Potential impacts of lower Snake River dams on salmon and steelhead survival in the ocean:

A scientific perspective about *delayed mortality*

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Contents

Executive Summary ... 1
Background ... 3
Potential Mechanisms for Delayed Mortality ... 6
Fish Condition (physiological stress and injury) ... 7
Estuary Arrival Timing ... 8
Estuary Resources ... 10
Knowledge Gaps & Future Research ... 11
Sublethal injury assessment ... 11
Estuary arrival timing analysis ... 11
Estuary Rearing ... 12
Conclusions ... 12
References ... 15

Executive Summary

Snake River salmon and steelhead abundance has declined precipitously over the past 100 years. Declines have been attributed to numerous natural and anthropogenic factors, including the construction of mainstem Columbia and Snake River hydropower dams. Juvenile fish migrating from the Snake River basin encounter eight mainstem hydropower dams. Although downstream passage survival is high at each dam, the cumulative impact of passing eight dams is a concern.

The National Oceanic and Atmospheric Administration (NOAA)[1] recently released a policy perspective asserting that the four lower Snake River dams need to be removed as part of a suite of actions aimed at rebuilding salmon and steelhead populations. Authors of the paper contend that direct and indirect impacts of the Federal Columbia River Power System (FCRPS) are the most important limiting factors for Snake River salmon and steelhead stocks. This marked a significant change in NOAA Fisheries policy and prompted discussions among state, tribal, and federal management agencies concerning the future of the lower Snake River dams.

It is widely accepted that juvenile salmon and steelhead mortality rates in the ocean are much higher than within the Snake and Columbia Rivers. However, some researchers believe that effects of passage through the FCRPS carry over into later life stages, contributing to high mortality in the ocean. This theory is commonly referred to as *delayed mortality.* Consequently, understanding the magnitude of delayed mortality is critical to assessing the potential benefits of removing the four lower Snake River dams.

Mount Hood Environmental (MHE)[2] was contracted by the Inland Ports and Navigation Group (IPNG)[3], to provide scientific perspective about mortality of juvenile salmon and steelhead caused by the lower Snake River dams. Specifically, our client sought information about the delayed mortality hypothesis. We were also asked to identify future research priorities to address critical data gaps related to the mechanisms and potential magnitude of delayed mortality.

Review of available literature revealed hundreds of scientific papers and reports pertinent to the topic of delayed mortality of salmon and steelhead in the Columbia Basin. The volume of relevant research conducted over the past three decades is vast, but an undisputed quantification of hydrosystem-related delayed mortality does not exist. It stands to reason that passage through the eight mainstem dams has carryover effects on juvenile salmon and steelhead, but whether that results in significant mortality is subject to scientific dispute.

Nevertheless, we identified three potential pathways for delayed mortality that merit further investigation. First, the four lower Snake River dams increase fish transit time through the mainstem Snake and Columbia Rivers, thereby delaying arrival of juvenile fish to the estuary.

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[1] NOAA Fisheries has jurisdiction over threatened and endangered salmon and steelhead populations.
[2] MHE has no conflicts of interest nor policy preference related to Snake River dam removal.
[3] IPNG is a collaboration of ports, businesses and public agencies who support navigation, energy, trade, economic development, and salmon recovery throughout the Pacific Northwest.

Altering the arrival timing of Snake River salmon and steelhead to the estuary could impact ocean survival, but the magnitude of this impact is unknown and depends on ocean conditions at the time of arrival. Second, sublethal injuries of juvenile fish during Snake River dam exposures are an unlikely but potential source of delayed mortality. While dam passage may result in acute stresses and injury, no studies have adequately linked internal injuries and physiological stressors to delayed mortality. Lastly, the estuary may serve as a potential bottleneck for Snake River salmon and steelhead production. However, the lower Snake River dams do not significantly alter habitat conditions in the estuary since flows are regulated by dozens of existing dams in the Columbia River and its tributaries. Moreover, habitat-altering activities in the estuary are also expected to continue (e.g., development and urbanization). Consequently, increasing the number of juvenile fish that successfully transit the Snake and Columbia Rivers may not yield a parallel response in adult salmon and steelhead returns.

We conclude that delayed mortality may be occurring in the ocean as a result of carryover effects from exposure to the Columbia River hydrosystem. However, mechanisms of delayed mortality are not well-defined, and the magnitude is unknown. Furthermore, it is unclear how removal of the lower Snake River dams would reduce hydrosystem-related delayed mortality because the mortality mechanism may be a function of broad-scale habitat changes caused by operation of the entire FCRPS, not exposure to individual dams. Whether Snake River dam breaching should be expected to reduce mortality of salmon in the ocean depends on the outcome of several important lines of research, including the relative benefit of advancing juvenile fish arrival time at the estuary, estuary habitat limitations, and sublethal injuries in fish that passed the Snake River dams.

