pheromones into the water. Furthermore, the study by Nilsen et al. (2015) suggests that chemical contaminants in sediments of the Columbia Basin could interfere with the effective release of these pheromones. The ISAB also noted that predation on salmonids by pinnipeds (as well as piscivorous fish and birds) is thought to be depensatory. As Pacific lamprey are a preferred prey of pinnipeds, this predation could also threaten lamprey recovery in the Columbia Basin. The paucity of scientific information about Pacific lamprey population dynamics make it extremely difficult to draw any firm conclusions, except that a concerted effort is needed to gather information to help recover this species ([ISAB/ISRP 2016-1](#)).

Historical Abundance Estimates

7. The Report's recalculation of historical salmon and steelhead abundance is suspiciously low and contrary to published literature. A more thorough inclusion of traditional knowledge and effects of industrial development would seem to lead to the opposite conclusion, (i.e., that the historical abundance estimates were conservative). We strongly object to the Report's assessment on historical abundance and request that it be removed from the document. At present, CRITFC is reviewing the analysis of Chapter III of the Report for comparison with the run size estimates adopted by the Northwest Power Planning Council in its Columbia Basin Fish and Wildlife program in 1987. We will share the results of this analysis with the ISAB for inclusion as an Appendix in the Report (see April 2016 [letter](#) from CRITFC to the ISAB).

Chapter III Goal. The ISAB included the chapter on pre-development capacity of the Columbia River Basin because recent evidence indicates density effects in the Basin are stronger than expected by most scientists, many of whom assumed that salmonid abundances and densities are extremely low relative to historical levels. That assumption seems reasonable given that most natural origin salmonids are listed as threatened or endangered under the Endangered Species Act (See Chapter I). However, given the recent evidence for density effects, we thought it prudent to examine the assumptions and quality of data used by a variety of investigators to estimate abundance of salmon and steelhead prior to significant development in the Basin, e.g., prior to 1850. Information in Chapter III helps to identify species having the greatest potential for density dependence given the change in accessible habitat and abundance over time (see Fig. III.3 in the ISAB report). The objective of this effort was not to revise restoration and mitigation goals in the Basin. Policymakers who consider both science and socioeconomic issues set those goals.

Information Considered. In Chapter III, the ISAB examined several approaches previously used to estimate pre-development abundances of salmon, including those based on 1) commercial landings, 2) extent of available freshwater habitat, and 3) daily salmon consumption by the Native American population in the Basin prior to 1800. Chapter III also considered the effect of ocean harvests (those extending northward through Southeast Alaska) on the abundance estimates and the effects of large-scale ocean climate phenomenon such as the PDO. A variety of investigations, representing different approaches and organizations, were described and cited in the report so that readers could see the range of assumptions used to estimate historical abundances. We did not attempt to describe every effort that has been undertaken because they represented small modifications to the approaches described in the report. ISAB authors also read reports about the tremendous importance of salmon to Native Americans and cited some of the more comprehensive publications on this topic (e.g., Campbell and Butler 2010, Hewes 1947, 1973, Suttles 1968, NPPC 1986, Schalk 1986). The ISAB acknowledged overharvest and degradation of salmonid habitat associated with the expansion of European settlers into the Basin in the mid to late 1800s and noted the construction of Swan Dam on the Snake River in 1907 that was not identified by Chapman (1986) when he discussed development of the Basin.

Our review of pre-development abundance estimates was not intended to discuss all previous estimates of historical abundance. The ISAB did examine analyses by Scholz et al. (1985) but did not describe them in Chapter III because they were nearly identical to approaches described by NPPC (1986), leading to values that were within the range reported by NPPC (1986). Both sources reconstructed total run size based on estimates of salmon consumption and commercial catch. NPPC (1986) also described an alternative approach that was essentially a blend of the primary NPPC analysis and that used by Chapman (1986). This alternative approach included additional assumptions about harvests by Native Americans and European settlers, but the resulting abundance estimates fell within the range of the primary analysis in NPPC (1986). In any case, it is important to note that if the commercial catch and commercial harvest rate assumptions were reasonably accurate, then there is no need to make further assumptions about salmon harvests by Native Americans and settlers when estimating salmon abundance in the Basin. This conclusion stems from the definition of harvest rate such that total abundance is calculated from the simple relationship: $Abundance = Catch / Harvest\ Rate$.

Assumptions. There are no direct estimates of pre-development abundances of salmon and steelhead—all have been reconstructed from various data by making important assumptions (Table 1). Therefore, it is essential to examine and compare the assumptions used by various investigators to approximate abundance in the pre-development period. Chapter III describes these assumptions so that readers can judge for themselves. Here, we briefly highlight some of the major assumptions, but we urge interested readers to examine the original reports and the ISAB report for additional detail.

Commercial Landings Approach. To estimate average annual abundance, NPPC (1986) and Scholz et al. (1985) both assumed a range of harvest rates from 50% to 85% to expand

maximum annual catches for each species (regardless of year). Given indications that Columbia salmon populations were being overfished in this period (Thompson 1951), a harvest rate of 50% seems too low whereas 85% seems realistic for overharvest of productive populations. NPPC (1986) and Scholz et al. (1985) both assumed that spring and fall Chinook salmon races each equaled 50% of the summer Chinook run. Although the all-time maximum reported commercial Chinook harvest was 2.3 million fish (in 1883), these authors both assumed the maximum catch for all races of Chinook was equivalent to 4.6 million fish. They justified this high value because spring and fall Chinook salmon were thought not to be exploited when the maximum Chinook harvest occurred in 1883. The NPPC (1986) approach led to an "average" run size of 9.6 to 16.3 million salmon and steelhead per year, based on assumed harvest rates of 85% and 50%, respectively (Table 1).

Although NPPC (1986) assumed no spring or fall Chinook salmon contributed to the reported catch in 1883, we note that harvest regulations and fishery openings during the early 1880s indicate that some spring and fall Chinook salmon would have been harvested and attributed to summer Chinook salmon. This would lead to inflated summer Chinook abundance (and therefore inflated spring and fall Chinook abundances). Wendler (1966) shows that during 1883, the year of maximum "summer" Chinook harvest, fishing was open in Washington and/or Oregon during April, May, June, July, and September, although some days were closed to fishing in each of these months. Chapman (1986) reviewed several historical documents and concluded that both late spring and summer Chinook salmon were harvested during 1881-1885. Thus, although the fishery targeted the summer run during this period, it is probable that some spring and possibly some fall Chinook salmon were taken in 1883 and counted as "summer" Chinook salmon.

