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A review of potential conservation and fisheries benefits of breaching four dams in the Lower Snake River (Washington, USA)

Adam J. Storch[a,*], Howard A. Schaller[b,1], Charles E. Petrosky[c,1], Robert L. Vadas Jr.[d], Benjamin J. Clemens[e], Gary Sprague[f,1], Norman Mercado-Silva[g], Brett Roper[h], Michael J. Parsley[i], Edward Bowles[j], Robert M. Hughes[k,l], Jay A. Hesse[m]

[a] Oregon Department of Fish and Wildlife, Ocean Salmon and Columbia River Program, 17330 Southeast Evelyn Street, Clackamas, OR 97015, USA
[b] U.S. Fish and Wildlife Service, 911 Northeast 11th Avenue, Portland, OR 97232, USA
[c] Idaho Department of Fish and Game, 600 South Walnut Street, Boise, ID 83707, USA
[d] Unaffiliated, Olympia, WA, USA
[e] Oregon Department of Fish and Wildlife, Corvallis Research Lab, 28655 Hwy 34, Corvallis, OR 97333, USA
[f] National Marine Fisheries Service, 650 Capitol Mall, Sacramento, CA 95814, USA
[g] Centro de Investigación en Biodiversidad y Conservación, Universidad Autónoma del Estado de Morelos, Av. Universidad 1001, Col. Chamilpa, C.P. 62209, Cuernavaca, Morelos, Mexico
[h] National Stream and Aquatic Ecology Center, U.S. Forest Service, 860 North 1200 East, Logan, UT 84321, USA
[i] Independent Fisheries Consultant, 191 Sooter Road, Underwood, WA 98651, USA
[j] Oregon Department of Fish and Wildlife, 4034 Fairview Industrial Drive Southeast, Salem, OR 97302, USA
[k] Amnis Opes Institute, 2895 Southeast Glenn Street, Corvallis, OR 97333, USA
[l] Department of Fisheries, Wildlife, & Conservation Sciences, 104 Nash Hall, Corvallis, OR 97331, USA
[m] Nez Perce Tribe Department of Fisheries Resources Management, 120 Beaver Grade, Lapwai, ID 83540, USA

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ABSTRACT

Abundances of important and imperiled fishes of the Snake River Basin continue to decline. We assessed the rationale for breaching the four lower Snake River Basin dams to prevent complete loss of these fishes, and to maximize their likelihood of recovery. We summarize the science surrounding Sockeye Salmon (*Oncorhynchus nerka*), Chinook Salmon (*O. tshawytscha*), steelhead (*O. mykiss*), Bull Trout (*Salvelinus confluentus*), White Sturgeon (*Acipenser transmontanus*), and Pacific Lamprey (*Entosphenus tridentatus*). From this, we drew ten conclusions: (1) development of the Columbia River System (including the Snake River Basin) has converted mainstem rivers into reservoirs, altering fish behavior and survival; (2) most populations currently record their lowest abundance; (3) the Columbia River System dams reduce productivity of diadromous fishes in the highest-quality spawning grounds that could buffer against future climate dynamics; (4) past actions have done little to reduce impacts or precipitate recovery; (5) the Columbia River System constrains survival and productivity of salmon, steelhead and Bull Trout; (6) Snake River Basin salmon and steelhead remain at high extinction risk; (7) eliminating migration impediments and improving mainstem habitats are essential for maintaining genetic diversity and improving Bull Trout persistence; (8) the lower Snake River Basin dams preclude passage of adult White Sturgeon, constraining gene flow and recruitment; (9) the lower Snake River Basin dams impede dramatically passage of adult and juvenile Pacific Lamprey, and (10) Snake River Basin Pacific Lamprey is at high risk of extirpation. Breaching the four lower Snake River Basin dams is an action likely to prevent extirpation and extinction of these fishes. Lessons from the Columbia River System can inform conservation in other impounded rivers.

1. Introduction

The development and operation of dams throughout the world has allowed humans to store and alter the timing and amount of water released downstream. However, growing evidence indicates that dams can negatively affect the ecological assembly and function of riverine systems (Poff and Hart, 2002). Decisions surrounding if, when, where, and how to breach dams are complex and depend on competing legal,

* Corresponding author.
E-mail address: adam.j.storch@odfw.oregon.gov (A.J. Storch).
[1] Retired.

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socio-political, ecological, and economic perspectives of risks and benefits, in addition to overarching factors (e.g., climate change) that affect all these parameters (Tullos et al., 2014; Bellmore et al., 2017; Foley et al., 2017).