Background

Snake River salmon and steelhead abundance has declined precipitously over the past 100 years. Declines are attributed to numerous natural and anthropogenic factors, including climate change, tributary and estuary habitat conditions, predation, fisheries, and migration impediments (including the construction of federal hydropower dams). A task force comprised of fisheries representatives from across the Columbia Basin recently concluded that the Federal Columbia River Power System (FCRPS) has the largest direct and indirect impact on Snake River salmon and steelhead stocks when compared to other factors (CBP Phase II Report). The National Oceanic and Atmospheric Administration (NOAA) also recently disseminated a perspective paper asserting that removal of the lower four Snake River Dams, in combination with other actions, was necessary to rebuild salmon and steelhead populations (NOAA 2022).

Direct impacts of the FCRPS on juvenile salmon and steelhead migration survival have been studied extensively. Direct mortality is defined as mortality that occurs while fish are residing in or migrating through the hydrosystem. Although juvenile fish survival through individual dams is high (Skalski et al. 2016), cumulative estimates of median mortality due to passage of eight mainstem Snake River and Columbia River dams range from 24-37% depending on species and life-history type (Figure 1). These estimates do not include mortality that occurs because of water impoundment upstream and altered flows downstream of the dams which modify river conditions, river ecology, and fish survival (Waples et al. 2008). However, it is difficult to precisely quantify direct mortality attributed to the hydrosystem relative to other sources, some of which are natural (Williams 2005).

In contrast to direct mortality, some have posited that hydrosystem impacts, referred to as carryover effects, manifest after fish have exited the FCRPS. Carryover effects are defined as cross-life-stage effects, in which the conditions experienced in one life stage carryover to affect an organism's performance and survival in subsequent life stages (Gosselin et al. 2021). Usage of the terms 'direct mortality' and 'indirect mortality' are often conflated with carryover effects and numerous other terms in the literature. Here, we will use the following distinctions: *direct mortality* occurs within the hydrosystem itself, while *carryover effects* occur after fish have left the hydrosystem and may lead to *delayed mortality*[4].

Although FCRPS dams are known to cause direct mortality to juvenile salmon and steelhead, it is also widely accepted that most juvenile fish perish within the first few months of life in the ocean, not during freshwater emigration. This is because predation rates in the estuary and ocean are high and juvenile fish growth and survival is strongly influenced by episodic presence of

[4] Delayed mortality most often refers to early ocean mortality that is related to earlier life-stage experiences in the freshwater environment, specifically within the Columbia River hydrosystem (Budy et al. 2002). Numerous terms have been used when describing long term effects of dam passage on fish, including carryover effects, latent mortality, and indirect mortality. These terms can have subtly different meaning, but they are all used to describe impacts that are observed weeks or months after dam exposure, or as a result of ecological changes caused by the dams.

food resources (Scheuerell et al. 2009; Sydeman and Bograd 2009; Wilson et al. 2021). Some researchers contend that fish passage through the FCRPS results in carryover effects that contribute to delayed mortality in the ocean (Haeseker et al. 2012). Delayed mortality is theorized to be caused by sublethal injuries, accumulated stress, and altered growth; conditions that ultimately leave fish more vulnerable to predation. In addition to physiological effects as a result of passage through the FCRPS, researchers have hypothesized that changes in estuary arrival timing increase early ocean mortality. The basis for this hypothesis is that fish that arrive at the estuary earlier tend to survive better, but passage through dams and reduced water velocity within the FCRPS prolong migration. These physiological and migration timing-related effects are thought to cause mortality weeks or even months after passage through FCRPS dams.

Understanding the magnitude of delayed mortality that occurs is critical to the perceived benefits of removing the four lower Snake River Dams. This is because expected improvements in emigration survival due to dam removal are not sufficient to achieve population rebuilding goals. For dam removal to markedly increase abundance of salmon and steelhead in the Snake River basin, a large increase in ocean survival must also occur. Some researchers contest that ocean survival rates will rise if Snake River dams are removed. Still, others argue that effects of dam exposure dissipate quickly after each passage event and early ocean survival is unrelated to dam passage.

Analysis presented in the Columbia River Systems Operations Environmental Impact Statement (USACE 2020) offer a vivid example of how differences in scientific opinion can influence the perceived fisheries benefits of Snake River dam removal. Salmon and steelhead population response to several different river operations scenarios were simulated with two life-cycle models. One model assumed significant hydrosystem-related delayed mortality occurs while the other did not. The model that included delayed mortality estimated a 140% increase in equilibrium adult salmon abundance in response to Snake River dam removal and the model that did not include delayed mortality predicted a 14% increase. In qualitative terms, these two analyses both predicted a positive response to dam removal, but there was an order of magnitude difference between the estimates.

