ISAB SAR and SAS Metrics Report

Challenges and Opportunities for Improved Estimation, Interpretation, and Use of Smolt to Adult Return (SAR) and Survival (SAS) Metrics for Salmon and Steelhead in the Columbia River Basin

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Report Cover

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ISAB Smolt-to-Adult Return (SAR) and Survival (SAS) Metrics Report

Contents

List of Tables

List of Figures

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Executive Summary

Estimates of survival and return are used extensively in salmon fisheries management and the assessment of hatcheries, habitat improvement projects, hydroelectric facility modifications, and other activities affecting salmon and steelhead (henceforth, for simplicity “salmon” unless steelhead are specified). The estimates are also used for time-series comparisons among species and populations, abundance forecasts at different locations and life stages, and understanding the effects of natural environmental processes on salmon. Though survival and return estimates are needed for salmon management, conservation, and research, the approaches for estimating these two metrics are varied and complex. Important attributes are not always sufficiently documented or standardized, complicating the interpretation and use of survival and return estimates.

This report reviews the estimation of smolt-to-adult return (SAR) and smolt-to-adult survival (SAS) for Columbia River Basin salmon, with a focus on terminology, methodology, data inputs, and other attributes affecting their use in management decisions and research, monitoring, and evaluation. At their core, SAR and SAS are related but different metrics to represent fundamental phases of salmonid life-history: survival of smolts to adulthood and return for spawning. We define SAS as the estimated proportion of smolts leaving some specified location that survive to adulthood and are either taken in ocean or freshwater fisheries, stray, or return to a designated location in the river system (e.g., a hatchery or stream). We use SAR to indicate the estimated proportion of smolts leaving a specified location that return to that or another designated location on their return as adults. The distinction between SAR and SAS, and the terms return and survival, should be clearly defined when used. SAR, as typically used in the Columbia River Basin, refers to smolt-to-adult return, and its use as a proxy for SAS or “marine survival” can cause confusion. Notably, salmon taken in ocean fisheries are considered to have survived for the purposes of estimating SAS, but they have not returned to their designated location in the river and thus do not count toward the SAR estimate. Consequently, the use of SAR to estimate survival relies on the assumption of little or no ocean fishery interceptions.

Estimating SAR and SAS requires designated locations where smolt and adult abundances are estimated. These locations are often not the same for the two estimators for a given cohort of smolts or for different stocks, and the methods for estimating abundance depend on the mark and recapture methodology and sampling techniques. Consequently, for a single cohort of smolts, SAR and SAS estimates may be similar or very different, and the choice of which estimate to report, or to report both, can affect our understanding of a population’s trend or the effects of management. Moreover, directly comparing SAR or SAS estimates that are produced with different tagging methods, from different locations, representing stocks of different origins and life histories, or different definitions of smolts and adults can introduce unintended biases and can lead to erroneous conclusions. These metrics are available for public use, so comparisons are commonly made based on data within and beyond the Columbia River Basin. Consequently, well-defined terms, transparent methods, and consistent application are important for sound science and use in the management process.

SAR and SAS estimates are fundamental to understanding the responses to adaptive management actions and the status and trends of salmon throughout the Columbia River Basin, so the overall goal of this report is to promote their clear and consistent use. To that end, we 1) review how SAR and SAS are commonly estimated and used for Columbia River Basin salmon, 2) discuss some of the key assumptions and limitations in their use, 3) present some of the complexities associated with the apparently simple terms “smolt, adult, return, survival” and 4) make recommendations to help practitioners and readers best use and understand these metrics. Our goal is neither to criticize past studies nor to discourage the use of these metrics. Rather, we seek to heighten awareness of the variation underlying their estimation and the pitfalls related to their inconsistent or unclear application.

This report does not advocate specific ways of estimating and interpreting salmon return and survival, but we provide examples of the use of SAR and SAS in the region that illustrate some of the issues we have identified. We also consider some of the complexities in estimating mortality from fishing and natural causes at sea. Apportioning mortality to different years and life stages has frustrated fisheries scientists for decades. Mortality during the early marine phase may determine the success of the cohort, but it is very difficult to estimate with any confidence. In the Columbia River Basin, this early marine phase has special importance because it is more plausibly linked to the delayed effects of smolt exposure to the hydrosystem during seaward migration than is mortality that occurs years later.

To illustrate the complexities associated with survival and return estimates and the progress being made in this regard, the report highlights two efforts that have addressed the need for consistency in SAR and SAS definitions, data collection, storage, sharing, and analysis. First, the Ad Hoc Supplementation Workgroup (AHSWG) was created in response to the ISAB and ISRP recommendations for an interagency evaluation of hatchery supplementation in the Columbia River Basin (ISRP and ISAB 2005-15). Their report provides a framework for integrated hatchery research, monitoring, and evaluation (AHSWG 2008), including standardized performance measures and definitions for natural population status and trends and hatchery effectiveness monitoring, including SARs. Second, the

Coordinated Assessment Partnership (CAP) is a basinwide collaborative effort to share standardized salmonid population metrics and high-level indicator data. It arose to improve data management, standardization, and sharing of research, monitoring, and evaluation information. Information is shared via a publicly accessible Coordinated Assessments Data Exchange System (CAX).

SAR and SAS estimates are essential to salmon conservation and management efforts in the Columbia River Basin and the broader science and management communities. Those who generate and use the estimates and manage data archives all contribute to their usability. We make the following summary recommendations to improve the estimation, interpretation, documentation, and usability of SAR and SAS metrics in the Columbia River Basin:

1. Provide clear study objectives and describe the application for studies using SAR and SAS.
2. Clearly define and consistently use the terms SAR, SAS, smolt, adult, return, and survival.
3. Describe how SAR and SAS are estimated and how time-series data are analyzed.
4. Report Passive Integrated Transponder (PIT)-tag detections for SAR components (downstream, ocean, upriver) where applicable.
5. Maintain the integrity of long-term SAR and SAS datasets by comparing results of different marking and analytical methods, developing robust conversions where appropriate, and reporting Coded Wire Tag (CWT)-based SAS estimates for representative stocks throughout the Basin.
6. Augment SAR reporting in publicly accessible databases to include SAS.
7. Where appropriate for the application, adjust SAR and SAS estimates to a common age at maturity and provide the rationale and methods for adjustments.
8. Use SAR and SAS metrics from surrogate populations with caution and explain how well the surrogate represents the population of interest.

The ISAB appreciates the significant effort of Columbia River Basin scientists to estimate SAR and SAS and the critical role these metrics play in salmon and steelhead management in the Basin. Our report builds on that work to improve future use and interpretation of SAR and SAS metrics.

Challenges and Opportunities for Improved Estimation, Interpretation, and Use of Smolt-to-Adult Return (SAR) and Survival (SAS) Metrics for Salmon and Steelhead in the Columbia River Basin

1. Introduction

Pacific salmon and anadromous trout (henceforth, for simplicity, "salmon") are exceptionally important in the culture, commerce, recreation, and ecology of the Pacific Rim, and their complex migration patterns, habitat requirements, and life history patterns pose special challenges for their conservation and management. They experience mortality in many distinct life stages and habitats: during incubation as embryos in the gravel, as they feed and grow in streams and lakes, as they migrate seaward, in the estuary, coastal waters, and open ocean where they feed and grow, in rivers as they migrate homeward and stage prior to spawning, and as they reproduce on the natal spawning grounds. The conservation needs arising from salmon life history and migrations have spurred the invention, development, and application of many methods for assessing their abundance, marking them, and keeping track of their movements and survival in the habitats that they sequentially use. Concurrently, extensive systems have been developed to collect, archive, and distribute data on salmon for the many entities responsible for their conservation and management, including but not limited to fishery managers, irrigators and other water users, hydroelectric dam operators, forest practice regulators, port authorities, and scientists trying to understand their population dynamics and forecast their future abundance. This report addresses the intersection between different salmon survival metrics, marking and analytical methodologies, and the needs of different management entities, scientists, and other interested parties.

The need to understand mortality in different habitats exists to some extent for all Pacific salmon populations (and Atlantic salmon as well: reviewed by Thorstad et al. 2012), but the populations in the Columbia River Basin face great challenges and have been extensively studied. Consequently, data generated from the Columbia River Basin are commonly used within the basin and in broader scientific literature on salmon ecology and conservation, and in public discourse regarding policies. This report draws from the scientific literature within and beyond the Columbia River Basin pertaining to salmon return and survival patterns and the techniques for studying them but is tailored to a readership primarily within the Columbia River Basin community, including those who collect and report data, and those who make decisions and policies based on such data.

In the Columbia River Basin, seaward migrating smolts are exposed to a complex suite of native and non-native predatory fishes, birds, mammals, and pathogens, and they encounter the hydrosystem at dams, bypass facilities, reservoirs, and transportation operations designed to mitigate hydrosystem effects. At sea, salmon are exposed to natural mortality that varies in time and space and typically has a large effect on the population's overall productivity. Several lines of evidence (detailed later in this report) indicate that much of the marine mortality occurs in the early period of ocean residence, and previous exposure to the hydrosystem may make the fish more vulnerable at this time. The duration of marine residence and exposure of immature and maturing salmon to predators and fisheries varies with species, population, sex, and year of ocean entry. As the surviving adults migrate through the estuary upriver to spawning sites and hatcheries, further mortality occurs from fishing, pinnipeds, delays, thermal stress, and disease. Estimates of salmon survival and return from the ocean are critical for understanding their life history and responses to disturbance, and for their conservation and management. However, estimation is complicated by the diverse agents of mortality, the broad ocean area where the losses occur (e.g., Holsman et al. 2012), the methodologies for estimating abundance and losses, and the extended spans of space and time over which mortality occurs.

The terms "smolt-to-adult survival" (SAS) and "smolt-to-adult return" (SAR) and are commonly used performance metrics in the science and management of Columbia River salmon (Figures 1 and 2), and SAS is widely used outside the Columbia Basin as well (e.g., coho salmon in Washington and British Columbia: Zimmerman et al. 2015; sockeye salmon across the Pacific Rim: Koenings et al. 1993; cutthroat trout in the Cowlitz River: Tipping and Blankenship 1993). The scientific literature also has many variants on this term; "marine survival" is very common for Pacific salmon (e.g., Thedinga et al. 1998) and Atlantic salmon (e.g., Thorstad et al. 2012), in some cases even if the fish are not yet smolts or entering the marine environment (Thorne and Ames 1987), and "juvenile-to-adult survival" has also been used (e.g., Evans et al. 2014; James et al. 2023). In some cases, "marine survival" is used to refer to the dynamics of populations without specific data on the numbers of smolt migrating to sea (Ohlberger et al. 2025).

The value of information on smolt-to-adult survival was recognized over a century ago, as evidenced by the scientists who marked smolts and examined fishery and escapement samples for such fish. For example, Barnaby (1944) reported on a series of marking studies using fin clips on sockeye salmon smolts from the Karluk River system in Alaska. "The average return from the marking of 3-year seaward migrants was 17.4 percent and for the 4-year seaward migrants was 25.7 percent" [p. 294]. The estimates included catch sampling at the cannery and the escapement, so these were, in effect, SAS estimates as the term is currently used: SAS is the proportion of seaward migrating smolts that survived to adulthood, including those taken in fisheries and those escaping to spawn.

The term SAR (sometimes "Survival from emigration to adult" or $S_{e\text{-}a}$, e.g., Copeland et al. 2024) is primarily used in the Columbia River Basin research and management communities, but elsewhere it has been used synonymously with "smolt survival" (e.g., Sobocinski et al. 2020) or "marine survival" (Taylor 1980; Holsman et al. 2012). We have not determined the first use of the term "smolt to adult return," but Raymond (1979) reported on fish marked with a series of brands in the Columbia River Basin. "The percentage of adults returning from the estimated number of juvenile chinook salmon and steelheads [sic] migrating downriver each year reflected the status of fish passage conditions in the Snake and Columbia rivers through the duration of this study (1966 to 1975)." [p. 513]. Outside the Columbia River Basin the concept is even older. For example, Forester (1954) studied Cultus Lake, B.C. sockeye salmon and reported "the number of seaward-migrating smolts for each year from 1927 to 1944 ... and the number of adults produced from each smolt seaward migration returning in the spawning escapement to the lake." [p. 350]. Foerster (1954) explicitly recognized that the returns were affected by fisheries (which could not be precisely estimated) and natural mortality, so these were essentially SAR estimates as the term is used.

Based on common but not universal usage, we define SAR as the proportion of smolts that survive all natural and fishery mortality between designated locations on their seaward and return migrations. In contrast, we define SAS as the proportion of smolts that survive to adulthood: those that return to a reference location plus those that are caught in ocean and river fisheries or stray and never arrive at the reference location (Figure 1). Note that Figure 1 is not a dichotomous key – the sampling and tagging approaches (described later) used to generate SAS and SAR estimates often differ. The juvenile and adult reference locations are sites where juveniles are marked, counted, and released as the starting point for the calculation process, and the sites where adult returns are estimated. Reference locations are typically dams, hatcheries, or tributaries (Figure 2).

There are many reasons for calculating SAR and SAS statistics for populations and population groups. These metrics are often used to monitor trends in hatchery and natural-origin populations, and to assess the effectiveness of activities designed to benefit these salmonids. Their wide usage over decades attests to their utility for assessing population status, and the terms SAR and SAS are ubiquitous in the world of Columbia River Basin salmon science and management. However, in the decades of reviewing scientific documents, the ISAB has noticed that the estimation methods often lack complete documentation, discussion of their comparability to other estimates is limited, and the validity of assumptions could be more clearly documented.

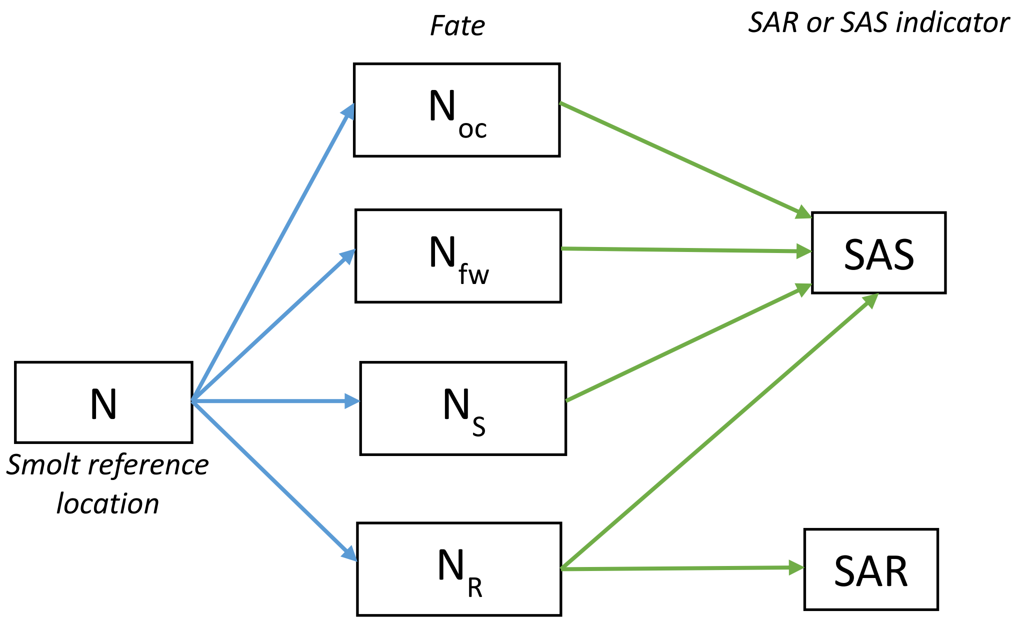


Figure 1. Diagram of an idealized salmon population depicting primary fates and definitions of SAS and SAR. N = number of smolts at a freshwater reference location; N_{oc} = number of adults from that cohort taken in ocean fisheries; N_{fw} = number of adults taken in freshwater fisheries below the adult reference location; N_s = number of adults that stray to areas downstream of the adult reference location; N_R = number of adults returning to the freshwater reference location. SAS = smolt-to-adult survival, where adults are the estimated numbers of those who survive to be harvested (N_{oc} + N_{fw}), plus those that stray (N_S), plus those that return (N_R). SAR = smolt-to-adult return, where adults are the estimated number of returns (N_R). Blue arrows link smolts (N_S) to their fate. Green arrows link the fate to the SAS and SAR indicators.

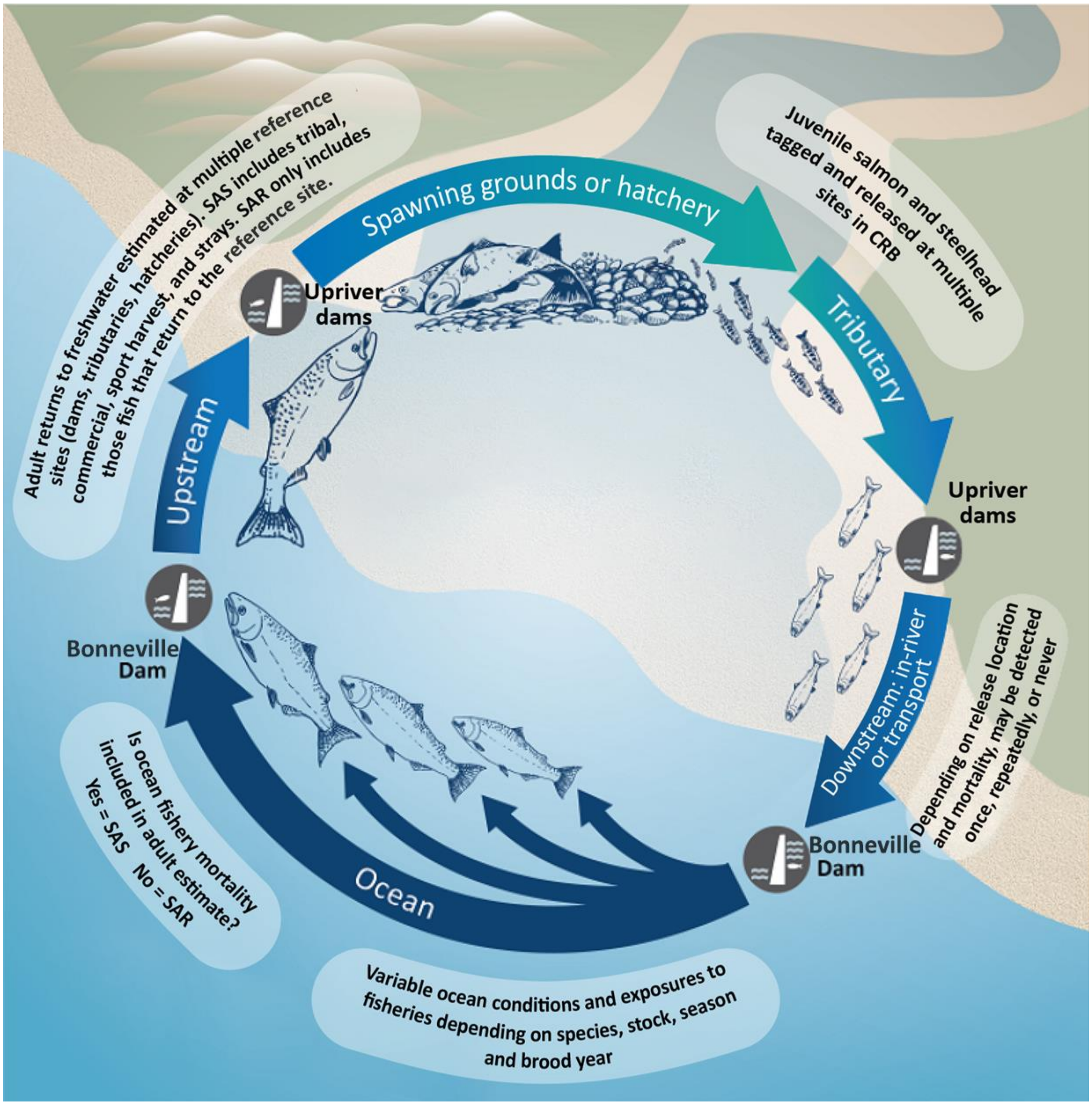


Figure 2. Graphical representative of SAS (smolt-to-adult survival) and SAR (smolt-to-adult return) definitions and reference locations for an illustrative Columbia River Basin (CRB) cohort of salmon, moving clockwise from the upper right. An important distinction between SAR and SAS is whether fisheries catch is included in the adult count. Salmon caught in ocean fisheries are included as survivors in SAS but not as returns in SAR. Adult returns to freshwater are estimated at a specified reference location using data collected at one or more sites (dams, tributaries, hatcheries). SAS includes ocean fishery harvest, all tribal, commercial, and sport harvest, strays, and returns in the adult count. SAR only includes estimated return to a specified adult reference location (typically a dam, tributary, or hatchery) in the adult count. (Source: Life cycle graphic modified from Figure 1 in Crozier et al. 2021).

In the Columbia River Basin, SAR and SAS goals have been adopted to guide salmon management and evaluate management actions and status and trends. For example, the mission of the Columbia River Fish and Wildlife Program of the Northwest Power and Conservation Council (NPCC) is to protect, mitigate, and enhance fish and wildlife populations in the Columbia River Basin affected by the development and operation of hydropower facilities. To do so, the Fish and Wildlife Program uses strategy performance indicators to track and assess implementation success. For anadromous fish populations, SAR is one such indicator. The 2020 Addendum to the 2014 Fish and Wildlife Program (NPCC 2014/2020) defines biological objective S2 as "contribute to achieving a smolt-to-adult return ratio (SAR) in the 2-6 percent range (minimum 2 percent; average 4 percent) for listed Snake River and upper Columbia salmon and steelhead, as well as for non-listed populations." This metric and threshold are widely referenced in scientific papers (e.g., Welch et al. 2020; Jacobs et al. 2024) and public discourse (e.g., Trout Unlimited online article). In the Fish and Wildlife Program's Comparative Survival Study (CSS), analysts estimate and update time series of SARs for many natural and hatchery-origin anadromous salmon population groups in relation to the 2-6% SAR objective (McCann et al. 2023). Similarly, the Lower Snake River Compensation Plan (LSRCP), implemented by the tribes and states and administered by the U.S. Fish and Wildlife Service, generates SAR and SAS metrics, and has developed SAR and SAS goals specific to hatchery programs.

Those who generate the time series of SAR and SAS estimates (e.g., the CSS and LSRCP) or other metrics of exploitation and smolt survival (e.g., the Chinook Technical Committee of the Pacific Salmon Commission) understand how the metrics are derived, including the assumptions, strengths, and limitations of each. However, readers of the very detailed and lengthy technical reports (which may not include needed caveats) produced by such entities, may not grasp their many complexities. When used with clarity, consistency, and care, these metrics provide important insights into salmon survival and thus inform pressing management and conservation problems and assessments, but failure to appreciate their nuances can be problematic.

1.1. Goals and Objectives

This report's overall goal is to promote clear and consistent reporting of SAR and SAS for accurate interpretation of trends and comparisons within and among subbasins and programs. Specifically, we 1) review how SAR and SAS are commonly estimated and used for Columbia River Basin salmon, 2) discuss some of their key assumptions and limitations, and 3) make recommendations to help users understand these metrics. We seek to foster scientific approaches and communication about the status of Columbia River Basin anadromous salmonids by explaining the importance of consistency in the terminology, definitions, methodology, and research and management application of SAR, SAS, and their component survival rates. We intend this report to be forward-looking and positive, thus references to past reports are not intended as criticisms, nor do we question prior analyses. To accomplish these goals and inspire further conversation on these important topics this report addresses the following objectives:

1. Review key terms related to life history and performance: smolt, adult, return, and survival.
2. Describe the life histories of Columbia Basin salmon related to calculating SAR and SAS.
3. Summarize SAR and SAS definitions and enumeration methods and describe their use in Columbia River Basin salmon management and research, monitoring, and evaluation.
4. Highlight examples where SAR and SAS metrics have been used in comparative studies and discuss their strengths and weaknesses for such comparisons.
5. Describe the utility of apportioning mortality to different life stages for SAR and SAS estimates.
6. Review methods and rationale for adjusting counts of adults to a common age for SAR and SAS estimates.
7. Characterize past and ongoing efforts in the Columbia River Basin to standardize terminology, definitions, and approaches to improve consistency, comparability, and quality of survival data.
8. Provide recommendations to improve consistency in terminology, definitions, and approaches to promote sound application in survival rate comparisons and management decisions.

2. Scope and Approach

Our report focuses on SAR and SAS metrics because of their importance for tracking the status and trends of salmon populations. We also consider what is known about stage-specific survival rates at sea. Losses at sea contribute strongly to SAS and SAR values, but, unlike losses during downstream migration of smolts to sea and upstream return migration of adults, it is very difficult to determine when and where fish died and what caused their death. Our geographical focus is the Columbia Basin, and we provide examples from many subbasins. However, we emphasize the Snake River, in part because of the wealth of data from there, and because of the heightened scrutiny of that area related to the Lower Snake River Compensation Plan, to the dams in the lower Snake River, and to the annual Comparative

Survival Study reports. Similarly, we focus on Chinook salmon, steelhead, and, to a lesser extent, sockeye salmon because the data on these species are richest, but the principles apply to other salmon as well. Our review includes both recent applications and older, influential works, and past ISAB and ISRP reports, such as:

- ISAB reviews of the Comparative Survival Study (see most recent, ISAB 2024-3)
- ISAB Review of the Coast-Wide Analysis of Chinook Salmon Smolt to Adult Returns (SARs) by Welch et al. (ISAB 2021-3)
- ISAB Comparison of Research Findings on Avian Predation Impacts on Salmon Survival (ISAB 2021-2)
- ISAB Dam Bypass Selectivity Report: Review of Analyses of Juvenile Fish Size Selectivity in Dam Bypass Systems and Implications for Estimating and Interpreting Fish Survival (ISAB 2021-1)
- ISAB Predation Metrics Report (ISAB 2016-1)
- ISRP Final Report: Mainstem and Program Support Category Review (ISRP 2019-2, pages 22-23)
- ISRP Lower Snake River Compensation Plan (LSRCP) Reviews and supporting materials (e.g., ISRP 2023-1 and ISRP 2014-6), and new information provided for this review
- StreamNet and the Coordinated Assessments Partnership

3. Review and Discussion of SAR and SAS

This section covers 1) definitions of smolts and adults as the terms pertain to SAS and SAR, 2) species and life history variants in the Columbia River Basin that are important for understanding SAR and SAS, 3) SAR and SAS definitions, distinctions, and relevant enumeration methods, and 4) applications of SAR and SAS in the Columbia River Basin with selected examples.

3.1. Basic biology of salmon smolts and adults, as related to SAR and SAS calculations

3.1.1. What is a smolt?

The first "S" in SAR and SAS is "Smolt." Smolts are salmonids making their first transition from freshwater to marine habitats. This transition involves a suite of physiological, morphological, and behavioral changes that are adaptive for downstream migration and life in salt water, and there is extensive scientific literature on these changes (Hoar 1976; McCormick 2012). The details of the internal (physiological) processes are not critical for estimating survival and return, but aspects of smolt timing are very important, as they differ markedly among and within species. In some cases, the increasing photoperiod and warming temperatures in spring synchronize circannual rhythms and initiate the cascade of physiological processes that prepare the fish to enter seawater and stimulate downstream migration in the spring. This classic smolt transformation process has been studied in species that migrate to sea after one or more years in fresh water, especially Atlantic salmon, steelhead, coho, and sockeye salmon (McCormick 1994).

This classic pattern is an oversimplification because salmonids often move downstream prior to smolting. Chinook salmon have long been known to vary greatly in juvenile migration patterns. They may leave their natal stream as newly emerged fry, as parr after feeding in the stream for a few weeks or months, or the following spring (Healey 1991; Apgar et al. 2021). Juveniles leaving in their first year of life are referred to as ocean-type (though Gilbert's [1913] original designation used the term sea-type) and older (i.e., yearling) migrants are referred to as stream-type (Healey 1991). In some populations, these juvenile life history types co-vary with adult migration timing (e.g., ocean-type juveniles are common in fall-returning adults and stream-type juveniles are common in populations with spring-returning adults: Taylor 1990). Some papers use terms for adult return timing when referring to the juvenile life type (e.g., use "fall Chinook" when they mean "ocean-type") or vice versa, but this is confusing and to be discouraged. This issue is especially confusing for summer Chinook salmon in the Columbia River Basin; those returning to the Snake River are generally stream-type, but those returning to the upper Columbia River are generally ocean type. The terms related to juvenile life history and adult return timing should not be used interchangeably.

As we detail in subsequent sections, the term "smolt" suggests a distinct condition, whereas it is a transformation process that may occur over a long distance and period of time (e.g., Berggren and Filardo 1993). Moreover, many salmon move downstream in different physiological conditions, so downstream movement and smolt transformation are not synonymous. Similarly, the term "adult" suggests a discrete status, but (as also detailed later in this report) it is also a process that takes place over many months and long distances. The terms "smolt" and "adult" are needed and useful, but they should be well defined and used precisely. Migration, growth, and mortality are processes that occur continuously, though not at equal rates, throughout the lives of salmon.

The timing, duration, routes, and success of downstream migration are related to environmental conditions (habitat features, water temperature and flow, etc.) and traits of the individuals such as size, growth rate, and stored energy. Consequently, migration patterns can differ markedly between natural-origin and hatchery populations, among natural populations, and among years. For example, genetically similar Chinook salmon smolts released from three hatchery facilities on the Deschutes River (entering the Columbia River just above The Dalles Dam) had survival rates that varied by an order of magnitude in each of the three years of the study among the facilities (Beckman et al. 1999). The link between smolt condition and growth rate can result in marked differences from the “conventional” patterns. High growth rates caused Chinook salmon from Yakima River and Willamette River populations to smolt in the fall of their first year rather than the following spring, as would be typical of these populations (Beckman and Dickhoff 1998). Diverse patterns can also occur in naturally rearing populations. Achord et al. (2007) injected PIT tags into wild Snake River Chinook salmon parr in different natal streams. Estimated survival to Lower Granite Dam varied greatly among populations and years, and migration timing was strongly affected by fixed factors (tagging site elevation) and by dynamic factors (temperature and stream flows). This study augmented previous findings that the offspring of wild spring and summer Chinook salmon from the Snake River populations migrated over a more protracted period than did the corresponding hatchery fish (Achord et al. 1996). However, the offspring of wild spring Chinook migrated later than the hatchery fish, but the offspring of wild summer Chinook migrated earlier than their hatchery counterparts.

These details about smolt physiology and migration are important for understanding SAR and SAS values. As detailed below, fish may move downstream and enter traps long before they undergo the smolt transformation and begin directed seaward migration. Put simply, not all fish moving downstream are smolts, not all fish released as smolts move downstream, and fish do not all move downstream in the same manner. Having said this, ISAB recognizes that one or a few life history forms may be the most common in a population, especially given the reduction in life history patterns that has occurred over time for many Columbia Basin natural populations. Thus, for some purposes using the typical form as the standard may be appropriate, but it is important to recognize the variation.

3.1.2. What is an adult?

As with “smolt,” the term “adult” can have different meanings in the context of SAR and SAS definitions. From the standpoint of reproduction and gene flow, any sexually mature – or maturing – fish is an adult, including anadromous males maturing a year younger than females of the population ("jacks") or two years younger ("mini-jacks"), or non-anadromous males. Jacks are distinguished from adult Chinook and coho salmon when counted at dams, not always included in returns to hatcheries, and their detection probability in carcass surveys is lower than larger and older salmon (e.g., Zhou 2002). Non-anadromous male Chinook salmon are essentially undetected in field surveys. For some species, such as coho salmon that mature after only a summer at sea as jacks or after a full year, large fish caught in marine waters are assumed to be destined to mature and spawn later that year. In contrast, other species and especially Chinook salmon may mature at any of several ages and so when caught at sea their maturity status is not known, unless examined in a scientific survey. These considerations (i.e., which ages of mature salmon constitute adults, and how to incorporate salmon of uncertain maturity status caught at sea in survival estimates) can complicate SAR and SAS analyses.