The breach of dams typically occurs when the costs of maintaining aging infrastructure and satisfying legal mandates exceed the advantages that a dam provides. In the U.S., such mandates are set forth by Federal Energy Regulatory Commission relicensing requirements, the Endangered Species Act (ESA; ESA, 1973), and other federal and state mandates (Bednarek, 2001; Bellmore et al., 2017; Foley et al., 2017). Despite constraints inherent in achieving this balance, the frequency of dam breaching has increased exponentially over the last several decades, particularly for relatively small dams in North America and Europe (O'Connor et al., 2015; Bellmore et al., 2017; Foley et al., 2017; Ding et al., 2019). In the U.S. alone, >1200 dams have been breached (Bellmore et al., 2017), and worldwide, 1449 studies examining responses to breach have been published through 2016 (Ding et al., 2019).

Breaching is commonly viewed as a form of river rehabilitation because it can help restore fluvial geomorphological and ecological processes, including river flows, water temperatures, sediment and particle transport, the structure and processes of river and riparian ecosystems (i.e., energy flow), and access to upstream and downstream habitats essential for aquatic macroinvertebrates and fishes to complete life cycles (Tullos et al., 2014; Poff and Hart, 2002; Bellmore et al., 2017; Foley et al., 2017). Increased habitat connectivity following dam breach can promote life history diversity within species (reviewed in Foley et al., 2017) and species diversity in general (Bednarek, 2001), with the responses of many ecosystem components–such as aquatic macroinvertebrates (Tullos et al., 2014) fishes, (Pess et al., 2014; Duda et al., 2021), sediment pulses (O'Connor et al., 2015) and large wood movement (Gregory et al., 2003)–occurring relatively rapidly.

Several intensive studies of the effects of breaching two large dams on the Elwha River (Washington, USA), provide an instructive example of how an ecosystem–where several components are monitored concomitantly–may respond to breach. This body of work has elucidated sediment dynamics and changes to river channel morphology and the floodplain (East et al., 2015; Magirl et al., 2015; Warrick et al., 2015; Ritchie et al., 2018); changes in returns of Pacific salmon (*Oncorhynchus* spp.; e.g., Liermann et al., 2017; Duda et al., 2020; Duda et al., 2021) and subsequent variation in nutrient acquisition by a river bird, the American Dipper (*Cinclus mexicanus*; Tonra et al., 2015); and recolonization of Pacific Lamprey (*Entosphenus tridentatus*; Moser and Paradis, 2017; Hess et al., 2020; Duda et al., 2021) and Bull Trout (*Salvelinus confluentus*; Brenkman et al., 2019; Duda et al., 2020; Duda et al., 2021). Examples from the Elwha River provide insights into how an ecosystem may respond from the breaching of dams in large river systems and highlights the ecological benefits of such endeavors.

In the late 1800s to early 1900s, populations of iconic fish species in the Columbia River Basin (U.S.A.) declined dramatically due in large part to industrial-scale overharvest. Although harvest has been managed to levels substantially reduced in recent decades, native fishes including salmon, steelhead (*O. mykiss*), Bull Trout, White Sturgeon (*Acipenser transmontanus*) and Pacific Lamprey continue to be impaired by the exclusion, alteration or destruction of spawning, nursery and migratory habitats (Nehlsen et al., 1991; Parsley et al., 2002; CRITFC, 2011; USFWS, 2015; Clemens et al., 2017a). Since completion of the dams and reservoirs of the Columbia River System (CRS; Fig. 1) in 1975, and despite considerable effort to improve habitat and provide for better passage conditions, native fish populations have been impaired, with many species or populations now facing extinction or extirpation. Nowhere is this decline more evident than in the Snake River Basin, even though a vast area of high-quality spawning and nursery habitat remains (Thurow, 2000; NOAA, 2017a). This basin once supported almost 50% of the Chinook Salmon and steelhead in the entire Columbia River Basin (TU, 2021). Considering this historic capacity, it stands to reason that the Snake River Basin now represents the best opportunity to promote broad-scale recovery. Yet, even after decades of attempts to mitigate the effects of impoundment, today only 1–2% of historic wild salmon and steelhead numbers return (Thurow et al., 2020) and all populations in the basin face extinction or extirpation (Williams et al., 1989; Nehlsen et al., 1991). Therefore, it seems clear that aggressive actions, not tried previously, are necessary. Within this context, we examined the need for, and likely efficacy of breaching the four lower Snake River (LSR) dams, to support the rehabilitation of salmon, steelhead, Bull Trout, White Sturgeon and Pacific Lamprey. We attempt to answer three questions specifically:

(1) Will breaching of the four LSR dams increase the likelihood that naturally produced populations of Snake Basin salmon and steelhead can persist into the future?

