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UNITED STATES DISTRICT COURT
DISTRICT OF OREGON
PORTLAND DIVISION

NATIONAL WILDLIFE FEDERATION, et al.,

Plaintiffs,

v.

NATIONAL MARINE FISHERIES SERVICE, et al.,

Defendants.

Case No.: 3:01-CV-00640-SI

2015 Declaration of Richard W. Zabel, Ph.D. National Marine Fisheries Service, West Coast Region

In support of Federal Defendant's' Cross-Motion for Summary Judgment

I, Richard W. Zabel, Ph.D., declare and state as follows:

1. I am Director of the Fish Ecology Division in the Northwest Fisheries Science Center of the National Marine Fisheries Service, an agency of the National Oceanic and Atmospheric Administration (hereafter “NOAA Fisheries”). I have been in this position since 2012. Previously, I have been employed by NOAA Fisheries since 1998 as a Mathematical Statistician, Team Leader, and Program Manager. The Fish Ecology Division has 70 full-time staff, along with numerous post-doctoral scholars and contractors. Our research is primarily focused on field studies and analyses to support management of threatened and endangered salmon populations. We conduct research on a broad range of topics, including: ocean and estuary ecology; watershed processes; ecosystem analysis; and survival and migration of salmonids through the Federal Columbia River Power System (FCRPS). As such, we examine processes affecting salmonids throughout their entire life cycle. In addition to my role as Division Director, my responsibilities included leading the development and implementation of the COMPASS model for the 2008 Biological Opinion, leading the Life-Cycle modeling team under the Adaptive Management Implementation Plan (AMIP), and providing supporting analyses (e.g., the Density Dependence analysis (Appendix C) for the 2014 Supplemental Biological Opinion).

2. I have worked at NOAA Fisheries for the past fifteen years. Previous to that I worked at the University of Washington as a Research Scientist and a post-doctoral Research Associate. I received a B.S. (with honors and distinction) and M.S. from the University of Michigan, Ann Arbor and a Ph.D. (in 1994) from the University of Washington, in the Quantitative Ecology and Resource Management program. I have published 40 peer-reviewed papers on salmon ecology and modeling.

3. For NMFS, I have participated in ESA consultations concerning the FCRPS since 2006. In preparation for this declaration, I have reviewed NMFS' FCRPS 2008, 2010 and 2014 biological opinions and supporting materials for these documents; and the declarations filed on behalf of the plaintiffs' motions for summary judgment by Anthony Nigro (Nigro) and Dr. Brendan M. Connors (Connors).

4. The purpose of this declaration is to address technical issues concerning analyses supporting the 2008 FCRPS Biological Opinion and the 2010 and 2014 FCRPS Supplemental Biological Opinions. I will begin by providing a brief description of Appendix C of the 2014 Supplemental Biological Opinion and its major conclusions. Finally, I will respond to concerns raised by the Connors and Nigro declarations.

Density Dependence in salmonid populations in the Interior Columbia River basin

5. The main conclusions of Appendix C are: 1) density dependence is occurring in Chinook and steelhead populations in the Interior Columbia River basin; and there is strong support for the hypothesis that decreases in observed Recruits per Spawner (R/S) in recent years resulted from density-dependent processes as the result of increased abundance. The recent report by the Independent Scientific Advisory Board (ISAB) on density dependence reached the same conclusion. (ISAB (2015), Exhibit 1¹).

Response to Connors Declaration

6. Connors does not dispute any of the major conclusions from Appendix C of the 2014 Supplemental Biological Opinion.

7. Instead, Connors presents a theoretical hypothesis to explain the existence of density dependence at relatively low densities. He postulates that the populations identified in Appendix

¹ Summary attached as Exhibit 1; the entire document is available at <https://www.nwcouncil.org/fw/isab/isab2015-1/>

C of the 2014 supplemental Biop are really meta-populations that are composed of subpopulations, with each subpopulation occupying “semi-discrete” habitat units. Further, he hypothesizes that these sub-populations “blink in and out,” and at low densities only a portion of the habitat patches are occupied. Because of this population contraction to a few discrete habitat patches, the meta-population would experience an “increased density dependent response ... even when overall meta-population abundance is low and not all spawning and rearing habitat is occupied.” Based on this hypothesis, Connors speculates that at the same level of abundance (i.e., spawners on the a-axis of Connors’ Figures 1C and 1D), the population would produce fewer recruits under a situation where certain subpopulations have “blinked off” compared to situation where all habitat patches are occupied (i.e., comparing curve B versus curve A in Connors Figure 1D). He then uses this hypothesis to assert that because freshwater habitat is underutilized, habitat actions will have little benefit until populations are at full capacity, and the only way to get to full capacity is to improve survival outside of spawning/rearing habitats. Although his hypothesis is plausible from a theoretical standpoint, I will argue below that it is highly speculative and has little empirical support for the following reasons: 1) Connors interpretation of meta-populations in the Columbia River basin is misconstrued; 2) available data on the spatial distribution of spawners are not consistent with Connors’ postulations; and 3) the mechanisms necessary for this hypothesis to occur are not consistent with observed salmon behavior.

8. Connors mischaracterizes meta-population dynamics in the interior Columbia River basin. The Interior Columbia Technical Recovery Team (ICTRT) spent several years defining populations (see “Independent Populations of Chinook, Steelhead, and Sockeye for Listed Interior Columbia ESUs” 2008 NOAA B191). They based their population designations on

genetic information, geography, life-history traits, morphological traits, and population dynamics. They state that “the populations identified in this document are independent groups of fish.” It is quite clear from the ICTRT document that the populations they defined, which are exactly the populations that comprise the analysis in Appendix C, do not constitute “meta-populations” as proposed by Connors in his declaration. They were designated as populations because the fish freely interbreed within the populations and thus do not demonstrate “source-sink” dynamics exhibited by meta-populations. This distinction is important because the concept that these populations are really meta-populations forms the cornerstone of the hypothesis that Connors puts forth to argue against the effectiveness of habitat actions.

9. Nonetheless, populations do spatially expand and contract with population density (Isaak and Thurow 2006), Exhibit 2. However, Connors’ characterization of these spatial patterns of populations is not consistent with data. Connors suggests that at low abundance, population subunits spatially contract and only utilize a portion of the available habitat, and that this is the current situation for populations in the Interior Columbia River basin. But Isaak and Thurow (2006) describe a different situation in the Salmon River basin based on recent spatially explicit spawner data. As population abundance increases, the use of stream segments by populations increases quickly to a threshold of about 70% of available stream segments, and this threshold is not surpassed even as abundance continues to increase substantially. Isaak and Thurow (2006) state that the remaining 30% of stream segments are likely unsuitable. These observations are in contrast to the population processes hypothesized by Connors, and further demonstrate that the foundation of Connors’ hypothesis lacks empirical support.

10. An important component of Connors’ hypothesis is that salmonid populations in the Columbia River basin exhibit different behavioral states depending on long-term trends in

abundance. When populations are depressed, they only occupy a proportion of habitat patches (i.e., Connors Figure 1B); when populations are abundant, they occupy all habitat patches (i.e., Connors' Figure 1A). This part of Connors' hypothesis is realistic. However, the second and incongruous part of Connors' hypothesis is that salmon populations somehow maintain these states across generations even as abundance changes. This is the only way to explain Connors' Figures 1C and 1D, which speculate that the population exhibits different density-dependent responses depending on its state. According to Connors, fewer smolts-per-spawner at a given spawner abundance are produced by populations under a depressed state compared to populations at an abundant state. In order for this to occur, individuals would need to pass up unoccupied habitats and instead spawn and/or rear in overcrowded habitats if population abundance in previous generations was depressed. This simply is not consistent with the observation from the studies discussed in my previous paragraph that as abundance increases, salmonid population quickly utilize available habitat, even at relatively low abundance. Further, Pess et al. (2014), Exhibit 3 concluded that salmonid populations quickly occupy habitat as it becomes available, which is inconsistent with Connors' hypothesis. Additionally, the ISAB (2015), Exhibit 1 at p. 200, concluded that although females can home to their natal areas within a watershed, they will move away from natal areas to spawn when densities are high. Not surprisingly, Connors offers no evidence in his declaration to support this proposed salmonid behavior. Nonetheless, this type of behavior is necessary to support Connors' claim that under current conditions, spawning and rearing habitat is underutilized and consequently habitat actions will be ineffective.

11. It should be noted that density dependence at low population abundance (that is, compared to population capacity) is not atypical for salmon populations. In fact, major

population models, including the Beverton-Holt model (probably the most common salmon population model) and Ricker model (used in Appendix C and by Nigro in his declaration) include density dependence at low abundance. This is typified by the trend of decreasing recruits-per-spawner as spawners increase (e.g., Connors' Figure 1C and Figure 1-4 in Appendix C). So, the observation of density dependence at low abundance is not unusual, but the relatively high magnitude of density dependence observed in contemporary salmonid populations is relevant to management of these populations. Several studies have offered explanations of this phenomenon. Achord et al. (2003), Exhibit 4, suggested that relative low nutrient levels in salmon streams could be important, and Walters et al. (2013 (2014 NOAA C023394)) concluded that habitat conditions could be important, with populations in more degraded habitats exhibiting a higher magnitude of density dependence than those located in wilderness areas. The ISAB (2015), Exhibit 1, noted that density dependence can occur throughout the life cycle, not just in spawning/rearing habitats. They also note that *overall* abundance (hatchery and wild fish combined) is greater than in historical periods for some ESUs, potentially leading to density dependent effects in migratory corridors, estuary, and ocean. In addition, the ISAB (2015), Exhibit 1, stated that altered ecosystems and large hatchery fish populations can support increased populations of predators, both native and non-native, which can put great pressures on wild populations, particularly when their abundance is low.

Response to Nigro Declaration (Paragraphs 23-36 and Appendix A)

12. Nigro presents simple models of population dynamics. This work has not been peer-reviewed.

13. It is not possible to reproduce the results. For instance, in Figure 8, Nigro compares SAR to Smolts/Spawner and also superimposes a line that represents combinations of SAR and

Smolts/Spawner to achieve replacement. In the figure legend, he presents the data sources for the figure. However, when I went to the sources to attempt to reproduce the figure, I found several discrepancies. First, across populations, the SARs were measured at different locations, making comparisons across populations infeasible. For instance, the SARs for the Snake River aggregate were measured from Lower Granite Dam (smolts) to return to the uppermost dam (Lower Granite Dam or Ice Harbor Dam) as adults. In contrast, the SARs from Copeland et al. (2014), Exhibit 5, for Idaho populations were measured from Lower Granite Dam (smolts) to Bonneville Dam as adults, which is the lowermost dam. So any mortality suffered by adults during migration through the hydrosystem is not reflected in the Copeland et al. (2014) SARs but is accounted for in the Snake River aggregate. Nigro makes no mention of whether these differences were taken into account. Further, the citation for the Oregon populations (Jonasson et al. 2014) does not provide SARs, so it is unclear how the values were derived in Figure 8. Another discrepancy is that in Figure 8, median SAR for Marsh Creek is less than 0.5%, but in figure 9, citing the same data source, median SAR for Marsh Creek is reported as 0.98%. In addition, Copeland et al. (2014), Exhibit 5, does not provide Smolts/Spawner data, so it is unclear how these values were derived. Finally, Nigro states the Smolts/Spawner values are median values across a number of years. But when I examine plots of Smolts/Spawner versus year (Figures 16 and 17 in Jonasson et al. 2014), the median values appear to be about twice as high as those represented in Figure 8. These higher values would put populations much closer to the replacement line. These issues reinforce that the analysis was not peer-reviewed, is not reproducible, and thus the overall conclusions are not supported.

14. In Figure 9, the data concerns continue. In this figure, adult abundances do not correspond to those contained in Copeland et al. (2014), Exhibit 5. Instead, they appear to be

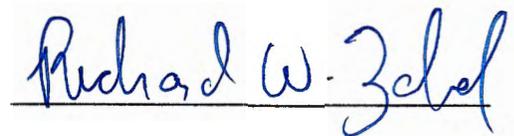
derived from the NMFS salmon database, as cited in Appendix A. Finally, Figure 9 appears to suffer from the same type of mismatch as contained in Figure 8. In this case, the adults for the SARs were measured at Bonneville Dam as they entered the hydrosystem, but the adults presented on the X axis were measured at the spawning site, over 1000 km upstream. These issues are also found in Figures 10, 12 and 13, rendering these analyses questionable.

15. In paragraphs 30-35, Nigro discusses the measurement of hydrosystem-related latent mortality by comparing Snake River populations to those located below the Snake River dams. In their review of post-Bonneville survival, the ISAB (2007 (2008 NOAA AR B.184)) stated:

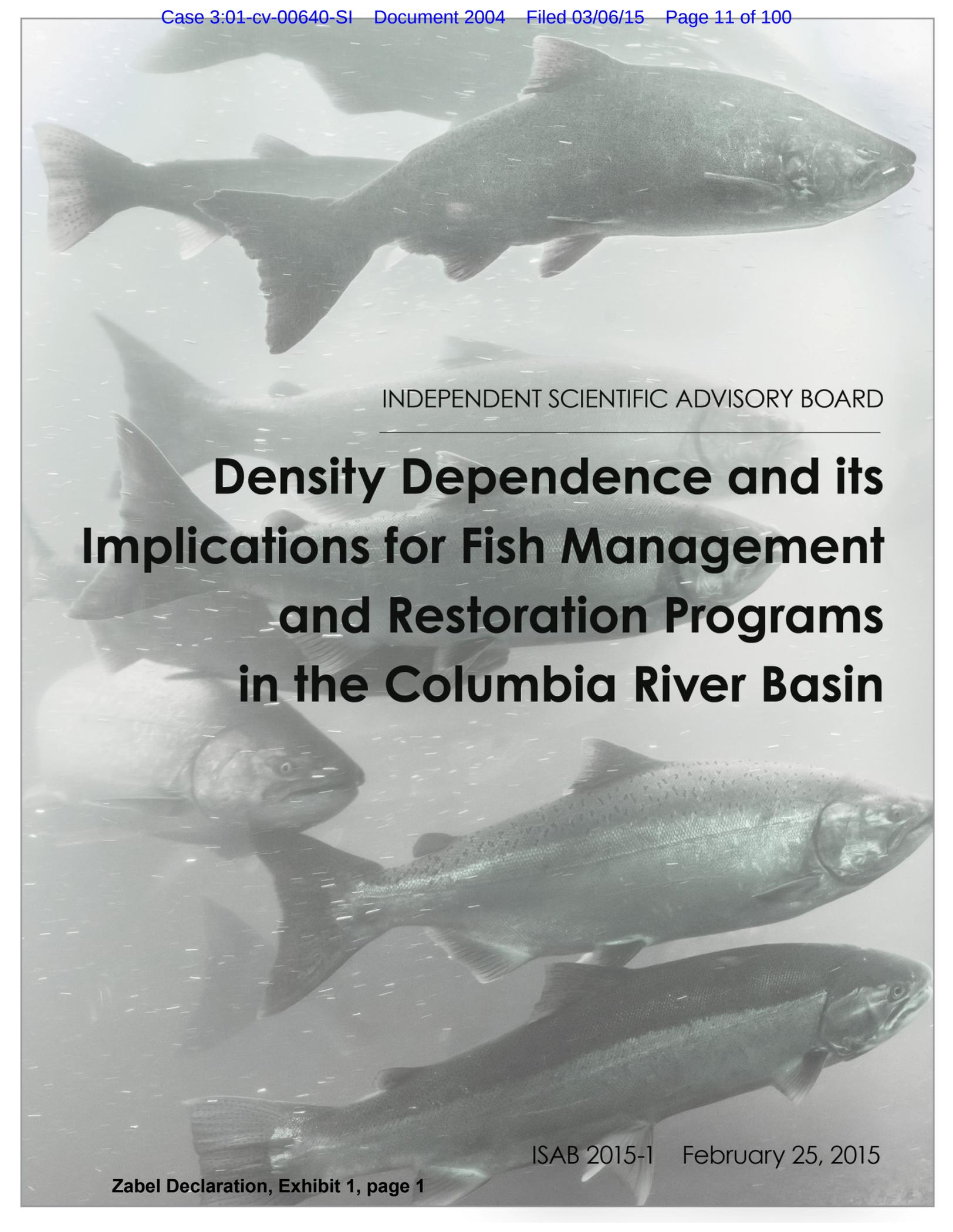
“The ISAB concludes that the hydrosystem causes some fish to experience latent mortality, but strongly advises against continuing to try to measure absolute latent mortality. Latent mortality relative to a damless reference is not measurable.”

16. In addition, the analysis has several flaws, beyond the issues with the underlying data. In particular, identifying the Ricker S_{max} as a population abundance target has little precedent in the field of fisheries management. Also, as demonstrated in Appendix C of the 2014 Supplemental Biological Opinion, the Ricker relationships typically have variability about them, and defining a point estimate for an abundance target is not reasonable because the estimate of S_{max} has uncertainty that is not being represented. Further, as demonstrated in the plots in Appendix A, most or all of the spawner estimates fall to the left of the abundance associated with S_{max} , and very few fall to the right. From a statistical standpoint, this makes it difficult to estimate S_{max} , further calling into question its use as a reference point in these plots. Again, these issues demonstrate that the analyses have not been thoroughly reviewed or documented, and that the conclusions are overly pessimistic.

I declare under penalty of perjury that the foregoing is true and correct. Executed on March 5, 2015, in Seattle, Washington.

A handwritten signature in blue ink that reads "Richard W. Zabel". The signature is written in a cursive style and is positioned above a horizontal line.

Richard W. Zabel, Ph.D.



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

ISAB 2015-1 February 25, 2015

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



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

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

W.E. Ricker 1954

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

Rose et al. 2001

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

Edmundson et al. 2003

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

Bugaev 2002

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

Y. Berra 1998

Key Words with Multiple Meanings

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

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

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

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

Executive Summary

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

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

The ISAB's key recommendations include:

Anadromous salmonids

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

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

Non-anadromous salmonids

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

Sturgeon

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

Lamprey

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

Summary

Preface

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

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

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

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

PART 1: Anadromous Salmonids

Chapter I. Introduction

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Chapter VI. Hatchery Effects on Density Dependence

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

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

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

Chapter VII. Predation Effects on Density Dependence

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

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

Chapter VIII. Management of Anadromous Salmonids in the Columbia Basin

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

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

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

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

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

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

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

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

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

Chapter IX. ISAB Recommendations, Part 1

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

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

- Use knowledge of mechanisms influencing density dependent growth, dispersal, and survival of anadromous salmonids to choose restoration actions that will most effectively increase habitat capacity and fish population productivity and abundance.
- In restoration planning, identify actions capable of reducing density dependence during each life stage, and integrate with actions designed to reduce mortality caused by density independent factors (e.g., water temperatures and flows).
- Consider density dependence when evaluating the success of restoration actions; fish response variables (growth, dispersal from the natal stream, survival, recruits) are typically influenced by fish density.

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

- Establish biologically based reference points to guide the need for management actions (via harvests, supplementation, and removal of surplus hatchery fish entering the spawning areas) and to quantify when too few or too many spawners are present to sustain natural populations.
- In setting harvest rates, account for current population productivity and habitat capacity, and adjust harvest through Adaptive Management as environmental conditions change.
- Recognize that large spawning escapements can provide ecosystem benefits and promote long-term sustainability but might also impose short-term costs to fishing communities or to the fish population if there is overcompensation (less recruitment with larger spawning abundances).
- Acknowledge that ecosystem-based fishery management may prove to be the best strategy over the long term given existing uncertainty about density dependent and ecosystem-scale processes.

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

- Clearly articulate anticipated benefits of supplementation actions and base these actions on established scientific principles.
- Estimate the abundance and proportion of hatchery and natural origin adults on spawning grounds, whenever possible, to target appropriate spawning densities that prevent the loss of productivity in natural populations, especially through overcompensation in the short term or domestication in the long term.
- Recognize that an integrated hatchery supplementation approach requires a self-sustaining natural salmon population, which in turn requires spawning densities that can be supported by the environment.

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

- Density effects in salmon populations that spawn in the lower Basin and in coho salmon populations throughout the Basin.
- Density effects on the growth and survival of juvenile salmonids emigrating downriver and rearing in the estuary and ocean.
- Predation on adult salmon by pinnipeds (seals and sea lions). Since compensatory mortality may pose a threat to ESA-listed populations, the ISAB recommends further quantification of mortality and evaluation of life cycle recruitment in salmon populations targeted by pinnipeds.

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

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

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

Chapter X. Non-Anadromous or “Resident” Trout

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Chapter XI. Kokanee

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

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

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

Chapter XII. Sturgeon

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

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

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

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

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

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

Chapter XIII. Pacific Lamprey

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

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

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

Chapter XIV. ISAB Recommendations, Part 2

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

Non-anadromous salmonids

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

- **Consider that in-stream habitat restoration is most likely to increase carrying capacity by reducing compensatory mortality and emigration.** The postulated mechanisms are related to increasing survival and decreasing emigration, rather than by affecting growth, fecundity, or immigration. Evidence from across many regions shows that increases can occur, but the true effects on survival and emigration occur at the riverscape scale and remain difficult to quantify.
- **Restore riparian vegetation to increase the input of terrestrial invertebrates,** which can improve growth and abundance and decrease emigration of salmonids.
- **Consider carefully the stocking of hatchery trout to avoid reducing carrying capacity for wild non-anadromous salmonids.** An investigation of stocking sterile hatchery rainbow trout did not detect effects on growth, survival, or recruitment, but this

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

- **Take steps to prevent invasions by non-native trout**, which can often replace native salmonids quickly (i.e., usurping carrying capacity), achieve higher density and biomass when they do replace them, and have ecosystem-scale effects on emerging insects that are key food resources for other wildlife. Removing non-native trout above barriers allows native salmonid populations to rebound to their former carrying capacity, and in relatively undisturbed watersheds without barriers, maintaining stronghold populations of native salmonids at high density may help to prevent invasions by non-native trout.
- **Consider the use of angling regulations and fishery closures to achieve conservation and sport fishing goals.** Studies of bull trout populations show populations rebounding from low abundance to achieve density goals for conservation, indicating that they were far below carrying capacity and that angling mortality was partly additive to natural mortality. Many populations of cutthroat and rainbow trout throughout the Rocky Mountains also have rebounded when restrictive angling regulations were applied, indicating that fishery management can be effective at increasing the density of resident trout.
- **Ensure that fishery managers consider the probable effects of density on survival, emigration, growth, and size/age at maturity.** For example, kokanee populations can crash due to food limitation following overstocking with kokanee fry. In the absence of detailed data for stock assessment, managers should use their knowledge of limiting factors and fishery management principles to target intermediate densities, rather than seeking the ecologically unrealistic goal of a higher abundance of larger fish.

Sturgeon

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

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

Lamprey

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

- **Initiate a concerted effort to gather information that would help the recovery of this species.** Toward that end, research in the Great Lakes has documented significant density dependent effects for populations of sea lamprey, which is related to the Pacific lamprey. These sea lamprey studies might provide a template for developing a similar understanding of Pacific lamprey.
- **Consider lessons learned about supplementation and density dependence in anadromous salmonids when planning future actions to propagate and translocate (i.e., supplement) lamprey within the Basin.** While the ecological lessons might not be directly transferrable, they can be used to guide management and restoration actions.

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

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

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

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

Appendix II. Density Effects during Spawning and Incubation

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

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

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

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

Network-scale spatial and temporal variation in Chinook salmon (*Oncorhynchus tshawytscha*) redd distributions: patterns inferred from spatially continuous replicate surveys

Daniel J. Isaak and Russell F. Thurow

Abstract: Spatially continuous sampling designs, when temporally replicated, provide analytical flexibility and are unmatched in their ability to provide a dynamic system view. We have compiled such a data set by georeferencing the network-scale distribution of Chinook salmon (*Oncorhynchus tshawytscha*) redds across a large wilderness basin (7330 km²) in central Idaho for 9 years (1995–2003). During this time, the population grew at a rate of 5.3 recruits per spawner, and redd numbers increased from 20 to 2271. As abundances increased, fish expanded into portions of the stream network that had recently been unoccupied. Even at the highest escapements, however, distributions remained clustered, and a limited portion of the network contained the majority of redds. The importance of the highest density spawning areas was greatest when abundances were low, suggesting these areas may serve as refugia during demographic bottlenecks. Analysis of variance indicated that redd numbers were strongly affected by local habitats and broad climatic controls, but also revealed a space–time interaction that suggested temporal instability in spatial patterns. Our results emphasize the importance of maintaining habitats with high densities of individuals, but also suggest that broader views may be needed to accommodate the dynamics of natural salmonid populations.

Résumé : Les plans d'échantillonnage spatial en continu, répétés dans le temps, fournissent une flexibilité d'analyse et sont sans pareil pour générer une perspective dynamique d'un système. Nous avons compilé une telle banque de données en établissant par géoréférencement la répartition à l'échelle du réseau des frayères de saumons quinnat (*Oncorhynchus tshawytscha*) dans un grand bassin versant sauvage (7330 km²) du centre de l'Idaho pendant 9 ans (1995–2003). Pendant cette période, la population a crû à un taux de 5,3 recrues par reproducteur et le nombre de frayères est passé de 20 à 2271. Au fur et à mesure de l'accroissement de l'abondance, les poissons ont envahi des sections du réseau hydrologique encore récemment inoccupées. Même dans les escarpements les plus élevés, cependant, la distribution demeure contagieuse et une partie restreinte du réseau abrite la majorité des frayères. L'importance des sites de frai à densité très élevée est maximale aux densités faibles, ce qui laisse croire que ces sites servent de refuges durant les goulots d'étranglement démographiques. Une analyse de variance indique que le nombre de frayères est très affecté par les habitats locaux et les facteurs généraux de contrôle climatique; elle montre aussi une interaction espace-temps qui laisse croire à une instabilité temporelle des patrons spatiaux. Nos résultats mettent l'emphase sur l'importante de préserver les habitats de grande densité de poissons, mais ils laissent aussi entrevoir que des perspectives plus larges seront peut-être nécessaires pour tenir compte de la dynamique des populations naturelles de saumons.

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Introduction

Pacific salmon populations have declined during the last century across much of North America outside of Alaska, especially at inland and southern peripheries of historical ranges (Nehlsen et al. 1991; Thurow et al. 2000). Many re-

maining populations persist at low levels, which has prompted federal protection under the US Endangered Species Act and costly restoration efforts. Initial attempts to restore populations focused on curtailment of adult harvests, supplementation of wild stocks with hatchery fish, and modification of hydrosystems to reduce mortality (Independent

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Scientific Group 1999). Results from these efforts have been mixed, and emphasis has recently turned to freshwater rearing habitats, where modeling results suggest that increases in juvenile survival could improve population growth rates (Kareiva et al. 2000; for an alternative view see Wilson 2003).