From the perspectives of fisheries management and efforts to understand the ecological processes controlling survival at sea, salmon are considered to have "survived" to adulthood if they remain alive after the earlier life stages when natural mortality rates are high and more variable. At this stage they recruit to (i.e., are exposed to) fisheries and are caught or return to rivers as maturing adults. Depending on the sex, species, and population, salmon may spend from a few months to several years at sea, resulting in variation in age-at-maturity and return. This varied marine residence period is especially marked in Chinook salmon. In this species, an individual might live long enough to recruit to fisheries and thus have "survived" yet not commence sexual maturation and homeward migration until the next or a future year.

Age composition and the concept of adulthood are important in the context of SAR and SAS estimates because, all other things being equal, the longer salmon remain in the ocean, the more likely they are to die there. Many Chinook salmon populations from California to Alaska have shown reductions in the proportion of older adults (Ohlberger et al. 2018), and such shifts complicate analysis of survival. Changes in smolt size and growth rates can affect age composition. Releasing bigger smolts from a hatchery yields higher proportions of jacks in coho and Chinook salmon compared to smaller smolts from the same facility (Bilton et al. 1982; Bilton 1984; Whitman 1987; Vøllestad et al. 2004), more sexually mature parr or mini-jacks in Chinook salmon (Larsen et al. 2004, 2006; Vøllestad et al. 2004), and younger female Chinook salmon (Quinn et al. 2004). As wild smolts are commonly smaller than hatchery-reared smolts from the same river, they often differ in age composition as adults. For example, Priest Rapids hatchery Chinook salmon sampled at sea averaged 70% age-4 and 30% age-5, but the wild Hanford Reach fish (with shared ancestry) were 44% age-4 and 56% age-5 (Norris et al. 2000). Similarly, Scheuerell (2005), Tattam et al. (2015), and Bosch et al. (2023) reported that larger wild Chinook salmon smolts were more likely to return at a younger age than were smaller smolts, although the effect varied among populations.

Another example of the greater ages at maturity in wild compared to hatchery origin adults was provided by Chen et al. (2023) for winter-run Chinook salmon in the Sacramento River system (Table 1). Depending on survival rates and exploitation at sea, regarding all these salmon as adults can distort an assessment of their ecological performance. Specifically, if hatchery fish spend fewer years at sea, their survival or return would be inflated relative to the natural origin fish if counted at face value. Carmichael and Messmer (1995) also reported differences in age composition for natural and hatchery-origin spring Chinook salmon in the Imnaha River system for the brood years (i.e., years in which the fish were spawned) 1982 to 1986 (Table 2). The total ages at maturity differ from the Sacramento River data, but the patterns are similar: younger age at maturity was observed in hatchery vs. natural-origin fish (and males vs. females).

Table 1. Proportional age composition of mature winter-run Chinook salmon in the Sacramento River system based on a combined sample of > 10,000 natural and hatchery-origin adults from 2005−2018, based on coded-wire tagged hatchery fish and scale samples from natural-origin fish (Chen et al. 2023).

Origin and sex	Age 2	Age 3	Age 4
Hatchery-origin males	0.30	0.62	0.08
Natural-origin males	0.19	0.44	0.37
Hatchery-origin females	0.11	0.84	0.05
Natural-origin females	0.07	0.85	0.08

Table 2. Proportional age composition of mature Imnaha River spring Chinook salmon from brood years 1982−1986 (Carmichael and Messmer 1995).

Origin and sex	Age 3	Age 4	Age 5
Hatchery-origin males	0.60	0.32	0.08
Natural-origin males	0.15	0.63	0.22
Hatchery-origin females	0.00	0.72	0.28
Natural-origin females	0.00	0.39	0.61

We can use the Imnaha River age-composition data in Table 2 to illustrate the connection between age at maturity and the estimation of survival. Let us assume that 400 adult salmon return: 100

males and 100 females each of natural and hatchery origin. The typical working assumption is that each salmon that returned is equivalent to the others. However, if we consider that age-4 is the standard, then fish returning at age-3 represent fewer age-4 equivalents because some might have died at sea in the intervening year. Likewise, fish returning at age-5 represent more than 1 age-4 fish because some that were alive at age-4 did not survive to age-5. Using the adjustments of 0.6 for age-3 fish and 1.25 for age-5 fish in Quinn et al. (2005) for similar marine ages, we would estimate the age-adjusted returns as 185 hatchery fish (78 males and 107 females) rather than 200, and 214.75 natural origin fish (99.5 males and 115.25 females). Thus, if these adults were produced from 10,000 smolts, the unadjusted SAR would be 2% for hatchery and 2% for wild fish, whereas the adjusted SARs would be 1.85% and 2.15%, respectively. In this example, the lower survival of the hatchery origin fish per unit of time at sea is masked by their tendency to mature at an earlier age. These estimates should not be taken literally, but they illustrate how differences in age at maturity can affect survival and return estimates.

The tendency for male Chinook salmon to mature without going to sea at all or return from the sea a year or two earlier than females of the population as jacks or mini-jacks (e.g., as described by Larsen et al. 2013) is a challenging form of life history variation from the standpoint of defining an adult. These male life history variants have long been known in wild populations (e.g., Rutter 1902), but their prevalence is often elevated in hatchery populations, resulting from faster early growth compared to naturally rearing fish. For example, Larsen et al. (2004) reported that “37-49% of the hatchery-reared males from this program undergo precocious maturation at 2 years of age and … a portion of these fish appear to residualize in the upper Yakima River basin throughout the summer” [p. 98]. Assuming an equal initial sex ratio, these data would indicate that ca. 20-25% of the total juvenile production adopted this life history pathway. Research in the Pahsimeroi River, Idaho indicated that 20% of the returning anadromous offspring had been sired by non-anadromous males (Steele et al. 2024). Ford et al. (2015) also reported that many juvenile Chinook salmon were sired by non-anadromous males of hatchery origin, but such males are also commonly produced by adults that spawned naturally (e.g., Koch et al. 2022). Regardless of their origin, in some cases these males can have a significant effect on the population’s gene pool, despite their lack of importance in fisheries or the population’s productivity. How jacks and non-anadromous males are treated in the context of counting adults for estimating SAR and SAS can affect the values and their interpretation.

Non-anadromous males occur in Chinook salmon and in *O. mykiss*, both non-anadromous females and males (i.e., rainbow trout) are common in natural resident (non-migratory) populations and as residualized fish produced by anadromous (steelhead) parents. Hatchery practices can affect the proportions of residuals (commonly males) produced by steelhead parents (e.g., the Winthrop National Fish Hatchery, Methow River: Tatara et al. 2019). Female rainbow trout can produce anadromous offspring (e.g., in the Yakima River: Courter et al. 2013), and blended complexes of natural and hatchery origin anadromous and non-anadromous *O. mykiss* occur as well (e.g., the Hood River: Christie et al. 2011). The decision on whether to include non-anadromous and early maturing fish as "adults" has clear implications for SAS or SAR estimates. The common practice of excluding them (especially non-anadromous forms) would decrease estimated survival estimates, whereas including them as adults would increase estimates. Thus, it is critical to clearly define the purpose and application of the estimates to align them and clarify exactly what data are included.

3.1.3. What is survival and what is return?

As with the terms smolt and adult, the "S" for "Survival" and "R" for "Return" in SAS and SAR need clear definitions and consistent use. Survival in SAS is the proportion of smolts (marked, detected, or counted at some location) that survive to be taken in fisheries plus those returning to spawning grounds or hatcheries. In many reports this is estimated from all the salmon taken in fisheries and those recovered in freshwater locations after expansion for subsampling. However, as explained above, summing the fish recovered can be misleading because maturity schedules vary from year to year, among populations or experimental groups, or for other reasons. For example, the Pacific Salmon Commission's Okanagan Work Group (2023) report listed the cumulative proportions of Okanagan Chinook salmon maturing at ages 3, 4, and 5. Over 23 brood years the age composition ranged widely (age 3: 0.7 - 13.5%, age 4: 6.4 - 52.1%, age 5: 55.4 - 99.3%). Because this variation affects apparent survival rates, they reported that "release for yearling smolts to age 3 survival" averaged 4.9% (range: 0.2 - 11.7%). Adjustment of survival to a standard age is common practice for some analyses, but in many other applications it is not done. We address this topic further in this report.

In the context of SARs, the term "Return" refers to adult salmon detected, recorded, or reconstructed at some specific location within the river system. The detection or reconstruction reference point depends on how the smolts were marked, adult detection capability, and the goals of the study. PIT-tagged fish can be detected with automated readers at one or more locations. For example, the 2023 Comparative Survival Study Annual Report listed their two primary adult detection points: Lower Granite Dam (LGR) and Bonneville Dam (BON), and the same two dams for smolts (though detections occur and could be reported at other locations). So, for some groups the SAR is from LGR – LGR, or LGR – BON, or BON – BON, and other combinations of locations could be used including in-stream detectors and hatcheries. If these locations are specified, and comparisons are made consistently, using LGR or another detection point can be very useful. However, use of any site complicates comparisons with populations that enter the Columbia River system below it because the populations would travel different distances to the estuary and thus experience different mortality regimes.

*A*ll SAR studies need not (and in practice cannot) have the same smolt and adult reference locations, but they must indicate how returns are estimated and to what extent they are comparable to estimates for other groups. The farther upriver the smolt and adult reference locations, the more difficult it is to identify and separate losses in the marine environment from those taking place during migration downstream and upstream. If the goal is to examine marine effects on survival, then PIT-tag data from smolts detected at Bonneville Dam to adults returning to Bonneville Dam, rather than locations farther upriver, provides the best approach. On the other hand, if the goal is to encompass as much of the life cycle as possible, then using an upriver location for smolts and adults is appropriate.

Salmon may die from natural causes or from fisheries (including retention and other forms of capture-related mortality) between their smolt and adult detection points. Whether natural mortality and fishing can be separated depends on how fish are marked. Few fisheries, especially marine, are sampled for passive integrated transponder (PIT) tags or genetic identity (parentage-based tagging – PBT) whereas most fisheries are sampled for coded wire tags (CWTs), making it routine to estimate fisheries catch after accounting for sampling effort and other considerations. Marine fisheries exploitation rates can vary greatly among species, populations, and years. For example, the PSC (2023) report on Okanagan River Chinook salmon indicated an average of 22.9% ocean exploitation rate (including catch and incidental fishing mortality, which they distinguished), with annual estimates ranging from 10.5% to 38.3% (Appendix E4). Some other stocks in the Columbia Basin have much higher exploitation rates, commonly 30-50% or higher, and other Chinook salmon have very low or negligible rates (e.g., Sharma and Quinn 2012), as do sockeye salmon and steelhead, likely resulting from their oceanic rather than coastal distributions (Beamish 2018). We note that the term exploitation rate should be defined when used. According to Walters et al. (2019), "In salmon fisheries, exploitation rate is defined as the proportion of the total stock that is taken as harvest, i.e., as (catch)/(number of fish at risk to harvest)."

Estimates of SAR rather than SAS are often reported for populations that are very lightly exploited in the ocean, often with a note added to the effect that ocean fishing rates are too small to be important. For example, upper Columbia River and Snake River spring (stream-type) Chinook salmon are very lightly exploited at sea (Waples et al. 2004, Table 3 below). The methods for estimating exploitation rates in that paper were not detailed as its primary purpose was population genetics and evolutionary lineages, but Sharma and Quinn (2012) examined fishery data and drew similar overall conclusions. In contrast, some upper Columbia River ocean-type, summer-run Chinook salmon have much higher ocean exploitation rates, as do lower river fall, ocean-type Chinook. A key difference between SAR and SAS is that SAR do not distinguish natural mortality and fisheries losses at sea.

Table 3. Estimated marine fishing exploitation rate (%, based on Pacific States Marine Fisheries Commission data), as reported by Waples et al. (2004, Appendix 2), categorized by region within the Columbia River system, river, season of adult return for Chinook salmon. Rivers listed together had identical estimates resulting from the use of index rates rather than rates specific to each population.

Basin	River	Run	Marine fishing (%)
Lower Columbia	Cowlitz, Kalama, Lewis	Spring	24
	Cowlitz, Kalama	Fall	46
	Lewis, Sandy	Late Fall	53
Willamette	McKenzie, N. Santiam, NF Clackamas	Spring	55
Mid-Columbia	Hanford Reach	Fall	39
	Warm Springs, NF John Day	Spring	1
	Deschutes	Summer-Fall	28
	Yakima	Spring	1
	Yakima	Fall	39
Upper Columbia	White, Nason, Chiwawa	Spring	1
	Wenatchee	Summer	68
	Methow, Twisp	Spring	2
	Methow, Similkameen	Summer	68
Snake	Lyons Ferry	Fall	36
	Minam, Lostine, March, Valley, Upper Salmon	Spring	1
	Imnaha, Secesh, Johnson	Spring-summer	1

Ocean fishery exploitation rates vary among stocks based on their marine distributions and among years for those with significant exploitation rates. Among 11 Columbia River Basin Chinook salmon stocks reported on by the Pacific Salmon Commission, exploitation rates of some increased while others decreased or changed little (Table 4). This example serves as a reminder that data on exploitation rates must be updated if estimates are included in survival and return models and used for management and evaluation decisions.

Table 4. Ocean (i.e., non-terminal) fishery exploitation (%) estimates for 11 Columbia River Basin Chinook salmon stocks as reported by the Pacific Salmon Commission (Chinook Technical Committee 2023). Data are reported for two decades separately (Appendix E4 provides annual estimates), and the most recent four years with complete data. The weighted mean was calculated using the numbers of years in each average. All stocks are hatchery produced other than the Lewis River and Hanford Reach Brights.

Chinook salmon stock	1999-2008	2009-2018	2018-2021	weighted mean
Cowlitz Fall Tule	37.9	22.3	19.0	28.7
Lewis River - Wild	34.3	32.6	41.6	34.5
Lower River Hatchery Tule	36.2	43.4	31.4	38.7
Spring Creek Tule	29.0	29.2	24.5	28.5
Willamette Spring	8.7	10.3	7.6	9.3
Columbia Upriver Bright	27.6	24.2	19.9	25.1
Hanford Wild Brights - Wild	29.5	30.8	21.5	29.0
Lyons Ferry Fingerling	13.7	18.1	12.2	15.4
Lyons Ferry Yearling	26.6	28.4	21.2	26.7
Similkameen Summer Yearling	27.2	25.2	10.4	24.1
Columbia River Summers	46.9	29.2	14.1	34.9

In reporting variation in exploitation rates over the years, the Chinook Technical Committee notes the distinction between catch and incidental mortality (Pacific Salmon Commission 2023):

> "Management strategies have changed considerably for fisheries of interest to the PSC since the PST was signed in 1985. Regulatory changes have included size limit changes, extended periods of Chinook Non-Retention (CNR) fisheries, mandatory release of Chinook salmon caught in some net fisheries, and MSFs [Mark Selective Fisheries] under various retention restrictions. Fisheries indices can be reported as either total mortality, or its components: catch mortality and incidental mortality (IM). Here we report total mortality for ISBM [Individual Stock-Based Management] fisheries, but the indices are split into components for AABM [Aggregate Abundance-Based Management] fisheries. Estimates of IM are essential for assessment of total fishery impacts, yet they cannot be determined directly from CWT recovery data. IM is estimated for both legal and sub-legal sized fish by

accounting for each of the following: (1) drop-off mortality of legal-sized fish in retention fisheries (CTC 2022b), (2) mortality of legal-size fish in CNR fisheries, (3) mortality of sublegal-size fish in both retention and CNR fisheries."

This distinction between catch and incidental fishing-related mortality emphasizes the many nuances in analyses of catch, exploitation, and other components of fishery-related mortality, as they relate to estimates of SAR and SAS.

Adults returning at different ages are typically combined to calculate and report SAR or SAS by brood year or smolt migration year (sometimes referred to as ocean entry year) rather than adult return year so that common factors like conditions in the ocean when the fish entered and subsequent fisheries are kept constant for the group. In stocks (and especially those from hatcheries) for which all smolts from a common brood year have the same ocean entry year, these conditions are essentially the same. However, for species with multiple smolt ages in wild populations, calculating survival or return by brood year vs. ocean entry or smolt migration year can yield quite different results. Hence, as with all these terms, it is important to explicitly state how reported results were calculated.

3.2. General life history patterns of Columbia River Basin salmonids

The anadromous salmonids of the Columbia River Basin vary greatly in the timing of seaward migration, return of adults, and spawning (Figure 3). These attributes affect their mortality patterns and mortality calculations. For example, juvenile chum and pink salmon migrate in early spring within days or weeks after emerging from the gravel and so are smaller as smolts than the other species. Once in the ocean, they typically migrate north along the continental shelf and then out into the Gulf of Alaska. Most Chum enter spawning tributaries in late October or early November and spawning peaks between the third week of November and early December. Chum salmon spawn at age-2 through age-5, although ages 3 and 4 are the most common; all pink salmon spawn at age-2. These two species are much less abundant in the Columbia River Basin compared to the other Pacific salmon and steelhead species, and they are also primarily distributed in the lower river and so are seldom included in SAR and SAS reports. However, the Columbia River system once supported an annual catch of over 500,000 adult chum salmon in some years (Fulton 1970; Johnson et al. 1997) and ca. 850,000 in 1928 (Fulton 1970). The ESU is currently listed as Threatened under the Endangered Species Act. The chum salmon spawning grounds are below Bonneville Dam and they likely have < 20,000 spawners annually (Table 43 in Ford 2022). In general, few chum salmon are counted at Bonneville Dam (but see e.g., Tomarow et al. 2007). Over the 20-year period from 2004 – 2023, counts at Bonneville Dam averaged 169 chum salmon based on DART (Data Access in Real Time – University of Washington). However, the 2023 count was 615 chum salmon and the 2024 count of 1135 was the highest since 1954, so they may be recovering. Chum salmon have open-ocean marine distributions (Urawa et al. 2018), and the exploitation of Columbia River chum salmon at sea is presumed to be very small. Thus, returns and survivals would be largely equivalent. From 2004 – 2023, counts at Bonneville Dam averaged 504 pink salmon on odd-numbered years and 9 on even-numbered years based on DART (Data Access in Real Time – University of Washington), consistent with the greater abundance of the odd-year run in the southern end of the species' distribution.

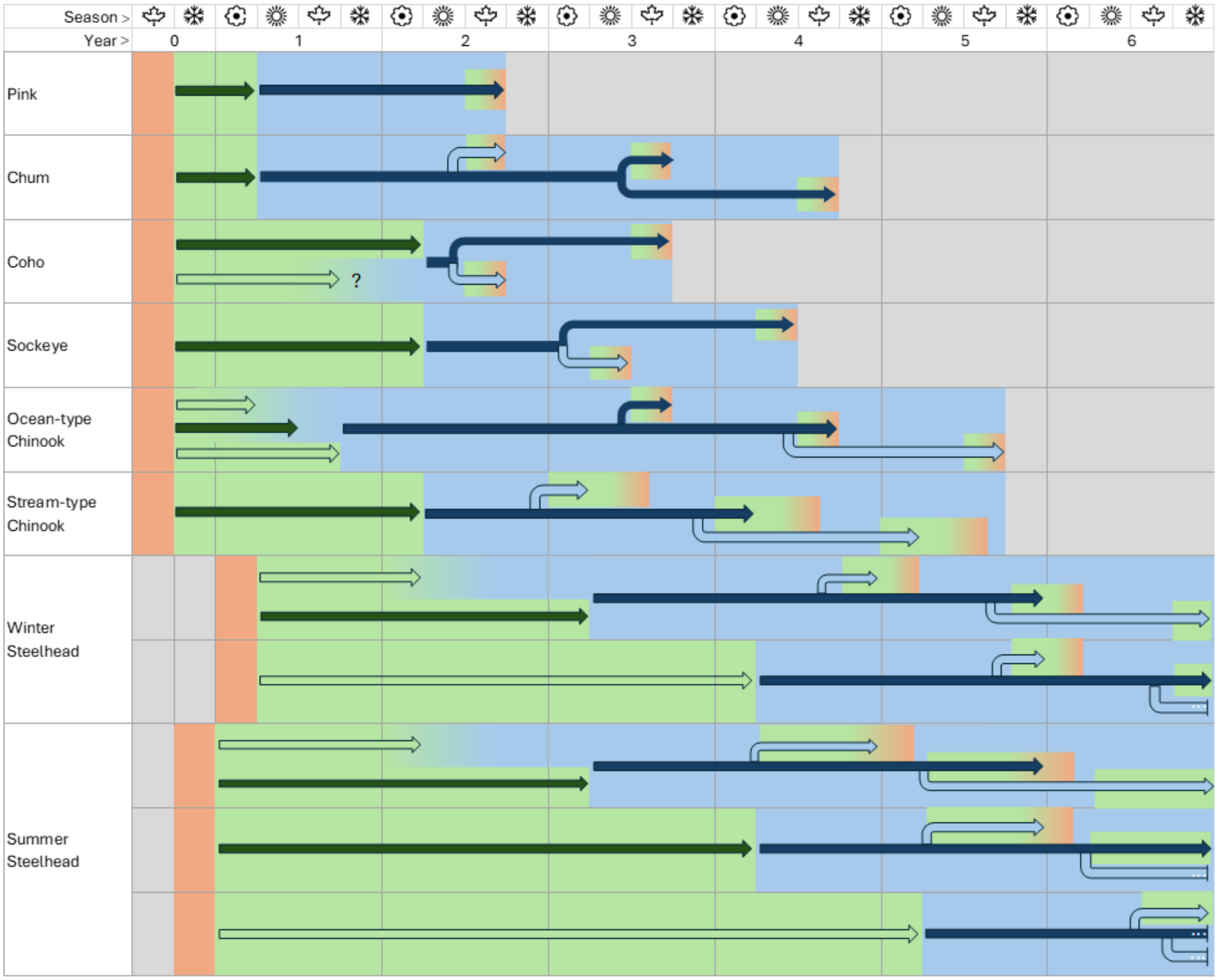
The distribution of sockeye salmon in the Columbia River Basin contracted greatly during the period of development (Fulton 1970; Mullan 1986; Nehlsen et al. 1991; Gustafson et al. 1997). They are now largely produced in the Lake Wenatchee and Okanagan Lake systems (Murauskas et al. 2021), with an ESA-listed population in the Sawtooth Valley, Idaho (Gustafson et al. 1997), and reintroduction efforts taking place in the Yakima River system (Matala et al. 2019). The Wenatchee and Okanagan populations differ in smolt size and timing (Peven 1987), and the Okanagan population has a higher proportion of age-3 (1.1) adults than does the Wenatchee population, which is dominated by age-4 (1.2) adults. Sockeye salmon tend to have an offshore marine distribution and are at most lightly exploited at sea. Throughout most of the species' range, the SAS of populations is estimated from smolt and adult abundance and estimates of fishery interceptions, but in the Columbia River Basin there are PIT tag programs for estimating returns. Notably, Murauskas et al. (2021) reported on PIT tag studies from 2012 – 2019 for Okanagan River basin sockeye salmon. Smolts were captured and tagged at five sites in the Okanagan River basin and detections were reported at McNary Dam as smolts, SAR to Bonneville Dam, and upstream travel and survival rate to McNary and Wells dams. Salient findings included the generally rapid migration rate and the high SAR for the smolts (0.4 - 6.1%), with significant year to year variation in SAR. Moreover, SAR values for the Skaha Lake (Canada) component exceeded those from the downstream Osoyoos Lake component of the population complex that spans the Canada/US border, at least in part because the Skaha Lake fish tended to mature at a younger age.

In another example of the use of PIT tags to estimate SAR for sockeye salmon, combined smolt detections at McNary Dam, adult detections at Bonneville Dam, and estimated fishery take below the dam revealed several findings pertinent to the present review (Williams et al. 2014). First, SAR estimates varied over 100-fold among years, from 0.2% in smolt year (i.e., year in which the fish migrated to sea as smolts) 1993 to 23.5% in 2008 (from Table 4 in their report). Second, the age composition of returning adults also varied greatly: from 1-4 years in fresh water prior to smolt migration and 1-3 years at sea. For example, in 2007, 46% had spent only one year at sea, but in 1994 and 1998, 68.4% and 56.8% had spent three years at sea, respectively (from Table 1 in their report). Consequently, SAR and age composition values averaged over many years can mask important inter-annual variation that informs interpretation of SAR and age-composition results.

The classic coho salmon life history involves a year of feeding in freshwater prior to seaward migration in the southern part of the range, with an increasing proportion of older smolts farther north (Weitkamp et al. 1995), followed by rapid migration through estuaries. In the Columbia River Basin, coho salmon are extensively produced in hatcheries, and these fish are released as smolts after one year of feeding. However, research has revealed much greater diversity in juvenile migration timing and habitat use among natural origin coho salmon, including downstream movements in the fall (e.g., Pess et al. 2011; Hance et al. 2016) seaward migration of subyearlings and use of estuaries. Such work has been documented in the Salmon River, Oregon (Jones et al. 2014, 2021), the Grays River in the lower Columbia River system (Craig et al. 2014), and elsewhere. Large disparities in estimates of marine survival in coho salmon between tag-based and abundance-based methods were attributed to juveniles moving from the natal habitat prior to smolt trapping (Cochran et al. 2019), illustrating the importance of this phenomenon. Thus, hatchery-produced smolts may not fully represent the life history of natural-origin smolts, and hatchery smolts are typically larger as well, producing a greater proportion of jacks. Coho salmon from the Columbia River Basin have a coastal distribution, resulting in considerable exploitation in marine fisheries, largely off the coast of Oregon and, to a lesser extent, Washington (Weitkamp 2012).

As noted above in the section of “what is a smolt,” Chinook salmon have great life history diversity across their range and within the Columbia River Basin and move throughout the year (Copeland et al. 2014; Bourret et al. 2016; Schroeder et al. 2016; Sorel et al. 2023). Downstream migrants range from newly emerged fry to fully developed yearling smolts. Their variation in size, timing, and travel rates affect susceptibility to predation (e.g., Hostetter et al. 2023), and when and where they are detected (e.g., with PIT tags or at traps). Some of this variation is an inherent feature of the species, and some aspects, notably use of reservoirs, are functions of habitat alteration (Connor et al. 2003, 2005). Chinook salmon populations vary in marine distributions, resulting in markedly different levels of exposure to fishing (Sharma and Quinn 2012), and in the timing of return migration. Chinook salmon also vary in age at maturity, including non-anadromous males and anadromous males that spent one or two fewer years at sea than females (i.e., jacks and mini-jacks, respectively). These forms of variation, combined with seasonal variation in river flow and temperature to which the life history variants are exposed, can complicate the interpretation of mark-recapture data on Chinook salmon.

Steelhead are typically classified based on the season when adults return from the ocean and whether final maturation occurs at sea, followed shortly by spawning, or in the river during a protracted period prior to spawning. The Columbia Basin has winter (ocean-maturing) and summer (river maturing) steelhead (Busby et al. 1996). However, the arrival and spawning of these forms can span an entire year, within even a single river such as the Kalama (Leider et al. 1986). In addition to variation in adult timing, juvenile life history also varies. Hatchery-origin steelhead are typically released as smolts after a year and age-2 is the mode for natural-origin smolts (Busby et al. 1996), but Peven et al. (1994) reported some age-7 smolts in the upper Columbia Basin and inferred that “a more or less continuous downstream movement of juveniles occurs that takes them to areas with more adequate food supplies” [p. 77]. Many juveniles move during the summer-fall transitional period within their natal stream, and some leave it (e.g., Lapwai Creek, Idaho: Myrvold and Kennedy 2016). Dobos et al. (2020) reported 12 different combinations of smolt and adult age in Fish Creek, Idaho steelhead, and noted that, “Diversity was most evident in juvenile movement and rearing strategies.” Not all downstream migrants are smolts, and not all will proceed to sea at the same rate. In addition, though the average timing of hatchery- and natural-origin smolts was only slightly different, the timing of hatchery-origin smolts was more compressed than that of the natural origin fish (Peven and Hays 1989). Given these differences in smolt age and migratory behavior, and the variation in adult return timing (primarily winter runs in the lower river and summer runs farther upriver, but with exceptions), counts estimated from tagging data must be interpreted cautiously.



Orange bars represent spawning season

Green arrows and background represent juvenile rearing until they migrate to sea

Darker green indicates the more prevalent form

Light blue arrows and background represent adults at sea until they return, beginning with the more prevalent juvenile form (i.e., in dark green)

The darker blue indicates the dominant form of returning adults

The green to orange gradient bars represent adult returns to freshwater and spawning season

Figure 3. Representation of the general life history patterns in Columbia River Basin salmonids. Variation within species and life history forms occurs among populations, especially in steelhead. These seasons are *not to be taken literally* (e.g., the incubation period may be more like 6 months than 3, etc.). In addition, repeat spawning (i.e., iteroparity) in steelhead is not shown, nor are the non-anadromous life history patterns often seen in steelhead/rainbow trout and Chinook salmon (e.g., precocious male parr).

3.3. SAR and SAS types and estimation methods

SAR is an estimate of the proportion of a cohort of smolts that survive all freshwater, estuarine, and ocean mortality agents between specified smolt and adult reference locations, whereas SAS is an estimate of the proportion of the cohort that returns to a freshwater reference location as adults (the SAR) plus those caught at sea and those that were caught or strayed in freshwater below the adult reference location. Methods to estimate SAR and SAS vary, depending on the strategies used for identifying abundance of smolt cohorts and the adult sampling of fisheries catch, strays and escapement (i.e., how, when, and where smolts are marked and their abundance is estimated, and how, when, and where adults are sampled and their numbers are estimated). Smolt cohorts may be identified by brood year (those spawned in a specific year, that may or may not all go to sea in the same year) or smolt migration year (those going to sea in a year but may or may not have all been spawned in the same year), and adults may or may not be pooled across age groups. Here we discuss some key distinctions pertaining to SAR and SAS estimation methodologies.

3.3.1. How are smolts marked and how are smolts and adults estimated?

SAR and SAS estimation rely on smolt cohorts being identifiable, either with extrinsic tags, intrinsic markers, or location-specific abundance estimates. Marking methodologies were reviewed in (ISAB/RP 2009), and this report's *Appendix. A brief history of tagging* provides a summary of various methods. Three main approaches are used in the Columbia River Basin, each with its own strengths and limitations: (1) coded wire tags (CWTs), (2) passive integrated transponder (PIT) tags, and (3) parentage-based tagging (PBT).

CWTs are typically applied to large numbers of fish in hatcheries (and some wild populations) prior to release but only group-specific data (e.g., mean fish mass and release date) are typically recorded, not data on individual fish. PIT tags are inserted into individual fish and data on each individual (e.g., body length, mass, tagging date and site) can be recorded and linked to the tag's unique identification code. The fractions of a population receiving CWT and PIT tags can vary considerably across populations. PBT is an alternative approach to CWT and PIT tagging that is based on genetic parentage assignments. Tissue samples taken from adults are genotyped, enabling the subsequent identification of their offspring and assignment to stock-of-origin and brood year (Beacham et al. 2019a, 2019b; 2020; Steele et al. 2013, 2019). Some important features of this method are that data on individual juveniles are not obtained prior to release, and that tissue samples are obtained from returning adults non-lethally. PBT has many positive attributes as a marking method; it is becoming increasingly common in Columbia River Basin hatcheries and can be applied to natural populations too.