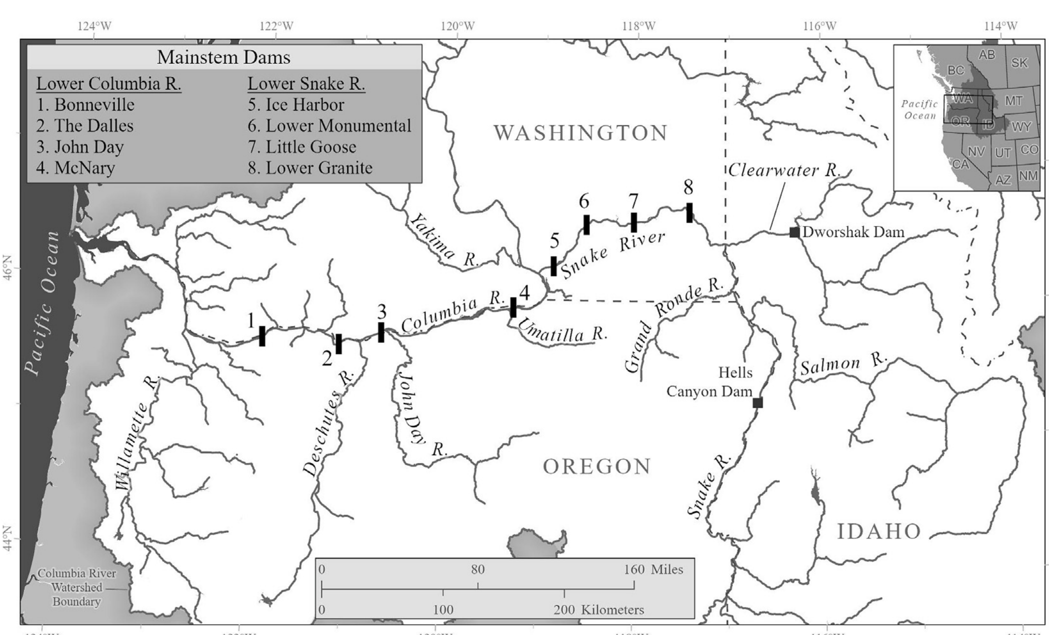

Fig. 1. Tributaries, dams, and reservoirs of the lower Columbia (i.e., contiguous U.S.) and lower Snake rivers.

(2) Would Snake River Basin salmon and steelhead reach healthy and harvestable levels if the four LSR dams were breached?
(3) Would other native fish species in the basin benefit from breaching the four LSR dams?

More broadly, we focus on the potential conservation and fishery benefits of breaching four dams in the Lower Snake River (LSR; Washington state, USA) as a case study to inform the rehabilitation of similarly impaired systems, in the U.S. and throughout the world.

2. Dams in the Columbia River system

Eight high-head dams currently span the Lower Columbia and Snake Rivers of Washington and Oregon (U.S.A.), constituting part of the CRS (Fig. 1). The dams are owned and operated by the U.S. Army Corps of Engineers (USACE) for the purposes of generating electricity, river navigation, recreation, and irrigation. Four of the eight dams impound the lower Columbia River in Washington and Oregon, including Bonneville (river kilometer [rkm] 235.1), The Dalles (rkm 309.0), John Day (rkm 347.6), and McNary (rkm 470.0). Installed beginning in the 1930s, operation of these lower Columbia River dams commenced between 1938 and 1971, and they currently provide partial juvenile and adult fish passage, particularly for salmon and steelhead (USACE, 2022a, b, c, d). The lower Snake River in Washington is impounded by four dams–Ice Harbor (rkm 15.6), Lower Monumental (rkm 66.9), Little Goose (rkm 113.1), and Lower Granite dams (rkm 173.0)–installed beginning in 1956 and first operational between 1962 and 1976. The four LSR dams provide some opportunity for volitional fish passage (juvenile and adults), with three of the dams (Lower Monumental, Little Goose and Lower Granite) supporting a juvenile transportation program meant to promote survival to the Columbia River Estuary by barging or trucking a proportion of outmigrants passed downstream mainstem dams (USACE, 2022e, f, g, h). These eight dams, and in particular the four LSR dams–owing largely to their deleterious effects on threatened and endangered salmon and steelhead populations–have been a source of contentious debate throughout the region for decades fueled by competing views on how and if to strike a balance between optimizing life-cycle survival of fishes to achieve long-term sustainability and certain socio-economic considerations.