The reason for using maximum 1-yr catch to estimate average pre-development run size is not adequately explained by NPPC (1986) and related investigations. In contemporary fisheries, maximum catch is associated with runs that are above average. Furthermore, annual salmon abundances are approximately log-normally distributed, indicating that maximum run size will be much further above the mean compared to a similar computation when the distribution of annual salmon abundances is approximated by a normal distribution (Hilborn and Walters 1992). Presumably maximum 1-yr catch was used for estimating average historical abundance in order to account for habitat degradation and overharvest that had already occurred during the period of reported commercial catch. Chapman (1986), who used peak 5-yr average annual catch values, referred to his abundance estimates as potential rather than average abundances because he recognized that peak catch is typically associated with peak runs.

Chapman (1986) used the peak 5-yr average annual commercial catch for each species and assumed harvest rates ranging from 48% to 88% to estimate "potential" abundance during the pre-development period. However, for sockeye salmon, the reported maximum 5-yr average annual catch was only 0.6 million fish (1889-1893), and there was some indication that sockeye abundance may have been higher during the previous 5-year period when only fishwheel catch data were available. Therefore, Chapman used the mean ratio of total sockeye catch to fishwheel catch (mean 23:1, range 11:1 to 41:1) during 1890-1893 to expand fishwheel catches

in 1883-1888. A regression relationship between sockeye catch in fish wheels and total sockeye catch was statistically non-significant ($n = 4$, $P = 0.46$, $R^2 = 0.29$); the highest fishwheel catch was associated with only a moderate total catch. Fishwheel/total catch ratios in 1889-1893 may not have been representative of catch ratios in 1883-1888 because fishwheel catches were much greater during the early period than during the period when the ratio was calculated. Nevertheless, Chapman (1986) calculated 1.9 million sockeye salmon as the maximum 5-yr annual average catch for the period 1883 to 1888 (rather than the reported maximum of 0.6 million sockeye). Combining these estimates for sockeye with other salmon and steelhead, Chapman's approach led to "potential" run size of 7.5 to 8.9 million salmon and steelhead per year, depending on whether the harvest rate was assumed to be optimal (i.e., unlikely for this period of reported overharvest) or probable (i.e., reflecting overharvest) (Table 1).

Early catch records provide landed weights by species rather than numbers of fish. Landed weight was converted to fish numbers using average weight per fish for each species and race of Chinook salmon. NPPC (1986) and Scholz et al. (1985) used more contemporary average values reported by Beiningen (1976), whereas Chapman (1986) used larger average fish weights reported during 1895 (Table 1). Thus, for a given biomass of landed catch, NPPC (1986) yielded a higher number of fish than did Chapman (1986).

NPPC (1986), Scholz et al. (1985), and Chapman (1986) selected maximum 1-yr or peak 5-yr annual catch for each species from a variety of years (spanning 1883 to 1928) to estimate average or potential abundance. The ISAB recognized that peak catch and runs of all six salmonid species do not occur in the same one-year or five-year period, so that summing abundance estimates for each species could overestimate *average* abundance estimate for all species combined. Chapman (1986) seemed to recognize this issue when identifying his estimates as "potential" abundance, but only Scholz et al. (1985) explicitly commented on it. Scholz et al. (1985) suggested that in a pristine environment, competition between the six species of salmonids would be minimal even at maximal abundances; therefore, it was reasonable to speculate that maximal abundances of all species could occur at the same time. However, more recent evidence indicates that salmonid species do compete for resources (e.g., Harvey and Nakamoto 1996, Sabo and Pauley 1997, Fausch 1998), suggesting that simultaneous maximal abundances for all species are unlikely.

To account for the observation that peak catch and runs of each species do not occur in the same year, the ISAB adjusted the NPPC (1986) and Chapman (1986) abundance estimates. The peak five-year average annual catch of all species combined (about 4.4 million fish in 1883-1887 based on expanded catch records; see report for details) 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, including estimates for all six species) 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 (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. The ISAB consider these values to represent above average runs of all species combined. Given year-to-year variations in species abundances, annual abundances could be much higher or lower than shown here. For example, Chapman (1986) reported evidence of "below-average runs and run failures" in the Columbia Basin for 1811 and 1826-1829, a time period before commercial fisheries and large-scale habitat degradation. Furthermore, large and relatively long-term swings in salmon abundance have been documented for salmon stocks prior to commercial fisheries (e.g., Drake et al. 2009), indicating that average abundance is influenced by both long-term and short-term environmental conditions. The ISAB report noted that the cool phase of the PDO prevailed during 1890 to 1924, suggesting that productivity during this period may have been relatively high (Mantua et al. 1997; <http://jisao.washington.edu/pdo/>; Jacobsen et al. 2012).

The ISAB report did not discuss the abundance estimate developed by Bonneville Power Administration (BPA) and noted by NPPC (1986) and Scholz et al. (1985). The BPA abundance estimate of 35 million salmon and steelhead was based on the simple assumption that fishwheels in the Columbia River captured 5% of the total run. The ISAB did not find support for this harvest rate, and the estimate of 35 million salmon and steelhead is inconsistent with analyses of reported total catch.

Habitat Approach. 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 accessible habitat. Quantity and quality of rearing and spawning habitat were not considered. This approach led to 6.3 million salmon plus an assumed 2 million steelhead (8.3 million total) (Table 1).

After the release of the ISAB Density Dependence Report, Pess et al. (in revision) examined the availability of spawning habitat prior to development and estimated that spawning habitat in the Basin above Bonneville Dam had the potential to support 108 million spawning salmon and steelhead (all species combined). However, they point out that factors other than the availability of potential spawning sites can limit the abundance of smolts and adults. For example, as discussed in the Density Dependence Report (Appendix II), spawning salmon have habitat preferences that extend beyond the stream characteristics considered in this analysis. Furthermore, density dependence may be especially important during the rearing rather than spawning stage for Chinook, coho, and steelhead that overwinter in freshwater streams.

Native American Nutritional Approach. Chapter III presented several estimates of salmon harvests by Native American tribes prior to the 1800s based on nutritional requirements. Key assumptions included population size (~50,000 to 62,000 people, circa 1780), per capita utilization rates (up to 3 lbs. of salmon per day, 365 days per year), and constant salmon availability for harvest each year regardless of how the environment affected salmon abundance (Table 1). Some high *per capita* consumption values reported by NPPC were based on the observation that caloric content of salmon declines significantly as they migrate to the

upper portions of the Basin. Some salmon may have been traded outside of the Basin, leading to harvest values higher than shown here. Harvest estimates ranged from 1.9 to 5.6 million fish per year depending on assumptions (e.g., NPPC 1986, Schalk 1986). Scholz et al. (1985) calculated harvests of 4.4 million salmon and steelhead, but they thought this estimate was conservative. Catch of steelhead was estimated to be 1.5 million fish even though steelhead are typically much less abundant than other anadromous salmonids. For example, in 1970-1986 total steelhead abundance in North America (hatchery plus wild) was estimated to be approximately 1.6 million fish per year (Light 1987). We are not aware of attempts to estimate harvest rates by Native Americans in the pre-development period so that total abundance could be calculated.