Some of the basic strengths and limitations of these tagging approaches are as follows: CWTs can be retrieved and monitored in fisheries and during sampling of returning adults, but codes cannot be read in live fish. PIT tags are detected in migrating smolts and adults at fixed PIT tag detectors in streams and at dams but are rarely monitored in fisheries, especially those at sea, and not monitored in all spawning grounds or at hatcheries. Unlike the remote detections of PIT-tags, PBT requires that the fish be physically sampled to acquire tissue for genotyping (but the fish need not be killed, unlike CWT), and this is typically done at a hatchery or dam but can be integrated into fishery sampling, as demonstrated by Beacham et al. (2019a, 2019b, 2020) for coho salmon in British Columbia and in most fisheries in the Columbia River Basin. Consequently, fish with these three kinds of tags have different detection probabilities, sampling constraints, and estimation methodologies that affect how they are used in estimating SAR and SAS.

The abundance of smolts in each cohort can be estimated in several ways, depending on the marking scheme. At one extreme, nearly all members of the smolt cohort may be counted at one place, such as a counting fence in a stream or in a hatchery. If absolute counts are not possible or detection is imperfect, abundance may be estimated from catches after accounting for sampling effort or detection probabilities using mark-recapture statistical models. The proportion of the population sampled is used to expand the sample counts to estimate the total counts.

Estimates of SAS typically require data on the fates of smolts marked in large groups with CWTs. CWTs, typically applied to pre-smolts prior to release from a hatchery, are subsequently recovered by sampling marine and freshwater fisheries, on spawning grounds, and at hatcheries. CWT recoveries are expanded based on estimates of the fraction of each stratum sampled, yielding estimates of numbers of tagged fish caught in fisheries, straying, and returning to their natal hatchery. In contrast, SAR estimates are typically based on the detection of PIT tags from returning salmon that had been tagged as smolts. Such detections typically occur in fish ladders at dams, in river reaches where fish can be constrained through arrays, and at hatcheries. Sampling may be close to 100% in some cases, but in others, the sampling fraction is estimated. As mentioned above, ocean fisheries are not normally sampled for PIT tags. Thus, natural and fishing mortality are combined, and SAR is estimated from the proportion of smolts with PIT tags that returned to the designated reference location.

The newer PBT approach for estimating survival and return has the potential to combine advantageous features of both CWTs and PITs. Assuming adequate samples of fish have been genotyped and appropriate tissue samples are gathered in fisheries, harvest rates can be computed, similar to those with CWTs. However, estimating PBT recaptures at dams and fishways is more difficult than with PITs as tissue sampling is required for the genetic analysis and complex sampling and estimation approaches are often required. This approach has tremendous future potential, but it is unlikely to fully replace either CWT or PIT-tags because each method has unique benefits. However, combining multiple methods has become common, providing benefits beyond the single method approaches for estimation.

The numbers of adults escaping fisheries to spawn are estimated from surveys (e.g., from boats or on foot), from weirs, dams, mark-recapture, and other methods, depending on access, river size, fish abundance, and other considerations (Knudsen 2000). PIT-tagged fish are typically detected as they ascend a dam, pass a weir or an instream detector, or on carcass surveys. CWTs are recovered in fisheries, during brood collection at hatcheries, or carcass recoveries on the spawning grounds. PBT-based SAR estimates are typically based on proportional sampling of adults passing a reference location such as Bonneville and Lower Granite dams, or in fisheries, at hatcheries, and on spawning grounds.

As with smolts, the numbers of returning adults must be estimated by considering sampling design and effort and detection probabilities using statistical models. In the case of CWTs, only a proportion of the run may be sampled for CWTs, so a key assumption is that fish are sampled in a representative manner (e.g., stratified, randomly) that can be expanded to the population level. For PIT tags, mark-recapture modeling is typically required to account for detection probabilities at dams and weirs. The methods and assumptions associated with PIT tag methods are described in Appendix A of the Comparative Survival Study 2023 report (CSS 2023).

For smolts with CWTs, ocean catches are estimated from coast-wide sampling, in-river catches are estimated from Columbia Basin wide fisheries sampling, and summary results are available through the Regional Mark Processing Center's Regional Mark Information System (RMIS). Typically, the fish from a given hatchery and year (and sometimes separate release groups) have different tag codes and data are reported for mean size (usually mass) and release date. Those caught in the ocean, in a river, or recovered on spawning ground surveys are sent to central processing labs where the codes are read and the fish assigned to the appropriate tag group which provides the hatchery, release year, mean size, and other strata. Expansion for the sampling fraction is required, and individual recovered tags often represent larger (sometimes much larger) numbers of like individuals. Thus, the estimated catch is an expansion of the number of CWT recoveries based on sampling rates and CWT marking rates (Nandor et al. 2010, Chapter 2).

Salmon taken in marine fisheries might not be maturing in the year when they were caught, but so-called “terminal recoveries” in rivers or hatcheries are assumed to be mature fish. When estimating SAS, salmon taken in fisheries and those that survive and return but stray to a non-natal site or “over-shoot” their natal site and fail to return must be estimated and added to those returning to the designated site. In the past these estimates were based on CWT programs, although PBT data are increasingly being used for this purpose. Escapement estimates may also depend on expansion factors for sampling at weirs and hatcheries, but RMIS is not set up to handle some of these more complex methods that have multiple expansion factors. The origin of strays on spawning grounds and at hatcheries are indicated based on tag codes or other marks. Straying rates vary among populations (e.g., Quinn et al. 1991) and species (Westley et al. 2013), but the strays are usually included in SAS estimates unless the goal of the program or study calls for them to be distinguished from salmon that homed.

If smolts are not marked with CWT, PIT tags, or PBT, as is the case for most naturally spawned salmon populations coast-wide, adults may still be identifiable to a geographical region, resulting in SAR and SAS estimates that are commonly referred to as “abundance-based.” Few estimates of SAS are available for natural populations in the Columbia Basin. To do so, adults are assigned to the population based on the location of return or by using intrinsic markers such as scale patterns or genotypes, the fish are assigned to the correct cohort by age determination of a subsample of, and surrogate CWT groups are used to estimate exploitation. This has been done for decades to study SASs of many sockeye salmon stocks (Koenings et al. 1993), for example, the Chilko River population in Fraser River system (e.g., Henderson and Cass 1991; Irvine and Akenhead 2013), the Kvichak River in Bristol Bay (e.g., Tillotson and Quinn 2016), and in a few Columbia Basin populations.

In some Columbia River Basin applications, SAS estimates that are based on brood years are derived using “cohort analysis” to estimate the youngest age’s cohort size in the ocean, prior to fishing. This is discussed by the Chinook Technical Committee (CTC 2023). Subject to several assumptions, age-specific cohort reconstruction involves summing CWT-based estimates of age-specific catch, non-retention mortality, escapement at age, and the cohort size of the next oldest age. In addition, cohort size is adjusted (i.e., increased) by accounting for (assumed) age-specific natural mortality (Appendix II of CTC 1988). The CTC uses cohort analysis to estimate smolt-to-age 2 or smolt-to-age-3 survival for 13 hatchery and 2 wild Chinook salmon stocks in the Columbia River Basin (for trends since the late 1970s, see Appendix E13 in CTC 2023). Although the CTC does not refer to these survival estimates as SASs, this is essentially what they are according to our definition when ocean age 2 or 3 is adopted as the reference life stage. A similar approach was used for comparing survival estimates among multiple Chinook salmon populations by Ruff et al. (2017).

3.4. Use of SAR and SAS in Columbia River Basin management, research, monitoring, and evaluation

This section reviews the main types of SAR and SAS estimates used in the management and research, monitoring, and evaluation (RM&E) of Columbia River Basin anadromous salmonids, the reasons for doing so, and the merits of using SAR vs. SAS, and PIT tag, CWT, and PBT methodologies. It also summarizes marking efforts, with a focus on the Lower Snake River (LSR, below Hells Canyon Dam) as an example, and the main sources of data (e.g., RMIS, PNAMP, StreamNet, LSRCP) related to SAR and SAS goals. Additional information on projects that involve tagging can be found on the Columbia Basin Fish and Wildlife Program website, https://www.cbfish.org. We end this section by discussing some key assumptions related to the major ways SAR and SAS are estimated and used.

The choice of using SAR, SAS, or both depends on the purpose and management application of the estimates and practical considerations such as the number of fish available to be marked and site-specific practical challenges for marking juveniles and collecting data on adults. Here we list some of the major management and RM&E applications of SAR and SAS in the Columbia River Basin.

- **Hatchery performance:** SAS and SAR are commonly used for determining optimum rearing and release strategies, assessing hatchery performance, and making adaptive management decisions. Hatchery programs often evaluate alternative strategies (e.g., broodstock source, rearing density, feed types, and growth rate, smolt size, release date and location) to best achieve specified management objectives such as survival, homing accuracy, spatial distribution of returns, and age composition (e.g., Feldhaus et al. 2016; Harstad et al. 2018). In the past, most such studies used CWTs, but PIT tags and PBT are increasingly used in some situations when assumptions of the analysis can be met and the performance metrics are appropriate (e.g., Harstad et al. 2018).

- **Status and trends:** SAS and SAR are key metrics used to monitor the status and trends in the post-release performance of most hatcheries in the Columbia River Basin. These monitoring programs have tended to rely on CWTs, but PIT tag and PBT approaches are increasingly common (reviewed by Steele et al. 2019; e.g., Horn et al. 2024). Some hatchery evaluation programs produce SAR estimates using two or all three methods, and there are very many combinations of operating agencies, hatcheries, stocks, release methods, and marking methods.

  The extent of marking to assess survival and return, and the complicated network of programs and data sources involved are exemplified by the LSRCP programs for Chinook salmon and steelhead. The spring/summer Chinook salmon program (Table 5) involves agencies from three states (IDFG, ODFW, WDFW), the USFWS, the Nez Perce Tribe, the Shoshone-Bannock Tribes, and the Confederated Tribes of the Umatilla Indian Reservation, as well as six fish production facilities—Sawtooth, Clearwater, Dworshak, Lookingglass, Lyons Ferry, and McCall—using direct or acclimated releases of smolts at 17 different locations with 12 different "stocks." The fall Chinook salmon program is somewhat simpler, with only two hatchery facilities and one stock, though they are released as sub-yearlings and yearlings, directly and after acclimation, at six locations. SAR is estimated using PBT and PIT tags, and SAS estimates primarily use CWTs with increasing use of combinations of PIT, PBT and CWT as well (Table 6). With respect to steelhead, five hatcheries produce smolts from eight stocks, including "B-run" and "A-run" fish (Table 7). B-run steelhead from the Clearwater and Salmon rivers are larger at a given age, primarily spend two years at sea, and arrive later at Bonneville Dam, whereas A-run steelhead are smaller for their age, tend to spend a single year at sea, and enter the river earlier (Busby et al. 1996). This categorization (unique to this system) is falling into some disfavor, but we mention it here because it is still used.

  The information in Tables 5, 6, and 7 demonstrates the exceptionally complicated and sophisticated marking programs that are used to estimate SAR/SAS for salmon and steelhead produced at these facilities, and the assessments that they allow. The many agencies, facilities, stocks, life history stages, release locations and methods, and the use of one, two, or three marking methodologies yields very many combinations. All smolts are identified through PBT, producing precise information on the parents of the returning fish, and PIT tags and CWTs are often applied as well.

- **Assessment of the influence of alternative hydrosystem operations and transportation:** Many studies have examined data on PIT-tagged fish detected at mainstem dams to evaluate and compare SARs of smolts experiencing different migratory conditions and routes through the mainstem to below Bonneville Dam (e.g., Faulkner et al. 2019), comparisons between wild and hatchery-origin fish (e.g., Achord et al. 1996), and how attributes of individual fish (e.g., size, origin, timing) affect their vulnerability to predation (e.g., Hostetter et al. 2012, 2023; Payton et al. 2023). PIT tags are also used to study migration timing (e.g., Achord et al. 1996), hypothesized to affect survival (Gosselin et al. 2021). As with hatchery-produced fish, estimation of SAR for wild populations is complex. For Chinook salmon (Table 8), there are multiple populations with SARs estimated from the population's home river to sea and back to the river in five cases (abundance based), from Lower Granite Dam out and back to Lower Granite Dam in nine cases for populations, Major Population Groups, and ESUs, from Lower Monumental Dam out and back to Lower Monumental Dam in one case, and from the Tucannon River to Ice Harbor Dam in another case.

  There are seven steelhead populations, MPGs and DPS combined. Five of which are assessed for SAR from Lower Granite Dam to Lower Granite Dam, one from Lower Monumental Dam to Lower Monumental Dam, and one from the Tucannon River to Ice Harbor Dam (Table 9). These tables reveal how much information is collected on the populations and how many different smolt and adult reference locations for SAR assessment are used. We note that not all SARs presented in Tables 8 and 9 are generated for hydrosystem assessment, though most are.

- **Fisheries management:** CWT marking programs are the basis for ocean fisheries management, including the assessment of international interceptions, in support of US – Canada Treaty obligations (e.g., Pacific Salmon Commission's 2023 Chinook Technical Committee Exploitation Rate Analysis), obligations to treaty tribes, and allocations among user groups within and between states. The losses to these fisheries are integrated into SAS estimates.

Table 5. Smolt-to-Adult Return (SAR) and Smolt-to-Adult Survival (SAS) assessment programs for Lower Snake River Compensation Plan Spring/Summer Chinook salmon hatcheries, including the release location map ID (see Figure 4), hatchery rearing facility, stock, life stage released, release method (direct or after acclimation), release location, the current methods used for SAR and SAS assessment: PBT = Parental Based Tag (universally applied), PIT = Passive Integrated Transponder Tag, CWT = Coded Wire Tag, and the operator. For IDFG SASs, variable fractions of the fish receive PIT and for all other SASs, except SBT egg outplants, variable fractions receive CWTs. SARs represent the return to the LSRCP project area above Lower Granite Dam for all programs except the Tucannon River. The SAS method indicates the SAR method plus the method for ocean and in-river harvest and straying estimation below the project area. All smolts are identified with PBT, but Lookingglass Hatchery SAR and SAS estimates use only CWT estimates, which often involve complex methods for spawning and return abundance estimation. “Surrogate” indicates that a representative CWT release group from the same hatchery is used in the SAS estimate. Information provided by the Idaho Department of Fish and Game (IDFG), Nez Perce Tribe (NPT), United States Fish & Wildlife Service (USFWS), Oregon Department of Fish and Wildlife (ODFW), Washington Department of Fish and Wildlife (WDFW), and Shoshone Bannock Tribes (SBT), compiled by the USFWS LSRCP office. All SAR and SAS estimates in the past, prior to PIT and PBT methods, were based on CWTS.

Release Location Map ID	Hatchery Rearing Facility	Stock	Life Stage	Release Method	Release Location	SAR Method	SAS Method	Operator
1	Sawtooth	Sawtooth	Smolt	Direct (includes 2 release groups)	Salmon River, Sawtooth Weir	PBT	PBT+PIT Conversion+ CWT Zone 1-5 Harvest	IDFG
2	Sawtooth	Sawtooth	Smolt	Direct	Salmon River, Yankee Fork	PBT	PBT+PIT Conversion+ CWT Zone 1-5 Harvest	IDFG
3	Clearwater	North Fork Clearwater River	Smolt	Direct	Clearwater Hatchery N F Clearwater River	PBT	PBT+PIT Conversion+ CWT Zone 1-5 Harvest	IDFG
3	Dworshak	North Fork Clearwater River	Smolt	Direct	NF Clearwater River	PBT	CWT	NPT/USFWS
4	Clearwater	Clear Creek/Powell	Smolt	Direct	Kooskia Hatchery, Clear Creek	PBT	PBT+PIT Conversion+ CWT Zone 1-5 Harvest	IDFG

Release Location Map ID	Hatchery Rearing Facility	Stock	Life Stage	Release Method	Release Location	SAR Method	SAS Method	Operator
5	Clearwater	Powell	Smolt	Direct	Lower Selway River	PBT	PBT+PIT Conversion+ CWT Zone 1-5 Harvest	IDFG
6	Clearwater	South Fork Clearwater River	Smolt	Direct	South Fork Clearwater River, Red River	PBT	PBT+PIT Conversion+ CWT Zone 1-5 Harvest	IDFG
7	Clearwater	Powell/ South Fork Salmon River	Smolt	Direct	Powell Satellite, Lochsa River	PBT	PBT+PIT Conversion+ CWT Zone 1-5 Harvest	IDFG
8	Dworshak/Nez Perce Tribal	North Fork Clearwater River	Smolt	Direct	Lapwai Creek	PBT	PBT+CWT	USFWS/NPT
9	Lookingglass	Catherine Creek	Smolt	Acclimated	Catherine Creek	CWT	CWT	ODFW/CTUIR
10	Lookingglass	Lostine River	Smolt	Acclimated	Lostine River	CWT	CWT	ODFW/NPT
11	Lookingglass	Upper Grande Ronde River	Smolt	Acclimated	Grande Ronde River	CWT	CWT	ODFW/CTUIR
12	Lookingglass	Lookingglass Creek	Smolt	Acclimated	Lookingglass Hatchery	CWT	CWT	ODFW
13	Lookingglass	Imnaha River	Smolt	Direct	Imnaha River	CWT	CWT	ODFW
13	Lookingglass	Imnaha River	Smolt	Acclimated	Imnaha River	CWT	CWT	ODFW
14	Lyons Ferry	Tucannon River	Smolt	Acclimated	Tucannon River	PIT	CWT	WDFW
15	McCall	South Fork Salmon River	Smolt	Direct	South Fork Salmon River, Knox Bridge	PBT	PBT+PIT Conversion+ CWT Zone 1-5 Harvest	IDFG
16	McCall	South Fork Salmon River	Eyed Egg	Direct	South Fork Salmon River, Curtis Creek	PBT	PBT+ Surrogate	SBT
17	McCall	South Fork Salmon River	Eyed Egg	Direct	South Fork Salmon River, Cabin Creek	PBT	PBT+ Surrogate	SBT

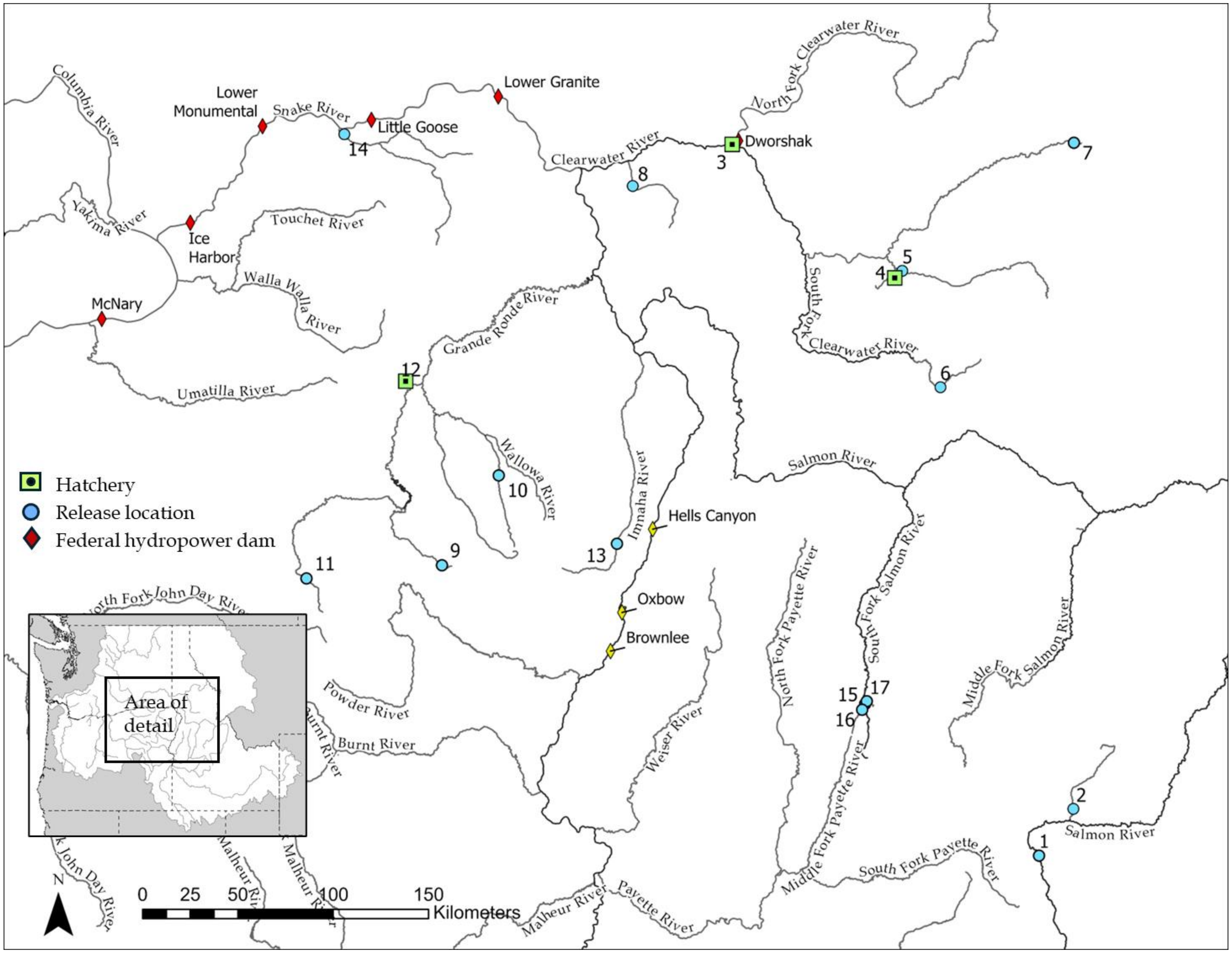


Figure 4. Smolt release locations for Lower Snake River Compensation Plan Hatchery produced Spring/Summer Chinook salmon tagged and released to estimate smolt-to-adult survival and smolt-to-adult return. Location designations correspond to stock, SAR/SAS tagging method, and associated metadata presented in Table 5.

Table 6. Smolt-to-Adult Return (SAR) and Smolt-to-Adult Survival (SAS) assessment programs for Lower Snake River Compensation Plan Fall Chinook salmon hatcheries, including the release location map ID (see Figure 5), hatchery rearing facility, life stage released, release method (direct or after acclimation), release location (numeral 2 for Captain Johns, Russel Bar, and Big Canyon refers to separate groups released at different times), and the current methods used for SAR and SAS assessment method: PBT = Parental Based Tag (universally applied), PIT = Passive Integrated Transponder Tag, CWT = Coded Wire Tag. For SAR, variable fractions of the fish receive PIT; for SAS, variable fractions receive CWTs. SARs represent the return to the LSRCP project area above Lower Granite Dam for all programs except for returns to Lyons Ferry Hatchery. The SAS method indicates the SAR method plus the method for ocean and in-river harvest and straying estimation below the project area. Information provided by ODFW, WDFW, and NPT, compiled by the USFWS-LSRCP office. All SAR and SAS estimates in the past, prior to PIT and PBT methods, were based on CWTs.

Release Location Map ID	Hatchery Rearing Facility	Stock	Life Stage	Release Method	Release Location	SAR Method	SAS Method	Operator
1	Irrigon	Snake River	Sub-Yearling	Direct	Couse Creek	PBT+PIT	PBT+PIT+CWT and/or PBT+PIT+PIT Conversion	ODFW
2	Irrigon	Snake River	Sub-Yearling	Direct	Wallowa River, Big Canyon Facility	PBT+PIT	PBT+PIT+CWT and/or PBT+PIT+PIT Conversion	ODFW
3	Lyons Ferry	Snake River	Yearling	Acclimated	Snake River, Lyons Ferry Hatchery	PBT+PIT	PBT+PIT+CWT and/or PBT+PIT+PIT Conversion	WDFW
3	Lyons Ferry	Snake River	Sub-Yearling	Acclimated	Snake River, Lyons Ferry Hatchery	PBT+PIT	PBT+PIT+CWT and/or PBT+PIT+PIT Conversion	WDFW
4	Lyons Ferry	Snake River	Sub-Yearling	Acclimated	Snake River, Captain Johns	PBT+PIT	PBT+PIT+CWT and/or PBT+PIT+PIT Conversion	WDFW/NPT
4	Lyons Ferry	Snake River	Sub-Yearling	Acclimated	Snake River, Captain Johns 2	PBT+PIT	PBT+PIT+CWT and/or	WDFW/NPT

Release Location Map ID	Hatchery Rearing Facility	Stock	Life Stage	Release Method	Release Location	SAR Method	SAS Method	Operator
							PBT+PIT+PBT Conversion	
5	Lyons Ferry	Snake River	Sub-Yearling	Acclimated	Salmon River, Russel Bar	PBT+PIT	PBT+PIT+CWT and/or PBT+PIT+PIT Conversion	WDFW/NPT
5	Lyons Ferry	Snake River	Sub-Yearling	Acclimated	Salmon River, Russel Bar 2	PBT+PIT	PBT+PIT+CWT and/or PBT+PIT+PIT Conversion	WDFW/NPT
6	Lyons Ferry	Snake River	Sub-Yearling	Acclimated	Clearwater River, Big Canyon	PBT+PIT	PBT+PIT+CWT and/or PBT+PIT+PIT Conversion	WDFW/NPT
6	Lyons Ferry	Snake River	Sub-Yearling	Acclimated	Clearwater River, Big Canyon 2	PBT+PIT	PBT+PIT+CWT and/or PBT+PIT+PIT Conversion	WDFW/NPT

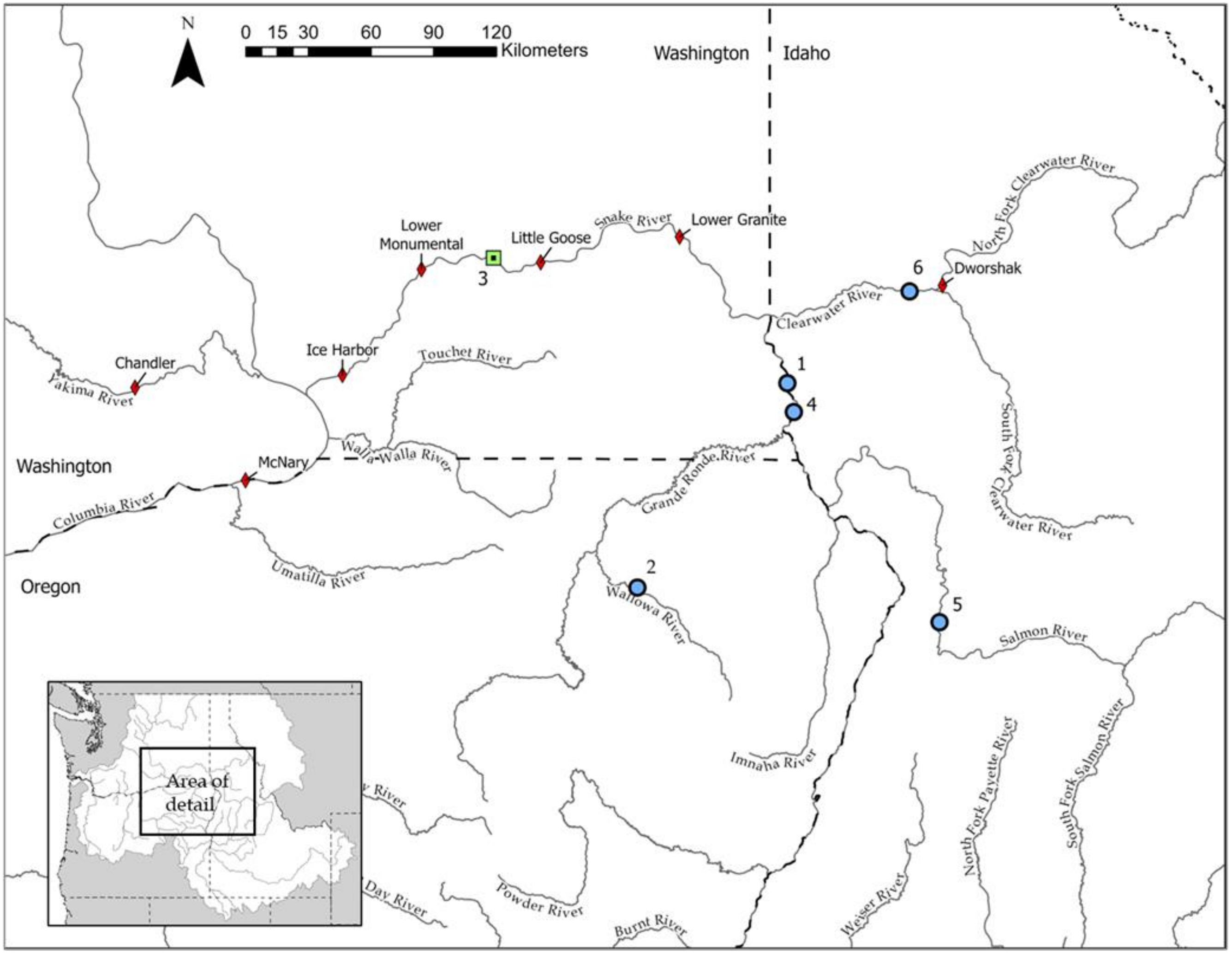


Figure 5. Smolt release locations for Lower Snake River Compensation Plan Hatchery produced Fall Chinook salmon tagged and released to estimate smolt-to-adult survival and smolt-to-adult return. Location designations correspond to stock, SAR/SAS tagging method, and associated metadata presented in Table 6.

Table 7. Smolt-to-Adult Return (SAR) and Smolt-to-Adult Survival (SAS) assessment programs for Lower Snake River Compensation Plan summer steelhead hatcheries, including the release location map ID (see Figure 6), hatchery rearing facility, stock (PRAS = Partial Recirculating Aquaculture System), life stage released, release method (direct or after acclimation), release location, the current methods used for SAR and SAS assessment : PBT = Parental Based Tag (universally applied), PIT = Passive Integrated Transponder Tag, CWT = Coded Wire Tag, and the operator. For SAS, in some programs variable fractions of the fish receive PIT or CWT. SARs represent the return to the LSRCP project area above Lower Granite Dam for all programs except the Tucannon River. The SAS method indicates the SAR method plus the method for harvest and straying estimation below the project area. All smolts are identified with PBT. Information provided by IDFG, ODFW, and WDFW and compiled by the USFWS-LSRCP office. All SAR and SAS estimates in the past, prior to PIT and PBT methods, were based on CWTs.