Most knowledge regarding the basic ecology of salmon comes from studies on freshwater environments. Unfortunately, most of this knowledge is derived from studies conducted at relatively small spatial and temporal extents (Fausch et al. 2002), which provides a poor fit to the broader spatiotemporal themes that underlie most species conservation efforts (e.g., metapopulation theory, source–sink dynamics, landscape ecology). Growing awareness of this gap, combined with advances in remote sensing, spatial sampling strategies, georeferencing capabilities, and broad usage of geographic information systems (Fisher and Rahel 2004) have motivated a new generation of studies designed to understand interpopulation processes (Rieman and Dunham 2000), the importance of natural disturbance regimes, terrestrial–aquatic linkages, and landscape genetics (e.g., Costello et al. 2003; Dunham et al. 2003; Miller et al. 2003).

Increasingly common among this new generation of studies are spatially continuous survey techniques (Fausch et al. 2002), which overcome many of the limitations associated with traditional sampling designs. Most sampling designs have two basic assumptions that must be met for valid inference to be drawn. First, the statistical population about which inference is desired must be correctly identified. Second, a statistically valid sample, involving the randomized selection of sample units, must be drawn from the population (Scheaffer et al. 1990). Inferential bias may still occur if broad-scale trends or unanticipated local factors impinge upon sample elements — a process that can result in spatially or temporally correlated error structures (Legendre 1993). The potential for this sort of bias has long been recognized in the temporal domain, where it motivates many books on the topic of time-series analysis. More recently, similar awareness has spread to the spatial domain, perhaps spurred by the emergence of theories that emphasize the importance of spatial context, connectivity, and habitat geometry (Hanski and Gilpin 1997). Regardless, insufficient or poorly designed sampling in either domain may yield a skewed picture of reality (Wiley et al. 1997). Spatially continuous sampling, especially if surveys are repeated through time, can minimize these error sources and provide more accurate system views that may yield novel insights to aquatic ecosystems (Fausch et al. 2002).

As one example, many biological systems are thought to be characterized by spatial variation in demographic rates, often referred to as source–sink dynamics (Pulliam and Danielson 1991). In practice, it is difficult to infer source–sink behavior in the absence of detailed demographic data (Watkinson and Sutherland 1995), which greatly restricts the spatial extents that can be studied. Changes in population size, however, often have profound and sometimes unpredictable effects on the distribution of a species because these adjustments are rarely uniform (Channell and Lomolino 2000). Populations occurring in productive habitats may show little change despite large declines in regional abundance, whereas less productive sink habitats may quickly

gain or lose populations, depending on the level of demographic support from source areas (Pulliam and Danielson 1991; Schlosser and Angermeier 1995). Simple observation of range contractions and expansions, therefore, if done using spatially continuous surveys so that the proportional contribution of different areas can be calculated, may reveal some areas to be more or less ephemeral. Although results would not provide conclusive proof for source–sink dynamics, insights might be gained regarding where more detailed studies should be conducted or which areas may be especially robust and therefore warrant conservation priority.

In this paper, we introduce a unique data set that consists of annual censuses of Chinook salmon (*Oncorhynchus tshawytscha*) nests, often referred to as redds, that have been georeferenced across a large wilderness basin located in central Idaho. Chinook salmon redds are readily observed because of their large size and high visibility for several weeks after construction. Although redd counts are often used as an index of abundance, the fact that they are the breeding structure for salmonid fishes suggests their distribution across a landscape may also serve as a useful proxy for understanding important biophysical processes (Montgomery et al. 1999). The goal of this paper is to describe the data set and examine spatial and temporal patterns in network-scale redd distributions. More specifically, we determine whether redds were randomly distributed in space, examine temporal changes in distributions relative to population size, decompose the variance associated with redd numbers to understand the relative importance of spatial and temporal factors, and discuss the conservation implications associated with these patterns. We also describe patterns associated with population expansion because salmon abundance increased dramatically during this study, probably stimulated by a combination of improved ocean productivity and juvenile migration conditions (Fish Passage Center 2003; Beamish et al. 2004).

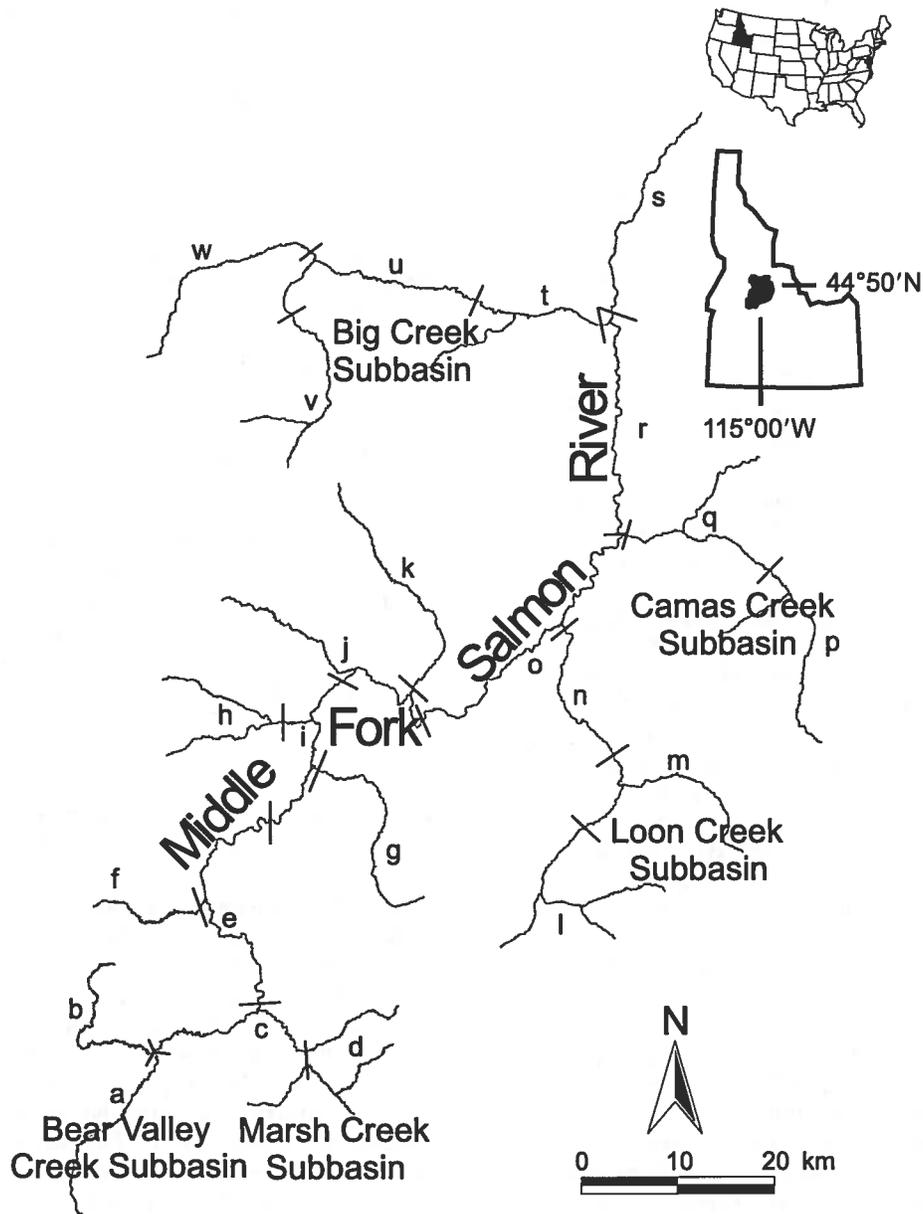
Materials and methods

Study area

This study was conducted in the Middle Fork of the Salmon River (MFSR) in central Idaho (Fig. 1). The MFSR drains 7330 km² of forested and steeply mountainous terrain in central Idaho that ranges in elevation from 1000 to 3150 m. Most of the area (>95%) is administered by the USDA Forest Service and was managed as a primitive area from 1930 to 1980 before receiving permanent protection as part of the Frank Church – River of No Return – Wilderness in 1980. As a result, road and trail densities are low and most areas exist in relatively pristine condition. Some areas continue to recover from the effects of grazing or mining, but cessation of many of these activities has occurred since wilderness designation and listing of Snake River salmon stocks under the Endangered Species Act. Natural disturbances from fires, hillslope movements, and floods persist, and these processes maintain a dynamic mosaic of landscape conditions.

Streams across much of the MFSR flow through narrow, V-shaped valleys, except for short reaches where valleys are unconfined. In the Bear Valley Creek and Marsh Creek subbasins, however, thick deposits of Quaternary alluvium and Pleistocene glacial drift fill the main valleys and result

Fig. 1. Stream network in the Middle Fork Salmon River that was accessible to Chinook salmon (*Oncorhynchus tshawytscha*) and was sampled for redds from 1995 to 2003. Letters next to stream segments denote areas used in later data summaries. Inset (upper right) shows location in Idaho, USA.

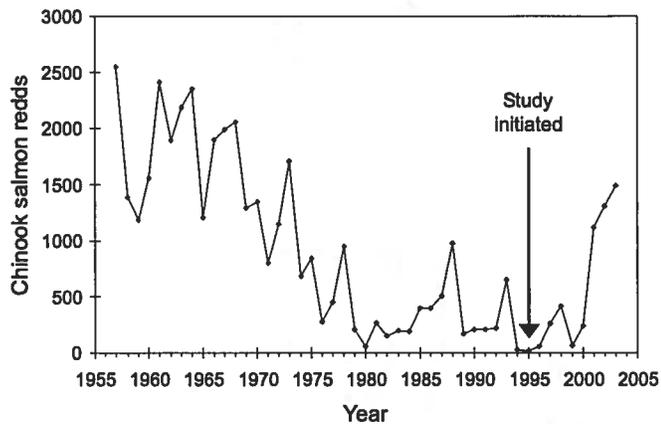


in broad, U-shaped valleys throughout these areas (Bond and Wood 1978). Channel morphologies in Bear Valley – Marsh Creek and other areas where valleys are not constrained consist of meandering pool–riffle sequences that are heavily used by spawning salmon. Channels associated with constrained valleys are usually higher-gradient planebed and step–pool configurations (*sensu* Montgomery and Buffington 1997). Stream hydrographs are driven by snowmelt runoff, with high flows occurring from April through June and low flows during the remainder of the year.

The Chinook salmon that occur in the MFSR are wild, indigenous fish and are referred to as spring–summer stocks based on the timing of adult migration past Bonneville Dam in the lower Columbia River (Matthews and Waples 1991). Redd counts conducted by the Idaho Department of Fish and Game at index sites within the MFSR since the 1950s sug-

gest that these populations have declined dramatically, although escapements increased during the span of this study (Fig. 2; Brown 2002). Chinook salmon enter the MFSR drainage in early summer, migrate to natal areas that occur primarily in larger tributaries, and stage in pools before spawning. Spawning time varies among sites, but redd construction usually begins during the last week of July at high elevations (1800–2100 m) and is completed by mid-September at low elevations (1000–1300 m; R. Thurow, unpublished data). Females deposit eggs in redds that are 2–4 m in diameter and are constructed in riffle crests or other areas that have similar hydraulic and substrate characteristics. Embryos incubate in the gravel and emerge as fry the following spring. Most juveniles rear in natal areas for one year before migrating seaward, although this time frame is variable (Bjornn 1971). Chinook salmon spend 1–3 years in

Fig. 2. Time series of Chinook salmon (*Oncorhynchus tshawytscha*) redd counts for index areas in the Middle Fork Salmon River. Data are from annual Idaho Department of Fish and Game surveys (Brown 2002).



the ocean, during which time growth is rapid and maturity is reached at total lengths ranging from 60 to 120 cm. Adult returns to the MFSR are dominated by age-4 and age-5 fish (Kiefer et al. 2002).

In addition to Chinook salmon, other fishes occurring within the MFSR include bull trout (*Salvelinus confluentus*), brook trout (*Salvelinus fontinalis*), westslope cutthroat trout (*Oncorhynchus clarkii lewisii*), rainbow trout (resident and anadromous forms; *Oncorhynchus mykiss*), mountain whitefish (*Prosopium williamsoni*), torrent sculpin (*Cottus rhotheus*), mottled sculpin (*Cottus bairdi*), shorthead sculpin (*Cottus confusus*), Pacific lamprey (*Lampetra tridentatus*), speckled dace (*Rhinichthys osculus*), longnose dace (*Rhinichthys cataractae*), largescale sucker (*Catostomus macrocheilus*), bridgelip sucker (*Catostomus columbianus*), reddsider shiner (*Richardsonius balteatus*), and northern pikeminnow (*Ptychocheilus oregonensis*; Thurow 1985).

Redd surveys

Low-level helicopter flights were used to conduct annual, spatially continuous surveys of Chinook salmon redds from 1995 to 2003 within that portion of the stream network (670 km) that was accessible to Chinook salmon (Fig. 1). Range determination was made by reviewing records of juvenile Chinook salmon occurrence (Thurow 1985), Idaho Department of Fish and Game redd survey reports (Brown 2002), and anecdotal accounts of spawning (Hauck 1953; Gebhards 1959) and by interviewing biologists familiar with the drainage. Aerial surveys were conducted between 0900 and 1800 h to facilitate visibility, and all surveys were conducted by the same observer (R. Thurow) at the end of the spawning period. During counts, the pilot maintained airspeeds of 20–40 km·h⁻¹ and altitudes of 15–50 m, depending on the surrounding terrain. When a redd was observed, a global positioning system (GPS; Pathfinder ProXL, Trimble, Sunnyvale, California) was used to georeference the location. In several sections of stream where tree canopy precluded aerial observation, trained observers walked the stream and recorded coordinates with a GPS at redd locations. All GPS locations were later differentially corrected and assembled into a geographic information system for use in subsequent analysis. Discerning Chinook salmon redds

from those of other fall-spawning salmonids was not problematic, given the large size of salmon redds as well as their distribution and timing of construction. Stream shading, habitat complexity, turbidity, and redd superimposition can affect the accuracy of redd counts (Dunham et al. 2001), but ongoing validation work suggests the relationship between aerial counts and “true” counts based on more reliable ground surveys is strong ($r = 0.78$, $n = 52$ reaches; R. Thurow, unpublished data).

Population expansion

Population growth was described in three ways. Inter-generational pairs of redd distributions were mapped for years when spawner-year abundance was especially low and many stream segments were unoccupied. Intergenerational lags were determined from female age structures estimated using finray cross-sections (Kiefer et al. 2002). Population expansion was also examined by splitting the network within each of the five major subbasins where most (87%) of the spawning occurred (labeled in Fig. 1) into contiguous, 500 m reaches and calculating the proportion of reaches that contained at least one redd during each survey year. Lastly, age structure information, combined with basin-wide redd count totals, were used to calculate population growth rates based on the number of recruits per spawner:

$$(1) \quad R = \frac{(N_{i4} + N_{i5} + N_{i6})}{N_i}$$

where R is recruits per spawner, N_i is the number of redds in spawner year i , and $N_{i4,5,6}$ are number of redds attributable to spawner year i four, five, and six years later, respectively.

Cumulative distribution curves

Similar to Walters and Cahoon (1985), we used cumulative distribution curves to summarize the spatial distribution of redds. Cumulative curves provide a visually intuitive means of describing a population, facilitate comparison to other distributions, and are simple to construct. This technique was applied by dividing the stream network into 23 segments of approximately equal length ($\mu = 28.2$ km, standard deviation = 2.1 km; Fig. 1). Summaries were also done using smaller segments, but results were qualitatively similar and are not presented. Attempts were made to place divisions at major tributary junctions and to maintain approximately equal segment sizes, which simplified randomization of redd distributions that were later used to construct null model distributions for comparison. Once the network was partitioned, the proportions of redds within individual stream segments were calculated and ranked relative to other stream segments within the same year. Cumulative proportions were then plotted against stream segment rank order.

Null model distributions were created by generating populations of 1000 curves from the random allocation of redds to stream segments. For each population of curves, the number of redds randomly allocated equaled the number of redds observed during one of the study years. We then calculated Shannon–Wiener diversity (Zar 1996) scores for the observed and randomized redd distributions. Higher scores were indicative of greater evenness. The form of the Shannon–Wiener diversity index used was as follows:

$$(2) \quad H' = \sum_{i=1}^k p_i \log p_i$$

where H' is Shannon–Wiener diversity, k is the number of stream segments, and p_i is the proportion of redds found in stream segment i . Diversity scores within individual years were compared and assigned probability values based on the proportion of the 1000 H'_{random} values that H'_{observed} exceeded. To determine whether discrepancies between observed and random distributions were related to population size, we regressed average $H'_{\text{random}} - H'_{\text{observed}}$ values against yearly redd totals. A trend was taken as evidence that changes in observed redd distributions were nonrandom and driven by biological processes related to fish movements or spatial variation in growth rates.

Space–time interaction

As a complement to the cumulative distributions, we considered whether the relative importance of individual stream segments remained constant through time. If no segment \times year interaction occurred, it would indicate that areas most important for spawning one year were important in other years. In the context of recovery planning, this scenario would be desirable because it allows easy identification of key areas and facilitates targeting of restoration activities on a small subset of reaches. The presence of an interaction is more problematic because it indicates that site selection through time is less consistent, and conservation or restoration activities may need to be more diffuse.

We tested for a segment \times year interaction using a repeated measures analysis of variance (ANOVA) design in which year was the repeated measure and the treatment factor was stream segment. Segments were bisected and redds were tallied by subsegments, which provided replicate samples and facilitated estimation of the interaction term (von Ende 2001). All factors were considered fixed, and the analysis was conducted in PROC MIXED in SAS (Littell et al. 1996) after redd counts were $\log_{10} + 1$ transformed to achieve residual normality. The MIXED procedure allowed specification of different covariance matrices to account for correlated error structures, so we initially ran the analysis using several error types to determine the most appropriate structure. The relative performance of different covariance structures was assessed using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). The covariance structures tested were a first-order, autoregressive structure; a banded Toeplitz matrix, which included lags out to 5 years (typically the maximum intergenerational lag); an unstructured matrix in which no a priori structure was assumed; and a standard covariance matrix, which assumed error independence (Littell et al. 1996). The Toeplitz matrix performed best and was used for the final analysis, although the choice of covariance structure had a minimal effect on the results.

Variance partitioning

We were also interested in determining the relative roles of spatial, temporal, and error sources on variance structure, as well as the effect that study duration may have had on the ability to accurately discern these roles. Variance structure is of interest because it reveals much about different types of biological, environmental, and sampling processes that may

be relevant (Wiley et al. 1997). In the present study, for example, spatial variability represented site-to-site differences in numbers of redds among stream segments that arose from local habitat factors that affected where salmon spawned (e.g., spawning gravels, suitable temperature regimes, adequate flow depths, etc.). Temporal variability, in contrast, represented yearly changes in redd numbers that occurred consistently, or synchronously, across stream segments. Broad-scale climatic factors that affected areas similarly, such as ocean productivity or flow conditions during juvenile migrations, would have fallen into this category. Interactions between spatial and temporal factors represent variability attributable to local, site-specific forcing factors. Examples could include spatial variation in density-dependent mortality factors or a stochastic event that altered habitat conditions within a stream segment after study initiation. Finally, residual variation lumps two sources of variability: those due to intrayear variability and measurement errors (Larsen et al. 2001). In this instance, intrayear variability resulted from differences in redd counts between the two subsegments used to estimate the segment effect, and measurement error stemmed from miscounts in the field, data transcription problems, or any other process that resulted in deviations from the actual number of redds.

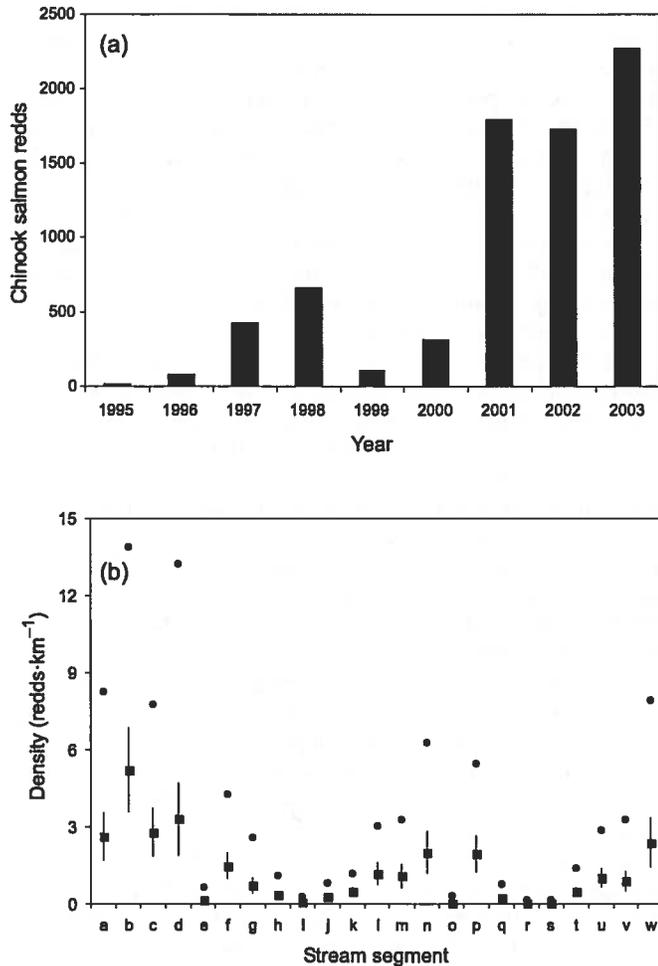
Variance partitioning was accomplished by decomposing total sums of squares (SS) into proportional contributions by segment, year, segment \times year interaction, and residual error. PROC VARCOMP was used to estimate SS because PROC MIXED does not use SS (Littell et al. 1996). Using the observed time series, SS were calculated using data from 1995, then data from 1995–1996, 1995–1997, etc. Answers derived from this approach, however, depended entirely on the observed data sequence, so we also calculated average variance contributions from analyses run on all possible yearly combinations in which years were not repeated. To determine variance contributions based on 1 year of data, nine separate analyses were run, variances were partitioned, and the proportional contribution of stream segment was calculated as an average across the nine analyses. This procedure was repeated for all possible combinations of 2 years of data, 3 years of data, etc., until the entire time series had been summarized accordingly.

Results

Stream conditions usually made it possible to count all designated areas each year, but high turbidities caused by thunderstorms limited visibility in parts of Loon and Camas creeks during 1995 and sections of Big Creek in 1997, 1998, and 2001. Basin-wide totals for redd counts ranged considerably — from 20 redds in 1995 to 2271 redds in 2003. Years of low escapements were intermixed with years of higher escapements, although the general trend was one of increase (Fig. 3a). In addition to temporal variation, spatial variability also occurred, and some segments of stream contained average redd densities as low as 0.023 redds·km⁻¹, whereas other segments averaged up to 5.2 redds·km⁻¹. Maximum redd densities for individual stream segments typically exceeded the mean density by a factor of three or four (Fig. 3b).

As recruits from the first redd surveys began to return, occupation of previously unused stream segments was rapid —

Fig. 3. (a) Basin-wide totals for annual Chinook salmon (*Oncorhynchus tshawytscha*) redds counted during aerial surveys from 1995 to 2003. (b) Mean redd densities (± 1 standard error) within stream segments shown in Fig. 1. Points above mean values indicate the maximum number of redds that occurred within a stream segment during this study.



increasing from 6 to 16 segments between 1995 and 1999 and from 16 to 22 segments between 1996 and 2000 (Fig. 4). Distributional expansions were less dramatic in subsequent years, given that baseline redd numbers were usually larger, but in some subbasins, these expansions appeared to be ongoing across the range of observed densities (Fig. 5a). In two subbasins with the highest redd densities, however, the proportion of 500 m reaches that were used for spawning appeared to approach asymptotes at ~70% of the network (Fig. 5b). These asymptotes were reached at low densities (≈ 3 redds·km⁻¹), and the proportion of reaches occupied then remained constant across a threefold density increase, which suggested that suitable reaches were rapidly colonized, but were not being fully utilized at the densities observed. Recruits per spawner during the 9 study years ranged from 2.7 to 9.1, with an average of 5.3 (Table 1).

Visual comparison of cumulative redd curves suggested that observed spawning distributions were more clustered than random distributions (Fig. 6). This observation was confirmed by the Shannon–Wiener diversity scores, in that

all $\bar{H}'_{\text{observed}}$ values were smaller than \bar{H}'_{random} scores, indicating p values < 0.001 . As redd numbers increased, distributions became less clustered, which resulted in flatter curve profiles, and decreased the proportion of redds that occurred in the densest spawning areas. Despite this pattern, no trend occurred in $H'_{\text{random}} - H'_{\text{observed}}$ values relative to population size ($b_1 = -1.51 \times 10^{-5}$; $df = 8$; $p = 0.35$), suggesting that changes in observed redd distributions occurred at rates similar to those expected in a random distribution.

The repeated-measures ANOVA suggested that a significant interaction occurred between year and stream segment ($F = 2.17$, $p < 0.001$, $df = 176$). Not unexpectedly, given the spatial and temporal variation in our data, sample year ($F = 95.8$, $p < 0.001$, $df = 8$) and stream segment ($F = 11.5$, $p < 0.001$, $df = 22$) also had significant effects on redd abundance. We repeated this analysis after excluding the 1995 data, reasoning that the low abundance and strongly clustered distribution observed that year may have unduly influenced our results, but all effects remained significant after this omission ($p < 0.001$).

Variance partitioning suggested that inference from fewer than 3–5 years of data would have resulted in a biased view regarding the relative importance of variance components. This pattern was similar in both the observed and permuted data sequences (Fig. 7). With 1 year of data, it was impossible to estimate a year effect ($df = 0$), so all variance was attributed to segment and residual error, which inflated the apparent importance of stream segments (65%–80% of total variation). Once multiple years of data were available, the strength of the segment effect decreased and stabilized at approximately 35% of total variation between years 3 and 5. Remaining variance components also stabilized by this time, with year, segment \times year, and residual error accounting for 40%, 13%, and 12% of total variation, respectively.