The strongest evidence available to support the delayed mortality hypothesis is the correlation between juvenile fish migration survival through FCRPS dams and the probability they will return from the ocean (Schaller and Petrosky 2007; Haeseker et al. 2012; Schaller et al. 2014). These results were compelling, but correlative analyses do not infer causation. Follow-up research found that fish size, which is also known to be correlated with survival in the ocean, influenced which route of passage fish used at FCRPS dams[5]. Smaller fish tended to select the routes of passage with the poorest survival, were most likely to be detected at the dams, and subsequently experienced the lowest ocean survival. When fish size is included as an explanatory

[5] Each dam offers three possible routes of fish passage: spillway, fish bypass, and powerhouse. Fish that pass via bypasses or powerhouses experience the lowest survival and tend to be smaller in size compared to those that pass via spillways.

variable within statistical models, the association between ocean survival and dam encounters is weak or no longer evident (Zabel et al. 2005; Faulkner et al. 2019; Gosselin et al. 2021).

A second line of evidence to support the delayed mortality hypothesis involves comparison of smolt-to-adult return rates for salmon and steelhead stocks originating from different regions throughout the Columbia Basin. For example, John Day River steelhead migrate downstream through three dams, while Snake River Spring Chinook migrate through eight dams. Storch et al. (2022) found that smolt-to-adult return rates to Bonneville Dam are consistently higher for fish that pass through fewer dams. The authors pointed to carryover effects of dam passage as the primary cause. However, Storch et al. (2022) did not account for differences in migration distance, which are also known to linearly influence emigration survival rates. Salmon and steelhead originating from the Snake River basin travel much farther than fish that originate in the mid-Columbia River region. Moreover, an earlier study with a similar comparative design found that survival of migrating juvenile Columbia River salmon and steelhead was higher than the same species migrating down the Fraser River, which does not have dams (Welch et al. 2008). Critics of these findings cite differences in habitat conditions and fish stocks between the two rivers. Comparative analyses such as Storch et al. (2022) and Welch et al. (2008) are persuasive case studies, but they do not conclusively support nor reject the delayed mortality hypothesis, nor are they used to inform mechanisms or causal relationships.

Other researchers have attempted to test the delayed mortality hypothesis with directed experimental studies. Rechisky et al. (2009) and Rechisky et al. (2014) tracked discrete cohorts of fish using acoustic telemetry as they migrated north along the Pacific Coast and compared their survival, finding no difference between fish from the Snake River and mid-Columbia River regions. The authors concluded ocean mortality is not related to passage through the FCRPS, but others have argued that fish size was a critical study constraint. Specifically, only large fish could be used in the study because of the weight burden imposed by the surgically implanted acoustic transmitters, limiting inferences to a subset of fish within each population.

The volume of research that has been published on the topic of delayed mortality over the past three decades is vast, yet two questions remain unanswered within the existing literature: *is hydrosystem-related delayed mortality a major contributor to low marine survival rates and, if so, how would early ocean survival rates change if the lower four Snake River dams were removed?*

The explanation that follows was crafted in response to a request for a concise summary of the available science pertaining to this question. In the process of reviewing the available literature, we compiled hundreds of papers and reports pertinent to the topic of delayed mortality of salmon and steelhead in the Columbia Basin. Indeed, there are hundreds more that we could have included in our literature database, but we selected only those papers that were most germane. Among the papers we reviewed, there were certain themes that emerged repeatedly, highlighting critical unknowns that made a clear answer to our thesis question impossible to apprehend. Alternatively, we offer our perspective about the delayed mortality theory and recommend topics for future study. If policy makers wish to obtain an accurate prediction of the outcome of Snake River dam removal, scientists must design empirical studies to quantify the influence of estuary habitat conditions on survival and the influence of lower Snake River dams on:

- Fish condition. Specifically, sublethal injury and prolonged stress response in emigrating juvenile fish.
- Estuary arrival timing and subsequent early ocean survival probability for juvenile salmon and steelhead.