Release Location Map ID	Hatchery Rearing Facility	Stock	Life Stage	Release Method	Release Location	SAR Method	SAS Method	Operator
1	Magic Valley	Pahsimeroi A	Smolt	Direct	Pahsimeroi Weir	PBT	PBT+PIT Conversion+ PBT Zone 1-5 Harvest	IDFG
1	Magic Valley	Upper Salmon River B	Smolt	Direct	Salmon River, Pahsimeroi River	PBT	PBT+PIT Conversion+ PBT Zone 1-5 Harvest	IDFG
2	Magic Valley	Upper Salmon River B	Smolt	Direct	Salmon River, Yankee Fork	PBT	PBT+PIT Conversion+ PBT Zone 1-5 Harvest	IDFG
3	Magic Valley	Sawtooth A or Pahsimeroi A	Smolt	Direct	Little Salmon River, Stinky Springs	PBT	PBT+PIT Conversion+ PBT Zone 1-5 Harvest	IDFG
4	Clearwater	South Fork Clearwater B	Smolt	Direct	SF Clearwater River, Meadow Creek	PBT	PBT+PIT Conversion+ PBT Zone 1-5 Harvest	IDFG
5	Clearwater	South Fork Clearwater B	Smolt	Direct	SF Clearwater River, Red House	PBT	PBT+PIT Conversion+ PBT Zone 1-5 Harvest	IDFG

Release Location Map ID	Hatchery Rearing Facility	Stock	Life Stage	Release Method	Release Location	SAR Method	SAS Method	Operator
6	Clearwater	South Fork Clearwater B	Smolt	Direct	SF Clearwater River, Newsome Creek	PBT	PBT+PIT Conversion+ PBT Zone 1-5 Harvest	IDFG
7	Irrigon	Imnaha	Smolt	Acclimated	Little Sheep Creek	CWT	PBT or CWT	ODFW
8	Irrigon	Wallowa	Smolt	Acclimated	Wallowa River, Big Canyon (OR)	CWT	PBT or CWT	ODFW
9	Irrigon	Wallowa	Smolt	Acclimated	Wallowa River, Wallowa Acclimation	CWT	PBT or CWT	ODFW
10	Magic Valley	Sawtooth A	Smolt	Direct	Salmon River, Sawtooth Weir	PBT	PBT+PIT Conversion+ PBT Zone 1-5 Harvest	IDFG
10	Hagerman	Sawtooth A	Smolt	Direct	Salmon River, Sawtooth Weir	PBT	PBT+PIT Conversion+ PBT Zone 1-5 Harvest	IDFG
10	Hagerman	Sawtooth A (PRAS)	Smolt	Direct	Salmon River, Sawtooth Weir	PBT	PBT+PIT Conversion+ PBT Zone 1-5 Harvest	IDFG
11	Hagerman	East Fork Salmon Natural	Smolt	Direct	East Fork Salmon River	PBT	PBT+PIT Conversion+ PBT Zone 1-5 Harvest	IDFG
12	Lyons Ferry	Wallowa	Smolt	Direct	Snake River, Lyons Ferry Hatchery	PIT	PBT+PIT	WDFW
13	Lyons Ferry	Tucannon-Mitigation	Smolt	Direct	Tucannon River (Lower)	PIT	PBT+PIT	WDFW
14	Lyons Ferry	Tucannon-Conservation	Smolt	Acclimated	Tucannon River, Curl Lake	PIT	PBT+PIT	WDFW
15	Lyons Ferry	Wallowa	Smolt	Acclimated	Grande Ronde River, Cottonwood Pond	PIT	PBT+PIT	WDFW

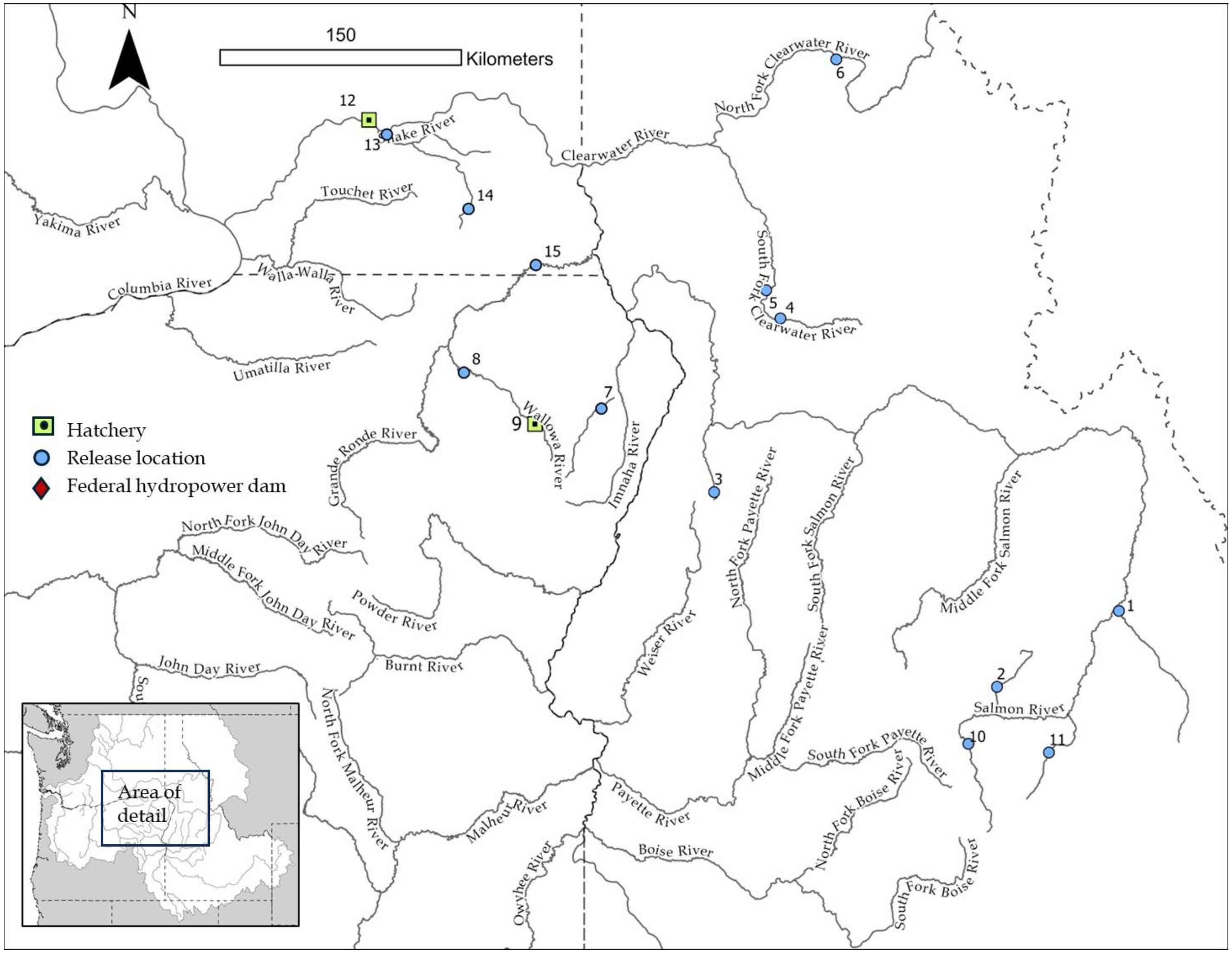


Figure 6. Smolt release locations for Lower Snake River Compensation Plan Hatchery produced Summer Steelhead tagged and released to estimate smolt-to-adult survival and smolt-to-adult return. Location designations correspond to stock, SAR/SAS tagging method, and associated metadata presented in Table 7.

Table 8. Smolt-to-Adult Return (SAR) assessment programs for natural origin Snake River Spring/Summer (Map ID 1-7) and Fall Chinook salmon, including the release location map ID (see Figure 7), population or group for conservation purposes (ESU = Evolutionary Significant Unit, MPG = Major Population Group), smolt and adult reference location (LGD = Lower Granite Dam, LMOD = Lower Monumental Dam), IHD = Ice Harbor Dam, and tagging method. PIT = Passive Integrated Transponder Tag. Abundance based estimates are derived from brood year specific smolt abundance estimates and the resulting adult returns. Information obtained from the StreamNet Coordinated Assessments Partnership Data Exchange (HLI categories and data), provided by the Fish Passage Center (FPC), NPT, WDFW, ODFW, and IDFG (Beeken et. al. 2024). End year represents the most recent migration or brood year estimate available.

Smolt Location Map ID	Population/Group	Location (smolt-adult reference)	Method	Agency	Years
1	Imnaha River (IR)	LGD-LGD	PIT	FPC	2006-2021
1	MF Salmon River MPG	LGD-LGD	PIT	FPC	2006-2021
1	SF Salmon River MPG	LGD-LGD	PIT	FPC	2006-2021
1	Upper Salmon River MPG	LGD-LGD	PIT	FPC	2006-2021
1	Snake River ESU	LGD-LGD	PIT	FPC	1994-2021
1	Snake River ESU	LGD-LGD	Abundance	IDFG	1996-2019
2	Tucannon River (TR)	LMOD-LMOD	PIT	FPC	2015-2020
3	Tucannon River (TR)	Tucannon-IHD	PIT	WDFW	2016-2020
1	Clearwater River MPG	LGD-LGD	PIT	FPC	2006-2021
1	Grande Ronde River MPG	LGD-LGD	PIT	FPC	2006-2021
4	Grande Ronde River (GR)	Grande Ronde-Grande Ronde	Abundance	ODFW	1994-2018
5	Wallowa/Lostine Rivers (WLR)	Lostine-Lostine	Abundance	ODFW	1997-2018
6	Minam River (MR)	Minam-Minam	Abundance	ODFW	2001-2018
7	Catherine Creek (CC)	Catherine Cr-Catherine Cr	Abundance	ODFW	1994-2018

Smolt Location Map ID	Population/Group	Location (smolt-adult reference)	Method	Agency	Years
3	Tucannon River (TR)	Tucannon-Tucannon	Abundance	WDFW	1985-2019
1	Fall Chinook- Snake River ESU	LGD-LGD	PIT	FPC	2008-2011

Table 9: Smolt-to-Adult Return (SAR) assessment programs for natural origin Snake River summer steelhead, including the release location map ID (see Figure 8), population or group for conservation purposes (MPG = Major Population Group, DPS = Distinct Population Segment), smolt and adult reference locations (LGD = Lower Granite Dam, ICD = Ice Harbor Dam, LMOD = Lower Monumental Dam), and tagging method (PIT = Passive Integrated Transponder Tag). Information obtained from the StreamNet Coordinated Assessments Partnership Data Exchange (HLI categories and data), provided by the FPC, NPT, WDFW and IDFG (Beeken et. al. 2024). The last years listed represent the most recent migration year estimates available.

Smolt Location Map ID	Population/Group	Location (smolt-adult reference)	Method	Agency	Years
1	Asotin Creek	LGD-LGD	PIT	FPC	2014-2020
2	Tucannon River	Tucannon-IHD	PIT	WDFW	2016-2020
1	Imnaha River	LGD-LGD	PIT	FPC	2006-2020
3	Tucannon River	LMOD-LMOD	PIT	FPC	2015-2020
1	Clearwater River MPG	LGD-LGD	PIT	FPC	2006-2020
1	Grande Ronde River MPG	LGD-LGD	PIT	FPC	2006-2020
1	Salmon River MPG	LGD-LGD	PIT	FPC	2006-2020
1	Snake River DPS (Inset map)	LGD-LGD	PIT	FPC	1997-2020

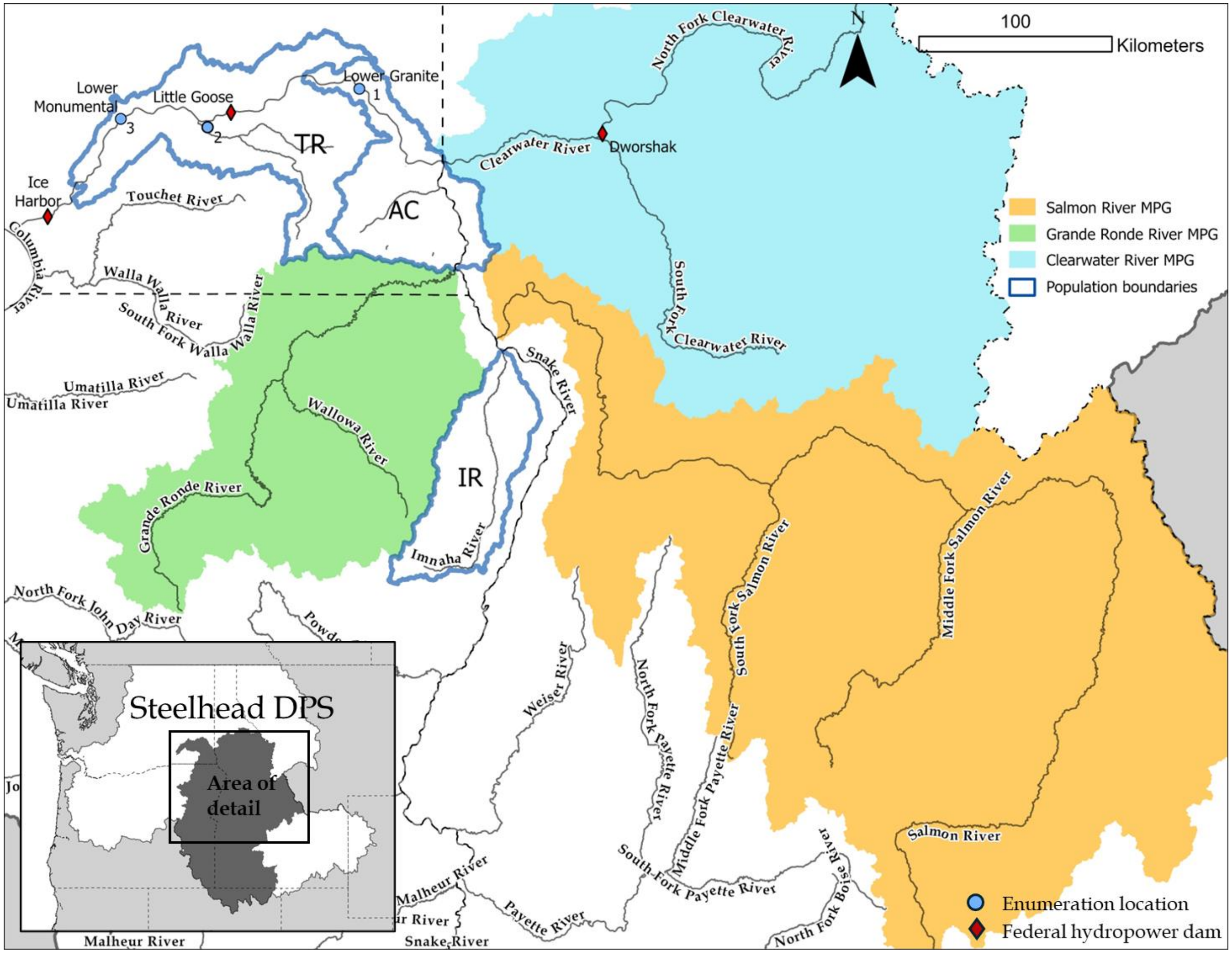


Figure 8. Smolt enumeration locations for natural origin Snake River Basin Summer Steelhead where smolt-to-adult return is estimated. Location designations correspond to population or MPG, SAR tagging method, and associated metadata provided in Table 9. Populations are delineated with blue borders and abbreviations and MPGs are delineated with colors. Inset map is the Snake River Steelhead DPS.

3.4.1. The Lower Snake River Compensation Plan Program: An Example of Management Application of SAR and SAS Estimates

The Lower Snake River Compensation Plan (LSRCP) Program illustrates the importance and value of SAS and SAR for assessing progress towards mitigation goals and management objectives. This federally funded program established specific adult return goals for fall Chinook salmon, spring/summer Chinook salmon, and steelhead prior to initiating hatchery production to mitigate the impacts of the four Lower Snake River dams (Ice Harbor, Lower Monumental, Little Goose, and Lower Granite). The annual adult return goals to the Compensation Plan area (above Lower Granite Dam for most of the spring/summer Chinook salmon and steelhead hatchery programs and Ice Harbor for fall Chinook salmon) are 18,300 fall Chinook salmon, 58,700 spring/summer Chinook salmon, and 55,700 steelhead. These goals were developed based on losses and impacts including spawning ground and in-river habitat inundation and dam construction and operation (United States Army Engineering District 1975).

Mitigation goals are specifically identified to address “in kind” and “in place” annual adult abundance losses of 48% of the base period of the late 1940s to early 1950s (prior to dam construction). The in-kind element addresses the species impacted, and the in-place element provides subbasin-specific annual adult return goals based on the estimated abundance at the time of dam construction. In addition to the return goals, there are specific combined harvest goals for the mainstem Columbia River and ocean based on an estimated 80% exploitation (i.e., proportion of adult fish that are harvested below the Compensation area) for Chinook salmon and 66.7% for steelhead (United States Army Engineer District 1975). The LSRCP Program has prioritized meeting the in-kind and in-place return goals to the compensation area over meeting the harvest objectives below the Compensation area.

As part of the LSRCP, each hatchery program has smolt production objectives, established during its design phase, and specific SAR and SAS objectives (also called targets) based on subbasin-specific annual goals for adult returns. The SAR and SAS objectives have been modified over time for some hatcheries due to reductions, or in most cases, increases in smolt production objectives as called for to address adaptive management needs. The adult return goals and SAR for the Oregon and Idaho programs are measured to the area above Lower Granite Dam and Washington’s are measured at dams downriver from Lower Granite Dams. SAS estimates incorporate harvest, natural mortality (for PBT and PIT based estimates, not CWT based estimates), strays below the compensation area, and adults that return to the compensation area. All SARs and SASs are estimated on a brood year basis.

The establishment of specific SAR and SAS objectives for each hatchery program provides benchmarks for assessing survival status and trends, determining success in meeting post-release survival objectives, and comparing performance over time within and between programs. The ISRP has completed multiple reviews of the LSRCP (see ISRP 2002-6, ISRP 2011-14, ISRP 2013-3, ISRP 2014-4, ISRP 2014-6, ISRP 2023-1) and has commended the LSRCP for the strength of its RM&E programs, specification of performance and management objectives, and the assessment of success in meeting performance objectives. The LSRCP supports an extensive RM&E program to assess the performance of each hatchery program. Annual age-specific adult return numbers are determined and compared to specific goals. Hatchery specific SAS and SAR values are estimated for each brood year, which provides a sound basis for assessing achievement of survival targets and post release performance. In addition, both SAR and SAS are used to determine hatchery-specific optimum rearing and release strategies.

The SAR and SAS targets and consistent methods for each hatchery program have provided the fishery managers and the ISRP with clear criteria and data for assessing success, evaluating trends, and comparing performance between programs. Some hatchery-specific survival datasets span nearly 40 brood years. The survival targets and long time-series of data have proven invaluable for informing fishery manager adaptive management decisions and ISRP reviews. These SAR and SAS estimates and the catch-escapement distributions were determined based on releases of smolts with CWT until the last decade or so when some programs shifted to PIT tags and PBT for SAR, and combinations of CWTs, PBT, and PIT tags for SAS (Tables 5, 6, 7). For the CWT-only based estimates, recoveries of adults (age 3-5) in all ocean and freshwater fisheries, strays, and returns to the subbasin of release are used for the SAS estimates.

The ISRP recently reviewed the LSRCP spring/summer Chinook salmon hatchery program (ISRP 2023-1) and calculated simple means of estimated SAR and SAS values for all hatchery programs in each subbasin (Figure 9, left panel). The ISRP determined that the SAR for brood years 2007-2016 were below current targets in all subbasins (Figure 9, right panel). In addition, SAR had declined compared with values during the previous decade or so, and the SAS values (Figure 10) were well below the targets in all subbasins with little harvest contributions to mainstem Columbia River or ocean fisheries.

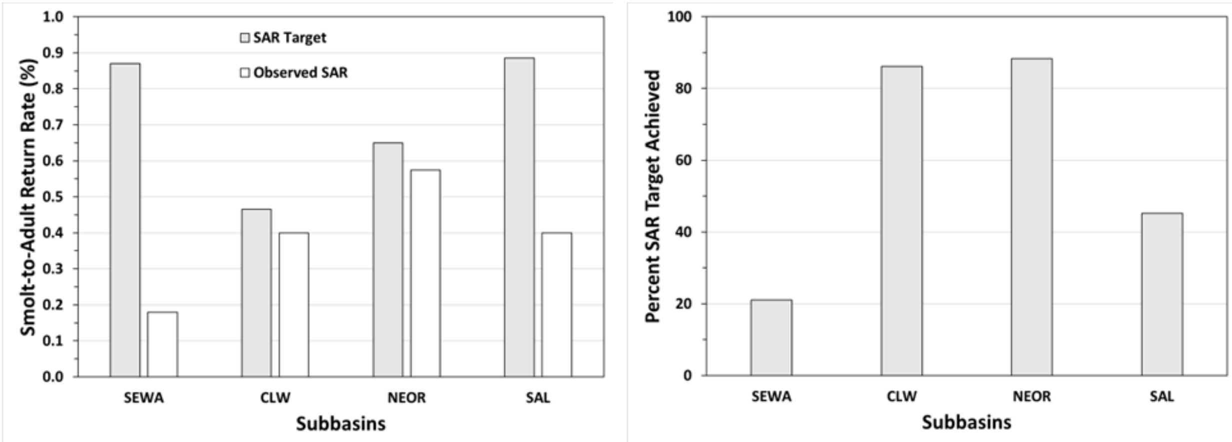


Figure 9. Average smolt-to-adult return estimates for spring/summer Chinook salmon in the four subbasins of the LSRCP Program for Brood Years 2007-2016 (left panel) and the average percentage of the SAR targets achieved (right panel). The geographic designations are Southeast Washington (SEWA), Clearwater (CLW), Northeast Oregon (NEOR), and Salmon (SAL). The data for SEWA are based on the original 1976 SAR target for the Tucannon River not including the Touchet River Program (ISRP 2023-1).

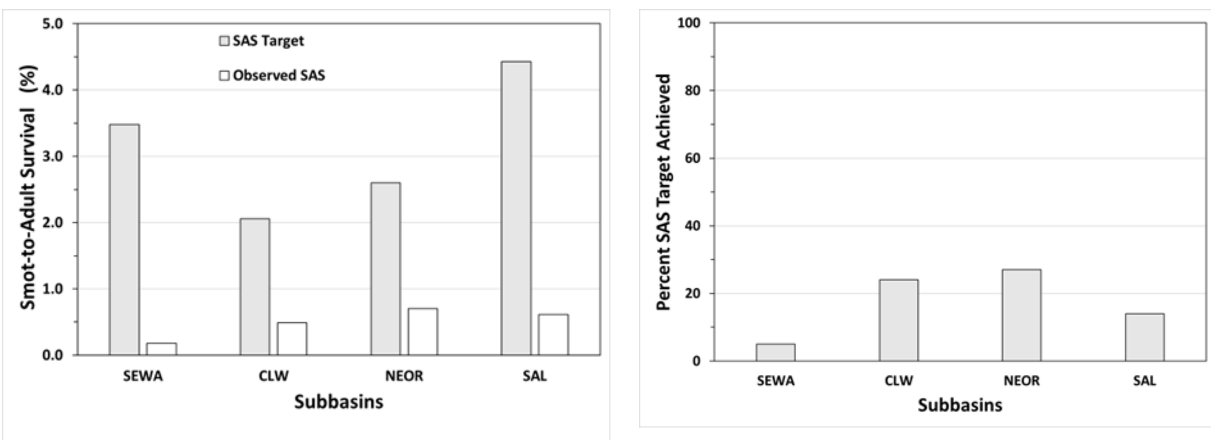


Figure 10. Average estimated spring/summer Chinook salmon smolt-to-adult survival rate for the four subbasins of the LSRCP Program for Brood Years 2007-2016 (left panel) and the average percent of the SAR targets achieved (right panel). The geographic designations are Southeast Washington (SEWA), Clearwater (CLW), Northeast Oregon (NEOR), and Salmon (SAL). The data for SEWA are based on the original 1976 SAR target for the Tucannon River not including the Touchet River Program (ISRP 2023-1).

In addition to the SAR and SAS estimates generated by each hatchery program, CWT recovery information is used to determine catch and escapement profiles. These profiles provide valuable information on exploitation rates and spatial distribution of recoveries over the years, differences in exploitation among hatchery stocks, and the proportions and spatial distributions of strays. Table 10 provides catch and escapement data from Feldhaus et al. (2022) for Grande Ronde and Imnaha River basin hatchery spring/summer Chinook salmon for the 2007-2016 brood years. These estimates were generated from CWT mark-recapture data. This reveals some of the variation of recovery location among populations, and variation in exploitation among years. Note the negligible effect of ocean fisheries on these populations. Straying to locations below Lower Granite Dam is low in all cases but straying above that dam varies from negligible to 10% in the case of the Upper Grande Ronde River population.

Table 10. Catch and escapement distribution (%) of Catherine Creek, Upper Grande Ronde River, Imnaha River, Lookingglass Creek, and Lostine River adult spring and summer Chinook salmon, brood years 2007-2016. For each brood year and population, the recoveries sum to 100%. Lower Granite Dam is abbreviated LGD (Feldhaus et. al 2022). (ISRP note: Estimates based on CWT recovery data which does not include the Snake River Tribal Fishery data).

Recovery Location	**Brood Year**										
	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	Mean
Catherine Creek											
Ocean	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.2
Columbia River											
Tribal Net	5.9	0.9	0.0	1.5	3.0	6.8	0.3	0.4	0.0	0.0	1.9
Commercial	3.4	1.1	2.1	2.4	2.2	2.4	1.4	0.4	0.0	0.0	1.5
Sport	5.8	10.5	7.0	6.7	3.2	8.0	25.5	13.2	0.0	0.0	8.0
Snake River											
Stray below LGD	0.2	0.2	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Stray-above LGD	10.2	6.9	5.7	9.4	2.7	15.3	5.6	4.9	8.4	2.0	7.1
Sport	0.2	3.7	2.6	3.0	2.0	0.7	0.0	3.0	1.2	2.5	1.9
Tribal	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Escapement to River	74.2	76.8	82.0	77.0	86.8	66.7	67.1	78.1	88.5	95.4	79.3
Upper Grande Ronde River											
Ocean	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.1
Columbia River											
Tribal Net	6.5	1.7	0.1	3.6	4.2	0.9	12.0	0.0	0.0	0.0	2.9
Commercial	0.6	2.2	0.0	2.9	0.8	4.8	0.0	1.2	1.4	0.0	1.4
Sport	2.8	11.3	1.4	5.1	4.0	13.0	6.8	11.1	6.2	0.0	6.2
Snake River											
Stray below LGD	0.0	0.2	0.0	0.1	0.0	0.3	0.0	0.0	0.9	0.0	0.2
Stray-above LGD	4.2	6.2	14.0	6.4	6.0	23.3	20.0	15.2	3.8	0.4	9.9
Sport	0.0	1.7	0.9	1.7	0.0	0.6	1.8	4.3	4.7	2.2	1.8
Tribal	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Escapement to River	85.8	76.6	83.5	80.3	85.1	57.1	59.3	67.1	83.0	97.4	77.5

Recovery Location	Brood Year										
	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	Mean
Imnaha River											
Ocean	0.1	0.2	0.0	0.0	0.3	0.2	0.4	1.3	0.5	0.2	0.3
Columbia River											
Tribal Net	14.2	6.1	2.6	9.8	19.6	9.0	6.1	0.3	1.7	0.0	6.9
Commercial	3.5	0.8	3.0	2.1	4.2	2.6	0.4	0.3	0.0	0.0	1.7
Sport	11.9	19.9	8.4	9.9	8.3	8.1	5.9	6.7	0.7	0.0	8.0
Snake River											
Stray below LGD	0.4	0.1	1.5	0.5	0.7	0.6	0.0	0.6	0.0	0.0	0.4
Stray-above LGD	0.0	0.3	0.1	0.2	0.0	0.0	0.1	0.0	6.5	0.0	0.7
Sport	0.0	0.0	3.7	1.6	0.9	0.3	0.2	2.9	0.4	0.2	1.0
Tribal	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Escapement to River	69.9	72.5	80.8	76.0	66.0	79.3	86.9	87.9	90.2	99.7	80.9
Lookingglass Creek											
Ocean	0.0	0.6	0.4	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Columbia River											
Tribal Net	4.3	3.7	2.0	4.5	4.1	5.5	0.0	0.0	0.0	0.0	2.4
Commercial	1.7	2.3	2.1	2.2	2.4	3.4	1.1	0.2	0.0	0.0	1.5
Sport	5.4	10.1	6.4	9.5	14.6	9.9	11.0	13.8	8.9	0.0	9.0
Snake River											
Stray below LGD	0.1	0.9	1.2	0.1	0.0	0.3	0.0	0.2	0.0	0.4	0.3
Stray-above LGD	18.2	0.5	9.4	7.4	1.5	3.3	2.2	6.9	0.6	0.6	5.0
Sport	1.4	2.7	0.0	0.7	0.2	1.3	0.0	2.7	0.0	1.2	1.0
Tribal	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Escapement to River	69.0	79.2	78.5	75.4	77.2	76.3	85.7	76.3	90.6	97.8	80.6
Lostine River											
Ocean	0.3	0.4	0.0	0.8	0.5	0.4	3.8	0.0	0.4	0.2	0.7
Columbia River											
Tribal Net	9.8	4.9	0.8	12.4	23.1	8.6	0.0	3.5	2.4	0.0	6.5
Commercial	1.6	0.7	0.8	1.0	4.4	2.7	0.0	0.2	0.0	0.0	1.1
Sport	7.4	9.6	0.0	8.0	13.0	7.1	4.4	8.8	3.8	0.0	6.2
Snake River											
Stray below LGD	0.4	0.4	0.4	0.9	0.2	0.5	1.1	0.3	0.6	0.2	0.5
Stray-above LGD	1.3	3.5	9.8	0.9	3.3	1.6	2.8	0.2	0.0	0.0	2.3
Sport	0.1	0.0	0.0	1.8	0.1	0.0	0.0	2.1	0.4	0.0	0.4
Tribal	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Escapement to River	79.2	80.4	88.2	74.1	55.5	79.0	87.9	84.8	92.3	99.6	82.1

We provide these details on the LSRCP to illustrate the importance of having clearly defined SAS and SAR terms, targets, and approaches that allow for sound comparisons between programs and for assessing performance trends within and among programs. Despite the diligent work by the LSRCP to standardize SAR and SAS approaches, the ISRP (2023-1) found that jacks were not consistently included in the survival estimates for spring/summer Chinook salmon, and no adjustment to a common return age was made in a few cases when adjustments would improve comparability. Thus, issues related to estimate equivalence to promote comparisons within and outside of a program remain.

Long-term datasets and performance assessments provide critical information for effective adaptive management. The PBT methodology being applied in the SAR and SAS estimation process within the LSRCP will provide many insights, but care is needed to ensure the compatibility and comparability of data based on PBT with the CWT-based approaches used in the past. We encourage practitioners to maintain the integrity and comparability of past estimates based on CWTs with new PBT-based estimates, and report on appropriate comparisons between methods.

3.4.2. Assessing Hatchery Optimum Rearing and Release Strategies

Studies to identify optimal rearing and release strategies for hatchery-produced salmon and steelhead are important for achieving adult return and survival objectives and maximizing production efficiency. Many factors that influence post-release survival of hatchery smolts have been investigated, e.g., smolt body size, release date and location, rearing density, exercise, feed type and regime, growth rates, acclimation, and natural rearing. SAR and SAS are the primary metrics in hatchery release studies to compare smolt-to-adult performance.

An example of the many studies to optimize hatchery strategies was on the effects of steelhead smolt release size (90 vs. 113 g) on SAS and straying (Clarke et al. 2014). The study, from release years 1986-1991, used paired-release replicate CWT groups of approximately 25,000 smolts, controlling for other rearing and release factors. SAS and associated methods were described as follows: “We [Clark et al.] estimated annual steelhead smolt-to-adult survival (SAS) rates and a stray rate index for each group using CWT recoveries from in-basin and out-of-basin locations. The estimated number of adult recoveries in a capture area equals the actual number of CWT recoveries multiplied by the sampling rate expansion factor. The total number of adults produced from each release group is the summation of adults captured in all areas (Johnson 1990). Smolt-to-adult survival is the percentage of smolts estimated to have been captured as adults from all locations ... Adult recovery information by capture area were obtained from the Regional Mark Information System.” The authors found that SAS varied greatly among years and was 42% higher for large compared to small smolts (average SAS: 1.31% vs.