Discussion

Spatial and temporal heterogeneity

Our data set linked a spatially continuous population census with almost a decade of observation. During this time, redd densities changed by two orders of magnitude, which provided a range of variability over which population performance could be examined. Similar to previous studies for a variety of salmonids, our results confirm that Chinook salmon spawning is a spatially and temporally heterogeneous process (Walters and Cahoon 1985; Magee et al. 1996; Pess et al. 2002). Preferred areas typically consisted of low-gradient, pool–riffle channels that flowed through wide, alluviated valleys, a finding which others have documented for this species (Vronskiy 1972; Montgomery et al. 1999; Burnett 2001). Specific mechanisms accounting for this linkage are poorly understood, but a suite of interacting factors probably plays a role. The simplest explanation is that pool–riffle channels have the greatest availability of microhabitats (substrate, flow, and depth combinations) that are suitable for spawning. However, these channels also occur in association with extensive alluvial deposits, which may act as aquifers to moderate temperature and flow regimes (Brunke and Gonser 1997), and their undulating bedforms may increase hyporheic exchange, thereby facilitating oxygen and waste

Fig. 5. Occurrence of Chinook salmon (*Oncorhynchus tshawytscha*) redds within five subbasins in the Middle Fork Salmon River.

(a) Patterns in subbasins where population expansion was ongoing (\blacktriangle , Loon Creek; \times , Camas Creek; \circ , Big Creek); (b) patterns in subbasins where population expansion appears to have reached an upper limit (\blacklozenge , Bear Valley Creek; \blacksquare , Marsh Creek).

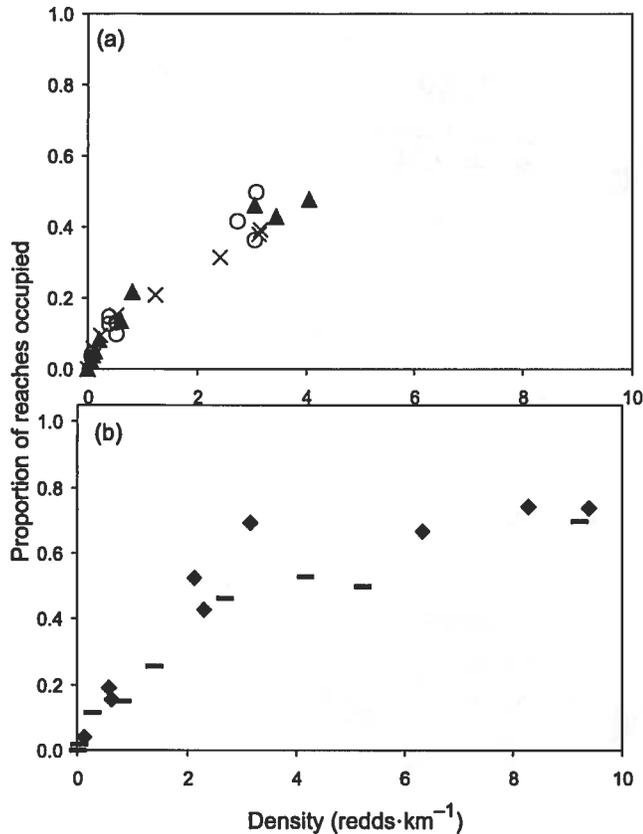


Table 1. Summary of recruits per spawner in an expanding population of Chinook salmon (*Oncorhynchus tshawytscha*) in the Middle Fork Salmon River.

Spawner year	<i>R</i>
1995	9.1
1996	5.9
1997	6.6
1998	3.9
1999	2.7 ^a
Average ^b	5.3

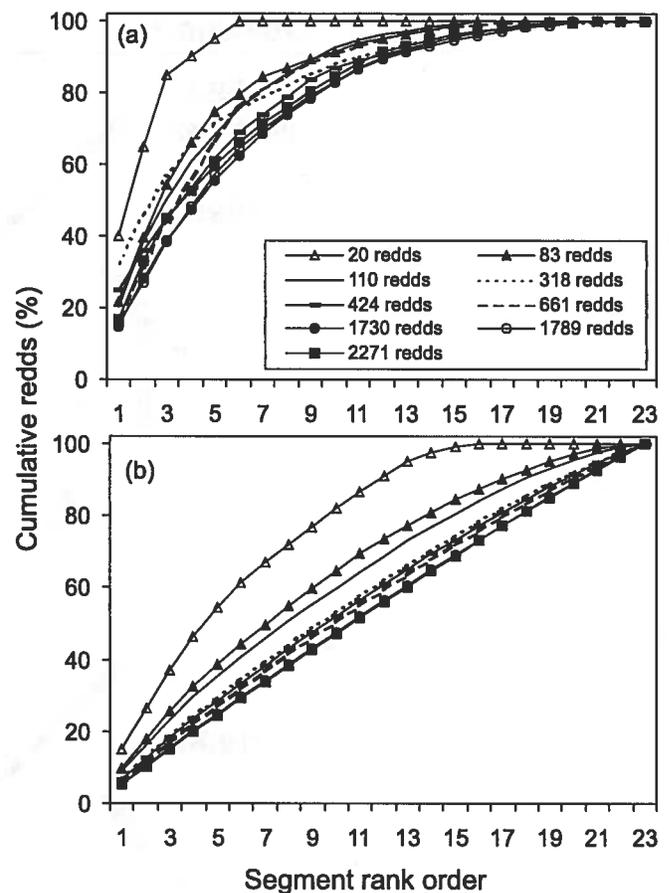
Note: Values were calculated using female age structures in return years and basin-wide redd count totals.

^aEstimate is biased low by lack of data on age-6 fish that returned in 2005.

^bAverage is weighted by relative population sizes determined by summing spawners and recruits.

exist, with populations in low density areas growing more rapidly than high density areas. That dispersal would play a role seems likely, given our observations of unoccupied stream segments that were later used by progeny from the earliest year classes, but determining the relative effects of both mechanisms will be challenging.

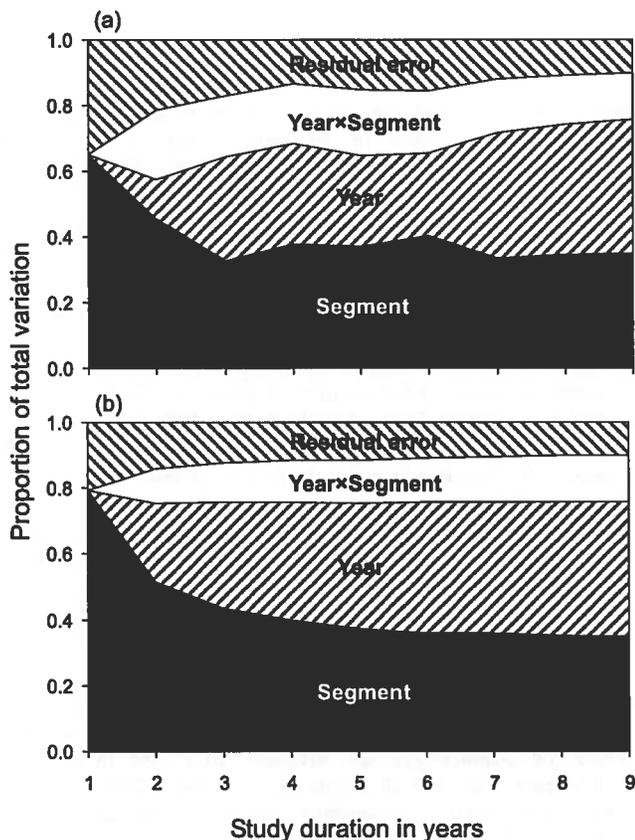
Fig. 6. Rank-ordered cumulative distributions for (a) observed redd distributions and (b) random redd distributions.



Chinook salmon populations grew rapidly during the course of this study, and the rate of this growth was higher than other values published for this species (McClure et al. 2003). Because the stream habitats in the MFSR have been protected by wilderness and primitive area designations for many decades, it is unlikely that this increase was caused by changes in spawning and rearing conditions. Instead, improved marine productivities and favorable juvenile migration conditions must have increased out-of-basin survival rates (Fish Passage Center 2003; Beamish et al. 2004). Although this population rebound probably occurred in response to the alignment of important environmental factors that were largely beyond management control, it was remarkable to note the resilience displayed by these populations. Such resilience suggests that attainment of robust population sizes may be achievable over several generations under the right conditions.

Variance partitioning provided several insights regarding the relative importance of factors that affected MFSR Chinook salmon. Compared with similar analyses performed with coho salmon (*Oncorhynchus kisutch*; Larsen et al. 2001), our data had a stronger temporal component and little residual variation. This suggested that variation from the combination of subsegments and measurement errors was low compared with the strength of signal from spatial and temporal factors. The strong year effect was due to large

Fig. 7. Relative importance of variance components as a function of study duration. (a) The pattern derived from the observed data sequence; (b) the average pattern derived from different yearly combinations of data.



interannual changes in redd numbers and the population growth that occurred during our study. The strength of this effect, combined with a relatively weak segment \times year interaction, also suggested concordant changes in redd numbers across sites, which corroborated earlier findings for these populations (Isaak et al. 2003). Increased synchrony is a recent phenomenon, the cause of which is unclear, but it may be related to loss of life history diversity or decreased importance of density-dependent factors at reduced population sizes (Isaak et al. 2003).

Variance partitioning results also suggested that inferences drawn from fewer than 3–5 years of study would have led to biased views regarding the relative importance of spatial and temporal components. Conversely, surveys conducted in excess of this temporal expanse were unnecessary — assuming, of course, that the only objective had been to accurately characterize these variance components. Because system behavior during the period of observation dictates when variance components stabilize — with some systems requiring decades and others a few years (Kratz 1995; Wiley et al. 1997) — generalizable recommendations regarding study duration are not possible. It is safe to conclude, however, that more than 1 year of data are desirable so that variance components inclusive of temporal factors can be estimated and that studies relying on space-for-time substitution may tend

to overestimate the importance of spatial attributes (Clinchy et al. 2002).

Conservation implications

Our results have several implications for population monitoring and prioritization of conservation efforts. Many early monitoring protocols were initiated using a series of index sites, which were often selected from accessible, high-density spawning areas (Larsen et al. 2001). Lack of randomization in site selection and shifts in fish distributions may bias inference from index samples and help mask population trends — a topic that we explore more fully with our data in a subsequent paper (J. Courbois, Northwest Fisheries Science Center, National Marine Fisheries Service, 2725 Montlake Boulevard East, Seattle, WA 98112, USA, unpublished data). Given the magnitude of declines that have occurred in many salmon stocks, however, optimal sampling strategies were not necessary for trend detection until recently. The new challenge will be to discern relatively small population changes that will allow for accurate assessments of expensive conservation and restoration efforts (Paulsen and Fisher 2005). Failure to do so may have negative consequences for depressed populations; therefore it is important that contemporary monitoring protocols be designed with appropriate statistical rigor (*sensu* Larsen et al. 2001).

With regard to habitat conservation, one of the commonalities emerging from many prioritization strategies is that the best remaining areas within a species' range should be protected (Epifanio et al. 2003; Groves 2003). In this context, "best" often connotes high density, and part of the rationale is that once limiting factors have been alleviated, protected areas can act as sources of colonists to fuel expansion into unoccupied habitats (Schlosser and Angermeier 1995). Our work supports this idea, in that the contribution of high-density areas appeared to be larger at low escapements, which suggests these areas may be particularly resistant to declines.

A strategy focused on protection of core populations may be useful in the short term, but longer perspectives will also be needed to accommodate the dynamics of natural systems (Hilborn et al. 2003). Even over the relatively short period encompassed by this study, we observed a segment \times year interaction, and population growth rapidly expanded spawning into areas where it had recently been absent. Over longer periods, we have documented dramatic changes in inter-population synchronies (Isaak et al. 2003), and anecdotal information suggests that spawning in mainstem areas may have once been much more prevalent (Hauck 1953; Meyer and Leidecker 1999). These factors highlight temporal variation in spatial distributions, the importance of suitable but unoccupied habitats, and the fact that populations will need room to expand during recovery (Cooper and Mangel 1998; Rieman and Dunham 2000). Conservation efforts that fail to accommodate future growth, and which seek to protect species only in high density or currently occupied areas, may artificially constrain populations and actually curtail future recovery possibilities.

Future applications

The challenges of conserving stream ecosystems extend beyond the knowledge that can be gained from traditional,

small-scale, site-specific studies and must be addressed in innovative ways. Fausch et al. (2002) provide a powerful argument for the necessity of studies conducted at landscape scales using continuous sampling techniques. Not only does the georeferencing that accompanies these surveys provide tremendous analytical flexibility, but a broader spatial extent facilitates a system view that is more commensurate with the scales at which important biophysical processes related to population persistence operate (Rieman and Dunham 2000). Although measurement errors will always remain a concern, researchers are less constrained by limitations associated with traditional sampling designs and instead may be limited chiefly by the array of interesting ideas that can be generated and tested.

By censusing the distribution of a commonly measured demographic parameter through time, we have generated a data set that has tremendous potential for revealing much about the dynamic nature of Chinook salmon in the MFSR. Currently, these data are being used in a host of studies to address key conservation issues for Chinook salmon, including examination of linkages between fine-scale genetic structure, demographic parameters, and environmental characteristics (H. Neville, University of Nevada-Reno, Department of Biology, Reno, NV 89577, USA, unpublished data), determination of dispersal ranges and environmental constraints using spatial autocorrelation analysis (D. Isaak, unpublished data), validation of hydrologic models for predicting basin-wide distributions of spawning substrates (Buffington et al. 2004), assessment of environmental covariates that affect habitat occupancy (D. Isaak, unpublished data), and validation of redd count methodologies (R. Thurow, unpublished data). We welcome opportunities for additional collaborations that would further explore the utility of these data.

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Re-colonization of Atlantic and Pacific rivers by anadromous fishes: linkages between life history and the benefits of barrier removal

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Abstract The last two decades have seen a rapid increase in barrier removals on rivers of the Northern Hemisphere, often for the explicit purpose of expanding the abundance, spatial distribution, and life history diversity of migratory fishes. However, differences in life history such as seasonal timing of migration and reproduction, iteroparity versus semelparity, and the extent of natal homing are likely to affect the capacity for expansion and re-colonization by taxa such as alosines, lamprey, and salmonids. We first review some basic life history traits that may affect re-colonization

by migratory fishes, and then present selected examples from Atlantic and Pacific basins to illustrate these patterns and their implications for the success of barrier removal as a measure to advance the goal of fish conservation. We conclude that diadromous fishes have the capacity to rapidly re-colonize newly available habitats, though the life history patterns of each species, the proximity to source populations in the same or nearby river systems, and the diversity of habitats available may control the patterns and rates of re-colonization.

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Introduction

Re-colonization of freshwater systems by migratory fishes has been an important process in the post-glacial ecology of the Northern Hemisphere, and the distributions of species reflect their pathways and capacities for taking advantage of vacant, suitable habitat (e.g., Lindsey and McPhail 1986; McPhail and Lindsey 1986). Euryhaline and diadromous fishes can move between watersheds via marine routes, facilitating colonization of previously glaciated habitat (though colonization via inland routes also took place). The processes of glacial retreat and colonization are generally viewed as having taken place in past millennia but in parts of Alaska they are contemporary processes (e.g.,

Milner and York 2001; Milner et al. 2000, 2008). In addition, natural and assisted re-colonization efforts have been important components of aquatic ecosystem restoration recently (Duda et al. 2008; Kesler et al. 2011) and in previous decades (Havey 1961; Roos 1991; Pess et al. 2012). Where fish ladders have been installed or culverts removed, streams have experienced natural colonization of upstream habitats, and self-sustaining populations were established within a decade (Bryant et al. 1999; Glen 2002; Anderson and Quinn 2007; Burdick and Hightower 2006; Pess et al. 2012; Anderson et al. 2013).

The rivers draining into the North Atlantic and Pacific oceans include many anadromous species (e.g., alosines, salmonids, lamprey, sturgeons, striped bass, sticklebacks) and a few catadromous species (notably eels but flounder in some cases). In addition, there are many fluvial migrants (Lucas and Baras 2001), including non-anadromous populations of facultatively anadromous species and entirely non-anadromous but migratory fishes such as catfish, cyprinids, and others. The patterns of life history (degree of iteroparity, parental care, size at maturity, seasonal timing of migration and breeding) also vary widely in these species and can influence the capacity for colonization. In addition, the mechanisms of migratory orientation, homing, and population structure vary greatly and likely affect colonization.

Colonization is hypothesized to depend on three factors: (1) Is the habitat accessible? (2) Does the species have the capacity to reach and use the habitat in the context of its life history? (3) Do the species' patterns of juvenile learning (e.g., olfactory imprinting), attraction to odors of conspecifics, or other mechanistic aspects of migration inhibit or encourage colonization of new habitat? Several large-scale restoration actions in river systems draining into the Atlantic and Pacific have occurred over the last several years, allowing scientists and managers to observe how re-colonization by different migratory fishes occurs and apply the lessons to future fish conservation efforts. In this paper we briefly review aspects of the life history of selected anadromous North American fishes, with a focus on species that are most often targeted for restoration. We then examine several case studies of re-colonization, considering the similarities and differences among rivers, species, and life histories. Lastly, we discuss the consequences of factors and how they affect fish conservation and restoration.

Life history of diadromous fishes: implications for colonization

Anadromous fishes are spawned in freshwater, rear as juveniles in freshwater for variable time periods, migrate to sea to grow to their adult size, and return to freshwater to spawn. Conversely, catadromous species are spawned at sea, enter freshwater to feed and grow, and migrate back to sea for reproduction. Fewer than 1 % of all fish species (~320 out of ~32,000) are diadromous, with over half of those being anadromous and approximately 25 % being catadromous; the others are amphidromous, spawned in freshwater, rearing for a period at sea and then returning to freshwater for further growth prior to maturation (McDowall 1988). While these migratory patterns between freshwater and the sea are uncommon among fishes, they are critical in understanding how reconnection of freshwater and marine environments through the removal of blockages to migration such as dams can lead to re-colonization of fish populations. Many of the anadromous fishes are very important in commercial, recreational, ceremonial or subsistence fisheries, yet some populations have been depleted to critical levels, and are protected under the U.S. Endangered Species Act (ESA) or comparable laws in other countries. Many factors caused these declines but habitat loss from impassable barriers was often a contributing factor (e.g., NRC 1996, 2004; McPhee 2002).

Among the diadromous fishes, anadromous species are much more common at higher latitudes than are catadromous species (McDowall 1988; Gross et al. 1988) and our review emphasizes the anadromous species. However, the catadromous eels (*Anguilla rostrata* in North America and *A. anguilla* in Europe; Tesch 2003) show fascinating patterns of migration and ecology (e.g., Helfman et al. 1987) and are of considerable conservation concern (Jonsson et al. 1999). The processes of colonization are likely very different between anadromous and catadromous fishes, as homing to the natal freshwater site for breeding is typical in anadromous fishes (but not universal, e.g., lamprey), whereas catadromous fishes breed at sea, and so their entry into freshwater is directed by other cues rather than detection of imprinted odors. The juvenile glass eels migrating upriver are not homing because they have never been to the river before, nor had their parents (in all

likelihood) been there either. Their migration may be stimulated by the presence of conspecifics (Briand et al. 2002) but flow and other environmental conditions also play a role (Sorensen and Bianchini 1986; Schmidt et al. 2009). Regardless of the mechanism, eels can colonize hundreds of kilometers upstream of former passage barriers and increase population abundance after dam removal (Hitt et al. 2012).

Anadromous mechanisms

The primary mechanism that allows for diadromy is the ability of fish to tolerate the osmotic differences between freshwater to the marine environments, and this is crucial for colonization from one basin to another via marine routes. These processes are best known in salmonids (Clarke and Hirano 1995), particularly the transition of smolts to sea (e.g., Hoar 1976; McCormick et al. 1998) that characterizes the semelparous species and steelhead trout, *O. mykiss*. Among salmonids, the facultatively anadromous, iteroparous species such as char (*genus Salvelinus*), and cutthroat trout (*O. clarki*) are seldom studied. Movements between basins during the spawning season are known in anadromous Dolly Varden, *S. malma* (Armstrong 1984; Bernard et al. 1995), and bull trout, *S. confluentus*; adults may breed in one river but enter other nearby rivers to feed or over-winter (Brenkman and Corbett 2005). The relatively large size of these fish (more tolerant of varying salinities than smaller fish) may contribute to their capacity to explore, and we expect that similar patterns may be revealed in cutthroat trout as well. This is consistent with the observation that Dolly Varden were the first salmonid in the newly de-glaciated Wolf Point Creek in Glacier Bay, Alaska (Milner et al. 2008). Osmoregulation studies in non-salmonids such as sturgeon indicate considerable variation from salmonid patterns, and also variation among species (e.g., McEnroe and Cech 1987; Krayushkina 1998; Kuz'michev et al. 2005). It is important to bear in mind these physiological aspects of each species' biology, as they may influence the capacity to colonize basins across a salinity gradient.

The population structure of migratory fishes, notably the anadromous ones, is largely controlled by their strong tendency to home to the natal site or site of first reproduction when mature and ready to breed. As McCleave (1967) pointed out, homing to the natal site

is a subset of the more general phenomenon of homing, including return to the site of previous reproduction (relevant to iteroparous species), and homing after natural or experimental displacement. Homing can be demonstrated directly, by the recovery of fish marked as juveniles in freshwater at the same site when they mature (Quinn 1993). However, persistent phenotypic differences in fish from different rivers convinced early researchers that fish homed (e.g., shad: Milner 1876), and differences in genetic markers provide additional evidence of homing (e.g., Atlantic salmon, *Salmo salar*: Primmer et al. 2006; Dionne et al. 2008; American shad, *Alosa sapidissima*: Hasselman et al. 2013).

Despite the strong homing impulse, dispersal from the natal site, or "straying," is necessary for post-glacial establishment and modern recovery of the species' range (Westley et al. 2013). Straying is typically defined as returning to spawn outside the river of origin (Westley et al. 2013), though the network structure of river systems can make it difficult to distinguish between straying and movement within rivers. Straying within watersheds and especially the tendency to migrate farther upriver, past the natal site (Keefer et al. 2008a) is especially important to re-colonization after dam removal, though straying from adjacent watersheds (i.e., via marine routes) also occurs. The phenomenon of straying has not been adequately explained on mechanistic or evolutionary grounds (Hendry et al. 2004), so it is difficult to determine how different factors will affect it. Is straying a failure to home, through inadequate learning, retention, or detection of imprinted odors, an alternative life history pattern, or a habitat choice (Quinn 1984)? In any case, straying can be viewed as an "exploratory behavior," that can contribute to population persistence, colonization, and range expansion (Secor 1999).

Olfactory imprinting for homing is particularly well studied in salmon and trout, and the imprinting has been hypothesized to be sequential, related to a combination of environmental stimuli, developmental and seasonal cues associated with smolt transformation and downstream migration (Hasler and Scholz 1983; Dittman and Quinn 1996). The involvement of imprinted odor memories to which fish return as adults is less often studied in other fishes than salmon but it has been reported in white suckers, *Catstomus commersonii*, (Werner and Lannoo 1994) and is likely a very

general phenomenon. However, the abilities of larval fishes to learn odors may depend on features of the structure and function of the olfactory organs, and the capacity of drifting pre-hatch embryos in the water column or larval fishes to detect and learn odors may not be as great as that of the larger salmon alevins and fry. To the extent that this is the case, homing to the natal stream may be less precise in non-salmonids unless the fish remain in the natal waters long enough to develop sufficient sensory capacity (see Horrall 1981 for a further discussion of this issue, with special reference to homing in salmonids compared to walleye, *Sander vitreus*, and white perch, *Morone americana*).

In addition to the learned odors from the stream's rocks, soil, plants and other chemical constituents, the odors of conspecifics can also play a role in guiding upstream migrants. Attraction to pheromones was hypothesized to influence salmon migrations (Nordeng 1971), and adult salmon are indeed attracted to the odors of juvenile conspecifics (Solomon 1973; Quinn et al. 1983; Groot et al. 1986), though this does not seem to be the primary source of odors leading salmon home (Brannon and Quinn 1990). Upstream-migrating adult sea lamprey, *Petromyzon marinus*, orient to pheromones from juveniles residing in streams rather than odors that they learned themselves earlier (Bjerselius et al. 2000; Vrieze et al. 2010, 2011; Johnson et al. 2012). However, sea lamprey quickly colonized the Great Lakes after they circumvented the Welland Canal (Bryan et al. 2005), and Pacific lamprey colonized the Babine Lake system in British Columbia (Farlinger and Beamish 1984), so pheromones may not be necessary for upstream migration and colonization. Attraction to species-specific odors has been documented in other diadromous species (e.g., the banded kokopu, *Galaxias fasciatus*: Baker and Montgomery 2001, and Atlantic eels: Briand et al. 2002, and references therein), and this is a fruitful area of further research with respect to colonization and migration patterns.

East versus West comparisons

The east and west coasts of North America share two genera of native diadromous fish: *Acipenser*, the sturgeons, and *Salvelinus*, the char. The west coast has four native genera of anadromous fish: *Oncorhynchus*, the Pacific salmon and trout, *Thaleichthys*, smelt,

and *Lampetra* and *Entosphenus*, lamprey. The east coast has six native genera of anadromous fish (*Salmo*, the Atlantic salmon; *Alosa*, the American shad; *Osmerus*, the smelt; *Microgadus*, the tomcod; *Morone*, the striped bass; and *Petromyzon*, the sea lamprey) and the typically catadromous genus of eels (*Anguilla*). Thus, there are some broad similarities (i.e., lamprey and sturgeon are common to both Pacific and Atlantic basins) and some important distinctions (i.e., the prevalence of *Oncorhynchus* spp. compared to prevalence of *Alosa* spp.). We now briefly consider several ecological mechanisms of importance to restoration and re-colonization efforts. Our taxonomic focus is limited to several major genera (*Oncorhynchus*, *Alosa*, and *Salmo*) and our geographic focus is limited to "the salmon-bearing" portions of the Atlantic and Pacific basins but we include some information on other taxa.

West coast: *Oncorhynchus* anadromy; the importance of straying, and colonization

Straying

Straying is a natural biological process that results in the establishment or re-establishment of populations (Pess 2009). Three generalizations have emerged from homing and straying studies that advance our understanding of how salmonids establish self-sustaining populations with respect to barrier removal. First, regardless of species or origin (wild vs. hatchery), most salmon home but some straying is always detected (Hendry et al. 2004; Quinn 2005). Salmon homing rates average 92 % (SD \pm 9.4 %) and the remaining 8 % stray (Hendry et al. 2004; Keefer et al. 2005; Keefer et al. 2008b). Thus a proportion of any salmon population will likely stray into newly created or accessible habitats once connectivity is restored, though the fraction can vary greatly.

A second generalization is that the amount of straying into a recipient stream is inversely correlated with geographical distance from the source, though other factors also influence the distribution of strays (Quinn 1993). Quinn and Fresh (1984) and Quinn et al. (1991) found that greater than 95 % of all fish that strayed were within 30 km of their home river system or hatchery release site, and other studies also found that most straying occurred to nearby sites (Labelle 1992; Unwin and Quinn 1993; Hard and Heard 1999; Candy and Beacham 2000; Keefer et al. 2008a).