Conclusions. Chapter III of the ISAB report on density dependence presents a range of estimates for the pre-development abundance of salmon and steelhead based on a several approaches and assumptions. The catch-based approach is the most direct method for estimating abundance given knowledge (or assumptions) about harvest rates. However, inferring historical capacity from historical abundance is complicated by further assumptions about the conditions that produced the maximum 1-yr and peak 5-yr annual catch, and whether these conditions would have been sustainable. In short, inferring carrying capacity from abundance requires assumptions about density dependence.

Nevertheless, all estimates show that contemporary abundances of salmon and steelhead remain far below pre-development values. For example, during 1986 to 2010, total annual salmon and steelhead abundance averaged approximately 2.3 million fish, including hatchery fish and ocean harvests extending through Southeast Alaska (see Figure III.1 in the ISAB report). The ISAB examined the historical abundance estimates (and assumptions) as an initial step to understand why density dependence in the Basin appears to be constraining productivity even when abundances remain low. As described in Chapter III, simple inspection of changes in abundance relative to the extent of accessible habitat since the late 1800s suggests that density effects may be higher than first expected for spring Chinook, fall Chinook, steelhead, and coho salmon (see Figure III.3 in the ISAB report). Subsequent chapters in the ISAB report examined evidence for density dependence by life stage of each species in each region of the Basin where quantitative data were available.

Table 1. Key assumptions used to estimate abundance of salmon and steelhead in the Columbia River Basin prior to development. See reports for additional details.

Commercial Catch Approach

NPPC (1986) ("average" abundance)

Maximum 1-yr catch for each species (years vary for each species)
 No spring or fall Chinook taken in 1883, year of maximum summer Chinook catch
 Spring Chinook: 50% of summer Chinook in 1883; Fall Chinook: 50% of summer Chinook in 1883
 Contemporary (1970s) fish weight to convert historic biomass to numbers (see Chapman 1986)
 Assumed harvest rates: 50% to 85%
 All species "average" abundance = sum of each species (9.6 to 6.3 million)

Scholz et al. (1985)

Maximum 1-yr catch (NPPC values); Assumed harvest rates: 50% to 66%

Chapman (1986) ("potential" abundance)

Peak 5-yr catch for each species (years vary for each species)
 Sockeye extrapolated from fishwheel catch assuming 23:1 ratio, 1883-1887
 Spring Chinook: 20% of April-July Chinook catch, 1890-1895
 Historic (1895) fish weights to convert historic biomass to numbers
 Assumed optimal harvest rates: 48% to 88% depending on species
 Assumed probable harvest rates: 80-88% depending on species
 All species "potential" abundance = sum of each species (7.5-8.9 million)

NPPC (1986) ("average" abundance alternative approach)

Maximum 1-yr commercial catch, each species, various years (8.7 million)
 Peak 5-yr commercial catch, each species, various years (6.6 million)
 Assumed Native American catch (879,000 fish); Assumed settler catch (879,000 fish)
 80% harvest rate applied to max 1-yr catch, Native American catch & settler catch
 67% harvest rate applied to peak 5-yr catch, Native American catch & settler catch
 All species "average" abundance = sum of each species (12.5 to 13.2 million)

BPA (in NPPC 1986)

Fishwheel catch = 5% of total commercial catch (35 million)

ISAB (2015)

Assumed NPPC and Chapman values for each species
 All species total adjusted because peak abundance for each species does not occur in same year
 (All-species potential capacity: 5 to 9 million)

PFMC (1979) & NPPC (1986) Habitat-based Approach

Salmon per linear mile accessible habitat to spawning grounds (river mouth thru mainstem and tributaries)
 Densities vary by region & species
 Rearing & spawning habitat not considered
 Steelhead abundance = 1.7x coho abundance
 No consideration of environmental variability or density dependence (8.3 million)

Native American Consumption Approach (NPPC 1986, Scholz et al. 1985)

Many investigators & various assumptions
 Prior to disease and population decline (~1780): 50,000 to 62,000 Native Americans in the Basin
 Per capita utilization: up to 3 lbs. per day, 365 days per year
 Consumption rates varied with Native group
 20% of salmon not eaten
 Contemporary fish weights to expand biomass to numbers
 No consideration of variable fish runs; trading outside of Basin not directly considered
 Up to 4.5 to 5.6 million fish harvested per year

Density Dependence Effects of Hatchery Fish in Freshwater Habitat

- 8. The ISAB states that current numbers of smolts, both natural-origin plus hatchery-origin, likely exceed historical levels and makes the simplistic inference that “throughout the interior Columbia River basin” freshwater habitat is being overwhelmed by the addition of hatchery juveniles and excessive numbers of returning hatchery-origin adults. This statement is misleading. It disregards the fact that hatcheries release juveniles at the smolt stage—fish that do not have long residence times in the tributaries, and thus compete minimally for resources prior to smoltification with wild parr/smolts. Also, much of the hatchery production in the Basin is from large lower river harvest augmentation programs whose adults generally do not return to natural spawning areas and thus do not compete with wild and supplementation hatchery adults. As opposed to interior freshwater habitat, more focus should be directed towards possible density dependent effects in the estuary and ocean.**

This overstates comments in the ISAB report. First, the ISAB Density Dependence Report references the ISAB Food Web report ([ISAB 2011-1](#)) and states that current smolt production may exceed historical abundances. Both ISAB reports highlight the uncertainty in estimating historical smolt production. Second, the ISAB report did not infer that “*throughout the interior Columbia River basin*” freshwater habitat is being “*overwhelmed by the addition of hatchery juveniles and excessive numbers of returning hatchery-origin adults.*” We did present pHOS data provided by the HSRG for each Chinook salmon ESU and each steelhead DPS in the Basin. These data indicate pHOS values ranging from approximately 35% to 75% depending on Chinook salmon ESU, and from 15% to 80% for steelhead DPS (see Fig. VI.1 in the ISAB report). Dialog on how to address high pHOS values is needed for those watersheds where hatchery spawners exceed the capacity of the watershed to support natural and hatchery salmon (see Sidebar 2).

We agree with the comment that hatchery smolts are typically released at the smolt stage (but see Venditti et al. 2015), which reduces the time that juvenile hatchery salmonids may compete with natural salmonids. Nevertheless, as noted in the density report, the ISAB ([2011-1](#)) used a bioenergetics approach to estimate the tremendous biomass of natural prey consumed by hatchery and wild yearling Chinook smolts (85% hatchery fish) as they emigrated from Lower Granite Dam to Bonneville Dam during a 13-14 day period. The high consumption rate highlighted the potential for competition for prey among smolts as they emigrate through the mainstem and estuary at a life stage requiring sustained feeding. However, as noted in the ISAB reports, few studies have examined competition for prey in the Columbia River mainstem, estuary, and ocean. This is why the ISAB/ISRP Critical Uncertainties report ([2016-1](#)) identified this topic as a high priority critical uncertainty.