0.92%). Smolt size did not affect age at maturity, but adults produced from large smolts strayed at a higher rate than small smolts (13.1% vs. 7.9%). This study provides a good example of the management application of SAS for evaluating hatchery rearing strategies, with a clear definition of SAS and sound methods for calculations and comparisons.

3.4.3. The Comparative Survival Study and the NPCC SAR Goal

The Comparative Survival Study (CSS) is a long-term research and monitoring program to assess the influence of hydrosystem operations on salmon and steelhead in the Columbia River Basin. The program has largely focused on evaluating the effects of mainstem flow augmentation, spill, transportation, and dam bypass encounters on SARs of Snake River spring/summer and fall Chinook salmon, summer steelhead, and sockeye salmon. The CSS was initiated in 1997 and is coordinated by the Fish Passage Center. The study is a cooperative large-scale multiagency effort of tribal, state, and federal entities. The CSS is an example of clear and consistent definitions, approaches, and management application of SARs, and here we focus on the CSS's use of SARs for Snake River salmon and steelhead survival assessments. We also discuss the importance of the NPCC's SAR goal and its value as a survival target for use by the CSS and the NPCC's Program Tracker-Strategic Performance Indicator assessment as criteria for assessing survival performance.

The CSS analyses address several questions including 1) Are direct and delayed impacts of the hydrosystem low enough to ensure sufficient survival to recover ESA-listed populations, 2) Is the SAR of barge-transported fish higher than that of fish that migrate in the river, and 3) Does the overall SAR (LGD-LGD) of listed natural-origin Snake River listed ESUs/DPSs meet the NPCC regional objective of 2-6% (4% average)? The CSS uses mark-recapture of hatchery and natural origin smolts identified with PIT tags (CSS 2023). Hatchery-origin juveniles are tagged at hatcheries and natural-origin fish are trapped and tagged at rivers and tributaries upstream of Snake and Columbia River mainstem dams. Recapture information is collected at mainstem dams for both juvenile and adult PIT-tagged individuals. The tagging, recapture, and analysis methods provide the ability to estimate and compare survival probabilities and other performance indicators through the life cycle. SAR estimates from the CSS are available in annual reports and from the Fish Passage Center (www.fpc.org).

Comparisons across release groups, species, subbasins, ESUs/DPSs, races, major population groups, origin, migration experience, (transported, in-river, bypass encounters) are possible when enough fish are tagged and survive to adulthood. Annual SAR estimates provide the most important high-level indicator in the broad array of survival comparisons used by the CSS. Multiple SAR types are determined including: smolts at LGR to adults at LGR, smolts at LGR to adults at BON, smolts below BON to adults at LGR, and other reference locations for the upper-and mid-Columbia River population groups. These reference locations all serve specific goals, and their various assumptions and treatment of the data can be confusing to readers unfamiliar with the data and analyses, especially because the CSS objectives, geographic scope, number of groups marked, and analytical approaches have expanded considerably over time.

The time-series of SARs generated by the CSS for population groups in the Columbia River Basin have proven valuable for addressing critical management questions and assessing success in achieving programmatic objectives like the NPCC's SAR objective to facilitate recovery. The SAR datasets include 24-27 outmigration years for Snake River wild and hatchery spring/summer Chinook salmon and summer steelhead, 13 years for Snake River sockeye salmon, and 12 years for Snake River hatchery-origin fall Chinook salmon. In addition, multiple long-term datasets for mid-Columbia Chinook salmon and steelhead have been generated. These datasets have been used, in combination with population modeling and other methods, to evaluate dam operation alternatives (including breaching), delayed mortality and bypass encounter effects, indications of climate change effects, influence of dam passage and in-river environmental variables, and upstream-downstream survival comparisons of Chinook salmon and steelhead from the Snake River and mid-Columbia Rivers.

The establishment of a specific SAR goal by the NPCC is important as it provides a benchmark for assessing performance of listed Snake and upper and mid-Columbia River salmon and steelhead by the CSS, the Council's Strategic Performance Indicators Program Tracker, and other projects. The goal highlights the importance of SARs as a "High Level Indicator" for tracking performance of natural populations, assessing management action effectiveness, and evaluating aspects of progress in recovery of ESA listed salmon and steelhead populations.

At this point we want to note that our emphasis on the Snake River and other interior populations indicated in the examples of LSRCP and CSS programs is illustrative and should not convey the impression that research, monitoring, and evaluation of salmonid production are limited to these areas. There are many spawning grounds and hatchery programs in tributaries of the Columbia River below Bonneville Dam that cannot be assessed by PIT-tag detectors at that dam for such populations, the assessment methodologies differ from those farther upriver. Moreover, many smolts originate from major tributaries of the Columbia River other than the Snake River. They travel different distances before they enter the mainstem and may encounter different numbers of dams on their way to the ocean. Their different routes and patterns of exposure to temperature, flow, predator communities, and habitats greatly complicate any comparisons in survival among them, above and beyond any differences in smolt size, timing, and other biological attributes (e.g., Bosch et al. 2023). Thus, notwithstanding the emphasis in many circles on interior populations, the survival of stocks throughout the Columbia Basin is important. Finally, processes affecting Columbia River stocks must be viewed in the context of marine survival patterns throughout the North American range (e.g., Chinook salmon: Kilduff et al. 2014; Ruff et al. 2017; Shelton et al. 2019; Welch et al. 2020) and these comparisons relied on CWT data.

3.5. Strengths and weaknesses of different approaches and applications

Many applications rely on comparisons of SAR or SAS estimates, including but not limited to comparisons over time, against benchmark values, and among and within populations. Problems can arise if SAR and SAS estimates are mixed, sources of data (CWT, PIT tag, and PBT) are mixed, different assumptions that affect the analyses are made, alternative stratification schemes are used, or populations are aggregated at different levels. SAR and SAS measure different things; they can be calculated in different ways and typically depend on marking methodologies with different attributes. In short, given the life history variation among and within populations, there is the potential for misinterpretation of SAR and SAS values, as detailed below in Section 5. It is important to bear in mind that PIT tags, CWT, PBT, and other forms of tagging are techniques or methodologies, whereas SAR, SAS, marine survival, exploitation rate, and such are performance metrics.

3.5.1. Should SAS, SAR, or both be used?

There is keen interest in the survival and return of salmon among scientists throughout their range, but which type of estimate or should both be used, and how do they differ? To many who work within the Columbia River Basin, the distinction between survival (SAS) and return (SAR) may seem academic if their concern is the absolute number of adults or the proportion of smolts returning as adults to their area of interest (e.g., a hatchery, spawning area, or standard detection point such as a dam to facilitate comparisons among groups). In many cases both estimates are used for the same group of fish, which provides the most robust survival information. They may have no control over fisheries in the ocean, and those fisheries may have little effect on the population of interest. However, for many populations, incorporating fisheries data may increase the statistical power to detect the effects of factors operating throughout the life cycle. Moreover, strays are sometimes a non-trivial fraction of the returning adult salmon, especially in ocean-type/fall run Chinook salmon (Westley et al. 2013), thus their treatment is important from the standpoint of estimating survival and distinguishing it from the return of salmon to a specific spawning area or hatchery.

To illustrate the range of differences between SAR and SAS, Table 11 shows data derived from information provided in the 2022-2023 Lower Snake River Compensation Plan Spring/Summer Chinook Program Review (USFWS 2022; and see ISRP 2023-1). Average SAR and SAS estimates were generated for 11 Chinook salmon populations, summarized below. The differences between SAR and SAS (resulting from exposure to fisheries, straying, patterns of natural mortality, and other factors) are negligible in some cases and much larger in others. Thus, not only do the average values of SAR and SAS vary among populations but the differences between SAR and SAS vary as well. Thus, the choice of which estimate to report should be considered carefully based on the populations of interest and the application.

Table 11. Average SAR and SAS values reported for 11 Chinook salmon populations evaluated by the ISRP as part of the assessment of the Lower Snake River Compensation Program, based on brood years 1998 – 2016. The smaller SAR values were calculated as percentages of the SAS values for comparison, and the populations are ranked from lowest to highest SAR as a percentage of SAS (USFWS 2022, ISRP 2023-1). The values are based on the number of marked smolts released from the hatchery or a stream location, including estimates based on multiple methods presented in Table 5. Adults include ages 3-5, except for the Tucannon, with no adjustment to a common age. The adult reference location for SAR is Lower Granite Dam for all site-stocks except the Tucannon-Tucannon.

Site - Stock	SAR Average %	SAS Average %	SAR % of SAS
Clearwater - Summer	0.26	0.43	60.5
Clearwater - Spring	0.29	0.40	72.5
South Fork Salmon – S Fork Salmon	0.72	0.91	79.1
Catherine Creek – Catherine Creek	0.38	0.46	82.6
Dworshak – Clearwater Spring	0.48	0.58	82.8
Imnaha – Imnaha	0.85	1.02	83.3
Sawtooth – Upper Salmon	0.36	0.43	83.7
Grande Ronde – Grande Ronde	0.40	0.46	87.0
Lookingglass – Catherine Creek	0.67	0.77	87.0
Lostine – Lostine	0.85	0.96	88.5
Tucannon – Tucannon	0.24	0.26	92.3
Average	0.50	0.61	82.3

3.5.2. PIT tag, CWT, or PBT?

SAR and SAS based on CWT, PIT tag, PBT and combinations of tagging methods provide complementary and partially overlapping information, thus their suitability depends on the application and the data required to address the question of interest. Survival comparisons among years and populations (within and especially outside the Columbia River Basin) need to carefully consider the assumptions and analytical methods that led to the estimates. Inconsistent or opaque combinations of estimates from different analyses can complicate interpretation. Welch et al. (2020) compared PIT-tag-based SAR and CWT-based SAS[1] estimates of survival to develop a correction factor. They noted the differences between methodologies and data and concluded that the correction factors produced estimates that were biased (i.e., deviated from 1:1) and differed among populations. They concluded that "A simple correction factor between PIT and CWT-based SAR estimates appears infeasible" [p. 202]. Further consideration of this topic can be found in a critique of the paper by the Fish Passage Center (2020) and the ISAB's (2021) review.

ODFW scientists compared SAR and SAS estimates for Imnaha and Wallowa stock hatchery summer steelhead produced using different combinations of data from CWT, PBT, and PIT-tags. The estimates follow similar patterns among years. However, the point estimates differ, and some calculation methods tend to yield higher estimates than others (Feldhaus, Greiner and Tattam, unpublished results). The overall conclusion is that the estimates of SAR and SAS for a given population and year may be very similar or much less so, and the attributes of PIT-tags, CWT, and PBT are sufficiently different that estimates based on them should not be combined or compared without clear and complete documentation and a good reason for doing so.

In general, CWT-based estimates are best suited for populations exposed to significant marine fisheries and for questions that do not require data on individual fish and require only a single, final return reference data point. They have the advantage of being readily compared with other populations within and outside the Columbia River Basin, and losses to natural mortality can be separated from losses to fisheries. However, in a large system like the Columbia River Basin, the considerable losses during downstream migration cannot be separated from losses to natural mortality at sea. In contrast, PIT-tags reveal the survival and detection date of individual fish at multiple specific locations and thus allow losses between those locations to be distinguished (e.g., between the hatchery of origin and Lower Granite Dam for immediate post-release performance, between Lower Granite Dam and Bonneville Dam for downriver survival and travel rate, from Bonneville Dam to sea and back there for survival and return timing, and from Bonneville Dam to Lower Granite Dam or some other point for upriver survival and travel rate). There is no necessity to report survival in multiple stages and environments for some applications, but in others it would allow more precise study of conditions in those environments and salmon mortality.

[1] Welch et al. (2021) analyzed SASs but called them SARs.

In addition to the benefits of multiple detections points for PIT-tags, they also have the great advantage of data specific to survival of individual fish between detection locations. For example, Faulkner et al. (2019) used PIT-tag data to study the relationships between mortality of Chinook salmon and steelhead smolts and their body size and use of bypass systems at dams. A growing body of scientific literature is revealing the importance of individual body size and especially date of marine entry for the fish's survival and age at maturity (Scheuerell 2005; Scheuerell et al. 2009; Bosch et al. 2023; Bond et al. 2024). Such information, and data on the travel rates of individual fish, are only available for PIT-tagged fish. Another use of tagging data, to estimate straying, can be accomplished with PIT tags (e.g., Pearsons and Miller 2023; Pearsons and O'Connor 2020, 2024) and CWT (Westley et al. 2013, 2015) and thus fish that return outside the target area can be assessed. However, not all PIT tag detections sites are equally effective, so detection probabilities need to be determined (Connolly et al. 2008; Connolly 2010).

PBT has the advantage over CWT that live as well as dead fish can be sampled (Steele et al. 2019). Moreover, in cases where hatchery-origin is indicated by a clipped adipose fin, PBT can accurately distinguish natural-origin from unclipped hatchery origin fish (e.g., Hargrove et al. 2021). However, PBT is most effective if all parents are genotyped and therefore generally more useful for hatcheries than wild populations. In addition, returning adults must be captured to obtain DNA samples, unlike PIT tags, which can be detected remotely, and no information is available on individual fish, a limitation that PBT shares with CWT. Although PBT could replace CWT programs in some cases if there was widespread adoption and extensive sampling in fisheries, it is unlikely to replace many PIT tag applications.

One important consideration when comparing survival estimates based on CWT, PIT and PBT is that CWT based estimates do not include as "survivors" adults lost to natural mortality (e.g., from thermal stress within the Columbia River) in the adult return abundance estimates because they are based on reconstructed expanded recoveries in fisheries and escapement. SAR estimates generated from PIT and PBT tagged smolts typically include adults that die from natural causes above the adult reference location. The inclusion of adult natural mortality in the PIT and PBT based SAR estimates creates comparability problems with CWT based estimates. The PIT and PBT based estimates better represent the true SAR value than the CWT based estimates because they use adult counts at the reference location.

3.6. Factors complicating use of SAS and SAR data

3.6.1. Juvenile life history variation

Life history variation, as described above, poses challenges for management applications of SAR and SAS estimates. There is variation within and among populations in when fish move downstream, how long it takes them to reach the ocean, and how they use river, reservoir, and estuary habitats during their migration. Timing of migration brings smolts into contact with different river conditions: flow, temperature, bypass system encounters and exposure to dams, predation pressure, and other sources of mortality and stress, as well as foraging opportunities. Thus, we urge caution when comparing populations that differ in juvenile life histories.

In addition to the effects of juvenile life history variation on travel patterns and survival within the river system and at sea, smolt size and migration timing also affect travel rate and survival. All other things being equal, larger smolts of a given cohort are more likely to survive than the smaller ones, but this effect must be assessed after considering the effect of smolt size on age at maturity (i.e., larger smolts are more likely to return after fewer years at sea compared to smaller ones from that cohort). In addition, larger wild smolts tend to migrate earlier in the season than smaller smolts, and smolt timing is related to survival (e.g., Scheuerell et al. 2009; reviewed by Quinn 2018). Such relationships are indicated by PIT tagged fish with individual records of size when tagged and movement history (e.g., Scheuerell et al. 2009) but cannot be inferred from CWT or PBT. For example, Bond et al. (2024) reported great variation among years in the relationships between PIT-tagged Snake River Chinook salmon smolt size, timing, and survival. In some cases, the survival patterns of a population of interest are not known from empirical data and another population for which data are available is used as a surrogate. This understandable practice can be reliable if they have sufficiently similar life histories and sizes, and similar down-river migration routes, distances, and timing, as these attributes affect survival and age at return. When the two populations differ in any of these attributes, caution is needed.

Interpretation of SAR and SAS data could also be affected by variations from the typical movement patterns, as revealed by PIT tags. Larsen et al. (2013) reported that spring Chinook mini-jack males displayed three different migration patterns: residents remained in the natal stream, fluvial fish migrated to mainstem rearing habitats, and anadromous fish spent weeks or months in marine waters. The patterns of migration affect when and where the fish will be detected, and their survival rate, as exemplified by work in Idaho by Copeland et al. (2014). These small fish can migrate long distances.

Zimmerman et al. (2003) reported round-trip migrations of ca. 1600 km from the Umatilla River, Oregon to the Columbia River estuary and back, and Johnson et al. (2012) reported mini-jacks traveling at least 2600 km from Idaho to the estuary and back in only about four months. If PIT tag detection histories reveal these patterns, then they can be excluded from analysis of returns or adjusted in some way. If so, it is essential to indicate how data for such fish are handled, and how alternative migrations such as mini-jacks are considered in sample expansions that involve assumptions about tagged and untagged fish and analyses that use CWT. Some studies (e.g., Bond et al. 2017) systematically exclude life history variants (and focus on dominant types) to simplify the analyses (of straying patterns, in this case). Given the sensitivity of early male maturation to size and the typical differences between wild and hatchery populations, such adjustments or acknowledgement of the use of data are very important.

3.6.2. Adult life history variation

Adult life history variation and the ways in which it is handled can affect SAR and SAS estimates and their interpretation. Studies using these and related metrics have differed in whether all fish are counted at face value or adjusted to a common age to account for the mortality risk to which salmon are exposed during each year spent at sea, and whether some or all early maturing life history types are excluded. Age at maturity and the incidence of alternative life history patterns commonly vary among hatchery-origin populations, natural-origin populations, and between these groups, complicating comparisons. Alternative male life history types (e.g., jacks, mini-jacks, and sexually mature parr) may constitute a large fraction of the population, and their inclusion or exclusion from calculations affects apparent survival and return patterns. More broadly, age-at-maturity variation exposes fish to different levels of natural mortality and fishing because they differ in duration and distribution at sea (e.g., Quinn et al. 2011). Variation in age composition among populations, brood years and return years can obscure genuine differences in mortality or create the false appearance of differences; thus, it is essential to be clear and consistent in how life history variation is incorporated into survival estimates.

The annual mortality rate at sea is difficult to determine, but fish maturing at an earlier age have less exposure to natural and fishing mortality. Consequently, adjusting adult returns to a common marine age facilitates comparisons among populations (e.g., one hatchery vs. another, a hatchery vs. a proximate wild population) that differ in age composition. So, for example, Coronado and Hilborn (1998a, 1998b) and Magnusson and Hilborn (2003) adjusted Chinook and coho salmon recoveries to age-3, which represented the great majority of the fish. Using similar logic, Quinn et al. (2005) studied

Puget Sound coho and Chinook salmon and indicated that "adjustment is necessary to account for the fact that salmon returning at a younger age (especially early maturing males) would experience lower cumulative natural mortality than those maturing later in life (see also Magnusson and Hilborn 2003). Changes in smolt size greatly affected age at maturity in these populations (Quinn et al. 2004; Vøllestad et al. 2004), so might produce spurious correlations with survival unless corrected. They used the following adjustment factors: Chinook: # age 1 × 0.3, # age 2 × 0.6, # age 3 × 1, # age 4/0.8, # age 5/0.72, and # age 6/0.65…" This is the equivalent of survival fractions of 50% between ocean years 1 and 2, 60% between ages 2 and 3, 80% between 3 and 4, and 90% between 4 and 5. However, some studies used different values (e.g., Carvalho et al. 2023), and others did not adjust for age at maturity in their estimates of survival and used the total estimated recovery across ages for a cohort of smolts (e.g., James et al. 2023). Both approaches are reasonable, but the inconsistency among studies hinders comparisons among them, and time series comparisons are compromised if deliberate or inadvertent changes in hatchery practices shift the age composition. Depending on the application, adjustment to a common age may be useful or it may introduce additional error because the assumed natural mortality rates are estimated rather than demonstrated and are fixed among years. We detail this topic further in the section below on mortality rates at sea and their incorporation into survival models.

Regardless of whether adults are adjusted to a common age, it is important to make clear how alternative life history patterns are handled. For example, Haeseker et al. (2012) stated that "For Chinook salmon, mini-jacks and jacks (0-ocean and 1-ocean, respectively) were not included in the adult return numbers, while for steelhead 1-ocean and older returns were considered adults" [p. 125]. Such clarity is very helpful; exclusion of jacks reduces survival estimates, relative to studies that included them, so the readers need to know how the data were handled.

3.6.3. Fisheries and predators

The vulnerability of salmon species and populations to predation is affected by the spatial and temporal distributions of salmon and their predators in different regions of the Pacific Ocean, Columbia River estuary, and river below and above Bonneville Dam. Consequently, comparisons of SAR and SAS among populations should clearly acknowledge this variation and explain to readers the implications for the analyses being conducted. For some populations, smolt survival and return of adults are almost exclusively affected by natural mortality rather than fishing.

Healey (1983) pointed out that, in general, stream-type Chinook salmon were less often taken in coastal marine fisheries compared to ocean-type Chinook, and he hypothesized that this resulted from the more offshore distribution of stream-type fish. Subsequent analyses have indicated that the difference in distributions does not stem from a distinction between juvenile life history types but from deep genetic differences between interior and coastal populations of Chinook salmon. Waples et al. (2004) concluded that "within the interior Columbia River Basin ... upstream of the Cascade crest, all spring-run populations form a coherent genetic group that is strongly divergent from all the summer- and fall-run populations" [p. 391-392]. They further reported that "many populations in the interior Columbia River Basin and upper Fraser River scarcely appear at all in any marine fisheries (marine harvest rates estimated to be below 5%, often below 1%)." Table 3, derived from Waples et al. (2004), shows this pattern (as does Table 10), whereas fall-run populations in the interior often had significant ocean interceptions during the period of record. Sharma and Quinn (2012) also found that upper Columbia River and Snake River stream-type Chinook indeed had negligible fishery interceptions until they reached terminal areas. Having clear evidence of the magnitude of exploitation on the population of interest is critical, and the use of appropriate surrogates is important, but Snake River spring/summer Chinook salmon, sockeye salmon, and steelhead are so lightly impacted by ocean fisheries that harvest likely has negligible effects in the context of natural mortality at sea.

For populations with minimal exposure to ocean fisheries, SAR and SAS can converge on similar estimates. For example, Schaller et al. (1999) stated that "Ocean harvest rates are very small for stream-type Chinook originating above Bonneville Dam, estimated at less than 1% based on a near absence of coded-wire tag (CWT) recoveries from ocean fishery mark recovery programs" [p. 1033]. Feldhaus et al. (2016) reported very low exploitation (0.1 - 1.8%, depending on experimental group) and similar SAR and SAS rates for Imnaha River Chinook salmon smolts. Petrosky et al. (2020, p. 789) used the terms survival and return interchangeably, "Smolt-to-adult survival rates (SARs) accounted for a majority of the variation in life cycle survival rates of Snake River Chinook Salmon." These SARs were based on PIT tag data and Petrosky et al. (2020, p. 791) explained that "Ocean fishery exploitation of both evolutionarily significant units (ESUs) is negligible (Schaller et al. 2000; PFMC 2011)." Similarly, Schaller et al. (2000, p. 1743) stated that "all the [upper Columbia River and Snake River] stream-type Chinook salmon harvest rates are less than 1%. This is in stark contrast with ocean-type Chinook salmon, which experience harvest rates in the range of 30–40% (PSC-CTC 1988; Peters et al. 1999)." Indeed, coastal runs of spring and fall Chinook experience much higher and exposure to fisheries along the coast, as we have pointed out in this report based on many published studies (e.g., Waples et al. 2004; Sharma and Quinn 2012) and the Chinook Technical Committee (2023). The different levels of exploitation to which the populations are exposed matter in the present context because they will result in more or less similarity between SAS and SAR.

After they encounter fisheries at sea, Columbia River populations are exposed to fisheries below Bonneville Dam and in the waters farther upriver, although each population's exposure depends on its run timing and destination. In-river treaty and non-treaty fisheries are sampled (e.g., pp. 8-14, Technical Advisory Committee 2023), and the estimated exploitation rates have been approximately 7-12% for upper Columbia River spring Chinook, 10-12% for Snake River spring/summer Chinook, 10-20% for steelhead, 30-45% for upper river (Columbia and Snake) fall Chinook, 5% for sockeye salmon, and < 5% for chum salmon, depending on year, stock, and other factors. Thus, both ocean and in-river harvesting should be considered when estimating and interpreting SAR and SAS values.

PIT-tagged fish may be detected at several dams during their homeward migration. Depending on the study goals, "return" may be considered to have occurred if the fish was detected at Bonneville Dam or some other location upriver. For example, Haeseker et al. (2012) calculated "ocean-adult survival" from the number of smolts detected at Bonneville Dam and the number subsequently detected as adults at Lower Granite Dam. Consequently, mortality at sea was pooled with losses during upriver migration. Such pooling of mortality complicates interpretation because fishing and *en route* natural mortality (e.g., from predators, thermal stress, pathogens, etc.) are not distinguished. The intensity of predation can depend on where predation occurs. Seasonal thermal patterns exert selection on salmon timing (e.g., sockeye: Quinn and Adams 1996; Crozier et al. 2011), as do pinniped predators (e.g., on Chinook salmon: Jepson et al. 2010; Plumb 2018; Sorel et al. 2021). This can create different levels of natural mortality among populations based on the timing and routes of migration, and also among years because predator populations have changed (Keefer et al. 2012; Tidwell et al. 2019; Wargo Rub et al. 2019; Braun et al. 2024). Consequently, SAR and SAS estimates that span long periods should be used carefully by considering the spatial and temporal variation in predation.

3.7. Limitations of SAR and SAS: apportioning mortality to different ages and life stages

SAR and SAS values incorporate mortality that occurs over a large portion of the salmon life cycle (Figure 2). Understanding mortality over shorter and more discrete portions of the life cycle, even just conceptually, helps interpret SAR and SAS estimates and characterize more specifically when in the life cycle mortality has a large influence in determining SAR and SAS values. This section summarizes what is known about mortality rates (i.e., over specified periods of time, as distinguished from total mortality) at sea and discusses the integration of harvest and mortality information at sea into survival metrics. We review some of the key studies on stage-specific mortality or survival rates. The portion of the life cycle encompassed by an SAR or SAS is mostly at sea, so we focus on ocean mortality, though depending on the sampling locations mortality in freshwater is also important.

3.7.1. Estimates of mortality rates at sea

Understanding the role of marine mortality is universally important in salmon management and conservation. There is broad agreement that the first few months at sea are critical in determining the overall survival of a cohort of smolts. This period is especially important for Columbia River salmon because inferences are drawn on delayed effects on survival of post-smolts that were exposed to stressful conditions during downstream passage but that survived to enter the ocean. Early marine mortality has been directly estimated from mark-recapture studies, though the papers reporting the results typically provide many caveats arising from methodological constraints. Moreover, combining results across studies is difficult because mortality was reported over different time periods, based on studies in different species, areas, years, with different methods. For example, Bax (1983) estimated the mortality rate of Hood Canal, Washington chum salmon fry to be 31% - 46% per day over the first 2-4 days. Wertheimer and Thrower (2007) estimated the daily mortality rate of chum salmon to be 8.1% for fish released early in the migration period and 3.9% per day for late releases over the first 21 days in southeastern Alaska marine waters. Fukuwaka and Suzuki (2002) estimated mortality rates of chum salmon to be 3.3% - 26.8% per day in the 14-43 days after release in Japan. Parker (1968) estimated 2-4% daily mortality rates of Bella Coola River pink salmon during the first 40 days. The mortality rate estimated by Bax (1983) was much higher than the other estimates and was measured over a much shorter period. The other three papers estimated about 4% mortality per day over the first month at sea for pink and chum fry, ca. 30 – 40 mm long. If this value was applied over 30 days, 1000 fry would be reduced to 294 survivors, or 29.4%.

The survival of smolts of species that enter the ocean at larger sizes compared to chum salmon has been studied using telemetry, a technique inappropriate for the small chum fry. For example, Moore et al. (2015) reported average survival fractions of 16% for wild steelhead smolts and 11% for hatchery origin steelhead from several Puget Sound rivers to the Strait of Juan de Fuca. Similarly, Welch et al. (2009) estimated ca. 20% survival of sockeye salmon smolts with acoustic transmitters from Cultus Lake, in the lower Fraser River system, to Queen Charlotte Strait ca. 500 km away, and Rechinsky et al. (2019) reported 8 – 14% survival of Chilko Lake sockeye salmon smolts downriver and through marine waters to a detection point 1044 km away. Survival rates per week were lowest in the Fraser River itself, highest from the estuary through the central Strait of Georgia, and intermediate from there to northeast Vancouver Island. Melnychuk et al. (2007) reported that early marine survival rate of Strait of Georgia steelhead was about 96.0-94.5% per day over ca. 27 days (and about half that daily survival rate during downriver migration). Such studies indicate high mortality rates during the riverine and early marine periods but come with several caveats. First, the tagging process may affect the fish's probability of survival, though this topic has been extensively investigated. Second, the fish used in studies are often quite large. For example, the Cultus Lake sockeye salmon smolts tagged by Welch et al. (2009) were ca. 160 – 180 mm and the steelhead tagged by Melnychuk et al. (2007) were about 180 mm. The migratory behavior and survival of these large fish may differ from patterns exhibited in smaller individuals.

The above-mentioned studies and others show substantial mortality of smolts during migration downstream in systems without dams (e.g., Furey et al. 2021). This is not a new discovery; mortality of seaward migrants in freshwater habitats has been reported over many decades (e.g., Hunter 1959; Ruggerone and Rogers 1984; Fresh and Schroder 1987; Wood 1987). Thus, when estimating SAR values, it is very helpful to distinguish between mortality occurring during migration down the river corridor from mortality that occurs at sea and on the upriver migration. SAS values (e.g., from CWT data) typically cannot distinguish the mortality in these habitats.

As an alternative to tracking individual fish to estimate survival, Beamish et al. (2012) used extensive field sampling and estimated that 6.9% of the hatchery-origin Cowichan River, BC, Chinook salmon smolts entering the Strait of Georgia survived to mid-July, 1.3% survived to mid-September, and only 0.8% remained by early October. In contrast, despite being much smaller, the wild Cowichan River fish enjoyed higher survival; 3.6 – 14.3% were estimated to have remained in early October. Such studies in comparatively confined marine waters such as the Salish Sea allow better estimates of early marine survival than are possible along the open Pacific Ocean coast, where dispersal and mortality are difficult to distinguish. However, Pearcy (1992) reported data for coho salmon along the Oregon coast, starting with the number released, then sampling at sea about 7 and 19 weeks later to estimate abundance, and finally by using the estimated number surviving to adulthood. Quinn (2018) summarized his work as follows, “from ocean entry on May 1 to June 17 the mortality rate was 2.92% per day for a total loss of 75.9% of the fish. From June 17 to September 11 the average mortality rate dropped to 0.91% per day but by the end of this period there were only 54.5% remaining of those present in mid-June. Then, from that September to September of the next year, the mortality rate averaged 0.35% per day, and 71.3% of the fish survived this year at sea.” Separation of mortality to sub-periods of the marine residence is feasible but requires targeted sampling studies that are expensive and whose generalization can be challenging.

One might ask why it matters when during their lives at sea salmon die, but in the Columbia River Basin this is very consequential. As Budy et al. (2002) noted, “The benefits these actions [removal of Snake River dams and improvements to the existing hydrosystem] are predicted to have in terms of salmon recovery hinge on whether the mortality that takes place in the estuary and early in their ocean residence is related to earlier hydrosystem experience during downstream migration.” [p. 35]. However, there is little basis for estimating this early ocean mortality fraction, hampering the ability to directly examine hydrosystem-induced delayed mortality (but see Rechinsky et al. 2009). For the most part, the published estimates of annual mortality rates at sea are little more than guesses, with only total mortality known with any degree of certainty. Ultimately, some confident level of calibration among tagging methods is necessary to address pressing questions regarding the early at-sea mortality of Columbia River Basin salmonids.