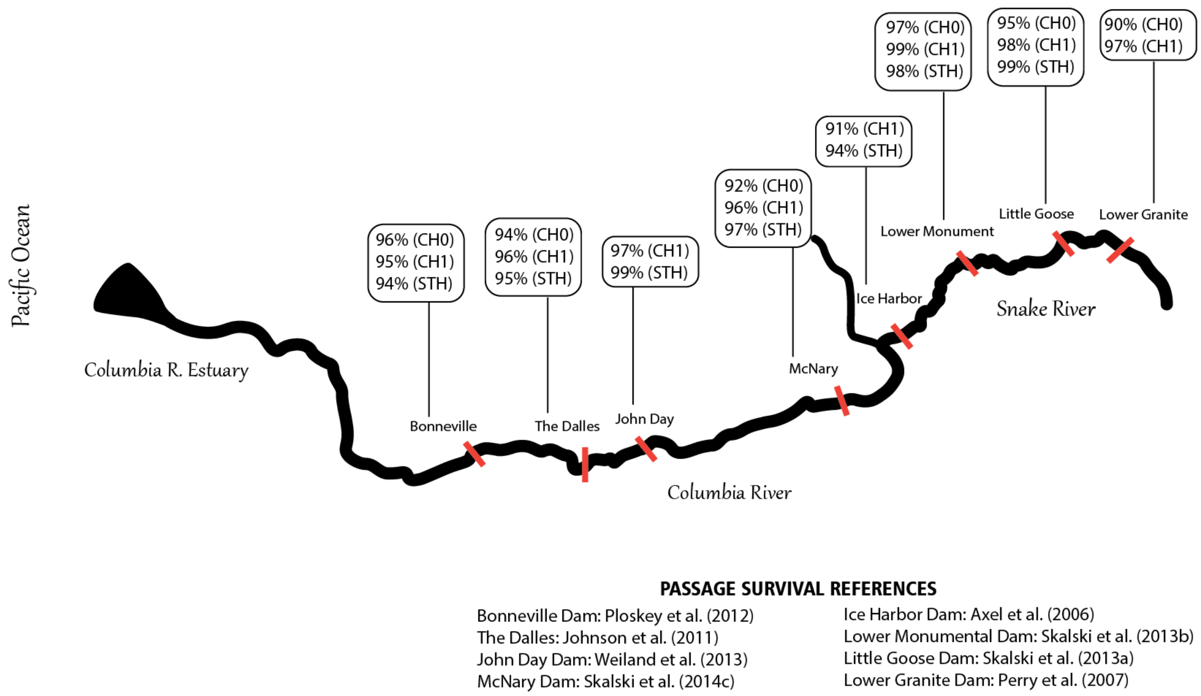

Figure 1. Summary of findings from studies of juvenile salmon and steelhead passage survival at the four lower Snake River and four mid and lower Columbia River FCRPS dams.

Potential Mechanisms for Delayed Mortality

Research on the topic of delayed mortality and carryover effects spans three decades, during which, numerous hydrosystem infrastructure upgrades (e.g., installation of bypass routes), operational changes (e.g., spill requirements), and policy changes have occurred. Therefore, this summary is limited to research that reflects current conditions experienced by Snake River salmon and steelhead. Additionally, the focus of this literature review is the mechanisms for carryover effects demonstrated via experiment or observation.

Fish Condition (physiological stress and injury)

Sublethal injuries caused by dam passage are a potential mechanism for carryover effects in juvenile salmonids. Internal injuries, including fractures and deformations, have been observed in salmonids that pass through hydroelectric turbines and pumps (Mueller et al. 2020). Salmonids are also particularly susceptible to barotraumas that do not necessarily result in visible injury or immediate mortality (Mueller et al. 2020). However, the authors did not evaluate salmonids in bypass facilities comparable to those of Snake River dams, and they observed fish for only 96 hours after passage. There is a low probability that juvenile salmonids will use passage routes through the Snake River dams that are associated with higher mortality and physical injury (e.g., turbines) (Skalski et al. 2021), thereby reducing the likelihood of certain sublethal injuries. Nevertheless, we are unaware of any studies that used x-ray and necropsies to examine sublethal injuries in fish that reach the estuary resulting from passage through Snake River hydroelectric dams.

Another type of sublethal injury in migrating salmonids can arise from exposure to high total dissolved gas (TDG). High TDG below dam spillways in FCRPS facilities can have long-term consequences for juvenile salmonids. For example, there is evidence that Chinook smolts that survived high TDG exposure had lower survival in the lower Columbia River and estuary compared to smolts exposed to low TDG (Brosnan et al. 2016). The effect of sublethal TDG exposure on ocean survival in Chinook and steelhead warrants further investigation.

Stress is another mechanism that has been implicated as a carryover effect from the FCRPS. This term is often misrepresented in the context of delayed mortality. We define stress as a physiological response that may include changes in cortisol, plasma glucose, and neurohormone levels, as well as humoral immune parameters. Plasma cortisol measured in fish using various passage routes is both measurable, generally short-lived (Ferguson et al. 2006; Ben Ammar et al. 2020), and does not differ from fish that do not pass the dams (Schreck et al. 2006). Studies evaluating immune system function among fish subjected to hydrosystem passage have mixed findings. For example, studies of fish passing through turbines suggest a persistent physiological stress that could impair the immune defense capacity (Thorstad et al. 2012, 2017), but Ammar et al. (2020) suggest the immune system might be enhanced. However, turbine passage is not the predominant route of passage in the FCRPS. There is some evidence that fish migrating through the mainstem Snake and Columbia Rivers have higher susceptibility to marine disease (*Listonella anguillarum*) compared to barged fish, which are loaded onto ships and transported downstream (Arkoosh et al. 2006), providing some evidence for hydrosystem-related stress. However, Schreck et al. (2006) found no evidence for a difference in Bacterial Kidney Disease prevalence between river migrants and barged fish. Given the weak and contradictory findings related to immune system stress as a primary mechanism for carryover effects, this topic warrants additional research, particularly as it relates to fish that have passed through the FCRPS and transitioned into their estuary and ocean life stages.