The primary evidence for density dependence involving hatchery salmon stems from hatchery adults spawning in rivers. A number of studies in the ISAB report show density dependent growth, emigration, and survival to the smolt stage and across the life cycle, indicating that the capacity to support both hatchery and wild salmon is exceeded in some years. This situation represents an opportunity to harvest surplus hatchery fish as a means to benefit people and

fish, as described in Sidebar 2. The ISAB report also described density dependence in some watersheds where there is little or no hatchery supplementation. As shown in Fig. 1 above, improved survival through the hydrosystem and ocean could lead to a higher equilibrium level (i.e., sustainability at higher spawning abundances).

Questions from the Council and Others

Density Dependence: Why Use the Label at All?

9. What about the use of the term, Density Dependence? It appears to be a convenient label for a variety of conditions that limit either the number or the size of hatchery populations and of native stocks in shared habitat. Why use the label at all?

Density dependence is the response of a population metric (e.g., survival, body growth, age at smolting, age at maturation) to population density (or abundance since habitat area is often constant). For example, fish survival typically declines as fish density increases because competition for resources increases. In contrast, some factors may influence salmon populations independently of density (e.g., temperature, flow fluctuations). However, density dependence may also interact with these physical factors; for example, density dependence is stronger when temperature is high (see Crozier et al. 2010).

Density dependence is the key to understanding how population abundance is regulated – that is, why populations do not grow without limit. That they do not is rather obvious, so the important questions are at what point does density (or abundance) begin to have a measureable effect on vital rates and at what point does it actually constrain further population growth? Ignoring fish density as a factor affecting survival or body growth can lead to erroneous conclusions and inefficient use of funding and human resources in restoration efforts. For example, in an extreme case, an agency or tribe might successfully improve stream habitat, but fill it with too many fish causing reduced growth and survival. If density effects were not considered, they might conclude that the restoration failed whereas in reality, it might have worked, but the restored habitat could not support the high density of fish. Alternatively, restoration activities in a tributary might reduce density-dependent and independent effects only to be constrained by density dependence in downstream habitats, including the mainstem and estuary.

Density dependence is important to monitor because, as an outcome, it reflects the response of the salmon population to the existing environment. Density effects due to competition are expected to be weak when abundance is low because many resources (food, habitat) are available per fish. However, density effects are expected to become evident as density increases. For this reason, it has been surprising to observe density dependence at abundances that are low relative to historical levels. This information suggests that more effort is needed to increase productivity and capacity of habitat and to improve survival through the hydrosystem in order to sustain larger populations.

Some ISAB members did not anticipate the widespread, relatively strong density dependence observed in the interior Basin, especially given the presumably low abundance. In general, they thought that density independent factors such as fluctuating temperatures, stream flows, or winter conditions would overwhelm the effect of density. It is well known that fluctuating environmental conditions can cause highly variable survival in a stream that might mask an underlying relationship between survival and density. The observation that density dependence is present in most populations highlights the importance of fish density in regulating salmon populations.

Sweet Spot between Too Few and Too Many Fish

10. Please define and explain the sweet spot between too few and too many fish in a given reach?

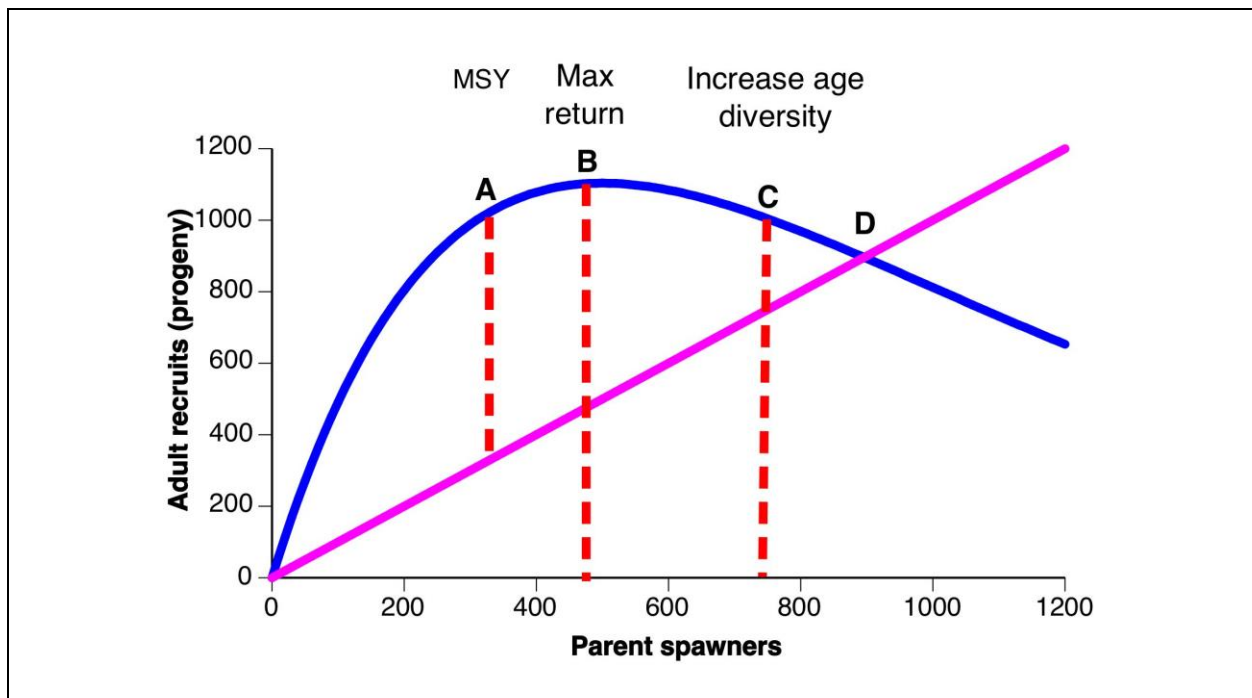


Fig. 3. Hypothetical example of adult salmon production in relation to parent spawning abundance (blue curved line). A) the location of maximum sustained yield (MSY) that is often targeted by fisheries managers, B) spawning escapement leading to the potential for maximum adult returns, C) spawning escapement that might lead to increased age diversity in some populations, and D) unfished equilibrium point where recruitment equals parent spawning escapement. See text for discussion.

Sustainable yield levels (“surplus fish”) are defined by the difference (i.e., vertical distance) between the recruitment curve (blue line) and the linear replacement line (purple) in Figure 3.