3.7.2. How do mortality rates change as salmon grow and age at sea?

In addition to field studies of early ocean mortality rates, there are other lines of evidence that initial rates are high and variable. For example, there is a long history of trying to forecast salmon runs using different methods, with varying levels of success (reviewed by Wainwright 2021). Many such studies point to environmental correlations between overall marine survival and conditions during the period just prior to or after ocean entry, consistent with the hypothesis that much of the variation in marine survival occurs in the early marine period. Such findings were reported for pink, chum, and sockeye salmon (e.g., Mueter et al. 2005), coho salmon (Hobday and Boehlert 2001), Chinook salmon from multiple populations (Sharma et al. 2013), California (Satterthwaite et al. 2014), and specifically the Columbia River Basin (e.g., Burke et al. 2013; Chasco et al. 2021). However, there are also indications of another major stanza of mortality during the first winter at sea, based on correlations with environmental conditions then (e.g., coho salmon: Logerwell et al. 2003). This has been termed the "critical size – critical time" hypothesis: that early ocean mortality is primarily related to predation whereas mortality in the first winter is affected more by physiological factors if the fish fail to achieve a critical size prior to winter (Beamish and Mahnken 2001). The relevance of this distinction between mortality immediately after ocean entry or later in the first year is that links to conditions experienced during downriver migration (e.g., powerhouse passages, transportation, etc.) are more plausible during the earliest ocean period than to conditions experienced many months later.

In addition to the evidence from correlations between environmental conditions when salmon enter the ocean and their overall survival, the strength of sibling relationships also indicates the extent of variation in survival after the first summer (for coho salmon) or first or second year (for Chinook, steelhead, and sockeye salmon). In the sibling relationship approach, the proportion of the smolt cohort that returns as jacks or some other number of years at sea is assumed to be constant, and the number of fish of one age-class each year can be used to forecast the number of older fish the next year (Peterman 1982a). This approach has been used for decades, though it is recognized that smolt size can affect the relationship (e.g., sockeye salmon: Peterman 1982a; reviewed as part of life history variation by Quinn et al. 2009). The sibling relationship approach is sometimes referred to as a jack index, and the relationship between the number of jacks in one year and the number of older salmon the next year is often strong. However, in some cases the jack index performed poorly (e.g., Winship et al. 2015 for California Chinook salmon), indicating that substantial variation in mortality may occur after the jack cohort returns, or that the population's age composition varied. The jack index also performed poorly for two Fraser River sockeye salmon stocks (Noakes et al. 1990). This weakness has long been known, and Peterman (1982b) inferred that significant variation in mortality occurred over the first 15 months (i.e., beyond the early residence period) at sea in sockeye salmon. Furthermore, the relationship between Asian pink salmon abundance and survival of Bristol Bay, Alaska, sockeye salmon (Ruggerone et al. 2016) indicates interactions after the first year, when the stocks overlap in the open ocean.

The question of when mortality occurs at sea and whether the rate is fixed after the highly vulnerable early period is important not only for the implication of hydrosystem-induced delayed mortality but because many researchers and management agencies have estimated the per-year mortality losses and in some cases use these estimates to adjust survival among years or populations to facilitate comparisons. Parker (1962) estimated mortality of juvenile and adult salmon in coastal waters and in the open ocean for sub-adults for multiple stocks of sockeye, pink, chum, coho and Chinook salmon. He concluded, (p. 585) “It is therefore suggested that ocean mortality may be relatively constant and similar for Pacific salmon while the coastal [mortality] is markedly different between species and geographic locations.” He estimated that, in general, “Ocean [not coastal] mortality is relatively constant and is of the order of magnitude of *q* [ocean mortality rate] = 0.32, S [survival] = 72% annually.”

Fredin (1965) estimated the annual natural mortality rates of Bristol Bay sockeye salmon with a variety of methods as 28.9% in their third year at sea and 19.5% in their second year. Karluk Lake sockeye salmon mortality was estimated at 28.2% in their last full year at sea. “The mortality rate during the year immediately preceding the last 2 months of ocean life of Bristol Bay sockeye that migrated to sea as 3-freshwater fish in 1956 and returned as mature 3-ocean fish in 1959 is estimated to be 28.9%. The average ocean mortality rate during the penultimate year of life of 3-ocean Bristol Bay sockeye is estimated to be 19.5% for the years 1956-57 to 1960-61. The natural mortality rate during the third year of ocean life of 3-freshwater Karluk sockeye is estimated to be 28.2%. Corresponding estimates of average monthly instantaneous mortality rates are 0.028, 0.018, and 0.031, respectively” [p. 33].

In contrast to the assumption that mortality rates are fixed after the early ocean period, Furnell and Brett (1986) built a growth and mortality model for Babine Lake, British Columbia, sockeye salmon, and mortality was estimated to decline on monthly time-steps as the fish grew. Mathews and Buckley (1976) similarly assumed that Puget Sound coho salmon mortality rates declined with body size throughout the marine period but noted that this was uncertain. “We assumed that the instantaneous rate of natural mortality at sea is inversely related to individual weight and thus decreases with marine life exponentially. Our reasoning for such a model is the assumption that marine natural mortality is mainly from predation; the larger the fish, the fewer the predators capable of eating it and the faster it is able to swim to avoid capture. Unfortunately, intuition must substitute for hard facts on these points” [p. 1678].

Henry (1978) estimated maturation and natural and fishing mortality of Columbia River Chinook salmon using adipose and ventral fin clips because this work pre-dated the CWT. This was derived from Henry (1971) using data on fish released from 1962 – 1965. Henry (1971) wrote, “These survival rates suggest that loss from mortality is at least 67 - 74 % in the 5th year, 56 -59 % in the 4th and 46 % in the 3rd year. These mortality levels are generally higher than estimates calculated by Cleaver for the 1961 brood (38-61 % in the 5^{th} year, 27 - 45 % in the 4th, and 30 - 53 % in the 3rd year” [p. 17]. These values imply higher mortality on older fish at sea, but natural mortality was not estimated directly, and it was concluded that because fishing mortality exceeded natural mortality for older fish, any error introduced by the values would not matter much. Ricker (1976) reviewed many studies, most of them on sockeye, and the one on Chinook salmon relevant to the Columbia River region was by Henry (1971) and Cleaver (1969), whose work was incorporated into Henry's papers. Ricker noted that "Neither Cleaver nor Henry had any objective estimate of noncatch mortality in the ocean, so they used a series of 6 trials of rates from M' = 0.02 to 0.08 per mo, the same for ages 2+, 3+, and 4+." Ricker's (1976) other estimate of marine survival of Chinook salmon was summarized as follows. "Parker (1960) obtained O.659 as an estimate of the natural survival rate of chinook salmon of southeastern Alaska. The corresponding instantaneous mortality rate is 0.417 per yr or 0.035 per month," but Parker (1960) remarked, "The rate of natural mortality is perhaps the most elusive parameter to determine" [p. 200].

Ricker (1976) stated further, "If we were to use some reasonable value for true natural mortality, say M = 0.015 per mo…" Iterating Ricker's (1976) estimate of m = 0.015 for 12 months yields an annual mortality of 16.6% or survival = 83.4%. Several studies over the past decades have used estimates of mortality after the first year at sea that rounded Ricker's value to 80%. For example, Jacobs et al. (2024) stated, "After the first winter at sea, we model the ocean survival of [Chinook] salmon as a function of an assumed annual ocean survival rate, φA = 0.80 (approximated from Ricker 1976)." Wilson (2003) used the same values, as did Kareiva et al. (2000), who noted, "No direct estimates of adult survival in the ocean exist for this ESU. We set $s_3 = s_4 = s_5 = 0.8$ [W. E. Ricker, J. Fish. Res. Board Can. 33, 1483 (1976)]." Thus, these values are commonly used, but it is important to recognize that they were based on at best very limited field work, conducted over 60 years ago before the invention of coded wire tags, using methods that the primary authors and Ricker himself acknowledged were very imprecise and inconsistent with other published models of marine mortality.

The conclusion reached by McGurk (1996) [p. 77] is largely still true, "There are few accurate estimates of instantaneous natural marine mortality rate ... for the seven species of Pacific salmon (genus *Oncorhynchus*), despite the importance of this information for reconstructing stock histories (Pacific Salmon Commission, 1992) and for modeling the dynamics of salmon populations (Ricker, 1962, 1976; Walters et al., 1978). For example, Ricker's (1976) review of marine mortality of Pacific salmon identified only three estimates of monthly *M* for the last year of sea life, which had no known bias and small sampling errors. No new estimates of marine *M* of Pacific salmon have been added to the primary scientific literature in the last 15 years (Groot and Margolis, 1991), although many estimates of smolt-adult survival have been reported."

3.7.3. Should survival estimates be adjusted to a common age at maturity?

Salmon survival in their early ocean period, though difficult to estimate with any precision, is much lower per unit of time than that experienced in their subsequent years at sea. However, the estimated mortality in the subsequent years at sea is often used to adjust the age composition of adults to a common age, facilitating comparisons of SAR and SAS among years and populations. As noted in the previous section, Ricker's (1976) review is typically the source of estimates of constant (e.g., 80%) survival, but there are other sources as well. For example, Kilduff et al. (2015) stated that, "We used cohort reconstruction to estimate the number of age 2 y (age 3 y) returns for subyearling (yearling) Chinook salmon (Magnusson and Hilborn 2003; Kilduff et al. 2014), assuming constant ocean survival rates for later ocean periods (0.5 for survival from age 2–3 y (3–4 y) for subyearling (yearling) releases and 0.8 for older ages)." The cited paper (Kilduff et al. 2014) adjusted for age in survival estimates using estimates of 0.5 from age-a to age-a+1, and assuming survival = 0.8 for all older years. However, Magnusson and Hilborn (2003), who Kilduff et al. (2015) also cited, did not do so. Magnusson and Hilborn (2003) stated that, "The age at return varies between regions, but most of the recoveries are … 3-5 year-old fall chinook salmon. Because of this variation, it was necessary to standardize the number of fish recovered (Coronado and Hilborn 1998) to allow a comparison of survival rates of the same species between regions. For Chinook $s_2 = 0.6$, $s_3 = 0.7$, $s_4 = 0.8$, and $s_5 = 0.9$ (Argue et al. 1983). This assumed adult ocean survival rate plays a minor role in the computations and should not be confused with the estimated smolt-to-adult survival rate that depends primarily on the first few months after release, when most of the mortalities occur."

Sharma et al. (2013) also studied Chinook salmon marine survival based on virtual cohorts at age-2, and used the same values as those in Magnusson and Hilborn (2003), stating, "From the CWT data, age-2 ocean abundances were constructed … NM [natural mortality] is assumed to occur in each age class before fishing mortality occurs and is assumed to be 40% to age-2 before fishing, 30% from age-2 to age-3, 20% from age-3 to age-4, and 10% from age-4 to age-5." Sharma et al. (2013) cited Argue et al. (1983) as the source of the estimates but Argue et al. (1983, p. 33) seem to have used fixed mortality rates for the last three years at sea. Thus, the scientific literature on estimated mortality rates at sea contains contradictions and inconsistencies. Notwithstanding these uncertainties, estimates of age-specific mortality at sea are incorporated into some fishery management processes. For example, the Pacific Salmon Commission's 2023 Chinook Technical Committee Exploitation Rate Analysis stated the assumption that, "For ocean age-2 and older fish, natural mortality varies by age but is constant across years. Natural mortality rates applied by age are: age 1 – age 2, 40%, age 2 – age 3, 30%, age 3 – age 4, 20%, and age 4 – age 5 and older, 10% (i.e., after fishing mortality and maturation of the age 4 cohort, 10% of the remaining immature fish die due to natural causes before moving to the next age class and before the commencement of fishing the next year)." These estimates are integrated into their Exploitation Rate Analysis (ERA). "The ERA relies on cohort analysis of CWT recoveries, a procedure that reconstructs the cohort size and exploitation history of a given stock and brood year (BY) using representative CWT data as a proxy (CTC 1988). The ERA provides brood- and stock-specific estimates of total, age- and fishery-specific exploitation rates, maturation rates, smolt to age-2 or age-3 survival rates, annual distributions of fishery mortalities used to compute CYERs [calendar year exploitation rates], and fishery indices for aggregate abundance-based (AABM) fisheries." CWT-based survival estimates are based on estimated exploitation rates, hence their importance for SAS and SAR comparisons.

3.7.4. Predation on large salmon can affect mortality rate estimates

Some analyses and models assume that the mortality rate (e.g., per year) is the same for the last several years at sea, and others assume declining mortality rates. The assumption of declining rates is intuitive, as many predators consume smaller than average prey because they are either gape-limited, or unable to capture and subdue larger prey. However, this may not be the case for salmon at sea because their primary predators (likely marine mammals and sharks), might be capable of capturing and consuming even large salmon. Ford and Ellis (2006) provided evidence that killer whales disproportionately consumed larger and older Chinook salmon over younger and smaller ones. Further evidence of predation on large/old Chinook salmon comes from acoustic tagging by Seitz et al. (2019) of fish 57 – 100 cm long, supported by modeling of the Yukon River Chinook salmon population by Manishin et al. (2021). The issue of predation on adult salmon is especially acute in the lower Columbia River. In recent years, sea lions have become very numerous, associated with non-fishing mortality (Wargo Rub et al. 2019), and they prey disproportionately on early returning stocks (Sorel et al. 2021). Thus, natural mortality of older and larger salmon may be significant, may vary among years and seasons, and therefore affect the interpretation of SAR and SAS estimates.

3.7.5. Inter-annual shifts in mortality rates

Given the changes in predator populations and other factors associated with mortality at sea, patterns from one period may not represent current or future patterns. Studies of this variation in mortality at sea have tended to focus on the effects of large-scale environmental factors (e.g., Beamish and Bouillon 1993; Mantua et al. 1997; Pyper et al. 2005; Wainwright 2021) to explain some of the great variation in survival among years, and to use climate and ocean-condition indices to help forecast future returns. Ten-fold to 20-fold variation in survival among years is routine in long-term data sets of many salmon species and populations (Quinn 2018). Fishery exploitation rates can be stable or vary over years (e.g., 47% to 14% for Columbia River summer Chinook, and 38% to 19% for Cowlitz River fall tule Chinook; Table 4). Analyses of return and survival patterns must explicitly consider the “non-stationary” nature of returns (e.g., Malick 2020). That is, patterns can change dramatically, and correlations with environmental variables that are prominent in one period can be weaker in subsequent years or decades. Notably, recent changes in the North Pacific Ocean may be affecting growth and survival of Columbia Basin salmon and steelhead. The ocean is warmer, temperature fluctuations are becoming more frequent (Laufkötter et al. 2020), and salmon abundances are exceptionally high, driven primarily by pink salmon (Ruggerone and Irvine 2018; Connors et al. 2024).

3.8. Efforts to provide consistency in SAR and SAS definitions, methods, and reporting

Consistency in SAS and SAR definitions, data collection and storage, analytical methods, and data sharing have been challenging for decades in the Columbia River Basin. Concerns with lack of consistency and documentation for all elements from definitions to data sharing have led to multiple efforts designed to improve data quality, consistency, and documentation. We highlight two efforts, one which is ongoing, to illustrate progress and how these issues and challenges can be addressed.

3.8.1. Ad Hoc Supplementation Monitoring and Evaluation Workgroup

The Ad Hoc Supplementation Workgroup (AHSWG) was created in direct response to the ISAB and ISRP recommendations that an interagency workgroup be formed to develop study designs to evaluate hatchery supplementation in the Columbia River Basin (ISRP and ISAB 2005-15). One of the key objectives that the AHSWG identified was “to describe a framework with which hatchery monitoring and evaluation activities may be standardized … for assessment of long-term and short-term effectiveness" (AHSWG 2008). In their findings they concluded "our review suggests that the diversity of data collection strategies, storage, and analysis approaches employed across the region places a substantial limit on our ability to combine data across projects to enable a coordinated large-scale analysis." In addition, the AHSWG stated that "the ability to aggregate project specific data in a large-scale design requires standardized protocols for M&E of salmon/steelhead populations in the basin, and organize these actions within a regional, muti-tiered framework."

The Final Report (AHSWG 2008) provides a framework for integrated hatchery research, monitoring, and evaluation. Within the framework, standardized performance measures and definitions for natural population status and trends and hatchery effectiveness monitoring are described for over 50 performance measures in the categories of abundance, survival-productivity, distribution, genetic, life-history, habitat, and in-hatchery measures. For application to the survival-productivity category of metrics, SAR is defined as the number of adults from a given brood year returning to a point (stream mouth, weir) divided by the number of smolts that left this point 1-5 years prior. Methods are described for four specific types of SARs including: tributary to tributary (i.e., the entire cycle), tributary to Lower Granite Dam (LGD), LGD to LGD, and LGD to tributary, for both hatchery and natural origin fish. Adult data are applied in two ways including the returns to the stream where the smolt estimates are obtained and returns to escapement monitoring sites (weirs, hatcheries, LGD). The methods recommended for each SAR type include a combination of calculations using PIT tag technology and/or direct counts of smolts and adults, and variance estimation methods are provided for each SAR type.

One of the methods described for SAR includes incorporation of all harvest (including ocean) below the adult reference point. There are no specific details provided to describe how this specific SAR would be determined. This specific SAR estimate includes all harvest and therefore represents an SAS; thus, the inclusion of this SAR type is confusing and inconsistent with the AHSWG SAR definitions. We are unaware of any supplementation evaluation projects that utilize SAS comparisons between hatchery and natural-origin fish to assess performance. This is likely a result of the difficulty in estimating ocean harvest for natural origin fish at a population scale.

The guidance provided by the AHSWG related to SARs represents one of the earliest attempts to standardize definitions and approaches. It represented a significant step forward in identifying the issues and providing clear recommendations for standardization, except for defining SAS as a type of SAR. It is unclear how broadly this guidance has been applied because there has been no follow up review of how extensively these definitions and methods have been utilized in supplementation studies in the Columbia River Basin.

3.8.2. Coordinated Assessment Partnership

The Coordinated Assessment Partnership (CAP) is the most recent effort to effectively share standardized salmonid population metrics and high-level indicator data. The goal is to share standardized salmonid performance data to meet regional management needs in the Pacific Northwest. This is a collaborative effort of Pacific Northwest and Columbia River Basin state, tribal, and federal agencies. CAP is sponsored by StreamNet and the Pacific Northwest Aquatic Monitoring Partnership (PNAMP). This effort originated in 2010 as the Coordinated Assessments for salmon and steelhead project, now known as CAP. The impetus and objectives of CAP arose from a series of multi-agency workshops that resulted in the development of an Anadromous Salmonid Monitoring Strategy (ASMS). The strategy highlighted the importance of data management, standardization, and sharing of research, monitoring, and evaluation information in the Columbia River Basin.

During early stages of the project, CAP focused on developing data exchange standards (DESs) for natural origin smolt-to-adult return (SAR), spawner abundance, and natural spawner recruits-per-spawner high-level indicators (HLIs) and associated metrics. Additional DESs have been completed for other natural origin HLIs and recently DESs for hatchery-origin fish HLIs and metrics, including SAR, have been developed. Metric and HLI data are shared via a publicly accessible Coordinated Assessments Data Exchange Data System (CAX). The CAP represents one of the largest data standardization and sharing efforts in the Columbia River Basin and is highly effective for standardizing, documenting, and sharing important salmon population performance information.

The DES is essential for effective data standardization and sharing by providing definitions and formal rules for data element structure, documentation, metadata, and data exchange. We examined the SAR DES to evaluate the specificity and effectiveness in addressing the standardization objective. The SAR DES contains 58 fields that describe essential characteristics and supporting metric data of each SAR dataset submitted for inclusion in the CAX. The fields require identification of species, ESU/DPS, race, population, smolt location, smolt definition, smolt abundance methods, adult location, return definition, return type, total adult return, outmigration year, SAR point estimate with confidence limits, and numerous other fields that further characterize and document the SAR estimates.

The complexity and magnitude of options that characterize the SAR for a specific group of fish, including the definitions for number of smolts and number of adult returns is necessary and important; however, it results in very many SAR types over a wide range of biological and geographical scales. For most data fields there are specific acceptable value descriptions to select from, often with numerous options. For example, the smolt definition field has five acceptable options and the adult return definition field includes ten options (presented below).

<u>Smolt Definition Field Acceptable values</u>:

1. Number of smolts marked
2. Smolts migrating past a point
3. Smolts migrating past multiple points
4. Juveniles leaving tributary mouth
5. Juveniles leaving population boundary

<u>Adult Return Field Acceptable values</u>:

1. Fish surviving to adulthood [*Potential returners before ocean harvest.*]
2. Returns to a dam [*Fish returning to a dam before removing broodstock or other removals at the dam.*]
3. Returns to population boundary [*Includes all fish that returned to the population boundary before any removals or mortalities, in the tributaries.*]
4. Returns to mouth [*Includes all fish that returned before any removals or mortalities, in the tributaries. Appropriate to use only if the mouth does not define the population.*]
5. Returns to spawning ground [*Fish in river available to spawn after removals, but before pre-spawn mortality, in the tributaries.*]
6. Returns to a weir [*Fish returning to weir before removing broodstock or other removals at the weir, in the tributaries.*]
7. Returns to a PIT tag array
8. Estimated number of spawners [*Fish available after all removals and pre-spawn mortality, in the tributaries (i.e., NOSA)*.]
9. Number of marked adult fish captured
10. Adult fish migrating to/past a point(s)

Currently there are 129 datasets housed in the CAX, mostly representing Columbia River Basin SARs. In some cases, there are multiple datasets for the same group of smolts and time-series with differences resulting from inclusion or omission of jacks or different smolt and adult enumeration locations. The many different types of SARs that can be reported are documented in the CAX and further illustrate some of the challenges inherent in achieving standardization and straightforward comparisons between different estimates. For example, SAR and SAS are not completely differentiated. However, the SAR DES includes all the required data and metadata needed to calculate and characterize both SAR and SAS values.

One of the acceptable options provided for data entry is the adult return definition of “fish surviving to adulthood” which falls within the normal definition of SAS. The harvested adjusted return field allows for inclusion of all ocean, mainstem, and tributary harvest to be included in the adult return estimate. The inclusion of “fish surviving to adulthood” and ocean harvest as options for inclusion in SAR estimates creates considerable confusion regarding the difference between SAR and SAS.

The CAP project and associated CAX have greatly improved the quality, quantity, and availability of natural-origin salmon and steelhead SAR data. The rigorous documentation requirements of all components of the estimates including methods, metrics, and metadata are highly beneficial and provide a sound basis for assessing whether specific datasets are suitable for comparative analysis. However, the many different types of SARs that the DES appropriately supports (resulting from the many different management questions, logistical constraints, methods, and reference locations) and that are currently posted highlight the ISAB’s concerns regarding the importance of clear definitions and approaches.

Consistency could be improved in the data exchange standards (DES) and data that are shared on the coordinated assessment exchange (CAX) if the differences between SAR and SAS were identified and SAS was presented as a separate High-Level Indicator. The current SAR DES contains all the fields and metrics required for SAS estimation. Providing both SAR and SAS data in the CAX, especially for hatchery origin fish, would be extremely valuable for a variety of comparative analyses and would better facilitate local and regional management decisions.

4. Conclusions and Recommendations

The ISAB acknowledges the difficulties in standardizing the methods used to estimate SAS and SAR and recognizes that diverse approaches and types of survival estimates are necessary to accommodate the available data, answer the specific questions for populations and locations, and address the diverse management needs. Constraints imposed by the many challenges in estimating survival and return further complicate standardization of these metrics. Salmonids are marked in different ways at many locations and detected at many locations as juveniles and adults. The resulting data are used to estimate survival within and beyond the Columbia River Basin for many purposes. While cognizant of these considerations, this section summarizes major conclusions and recommendations to improve consistency in terminology, definitions, and approaches to promote more robust SAR and SAS comparisons and ensure accurate information is used to inform management decisions. These recommendations are organized around the use of terminology, reporting of SARs and SASs, consideration of assumptions in comparative studies, consideration of ocean natural mortality, communication between practitioners and users, and the need to develop more accurate and precise SAR and SAS objectives.

The term “smolt” should be used with care, especially in the large and complex Columbia River Basin with species that migrate to sea after variable periods in streams, along direct and indirect pathways, and at different times of the year. This variation in migratory behavior and life history has been emphasized in this report for Chinook salmon, but wild steelhead also vary considerably in smolt age and movement patterns. Not all downstream migrants are smolts, they do not all proceed to sea at the same rate, and some fish released as smolts from hatcheries do not migrate to sea at all. Consequently, emphasis should be placed on the location and time of marking and detection so that readers can fully understand the status of the fish being studied.

Similarly, the term “adult” needs to be carefully defined in reports on Columbia Basin salmonids. For example, are all sexually mature fish included, only those that went to sea, or only those of certain ages (i.e., excluding precocious male parr, mini-jacks, and jacks)? Estimates of fisheries exploitation, survival, and return should indicate which ages are included, whether there was any adjustment to a common age, and if so, how this was done. Otherwise, shifts in age composition or differences among stocks can be masked or biased. Populations or sub-groups differing in age composition will likely differ in exposure to natural mortality and fisheries.

The distinction between SAR and SAS, and the terms return and survival, should be clearly defined when used. SAR, as typically used in the Columbia River Basin, refers to smolt-to-adult return, and its use as a proxy for SAS can cause confusion. Salmon taken in ocean fisheries are not routinely sampled for PIT tags or PBT, so fishing and natural mortality cannot be distinguished using these methods. Consequently, the use of SAR to estimate survival from natural mortality agents relies on the assumption that ocean fishery interceptions are very small (e.g., Schaller et al. 1999; Petrosky et al. 2020). If this is the case, and if in-river fisheries are monitored, and adult counts are made at one location, SAR estimates based on PIT tags may be largely equivalent to SAS. However, for populations exposed to substantial exploitation at sea, the two metrics can be quite different.

We also urge caution in only using average values for comparisons without measures of variability or dispersion. As noted in this report, average values can mask important variation in annual estimates of survival or age composition among years and populations. When standardizing SAR and SAS metrics to a common smolt, adult, or return age to facilitate comparisons, practitioners should state all underlying assumptions, and present supporting data. Some modeling procedures may be needed to properly account for the high levels of variation in fish life history, survival, environmental conditions, and other metrics of interest.

Consistency would be improved in publicly shared data if differences between SAR and SAS were clear and if both were defined and presented as high-level indicators of program and system performance. Providing both SAR and SAS data in the Coordinated Assessments Data Exchange Data System, especially for hatchery-origin fish, would be valuable for many comparative analyses and better support application to local and regional management decisions.

PIT and PBT marking and associated analytical methodologies used to estimate SAR and SAS (e.g., within the LSRCP) may not provide comparable estimates with the historical CWT-based approaches and thus complicate future time-series analyses. Practitioners should maintain the integrity and comparability of estimates for consistency with earlier estimates and ensure that estimates based on newer approaches can be readily compared to historical estimates. Robust conversion factors between metrics based on CWT, PIT, PBT and combinations should be investigated. Given the emerging development of the use of PBT, along with combinations of PBT, PIT tag, and CWT approaches for estimating SAR and SAS in the Columbia River Basin, a comprehensive analysis should be conducted to compare the results produced from these approaches. Datasets are available for multiple hatchery stocks where SAR and SAS estimates can be derived from PBT, PIT tag, CWT, and combinations of these methods. Clear description of the differences in the methods, what area-specific adult harvest, strays, and other losses are included in each method, and development of conversion factors to allow comparisons between methods would be a valuable contribution to the application of SAR and SAS to fisheries management in the Columbia River Basin. At a minimum, it is important to determine, as precisely as possible, annual exploitation rates for all populations that regularly receive CWTs and to compare estimated survival and return rates based on CWTs with those based on PIT tags, PBT, and the combinations for populations/hatchery stocks with more than one marking method.

4.1. Summary Recommendations

Recommendation 1. Provide clear objectives and applications for studies using SAR and SAS.

Clearly stated objectives and management applications are key to understanding the purpose and adequacy of the metrics and methods for the intended application. The more specific the questions, the easier it is to assess the analyses and assumptions.

Recommendation 2. Define SAR, SAS, and related terms clearly, and use them consistently.

- Specify if estimates are SAR or SAS with clear definitions.
- Identify the smolt and adult reference locations.
- Describe the life stage and methods of marking and estimating smolt abundance.
- Indicate which life history forms are considered “adults” and which are not counted as such.
- Define and consistently use terms related to fishing such as exploitation rate and harvest.

Recommendation 3. Provide clear descriptions of how SAR, SAS and related terms are estimated.

- Provide detailed sampling and analytical methods for estimating SAR and SAS including approaches for smolt and adult estimates.
- Provide measures of variability and dispersion for SAR and SAS estimates.
- Clearly articulate key assumptions for sampling design, data collection, and analyses.
- Document the methods and data treatment, incorporation of strays, detection probabilities, ocean mortality, fishery harvests, etc.

- Describe the methods for time-series data analysis and comparisons of survival estimates between populations.

Recommendation 4. Augment SAR reporting in publicly accessible databases to include SAS and component life stage specific survival where possible.

- Currently, SAR data are reported by various practitioners using various databases, but no consistent, publicly accessible reporting of SAS exists. Providing hatchery and natural origin SAR and SAS data would facilitate useful comparative analyses to guide local and regional management decisions. For example, it might be possible for the CAX to modify the data exchange standard and clearly distinguish SAR and SAS and provide SAS as an option as a high-level indicator in the Coordinated Assessments CAX database.
- We also encourage reporting of the component survival patterns (e.g., upper-most smolt detection to Bonneville Dam, Bonneville Dam to Bonneville Dam, and Bonneville Dam to upper-most detection) to better characterize survival patterns by life stage, habitat, and period. Doing so would facilitate analyses of the factors associated with in-river losses of smolts, losses at sea, and in-river losses of adults.

Recommendation 5. Maintain the integrity of long-term SAR and SAS datasets by comparing results of different marking and analytical methods and developing robust conversions.

We recognize that many factors are considered in selecting a marking method, analytical approach, and geographic scale for estimating SAR and SAS. Approaches are tailored to local conditions, available data, and specific research and management questions, but clear documentation of analyses will facilitate comparisons with other studies. We encourage practitioners to maintain the integrity and comparability of the past SAR and SAS estimates based on CWTs with new approaches and to develop robust conversion factors. Given the increasing use of PBT and combinations of PBT, PIT tag, and CWT approaches for estimating SAR and SAS in the Columbia River Basin, a comprehensive analysis should be conducted to compare the results produced by these approaches.

Recommendation 6. Where appropriate, adjust SAR and SAS estimates to a common age and explain any adjustments.

Depending on the application, adjustment to a common age at maturity may be needed, informative, or unnecessary for interpretation of SAR and SAS estimates. If the age composition of the salmon of interest differs between groups or changes over time, their exposure to natural mortality at sea and to fisheries may differ. Age composition differences might be insufficient to affect survival comparisons, but they should be acknowledged; where age differences are important, age adjustments should be considered as an option and clearly explained if they are used.

Recommendation 7. Be cautious when using surrogates and provide clear explanations of how well the surrogate represents the population of interest.

Describe the information used to determine the adequacy of the surrogate group to represent the less studied group (e.g., one river to another or wild to hatchery within a river), including similarity in life history and survival patterns, marking methods, and analysis of survival rate estimates.