Keefer et al. (2008a) found that two types of straying behavior, overshooting a natal stream and the temporary use of another tributary, declined exponentially with increasing distance from the natal tributary. Because nearby populations are most likely to seed newly available habitats, metapopulation concepts aid our understanding of salmon population dynamics (Cooper and Mangel 1999; Schtickzelle and Quinn 2007).

A third generalization that emerges is that straying rates differ among salmon species (Quinn 1984; Hendry et al. 2004; Quinn 2005). Hard evidence to support this generalization is scarce because there have not been controlled experiments on all species in the same river, and data on wild populations are very limited. Nevertheless, sockeye salmon (*O. nerka*) tend to have very low straying rates (<0.8 %), whereas coho (*O. kisutch*), Chinook (*O. tshawytscha*), steelhead (*O. mykiss*), and Atlantic salmon were reported to have similar and somewhat higher rates (7.8, 6.2, 7.7, and 7.7 %), and chum (*O. keta*) and pink salmon (*O. gorbuscha*) had the highest rates (19.1 and 15.4 %: Hendry et al. 2004). Recent examination of straying rates from the same hatcheries revealed marked differences between species: coho salmon (0.52 %), Chinook salmon (15.3 %), and steelhead (1.2 %: Westley et al. 2013), and also differences among life history types of Chinook salmon. Notwithstanding the difficulties in determining empirical rates of straying among species, why might one expect them to vary? Quinn (1984) hypothesized that there is a dynamic equilibrium between homing and straying in all populations, and that three main factors influence the relative frequency of homing and straying among species: (1) variation in the stability of the habitat, as it affects the certainty of reproductive success (e.g., variation in number of recruits per spawner), (2) the extent of specialization for freshwater habitats, (3) variation in age of maturity, and the extent of iteroparity. Thus if a stream is stable in the recruitment of salmon due to attenuated flow conditions during spawning and incubation, such as a river flowing from a lake, then variation in recruitment would be less and consequently homing would be favored over straying. Conversely, in spawning areas prone to dynamic changes that produce great variation in egg-fry survival (e.g., systems with large variation in flow conditions such as coastal, rain-dominated watersheds), straying might be more prevalent.

An illustration of the role of straying in species' persistence in the face of environmental disruption is provided by the eruption of Mt. St. Helens, Washington on 18 May 1980. When Toutle River origin fish returned (e.g., fall 1980, 1981) they encountered drastically degraded habitat and elevated turbidity from volcanic ash and silt (Leider 1989). Faced with these conditions, Toutle River steelhead straying rates increased from 16 to 45 % after the eruption, and most strays entered watersheds with lower turbidity (Leider 1989). However, within 4 years, or one life cycle of steelhead, straying into nearby rivers decreased to pre-eruption levels and densities of spawning steelhead in two of the major tributaries that returned to pre-eruption streambed elevation had steelhead redd densities that went from 0 to 5.7–21.5 redds km⁻¹ within 7 years of the eruption (Lucas and Pointer 1987; Leider 1989; Bisson et al. 2005). It cannot be determined if the steelhead strayed because they could not identify their natal river because of the ash or because they sensed that the stream was no longer suitable for reproduction. However, experiments indicated that the presence of suspended volcanic ash did not prevent home-stream recognition by Chinook salmon but that they tended to avoid ash-laden water (Whitman et al. 1982). Conversely, as stream conditions changed and sediment concentrations decreased, salmon apparently recognized the change and returned to their natal systems (Bisson et al. 2005).

The second element of Quinn's (1984) hypothesis was that species with less extensive use of freshwater habitats might stray at higher levels than species with extensive specialization for freshwater. For example, the population-level patterns of disease resistance (Buchanan et al. 1983; Bower et al. 1995), migratory orientation (Raleigh 1971; Brannon 1972) and other forms of behavior and morphology (Rosenau and McPhail 1987; Swain and Holtby 1989) that characterize species such as steelhead, Chinook, coho and sockeye salmon may reflect the longer periods of freshwater residence compared to chum and pink salmon. For pink and chum salmon that spawn in the lower portions of coastal streams, conditions are very similar among the streams available to them, and straying to a nearby non-natal stream may not have a large effect on fitness (Quinn 2005). Lower levels of genetic difference between populations as a function of spatial separation in pink and chum salmon compared

to the other species (Hendry et al. 2004) is consistent with this hypothesis but not direct proof of it.

Quinn (1984) also hypothesized that straying is inversely related to variation in age of maturity because parents whose offspring will all spawn in a single year are more at risk of having no grandchildren (owing to some future one-time disaster) than those with offspring spawning in different calendar years. At one end of the spectrum are pink salmon with a fixed 2-year cycle. As Bakshantansky (1980) pointed out, an event occurring in a stream can extirpate an entire year class of this species. It may thus optimize the parents' fitness to have some offspring home and have others stray, to reduce the probability that the entire line will be lost. Chinook salmon are at the other end of the spectrum, varying more in total age than the other Pacific salmon species. Thus, even with the complete loss of one or more year classes and no straying, the parents might still have some surviving grandchildren. Variation in age at maturity is thus a form of straying in time to balance the straying in space. However, recent data challenge the hypothesis that straying is inversely related to variation in age; coho salmon had a lower average straying rate than Chinook salmon in the same river, even though they have less variation in age at spawning (Westley et al. 2013).

Colonization

We hypothesize that the rate of re-colonization is most likely affected by four key factors: the species' presence in the same or nearby watershed(s); productivity of the nearby (donor) population; suitability of newly available habitat for the species; and the presence of life history variants in the donor population to take advantage of the newly opened habitat.

In addition to the studies specifically focused on homing and straying, there have been studies of colonization by salmon to new, naturally created habitats (Leider 1989; Milner and Bailey 1989; Milner and York 2001; Milner et al. 2008) or recently opened/re-opened habitats (Bryant et al. 1999; Young 1999; Burger et al. 2000; Glen 2002; Pess et al. 2003, 2012; Milner et al. 2007; Anderson et al. 2008; Kiffney et al. 2009; Anderson et al. 2013). The time general period for colonization and establishment of self-replacing populations, regardless of whether the new habitats were newly opened or re-opened, was ~5–30 years, and mostly ~10–20 years (Withler 1982; Bryant et al.

1999; Young 1999; Burger et al. 2000; Glen 2002; Pess et al. 2003, 2012; Milner et al. 2008; Kiffney et al. 2009; Anderson 2011) (Fig. 1). Colonizing salmon populations often showed an exponential growth phase ~18–108 % per generation (Table 1).

Pink salmon, coho salmon, sockeye salmon, and Dolly Varden (*Salvelinus malma*) colonized new streams that had recently formed due to de-glaciation in Glacier Bay and established self-sustaining populations within 20 years (Milner et al. 2008). Where fish ladders were installed or culverts removed, natural colonization led to self-sustaining populations in 1–5 years (Bryant et al. 1999; Glen 2002; Pess et al. 2003). Recolonization and establishment of pink salmon in the Fraser River above Hell's Gate landslide required approximately 20 years to establish large spawning populations (Pess et al. 2012).

One of the most important attributes associated with successful salmon colonization in newly opened habitats is the link between compatible life history adaptations and geographic, hydrologic, and ecological characteristics (Quinn 1984; Allendorf and Waples 1996; Burger et al. 2000). For example, as the Glacier Bay landscape evolved over time, certain habitat features such as lakes became separated from the stream network, resulting in a loss of sockeye salmon populations (Milner et al. 2007). Burger et al. (2000) also found that life history adaptation needed to be compatible with local habitat conditions for sockeye salmon donor populations to successfully colonize a lake system in Alaska after passage facilities allowed them to circumvent a waterfall, underscoring the need to consider life history traits and genetic adaptations in other introduction programs. Further evidence for the link between life history adaptation and environmental and ecological condition again comes from Glacier Bay, Alaska. Milner and Bailey (1989) compared the salmonid spawning density in two recently de-glaciated, geomorphically similar, and adjacent streams. They found that low turbidity, a higher proportion of preferred spawning temperature range (12–15° C), and a more attenuated hydrology were dominant factors associated with higher spawning density. Colonization of these streams over time varied for each species and resulted in more cold water oriented species colonizing first (i.e., Dolly Varden), while pink, coho, and chum salmon appeared 2–10 years later as temperatures warmed (Milner et al. 2008). The sequential

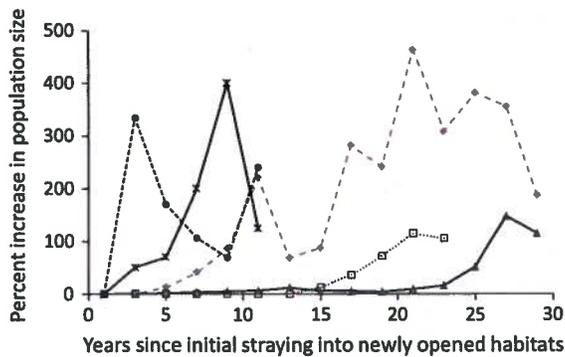


Fig. 1 Percent increase in population size of several salmon populations over time along the Eastern Pacific Rim. *Solid black dots with hashed black line* represent Cedar River, Washington State coho salmon (Kiffney et al. 2009). *Solid black line with stars* represent Cedar River, Washington State Chinook salmon (Kiffney et al. 2009). *Solid grey diamonds with grey hashed line* represent Fraser River, British Columbia pink salmon (Pess et al. 2012). *Open dark squares dark hashed line* represent Glacier Bay, AK pink salmon (Milner et al. 2007). *Solid grey triangles with solid black line* represent percent increase in South Fork Skykomish pink salmon above Sunset falls, Washington State. Population size of the Cedar coho and Chinook salmon is 100 s; 100,000 s for Fraser River pink salmon; 10,000 s for South Fork Skykomish pink salmon, and 1,000 s for Glacier Bay, AK pink salmon

colonization by species over a changing temperature regime also suggests ongoing exploratory behavior by all of these species and a non-random pattern to the colonization.

Another excellent example of the link between life history adaptation and environmental and ecological condition with respect to recolonization is the juvenile coho salmon in the Cedar River watershed of Washington, USA. Juvenile coho salmon typically rear in freshwater habitats for a year prior to seaward migration. Anderson et al. (2013) used a combination of DNA-based parentage analysis and mark–recapture

techniques to document dispersal by juvenile coho salmon in the initial stages of re-colonization following installation of fish passage structures at a dam. Over 25 % of the offspring were outside the area where their parents had spawned, and moved as much as 6.3 km (median = 1.5 km) upstream from the redd locations. Juvenile coho salmon also colonized tributaries where spawning had not taken place, providing a secondary process of spatial expansion following initial colonization by adults (Anderson et al. 2008; Pess et al. 2011; Anderson et al. 2013).

As previously mentioned, most salmonids home to their natal streams to spawn but some (usually <10 %) stray. This entry into recipient streams is inversely correlated to geographic distance from the natal site, and can lead to the establishment of new populations in ~5–30 years, with population growth rates during the initial phase of ~20–100 % per generation. In contrast to the rich literature on salmonids on the west coast, the information on straying and colonization by other anadromous fishes is more limited. There are two sturgeon species on the west coast, the white sturgeon, *Acipenser transmontanus* and the green sturgeon, *A. medirostris*, and the latter is more strongly anadromous in behavior and ecology (Moyle 2002; Wydoski and Whitney 2003). Fish ladders and other passage structures at dams designed for salmonids do not function well for these large-bodied fish, resulting in largely isolated populations (Parsley et al. 2007; Cocherell et al. 2011). Pacific lamprey, *Lampetra tridentata*, also do not use salmon ladders well, though for other reasons, and there is considerable work on the need to modify dams to facilitate their passage (Jackson and Moser 2012; Moser et al. 2002a, b, 2011). Indeed, a recent review indicated that in general salmonids are more successful at using passage facilities than non-salmonids (Noonan et al. 2012).

Table 1 Estimated annual rates of increase based on the exponential growth phase of six colonizing populations (Pess et al. 2012; Milner et al. 2007; Kiffney et al. 2009; Anderson 2011)

Species	Location	Population growth rate (r)
Pink salmon	Fraser River (Above Hell's Gate), British Columbia, Canada	1.18
Pink salmon	Glacier Bay, Southeast Alaska	2.01
Pink salmon	South Fork Skykomish, Puget Sound, Washington State	1.18
Coho salmon	Cedar River, Puget Sound, Washington State	2.08
Chinook salmon	Cedar River, Puget Sound, Washington State	1.95
Chinook salmon	South Fork Skykomish, Puget Sound, Washington State	1.28

Colonization opportunities, particularly for salmonids, have been or are being created throughout the Western United States with the removal of both small and large dams. Notable dam removals that have occurred or are occurring in the Western US include Marmot Dam on the Sandy River, Oregon, Condit Dam on the Little White Salmon River, Washington, Savage Rapids Dam on the Rogue River, Oregon, and the Elwha and Glines Canyon dams on the Elwha River in Washington state (http://en.wikipedia.org/wiki/Dam_removal). Passage facilities have recently been implemented in other locations such as the Cedar River in Washington State (Anderson and Quinn 2007), and there are recent on-going efforts to move salmonids above large dams with no passage facilities such as the Cowlitz River, Washington State (<http://cowlitzfish.net/>) and the Willamette River, Oregon (Keefer et al. 2013).

East Coast: Multispecies anadromy dominated by alosines

The life history patterns of the diverse, native anadromous species on the east coast of North America differ in many ways from those on the west coast. Unlike the west coast, the east coast was not dominated by salmonids. Atlantic salmon were never as abundant as the alosines that shared many of the same rivers, particularly in the southern portion of the Atlantic salmon's North American range. In addition, Atlantic salmon are a single species, with brook trout (*Salvelinus fontinalis*) as the other native salmonid other than Arctic char, whereas there are five species of Pacific salmon, plus two anadromous trout species, and three species of anadromous char. We thus focus our east coast review on community interactions, recolonization patterns, and restoration outcomes with a particular emphasis on the southern portion of the Atlantic salmon's North American range. These patterns and observations would likely shift substantially as the geographic focus moves north and Atlantic salmon become one of the very few diadromous species able to tolerate the challenging climate of northern Quebec and Labrador.

Community interactions

Historically, numerous east coast rivers had large runs of sturgeon (*Acipenseridae*), striped bass (*Moronidae*)

and alosines (*Clupeidae*), which dominated most systems from New England to northern Florida (Stevenson 1899; Limburg and Waldman 2009). Within New England, abundant runs of Atlantic salmon, rainbow smelt (*Osmerus mordax*), and sea lamprey (*Petromyzon marinus*) were ubiquitous as well (Moring 2005), although alosines were likely the most abundant species (Foster and Atkins 1869; Limburg and Waldman 2009).

A growing body of evidence suggests that the formerly abundant runs of other diadromous species, alosines, sea lamprey and rainbow smelt in particular, provided demographic security to Atlantic salmon and sustained ecological functions required by Atlantic salmon through a series of interspecific interactions. Saunders et al. (2006) hypothesized that these other species provided demographic benefits to Atlantic salmon through four specific mechanisms: nutrient cycling (i.e., marine-derived nutrient deposition), habitat conditioning, providing alternative prey for predators of salmon (i.e., prey buffer), and serving as prey for juvenile and adult salmon. These hypotheses are difficult to test, given the severely depressed abundance levels of many of the species, but there is evidence of their individual effects. The role of marine-derived nutrient deposition was recently evaluated by Guyette et al. (2013) using carcass analogs to simulate nutrient deposition by sea lamprey carcasses in headwater tributaries of the Penobscot River, Maine. Guyette et al. (2013) provided clear evidence of enhanced growth (e.g., 33–48 % greater mass) experienced by juvenile Atlantic salmon in treatment reaches. Further, evaluations of the potential for sea lamprey to “condition” the freshwater habitat of Atlantic salmon by Hogg (2012) showed that bioturbation was associated with sea lamprey nest construction in sympatric reaches of Atlantic salmon habitat. A suite of abiotic effects such as increased permeability and decreased embeddedness, and biotic effects (e.g., abundance of benthic organisms) were detectable immediately and for several months after lamprey spawning (Hogg 2012). Further research may elucidate the potential role of sea lampreys as ecosystem engineers (sensu Brown 1995) in freshwater habitats important to Atlantic salmon production in similar ways that bioturbation studies from the West Coast (e.g., Montgomery et al. 1996) have provided evidence of intraspecific interactions for Pacific salmon species. Some evaluations of the roles of river herring

as a prey buffer for emigrating Atlantic salmon smolts are currently underway (NMFS unpublished data), and the role of rainbow smelt as an important food source, particularly for re-conditioning kelts, is already well recognized (Saunders et al. 2006).

Although refinement and testing of these hypotheses remain a priority, recovery of the last remnant stocks of Atlantic salmon in the United States are moving forward on the basis of a multi-species approach to Atlantic salmon recovery. For example, the National Marine Fisheries Service specifically identified “freshwater and estuary migration sites with abundant, diverse native fish communities to serve as a protective buffer against predation” as a primary constituent element of Critical Habitat for the endangered Gulf of Maine Distinct Population Segment of Atlantic salmon (USOFR 2009a, b). Thus, understanding the factors limiting restoration of the suite of east coast diadromous fish is important in its own right, but also in the context of recovering Atlantic salmon in the US.

Re-colonization patterns and restoration outcomes

There is a wide range in our understanding of genetic structure, homing rates, and life history variation among native species on the east coast. For Atlantic salmon, the general pattern of philopatry coupled with distinct river-specific adaptation is well studied (Klemetsen et al. 2003; Garcia de Leaniz et al. 2007), as is the importance of life history variation (Saunders and Schom 1985; Vähä et al. 2008). Life-stage specific vital rates are also available for Atlantic salmon, permitting the development of very detailed life history models (e.g., Juanes et al. 2009). Atlantic salmon homing rates are quite high (roughly 98 % reported by Baum and Spencer 1990, in general accord with those reviewed by Stabell 1984). Studying homing rates in the southern portion of the North American portion of the range of Atlantic salmon is complicated by the presence of many dams with inefficient fishways, low post-spawning survival of kelts, and substantial hatchery influence in many cases. In contrast with Pacific salmon, Atlantic salmon are iteroparous and this appears to be an important component of the Atlantic salmon’s “bet hedging” strategy (see Klemetsen et al. 2003). McCleave (1967) stated that iteroparity may increase the rate of homing

due to previous experience, though empirical evidence remains sparse.

While the importance of homing, straying, and life history variation described above for west coast salmonids is likely as significant in non-salmonid anadromous fishes, substantially less information is available for the alosines, sea lamprey, and sturgeon. For example, Hasselman and Limburg (2012) searched Thomson Scientific’s Web of Science and found that the keywords “*Alosa* AND *genetic*” revealed 34 publications; “*Salmo* AND *genetic*” revealed 1,721 publications; “*Oncorhynchus* AND *genetic*” revealed 1,914 publications. This anecdote illustrates the comparative dearth of genetic information of alosines compared to Atlantic and Pacific salmon; this pattern generally holds true for other kinds of information (e.g., life history variation), and other kinds of fishes.

Like other clupeids, the alosines are schooling fish that tend to be broadcast spawners (e.g., Loesch and Lund 1977) with no parental care (Fay et al. 1983). These life history traits contrast sharply with salmonids, and the differences are largely consistent with their respective evolutionary lineages (see McDowall 1993, 1997; Dodson 1997; Dodson et al. 2009). These basic differences in life history are relevant to restoration and re-colonization in at least three major ways. First, schooling behavior (i.e., the desire to pass upstream together), coupled with relatively large body size of American shad creates great difficulty for upstream passage even in state-of-the-art fishways. American shad and other alosines tend not to leap (Larinier and Travade 2002), they avoid submerged orifices (Monk et al. 1989), and they tend to be very sensitive to turbulence and shadows (Haro and Castro-Santos 2012). Large fishways with lower slopes, little air entrainment, and fewer eddies are thought to be more effective for passing American shad (Larinier and Travade 2002), but the current lack of quantitative field evaluations and variation in passage efficiency when such studies are conducted have led to conclusions that high performance of upstream passage for American shad cannot be achieved (Haro and Castro-Santos 2012). Few large fishways that would accommodate the large body size and schooling behavior of American shad have been built on eastern rivers. Evaluations of scaled-down versions of traditional fishways, modeled after Columbia River-style fishways, produced disappointingly low efficiency

estimates (e.g., Rideout et al. 1985) and full size evaluations of these types of fishways have yet to be undertaken broadly (Haro and Castro-Santos 2012). In some instances, fish lifts have successfully passed American shad, but problems with siting, attraction, and peak-run capacity still need to be resolved (Haro and Castro-Santos 2012). Presumably, the presence of relatively large fishways that can accommodate large-bodied, schooling fish is at least partially responsible for the colonization of rivers along the west coast, especially their numerical and spatial expansion in the Columbia River following the construction of The Dalles Dam in 1957 (Quinn and Adams 1996; Hasselman et al. 2012; Hinrichsen et al. 2013). Conversely, the relative absence of such fishways on the east coast has likely inhibited the colonization by shad in rivers (Hinrichsen et al. 2013).

Second, stock-specific adaptations are not well documented in alosines and their importance to restoration and re-colonization is largely unknown. While there is evidence of philopatry among alosines (e.g., Carscadden and Leggett 1975; Hendricks et al. 2002), quantitative estimates of homing and straying are also largely unknown. Some inferences can be made from tagging studies (Jessop 1994), and genetic techniques offer hope of refining these estimates (Palkovacs et al. 2013). Although information is currently limited, there is substantial life history variation (e.g., Limburg 1998) including population-specific iteroparity rates and ages at maturation (Leggett and Carscadden 1978) in American shad. Leggett and Carscadden (1978) concluded that the higher rate of iteroparity in the northern portion of the American shad's range was a bet-hedging strategy because of the more unpredictable spring and early summer climatic conditions. For river herring, Gahagan et al. (2012) recently described high movement rates across salinity boundaries for age-0 alewives and blueback herring, particularly in systems where movement between riverine and estuarine habitats was unrestricted. Roughly 16 % of all fish examined moved between freshwater and marine habitats multiple times in their early life history (Gahagan et al. 2012). This finding contrasts sharply with the widely held view that juvenile river herring emigration is unidirectional and deterministic (i.e., always proceeds directly downstream). Limburg (1998) hypothesized that recurring migrations of juvenile alosines between lower river and near shore marine habitats were the

result of schooling, whereby juvenile alosines are entrained in schools of adult spawners. Limburg (1998) further hypothesized that this may be an important exploratory mechanism for potential colonizers. Unfortunately, there is great uncertainty regarding the heritability of these patterns of life history, habitat use, and migration timing. There is, however, more historic (Nolan et al. 1991) and recent work describing patterns of genetic structure in American shad (Hasselman et al. 2010, 2013) and river herring (Palkovacs et al. 2013).

Third, at high latitudes American shad may exhibit serial spawning and batch fecundity, whereby spawning events occur in several pulses and progress in a downstream direction as the season advances (Maltais et al. 2010). This has been observed in both semelparous and iteroparous populations of American shad (Olney et al. 2001). The phenomenon of serial spawning, coupled with higher degrees of iteroparity at higher latitudes (Leggett and Carscadden 1978), suggests that poor downstream survival of adults (Leggett et al. 2004) as well as juveniles (Harris and Hightower 2012) may negate otherwise effective restoration actions. Serial spawning is poorly understood in river herring as well as American shad. Frank et al. (2009) recently hypothesized that the phenomenon commonly referred to as "fallback" may actually be part of the normal spawning migration behavior of anadromous alewives. This would have substantial ramifications for how we view alosine migrations. In an undammed system, serial spawning would ensure substantial variation in life history even within a family group. Prior to the observations by Maltais et al. (2010), Olney et al. (2001) hypothesized that serial spawning may increase the probability of finding favorable environmental conditions for the survival of the larval American shad by dispersing them over time and space. Thus, life history variation may be environmentally mediated by processes such as serial spawning, but the extent to which these characteristics (i.e., tendency to spawn serially) may be heritable is largely unknown. Further refinement and testing of hypotheses regarding the genetic and environmental influences of serial spawning and other life history variants in alosines is needed.

Among the least studied of the east coast diadromous fishes is the sea lamprey (*Petromyzon marinus*; Clemens et al. 2010), for which even basic assessments such as regional abundance trends of adult

returns are unavailable (Nislow and Kynard 2009). Sea lamprey are best known for the extensive control programs in the Great Lakes where they are a non-native invasive species but they are native to the east coast and there is building evidence that they provide important ecological services to the watersheds, and that efforts to restore sea lampreys may assist the restoration attempts for other species (Hogg 2012). Recent evidence indicated that they quickly re-colonized upstream habitat after removal of small dams (Hogg et al. 2013).

On the east coast, true re-colonization studies are quite rare even though there have been many dam removals during the past 15 years, and we focus here on responses of alosines. Removals of Edwards Dam (Kennebec River, Maine) and Quaker Neck Dam (Neuse River, North Carolina) (Fig. 2) resulted in upstream migration of alosines and other anadromous fishes (O'Donnell et al. 2001; Burdick and Hightower 2006), yet the observations of these species upstream of the recently removed Embury Dam (Rappahannock River, Virginia) have been limited in distance and numbers (Allan Weaver, Virginia Dept. Game Inland Fisheries, pers.com.). When dams are removed or planned to be removed, various types of stocking are often implemented. For example, prior to the removal of the Edwards Dam in 1999, the Maine Department of Marine Resources had already transferred roughly 600,000 adult alewife and 8.4 million American shad fry to upstream reaches. Millions of adult alewives now return to the Kennebec River annually but the question remains whether the dam removal or the stocking led to the “success”.

Numerous rivers flowing into Long Island Sound did not have dams removed but have had fish passage facilities constructed and now have fish runs which are monitored at those facilities. Shad runs occur in the Housatonic, Naugatuck, Shetucket, and Pawcatuck rivers (S. Gephard, unpublished data) (Fig. 2). The Connecticut River hosts the largest run of American shad in Long Island Sound; in 2012, nearly 490,000 American shad were passed at the first dam (<http://www.fws.gov/r5crc/Stuff/stuff.html>). To the west, the Quinnipiac River had a shad count of seven for the first time at the first dam in 2012 (Connecticut Department of Energy and Environmental Protection (CTDEEP), Old Lyme, CT, unpublished data). Shad have been reported in only 2 of the last 15 years at the first dam on Whitford Brook (20 km east of the Connecticut

River) but other rivers have had far more consistent counts. The Pawcatuck River, 8 km west of Whitford Brook, has averaged 888 at the first dam over the past 34 years (RI DEM Arcadia, RI, unpublished data). No shad are observed in other numerous streams along the shoreline of Long Island Sound, suggesting that straying may be relatively rare.