The spawning abundance that produces maximum sustained yield (MSY) is shown by point A on the graph. The spawning abundance that produces maximum adult returns is shown by point B. Point A is the "sweet spot" for those seeking to maximize sustainable yield, but Point B is the "sweet spot" for those seeking to maximize abundance or availability (but with smaller harvests). Point C identifies a spawning escapement level that may lead to increased age diversity in response to density dependent growth of juveniles (see Sidebar 1; Tattam et al. 2015). Spawning levels exceeding the unfished equilibrium point (point D) are not sustainable (return per spawner (R/S) is less than 1) and the population will decline towards the equilibrium in the succeeding generation. Thus, from the perspective of sustainable fisheries, the "sweet spot" lies above the spawning level producing MSY (point A) but below the unfished equilibrium (point D). It is worth noting, however, that spawning escapements in excess of the equilibrium point do occur in natural populations (especially in unfished areas), and these occasional large escapements may benefit the ecosystem and help to maintain salmon productivity (i.e., the underlying basis for the recruitment curve). However, those large spawning escapements cannot be sustained.

From a salmon viability perspective, concerns arise when 1) the unfished equilibrium point occurs at a very low abundance (as we often see in the Basin), and 2) when domesticated hatchery fish are pushing the population above the unfished equilibrium point such that R/S is often below 1. Interbreeding with domesticated hatchery fish likely inhibits the development or persistence of locally adaptive traits that enhance the intrinsic productivity (i.e., R/S at low S) and viability of the natural population. In the Columbia Basin, many "surplus" hatchery fish are going unharvested. This defeats the primary intent of hatcheries to mitigate lost harvests. Furthermore, an integrated hatchery approach, as defined by the HSRG, cannot exist when the natural population is not sustainable, i.e., when R/S is often below 1. If hatchery fish were genetically identical to the natural origin fish (no domestication or other hatchery breeding effects), then intrinsic productivity would not decline, but even so, the habitat would not be able to support the desired abundance level without continued release of hatchery fish.

Salmon fisheries (and the associated spawning escapement) are typically managed to achieve some level of sustainable harvests over time. In recent decades, this has often led to a narrow range in parent spawning escapements. For a number of reasons, it may be beneficial to periodically allow for a large spawning escapement—one that is beyond the level leading to maximum return. This approach may be needed to maintain the ecosystem that underpins the recruitment curve, plus collecting additional data at high abundances may uncover unexpected benefits of larger escapements (see response to Question 4).

The ISAB recommended the development of biologically based escapement goals, also known as reference points. Biologically based reference points are often developed from recruitment curves, which reflect density dependence. Other biologically based goals include recovery goals developed by the ICTRT, but these goals typically assume minimal density dependence. Managers may use these relationships to implement policy to, for example, increase the potential for maximizing harvests, to achieve maximum returns, increase diversity in age at maturation, or to minimize risk of small future population size. Fish "tell" managers how many

spawning fish are needed to achieve a targeted policy within the existing constraints of the environment, provided managers are “listening” with an appropriate monitoring program.

Is Density Dependence Self-correcting?

11. Is the density dependence effect self-correcting, so not really something we need to manage?

An unfished population will fluctuate around the equilibrium point in response to density and density independent factors. To diminish density effects and increase sustainable yield (or total adult returns), managers of salmon fisheries aim to reduce spawning abundance by choosing spawning escapement targets between points A and D in Figure 3 (see question 10). A special concern arises when the population is relatively small (e.g., overfished or experiencing degraded habitat) and there is risk of compensatory density dependence. This might occur, for example, if environmental conditions or adverse events cause a sharp reduction in salmon smolt abundance, such that an unusually large proportion of the remaining smolts could be eaten by predators. However, a predator population that is dependent on salmon would move or eventually decline once there are too few salmon, at which point the salmon population would likely recover.

As described above and in the ISAB report, compensatory density dependence is ecologically necessary for a fishery to be sustainable, and understanding density dependence is key to managing fisheries. Managers need to investigate the density dependent relationship to be able to maximize the potential for “large” future harvests or for large future adult returns. Data must be examined to determine whether progeny (recruits) might actually decline with additional parent spawners (overcompensation, as in Fig. 3 above). When hatchery fish supplement the natural origin population, then density effects should be examined to determine if the spawning abundance target is sustainable (i.e., is $R/S > 1$, on average?). Otherwise, continual supplementation of the natural population with domesticated hatchery fish is expected to erode adaptive traits of the natural population and reduce population viability and the capacity of the habitat to support natural origin fish (e.g., Buhle et al. 2013, 2014; Scheuerell et al. 2015, Venditti et al. 2015).

Management of salmon density becomes more important when hatchery fish are spawning with the natural population. Hatchery fish increase overall density and thus reduce the productivity of the natural population demographically through density dependence in the short term. The presence of numerous hatchery fish also confounds interpretation of productivity and capacity from the recruitment relationship. Because domesticated hatchery fish are less genetically adapted to the natural stream conditions, they can also reduce the intrinsic productivity of the overall natural spawning population in the long term. As stated above, a key question arising from supplementation of Snake River salmonids is, *“at what level of supplementation do genetic and ecological risks outweigh demographic benefits, indicating that hatchery supplementation should be scaled back (Cooney 2013)?”*

Comparison of Freshwater Carrying Capacity to Delisting Goals

12. The factor that might limit recovery is whether freshwater carrying capacity is too low to support a population at a viable abundance. Has the ISAB compared the capacities of populations, measured by stock-recruitment functions, to abundance delisting goals set for them in recovery plans? If so, what were the results? If not, should this comparison be completed to better understand capacity limitations on recovery?

In the ISAB report, we did not directly compare the stock-recruitment capacity estimates with minimum abundance thresholds and delisting goals. We believe such a comparison would be very worthwhile.

There is evidence, however, that density dependence is constraining recovery. ICTRT (2007) identified minimum abundance thresholds (MAT) values for populations examined of 500 to 1,000 spawners for small to large populations. Many of the populations examined in the ISAB report experienced adult return per spawner (R/S) less than 1 at abundances that appeared to be less than MAT (see CSS 2015 Appendix Table B.70, Ford et al. 2011, Northwest Fisheries Science Center 2015). These populations also showed evidence of strong density dependence, although density independent factors also contributed to low productivity. In other words, density dependence (associated with current habitat conditions) is inhibiting recovery of salmon populations. When developing minimum abundance thresholds, the ICTRT (2007) recommended that Major Population Groups should not consistently fall below replacement ($R/S < 1$), but they also explicitly assumed density effects were minimal at the current low abundances. The ICTRT (2007) apparently did not realize that capacity would be exceeded at spawner levels lower than the minimum abundance thresholds. As described above (e.g., CSS 2015), greater survival in relation to density independent factors, such as the hydrosystem, can also lead to a higher equilibrium level ($R/S = 1$).

Density Dependence in Pristine Habitat: Marine Derived Nutrients

13. We generally support habitat improvements, especially in populations where freshwater capacity appears to be impaired and too low to support recovery goals. However, there are many populations that are in relatively pristine unaltered freshwater tributary habitat that are well below viability goals. If freshwater capacity is too low in these pristine habitats, the ISAB appears to recommend that we improve marine derived nutrient inputs into those areas. We believe that this can only be accomplished by improving SARs to increase wild adult returns to those areas. Does the ISAB agree with this approach? Does it have alternative ideas?