5. Appendix. A brief history of tagging methods

The ISRP and ISAB issued a joint report in 2009 detailing the use of different marking and tagging methodologies, including applied and natural marks, in the Columbia River Basin (ISAB/ISRP 2009-1). Our goal here is not to duplicate that report, nor the many details presented in McKenzie et al. (2012) but to briefly summarize some of the primary marking methods for assessing salmonid survival. Our emphasis is on the different periods over which they were developed and their strengths and weaknesses. Readers are directed to the report (ISAB/ISRP 2009-1) for details, though there have been some changes since that report, and the relative use of approaches is changing. We omit some of the older methods such as ventral fin clips and branding that are not currently in wide use.

The movements of salmonids and their natural and fishing mortality ages have been estimated using techniques that were developed decades apart. For example, pioneering work on acoustic tagging was conducted with adult steelhead and Chinook and coho salmon in the forebay of Bonneville Dam in 1957 (Johnson 1960). As technology advanced, transmitters were miniaturized, standardized, and manufactured in quantity (most of the early researchers made their own) and came into wider use (Stasko and Pincock 1977). The development of fixed receiver stations that log data allowed the deployment of lines of receivers to detect migrating salmon and thus estimate survival over specific periods and distances (Voegeli et al. 1998; Welch et al. 2003), which was impossible when fish had to be followed by researchers in boats. These techniques can provide important information on, for example, survival in the early ocean period.

Coded Wire Tags (CWTs) were invented in the early 1960s (Jefferts et al. 1963) and revolutionized quantitative salmon research by allowing great numbers of smolts to be marked before release and then sampled in fisheries, spawning grounds, and hatcheries (Johnson 1990; Nandor et al. 2010). In the typical case, the tag is inserted in the fish’s cranial cartilage and its presence signaled by the excision of the adipose fin. Extraction of the tag for reading necessitates the death of the fish, so sequential detections are not possible. In most applications, one code is applied to an entire release group from a hatchery (or, less commonly, a wild population); thus, data on individual fish such as size and date are seldom collected (Peterson et al. 1994). Moreover, it took some years before the use of CWTs was widespread, and computerized data management systems were needed to facilitate their use (Johnson 1990).

Passive Integrated Transponder (PIT) tags for fish were developed in the 1980s (Prentice et al. 1990a, 1990b) and have improved significantly over the last few decades. PIT tags have offsetting advantages and disadvantages, relative to CWTs. PIT tags have a short detection range but can be detected remotely by fixed receiver stations in constricted areas of streams, in dam passageways, in open-ended weirs, nets, and floating barges, permitting multiple records of the passage of individuals. Mobile receivers can also be used in small streams to detect free-living fish, and at water bird colonies to estimate mortalities by detecting tags passed by predators. The tags are unique, and data specific to the individual such as size, date, and location of tagging, are routinely recorded. They are smaller than acoustic transmitters and so can be used with smaller fish, though they are larger than CWTs. Unlike CWTs, the presence of a PIT tag is not normally indicated by a clipped adipose fin, and they are not routinely sampled in ocean fisheries. The large network of PIT tag detectors at mainstem dams and tributary systems of the Columbia River make these tags an appealing method to assess various life-cycle metrics (e.g., migration rate and survival from release at a hatchery to a dam, from one dam to another, etc.). However, PIT tags with large-enough read ranges have not been generally available for the smallest salmon (< ~ 60 to 75 mm), and the tagging process and expense reduce their practicality for very large numbers of fish.

The development of techniques to produce bands on the otoliths of embryos or alevins by abrupt changes in thermal regime during incubation (Brothers 1990; Volk et al. 1990) allowed mass-marking of vast numbers of fry. This technique is primarily used for sockeye, chum, and pink salmon (Oxman et al. 2018), though the technique works on other species as well. However, otolith extraction necessitates the death of the fish, and only large groups are routinely marked. Thus, data on individual fish are unavailable, and sequential detections are not possible. Otolith marking is not extensively used in the Columbia River Basin (ISAB/ISRP 2009). Most recently, sampling the DNA from all adults spawning at a hatchery allows their offspring to be identified by parentage. This technique, known as parentage-based genetic tagging (PBT), was reviewed by Steele et al. (2019), and recent examples include the work of Beacham et al. (2019a, 2019b, 2020) and Horn et al. (2024).

The different marking techniques were developed and evolved during different periods, and their applications have not been part of a coordinated effort to study a single problem or suite of problems. Rather, the techniques arose and have been used to address related but different issues, and there was no plan to make them interchangeable. They have been used and overseen by agencies with different missions and for different purposes (e.g., management of US and Canadian fisheries, experiments on hatchery treatments to improve survival, comparisons of performance of wild and hatchery origin salmon, assignment of mortality to specific predators, and optimal management of river flows for salmon survival). The methodologies can provide not only estimates of survival and fisheries exploitation but other very important types of data on marine distribution, homing, and straying, and are thus essential tools for salmon management. However, interpretation of data produced by the techniques must be tempered with an understanding of their limitations.

The various approaches used (e.g., CWTs, PIT tags, radio, acoustic, and combined acoustic and radio tags, otolith marking, and PBT have unique strengths and weaknesses for estimating natural and fishing mortality of cohorts or the fate of individual fish (ISAB/ISRP 2009; Drenner et al. 2012). Consequently, it is difficult to combine or compare estimates based on the different approaches because they differ so much. As noted above, salmon taken in ocean fisheries are commonly sampled for CWTs but not PIT tags or PBT, and PIT tags are routinely detected repeatedly and remotely at fixed stations including dams during the fish's downstream and upstream migrations, but CWTs, otolith marks, and PBT are not read remotely. Importantly, these approaches can provide estimates of total survival at sea (with or without the ability to distinguish natural mortality from fishing) but only telemetry can indicate survival at sea, and that is limited to certain coastal regions. It is generally believed that the highest and the most variable mortality rates occur when the fish are small, soon after they enter marine waters and prior to fishing mortality. This phase is also especially important with respect to Columbia River Basin populations because of delayed effects of exposure to stressors during downstream migration (e.g., passage structures at dams and transportation), which have been hypothesized to adversely affect fish that survived to Bonneville Dam (e.g., Gosselin et al. 2017; but see Rechinsky et al. 2009 for evidence to the contrary).

6. References Cited

Achord, S., G. M. Matthews, O. W. Johnson, and D. M. Marsh. 1996. Use of passive integrated transponder (PIT) tags to monitor migration timing of Snake River chinook salmon smolts. North American Journal of Fisheries Management 16:302-313.

Achord, S., R. W. Zabel, and B. P. Sandford. 2007. Migration timing, growth, and estimated parr-to-smolt survival rates of wild Snake River spring-summer Chinook salmon from the Salmon River basin, Idaho, to the Lower Snake River. Transactions of the American Fisheries Society 136:142-154.

Ad Hoc Supplementation Monitoring and Evaluation Workgroup (AHSWG). 2008. Recommendations for broad scale monitoring and evaluation to evaluate the effects of hatchery supplementation on the fitness of natural salmon and steelhead populations. Final Report, Northwest Power and Conservation Council, Portland.

Anadromous Salmonid Monitoring Workshop Contributors. 2010. Anadromous salmonid monitoring strategy – Columbia Basin Coordinated Anadromous Monitoring Workshop. Version 30062010. Northwest Power and Conservation Council, Portland.

Apgar, T. M., J. E. Merz, B. T. Martin, and E. P. Palkovacs. 2021. Alternative migratory strategies are widespread in subyearling Chinook salmon. Ecology of Freshwater Fish 30:125-139.

Argue, A. W., R. Hilborn, R. M. Peterman, M. J. Staley, and C. J. Walters. 1983. Strait of Georgia chinook and coho fishery. Canadian Bulletin of Fisheries and Aquatic Sciences 211.

Barnaby, J. T. 1944. Fluctuations in abundance of red salmon, *Oncorhynchus nerka* (Walbaum), of the Karluk River, Alaska. Fishery Bulletin 50:237-295.

Bax, N. J. 1983. Early marine mortality of marked juvenile chum salmon (*Oncorhynchus keta*) released into Hood Canal, Puget Sound, Washington, in 1980. Canadian Journal of Fisheries and Aquatic Sciences 40:426-435.

Beacham, T. D., C. Wallace, K. Jonsen, B. McIntosh, J. R. Candy, D. Willis, C. Lynch, J. S. Moore, L. Bernatchez, and R. E. Withler. 2019a. Comparison of coded-wire tagging with parentage-based tagging and genetic stock identification in a large-scale coho salmon fisheries application in British Columbia, Canada. Evolutionary Applications 12:230-254.

Beacham, T. D., C. Wallace, K. Jonsen, B. McIntosh, J. R. Candy, D. Willis, C. Lynch, and R. E. Withler. 2019b. Variation in migration pattern, broodstock origin, and family productivity of coho salmon hatchery populations in British Columbia, Canada, derived from parentage-based tagging. Ecology and Evolution 9:9891-9906.

Beacham, T. D., C. Wallace, K. Jonsen, B. McIntosh, J. R. Candy, D. Willis, C. Lynch, and R. E. Withler. 2020. Insights on the concept of indicator populations derived from parentage-based tagging in a large-scale coho salmon application in British Columbia, Canada. Ecology and Evolution 10:6461-6476.

Beamish, R. J., editor. 2018. The Ocean Ecology of Pacific Salmon and Trout. American Fisheries Society, Bethesda, Maryland.

Beamish, R. J. and D. R. Bouillon. 1993. Pacific salmon production trends in relation to climate. Canadian Journal of Fisheries and Aquatic Sciences 50:1002-1016.

Beamish, R. J. and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Progress in Oceanography 49:423-437.

Beamish, R. J., R. M. Sweeting, C. M. Neville, K. L. Lange, T. D. Beacham, and D. Preikshot. 2012. Wild chinook salmon survive better than hatchery salmon in a period of poor production. Environmental Biology of Fishes 94:135–148.

Beckman, B. R. and W. W. Dickhoff. 1998. Plasticity of smolting in spring chinook salmon: relation to growth and insulin-like growth factor-I. Journal of Fish Biology 53:808-826.

Beckman, B. R., W. W. Dickhoff, W. S. Zaugg, C. Sharpe, S. Hirtzel, R. Schrock, D. A. Larsen, R. D. Ewing, A. Palmisano, C. B. Schreck, and C. V. W. Mahnken. 1999. Growth, smoltification, and smolt-to-adult return of spring chinook salmon from hatcheries on the Deschutes River, Oregon. Transactions of the American Fisheries Society 128:1125-1150.

Beeken, N., J. S. Hargrove, A. C. Harris, M. Davison, T. Copeland, L. Chiaramonte, and N. R. Smith. 2024. Wild adult steelhead and Chinook salmon abundance and composition at Lower Granite Dam, spawn year 2023. Research Report 24-12. Idaho Department of Fish and Game. Boise, Idaho.

Berggren, T. J., and M. J. Filardo. 1993. An analysis of variables influencing the migration of juvenile salmonids in the Columbia River Basin. North American Journal of Fisheries Management 13:48-63.

Bilton, H. T. 1984. Returns of Chinook salmon in relation to juvenile size at release. Canadian Technical Report of Fisheries and Aquatic Sciences 1245:1-33.

Bilton, H. T., D. F. Alderdice, and J. T. Schnute. 1982. Influence of time at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. Canadian Journal of Fisheries and Aquatic Sciences 39:426-447.

Bond, M. H., B. Chasco, and R. W. Zabel. 2024. Estimating the effects of smolt size and migration timing on salmon marine survival using a multivariate mixed-effect model. Journal of Applied Ecology 61: 2549-2561.

Bond, M. H., P. A. H. Westley, A. H. Dittman, D. Holecek, T. Marsh, and T. P. Quinn. 2017. Combined effects of barge transportation, river environment, and rearing location on straying and migration rate of Snake River fall-run Chinook Salmon. Transactions of the American Fisheries Society 146:60-73.

Bosch, W. J., S. N. Pandit, B. P. Sandford, G. M. Temple, M. V. Johnston, and D. A. Larsen. 2023. Effects of volitional emigration timing and smolt size on survival and age-at-return in a Pacific salmon hatchery population. Environmental Biology of Fishes 106:1037-1059.

Bourret, S. L., C. C. Caudill, and M. L. Keefer. 2016. Diversity of juvenile Chinook salmon life history pathways. Reviews in Fish Biology and Fisheries 26:375-403.

Braun, M. W., B. K. van der Leeuw, and K. S. Tidwell. 2024. 2023 evaluation of pinniped predation on adult salmonids and other fish in the Bonneville Dam tailrace. U. S. Army Corps of Engineers, Cascade Locks, OR.

Brothers, E. B. 1990. Otolith marking. American Fisheries Society Symposium 7:183-202.

Budy, P., G. P. Thiede, N. Bouwes, C. E. Petrosky, and H. A. Schaller. 2002. Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. Transactions of the American Fisheries Society 22:35–51.

Burke, B. J., W. T. Peterson, B. R. Beckman, C. Morgan, E. A. Daly, and M. Litz. 2013. Multivariate models of adult Pacific salmon returns. PLoS ONE 8:e54134.

Busby, P. J., T. C. Wainwright, G. J. Bryant, L. J. Lierheimer, R. S. Waples, F. W. Waknitz, and I. V. Lagomarsino. 1996. Status review of west coast steelhead from Washington, Idaho, Oregon and California. Technical Memorandum NWFSC-27. National Marine Fisheries Service Seattle.

Carmichael, R. W. and R. T. Messmer. 1995. Status of supplementing Chinook salmon natural production in the Imnaha River basin. American Fisheries Society Symposium 15:284-291.

Carvalho, P. G., W. H. Satterthwaite, M. R. O'Farrell, C. Speir, and E. P. Palkovacs. 2023. Role of maturation and mortality in portfolio effects and climate resilience. Canadian Journal of Fisheries and Aquatic Sciences 80:924-941.

Chasco, B., B. Burke, L. Crozier, and R. Zabel. 2021. Differential impacts of freshwater and marine covariates on wild and hatchery Chinook salmon marine survival. PLoS ONE 16:e0246659.

Chen, E. K., W. H. Satterthwaite, B. J. Kormos, Rachel C. Johnson, C. C. Phillis, and S. M. Carlson. 2023. Age structure of natural versus hatchery-origin endangered Chinook salmon and implications for fisheries management in California. Marine Ecology Progress Series 723:37-55.

Chinook Technical Committee. 1988. Joint Chinook technical committee report 1987 annual report. Pacific Salmon Commission.

Chinook Technical Committee. 2023. Joint Chinook technical committee report: 2022 exploitation rate analysis. Pacific Salmon Commission.

Christie, M. R., M. L. Marine, and M. S. Blouin. 2011. Who are the missing parents? Grandparentage analysis identifies multiple sources of gene flow into a wild population. Molecular Ecology 20:1263-1276.

Clarke, L. R., M. W. Flesher, and R. W. Carmichael. 2014. Hatchery steelhead smolt release size effects on adult production and straying. North American Journal of Aquaculture 76:39-44.

Cleaver, F. C. 1969. Effects of ocean fishing on 1961-brood fall chinook salmon from Columbia River hatcheries. Fish Commission of Oregon, Research Reports 1 (1), 76 p.

Cochran, S. M., S. Ricker, C. Anderson, S. P. Gallagher, and D. M. Ward. 2019. Comparing abundance-based and tag-based estimates of coho salmon marine survival. Fisheries Management and Ecology 26:165-171.

Comparative Survival Study (CSS). 2023. Comparative Survival Study of PIT-tagged Spring/Summer/Fall Chinook, Summer Steelhead, and Sockeye. 2023 Annual Report. Fish Passage Center. Available online: link.

Connolly, P.J., I.G. Jezorek, K.D. Martens, and E.F. Prentice. 2008. Measuring performance of two stationary interrogation systems for detecting downstream and upstream movement of PIT-tagged salmonids. North American Journal of Fisheries Management 28:402-417.

Connolly, P.J. 2010. Guidelines for calculating and enhancing detection efficiency of PIT tag interrogation systems. Chapter 7; Pages 119-125 *in* K.S. Wolf, and J.S. O'Neal, editors. Tagging, Telemetry and Marking Measures for Monitoring Fish Populations—A compendium of new and recent science for use in informing technique and decision modalities. Pacific Northwest Aquatic Monitoring Partnership Special Publication 2010-002.

Connor, W. P., R. K. Steinhorst, and H. L. Burge. 2003. Migrational behavior and seaward movement of wild subyearling fall chinook salmon in the Snake River. North American Journal of Fisheries Management 23:414-430.

Connor, W. P., J. G. Sneva, K. F. Tiffan, R. K. Steinhorst, and D. Ross. 2005. Two alternative juvenile life history types for fall chinook salmon in the Snake River basin. Transactions of the American Fisheries Society 134:291-304.

Connors, B., G. T. Ruggerone, and J. R. Irvine. 2024. Adapting management of Pacific salmon to a warming and more crowded ocean. ICES Journal of Marine Science, 82 (1): fsae135, https://doi.org/10.1093/icesjms/fsae135

Copeland, T., J. D. Ebel, R. N. Kinzer, and M. P. Corsi. 2024. How do management goals for wild Chinook Salmon align with feasibility? Fisheries 49:412-422.

Copeland, T., D. A. Venditti, and B. R. Barnett. 2014. The importance of juvenile migration tactics to adult recruitment in stream-type Chinook Salmon populations. Transactions of the American Fisheries Society 143:1460-1475.

Coronado, C. and R. Hilborn. 1998a. Spatial and temporal factors affecting survival in coho salmon (*Oncorhynchus kisutch*) in the Pacific Northwest. Canadian Journal of Fisheries and Aquatic Sciences 55:2067-2077.

Coronado, C. and R. Hilborn. 1998b. Spatial and temporal factors affecting survival in coho and fall chinook salmon in the Pacific Northwest. Bulletin of Marine Science 62:409-425.

Courter, I. I., D. B. Child, J. A. Hobbs, T. M. Garrison, J. J. Glessner, and S. Duery. 2013. Resident rainbow trout produce anadromous offspring in a large interior watershed. Canadian Journal of Fisheries and Aquatic Sciences 70:701–710.

Craig, B. E., C. A. Simenstad, and D. L. Bottom. 2014. Rearing in natural and recovering tidal wetlands enhances growth and life-history diversity of Columbia Estuary tributary coho salmon *Oncorhynchus kisutch* population. Journal of Fish Biology 85:31-51.

Crozier, L.G., B. J. Burke, B. E. Chasco, D. L. Widener, and R. W. Zabel. 2021. Climate change threatens Chinook salmon throughout their life cycle. Communications Biology 4, 222. https://doi.org/10.1038/s42003-021-01734-w (also see NOAA online article).

Crozier, L. G., M. D. Scheuerell, and R. W. Zabel. 2011. Using time series analysis to characterize evolutionary and plastic responses to environmental change: A case study of a shift toward earlier migration date in sockeye salmon. American Naturalist 178:755-773.

Dobos, M. E., B. J. Bowersox, T. Copeland, and E. J. Stark. 2020. Understanding life history diversity of a wild steelhead population and managing for resiliency. North American Journal of Fisheries Management 40:1087-1099.

Drenner, S. M., T. D. Clark, C. K. Whitney, E. G. Martins, S. J. Cooke, and S. G. Hinch. 2012. A synthesis of tagging studies examining the behaviour and survival of anadromous salmonids in marine environments. PLoS ONE 7:e31311.

Evans, A. F., N. J. Hostetter, K. Collis, D. D. Roby, and F. J. Loge. 2014. Relationship between juvenile fish condition and survival to adulthood in steelhead. Transactions of the American Fisheries Society 143:899-909.

Faulkner, J. R., B. L. Bellerud, D. L. Widener, and R. W. Zabel. 2019. Associations among fish length, dam passage history, and survival to adulthood in two at-risk species of Pacific salmon. Transactions of the American Fisheries Society 148:1069-1087.

Feldhaus, J. W., T. L. Hoffnagle, and R. W. Carmichael. 2016. The influence of size at release on performance of Imnaha River Chinook Salmon hatchery smolts. North American Journal of Fisheries Management 36:363-374.

Feldhaus, J., E. Brandt, I. Tattam, S. Vatland, C. Crump, and L. Naylor. 2022. 2022 Grand Ronde and Imnaha River basin Spring Chinook Hatchery Review. 2022 ISRP Review Materials, Lower Snake River Compensation Plan Office, Boise, Idaho.

Fish Passage Center (FPC). 2020. Technical review of Welch et al. (2020), titled, A synthesis of the coast-wide decline in survival of West Coast Chinook Salmon (Oncorhynchus tshawytscha, Salmonidae). Memorandum from Michele DeHart (FPC) to Bill Tweit (WDFW), Tucker Jones (ODFW), and Margaret Filardo (citizen). December 4, 2020. https://www.fpc.org/documents/memos/53-20.pdf

Foerster, R. E. 1954. On the relation of adult sockeye salmon (*Oncorhynchus nerka*) returns to known smolt seaward migrations. Journal of the Fisheries Research Board of Canada 11:339-350.

Ford, J. K. B. and G. M. Ellis. 2006. Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia. Marine Ecology Progress Series 316:185-199.

Ford, M. J., editor. 2022. Biological Viability Assessment Update for Pacific Salmon and Steelhead Listed Under the Endangered Species Act: Pacific Northwest. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-171. https://doi.org/10.25923/kq2n-ke70

Ford, M., T. N. Pearsons, and A. Murdoch. 2015. The spawning success of early maturing resident hatchery Chinook Salmon in a natural river system. Transactions of the American Fisheries Society 144:539-548.

Fredin, R. A. 1965. Some methods for estimating ocean mortality of Pacific salmon and applications. Journal of the Fisheries Research Board of Canada 22:33-51.

Fresh, K. L., and S. L. Schroder. 1987. Influence of the abundance, size, and yolk reserves of juvenile chum salmon (*Oncorhynchus keta*) on predation by freshwater fishes in a small coastal stream. Canadian Journal of Fisheries and Aquatic Sciences 44:236-243.

Fukuwaka, M., and T. Suzuki. 2002. Early sea mortality of mark-recaptured juvenile chum salmon in open coastal waters. Journal of Fish Biology 60:3-12.

Fulton, L. A. 1970. Spawning areas and abundance of steelhead trout and coho, sockeye, and chum salmon in the Columbia River Basin – past and present. Special Scientific Report – Fisheries 618. National Marine Fisheries Service, Washington, D.C. 37 p.

Furnell, D. J., and J. R. Brett. 1986. Model of monthly marine growth and natural mortality for Babine Lake sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 43:999-1004.

Gilbert, C. H. 1913. Age at maturity of the Pacific coast salmon of the genus Oncorhynchus. Bulletin of the Bureau of Fisheries 32:1-22.

Gosselin, J. L., E. R. Buhle, C. Van Holmes, W. N. Beer, S. Iltis, and J. J. Anderson. 2021. Role of carryover effects in conservation of wild Pacific salmon migrating regulated rivers. Ecosphere 12:e03618.

Gosselin, J. L., R. W. Zabel, J. J. Anderson, J. R. Faulkner, A. M. Baptista, and B. P. Sandford. 2017. Conservation planning for freshwater–marine carryover effects on Chinook salmon survival. Ecology and Evolution 8:319-332.

Gustafson, R. G., T. C. Wainwright, G. A. Winans, F. W. Waknitz, L. T. Parker, and R. S. Waples. 1997. Status review of sockeye salmon from Washington and Oregon. NOAA Technical memorandum NMFS-NWFSC-33. National Marine Fisheries Service, Seattle.

Haeseker, S. L., J. A. McCann, J. Tuomikoski, and B. Chockley. 2012. Assessing freshwater and marine environmental influences on life-stage-specific survival rates of Snake River spring–summer Chinook Salmon and Steelhead. Transactions of the American Fisheries Society 141:121-138.

Hance, D. J., L. M. Ganio, K. M. Burnett, and J. L. Ebersole. 2016. Basin-scale variation in the spatial pattern of fall movement of juvenile coho salmon in the West Fork Smith River, Oregon. Transactions of the American Fisheries Society 145:1018-1034.

Hargrove, J. S., C. A. Camacho, W. C. Schrader, H. H. Powell, T. A. Delomas, J. E. Hess, S. R. Narum, and M. R. Campbell. 2021. Parentage-based tagging improves escapement estimates for ESA-listed adult Chinook salmon and steelhead in the Snake River basin. Canadian Journal of Fisheries and Aquatic Sciences 78:349-360.

Harstad, D. L., D. A. Larsen, J. Miller, I. Adams, D. K. Spangenberg, S. Nance, L. Rohrbach, J. G. Muraskas, and B. R. Beckman. 2018. Winter-rearing temperature affects growth profiles, age of maturation, and smolt-to-adult returns for yearling summer Chinook Salmon in the upper Columbia River Basin. North American Journal of Fisheries Management 38:867-885.

Healey, M. C. 1983. Coastwide distribution and ocean migration patterns of stream- and ocean-type chinook salmon, Oncorhynchus tshawytscha. Canadian Field-Naturalist 97(4):427-433.

Healey, M. C. 1991. Life history of chinook salmon (Oncorhynchus tshawytscha) Pages 311-393 in C. Groot, and L. Margolis, editors. Pacific Salmon Life Histories. University of British Columbia Press, Vancouver.

Henderson, M. A. and A. J. Cass. 1991. Effect of smolt size on smolt-to-adult survival for Chilko Lake sockeye salmon (Oncorhynchus nerka). Canadian Journal of Fisheries and Aquatic Sciences 48:988-994.

Henry, K. A. 1971. Estimates of maturation and ocean mortality for Columbia River hatchery fall chinook salmon and the effect of no ocean fishing on yield. Research Reports of the Fish Commission, Oregon 3:13-27.

Henry, K. A. 1978. Estimating natural and fishing mortalities of chinook salmon, Oncorhynchus tshawytscha, in the ocean, based on recoveries of marked fish. Fishery Bulletin 76:45-57.

Hoar, W. S. 1976. Smolt transformation: evolution, behavior, and physiology. Journal of the Fisheries Research Board of Canada 33:1233-1252.

Hobday, A. J. and G. W. Boehlert. 2001. The role of coastal ocean variation in spatial and temporal patterns in survival and size of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 58:2021-2036.

Holsman, K. K., M. D. Scheuerell, E. Buhle, and R. Emmett. 2012. Interacting effects of translocation, artificial propagation, and environmental conditions on the marine survival of Chinook salmon from the Columbia River, Washington, U.S.A. Conservation Biology 26:912-922.

Horn, R. L., H. M. Nuetzel, B. Johnson, C. Kamphaus, J. Lovrak, K. Mott, T. Newsome, and S. R. Narum. 2024. Utility of parentage-based tagging for monitoring Coho salmon (*Oncorhynchus kisutch*) in the interior Columbia River Basin. Evolutionary Applications 17:e13607.

Hostetter, N. J., A. F. Evans, D. D. Roby, and K. Collis. 2012. Susceptibility of juvenile steelhead to avian predation: the influence of individual fish characteristics and river conditions. Transactions of the American Fisheries Society 141:1586-1599.

Hostetter, N. J., A. F. Evans, Q. Payton, D. D. Roby, D. E. Lyons, and K. Collis. 2023. A review of factors affecting the susceptibility of juvenile salmonids to avian predation. North American Journal of Fisheries Management 43:244-256.

Hunter, J. G. 1959. Survival and production of pink and chum salmon in a coastal stream. Journal of the Fisheries Research Board of Canada 16:835-885.

Irvine, J. R., and S. A. Akenhead. 2013. Understanding smolt survival trends in sockeye salmon. Marine and Coastal Fisheries 5:303-328.

ISAB (Independent Scientific Advisory Board). 2016-1. Predation Metrics Report. Northwest Power and Conservation Council, Portland, Oregon. ISAB Report 2016-1. Available online: link.

ISAB (Independent Scientific Advisory Board). 2021-1. ISAB Dam Bypass Selectivity Report: Review of Analyses of Juvenile Fish Size Selectivity in Dam Bypass Systems and Implications for Estimating and Interpreting Fish Survival. Northwest Power and Conservation Council, Portland, Oregon. ISAB Report 2021-1. Available online: link.

ISAB (Independent Scientific Advisory Board). 2021-2. ISAB Comparison of Research Findings on Avian Predation Impacts on Salmon Survival. Northwest Power and Conservation Council, Portland, Oregon. ISAB Report 2021-2. Available online: link.

ISAB (Independent Scientific Advisory Board). 2021-3. ISAB Review of the Coast-Wide Analysis of Chinook Salmon Smolt to Adult Returns (SARs) by Welch et al. Northwest Power and Conservation Council, Portland, Oregon. ISAB Report 2021-3. Available online: link.

ISAB (Independent Scientific Advisory Board). 2024-3. ISAB Review of the Comparative Survival Study (CSS) Draft 2024 Annual Report. Northwest Power and Conservation Council, Portland, Oregon. ISAB Report 2024-3. Available online: link.

ISAB/ISRP (Independent Scientific Advisory Board/Independent Scientific Review Panel). 2009-1. Tagging Report: A comprehensive review of Columbia River Basin fish tagging technologies and programs. Northwest Power and Conservation Council, Portland, Oregon. ISAB/ISRP Report 2009-1. Available online: link.

ISRP (Independent Scientific Review Panel). 2014-6. Summary Review of the Lower Snake River Compensation Plan 2011-2014. Northwest Power and Conservation Council, Portland, Oregon. ISRP Report 2014-6. Available online: link.

ISRP (Independent Scientific Review Panel). 2019-2. Mainstem and Program Support Category Review. Northwest Power and Conservation Council, Portland, Oregon. ISRP Report 2019-2. Available online: link.

ISRP (Independent Scientific Review Panel). 2023-1. Review of LSRCP Spring/Summer Chinook Production Program, 2022-2023. ISRP Report 2023-1. Northwest Power and Conservation Council, Portland, Oregon. Available online: link.

ISRP/ISAB (Independent Scientific Review Panel/Independent Scientific Advisory Board). 2005-15. Monitoring and Evaluation of Supplementation Projects. Northwest Power and Conservation Council, Portland, Oregon. ISRP/ISAB Report 2005-15. Available online: link.

Jacobs, G. R., R. F. Thurow, C. E. Petrosky, C. W. Osenberg, and S. J. Wenger. 2024. Life-cycle modeling reveals high recovery potential of at-risk wild Chinook salmon via improved migrant survival. Canadian Journal of Fisheries and Aquatic Sciences 81:297-310.

James, S. E., B. Doherty, S. P. Cox, I. A. Pearsall, and B. Riddell. 2023. Size and timing of hatchery releases influence juvenile-to-adult survival rates of British Columbia Chinook (*Oncorhynchus tshawytscha*) and coho (*Oncorhynchus kisutch*) salmon. Canadian Journal of Fisheries and Aquatic Sciences 80:700-718.

Jefferts, K. B., P. K. Bergman, and H. F. Fiscus. 1963. A coded wire identification system for macro-organisms. Nature 198:460-462.

Jepson, M. A., M. L. Keefer, G. P. Naughton, C. A. Peery, and B. J. Burke. 2010. Population composition, migration timing, and harvest of Columbia River Chinook salmon in late summer and fall. North American Journal of Fisheries Management 30:72-88.

Johnson, J. H. 1960. Sonic tracking of adult salmon at Bonneville Dam, 1957. Fishery Bulletin 60:471-485.

Johnson, J. K. 1990. Regional overview of coded wire tagging of anadromous salmon and steelhead in northwest America. American Fisheries Society Symposium 7:782-816.