3. Salmon and steelhead

Development of the CRS converted 518 km of free-flowing river into a series of dams and reservoirs, affecting native fish populations dramatically. Prior to this transformation, the Columbia River ecosystem was a network of complex, interconnected habitats created, periodically altered, and maintained by natural physical processes (ISG, 1999; Williams, 2006), whereby passage to and from upriver habitats by anadromous fishes was largely unimpeded by modern anthropogenic factors such as impoundment. Today, the Columbia River ecosystem bears little resemblance to a naturally flowing river, and salmon and steelhead face increased constraints on survival owing to several factors including reduced water velocity, potentially lethal reservoir temperatures, migration delays and increased biotic interactions (predation, competition and/or disease), injury and other stressors that occur during dam and reservoir passage (Budy et al., 2002; Cannamela et al., 2019). For juveniles, these factors depress rates of survival, both directly and indirectly, during seaward migration. Further, effects of the hydrosystem can manifest in reduced ocean survival and, ultimately, rates of adult returns. Snake River populations in particular are likely impaired by substantial delayed mortality in the marine environment because of out-migration experiences (Deriso et al., 2001; Williams et al., 2005; Schaller and Petrosky, 2007; Buchanan et al., 2011; Marmorek et al., 2011; Schaller et al., 2014a).

Since the 1980s, several strategies to promote the recovery of salmon and steelhead have been implemented. These include: major structural modifications at dams to improve passage survival; extensive collection and transportation of juvenile salmon to the Columbia River Estuary; rehabilitation and enhancement of spawning and rearing habitat in central Idaho, southeast Washington, and northeast Oregon; rehabilitation of estuary habitat; extensive hatchery supplementation; regulations to reduce rates of harvest; reduced timber harvest and road development in public lands; intensive programs to control avian, piscivorous and mammalian predators; increased flows through CRS reservoirs; and increased spill over CRS dams to aid fish passage. However, efforts to date have not reversed or appreciably slowed the continued decline of these species (Lichatowich, 2013; Rieman et al., 2015).

3.1. *Desired status*

Previous regional goals seeking to rehabilitate salmon and steelhead populations in the Columbia River Basin had often been based on ESA delisting criteria (ESA, 1973) that consider the probability of functional extirpation or whether minimal abundance thresholds have been achieved to allow for long-term persistence. Recently, the Columbia Basin Partnership (CBP), in its Phase 2 Report (NMFS, 2020), consolidated and aligned abundance goals while detailing a common vision to realize sustainable populations of salmon and steelhead in the basin. These new goals were adopted subsequently by the Northwest Power and Conservation Council (NPCC, 2020) and endorsed by others in the region (NMFS, 2020). The CBP Phase 2 Report, and concurrence among several bodies, puts into stark relief the urgency to achieve these goals, thereby restoring healthy and harvestable populations.

Further, in 2020 the NPCC reaffirmed the prior benchmark of smolt-to-adult returns (SAR) averaging 4% (range: 2%–6%) for spring/summer Chinook Salmon (NPCC, 2020). As the NPCC notes, a minimum SAR of 2% is required to consistently maintain existing populations, whereas SARs >2% indicate degrees of population growth (Marmorek et al., 1998; Peters and Marmorek, 2001; McCann et al. 2017, 2018; Petrosky et al., 2020). Smolt-to-adult return rates ≥4% achieved on a regular basis should promote a high likelihood of recovery (i.e., consistent generational increases in abundance, Petrosky et al., 2020). The Independent Scientific Advisory Board (ISAB, 2017; ISAB, 2018) has reviewed in detail the 2–6% SAR objective and identified extensive evidence to support these goals, noting that "SAR objectives provide a readily measured, first-order objective for restoring stocks."

3.2. *Quasi extinction thresholds (QETs) and population declines*

QETs are used to assess extinction risk and population viability, representing tipping points for population collapse in conservation science. Populations falling below QETs face high genetic, demographic, and environmental risks–increasing the probability of extirpation or extinction, constraining resilience, and limiting substantially the potential for recovery (Gilpin and Soulé, 1986; Simberloff, 1988; Fagan and Holmes, 2006). The QET for salmon and steelhead is commonly accepted as being met when the abundance of natural-origin spawning adults is ≤50 individuals per year for four consecutive years (ICTRT, 2007). Under this definition, Johnson et al. (2021) estimated 42% of populations of ESA-listed Snake River spring/summer Chinook Salmon currently have reached QET and 77% of those populations are predicted to drop to levels ≤50 adult spawners by 2025. Similarly, 19% of summer steelhead populations originating in the Snake River Basin are currently at or below QET and 44% of populations are expected to drop below 50 adult spawners by 2025 (Johnson et al., 2021). Bowles (2021) conducted analyses pointing to a similar dire situation, where an estimated 29% of Snake River spring/summer Chinook Salmon populations are now at QET and 39% are predicted to drop to QET by 2025. For summer steelhead, 13% are currently at QET and 62% of populations are predicted to have fallen to or below QET by 2025 (e.g., Fig. 2).