Please see ISAB response to Question 2 and the recent analysis by the CSS (2015). Increasing productivity in the hydrosystem by 20% would likely lead to ~20% increase in SARs and, as shown in Fig. 1, this would shift the unfished equilibrium point to the right. In other words, the watershed would be able to sustain a larger population, which would return more nutrients to

the ecosystem. It should be noted, however, that the positive influence of these nutrients on the ecosystem might take decades to be fully expressed. For instance, it takes many years for trees assimilating marine-derived nutrients to grow large and then fall into streams to create habitat.

Many spring/summer Chinook produced in the “pristine” areas emigrate downriver as subyearlings and overwinter there. Copeland et al. (2014) suggested that survival of these subyearling emigrants is critical for population recovery. However, these important subyearling life history types (i.e., fry and parr emigrants) encounter degraded rearing habitats in lower tributaries and mainstem areas that reduce their survival. Also, the ISAB wonders if the habitats in these areas (Middle Fork Salmon River) are as pristine as some people think. While they may “appear” to be in good ecological condition, alterations from beaver trapping, mining, grazing, wood snagging and other widespread land uses in the 1800s most likely impacted the carrying capacity and productivity of rivers in ways that are not yet fully appreciated (see Turner et al. 1990, Lichatowich 1999, ISAB 2011-4, and others).

Smolts per Spawner and Smolt to Adult Return Rate

14. We would like the ISAB to expand on its discussion of smolts per spawner and SARs. The report includes a figure on page 130 that compares smolt to adult return and smolts per spawner. The ISAB discusses this largely from the perspective that observed SARs will require a certain level of smolts per spawner, but the ISAB ultimately concludes that major actions are necessary to increase both smolts/spawner and SARs. Could the ISAB elaborate further on this discussion?

This example involves strong density dependence shown by Snake River spring/summer Chinook salmon during the spawner to smolt stage. Figure 4 shows the minimum number of smolts per spawner (>72 smolts) needed to support a sustainable population at current SAR (geometric mean 1.4%). However, total spawning abundances are often too high to produce more than 72 smolts per spawner, indicating the abundance is not self-sustainable. Hatchery fish spawning in the streams are often maintaining high spawning densities. Selective removal of some hatchery fish would decrease spawning density, help increase smolts per spawner, and promote natural sustainability at a smaller population size. Alternatively, increased smolts per spawner may be achieved via habitat restoration actions.

Sustainability also would be enhanced by increasing SARs. This could be achieved by increasing survival of smolts through the hydrosystem, as discussed by CSS (2015). If SAR was increased to 4%, for example, then a sustainable population could be reached with 25 or more smolts per spawner rather than >72 smolts per spawner (Figure 4a). Figure 4 presents a method for estimating smolts per spawner necessary to produce a sustainable population given a specific SAR value. These relationships can be used to estimate how much benefit may be gained from improvements in the hydrosystem, smolts per spawner via habitat actions, and by harvesting surplus hatchery fish (i.e., reducing spawner density).

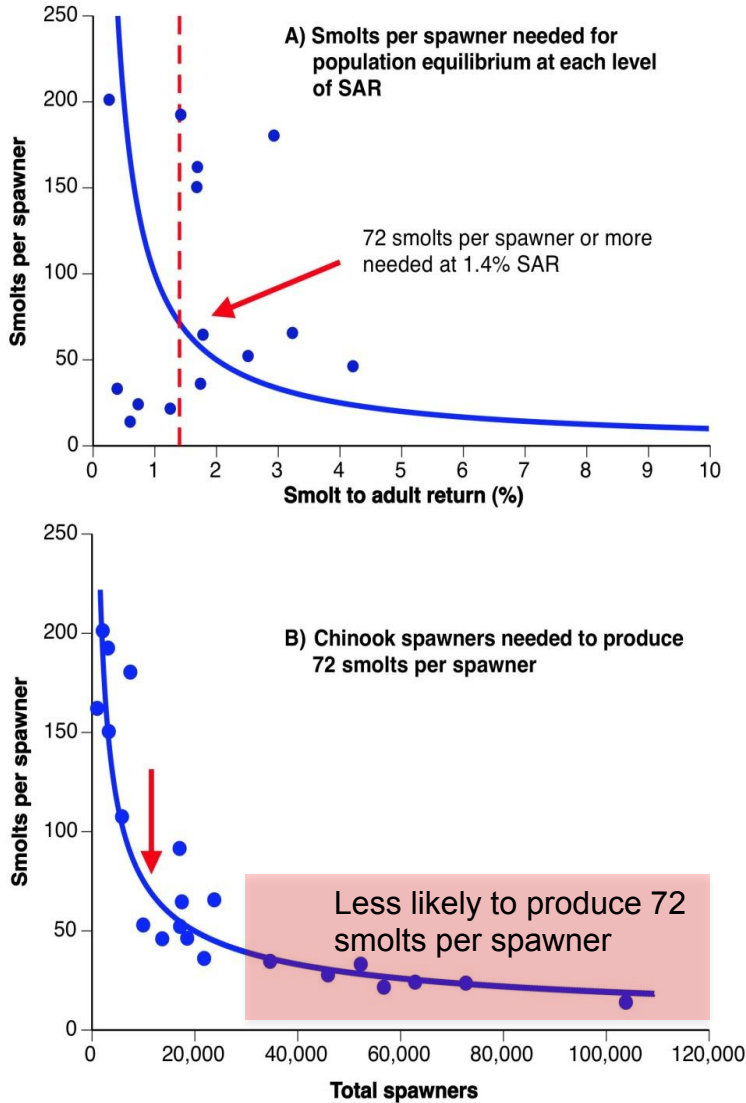


Fig. 4. Smolts per spawner needed to achieve replacement (equilibrium) in relation to the rate of smolt-to-adult return (SAR) (A), and the empirical relationship between smolts per spawner and total spawners of Snake River spring/summer Chinook (B). In panel (A), smolt per spawner values below the solid 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 VIII.1 in the ISAB report).

Spawning Areas: Clumping and Egg Superimposition

15. Spawning fish often utilize the same spawning areas - even when other habitat appears available—something the ISAB referred to as “clumping.” Superimposition of the eggs can occur. Does this phenomenon reduce the effectiveness of habitat improvement to enhance this particular part of the life history? (Page 198)

The text on page 198 of the ISAB report describes studies showing that salmon typically spawn in a very small percentage of the stream area. Maturing salmon migrate (home) back to their natal stream, and they are very good at identifying the complex suite of habitat characteristics that will support their eggs. The vast majority of stream habitat does not provide good spawning habitat, as documented in the report. As spawning abundances increase, spawners may spread out to some degree and occupy less favorable habitats, or high densities may lead to redd superimposition.