Estuary Arrival Timing

The highest mortality in juvenile salmonids from the Columbia River basin occurs during early ocean residence as fish transition from freshwater to the estuary and ocean. There is also a strong relationship between arrival timing to the estuary and marine survival (Chasco et al. 2021). This is because ocean conditions vary, as does physiological readiness for ocean entry.

Whether ocean conditions are favorable or unfavorable at the time of arrival influences growth opportunity for juvenile salmonids (Figure 2). Ocean conditions vary from year to year, with cool ocean phases generally providing a more productive environment for fish. Indeed the effect of arrival timing on ocean survival varies across years and depends on the cool/warm phase (Gosselin et al. 2018) and copepod composition[6] (Miller et al. 2014). During years with favorable conditions, early ocean arrival may support better growth and survival simply by increasing the amount of time spent foraging and growing in the productive marine environment compared to the freshwater environment (Weitkamp et al. 2015). Conversely, fish arriving when conditions are suboptimal may experience reduced growth and poor survival.

Arrival timing may also impact survival if it is not synced with the physiological development necessary for ocean entry (i.e., sea-water preparedness). This includes degree of smoltification[7], fish condition, and size. Fish may arrive at the estuary at varying degrees of development and sizes, affecting their disposition for saltwater entry. Fish that require additional growth or development in the estuary before ocean entry are more vulnerable to predation, resulting in high rates of mortality (Schreck et al. 2006; Kennedy et al. 2007).

Ocean arrival timing is influenced by the aggregate of conditions encountered in freshwater and includes exposure to the FCRPS. Although myriad environmental factors influence this timing (e.g., SWE, carrying capacity in the freshwater rearing habitat, genetics, etc.), we will focus on demonstrable hydrosystem effects: fish transportation and flow regulation.

The most obvious way that arrival timing is disrupted is through barging, or transportation of fish around the hydrosystem. The impacts of barging can have both positive and negative implications for survival depending on the ocean conditions (Gosselin et al. 2018). For fish leaving the Snake River basin, barging accelerates migration from several weeks to only a few days. Although, fish that arrive early to the estuary tend to encounter more productive ocean conditions (Scheuerell et al. 2009), fish that are barged early in the migration season have lower survival (Gosselin et al. 2018), likely because they arrive smaller and less physiologically prepared for saltwater.

[6] Copepods are small crustacean species found in aquatic environments and are an important part of the food web, often used as indicators of biodiversity. Copepods are a prey source for larger species that in turn support the diet of salmonids.

[7] Smoltification (also known as Parr-Smolt transformation) is a complex series of physiological changes where young salmonid fish adapt from living in fresh water to living in seawater. Physiological changes during smoltification include modified body shape, increased skin reflectance, and increased Na+/K±ATPase in the gills.

The hydroelectric dams and their reservoirs also influence water velocity, which can affect estuary arrival timing. The transit time of juveniles through the reservoirs is dependent on flow, which is currently a function of operational spill. There exist regulatory spill minimums during the outmigration period, though it is unclear how transit time under these minimums would compare to transit time in a free-flowing river scenario. Historic flow data suggest that water transit time from the Snake River to Bonneville Dam has increased from several days to several weeks (NOAA unpublished *in* Waples et al. 2008). The increased transit time is a function of water impoundments upstream of the lower Snake River dams, as well as the eight mainstem dams. Correspondingly, juvenile salmonids take three times longer to migrate downstream (Raymond 1979), substantially longer than pre-dam construction. This is consistent with current monitoring of tagged fish from the Snake River, which indicates transit through impounded sections of the lower Snake and Columbia Rivers takes approximately three weeks.

Lastly, water temperature is modified by flow regulation and impoundment of water in the hydrosystem. Dam-related temperature increases generally occur during the summer months and may affect temperatures by more than 3.0 °C relative to free-flowing conditions (EPA 2021). However, Snake River Chinook salmon and steelhead trout emigration occurs in the spring when these temperature effects are expected to be less than 1°C. During the spring migration period, warmer water temperatures have been linked to increased survival in Chinook (Gosselin et al. 2018), suggesting that warmer temperatures may improve performance and growth. However, it is unclear how hydrosystem-related water temperature increases might influence the food web in the river and estuary relative to larger climatic shifts in temperature.