Johnson, J., T. Johnson, and T. Copeland. 2012. Defining life histories of precocious male parr, minijack, and jack Chinook salmon using scale patterns. Transactions of the American Fisheries Society 141:1545-1556.

Johnson, O. W., W. S. Grant, R. G. Kope, K. G. Neely, F.W. Waknitz, and R.S. Waples. 1997. Status review of chum salmon from Washington, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-32. NOAA-Fisheries, Seattle.

Jones, K. K., T. J. Cornwell, D. L. Bottom, L. A. Campbell, and S. Stein. 2014. The contribution of estuary-resident life histories to the return of adult *Oncorhynchus kisutch*. Journal of Fish Biology 85:52-80.

Jones, K. K., T. J. Cornwell, D. L. Bottom, S. Stein, and S. Starcevich. 2021. Interannual variability in life-stage specific survival and life history diversity of coho salmon in a coastal Oregon basin. Canadian Journal of Fisheries and Aquatic Sciences 78:1887-1899.

Kareiva, P., M. Marvier, and M. McClure. 2000. Recovery and management options for spring/summer chinook salmon in the Columbia River Basin. Science 290:977-979.

Keefer, M. L., R. J. Stansell, S. C. Tackley, W. T. Nagy, K. M. Gibbons, C. A. Peery, and C. C. Caudill. 2012. Use of radiotelemetry and direct observations to evaluate sea lion predation on adult Pacific salmonids at Bonneville Dam. Transactions of the American Fisheries Society 141:1236–1251.

Kilduff, D., L. Botsford, and S. Teo. 2014. Spatial and temporal covariability in early ocean survival of Chinook salmon (*Oncorhynchus tshawytscha*) along the west coast of North America. ICES Journal of Marine Science 71(7):1671–1682.

Kilduff, D. P., E. Di Lorenzo, L. W. Botsford, and S. L. H. Teo. 2015. Changing central Pacific El Niños reduce stability of North American salmon survival rates. Proceedings of the National Academy of Sciences 112: 10962-10966.

Knudsen, E. E. 2000. Managing Pacific salmon escapements: the gaps between theory and reality. Pages 237-272 in E. E. Knudsen, C. R. Steward, D. D. MacDonald, J. E. Williams, and D. W. Reiser, editors. Sustainable fisheries management: Pacific salmon. Lewis Publishers, Boca Raton, Florida.

Koch, I. J., T. R. Seamons, P.F., Galbreath, H.M. Nuetzel, A. P. Matala, K. I. Warheit, D. E. Fast, M. V. Johnston, C. R. Strom, S.R., Narum, and W. J. Bosch. 2022. Effects of supplementation in upper Yakima River Chinook Salmon. Transactions of the American Fisheries Society 151:373-388.

Koenings, J. P., H. J. Geiger, and J. J. Hasbrouck. 1993. Smolt-to-adult survival patterns of sockeye salmon (*Oncorhynchus nerka*): effects of smolt length and geographic latitude when entering the sea. Canadian Journal of Fisheries and Aquatic Sciences 50:600-611.

Larsen, D. A., B. R. Beckman, K. A. Cooper, D. Barrett, M. Johnston, P. Swanson, and W. W. Dickhoff. 2004. Assessment of high rates of precocious male maturation in a spring chinook salmon supplementation hatchery program. Transactions of the American Fisheries Society 133:98-120.

Larsen, D. A., B. R. Beckman, C. R. Strom, P. J. Parkins, K. A. Cooper, D. E. Fast, and W. W. Dickhoff. 2006. Growth modulation alters the incidence of early male maturation and physiological development of hatchery-reared spring Chinook salmon: a comparison with wild fish. Transactions of the American Fisheries Society 135:1017-1032.

Larsen, D. A., D. L. Harstad, C. R. Strom, M. V. Johnston, C. M. Knudsen, D. E. Fast, T. N. Pearsons, and B. R. Beckman. 2013. Early life history variation in hatchery- and natural-origin spring Chinook Salmon in the Yakima River, Washington. Transactions of the American Fisheries Society 142:540-555.

Laufkötter, C., J. Zscheischler, and T. L. Frölicher. 2020. High-impact marine heatwaves attributable to human-induced global warming. Science 369:1621-1625.

Leider, S. A., M. W. Chilcote, and J. J. Loch. 1986. Comparative life history characteristics of hatchery and wild steelhead trout (*Salmo gairdneri*) of summer and winter races in the Kalama River, Washington. Canadian Journal of Fisheries and Aquatic Sciences 43:1398-1409.

Logerwell, E. A., N. Mantua, P. W. Lawson, R. C. Francis, and V. N. Agostini. 2003. Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. Fisheries Oceanography 12:554-568.

Magnusson, A., and R. Hilborn. 2003. Estuarine influence on survival rates of coho (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus tshawytscha*) from hatcheries on the U.S. Pacific coast. Estuaries 26:1094-1103.

Malick, M. J. 2020. Time-varying relationships between ocean conditions and sockeye salmon productivity. Fisheries Oceanography 29:265-275.

Manishin, K. A., C. J. Cunningham, P. A. H. Westley, and A. C. Seitz. 2021. Can late stage marine mortality explain observed shifts in age structure of Chinook salmon? PLoS ONE 16:e0247370.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78:1069-1079.

Matala, A. P., S. R. Narum, B. P. Saluskin, M. V. Johnston, J. E. Newell, D. E. Fast, and P. F. Galbreath. 2019. Early observations from monitoring a reintroduction program: Return of Sockeye Salmon to a nursery lake of historical importance. Transactions of the American Fisheries Society 148:271-288.

Mathews, S. B., and R. Buckley. 1976. Marine mortality of Puget Sound coho salmon (*Oncorhynchus kisutch*). Journal of the Fisheries Research Board of Canada 33:1677-1684.

McCann, J, B. Chockley, E. Cooper, G. Scheer, R. Tessier, S. Haeseker, B. Lessard, T. Copeland, J. Ebel, A. Storch, D. Rawding. 2023. Comparative survival study of PIT-tagged spring/summer/fall Chinook, summer steelhead, and sockeye. 2023 Annual Report to the Bonneville Power Administration. Portland, OR.

McCormick, S. D. 1994. Ontogeny and evolution of salinity tolerance in anadromous salmonids: hormones and heterochrony. Estuaries 17:26-33.

McCormick, S. D. 2012. Smolt physiology and endocrinology. Fish Physiology 32:199-251.

McGurk, M. D. 1996. Allometry of marine mortality of Pacific salmon. Fishery Bulletin 94:77-88.

McKenzie, J., B. Parsons, A. Seitz, R. K. Kopf, M. Mesa, and Q. Phelps, editors. 2012. Advances in Fish Tagging and Marking Methodology, volume 76. American Fisheries Society, Bethesda, Maryland.

Melnychuk, M. C., D. W. Welch, C. J. Walters, and V. Christensen. 2007. Riverine and early ocean migration and mortality patterns of juvenile steelhead trout (*Oncorhynchus mykiss*) from the Cheakamus River, British Columbia. Hydrobiologia 582:55-65.

Moore, M. E., B. A. Berejikian, F. A. Goetz, A. G. Berger, S. S. Hodgson, E. J. Connor, and T. P. Quinn. 2015. Multi-population analysis of Puget Sound steelhead survival and migration behavior. Marine Ecology Progress Series 537:217-232.

Mueter, F. J., B. J. Pyper, and R. M. Peterman. 2005. Relationships between coastal ocean conditions and survival rates of Northeast Pacific salmon at multiple lags. Transactions of the American Fisheries Society 134:105-119.

Mullan, J. W. 1986. Determinants of sockeye salmon abundance in the Columbia River, 1880's - 1982: A review and synthesis. Biological Report 86(12) U. S. Fish and Wildlife Service, Leavenworth, Washington. 135 p.

Murauskas, J., K. Hyatt, J. Fryer, E. Koontz, S. Folks, R. Bussanich, and K. Shelby. 2021. Migration and survival of Okanagan River Sockeye Salmon *Oncorhynchus nerka*, 2012- 2019. Animal Biotelemetry 9:1-16.

Myrvold, K. M., and B. P. Kennedy. 2016. Juvenile steelhead movements in relation to stream habitat, population density, and body size: consequences for individual growth rates. Canadian Journal of Fisheries and Aquatic Sciences 73:1520-1529.

Nandor, G., J. R. Longwill, and D. L. Webb. 2010. Overview of the coded wire tag program in the Greater Pacific Region of North America. Pages 5-46 *in* K. S. Wolf, and J. S. O'Neal, editors. Telemetry, and marking measures for monitoring fish populations—a compendium of new and recent science for use in informing technique and decision modalities. Pacific Northwest Aquatic Monitoring Partnership.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4-21.

Noakes, D. J., D. W. Welch, M. Henderson, and E. Mansfield. 1990. A comparison of preseason forecasting methods for returns of two British Columbia sockeye salmon stocks. North American Journal of Fisheries Management 10:46-57.

Norris, J. G., S.-Y. Hyun, and J. J. Anderson. 2000. Ocean distribution of Columbia River upriver bright fall chinook salmon stocks. North Pacific Anadromous Fish Commission Bulletin 2:221-232.

Northwest Power and Conservation Council (NPCC). 2014/2020. 2014/2020 Columbia River Basin Fish and Wildlife Program. NPCC. Portland, Oregon. Available online (link).

Ohlberger, J, E. R. Buhle, T. W. Buehrens, N. W. Kendall, T. Harbison, A. M. Claiborne, J. P. Losee, J. Whitney, and M. D. Scheuerell. 2025. Declining marine survival of steelhead trout linked to climate and ecosystem change. Fish and Fisheries doi.org/10.1111/faf.12878

Ohlberger, J., E. J. Ward, D. E. Schindler, and B. Lewis. 2018. Demographic changes in Chinook salmon across the Northeast Pacific Ocean. Fish and Fisheries 19:533-546.

Okanagan Work Group. 2023. Okanagan Chinook: summary of findings and considerations for future actions. Pacific Salmon Commission Technical Report 51. Vancouver, British Columbia. 166 pages.

Oxman, D. S., K. W. McNeel, and A. R. Munro. 2018. Otolith marking. Pages 1000-1019 *in* R. J. Beamish, editor. The ocean ecology of Pacific salmon and trout. American Fisheries Society, Bethesda, Maryland.

Parker, R. R. 1960. Critical size and maximum yield for chinook salmon (*Oncorhynchus tshawytscha*). Journal of the Fisheries Research Board of Canada 17: 199-210.

Parker, R. R. 1962. Estimations of ocean mortality rates for Pacific salmon (*Oncorhynchus*). Journal of the Fisheries Research Board of Canada 19(4):561-589.

Parker, R. R. 1968. Marine mortality schedules of pink salmon of the Bella Coola River, Central British Columbia. Journal of the Fisheries Research Board of Canada 25(4):757-794.

Payton, Q., J. K. Fryer, T. Garrison, and A. F. Evans. 2023. Estimating cause-specific mortality and survival of juvenile fall Chinook salmon: an investigation of avian predation across large spatial scales. North American Journal of Fisheries Management 43:569–585.

Pearcy, W. G. 1992. Ocean ecology of North Pacific salmonids. Washington Sea Grant Program, University of Washington, Seattle.

Pearsons, T. N., and M. D. Miller. 2023. Stray compositions of hatchery-origin Chinook Salmon and steelhead in natural spawning populations of the upper Columbia watershed. Transactions of the American Fisheries Society 152:515–529.

Pearsons, T. N., and R. R. O'Connor. 2020. Stray rates of natural-origin Chinook Salmon and Steelhead in the Upper Columbia River Watershed. Transactions of the American Fisheries Society 149:147-158.

Pearsons, T. N., and R. R. O'Connor. 2024. Comparisons of donor stray percentages between hatchery- and natural-origin Chinook Salmon and steelhead in the upper Columbia watershed. North American Journal of Fisheries Management.

Pess, G. R., and coauthors. 2011. The influences of body size, habitat quality, and competition on the movement and survival of juvenile coho salmon, *Oncorhynchus kisutch*, during the early stages of stream re-colonization. Transactions of the American Fisheries Society 140:883-897.

Peterman, R. M. 1982a. Model of salmon age structure and its use in preseason forecasting and studies of marine survival. Canadian Journal of Fisheries and Aquatic Sciences 39:1444-1452.

Peterman, R. M. 1982b. Nonlinear relation between smolts and adults in Babine Lake sockeye salmon *(Oncorhynchus nerka)* and implications for other salmon populations. Canadian Journal of Fisheries and Aquatic Sciences 39:904-913.

Peterson, N. P., E. F. Prentice, and T. P. Quinn. 1994. Comparison of sequential coded-wire and passive integrated transponder tags for assessing overwinter growth and survival of juvenile coho salmon. North American Journal of Fisheries Management 14:870-873.

Petrosky, C. E., H. A. Schaller, E. S. Tinus, T. Copeland, and A. J. Storch. 2020. Achieving productivity to recover and restore Columbia River stream-type Chinook Salmon relies on increasing smolt-to-adult survival. North American Journal of Fisheries Management 40:789–803.

Peven, C. M. 1987. Downstream migration timing of two stocks of sockeye salmon on the Mid-Columbia River. Northwest Science 61:186-190.

Peven, C. M., and S. G. Hays. 1989. Proportions of hatchery and naturally produced steelhead smolts migrating past Rock Island Dam, Columbia River, Washington. North American Journal of Fisheries Management 9:53-59.

Peven, C. M., R. R. Whitney, and K. R. Williams. 1994. Age and length of steelhead smolts from the mid-Columbia River Basin, Washington. North American Journal of Fisheries Management 14:77-86.

Plumb, J. M. 2018. A bioenergetics evaluation of temperature-dependent selection for the spawning phenology by Snake River fall Chinook salmon. Ecology and Evolution 8:9633-9645.

Prentice, E. F., T. A. Flagg, and C. S. McCutcheon. 1990a. Feasibility of using implantable passive integrated transponder (PIT) tags on salmonids. American Fisheries Society Symposium:317-322.

Prentice, E. F., T. A. Flagg, C. S. McCutcheon, D. F. Brastow, and D. C. Cross. 1990b. Equipment, methods, and an automated data-entry station for PIT tagging. American Fisheries Society Symposium 7:335-340.

PSC (Pacific Salmon Commission). 2023. Specifications and Definitions for the Exchange of Coded Wire Tag Data for the North American Pacific Coast. PSC Format Version 4.2.

Pyper, B. J., F. J. Mueter, and R. M. Peterman. 2005. Across-species comparisons of spatial scales of environmental effects on survival rates of Northeast Pacific salmon. Transactions of the American Fisheries Society 134:86-104.

Quinn, T. P. 2018. The Behavior and Ecology of Pacific Salmon and Trout, second edition. University of Washington Press, Seattle.

Quinn, T. P., and D. J. Adams. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. Ecology 77:1151-1162.

Quinn, T. P., J. Chamberlin, and E. L. Brannon. 2011. Experimental evidence of population-specific spatial distributions of Chinook salmon, *Oncorhynchus tshawytscha*. Environmental Biology of Fishes 92:313-322.

Quinn, T. P., B. R. Dickerson, and L. A. Vøllestad. 2005. Marine survival and distribution patterns of two Puget Sound hatchery populations of coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon. Fisheries Research 76:209-220.

Quinn, T. P., K. Doctor, N. Kendall, and H. B. Rich. 2009. Diadromy and the life history of sockeye salmon: nature, nurture, and the hand of man. American Fisheries Society Symposium 69:23-42.

Quinn, T. P., R. S. Nemeth, and D. O. McIsaac. 1991. Homing and straying patterns of fall chinook salmon in the lower Columbia River. Transactions of the American Fisheries Society 120:150-156.

Quinn, T. P., L. A. Vøllestad, J. Peterson, and V. Gallucci. 2004. Influences of fresh water and marine growth on the egg size – egg number tradeoff in coho and chinook salmon. Transactions of the American Fisheries Society 133:55-65.

Raymond, H. L. 1979. Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966-1975. Transactions of the American Fisheries Society 108:505-529.

Rechisky, E. L., A. D. Porter, T. D. Clark, N. B. Furey, M. K. Gale, S. G. Hinch, and D. W. Welch. 2019. Quantifying survival of age-2 Chilko Lake sockeye salmon during the first 50 days of migration. Canadian Journal of Fisheries and Aquatic Sciences 76:136-152.

Rechisky, E. L., D. W. Welch, A. D. Porter, M. C. Jacobs, and A. Ladouceur. 2009. Experimental measurements of hydrosystem-induced delayed mortality in juvenile Snake River spring Chinook salmon (*Oncorhynchus tshawytscha*) using a large-scale acoustic array. Canadian Journal of Fisheries and Aquatic Sciences 66:1019-1024.

Ricker, W. E. 1976. Review of the rate of growth and mortality of Pacific salmon in salt water, and noncatch mortality caused by fishing. Journal of the Fisheries Research Board of Canada 33:1483-1524.

Ruff, C. P., J. H. Anderson, I. M. Kemp, N. W. Kendall, P. A. McHugh, A. Velez-Espino, C. M. Greene, M. Trudel, C. A. Holt, K. E. Ryding, and K. Rawson. 2017. Salish Sea Chinook salmon exhibit weaker coherence in early marine survival trends than coastal populations. Fisheries Oceanography 26:625–637.

Ruggerone, G. T., and J. R. Irvine. 2018. Numbers and biomass of natural- and hatchery-origin Pink Salmon, Chum Salmon, and Sockeye Salmon in the North Pacific Ocean, 1925–2015. Marine and Coastal Fisheries 10:152-168.

Ruggerone, G. T. and D. E. Rogers. 1984. Arctic char predation on sockeye salmon smolts at Little Togiak River, Alaska. Fishery Bulletin 82:401-410.

Ruggerone, G. T., B. A. Agler, B. M. Connors, E. V. Farley Jr, J. R. Irvine, L. I. Wilson, and E. M. Yasumiishi. 2016. Pink and sockeye salmon interactions at sea and their influence on forecast error of Bristol Bay sockeye salmon. North Pacific Anadromous Fish Commission Bulletin 6:349–361.

Rutter, C. 1902. Natural history of the quinnat salmon. A report on investigations in the Sacramento River 1896-1901. U.S. Fish Commission Bulletin 22:65-141.

Satterthwaite, W. H., S. M. Carlson, S. D. Allen-Moran, S. Vincenzi, S. J. Bograd, and B. K. Wells. 2014. Match-mismatch dynamics and the relationship between ocean-entry timing and relative ocean recoveries of Central Valley fall run Chinook salmon. Marine Ecology Progress Series 511:237–248.

Schaller, H. A., C. E. Petrosky, and O. P. Langness. 1999. Contrasting patterns of productivity and survival rates for stream type chinook salmon (*Oncorhynchus tshawytscha*) populations of the Snake and Columbia rivers. Canadian Journal of Fisheries and Aquatic Sciences 56:1031–1045.

Schaller, H. A., C. E. Petrosky, and O. P. Langness. 2000. Reply to Zabel and Williams comments on "Contrasting patterns of productivity and survival rates for stream-type Chinook Salmon (*Oncorhynchus tshawytscha*) of the Snake and Columbia rivers" by Schaller et al. (1999). Canadian Journal of Fisheries and Aquatic Sciences 57:1742-1746.

Scheuerell, M. D. 2005. Influence of juvenile size on the age at maturity of individually marked wild Chinook salmon. Transactions of the American Fisheries Society 134:999-1004.

Scheuerell, M. D., R. W. Zabel, and B. P. Sandford. 2009. Relating juvenile migration timing and survival to adulthood in two species of threatened Pacific salmon (*Oncorhynchus* spp.). Journal of Applied Ecology 46:983-990.

Schroeder, R. K., L. D. Whitman, B. Cannon, and P. Olmsted. 2016. Juvenile life-history diversity and population stability of spring Chinook salmon in the Willamette River basin, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 73:921-934.

Seitz, A. C., M. B. Courtney, M. D. Evans, and K. Manishin. 2019. Pop-up satellite archival tags reveal evidence of intense predation on large immature Chinook salmon (*Oncorhynchus tshawytscha*) in the North Pacific Ocean. Canadian Journal of Fisheries and Aquatic Sciences 76:1608-1615.

Sharma, R. and T. P. Quinn. 2012. Linkages between life history type and migration pathways in freshwater and marine environments for Chinook salmon, *Oncorhynchus tshawytscha*. Acta Oecologica 41:1-13.

Sharma, R., L. A. Vélez-Espino, A. C. Wertheimer, N. J. Mantua, and R. C. Francis. 2013. Relating spatial and temporal scales of climate and ocean variability to survival of Pacific Northwest Chinook salmon (*Oncorhynchus tshawytscha*). Fisheries Oceanography 22:14-31.

Shelton, A. O., W. H. Satterthwaite, E. J. Ward, B. E. Feist, and B. Burke. 2019. Using hierarchical models to estimate stock-specific and seasonal variation in ocean distribution, survivorship, and aggregate abundance of fall run Chinook salmon. Canadian Journal of Fisheries and Aquatic Sciences 76:95-108.

Sobocinski, K. L., N. W. Kendall, C. M. Greene, and M. W. Schmidt. 2020. Ecosystem indicators of marine survival in Puget Sound steelhead trout. Progress in Oceanography 188:1-27.

Sorel, M. H., A. R. Murdoch, R. W. Zabel, J. C. Jorgensen, C. M. Kamphaus, and S.J. Converse. 2023. Juvenile life history diversity is associated with lifetime individual heterogeneity in a migratory fish. Ecosphere 14:e4366.

Sorel, M. H., R. W. Zabel, D. S. Johnson, A. M. Wargo Rub, and S. J. Converse. 2021. Estimating population-specific predation effects on Chinook salmon via data integration. Journal of Applied Ecology 58:372-381.

Stasko, A. B. and D. G. Pincock. 1977. Review of underwater biotelemetry, with emphasis on ultrasonic techniques. Journal of the Fisheries Research Board of Canada 34:1261-1285.

Steele, C. A., E. C. Anderson, M. W. Ackerman, M. A. Hess, N. R. Campbell, S. R. Narum, and M. R. Campbell. 2013. A validation of parentage-based tagging using hatchery steelhead in the Snake River basin. Canadian Journal of Fisheries and Aquatic Sciences 70:1046–1054.

Steele, C. A., M. Hess, S. Narum, and M. Campbell. 2019. Parentage-based tagging: reviewing the implementation of a new tool for an old problem. Fisheries 44:413-422.

Steele, C. A., A. Harris, M. Campbell, and D. A. Venditti. 2024. Inferring precocial Chinook Salmon production through single-parentage assignments. Transactions of the American Fisheries Society 153:494-504.

Tatara, C. P., D. A. Larsen, M. R. Cooper, P. Swanson, M. A. Middleton, J. T. Dickey, D. Harstad, M. P. Humling, C. R. Pasley, and B. Berejikian. 2019. Age at release, size, and maturation status influence residualism in hatchery steelhead. North American Journal of Fisheries Management 39:468-484.

Tattam, I. A., J. R. Ruzycki, J. L. McCormick, and R. W. Carmichael. 2015. Length and condition of wild Chinook salmon smolts influence age at maturity. Transactions of the American Fisheries Society 144:1237-1248.

Taylor, E. B. 1990. Environmental correlates of life-history variation in juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). Journal of Fish Biology 37:1-17.

Taylor, S. G. 1980. Marine survival of pink salmon fry from early and late spawners. Transactions of the American Fisheries Society 109:79-82.

Technical Advisory Committee for U.S. v. Oregon. 2023. 2023 Annual Report: Abundance, Stock Status, Harvest, and Endangered Species Act Impacts - Summary of 2022 Fisheries and Fish Runs.

Thedinga, J. F., S. W. Johnson, and K. V. Koski. 1998. Age and marine survival of ocean-type chinook salmon Oncorhynchus tshawytscha from the Situk River, Alaska. Alaska Fishery Research Bulletin 5:143-148.

Thorne, R. E. and J. J. Ames. 1987. A note on variability of marine survival of sockeye salmon (*Oncorhynchus nerka*) and effects of flooding on spawning success. Canadian Journal of Fisheries and Aquatic Sciences 44:1791-1795.

Thorstad, E. B., F. Whoriskey, I. Uglem, A. Moore, A. H. Rikardsen, and B. Finstad. 2012. A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt period. Journal of Fish Biology 81: 500-542.

Tidwell, K. S., B. A. Carrothers, K. N. Bayley, L. N. Magill, and B. K. van der Leeuw. 2019. Evaluation of pinniped predation on adult salmonids and other fish in the Bonneville Dam tailrace, 2018. U. S. Army Corps of Engineers, Cascade Locks, Oregon.

Tillotson, M. D. and T. P. Quinn. 2016. Beyond correlation in the detection of climate change impacts: Testing a mechanistic hypothesis for climatic influence on sockeye salmon (Oncorhynchus nerka) productivity. PLoS ONE 11:e0154356.

Tipping, J. M. and H. L. Blankenship. 1993. Effect of condition factor at release on smolt-to-adult survival of hatchery sea-run cutthroat trout. Progressive Fish-Culturist 55:184-186.

Tomarow, L.M., W. van der Naald, R.R. Brooks, T.A. Jones, and T.A. Friesen 2007. Evaluation of Chum and Fall Chinook Salmon Spawning Below Bonneville Dam. Annual Report. Oregon Department of Fish and Wildlife, Project No. 1999-003-01. Bonneville Power Administration, Portland Oregon United States Army Engineer District. 1975. Special Report – Lower Snake River Fish and Wildlife Compensation Plan. U. S. Army Corps of Engineers, Walla Walla, Washington.

US Army Engineer District. 1975. Special Report. Lower Snake River Compensation Plan. Walla Walla, Washington.

USFWS (United States Fish and Wildlife Service). 2022. Table 2. ISRP assessment of the reporting of objectives and performance metrics in individual hatchery program reports, prepared for the 2022 LSRCP Spring Chinook Program Review, encompassing brood years 1998-2016. USFWS-LSRCP, Boise, Idaho. Available online: link.

Urawa, S., T. D. Beacham, M. Fukuwaka, and M. Kaeriyama. 2018. Ocean ecology of Chum Salmon. Pages 161-318 in R. J. Beamish, editor. The Ocean Ecology of Pacific Salmon and Trout. American Fisheries Society, Bethesda, Maryland.

Voegeli, F. A., G. L. Lacroix, and J. M. Anderson. 1998. Development of miniature pingers for tracking Atlantic salmon smolts at sea. Hydrobiologia 371/372:35–46.

Volk, E. C., S. L. Schroder, and K. L. Fresh. 1990. Inducement of unique otolith banding patterns as a practical means to mass-mark juvenile Pacific salmon. American Fisheries Society Symposium 7:203-215.

Vøllestad, L. A., J. Peterson, and T. P. Quinn. 2004. Effects of fresh water and marine growth rates on early maturity in male coho and chinook salmon. Transactions of the American Fisheries Society 133:495-503.

Wainwright, T. C. 2021. Ephemeral relationships in salmon forecasting: A cautionary tale. Progress in Oceanography 193:102522.

Walters, C., K. English, J. Korman, and R. Hilborn. 2019. The managed decline of British Columbia's commercial salmon fishery. Marine Policy 101:25-32.

Waples, R. S., D. J. Teel, J. M. Myers, and A. R. Marshall. 2004. Life-history divergence in chinook salmon: historic contingency and parallel evolution. Evolution 58:386-403.

Wargo Rub, A. M., N. A. Som, M. J. Henderson, B. P, Sandford, D. M. Van Doornik, D. J. Teel, M. J. Tennis, O. P. Langness, B. K. van der Leeuw, and D. D. Huff. 2019. Changes in adult Chinook salmon (*Oncorhynchus tshawytscha*) survival within the lower Columbia River amid increasing pinniped abundance. Canadian Journal of Fisheries and Aquatic Sciences 76:1862-1873.

Weitkamp, L. 2012. Marine distributions of coho and Chinook salmon inferred from coded wire tag recoveries. American Fisheries Society Symposium 76:191-214.

Weitkamp, L. A., T. C. Wainwright, G. J. Bryant, G. B. Milner, D. J. Teel, R. G. Kope, and R. S. Waples. 1995. Status review of coho salmon from Washington, Oregon, and California. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, NMFS-NWFSC-24.

Welch, D. W., G. W. Boehlert, and B. R. Ward. 2003. POST - the Pacific Ocean salmon tracking project. Oceanologica Acta 25:243-253.

Welch, D. W., A. D. Porter, and E. L. Rechisky. 2020. A synthesis of the coast-wide decline in survival of West Coast Chinook Salmon (*Oncorhynchus tshawytscha*, Salmonidae). Fish and Fisheries 22:194-211.

Welch, D. W., M. C. Melnychuk, E. R. Rechisky, A. D. Porter, M. C. Jacobs, A. Ladouceur, R. S. McKinley, and G. E. Jackson. 2009. Freshwater and marine migration and survival of endangered Cultus Lake sockeye salmon (*Oncorhynchus nerka*) smolts using POST, a large-scale acoustic telemetry array Canadian Journal of Fisheries and Aquatic Sciences 66:736-750.

Wertheimer, A. C., and F. P. Thrower. 2007. Mortality rates of chum salmon during their early marine residency. American Fisheries Society Symposium 57:233–247.

Westley, P. A. H., T. P. Quinn, and A. H. Dittman. 2013. Rates of straying by hatchery-produced Pacific salmon (*Oncorhynchus* spp.) and steelhead (*Oncorhynchus mykiss*) differ among species, life history types, and populations. Canadian Journal of Fisheries and Aquatic Sciences 70:735-746.

Westley, P. A. H., A. H. Dittman, E. J. Ward, and T. P. Quinn. 2015. Signals of climate, conspecific density, and watershed features in patterns of homing and dispersal by Pacific salmon. Ecology 96:2823-2833.

Whitman, R. P. 1987. An analysis of smoltification indices in fall chinook salmon (*Oncorhynchus tshawytscha*). M. Sc. thesis, University of Washington, Seattle.

Williams, J. G., S. G. Smith, J. K. Fryer, M. D. Scheuerell, W. D. Muir, T. A. Flagg, R. W. Zabel, J. W. Ferguson, and E. Casillas. 2014. Influence of ocean and freshwater conditions on Columbia River sockeye salmon *Oncorhynchus nerka* adult return rates. Fisheries Oceanography 23:210-224.

Wilson, P. H. 2003. Using population projection matrices to evaluate recovery strategies for Snake River spring and summer Chinook Salmon. Conservation Biology 17:782–794.

Winship, A. J., M. R. O'Farrell, W. H. Satterthwaite, B. K. Wells, and M. S. Mohr. 2015. Expected future performance of salmon abundance forecast models with varying complexity. Canadian Journal of Fisheries and Aquatic Sciences 72:557-569.

Wood, C. C. 1987. Predation of juvenile Pacific salmon by the common merganser (*Mergus merganser*) on eastern Vancouver Island. I: Predation during the seaward migration. Canadian Journal of Fisheries and Aquatic Sciences 44:941-949.

Zhou, S. 2002. Size-dependent recovery of chinook salmon in carcass surveys. Transactions of the American Fisheries Society 131:1194-1202.

Zimmerman, C. E., R. W. Stonecypher, Jr., and M. C. Hayes. 2003. Migration of precocious male hatchery chinook salmon in the Umatilla River, Oregon. North American Journal of Fisheries Management 23:1006-1014.

Zimmerman, M. S., J. R. Irvine, M. O'Neill, J. H. Anderson, C. M. Greene, J. Weinheimer, M. Trudel, and K. Rawson. 2015. Spatial and temporal patterns in smolt survival of wild and hatchery Coho Salmon in the Salish Sea. Marine and Coastal Fisheries 7:116-134.