Shad re-colonization of reconnected habitat within a natal river in the northeastern United States can proceed quickly, regardless of the low population levels. Immediate use of upstream habitats was seen in the Westfield River, a tributary to the Connecticut River at river kilometer (RKM) 95 and Farmington River at RKM 80 once fishways were installed at their respective dam sites (Fig. 3). Both rivers had shad runs to the base of the dams prior to fishway construction but the increase in shad abundance over time was greater in the Westfield River than the Farmington River. The Farmington River fishway at Rainbow Dam is considerably larger than the one at the Westfield River dam site (approximately 15 m high and 241 m long), making ascent difficult for shad. In the Shetucket River, draining directly into Long Island Sound, shad immediately moved upstream once fish passage facilities were installed (Fig. 2).

Self-sustaining populations above these dam sites are likely constrained by anthropogenic factors unrelated to the species' tendency for colonization. For example, the Rainbow Dam fishway is an unsuitable design for shad and many die attempting to ascend (S. Gephard, personal observation). Thus, the lack of population rebuilding observed over the last two decades is not surprising. The Greeneville Dam fish lift on the Shetucket River provides access to only a small area of upstream habitat that may be near its carrying capacity, resulting in a relatively stable but small population. The West Springfield Dam fishway on the Westfield River is the most effective fishway of the three and provides access to 21 km of suitable habitat, resulting in an expanding shad population in the Westfield River. While long-term success of restoration efforts has varied between the three locations, the data demonstrate the species' strong urge to continue upstream into habitat not previously occupied.

Until recently, empirical evidence of straying by river herring (alewife and blueback herring) has been completely lacking. Hogg (2012) and Gardner et al. (2011) captured adult alewife in previously

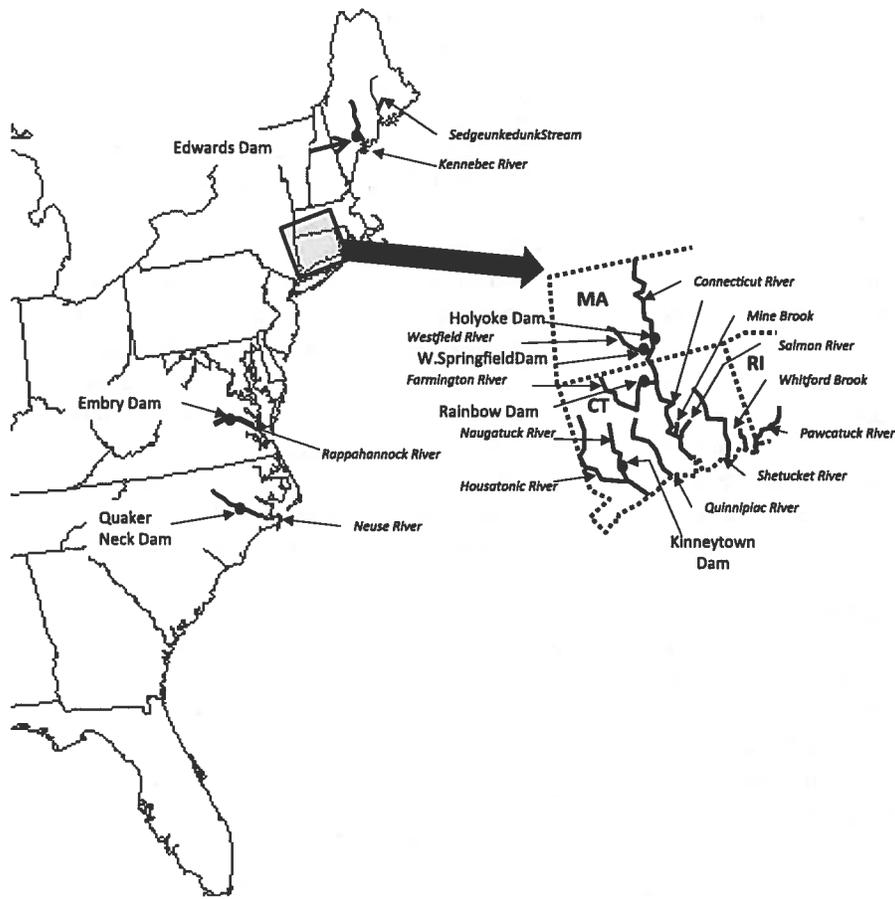


Fig. 2 Select rivers and dams along the Eastern seaboard of the United States. Inset map includes detailed area of rivers draining into Long Island Sound and their associated dams

inaccessible reaches of Sedgeunkedunk Stream, Maine shortly after dam removals in 2008 and 2009. Further, Hogg (2012) observed downstream emigration of juvenile alewife at the outlet of Fields Pond on this stream, confirming successful reproduction and recolonization of alewives in a pond that had been inaccessible prior to dam removal. Alewives have also been observed spawning in Connecticut River tributaries where there is no nursery habitat. For example, Mine Brook in East Hampton, CT has very limited (<300 m) fast flowing rocky habitat before alewives encounter a 6 m barrier waterfall yet alewives have been observed spawning there in some of the last 10 years (S. Gephard, pers. obs.). Residence time of drifting larvae would be extremely limited in this small brook so imprinting seems unlikely, leading to the conclusion that this spawning run and others like it

may represent straying. Moreover, recent studies have inferred straying rates from genetic analyses. Palkovacs et al. (2013) examined genetic patterns of isolation by distance (IBD) to conclude that straying rates are generally higher in alosines than salmon, and that blueback herring stray more than alewife. Notwithstanding the limitations of the IBD analysis (Bradbury and Bentzen 2007), this conclusion is consistent with observations from these New England streams (S. Gephard, pers. obs.).

Sea lamprey runs in Long Island Sound tributaries have been limited to a very few streams after industrialization (Whitworth 1996). The Connecticut River hosts the largest run in Long Island Sound, averaging 38,000 lamprey lifted annually during the last 20 years (<http://www.fws.gov/r5csrc/Stuff/stuff.html>). Only eight tributaries in Long Island Sound in

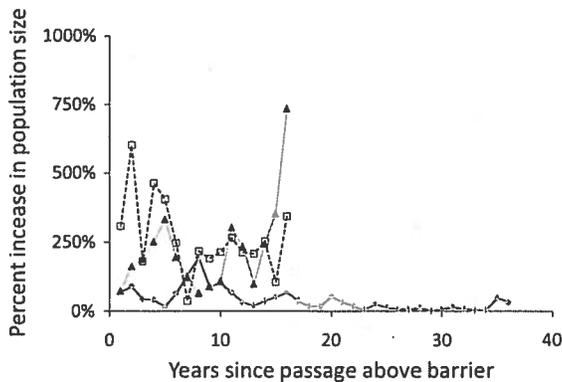


Fig. 3 Shad counts at three Long Island Sound fishways beginning the first year of operation of each fishway (CTDEEP and USFWS unpublished data). *Open squares with dashed black lines* is the Shetucket River (Greeneville dam fishlift) (ave. shad population 2.317 ± 1.287), *grey diamond with solid black line* is the Farmington River (Rainbow dam fishway) (ave. shad population 504 ± 491), and the *black triangle with grey solid line* is the Westfield River (West Springfield dam fishway) (ave. shad population 3.038 ± 2.300)

Connecticut host sea lamprey runs, and most of them are believed to number <1,000 and in most cases <100 individuals per year (CTDEEP, Old Lyme, CT, unpublished data). The tendency to be attracted to the pheromones produced by resident ammocoetes (noted previously), coupled with the paucity of established runs in Connecticut streams, suggest low re-colonization potential for the species.

Results from different restoration strategies in two Long Island Sound tributaries support the view that sea lamprey have limited re-colonization ability. The Shetucket River Greeneville Dam Fishlift and the Naugatuck River Kinneytown Dam Fishway were operated for the first time in 1996 and 2000, respectively, with no prior stocking of sea lamprey and the assumption that no lampreys were present downstream of the dams (Whitworth 1996). No lampreys were passed in the 6–8 years of operation (Fig. 4), though a few lamprey were counted at the Greeneville Fishlift on the Shetucket River during the past 17 years, demonstrating that some straying occurred (Fig. 4). Un-spawned adult lamprey were transplanted into habitat upstream of the Kinneytown Dam in 2004 ($N = 63$) and 2005 ($N = 110$) to support a re-colonization study that successfully produced ammocoetes (Starr 2007). During the next several years, the number of adult sea lampreys counted at the Kinneytown Fishway increased dramatically, presumably in

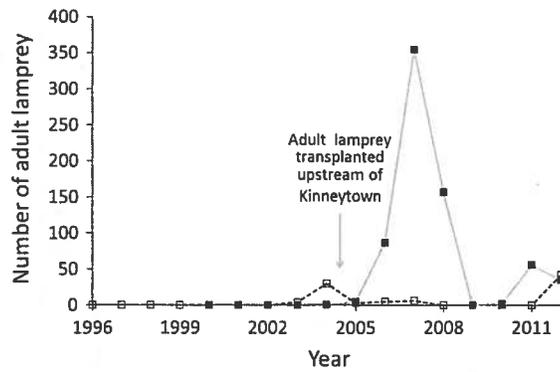


Fig. 4 Adult sea lamprey counts on the Shetucket River (Greeneville dam fishlift), Shetucket River and Naugatuck River (Kinneytown dam fishway, Naugatuck River. *Open rectangles with a hashed black line* denote the Shetucket River, while the *solid grey line* and *solid black rectangles* denote the Naugatuck River (CTDEEP, unpublished data)

response to the presence of ammocoete pheromones (Fig. 4). Similar returns were not seen at the Greeneville Fishlift where no transplantation occurred, suggesting that sea lamprey colonization of unoccupied streams is slower compared to streams with ammocoetes.

The Westfield River's West Springfield fishway and the Farmington River's Rainbow fishway both had sea lampreys nesting below the dams but no transplantation of sea lampreys above the dams prior to fishway operation. In both cases, sea lamprey immediately used the fishways in large numbers, resulting in consistent counts of lamprey in the thousands (Fig. 5). Sea lamprey nest surveys on the Salmon River, a Connecticut River tributary, documented many nests in headwater habitat approximately 5 rkm upstream of typical ammocoete habitat (CTDEEP, Old Lyme, unpublished data) demonstrating that upstream penetration is common and likely evolved to ensure that eggs and larvae drift downstream into suitable habitat. Similar patterns with sea lamprey in the Sedgeunkunk Stream, Maine have recently been observed. A spawning population of sea lamprey existed below two impassable dams prior to their removal beginning in 2008. Within 1 year of dam removal, sea lamprey re-colonization proceeded as far upstream as the first natural barrier (roughly 5 km; Hogg et al. 2013). These data and observations demonstrate that lateral colonization of unoccupied streams by sea lamprey may be slow but upstream colonization of unoccupied habitat within occupied streams can be rapid.

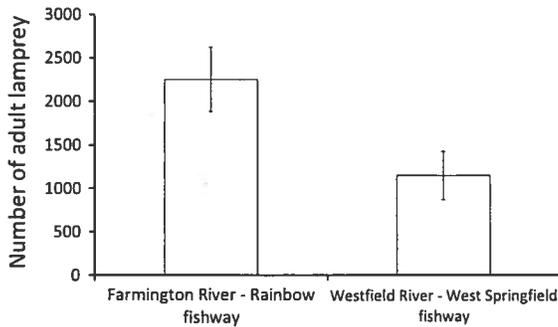


Fig. 5 Average number of sea lamprey passed in the Farmington River (Rainbow fishway) (1976–2012) and the Westfield River (West Springfield fishway) (1996–2012). Lines with perpendicular marks are standard error estimates, respectively. Lampreys were not counted at the Rainbow fishway in 1976–1977 (CTDEEP and MDFW unpublished data)

A colonization model

The preceding observations lead us to offer a conceptual model to compare the relative tendency for prominent North American east and west coast diadromous species to colonize new habitat (Fig. 6). This conceptual model between species provides a starting point for those involved in management actions associated with the elimination of migratory barriers and expansion of diadromous fish populations. For example, given the apparent tendency of sea lamprey to not stray (laterally across watershed boundaries) and apparent genetic panmixis in the Atlantic population (Bryan et al. 2005) there may be no reason not to transplant adults to accelerate colonization of vacant streams.

Alosines, on the other hand, have an intermediate tendency to stray and the decision to re-introduce fish may be influenced by local conditions. If a vacant stream is located between two streams with strong runs of the targeted alosine species, re-colonization may occur without reintroduction. Rivers that are distant or unique from extant runs may slow to re-colonize, so reintroduction may accelerate the pace of recolonization. If stocking is used, other issues of population structure and the swamping of native genotypes require careful consideration. Lastly, some rivers targeted for Atlantic salmon restoration in New England (e.g., the Connecticut) are over 500 km away from the nearest extant population. Given the species' limited tendency to stray, natural re-colonization

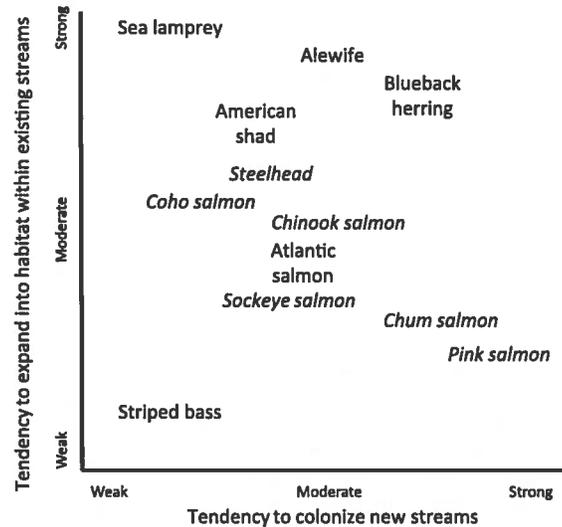


Fig. 6 A conceptual model of the potential for recolonization by East and West Coast of North America diadromous fish species. Italicized species are West Coast salmonids

would likely take an extremely long time or might not occur in the foreseeable future without assistance.

The tendency for west coast salmonids to colonize new streams or expand into habitats within existing streams is ultimately related to the compatibility between specific life history adaptations of each species and the physical and ecological characteristics of the new habitats (Quinn 1984; Allendorf and Waples 1996; Burger et al. 2000). Several specific factors will also directly affect colonization by salmon. These include natural barriers (assuming artificial barriers are removed), distance from the source population, initial population size, straying rate, interactions with existing fish populations, and intraspecific competition for food and space (Pess 2009; Pess et al. 2012). Identifying and understanding how each of the variables affects species-specific salmonid recolonization provides a template for salmonid response in any watershed. For example, pink salmon which typically have larger but highly variable population sizes, higher straying rates, minimal variation in life history characteristics, and a short freshwater residence are prime candidates for the colonization of newly opened habitats (Quinn 2005). Other species such as steelhead have lower population sizes, lower straying rates, greater variation in their life history, and greater freshwater residence time are thus less likely to establish spawning populations first.

Conversely, pink salmon colonization may be limited in their more modest jumping ability and ability to maneuver past barriers compared to steelhead.

One important factor to consider is metapopulation dynamics. A metapopulation can be broadly defined a suite of local populations inhabiting distinct patches of suitable habitat, which interact through dispersal, and persist through time between stochastic extinctions and re-colonizations (Schtickzelle and Quinn 2007). Both theoretical and empirically derived metapopulation models have been used and developed to explain the interaction of local populations and the potential for colonization of diadromous fishes (Cooper and Mangel 1999; Young 1999; Thorrold et al. 2001; Pess et al. 2012) but in general this body of theory has not been as strongly linked to conservation efforts for migratory fishes as it might be.

Conclusions and recommendations

Diadromous fishes can re-colonize newly available habitats, though life history patterns, proximity to source populations, physical capacity to surmount barriers or use artificial ladders, and diversity of habitats available may control the patterns and rates of recolonization. Straying and life history variation are integral parts of the biology of each species, allowing it to persist in the face of varying environmental conditions. These features, inferred from the west coast salmonid examples, and east coast alosine restoration efforts, function at the population level. However, the genetic architecture behind these life history traits at the individual level, where selection occurs, is even less well understood than it is at the population level. To advance the understanding of re-colonization we have offered several examples to illustrate the likely factors influencing the pace of natural re-colonization in previous sections. Re-colonization rate is most likely affected by four factors: accessibility, proximity to a donor stock, productivity and condition of the donor stock, and habitat suitability for the species and life history variant. These factors are the basis of our conceptual model to assist those weighing various re-colonization options. This conceptual model requires refinement and scrutiny through the development of quantitative models and empirical evidence.

Regardless of the factors that influence recolonization, barrier removal and assisted migration are the two main restoration actions that can be utilized as a restoration strategy. Identifying the targeted species, understanding the life history patterns between and within species, having information on the four preceding factors affecting colonization rate, and knowing if the focal populations are natural, transplanted, or of hatchery origin will help identify which restoration strategy is utilized (Anderson et al. 2013). Species with higher stray rates across watersheds, a relatively simple set of life history patterns, and are naturally occurring may not need any prompting, thus barrier removal could suffice to bring colonizers. Conversely, a species that seldom strays, does not move much within a stream, and has a relatively complex life history and specific habitat needs may need assisted migration or reintroduction.

Lastly, few examples of true re-colonization experiments exist, partly because they are often confounded by the artificial re-introduction of fish. There is typically more effort to stock streams to accelerate the pace of restoration but less effort to evaluate the costs and benefits of natural re-colonization versus stocking. Regardless of whether or not fish are stocked into a stream as part of a restoration plan, our review suggests that the elimination of migratory barriers will often result in upstream colonization of vacant habitat, even if different species do so at different rates.

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REPORT

Density-dependent mortality in Pacific salmon: the ghost of impacts past?

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Abstract

Conservation biologists often ignore density dependence because at-risk populations are typically small relative to historical levels. However, if populations are reduced as a result of impacts that lower carrying capacity, then density-dependent mortality may exist at low population abundances. Here, we explore this issue in threatened populations of juvenile chinook salmon (*Oncorhynchus tshawytscha*). We followed the fate of more than 50 000 juvenile chinook in the Snake River Basin, USA to test the hypothesis that their survival was inversely associated with juvenile density. We also tested the hypotheses that non-indigenous brook trout and habitat quality affect the presence or strength of density dependence. Our results indicate that juvenile chinook suffer density-dependent mortality and the strength of density dependence was greater in streams in which brook trout were absent. We were unable to detect an effect of habitat quality on the strength of density dependence. Historical impacts of humans have greatly reduced population sizes of salmon, and the density dependence we report may stem from a shortage of nutrients normally derived from decomposing salmon carcasses. Cohorts of juvenile salmon may experience density-dependent mortality at population sizes far below historical levels and recovery of imperiled populations may be much slower than currently expected.

Keywords

Chinook salmon, density dependence, extinction, fisheries, hydropower dams, non-indigenous species, *Oncorhynchus tshawytscha*.

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INTRODUCTION

One of the most contentious issues in ecology is the degree to which density-dependent processes determine the size or allow persistence of populations (Turchin 1999). After decades of debate, most researchers now agree that most (but not all) populations are regulated and thus persist in the face of environmental variability (Hixon & Webster 2002). While some controversy about the importance of density dependence as an agent of regulation certainly remains (Sale & Tolimieri 2000), it is clear that the scientific basis of conservation and natural resource management depends, in part, in understanding the density-dependent mechanisms that regulate populations (e.g. Fagan *et al.* 2001; Gundersen *et al.* 2002).

Conservation biologists often ignore density dependence because at-risk populations are typically small relative to historical levels and are assumed immune to compensatory

mortality associated with competition or density-dependent predation. Many recent population risk analyses based on either diffusion models (e.g. Dennis *et al.* 1991) or matrix projection models (Doak *et al.* 1994; Menges 1992; Kareiva *et al.* 2000; Hinrichsen 2002) have not included density dependence. However, if populations are reduced as a result of habitat loss or degradation, introduction of exotic competitors, or other impacts that lower carrying capacity, then density-dependent mortality may exist at low population abundances and will have important effects on estimates of population growth, risk of extinction, probability of recovery or other parameters of conservation concern.

Populations of salmon may experience density dependence at low population abundance because of their unique life histories. Many salmon populations utilize nutrient-poor streams as spawning/rearing areas. In these systems, the delivery of nutrients derived from decomposing salmon

carcasses appears to be crucial to the growth of juvenile salmon (Larkin & Slaney 1997). Thus, the abundance of returning adults may determine carrying capacity during the freshwater rearing phase. If this feedback between abundance of adults and population regulation of juveniles exist, it may have important consequences for restoring the many at-risk salmon populations worldwide.

Here, we explore this issue in threatened populations of juvenile chinook salmon (*Oncorhynchus tshawytscha*) from the Snake River, a major tributary of the Columbia River. Over the last 100 years, these populations have suffered from two major impacts: heavy fishing in the early part of the 1900s (Levin & Schiewe 2001) and dam construction during the 1960s and 1970s (Levin & Tolimieri 2001). These two impacts in concert with a natural downturn in ocean productivity (Beamish *et al.* 1999) have landed chinook from the upper portions of the Columbia River Basin on the US endangered species list. Previous analyses of time series using data from the last 20 years show little evidence supporting density dependence in Snake River chinook (Kareiva *et al.* 2000; Zabel & Levin 2002) – the expected result in a system where population declines are the result of harvesting by humans or hydropower systems. However, based on the mechanisms described above, there is cause for a more detailed examination of density dependence, particularly during the freshwater phase. The extreme reduction in salmon abundance caused by harvest and dams may have produced a nutrient deficit that would lower carrying capacity and result in compensatory mortality of fish even when densities are depressed (cf. Bilby *et al.* 1998; Gresh *et al.* 2000).

We followed the fate of more than 50 000 individually tagged juvenile chinook salmon in tributaries of the Snake River to test the hypothesis that their survival was inversely associated with juvenile density. Additionally, because densities of fish and habitat quality can co-vary and thus mask the strength of density dependence (Shima & Osenberg in press), we examined the consistency of patterns of covariation between survival, density and habitat quality. Finally, the presence of non-indigenous brook trout may influence the importance of density dependence by competing with or preying on juvenile chinook. Accordingly, we examined the consistency of patterns of association between survival and juvenile density in sites with and without exotic brook trout.

METHODS

Our study sites were located in the 36 000 km² Salmon River basin. The Salmon river drains into the Snake River 303 km above the mouth of the Snake River. Human population density in this region is low and timber harvesting, mining and agriculture are the dominant land

use practices. The US Forest Service and the Bureau of Land Management manage 89% of the Salmon River basin with 27% of the basin designated and managed as wilderness area. Detailed descriptions of these study sites can be found in Levin *et al.* (2002) and Schaller *et al.* (1999). Non-indigenous brook trout are ubiquitous throughout the Salmon River basin and are associated with significantly lower survival of juvenile chinook (Levin *et al.* 2002). We selected eight study sites in which at least 5 years of data were available between 1992 and 2000. Streams were only sampled in years when chinook abundance was relatively high (collection permits are not granted when fish abundance is low). Additionally, only a subset of streams were sampled in 2000 because of forest fires near our study sites.

Beginning in 1988, the National Marine Fisheries Service (NMFS) began a programme to individually tag wild chinook parr (actively feeding juvenile salmon residing freshwater) in the Salmon River Basin with passive integrated transponder (PIT) tags. An expansion of this programme in 1992 provided data that allowed us to estimate rates of juvenile survival of salmon (Achord *et al.* 1994). During July and August of each year (when chinook are 2–5 months post-emergence), NMFS electrofished with supplemental seining in an effort to collect chinook salmon for tagging with minimal impact on the fishes (Achord *et al.* 1996). Modified syringes and needles were used for PIT tagging (Prentice *et al.* 1990), and they, along with PIT tags were disinfected for a minimum of 10 min with ethanol before tagging. PIT tags (12 mm in length) each contain a unique code, and are inserted into the body cavities of juvenile chinook (>54 mm FL), where they remain for the lifetime of the fish. Details of tagging and fish release are described elsewhere (Achord *et al.* 1996).

When fish migrate downstream the spring after they are tagged, they pass through dam bypass systems equipped to automatically detect each tag. We were interested in survival from the point of release in streams to the Lower Granite Dam, the first dam they encounter on the seaward migration. As PIT tags are detected at Lower Granite Dam and dams downstream, survival can be calculated using the Cormack–Jolly–Seber procedure (Cormack 1964; Jolly 1965; Seber 1965). Survival from point of release to Lower Granite Dam was estimated as

$$\hat{S} = \frac{n/\hat{p}}{R}$$

where n is the number of fish detected at Lower Granite Dam, \hat{p} is the probability of detection at Lower Granite Dam, and R is the release number. Probability \hat{p} was based on the number of fish not detected at Lower Granite Dam but detected at downstream dams, and the numbers detected at both Lower Granite and downstream dams (Burnham *et al.* 1987). Further detail of procedures to

estimate survival for these populations are provided by Smith *et al.* (2002).

Rigorous estimates of the density of chinook parr are not available for our study sites; however, when collecting fish for tagging, the distance in kilometres covered in each stream and the number of chinook captured were recorded (e.g. Achord *et al.* 1997). As three experienced personnel did over 90% of the electrofishing following standardized protocols, the number of fish captured per kilometre provides a reasonable estimate of relative parr density. In addition to chinook, the number of non-indigenous brook trout captured was also enumerated. Levin *et al.* (2002) concluded that estimates of brook trout densities were unreliable, but that sites could be reliably separated into those where brook trout were common vs. those in which they were rare.

To explore the hypothesis that survival of chinook parr was associated with parr density we used linear mixed models that allowed us to consider complex autoregressive error structures. We used survival of parr as the response variable, year as a main effect and parr density as a covariate. Secondly, we examined survival of parr as a function of brook trout (common vs. rare) and parr density. In both cases, we first fit the fully saturated model and subsequently removed non-significant interactions from the model. We used Akaike's Information Criterion (AIC) to compare models in which we considered autoregressive error structures to those in which we did not. As standard autoregressive error structures assume equal spacing of samples, and our data did not conform to this requirement (as not all years were sampled), we modelled the autocorrelation using the spatial power law (Littell *et al.* 1996). This procedure produces a covariance structure in which correlations decline as a function of time in a manner directly analogous to a first-order autoregressive process. When AIC indicated that inclusion of correlated errors did not improve the fit of the model, we did not include the complex error structures.

To determine if habitat quality might mask the strength of density dependence (Shima & Osenberg, in press) we used a general linear model in which chinook survival was the response variable, and parr density, habitat and the interaction of parr density and habitat were independent variables. A significant interaction between habitat and parr density indicates that the relationship between density and survival varies among habitats. Levine's test (Wilkinson *et al.* 1996) indicated that variances were homogeneous ($F = 0.312$; $P = 0.58$). To characterize habitat, we used an index of habitat developed by Levin *et al.* (2002) that explained differences in survival of chinook parr in the Salmon River Basin. This habitat index is the first principal component of seven diverse measures of habitat that appear to be important to chinook. These are the percentage of non-forested riparian wetlands, maximum air temperature,

the number of water diversions, percentage of rangeland, millimetres of precipitation, percentage of granite bedrock and hill slope. As our measure of habitat was time invariant (Levin *et al.* 2002) we used average survival and density from individual sites as variables in this analysis.