Most proposals reviewed by the ISRP do not specifically target restoration of spawning versus rearing habitat. The ISAB density dependence report does recommend identification of whether spawning or rearing habitat is limiting production, but few habitat restoration studies currently do so. Colonization of newly restored spawning areas (e.g., barrier removal) will depend in part on densities of spawners in the adjacent reach. Supplementation efforts may be used to facilitate colonization (Venditti et al. 2015). Future spawners may be attracted to chemicals produced by previous spawners.

Here are two studies related to this issue:

Isaak and Thurow (2006) examined the spatial distribution of spawning spring/summer Chinook salmon in the Middle Fork Salmon River during a period of increasing spawner abundances (1995-2003). This watershed is much less disturbed by humans relative to other streams and few, if any, hatchery salmon spawn here. As abundances increased from 20 to 2271 spawners, fish expanded into portions of the stream network that had been recently unoccupied. However, at the higher spawning abundances, distributions remained clustered and a limited portion of the network contained the majority of redds. The high density spawning areas were especially important to recruitment when abundances were low, suggesting these areas may serve as refugia during demographic bottlenecks. Strong density dependence has been observed in tributaries of the Middle Fork Salmon River (Fig. V.1 of the ISAB density report). This study indicates that salmon may seek out high quality habitats when abundances are both low and high. This could help maintain competition for spawning and rearing habitat even when densities are low.

Atlas et al. (2015) describe a spatial contraction hypothesis that provides a mechanism leading to strong density dependence at very low abundances of salmonids. This study is based on steelhead in the Keogh River, Vancouver Island. The hypothesis states that when spawner density is low, spawning populations contract to a small area, making density effects higher than expected because the population is no longer dispersed across the entire range of habitat

that was occupied when the population was larger. This hypothesis supports the idea of increasing spawning escapement so that salmon might recolonize unused habitat. Although sub-optimal clumping of spawners throughout the available habitat could increase density effects and reduce productivity, the empirical evidence in this study is weak.

Adequacy of Current Fishery Escapement Targets

16. There are escapement targets used by the states in fisheries—why aren't these adequate? Should escapement numbers include both minimum and maximum targets?

Some biologically based spawning goals have been developed in the Basin, as noted in the report. However, many goals seem to be based on the expert opinion of managers rather than quantitative analyses of spawning stock and recruitment. These management goals are generally adequate for maintaining some level of future harvest. The ISAB encourages the development and use of biologically based goals (e.g., spawner recruit relationships) so that recruitment in relation to parent spawners can be evaluated and used to make informed decisions. This information can be used to monitor and quantify effectiveness of habitat restoration activities and performance of fisheries harvest management. In the Columbia, where many natural populations are depressed, managers may wish to target the equilibrium point and harvest hatchery fish exceeding this level. Periodic high spawning escapements may benefit the ecosystem as discussed above.

Salmon escapement targets often include lower and upper goals in part because there is considerable variability in recruitment data and reference points are not precisely estimated. Managers typically try to reduce fishing mortality when escapements approach the lower goal. In some watersheds (e.g., Fraser River), managers account for high in-river mortality due to temperature and flow when managing the sockeye fishery, thereby increasing the likelihood of reaching the spawning goals.

Predation Concerns for Weak Populations

- 17. Your report notes on page 124 that the management goal of spring Chinook counted at Bonneville Dam have been met or exceeded each year since 2008. Shouldn't we also be concerned with weaker populations like upper Columbia spring Chinook?**
- a. Is it possible endangered populations like upper Columbia spring Chinook are experiencing compensatory density dependence (a population's growth rate *decreases* at low densities, opposite of what's expected at low population levels) from pinniped and avian predation?**
 - b. Is it possible that pinniped predation is counteracting positive reactions to other areas of improvement in the life cycle?**

Yes, it is possible that compensatory density dependence is occurring, but that said, the critical issue is whether predation causes the cumulative mortality rate (over the entire life cycle) for endangered populations to become compensatory. As we state in our density dependence report, it is not particularly surprising or alarming to find that predation mortality is compensatory over certain life stages, but this may not cause a problem as long as sufficient compensation can occur at other life stages. Compensation also means that predation will become less and less serious for a population that is already increasing. These issues will be considered further by the ISAB as part of its 2016 assignment to review procedures to develop a common metric to measure the effects of predation on Columbia River salmonids. The ISAB intends to complete and post its predation metric report in September 2016.

Lessons from Populations Not Showing Density Dependence

18. You note on page 139 that 25 of 27 spring/summer Chinook populations exhibit strong density dependence. Is there something we can learn from the two populations that are not showing signs of density dependence?

Yes, it is worthwhile to look into why density dependence is evident in many but not all populations. In order to detect density effects, the investigator must have sufficient contrast (range) in the density variable, such as spawner abundance, and data quality must be reasonably high. Without a range in values, density effects may not be apparent even when it is strong. If data are sufficient, then other factors such as habitat quality and quantity may be relatively high, or density may not be sufficiently high to show an effect.

Density dependence was not detected in the Wenaha River (Grande Ronde watershed) in the Snake River Basin and the Wenatchee River in the upper Columbia Basin despite a considerable range in spawning densities. Fig. V.1 in the ISAB report shows that there is some indication of density dependence in both populations but the regression was not statistically significant. In general, the Wenatchee River Basin is subjected to moderate land use, whereas the Wenaha River experiences fewer disturbances. It would be worthwhile to further explore density effects in all of these populations, including how the percentage of hatchery fish influences productivity at spawning levels above replacement (i.e., the spawning density above which $R/S < 1$). Furthermore, it would be worthwhile to evaluate the strength of overcompensation in these populations. The ISAB did not have access to the raw data, and the findings were based on linearized Ricker recruitment plots, which do not reveal the degree of overcompensation.

Hatchery Fish Contribution to Abundance

19. The concern seems to be about returns per spawner of less than 1, i.e., where the number of returning progeny is less than the parents that produced them. But even if 10,000 hatchery fish on the spawning grounds only returns 8,000 natural origin fish, isn't that still better than no hatchery fish?

The answer to this question depends on the goal. If the goal is to foster a self-sustaining wild salmon population, then the scenario described in the question will likely be counter-productive in the long term. A primary reason for producing hatchery fish is typically to provide fish for harvests while minimizing impacts on wild salmon. Please see ISAB responses to questions 3 and 4.

Density Dependence Effects of Hatchery Fish Compared to Natural-origin Fish

20. Is the science clear that lower productivity is caused by the number of fish (density) rather than the type of fish (hatchery)? For example, can you be sure that if we had the same returns but all fish were natural origin that productivity would still be low? If the problem could be hatchery fish, aren't the policy solutions different?