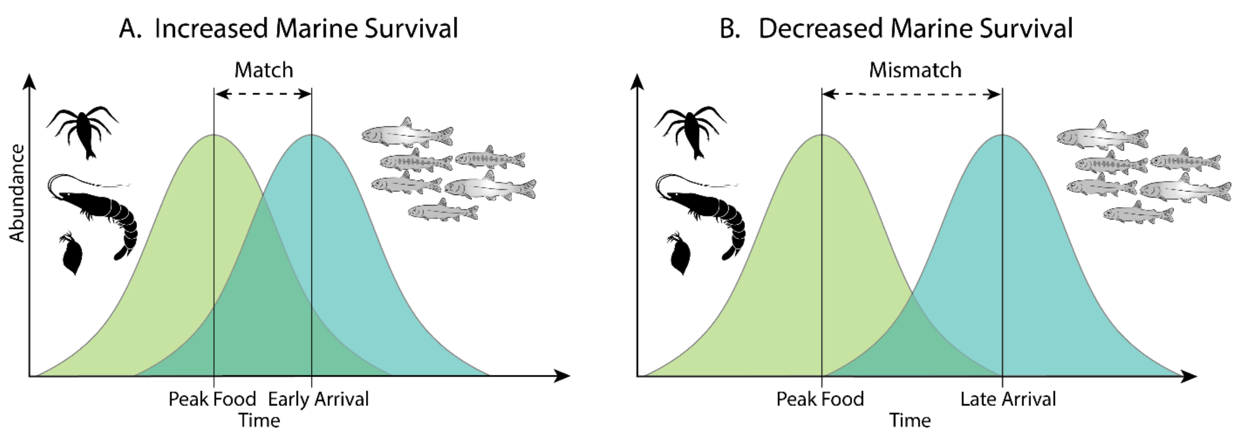

Figure 2. A conceptual example of how juvenile salmon and steelhead arrival timing at the estuary overlaps with food availability. Figure adapted from Cushing (1990) and Wilson et al. (2021).

Estuary Resources

Migration through the Lower Columbia River Estuary is an essential part of the lifecycle in anadromous salmonids. The estuary functions as a productive feeding area capable of sustaining increased growth rates, a temporary refuge from marine predators, and a physiological transition zone where juvenile fish can gradually acclimate to saltwater (Bottom et al. 2005). While historical information about juvenile salmonid use of the estuary is scant, reporting from the early 20th century indicates that juvenile Chinook Salmon spent extensive time rearing in the estuary and subyearling Chinook increased 20 to 66 percent in length while in the estuary (Rich 1920). Since the late 1800s, more than 65 percent of the vegetated tidal wetlands in the estuary have been lost due to agriculture and urban development, among other factors.

Despite drastic changes to physical habitat and predator abundance in the estuary over the past 150 years, it remains critical habitat for juvenile salmonids, particularly with respect to their growth. Indeed, there is a significant link between estuary wetland habitat quality and quantity and resource availability for juvenile salmonids (Roegner and Johnson 2023). Recently, it has been demonstrated that juvenile steelhead and Chinook are actively feeding and growing as they move through the estuary and this rapid growth may increase marine survival (Weitkamp et al. 2022). In part, this is because size influences susceptibility to predators, the timing of ocean entry, and feeding opportunity.

Flow regulation is the primary mechanism by which the FCRPS may influence growth conditions for fish within the estuary. Flow regulation affects habitat area and quality (resulting in reduced estuary carrying capacity[8]) and water temperature in the estuary. For example, peak river flows are correlated with sediment transport from the Columbia River to the estuary, a key process affecting the quantity and quality of estuarine habitat for salmon (Bottom et al. 2005). Floods during historic peak flow events brought important nutrients to the estuary that supported the food web, connected habitats, and influenced salinity intrusion (mixing of freshwater with saltwater), all of which have a direct impact to fish or their habitat. Because peak flows are regulated by the extensive network of dams throughout the Columbia River Basin, they are now much lower than natural peak flows (Waples et al. 2008).

There is also an interaction between in-river growth, estuary rearing, and ocean growth. A recent study found that Chinook salmon that grew slower during freshwater residence experienced increased mortality during early ocean residence (Norrie et al. 2022). One explanation is that higher growth rates in freshwater are related to seawater-preparedness (smoltification and size). Consequently, individuals that are more developed for seawater entry may move through the estuary faster and experience lower predation risk (Dietrich et al. 2016). This is consistent with other findings that early marine growth (including the estuary) is positively related to survival (Miller et al. 2014).

[8] Carrying capacity refers to the maximum number of organisms that an area or an ecosystem can support. In this case, carrying capacity refers to the number of juvenile salmonids the estuary can support.

It is well established that habitat areas and rearing opportunities in the estuary have diminished over the last century. While restoration has resulted in notable improvements, influence of the estuary on Chinook Salmon and steelhead trout survival is less clear. Though flow regulation has significantly altered habitat and the condition of fish arriving to the estuary, it is impossible to assess effects of the FCRPS on estuary conditions, which are significantly impacted by agriculture, urbanization, and climate change. Moreover, removal of the lower Snake River dams will not alter flow conditions in the estuary, since flows would still be regulated by the remaining network of dams in the Columbia River and its tributaries. Estuary resources may be episodic or finite, and predator abundance increases with salmonid prey availability. Therefore, additional research is needed to estimate the relationship between the number of juvenile salmon arriving to the estuary and the number of adult fish that return.