RESULTS

The density of chinook parr varied significantly among our study sites ($F_{7,36} = 4.09$; $P = 0.002$; Fig. 1). Our estimates of parr density, averaged across years, ranged from a low of 115 (SE 26.2) per km in Lower Big Creek to a high of 704.2 (SE 130.9) in the South Fork of the Salmon River.

During the study period a total of 52 239 juvenile chinook salmon were tagged in our eight study sites. Estimates of survival varied greatly among sites ($F_{7,34} = 11.67$; $P < 0.0001$; Fig. 2). Average survival ranged from 12.6% (SE 1.8%) in Valley Creek to a high of 36% (SE 2.9%) in Lower Big Creek. Survival also varied among tagging years with a high of 25% (SE 3.8%) in 1998 and a low of 14.5% (SE 2.8%) in 1994 (Fig. 2). Overall, juvenile survival of chinook averaged 19.7% (SE 1.3%).

Survival of chinook parr showed a strong negative relationship with their initial density (Table 1; Fig. 3). The interaction of parr density and year was not significant in our ANCOVA model (Table 1), indicating that the negative association of parr density and survival was consistent over the time frame of our study. The average proportion of fish surviving at high densities (>700 chinook km^{-1}) was about

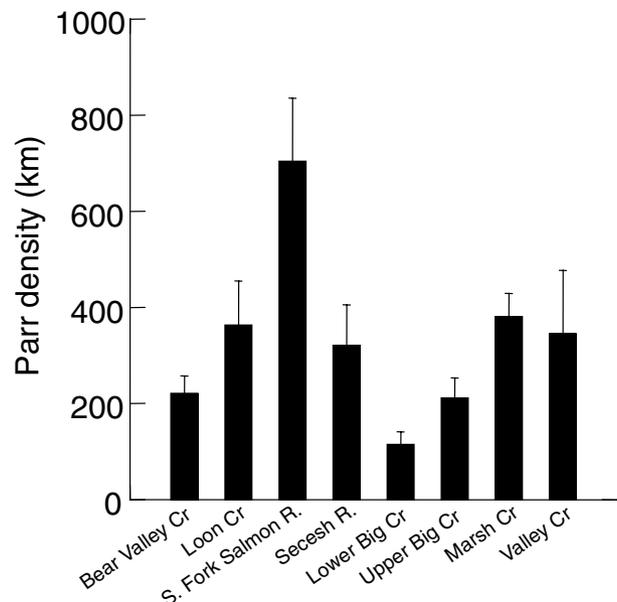


Figure 1 Mean density of chinook salmon parr per kilometre of stream in several sites in the Snake River Basin, USA.

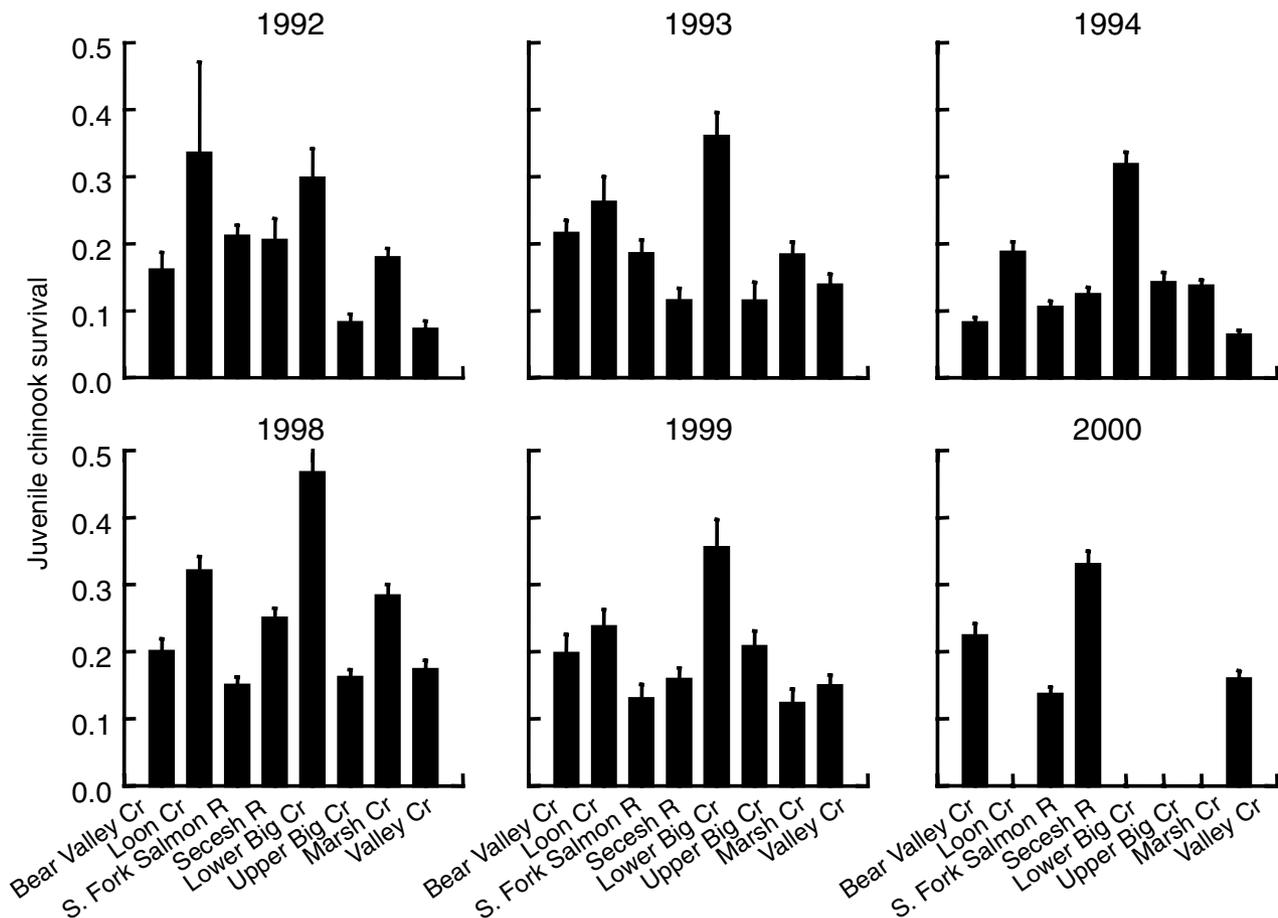


Figure 2 Estimates of juvenile chinook survival in the Snake River Basin from the summer of their first year when they were tagged to the following spring. Error bars are 1 SE. The designated years are tagging years.

Table 1 Results of analysis of covariance testing the null hypothesis of no difference in the association of juvenile chinook survival with the density of juvenile chinook (covariate) or year (main effect)

Source	SS	d.f.	MS	<i>F</i>	<i>P</i> -value
Year	0.031	1	0.031	13.77	0.001
Site	0.186	7	0.027	11.67	<0.001
Parr density	0.027	1	0.027	11.76	0.002
Error	0.078	34	0.002		

Interaction terms were not significant ($P > 0.70$) and were removed from the model. AIC indicated that the inclusion of an autoregressive error structure did not improve the fit of the model, and thus we used a simple variance–covariance matrix of errors.

half that at low (<150 chinook km^{-1}) densities (Fig. 3). Survival at low densities appeared more variable than survival at high densities with survival estimates at low densities ranging from below 0.1 to nearly 0.5.

Some of the variability about the relationship between chinook survival and density may be the result of interactions with non-indigenous brook trout. Survival of chinook parr in streams with brook trout was significantly lower than in streams without brook trout (23.8% vs. 15.7%; Fig. 4). The strength of density-dependent survival differed among streams with brook trout vs. those without brook trout (Table 2, Fig. 4). In streams in which brook trout were absent, the relationship between survival and density was strong and highly significant ($r^2 = 0.38$; $P = 0.002$; Table 3). Survival in high-density streams was less than half that of low-density streams (Fig. 4). In contrast, when brook trout were present, the association of chinook survival and density disappeared ($r^2 = 0.13$; $P = 0.1$; Table 3).

We were unable to detect a direct effect of habitat on average survival of chinook parr ($t = 0.60$; $P = 0.58$). The interaction of parr density and habitat was also not significant ($t = 0.59$; $P = 0.58$), and thus we were unable

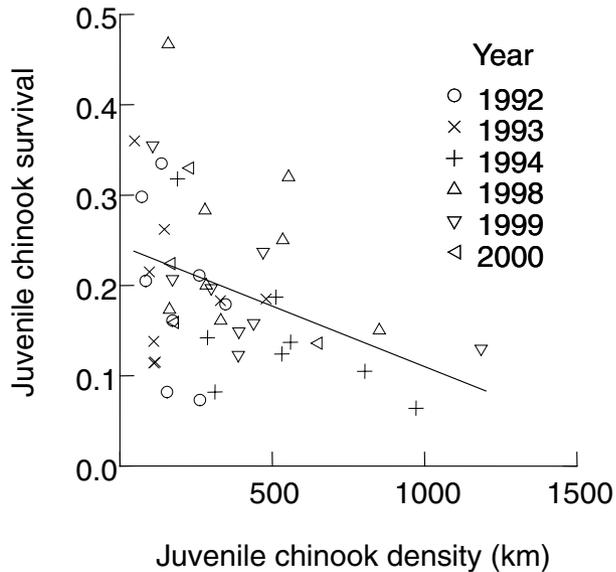


Figure 3 Survival of juvenile chinook salmon (from the summer of their first year until the following spring) as a function of the density of juvenile chinook (per km of stream) in 6 years. Each data point represents survival in a site.

to detect any evidence that the negative association between parr density and survival varied as a function of habitat.

DISCUSSION

Density-dependent population growth forms the basis of resource management in both terrestrial (e.g. Kokko 2001; Jonzen *et al.* 2002) and marine systems (e.g. Stenseth *et al.* 1999; Fromentin *et al.* 2001). Indeed, the basis for setting sustainable harvest rates relies on the notion that at lower densities, population growth is greater than at higher densities (Rose *et al.* 2001). At population sizes that are

low relative to historical levels, we expect population dynamics to be a function of the maximum annual reproductive rate (Myers 2001). However, for the populations we examined, this does not seem to be the case. During the time period of our study, populations (for which long-term data are available) in the Salmon River Basin had declined more than 90% from the 1960s. If carrying capacity of streams is set by availability of rearing habitat (Nickelson *et al.* 1992; Bradford *et al.* 1997), which has not changed appreciably at our study sites (Petrosky *et al.* 2001), then fish should be released from competition and not show evidence of density-dependent mortality. Instead, our results indicate that juvenile chinook suffer density-dependent mortality despite their depleted state.

We hypothesize that the evidence of density dependence we report stems from a shortage of nutrients derived from decomposing salmon carcasses. As more than 95% of the body mass of salmon is accumulated while fish are in the sea (Pearcy 1992), the return of adult salmon results in a transfer of nutrients from marine to freshwater habitats. These marine-derived nutrients are now recognized to play an important role in the ecology of riparian habitats in the Pacific north-west (Gresh *et al.* 2000). The extreme reduction in salmon abundance caused by historical over-harvest and hydropower systems ostensibly has resulted in a nutrient deficit in the spawning and rearing streams we investigated (cf. Bilby *et al.* 1998). Thus, while the number of salmon per unit area declined, the number of salmon per unit resource has not. As a consequence, juvenile chinook should exhibit density-dependent mortality even at low population sizes because carrying capacity is a function of population size.

If our hypothesis is correct, then our views of recovery of decimated chinook populations must be modified. Harvest rates have long been reduced, impacts from hydropower were largely mitigated in the last 20 years

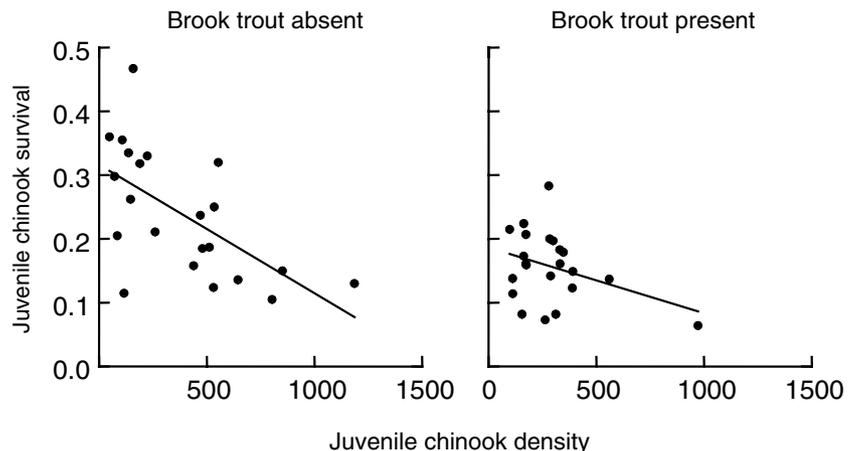


Figure 4 Survival of juvenile chinook salmon (from the summer of their first year until the following spring) as a function of the density of juvenile chinook (per km of stream) in sites in which non-indigenous brook trout were present or absent.

Effect	Numerator d.f.	Denominator d.f.	<i>F</i>	<i>P</i> -value	
(A) Tests of fixed effects					
Brook trout	1	6	8.57	0.026	
Year	4	8	2.44	0.131	
Density	1	8	2.71	0.138	
Brook trout* Density	1	8	6.09	0.039	
Covariance parameter	Subject	Estimate	SE	<i>Z</i>	<i>P</i> -value
(B) Covariance parameter estimates					
Autocorrelation (spatial power)	Site	0.87	0.089	9.69	0.001
Residual		0.004	0.002	2.12	0.02

Table 2 Results of linear mixed model testing the null hypothesis of no difference in the association of juvenile chinook survival with the density of juvenile chinook, and the presence or absence of brook trout and year

An autoregressive error structure using the spatial power law was included in the final model. The interaction juvenile chinook and year was not significant ($P = 0.98$) and was removed from the model.

Table 3 Results of regression analyses testing the association of juvenile chinook survival as a function the density of juvenile chinook with and without brook. These results describe the effects of brook trout on the survival–density relationship, but statistical conclusions were drawn from the full linear mixed model (see methods)

Effect	Coefficient	SE	<i>t</i>	<i>P</i> -value
Brook trout present				
Constant	0.186	0.021	9.086	<0.001
Density	−0.001	0.00006	1.727	0.10
Brook trout absent				
Constant	0.316	0.028	11.206	<0.001
Density	−0.002	0.00005	3.48	0.002

(Levin & Tolimieri 2001), and ocean productivity has recently shifted to favour survival of Snake River chinook salmon (McFarlane *et al.* 2000). If one assumes a carrying capacity that is determined by the physical habitat (Beechie *et al.* 1994), then a fairly rapid return to historical levels may occur. In contrast, if marine-derived nutrients limit population size, then cohorts of juvenile salmon will experience density-dependent mortality at population sizes far below historical levels and recovery would be much slower than in the former case.

We have suggested elsewhere that non-indigenous brook trout are an important influence on chinook populations in the Salmon River Basin (Levin *et al.* 2002), and our results here further emphasize the importance of brook trout in this system. The density of chinook parr was about 30% lower in streams with brook trout vs. those without brook trout (Fig. 4). While we do not know the mechanisms by which brook trout affect

juvenile chinook, our data are consistent with the notion that brook trout prey upon chinook eggs or juveniles, and this reduction in density was sufficient to reduce the effects of density-dependent mortality. Thus, brook trout not only reduce survival of chinook, they may also fundamentally alter the mechanisms that determine chinook population size.

Recent modelling efforts have suggested that modest reductions in juvenile mortality of chinook could reverse the recent declines of the stocks we investigated (Kareiva *et al.* 2000). These populations, however, occur in areas where the physical habitat has not been significantly degraded, and thus some have suggested there is little scope for improving the survival of juvenile chinook while they rear in freshwater (Collie *et al.* 2000). Our results suggest that such conclusions may be incorrect. If nutrients limit population size, a programme of nutrient or salmon-carcass supplementation (Wipfli *et al.* 1999) would reduce the compensatory mortality we observed and increase rates of survival as populations of juvenile chinook grow towards their historical levels. The massive tagging effort of which we took advantage of in this paper was not designed to test for density dependence, but there is clearly a need to employ manipulative experiments to more rigorously test the patterns we report here. Nonetheless, our results suggest that recovery of salmon populations may be hindered by decades of historical human impacts.

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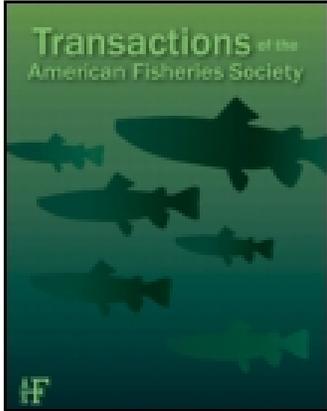
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ARTICLE

The Importance of Juvenile Migration Tactics to Adult Recruitment in Stream-Type Chinook Salmon Populations

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Abstract

The existence of multiple migration tactics within a population has been observed for several fish species, and they may contribute differentially to adult recruitment. Relative contribution by juveniles using the same habitats on different schedules is variable; therefore, understanding and conserving this diversity should be important to fisheries managers. We investigated adult recruitment by two distinct juvenile migration tactics in several spawning populations of stream-type Chinook Salmon *Oncorhynchus tshawytscha* in Idaho: those leaving the spawning grounds as subyearlings during June through November (downstream rearing, or DSR, type) and those emigrating from natal areas 1 year after emergence (natal reach rearing, or NRR, type). The DSR type had greater juvenile abundance in all populations, although the NRR type exhibited better survival from the natal reach to the migratory corridor. The DSR type had greater survival from smoltification to adult return to freshwater compared with the NRR type. More DSR emigrants than NRR emigrants returned to freshwater as adults, although the difference was influenced by cohort and population. Adult recruits to stream-type Chinook Salmon populations in Idaho are comprised mostly of DSR emigrants, i.e., fish that dispersed from their natal habitats and reared in reaches downstream. This finding is ubiquitous, although the size of the effect depends on cohort and population. We demonstrated that juvenile Chinook Salmon in Idaho do indeed use downstream rearing habitats effectively, thereby increasing recruitment of adults back to the spawning gravels in these populations. This study illustrates how dispersive life histories are essential to achieve the full productive potential of migratory stream fish populations.

The return of spawning salmon to their natal areas is remarkable in its accuracy and in the consistency of its timing (Quinn 2005). Less is known about emigration, i.e., the downstream migration of juveniles. Recent work has led to a greater appreciation of the variation in the ways that juvenile salmon accomplish their journeys (e.g., Trudel et al. 2009), but the relative importance of how this life history diversity translates into adult recruitment is poorly understood.

The existence of multiple migratory life history types within a population has been observed for several fish species (Secor 1999). The life histories within a cohort of juvenile migratory fish often contribute differentially to recruitment into the adult population (Reimers 1973; Limburg 2001; Copeland and Venditti 2009). Given sufficient temporal variability, juveniles using the same habitats on different schedules may

have very different fates. Relative contribution by life history types is temporally variable; therefore, understanding and conserving this diversity should be important to fisheries managers (Hilborn et al. 2003; Kerr et al. 2010; Petitgas et al. 2010).

Many salmon populations in the Pacific Northwest are listed under the U.S. Endangered Species Act (Good et al. 2005). For effective conservation, population bottlenecks must be identified in order to be ameliorated. However, variations in life history, as identified above, may be affected differentially by proposed conservation measures. Habitat restoration has often been implemented with the goal of increasing returns of adult salmon (Katz et al. 2007). These are typically enhancements within spawning tributaries, which benefit most the portion of the population that resides there until smoltification. Characteristics of good spawning habitat are to some

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degree opposed to the characteristics of good rearing habitat, i.e., cold, well-oxygenated, sterile streams are ideal environments for incubating embryos, but juveniles need food and warmer temperatures for digestion (Mundie 1969; Quinn 2005). Therefore, rearing habitat limitations, rather than inadequate spawning gravels, are more likely to affect juvenile production in salmon populations (Quinn 2005).

Pacific salmon (genus *Oncorhynchus*) exhibit a continuum of life histories with respect to anadromy, which is one of the defining characteristics of the genus (Quinn and Myers 2004). Species, populations, and even individuals within populations may vary with respect to the time they spend in freshwater before emigrating to the sea as a smolt (Quinn 2005). For example, populations of Chinook Salmon *O. tshawytscha* are often classified (following Healey 1991) as stream-type (that is, they have an extended freshwater rearing phase and enter the ocean as yearlings) or ocean-type (they rear in freshwater for a shorter time and enter the ocean before their first winter as a subyearling). Within these broad categories there is considerable variation in how individual Chinook Salmon use the accessible freshwater habitat (e.g., Reimers 1973).

Dispersal of juvenile salmon for rearing and wintering is likely of demographic importance in populations with extended freshwater rearing. In some cases, juveniles disperse into small, nonnatal tributaries to rear or spend the winter (e.g., Murray and Rosenau 1989; Erkinaro et al. 1997; Bradford et al. 2001; Daum and Flannery 2011). On the Oregon coast, Coho Salmon *O. kisutch* use intermittent streams during the winter, even though these reaches are dry during the summer (Ebersole et al. 2006). Levings and Lauzier (1991) found that the main-stem reaches of the Fraser River basin, British Columbia, were used as winter habitat by juvenile Chinook Salmon. Large-scale dispersal by juvenile salmon should be important in large river basins where the habitats that can support downstream rearing are connected to natal reaches.

There are limitations to juvenile production by stream-type Chinook Salmon populations in relatively unaltered habitats in Idaho (Copeland and Venditti 2009; Walters et al. 2013). Here we present a more intensive investigation of the recruitment of natural-origin Chinook Salmon exhibiting two juvenile migration tactics. Juveniles of the first type (downstream rearing, or DSR) initially disperse downstream from natal habitat as parr, winter downstream in nonnatal reaches, and then enter the migration corridor as yearling smolts the following spring. Juveniles of the second type (natal-reach rearing, or NRR) rear in their natal habitat for roughly 1 year after emergence until the onset of smoltification and active seaward migration. Biologists have long known that DSR emigrants use downstream-rearing and wintering habitats in the lower stretches of the Salmon and Grande Ronde rivers or in the middle reaches of the Snake River (Chapman and Bjornn 1969; Raymond 1979; Figure 1), but explicit information on their early life history and fate through adulthood is lacking. Our goal was to elucidate the demographic importance of the two juvenile

migration tactics in 11 stream-type Chinook Salmon populations in Idaho by providing comparisons of (1) estimated emigrant abundance at exit from the natal reach, (2) estimated survival from natal reach to migration corridor entry, (3) estimated survival from migration corridor to adult return to freshwater, and (4) estimated total adult recruitment to freshwater as well as survival from natal reach to adult.

We made several predictions regarding survival among the stages defined above and number of adult recruits of each type. We knew that abundance of DSR emigrants would exceed abundance of NRR emigrants of the same cohort (Walters et al. 2013). A clear contrast in rate of survival from emigration from natal areas to migration corridor entry was anticipated because a portion of the DSR marked at emigration from natal areas die during the winter before the NRR from the same cohort were marked (hypothesis $[H]_1$: DSR < NRR). We hypothesized that the influence of initial emigration timing would become negligible after migration corridor entry because both DSR and NRR juveniles would be large, actively migrating smolts (H_2 : DSR = NRR). Given H_1 and H_2 , we hypothesized that survival from natal reach to adult would likely favor the NRR emigrants (H_3 : DSR < NRR), but the DSR type would return more adults to freshwater because DSR emigrants were numerically dominant (H_4 : DSR > NRR). We knew a priori that there would be differences among populations and among cohorts; therefore, these were included as factors in the analysis, but our focus was the comparison of the two types.

METHODS

Study populations.—We examined juvenile production for nine Chinook Salmon populations in Idaho (Figure 1) for 11 cohorts (fish spawned during 1997–2007). All populations are part of the Snake River spring–summer Chinook Salmon Evolutionarily Significant Unit, which is listed as threatened under the U.S. Endangered Species Act (NMFS 1992). All Snake River spring–summer Chinook Salmon are considered to have a stream-type life history (Good et al. 2005). Snake River spring–summer Chinook Salmon are genetically distinct from Chinook Salmon from other parts of the Columbia River basin and from the fall Chinook Salmon within the Snake River, which have an ocean-type life history (Waples et al. 2004; Narum et al. 2007). However, approximately one-third of the smolts from the Pahsimeroi River population emigrate to the ocean as subyearling smolts, which have very low adult return rates (Copeland and Venditti 2009; D. A. Venditti, unpublished data), so only the DSR and NRR emigrants from the Pahsimeroi River are used in this analysis.