Management of density becomes more important when domesticated hatchery fish are spawning with the natural population. Hatchery fish increase overall density and thus reduce the productivity of the natural population demographically through density dependence in the short term. Because domesticated hatchery fish are less genetically adapted to the natural stream conditions, they can also reduce the intrinsic productivity of the overall natural spawning population in the long term.

The science is not yet clear, but recent studies suggest that the short-term effects of density on productivity are not the same for hatchery and natural origin fish (see pages 112-120 of ISAB 2015-1). In coastal Oregon, stray hatchery spawners had a much stronger (5x) negative density dependent effect on coho productivity than did natural-origin spawners (Buhle et al. 2009). Models presented in Buhle et al. (2009) predict that at any given spawning density, a spawning population that includes hatchery fish will produce fewer recruits than one that is entirely natural and that the presence of hatchery spawners will reduce the carrying capacity (maximum abundance) of the natural population. A similar modeling study of Snake River spring/summer Chinook populations (Buhle et al. 2013, 2014) suggests 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. Another modeling study based on data from 30 Chinook, 23 steelhead, and 18 coho populations (Chilcote et al. 2011, 2013) predicted that intrinsic productivity of spawning populations consisting of 50% hatchery fish would decline by 74% compared to a population consisting entirely of natural-origin salmon.

New References

Please see the full ISAB Density Dependence Report for other references noted above.

Atlas, W.I., T.W. Buehrens, D.J.F. McCubbing, R. Bison, and J.W. Moore. 2015. Implications of spatial contraction for density dependence and conservation in a depressed population of anadromous fish. *Canadian Journal of Fisheries and Aquatic Sciences* 72:1682-1693.

Collins, S.F., A.M. Marcarelli, C.V. Baxter, and M.S. Wipfli. 2015. A Critical Assessment of the Ecological Assumptions Underpinning Compensatory Mitigation of Salmon-Derived Nutrients. *Environmental Management* 56:571–586.

Comparative Survival Study (CSS). 2015. Comparative Survival Study of PIT-tagged Spring/Summer/Fall Chinook, Summer Steelhead, and Sockeye 2015 Annual Report. Prepared by Comparative Survival Study Oversight Committee and Fish Passage Center.

Drake, D., R.J. Naiman, B. Finney, and I. Gregory-Eaves. 2009. Long-term perspectives on salmon abundance: evidence from lake sediments and tree rings. *American Fisheries Society Symposium* 71:65-75.

Ford M.J. (ed.), T. Cooney, P. McElhany, N. Sands, L. Weitkamp, J. Hard, M. McClure, R. Kope, J. Myers, A. Albaugh, K. Barnas, D. Teel, P. Moran, and J. Cowen. 2011. Status review update for Pacific salmon and steelhead listed under the Endangered Species Act: Northwest. U.S. Department of Commerce, NOAA Technical Memorandum NWFSC 113:1-281.

Harvey, B.C. and R.J. Nakamoto. 1996. Effects of steelhead density on growth of coho salmon in a small coastal California stream. *Transactions of the American Fisheries Society* 125:237-243.

Hatchery Scientific Review Group (HSRG). 2015. Annual report to Congress on the science of hatcheries, 2015. A report on the application of up-to-date science in the management of salmon and steelhead hatcheries in the Pacific Northwest. Available: www.hatcheryreform.us/hrp/reports/hatcheries/downloads/HSRG_Report%20to%20Congress_2015.pdf (accessed July 2016).

Interior Columbia Technical Recovery Team (ICTRT). 2007. Viability criteria for application to interior Columbia Basin salmonid ESUs. Review draft. March 2007. U.S. Department of Commerce. NOAA Fisheries. Available: www.nwfsc.noaa.gov/trt/trt_documents/ictrt_viability_criteria_reviewdraft_2007_complete.pdf (accessed July 2016).

ISAB/ISRP. 2016. Critical uncertainties for the Columbia River Basin Fish and Wildlife Program. ISAB/ISRP Document 2016-1. Prepared for the Northwest Power and Conservation Council. Available: www.nwcouncil.org/fw/isab/isabisrp2016-1 (accessed July 2016).

- Marcarelli, A.M., C.V. Baxter, and M.S. Wipfli. 2014. Nutrient additions to mitigate for loss of Pacific salmon: consequences for stream biofilm and nutrient dynamics. *Ecosphere* 5(6):69. Available: <http://dx.doi.org/10.1890/ES13-00366.1> (accessed July 2016).
- Naiman, R.J., R.E. Bilby, D.E. Schindler, and J.M. Helfield. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems* 5:399-417.
- Naiman, R.J., J.M. Helfield, K.K. Bartz, D.C. Drake, and J.M. Honea. 2009. Pacific salmon, marine-derived nutrients and the characteristics of aquatic and riparian ecosystems. Pages 395-425, in: A.J. Haro, K.L. Smith, R.A. Rulifson, C.M. Moffitt, R.J. Klauda, M.J. Dadswell, R.A. Cunjak, J.E. Cooper, K.L. Beal, and T.S. Avery, editors. *Challenges for Diadromous Fishes in a Dynamic Global Environment*. American Fisheries Society Symposium 69. Bethesda, Maryland.
- Nilsen, E.B., W.B. Hapke, B. McIlraith, and D. Markovchick. 2015. Reconnaissance of contaminants in larval Pacific lamprey (*Entosphenus tridentatus*) tissues and habitats in the Columbia River Basin, Oregon and Washington, USA. *Environmental Pollution* 201:121-130.
- NOAA Fisheries. 2015. Proposed ESA recovery plan for Snake River fall Chinook salmon (*Oncorhynchus tshawytscha*). U.S. Department of Commerce, National Marine Fisheries Service.
- Northwest Fisheries Science Center. 2015. Status review update for Pacific salmon and steelhead listed under the Endangered Species Act: Pacific Northwest. U.S. Department of Commerce, National Marine Fisheries Service.
- Pess, G.R., B. McMillan, T.J. Beechie, and H. Imaki. Historic potential spawning abundance estimates for Columbia River Basin salmon and steelhead in areas above Bonneville Dam. *North American Journal of Fisheries Management*, *in revision*.
- Tattam, I.A., J.R. Ruzycski, J.L. McCormick and R.W. Carmichael. 2015. Length and condition of wild Chinook salmon smolts influence age at maturity. *Transactions of the American Fisheries Society* 144:237-248.
- Turner, B.L. and 5 others (eds). 1990. *The Earth as Transformed by Human Action*. Cambridge.
- Venditti, D., R. Kinzer, K. Apperson, B. Barnett, M. Belnap, T. Copeland, M. Corsi, T. Gross L. Janssen, R. Santo, K. Tardy, and A. Teton. 2015. Idaho Supplementation Studies: Project Completion Report 1991 – 2014. IDFG Report 15-18.
- Wipfli, M. and C. Baxter. 2010. Linking Ecosystems, Food Webs, and Fish Production: Subsidies in Salmonid Watersheds. *Fisheries* 35:373-387.