Knowledge Gaps & Future Research

Hypothesized mechanisms for delayed mortality of Snake River salmon and steelhead have been identified in the science literature, but they are not supported by conclusive empirical observations. Further, the proportion of Snake River salmon and steelhead that experience carryover effects from the FCRPS is unknown. Therefore, we identified three primary topics for future research necessary to address these scientific uncertainties, including sublethal injury, estuary arrival timing, and estuary conditions (Figure 3).

Sublethal injury assessment

Snake River salmonids should be examined for nonlethal injuries when they arrive at the Columbia River estuary. X-ray images, necropsy exams, and pathological reports should be conducted on a subsample of fish. These data can be used to link passage routes and demographic information to the frequency of injury and stress. That relationship, if present, can then be used to model the population-level effect of sublethal stress and injury.

Estuary arrival timing analysis

Weekly or biweekly predictions of estuary and near-shore ocean conditions should be combined with arrival of discrete cohorts of juvenile Snake River salmon and steelhead under current conditions and under a dam breach scenario. Previous research by Scheuerell et al. (2009) and Tiffan et al. (2009) can be leveraged along with water travel time analyses described in the Columbia River Systems Operations Environmental Impact Statement (USACE 2020). Predicted differences in estuary arrival time and associated marine survival for the no-breach and breach scenarios could then be used to approximate the magnitude of expected increase in adult fish returns following dam breaching. A weakness of this modeling exercise is that it assumes delayed estuary arrival time is the only mechanism for indirect mortality. However, if Snake River dams indirectly cause low marine survival, altered estuary arrival timing may be the primary mechanism.

Estuary Rearing

Estuary rearing is a key life stage often overlooked by researchers. During this period, juvenile salmonids may be resource-limited, depending on ocean conditions. Although the Snake River dams do not have a direct influence on estuary conditions, developing a relationship between estuary conditions and ocean survival is paramount to understanding how a breaching scenario may or may not improve survival. If estuary conditions are limiting, increased survival of juvenile fish through the hydrosystem may have little impact on adult returns.

Conclusions

Impacts of the FCRPS on Snake River salmon and steelhead include direct and indirect effects. Direct effects of dam passage have been thoroughly studied, and prospective benefits of removing the lower four Snake River dams on juvenile fish migration survival are relatively simple to quantify. However, carryover effects that may result in delayed morality are difficult to measure. The scientific basis for carryover effects in salmon and steelhead transiting the FCRPS is well established, but the magnitude of hydrosystem-related delayed mortality that can be assigned to the lower Snake River dams remains unknown.

In order to assess the potential survival benefits associated with removal of the Lower Snake River dams, carryover effects caused by broad-scale influence of the FCRPS (e.g. river flow and estuary habitat modification) must be differentiated from carryover effects associated with the Snake River dams (e.g. migration delay or injury). Indeed, effects of individual dam exposures versus the entire hydrosystem are distinct. For example, breaching the four lower Snake River dams will increase juvenile fish migration survival through the FCRPS. Breaching will also likely reduce water transit time and fish transit time, thereby expediting arrival of smolts at the estuary. Altering the arrival timing of Snake River salmon and steelhead to the estuary is a potentially significant carryover effect, though the magnitude of this impact is unclear because the effect depends on ocean conditions at the time of arrival. Conversely, removal of the Snake River dams will not improve habitat conditions in the estuary since flows would still be regulated by dozens of additional dams in the Columbia River and its tributaries. Notably, spring freshets originating from the Snake River and other inland tributaries would remain restricted. The suppression of natural flow reduces sediment and nutrient transport and influences circulation and salinity intrusion in the estuary (Weitkamp 1994), thereby altering the characteristics and quality of estuary habitat. Breaching Snake River dams will not change habitat carrying capacity in the estuary, therefore it may continue to be a bottleneck for survival. Specifically, if estuary habitats are already at or near capacity, incremental improvements in migration survival and reductions in carryover effects are unlikely to result in large increases in adult fish returns to the Snake River basin.

Given the uncertainties associated with the delayed mortality hypothesis, it may be tempting to cite previous dam removal efforts, such as the Elwha River in Washington, as evidence for lower Snake River dam removal benefits, thereby circumventing the need for further study. However, this would be inappropriate as there is no existing analog to the Snake River dams. Numerous dams have been removed in the past 30 years at sites *without* fish passage, including Elwha and Glines Canyon Dams. In some cases, these projects resulted in rapid recolonization of newly accessible habitat (Duda et al. 2021). Improvements to salmon habitats and ecosystem functions have also been empirically and conceptually modeled (Bellmore et al. 2019). However, the majority of dam removal projects in the United States over the past two decades have not been monitored, or, if monitoring is occurring, results have not been published (Foley et al. 2017). Moreover, we are unaware of any large hydroelectric dams with fish passage at the scale of those in the lower Snake River that have been breached and subsequently monitored.