Data collection.—Emigrating Chinook Salmon juveniles were collected by a rotary screw trap, typically located near the lower extent of major spawning areas. The traps were deployed as early as possible in the spring (usually early March) and operated until the formation of ice prevented trap

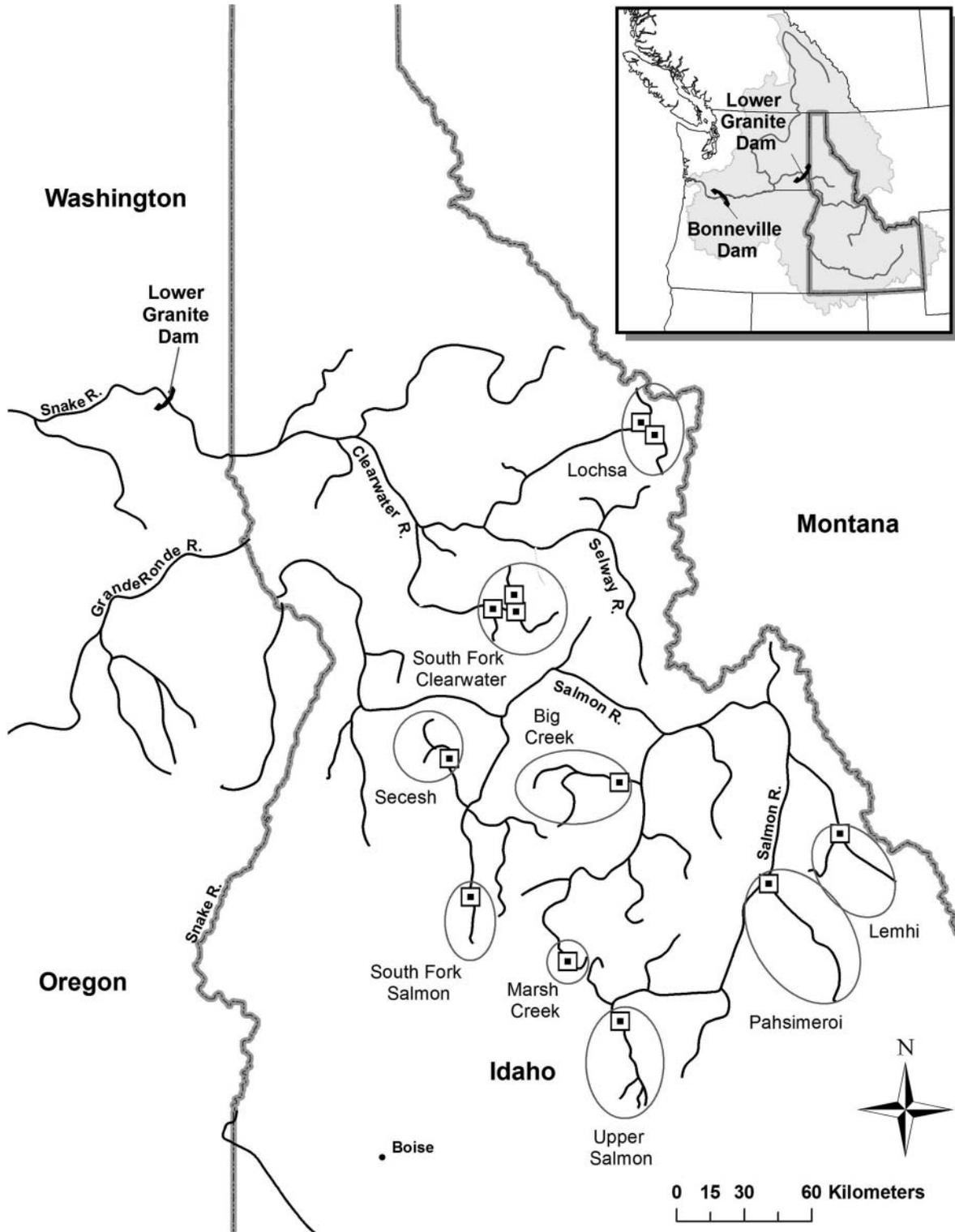


FIGURE 1. Location of study reaches and Chinook Salmon populations in Idaho. Squares indicate locations of rotary screw traps. Inset shows the study area in relation to the Columbia River basin and Bonneville Dam.

operation (usually the middle of November). Before they were processed, all fish were anesthetized with a buffered solution of tricaine methanesulfonate (MS-222). Trap tenders processed fish at least once daily. Fish were counted and measured, and a subsample was tagged with a PIT tag. The transponder in these tags emits a unique code that can be read by a detector when the tag passes through a magnetic field (Prentice et al. 1990). All fish were measured to the nearest 1 mm from the tip of the snout to the fork of the caudal fin (FL) and scanned for the presence of a PIT tag. Size and visual characteristics (e.g., silver color and parr marks) were used to distinguish NRR (which emigrate directly to the ocean) and DSR (which winter downstream from the trap and emigrate the following spring) for 2–4-week period when both migratory types were captured concurrently (Figure 2). After processing, all PIT-tagged fish were released approximately 0.5 km upstream from the trap. Efficiency of the trap was calculated from recaptures of these fish. Recaptured fish and any individuals not tagged were released below the trap.

Tagging procedures followed recommendations of the PIT Tag Steering Committee (1999). Natural-origin fish (as evidenced by an intact adipose fin) ≥ 60 mm FL were eligible for tagging (see procedures below). We assumed there was no size-related effect from tagging on growth or survival within the size range tagged (see Ombredane et al. 1998). Tags were injected into the body cavity using a hypodermic needle. Needles and tags were sterilized in ethanol for 10 min prior to and between uses. Essentially all NRR emigrants trapped were tagged. We tagged DSR emigrants at a rate determined by the expected number of emigrants and the number of tags available for the year, which spread tagging effort over the entire migratory period. Tagging data were recorded into a computer file each day and were uploaded to the central repository for all PIT-tagging activities in the Columbia Basin (PIT Tag Information System [PTAGIS], www.ptagis.org) within 48 h.

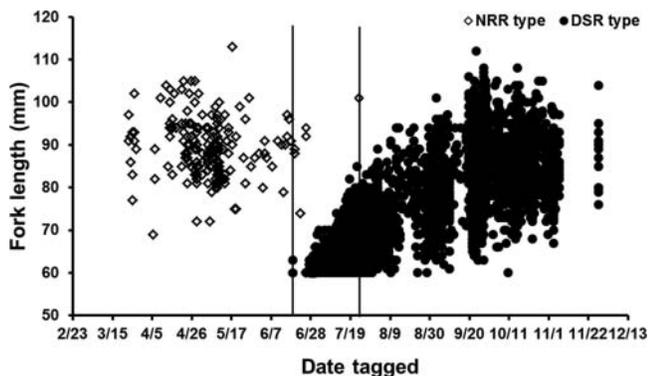


FIGURE 2. An example of the separation between natal-reach-rearing (NRR) and downstream-rearing (DSR) types of Chinook Salmon based on length and time of capture. Data are from individuals tagged from the Marsh Creek population in 2008. The NRR are from the 2006 cohort, and the DSR are from the 2007 cohort. Vertical lines indicate the period of time when the two types were collected concurrently. Dates are given as month/day.

We queried the PTAGIS database for detections of tagged fish as they entered the migratory corridor as smolts at Lower Granite Dam and as returning adults ascending Bonneville Dam (Figure 1). Lower Granite Dam (695 km from the ocean) is the first dam encountered by smolts during seaward migration. Smolts pass the dam primarily through turbine intakes or over the spillway when water is spilled. A portion of the PIT-tagged smolts entered the turbine intakes and was routed away from the powerhouse by submersible bar screens into a bypass fitted with PIT tag monitors that detected PIT-tagged fish with nearly 100% efficiency (Prentice et al. 1990). Bonneville Dam (234 km from the ocean) is the first dam encountered by adults returning to freshwater, and above this point other potentially confounding factors come into play (e.g., nonselective harvest and spill management); therefore, this is a logical endpoint for our study. The ladders that provide adult passage are also equipped with highly efficient PIT tag monitors (i.e., probability of detection ≈ 1.0 ; Fryer et al. 2012). We downloaded the detection data for both juveniles and adults from the central database. Detection information was linked to the tagging information.

Data analyses.—Abundance of each emigrant type as they exited the natal reach (natural-origin fish only) was estimated with mark–recapture software designed specifically for time-stratified rotary screw trap data developed by Steinhorst et al. (2004). Periods during which the DSR and NRR passed the traps were further stratified based on changes in flow, temperature, or other variables that affect trap efficiency. Abundance of all emigrants from a cohort by type was estimated using a summation of Bailey’s modified estimator (Ricker 1975),

$$N_j = \sum_{i=1}^k c_i(m_i + 1)/(r_i + 1),$$

where N_j is number of emigrants of type j , k is the number of periods designated, c_i is the number of all fish captured, m_i is the number of tagged fish released in period i , and r_i is number of recaptures in period i . The estimator was computed using an iterative maximization of the log likelihood, assuming fish are captured independently with probability p_i (equivalent to trap efficiency) and tagged fish mix thoroughly with untagged fish. To get population abundance in populations with more than one trap, abundances were summed because the traps were sampling different tributaries (e.g., in the South Fork Clearwater River population; Figure 1). The point estimates of abundance from each population are used for determining tagging rates. There was no spawning observed in Marsh Creek in 1999; therefore, we excluded that cohort from the analysis. The Big Creek rotary screw trap was first run in 2007, so there are only data from the 2006 and 2007 cohorts for that population.

We estimated survival of each migratory type based on the number of tags placed and then detected at Lower Granite and

Bonneville dams. Survival from trap to Lower Granite Dam (S_{t-l}) and the probability of detection at the dam were computed using a Cormack–Jolly–Seber model implemented by SURPH software (Lady et al. 2010). Survival from smolt emigration at Lower Granite Dam to adult return to Bonneville Dam, commonly referred to as smolt-to-adult return (SAR) rate, was computed as the number of PIT tags detected on adult return at Bonneville Dam divided by the number of tags passing Lower Granite Dam (tags detected in juveniles adjusted for detection probability). Survival rate of fish passing the traps to adulthood (S_a) was estimated by dividing the number of adult detections by the number of PIT tags placed in each cohort because detection probability of adults ascending the Bonneville Dam fish ladders is essentially 1.0 (Fryer et al. 2012) and therefore equivalent between migratory types.

Our goal was to understand the importance of the migratory types to population dynamics, which requires an estimate of adult abundance. Total adult recruitment back to freshwater was the number of tags detected expanded by the tagging rate for each combination of migration tactic, cohort, and population. The tagging rate was estimated by dividing the number of tags placed by the abundance of each emigrant type as they exited the natal reach.

We used a model selection approach to inference. Models were compared and a final model selected for inference based on Akaike's information criterion (AIC) corrected for small sample sizes (AIC_c), which is a quantitative metric that measures a tradeoff of model fit versus parsimony (Burnham and Anderson 2002). We report the ANOVA statistics for each selected model. Acceptable risk of type 1 error was set at 0.05. All models were implemented as general linear models using Systat version 13. Performance of each selected model was assessed by inspection of the residuals.

Each survival metric (S_{t-l} , SAR, S_a) was compared between types by taking the natural logarithm of partitioned survival by DSR emigrants over that of NRR emigrants for each population by cohort. Therefore, we tested the ratio of survival, i.e., \log_e (DSR S /NRR S), which is interpreted as the number of DSR surviving for each surviving NRR emigrant. Thus, the global model was

$$\text{Log}_e(\text{DSR } S/\text{NRR } S) = \beta_o + \beta_{yr} + \beta_{pop} + \varepsilon,$$

where β_o is the overall mean, β_{yr} is the cohort effect, β_{pop} is the population effect, and ε is residual error. We tested for an interaction between population and cohort with Tukey's test of additivity (Steel et al. 1997). Briefly, predicted values from the main effects model are output and the analysis is rerun using the squared predicted values as a regressor. In this analysis, each cohort by population combination is considered a replicate. We excluded year-class failures from the SAR and S_a analyses (i.e., no adults detected from either type). There were several instances in which adults were detected from one type

but not from the other, so we added a small constant to each SAR and S_a estimate. The minimum observed SAR (0.001101) and S_a (0.000174) were used, which approximate the lowest survival that was detectable. Given that there were more zeros in NRR returns, these additions provided conservative metrics with which to test hypotheses. The value of β_o was used to evaluate hypotheses H_1 , H_2 , and H_3 .

Total adult recruitment was modeled using a square-root transformation before analysis ($y' = \sqrt{y+0.5}$) to address parametric model assumptions (Zar 1999). There may be differences among cohorts and populations, so these were included to account for their effects and potential interactions. The global model used was then

$$N = \beta_o + \beta_{type} + \beta_{yr} + \beta_{pop} + (\beta_{type} \times yr) + (\beta_{type} \times \beta_{pop}) + (\beta_{pop} \times \beta_{yr}) + \varepsilon,$$

where β_{type} is the effect of emigrant type and the other parameters are as defined above. Because we were specifically interested in the effects of emigrant type, only models with that effect were evaluated. Models considered included the global model, main effects only, and all possible combinations of two-way interactions. The primary interest is in the difference between adult recruitment by type, so the value of β_{type} was used to evaluate hypothesis H_4 .

RESULTS

There were 330,336 juvenile Chinook Salmon PIT-tagged among the 11 cohorts represented in this study, and of these 0.3% were detected as adults returning to Bonneville Dam. We PIT-tagged 2.2% of the DSR emigrants and 10.4% of the NRR emigrants. There were 906 DSR tags and 226 NRR tags detected as adults at Bonneville Dam. The abundance of DSR emigrants exiting the natal reaches was much greater than that of the NRR emigrants, averaging 85.8% of the juvenile production over all populations and cohorts. The average proportion of DSR emigrants ranged from 98.9% in the Secesh population to 70.8% in the South Fork Clearwater population. Selected details of trapping results and estimates used in the analyses are presented in Table A.1 in the Appendix.

Differential Life Stage Survival

Survival from trap to Lower Granite Dam was almost always higher for NRR emigrants than for DSR emigrants (Figure 3). The average \log_e ratio of S_{t-l} was -0.89 , i.e., survival of NRR emigrants was 2.4 times higher on average. The only positive \log_e ratio was in the 2007 cohort from the Secesh River, in which S_{t-l} was higher for DSR emigrants. All other $\log_e S_{t-l}$ ratios were negative and ranged from -0.01 to -2.52 .

Model selection for S_{t-l} was not straightforward. The AIC_c for the full model was 58.95 but the main effects were not significant, making their interaction hard to interpret. The next

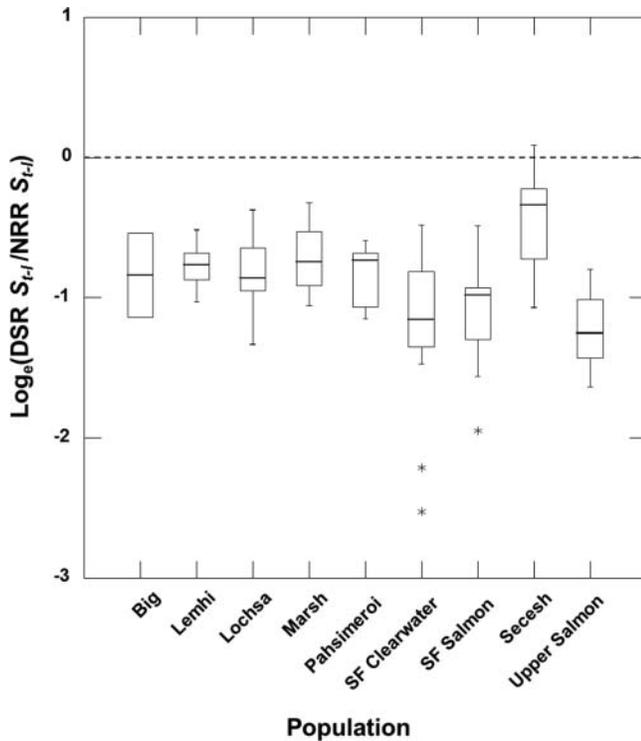


FIGURE 3. \log_e ratios of survival of Chinook Salmon from the trap to Lower Granite Dam (S_{t-l}). Points above zero (dashed line) indicate better survival by downstream-rearing emigrants; points below zero indicate better survival by natal-reach-rearing emigrants. Boxes represent the middle 50% of the observations and the median is shown by the bisecting line. Whiskers show range of values within 1.5 times the interquartile range. Outliers are represented by asterisks (*).

best model had an AIC_c of 60.21 (a difference of <2), indicating an equivalent amount of support (Burnham and Anderson 2002), so we selected that model for inference. The selected model of relative juvenile survival included both population and cohort effects (Table 1). The estimate of β_o (-0.90) was significantly less than zero ($F = 628.3$, $P < 0.001$); therefore, survival to Lower Granite Dam was significantly greater for NRR emigrants. The predicted difference between DSR S_{t-l} and NRR S_{t-l} was least in the Secesh population and greatest in the South Fork Clearwater population. Similarly by cohort, the predicted difference between DSR S_{t-l} and NRR S_{t-l} was greatest in the 2001 cohort and least in the 1998 cohort. However, note that S_{t-l} estimates for DSR emigrants included winter mortality whereas S_{t-l} for NRR emigrants did not because the latter were not tagged until exiting the natal reach after winter.

Relative SAR was more variable but tended to favor DSR emigrants (Figure 4). The average \log_e SAR ratio was 0.50, which means that DSR SAR was 1.6 times higher on average. However, values ranged from -3.1 to 3.7 . The extremes occurred when adults of one emigrant type but not the other were detected in a cohort. Of the 78 cohorts that produced an adult recruit, there were 26 instances of zero returns by one type when the other produced adults. In 18 of these 26 instances, the NRR type produced no adults.

The best model of relative SAR included a population effect (Table 1). This model had an AIC_c weight > 0.99 , indicating it essentially was the only supportable model. The estimate of β_o (0.43) was significantly greater than zero ($F = 8.64$, $P < 0.004$); therefore, predicted survival from Lower Granite Dam to adult return was significantly greater for DSR

TABLE 1. Results of ANOVA of the selected models for survival from natal reach to Lower Granite Dam (S_{t-l}), smolt-to-adult survival (SAR), survival to adulthood (S_a), and number of adult returns (number) for Chinook Salmon.

Source	Sums of squares	df	Mean squares	F-ratio	P-value
\log_e ratio S_{t-l}					
Population	5.48	8	0.69	8.43	<0.001
Cohort	4.75	10	0.48	5.85	<0.001
Error	5.69	70	0.08		
\log_e ratio SAR					
Population	33.48	8	4.19	2.69	0.01
Error	107.22	69	1.55		
\log_e ratio S_a					
Population	74.67	8	9.33	4.22	<0.001
Error	152.62	69	2.21		
Number					
Population	2,635.91	8	329.49	15.17	<0.001
Cohort	1,669.74	10	166.97	7.69	<0.001
Type	1,665.05	1	1,665.05	76.66	<0.001
Population \times Type	2,389.61	8	298.70	13.75	<0.001
Cohort \times Type	720.06	10	72.01	3.32	<0.001
Error	3,040.65	140	21.72		

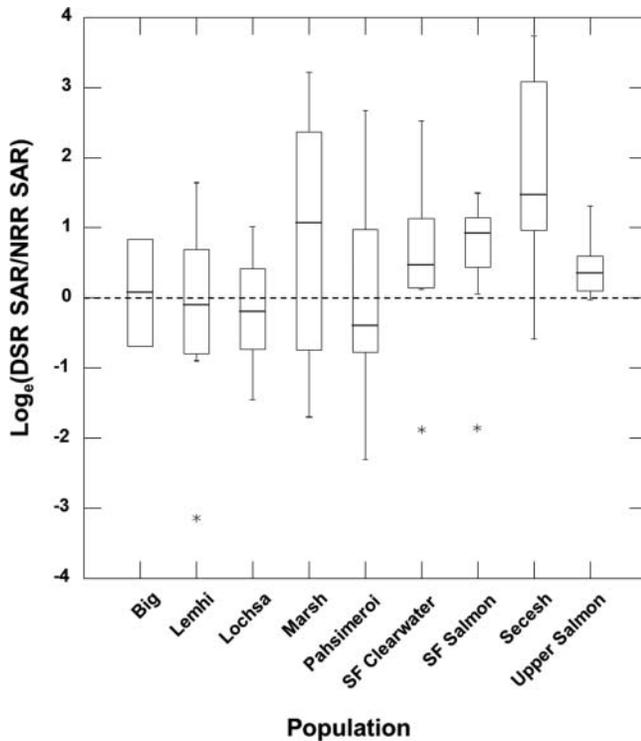


FIGURE 4. Log_e ratios of smolt-to-adult return (SAR) rate for Chinook Salmon. Points above zero (dashed line) indicate better survival by downstream-rearing emigrants; points below zero indicate better survival by natal-reach-rearing emigrants. Boxes represent the middle 50% of the observations and the median is shown by the bisecting line. Whiskers show range of values within 1.5 times the interquartile range. Outliers are represented by asterisks (*).

emigrants. The predicted log_e SAR ratio favored DSR emigrants in six populations and NRR emigrants in three populations. The ratio of DSR SAR to NRR SAR was highest in the Secesh and lowest in the Lemhi populations.

Survival rate to adulthood (S_a) was extremely variable (Figure 5), averaging 0.38% over type, populations, and years. Note that the average includes cohort failures, which are omitted from the models reported below. Survival among cohorts that returned adults varied from 0.11% in the 1999 cohort to 1.13% in the 2006 cohort. Among populations, S_a was greatest for Big Creek (1.56%), but this was based only on two cohorts when there were better-than-average returns in all populations. For the other populations, S_a varied from 0.11% (South Fork Clearwater) to 0.50% (Lemhi River). Averaging over all population and cohort combinations, mean S_a was 0.32% and 0.43% for DSR emigrants and NRR emigrants, respectively.

The differential rate at which migrants returned as adults was not influenced by cohort but there were differences among populations (Table 1). This model also had an AIC_c weight > 0.99 , indicating it essentially was the only supportable model. The ratio of DSR S_a to NRR S_a was highest in the Secesh and lowest in the Lemhi populations. The estimate of β_o (-0.11) was not significantly different from zero ($F = 0.35$, $P = 0.56$);

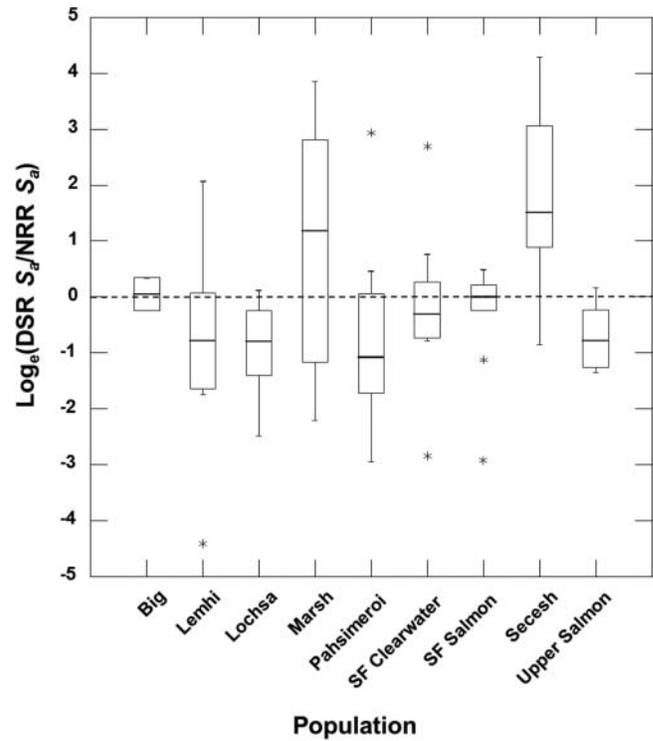


FIGURE 5. Log_e ratios of survival of Chinook Salmon from the trap to adult recruitment (S_a). Points above zero (dashed line) indicate better survival by downstream-rearing emigrants; points below zero indicate better survival by natal-reach-rearing emigrants. Boxes represent the middle 50% of the observations and the median is shown by the bisecting line. Whiskers show range of values within 1.5 times the interquartile range. Outliers are represented by asterisks (*).

therefore, survival from the natal reach to adult return to freshwater was equivalent between types after population and cohort effects were accounted for.

Total Adult Recruitment

We estimated that 23,449 adults returned to freshwater from our study populations from the 11 cohorts. Of these, 89.5% were returning DSR emigrants. The highest overall recruitment was by the 2006 cohort with 4,601 adult recruits. The lowest overall recruitment was by the 1999 cohort with only 45 recruits. There were 12 instances of recruitment failure among the study populations, of which half were in the 1999 cohort. The South Fork Clearwater and Lochsa populations each had three failures: the 1999, 2001, and 2005 cohorts. In most cases the majority of the returning adults were DSR emigrants (Figure 6). Conversely, adult spawning cohorts composed mostly of returning NRR emigrants only occurred when adult recruitment was very low. The cohorts dominated by NRR recruits (14 out of 78) had an average estimated return of only 36 fish.

For inferences about total adult recruitment, we selected the model including all main effects plus two interactions:

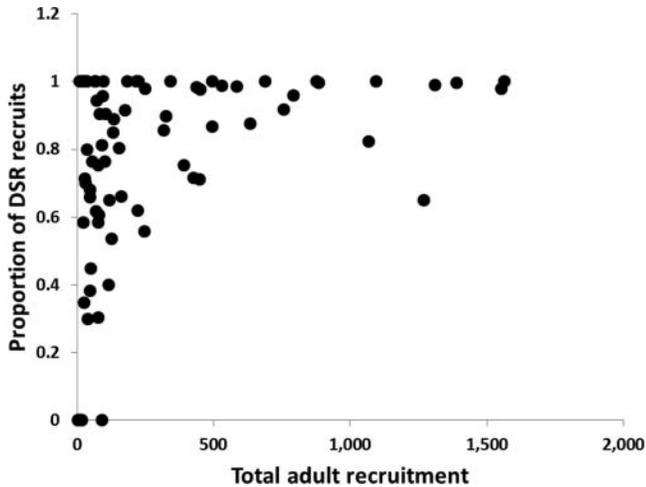


FIGURE 6. Proportion of the adult Chinook Salmon recruits that exhibited the downstream-rearing tactic (DSR) in relation to total adult recruitment for each population and cohort.

between emigrant type and population, and between emigrant type and cohort (Table 1). The selected model was 32.8 times (AIC_c weight, 0.97) more likely than the next best model (AIC_c weight, 0.03), which had the main effects and one interaction term (emigrant type and population). The selected model always predicted more DSR emigrants than NRR emigrants to return, which was supported by PIT tag observations. Migrant type had a significant effect on the number of returning adults ($\beta_{type} = 3.64$; Table 1). The predicted difference between types was lowest in Pahsimeroi, followed by Lochsa, South Fork Clearwater, and Lemhi populations, respectively (Figure 7).

DISCUSSION

Our goal was to compare the demographic performance of the DSR and NRR types in order to increase understanding of the dynamics of the Chinook Salmon study populations. We confirmed that NRR emigrants survive from natal reach to the migration corridor at a greater rate (H_1 : DSR < NRR). However, the second prediction (H_2 : DSR = NRR) was refuted because we found that SARs were not equivalent; therefore, the influence of type was not negligible after entering the migratory corridor (DSR > NRR). Consequently, the third prediction (H_3 : DSR < NRR) was refuted because survival from natal reach to adult was equivalent between types (DSR = NRR). Total adult recruitment to stream-type Chinook Salmon populations in Idaho is comprised mostly of fish that dispersed from their natal habitats and reared in reaches downstream prior to smoltification (DSR type), although the size of the effect depended on cohort and population. This result corroborated our last prediction (H_4 : DSR > NRR).