We conclude that carryover effects and delayed mortality are likely occurring as a result of exposure to the Columbia River hydrosystem, but the magnitude of effect on marine survival attributable to the lower Snake River dams is unknown. Whether dam breaching should be expected to markedly increase adult salmon and steelhead returns depends on the outcome of several important lines of research. These include the relative benefit of advancing estuary arrival timing of juvenile fish, estuary habitat limitations, and sublethal injuries caused by the Snake River dams.

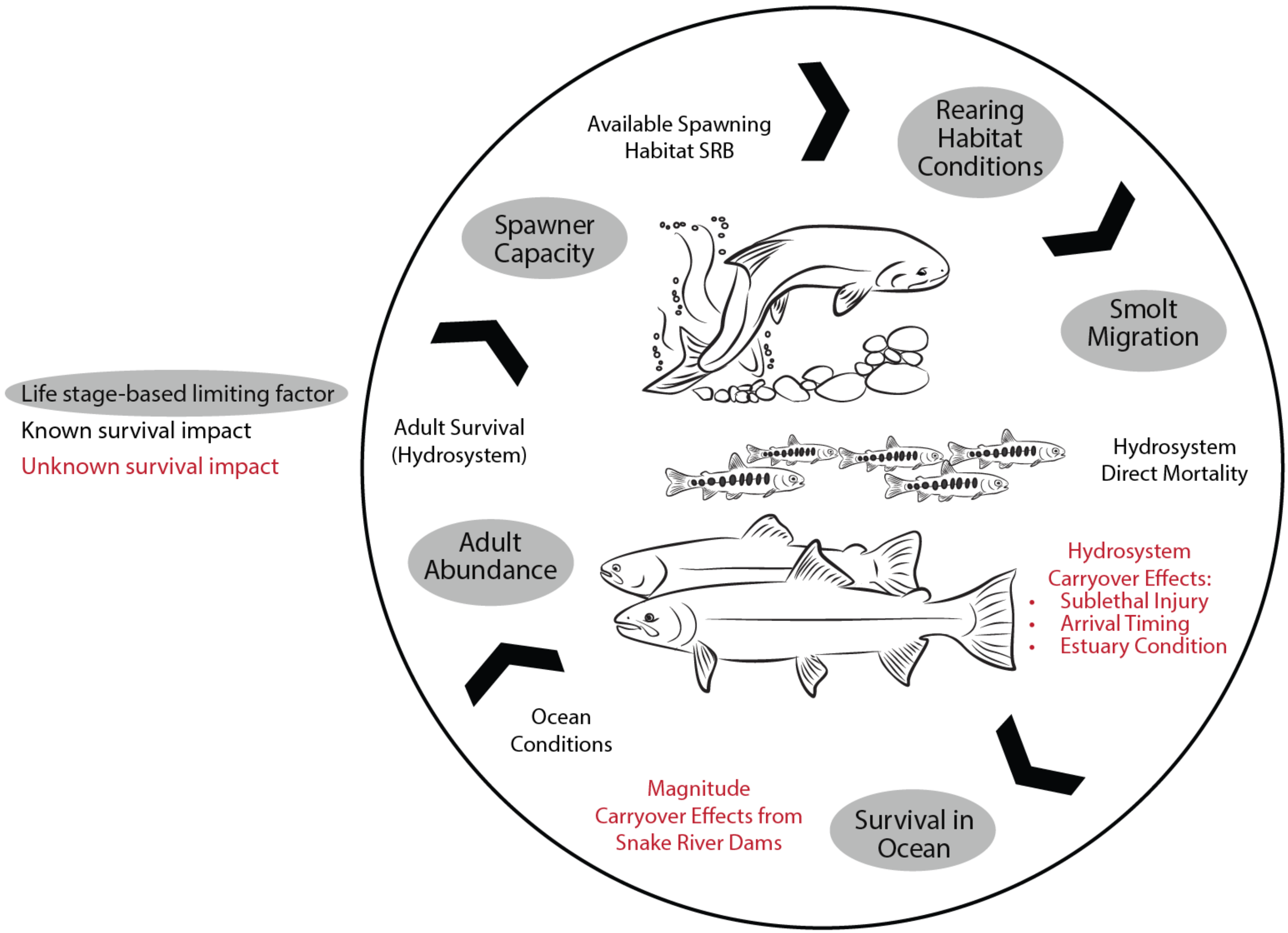

Figure 3. Limiting factors that influence salmon and steelhead survival from one life stage to another.

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