We conclude that DSR emigrants are the more productive juvenile type in stream-type Chinook Salmon populations in

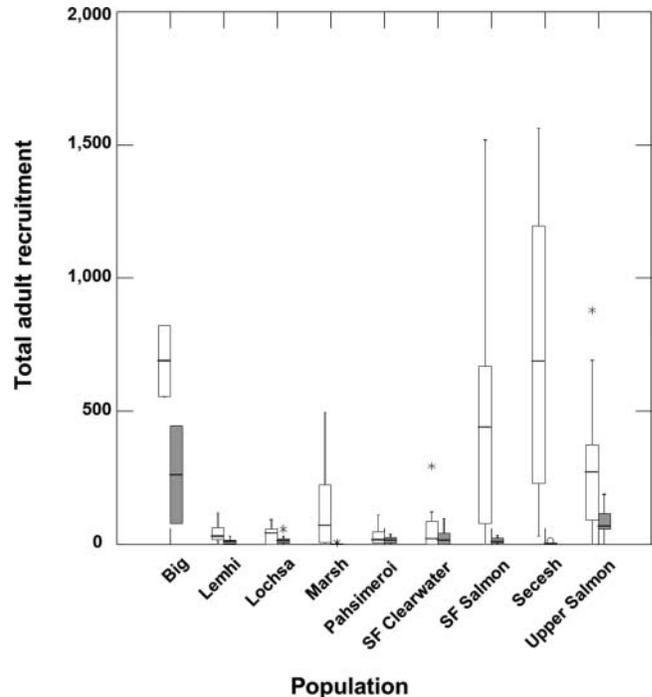


FIGURE 7. Comparison of total adult recruitment by emigrant type and population for Chinook Salmon. For each population, data for downstream-rearing emigrants are on the left (open boxes) and natal-reach-rearing emigrants are on the right (shaded boxes). Boxes represent the middle 50% of the observations and the median is shown by the bisecting line. Whiskers show range of values within 1.5 times the interquartile range. Outliers are represented by asterisks (*).

Idaho. The relative survival advantage between the two types ($\log_e S_a$) varies around zero among populations. However, the numerical advantage of the DSR type carries through to adult recruitment back to freshwater, although ratios of survival rates were much more variable than the numerical effect. The numerical advantage of adults produced from DSR emigrants arises from a greater abundance at exit from natal reaches but was not constant in time. For example, in cohorts returning fewer than 100 fish, NRR emigrants dominated numerically (Figure 6). Logically, relative fitness was greater for the NRR type for those populations at those times. We discuss the implications of our results for fitness and population dynamics below.

Demographic Effects of Diversity in Juvenile Migration Tactics

Our study demonstrates the importance of different migratory tactics to population recruitment and resilience. Diversity in migratory life histories spreads demographic risk (Kerr et al. 2010) and some life histories may tend to produce most of the spawning population. The more dispersive type is often the more productive component of the population (e.g., Kraus and Secor 2005), as we also found. In effect, the dispersive

type expands the niche of the population to take advantage of a greater expanse of the accessible habitat, resulting in greater adult recruitment to the spawning population (e.g., Neville et al. 2006; Morita et al. 2009; Anderson et al. 2013).

The fitness of a migratory life history is sensitive to the costs of movement (Gross 1987; Hendry et al. 2004); therefore, migratory fishes need connected stream reaches with rearing habitats of good quality to use (Northcote 1997). Connectivity to high-quality rearing habitats is important, even if these areas are not used for spawning and are distant from natal reaches (Anderson et al. 2013). Nonnatal habitats can provide significant survival and growth advantages for juvenile salmon, especially through winter (Ebersole et al. 2006). There may be indirect synergistic benefits to individual fitness from the ability to use a suite of habitats because juveniles that rear well tend to have good life performance (Lindström 1999; Metcalfe and Monaghan 2001; Taborsky 2006). The populations in this study have several hundred kilometers of river between their natal reaches and Lower Granite Dam (266 to 747 km), below which there is no record of them rearing. Much of this area above the dam is within statutory wilderness and therefore is affected minimally by anthropogenic factors, and also offers the riverscape connectivity necessary for dispersive life histories to be successful (Baguette et al. 2013). Population dynamics of stream fishes are greatly affected by the ability to move among habitats and exploit food resources (Schlosser 1995; Northcote 1997; Wipfli and Baxter 2010). Watersheds with a high degree of habitat complementation and connectivity support more robust salmon runs than watersheds with lower habitat complementation and connectivity (Kim and Lapointe 2011).

To advance our knowledge of the dynamics of these populations, it is necessary to understand the fitness values of the emigrant types that comprise them and when each type is likely to be successful. It is unclear from the data in hand at what point DSR emigrants may achieve a true survival advantage over NRR emigrants. In this study, winter survival is accounted for in DSR emigrants, whereas it is not in NRR emigrants. Winter can be a stressful season for young salmonids (Cunjak et al. 1998; Huusko et al. 2007; Brown et al. 2011). If winter survival is accounted for in the NRR type, DSR fitness may be higher than NRR fitness, but we do not have reliable survival estimates in the natal reaches of the study populations. Smith and Griffith (1994) reviewed studies of winter survival in 24 populations of juvenile salmonids exposed to prolonged periods of 0°C temperatures and estimated mean survival was 0.50 (SD = 0.18). Mitro and Zale (2002) estimated winter survival was 0.20 in good habitat for young Rainbow Trout *O. mykiss* in Henrys Fork in Idaho near our study area (we use this as a benchmark for severe winter conditions). Clearly, there should be some amount of winter mortality on fish remaining in their natal reaches until emigration.

We conducted a thought experiment to examine the likely consequences of winter mortality on relative fitness between the emigrant types. Consider S_w^* , the NRR winter survival threshold at which S_a is equivalent between types. This threshold is related to S_a by $\log_e(1) = \log_e[\text{DSR } S_a / (\text{NRR } S_a \times S_w^*)]$, which simplifies to $S_w^* = \text{DSR } S_a / \text{NRR } S_a$. For the 1998 cohort in the upper Salmon River, the closest data point to the model intercept β_0 (-0.11), S_w^* is 0.92. On average across the data set, likely winter survival will be such that the DSR type should have higher relative fitness. The S_w^* will vary among populations and is lowest for the Lochsa population (0.32). Severe winter conditions imply that the DSR migrant type has the higher relative fitness in all populations. Winter severity will vary, which may explain why there was a significant cohort effect on total adult recruitment but not on S_a . Certainly, the presence of significant population and cohort effects on total adult recruitment imply that relative fitness is not constant. This thought experiment underscores the importance to salmon conservation of dispersive life histories and the rearing and wintering habitats that support them; however, no studies have yet demonstrated that alternative migratory tactics have equal or unequal average fitness in salmonid fishes (Dodson et al. 2013).

Juvenile Chinook Salmon exhibiting the DSR migration tactic achieved a survival advantage over the NRR emigrants in SAR. Theoretically, dispersing individuals may accrue benefits by avoiding conspecific competition or deteriorating environmental conditions but incur costs by expenditures of limited time and energy as well as the risk of failure, i.e., mortality (Bowler and Benton 2005; Baguette et al. 2013). In this case, we hypothesize that the proximate advantages of downstream rearing are (1) earlier and easier final emigration the following spring and (2) increased overwinter survival and additional growth opportunity. These two hypotheses are not mutually exclusive.

In terms of demography, dispersive life history types increase population productivity and resilience, but resident life histories enhance stability, and thus both contribute to population persistence (Kerr et al. 2010). In the stream-type Chinook Salmon populations of Idaho, the capacity of the habitat to produce NRR emigrants is limited, whereas production of DSR emigrants is less constrained (Walters et al. 2013). In most of Idaho, the salmon spawning reaches are infertile (Sanderson et al. 2009) and have a short growing season. Salmon spawning is concentrated by philopatry, but rearing space and food usually limit smolt production rather than spawning habitat (Quinn 2005). This tension impels movement by juveniles to prepare for successful emigration to, and survival in, the ocean. The tradeoff between freshwater foraging opportunities versus winter mortality encourages diversity in migratory life histories (Dodson et al. 2013). Given limitations in spawning reaches, the DSR type should be more important in recovery as abundance is increasing, while the

NRR emigrants should buffer the population during periods of low abundance (Figure 6).

Implications for the Snake River Basin

For population-specific assessment and management of Chinook Salmon in the Snake River basin, a better understanding of rearing and winter habitats is needed. Migrating salmonids often show fidelity to feeding and refuge habitats (Northcote 1997); therefore, specific reaches may be important to a population. In interior Oregon, Tattam (2006) found that most individuals of a steelhead (anadromous Rainbow Trout) population spent the winter in a relatively short reach in the main stem of the South Fork John Day River. Confined use of habitat increases population vulnerability to catastrophe. In this study, we demonstrated recruitment of fish from downstream rearing habitats into the adult population, but we do not know the extent of these habitats. However, DSR emigrants typically arrive at Lower Granite Dam approximately a month earlier than the NRR emigrants (Venditti et al. 2005), suggesting that habitats occupied by DSR emigrants during winter are a significant distance downstream from the natal reaches. Our results suggest a broad focus is needed in restoration plans and that rearing reaches downstream from spawning grounds should also be addressed. In general, this study has interesting demographic implications for how migratory populations of stream fish use accessible habitats and how managers may use this understanding to increase adult recruitment.

Similarly, management of the migration corridor is focused on the aggregate rather than specific populations of concern. If there are weak stocks, the aggregate approach may inhibit effectiveness of recovery actions. Early ocean entrance seems to be important to survival to adulthood (Scheuerell et al. 2009). Several studies have demonstrated that delayed emigration to the ocean results in lower survival (Petrosky and Schaller 2010; Haeseker et al. 2012). Because DSR emigrants have a different timing into the migration corridor (Venditti et al. 2005), management actions in the migratory corridor may affect populations differently.

In summary, juvenile salmon migrate to the ocean where they can maximize growth and therefore eventual fecundity. Stream-type Chinook Salmon in Idaho spawn in some of the highest, most remote locations accessible. Here they potentially overseed the rearing capacity of natal habitats with eggs but maximize early survival and therefore production of fry, even though current adult escapements are well below historical abundance. However, these streams are infertile with short growing seasons and harsh winters. It is logical that salmon populations constrained by rearing and wintering habitat in natal reaches would exhibit some amount of juvenile movement to avoid these constraints. We demonstrated that juvenile Chinook Salmon in Idaho do indeed use downstream rearing habitats effectively, thereby increasing recruitment of adults back to the spawning gravels in these populations. This study

illustrates how dispersive life histories are essential to achieve the full productive potential of migratory stream fish populations.

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Appendix: Trap and Population Statistics

TABLE A.1. Summary of trap operations and values used in the analyses of Chinook Salmon by population, cohort, and tactic. These include number of tags placed and estimates of trap efficiency, juvenile abundance (juvenile \hat{N}), survival from trap to Lower Granite Dam (S_{t-l}), smolt-to-adult return rate (SAR), survival from trap to adult (S_a), and total adult recruitment (adult \hat{N}). Tactics are downstream rearing (DSR) or natal-reach rearing (NRR).

Cohort	Tactic	Tags	Trap efficiency	Juvenile \hat{N}	S_{t-l}	SAR	S_a	Adult \hat{N}
Big Creek								
2007	DSR	3,185	0.0923	46,555	0.3970	0.0301	0.0119	555
	NRR	829	0.1000	9,331	0.6810	0.0124	0.0084	79
2006	DSR	5,454	0.2372	44,461	0.2580	0.0718	0.0185	823
	NRR	725	0.0400	18,981	0.5140	0.0456	0.0234	445
Lemhi								
2007	DSR	3,223	0.0991	28,928	0.3335	0.0093	0.0031	90
	NRR	340	0.1997	1,190	0.7172	0.0041	0.0029	4
2006	DSR	3,327	0.3440	12,909	0.3175	0.0293	0.0093	120
	NRR	258	0.2610	644	0.7539	0.0308	0.0233	15
2005	DSR	2,452	0.2743	11,052	0.3281	0.0394	0.0061	68
	NRR	310	0.3162	1,206	0.7200	0.0086	0.0032	4
2004	DSR	2,063	0.1584	9,951	0.2658	0.0055	0.0015	14
	NRR	409	0.3374	1,312	0.6800	0.0108	0.0073	10
2003	DSR	1,613	0.1491	6,375	0.1961	0.0000	0.0000	0
	NRR	383	0.2559	1,590	0.4700	0.0000	0.0000	0
2002	DSR	4,147	0.2167	17,981	0.2646	0.0046	0.0012	22
	NRR	586	0.2872	2,000	0.5300	0.0000	0.0000	0
2001	DSR	2,580	0.0792	40,429	0.1712	0.0045	0.0008	31
	NRR	370	0.1005	2,898	0.4800	0.0113	0.0054	16
2000	DSR	1,908	0.1283	10,836	0.3109	0.0084	0.0026	28
	NRR	199	0.1313	1,489	0.5200	0.0097	0.0050	7
1999	DSR	1,918	0.1434	12,246	0.2743	0.0000	0.0000	0
	NRR	142	0.1631	852	0.5800	0.0243	0.0141	12
1998	DSR	1,847	0.1486	10,739	0.3693	0.0147	0.0054	58
	NRR	283	0.1555	1,818	0.6700	0.0158	0.0106	19
1997	DSR	3,586	0.1597	40,425	0.3788	0.0029	0.0011	45
	NRR	623	0.1293	4,930	0.7400	0.0087	0.0064	32

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TABLE A.1. Continued.

Cohort	Tactic	Tags	Trap efficiency	Juvenile \hat{N}	S_{t-l}	SAR	S_a	Adult \hat{N}
Lochsa								
2007	DSR	1,020	0.2635	4,604	0.3763	0.0182	0.0069	32
	NRR	175	0.1372	1,287	0.8906	0.0128	0.0114	15
2006	DSR	2,187	0.4207	6,137	0.2522	0.0272	0.0069	42
	NRR	163	0.0902	2,128	0.6773	0.0091	0.0061	13
2005	DSR	1,508	0.2059	9,861	0.1655	0.0000	0.0000	0
	NRR	116	0.0442	2,166	0.5531	0.0000	0.0000	0
2004	DSR	3,398	0.2250	27,780	0.2769	0.0064	0.0018	49
	NRR	358	0.0750	5,707	0.6543	0.0085	0.0056	32
2003	DSR	2,130	0.1631	81,849	0.2145	0.0000	0.0000	0
	NRR	515	0.0998	4,998	0.5347	0.0036	0.0019	10
2002	DSR	2,964	0.1672	41,443	0.1768	0.0057	0.0010	42
	NRR	351	0.0706	4,624	0.3325	0.0171	0.0057	26
2001	DSR	3,259	0.2046	38,426	0.1012	0.0000	0.0000	0
	NRR	426	0.0815	5,014	0.3834	0.0000	0.0000	0
2000	DSR	2,288	0.2027	53,563	0.2025	0.0086	0.0017	94
	NRR	168	0.1014	1,705	0.4052	0.0147	0.0060	10
1999	DSR	623	0.2113	4,735	0.3814	0.0000	0.0000	0
	NRR	284	0.0654	4,025	0.5538	0.0000	0.0000	0
1998	DSR	1,226	0.0890	13,794	0.3418	0.0143	0.0049	68
	NRR	360	0.0640	7,045	0.4983	0.0167	0.0083	59
1997	DSR	2,764	0.1607	50,400	0.3054	0.0047	0.0014	73
	NRR	704	0.0782	12,234	0.5901	0.0024	0.0014	17
Marsh Creek								
2007	DSR	6,324	0.2216	39,412	0.3272	0.0174	0.0057	224
	NRR	265	0.3596	1,053	0.4514	0.0000	0.0000	0
2006	DSR	7,051	0.2708	31,834	0.3714	0.0363	0.0135	429
	NRR	190	0.2895	691	0.6300	0.0167	0.0105	7
2005	DSR	4,489	0.1663	36,077	0.2527	0.0106	0.0027	96
	NRR	79	0.3333	228	0.5900	0.0000	0.0000	0
2004	DSR	2,118	0.1395	18,700	0.2088	0.0023	0.0005	9
	NRR	211	0.3684	854	0.5200	0.0000	0.0000	0
2003	DSR	2,520	0.2715	207,358	0.1000	0.0000	0.0000	0
	NRR	729	0.3478	2,142	0.2800	0.0049	0.0014	3
2002	DSR	3,920	0.2520	139,993	0.1554	0.0000	0.0000	0
	NRR	2,174	0.4423	6,226	0.3300	0.0014	0.0005	3
2001	DSR	3,127	0.4334	112,584	0.1672	0.0019	0.0003	36
	NRR	650	0.3812	2,084	0.4800	0.0000	0.0000	0
2000	DSR	1,566	0.1642	14,823	0.3602	0.0142	0.0051	76
	NRR	119	0.2542	465	0.5400	0.0311	0.0168	8
1998	DSR	2,124	0.1024	61,880	0.3020	0.0265	0.0080	495
	NRR	263	0.1686	1,694	0.6300	0.0000	0.0000	0
1997	DSR	2,180	0.1892	29,396	0.3321	0.0069	0.0023	67
	NRR	157	0.0921	1,881	0.6900	0.0000	0.0000	0
Pahsimeroi								
2007	DSR	856	0.0928	10,610	0.2841	0.0041	0.0012	12
	NRR	77	0.0548	1,080	0.5124	0.0507	0.0260	28
2006	DSR	860	0.1730	6,407	0.2200	0.0793	0.0174	112
	NRR	276	0.1451	1,853	0.6700	0.0162	0.0109	20

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JUVENILE MIGRATION TACTICS OF CHINOOK SALMON

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TABLE A.1. Continued.

Cohort	Tactic	Tags	Trap efficiency	Juvenile \hat{N}	S_{r-l}	SAR	S_a	Adult \hat{N}
2005	DSR	2,374	0.0624	46,065	0.2300	0.0073	0.0017	78
	NRR	817	0.1243	6,595	0.5500	0.0067	0.0037	24
2004	DSR	1,995	0.1276	14,029	0.2027	0.0074	0.0015	21
	NRR	1,461	0.2244	6,731	0.6400	0.0021	0.0014	9
2003	DSR	1,920	0.0935	37,977	0.2200	0.0000	0.0000	0
	NRR	1,422	0.2392	6,187	0.4300	0.0065	0.0028	17
2002	DSR	2,639	0.1063	26,394	0.2300	0.0033	0.0008	20
	NRR	810	0.2518	3,433	0.4800	0.0051	0.0025	8
2001	DSR	2,721	0.0794	36,176	0.1992	0.0000	0.0000	0
	NRR	1,304	0.2452	6,189	0.5800	0.0013	0.0008	5
2000	DSR	320	0.0614	5,610	0.2100	0.0149	0.0031	18
	NRR	127	0.0439	4,083	0.6100	0.0000	0.0000	0
1999	DSR	1,434	0.1622	10,316	0.2700	0.0000	0.0000	0
	NRR	120	0.1391	1,924	0.5300	0.0000	0.0000	0
1998	DSR	825	0.1109	15,751	0.3700	0.0131	0.0048	76
	NRR	320	0.1234	2,646	0.7400	0.0211	0.0156	41
1997	DSR	878	0.1408	7,855	0.3602	0.0063	0.0023	18
	NRR	478	0.1261	3,485	0.7300	0.0115	0.0084	29
Secesh								
2007	DSR	4,265	0.0546	128,935	0.2521	0.0270	0.0068	877
	NRR	409	0.1659	1,685	0.2310	0.0000	0.0000	0
2006	DSR	4,971	0.2475	55,098	0.2772	0.0450	0.0125	687
	NRR	176	0.0000	0	0.4945	0.0000	0.0000	0
2005	DSR	3,325	0.1896	227,198	0.1943	0.0294	0.0057	1,298
	NRR	616	0.1070	2,422	0.2681	0.0182	0.0049	12
2004	DSR	3,516	0.1433	392,659	0.1318	0.0302	0.0040	1,563
	NRR	514	0.0636	3,739	0.1853	0.0000	0.0000	0
2003	DSR	4,764	0.1039	876,489	0.1436	0.0015	0.0002	184
	NRR	1,108	0.1786	4,613	0.2367	0.0000	0.0000	0
2002	DSR	3,327	0.1412	568,760	0.0951	0.0063	0.0006	342
	NRR	1,026	0.0982	6,619	0.2770	0.0000	0.0000	0
2001	DSR	6,967	0.1886	747,244	0.0990	0.0029	0.0003	215
	NRR	1,067	0.1231	5,471	0.2369	0.0000	0.0000	0
2000	DSR	5,232	0.2402	357,372	0.1596	0.0192	0.0031	1,093
	NRR	436	0.2180	1,355	0.4279	0.0000	0.0000	0
1999	DSR	5,390	0.2888	45,092	0.3463	0.0021	0.0007	33
	NRR	716	0.2877	2,025	0.4182	0.0000	0.0000	0
1998	DSR	3,604	0.1477	103,977	0.3181	0.0419	0.0133	1,385
	NRR	351	0.1381	1,441	0.3223	0.0088	0.0028	4
1997	DSR	6,601	0.1231	177,971	0.2640	0.0052	0.0014	243
	NRR	287	0.2438	1,378	0.3429	0.0102	0.0035	5
South Fork Clearwater								
2007	DSR	3,371	0.3538	27,404	0.1876	0.0127	0.0024	65
	NRR	818	0.1673	6,761	0.3035	0.0000	0.0000	0
2006	DSR	1,592	0.3198	7,171	0.1965	0.0064	0.0013	9
	NRR	1,103	0.1579	9,643	0.3405	0.0053	0.0018	17
2005	DSR	683	0.0846	7,444	0.0818	0.0000	0.0000	0
	NRR	2,329	0.2726	10,192	0.3565	0.0000	0.0000	0

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TABLE A.1. Continued.

Cohort	Tactic	Tags	Trap efficiency	Juvenile \hat{N}	S_{t-l}	SAR	S_a	Adult \hat{N}
2004	DSR	2,725	0.1671	72,679	0.1453	0.0101	0.0015	107
	NRR	570	0.1222	15,795	0.4689	0.0075	0.0035	55
2003	DSR	5,736	0.1684	139,993	0.1584	0.0011	0.0002	24
	NRR	3,881	0.1792	26,053	0.5027	0.0000	0.0000	0
2002	DSR	3,141	0.1445	192,887	0.0519	0.0123	0.0006	123
	NRR	2,434	0.1212	36,072	0.4739	0.0017	0.0008	30
2001	DSR	1,028	0.1000	94,471	0.0341	0.0000	0.0000	0
	NRR	2,800	0.1200	27,228	0.4257	0.0000	0.0000	0
2000	DSR	902	0.1300	19,463	0.1615	0.0069	0.0011	22
	NRR	1,832	0.2400	16,298	0.5510	0.0030	0.0016	27
1999	DSR	411	0.2595	1,802	0.2201	0.0000	0.0000	0
	NRR	324	0.1869	1,739	0.4898	0.0000	0.0000	0
1998	DSR	2,372	0.1993	116,223	0.2055	0.0123	0.0025	294
	NRR	1,767	0.1923	19,047	0.4716	0.0108	0.0051	97
1997	DSR	1,825	0.0399	528,900	0.1706	0.0000	0.0000	0
	NRR	1,444	0.1836	32,445	0.4569	0.0061	0.0028	90
South Fork Salmon								
2007	DSR	5,975	0.1996	52,946	0.2401	0.0230	0.0055	292
	NRR	1,491	0.3116	4,866	0.6100	0.0110	0.0067	33
2006	DSR	2,203	0.1762	69,770	0.2287	0.0476	0.0109	760
	NRR	944	0.4034	3,004	0.5800	0.0183	0.0106	32
2005	DSR	5,533	0.2878	63,248	0.2333	0.0108	0.0025	160
	NRR	2,008	0.4648	5,977	0.3800	0.0066	0.0025	15
2004	DSR	4,351	0.2889	313,995	0.1350	0.0136	0.0018	577
	NRR	1,561	0.4358	6,443	0.3600	0.0036	0.0013	8
2003	DSR	2,566	0.2020	546,670	0.1305	0.0000	0.0000	0
	NRR	2,583	0.3666	7,562	0.3800	0.0000	0.0000	0
2002	DSR	3,449	0.1290	761,350	0.0948	0.0061	0.0006	441
	NRR	1,375	0.2656	5,121	0.3800	0.0057	0.0022	11
2001	DSR	2,246	0.1588	659,711	0.0656	0.0204	0.0013	881
	NRR	587	0.3325	2,354	0.4600	0.0037	0.0017	4
2000	DSR	1,312	0.1721	132,065	0.1071	0.0000	0.0000	0
	NRR	650	0.3167	3,813	0.5100	0.0060	0.0031	12
1999	DSR	1,394	0.0979	194,042	0.1900	0.0000	0.0000	0
	NRR	480	0.2312	6,888	0.4800	0.0000	0.0000	0
1998	DSR	4,478	0.0932	242,991	0.2008	0.0311	0.0063	1,519
	NRR	1,582	0.1575	9,055	0.3800	0.0100	0.0038	34
1997	DSR	2,811	0.0668	366,613	0.1559	0.0091	0.0014	522
	NRR	949	0.1916	6,932	0.5200	0.0020	0.0011	7
Upper Salmon								
2007	DSR	1,579	0.0196	74,983	0.2070	0.0275	0.0057	427
	NRR	1,210	0.2264	5,728	0.6300	0.0184	0.0116	66
2006	DSR	3,331	0.0349	112,624	0.1938	0.0403	0.0078	879
	NRR	369	0.0351	9,964	0.6600	0.0287	0.0190	189
2005	DSR	4,094	0.0167	257,673	0.1576	0.0171	0.0027	692
	NRR	575	0.0464	12,010	0.5800	0.0090	0.0052	63
2004	DSR	4,456	0.0555	177,721	0.1313	0.0137	0.0018	319
	NRR	1,634	0.0919	17,682	0.5700	0.0129	0.0073	130

(Continued on next page)

JUVENILE MIGRATION TACTICS OF CHINOOK SALMON

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TABLE A.1. Continued.

Cohort	Tactic	Tags	Trap efficiency	Juvenile \hat{N}	S_{t-l}	SAR	S_a	Adult \hat{N}
2003	DSR	2,982	0.1261	137,286	0.1034	0.0032	0.0003	46
	NRR	4,126	0.1232	47,435	0.5300	0.0027	0.0015	69
2002	DSR	4,194	0.0955	193,337	0.1086	0.0066	0.0007	138
	NRR	2,507	0.1965	34,049	0.4700	0.0068	0.0032	109
2001	DSR	3,587	0.1224	164,990	0.1283	0.0065	0.0008	138
	NRR	2,649	0.1771	28,182	0.5200	0.0058	0.0030	85
2000	DSR	2,557	0.1448	59,827	0.1687	0.0301	0.0051	304
	NRR	695	0.0409	28,096	0.5900	0.0073	0.0043	121
1999	DSR	908	0.0864	14,691	0.2487	0.0000	0.0000	0
	NRR	384	0.1882	1,991	0.6200	0.0000	0.0000	0
1998	DSR	1,019	0.0402	30,750	0.2617	0.0337	0.0088	272
	NRR	527	0.1061	4,868	0.5800	0.0164	0.0095	46
1997	DSR	353	0.0523	8,020	0.2922	0.0097	0.0028	23
	NRR	279	0.0291	14,683	0.6600	0.0054	0.0036	53