Low abundances within Snake River spring/summer Chinook and steelhead populations are driven by a persistent pattern of low SARs in

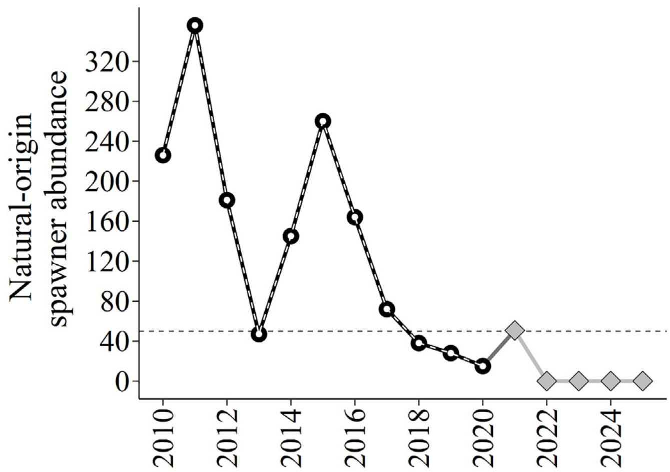

Fig. 2. Natural-origin spawner abundance of summer steelhead, as estimated directly (black circles/lines) from both a model fitted to the original times series (white circles/lines) and projections (diamonds) based on Auto-Regressive Integrated Moving Average (ARIMA) models fit to the entire original time series (pre-2020). The dashed horizontal line represents the threshold at which quasi-extinction is assessed (i.e., ≤50 natural origin spawners). Data are for Secesh River summer steelhead, but trends are indicative of the status of many salmon and steelhead populations in the Snake River Basin (Bowles, 2021).

recent decades (McCann et al. 2017, 2018; Petrosky et al., 2020). Spring/summer Chinook SARs have averaged less than 1% over approximately the past twenty years, resulting in generational declines in population abundance throughout the basin. Over the same period, SARs for steelhead have averaged less than 2%, also resulting in population declines (McCann et al., 2017, 2018, 2020). Low abundances are perpetuated by poor SARs and pose a very high demographic and genetic risk to the persistence of the populations and may lead to extirpation (McElhany et al., 2000; ICTRT, 2007; Thompson et al., 2019; Petrosky et al., 2020).

3.3. Hydrosystem effects

Rates of smolt-to-adult return for populations of salmon and steelhead in the Columbia River Basin reflect the influence of various factors acting throughout the life-cycles of fishes in each population. These factors include temperature and flow conditions during outmigration, direct effects of hydro-system passage, estuary survival, delayed mortality, ocean conditions, predation, harvest, and freshwater temperatures and flow conditions during the adult return.

While there are several factors that may dictate SARs in any given year, the strong influence of hydrosystem effects is evident when comparing the success of populations in different subbasins throughout the system. Populations of yearling Chinook Salmon and steelhead in the Columbia River Basin that migrate past four or fewer mainstem dams survive at rates higher than those that must pass eight dams (see Dams of the CRS; Fig. 1). For example, wild spring/summer Chinook salmon originating in the Yakima River Subbasin, that pass four mainstem dams on their way to the Pacific Ocean, have exhibited SARs of approximately 2% (migration years 2000–2018; geometric mean SAR = 2.44%), whereas Chinook Salmon originating in the John Day Basin (passing three dams during juvenile outmigration) have generally returned as adults at rates above 3% (migration years 2000–2018; geometric mean SAR = 3.52%). In contrast, Snake River spring/summer Chinook Salmon that pass eight mainstem dams during outmigration survive to adulthood at considerably lower rates than their downstream counterparts (geometric mean SAR = 0.91%; migration years 2000–2018; McCann et al., 2021, Fig. 3).

This effect is also evident for summer steelhead. For fish originating in the Yakima and John Day subbasins (above four and three mainstem dams, respectively), SARs consistently met or exceeded 4% (migration $\text{years}_{\text{Yakima}}$ = 2002–2018, geometric mean $\text{SAR}_{\text{Yakima}}$ = 4.42%; migration $\text{years}_{\text{John Day}}$ = 2004–2018, geometric mean $\text{SAR}_{\text{John Day}}$ = 4.62%). For wild summer steelhead out-migrating from the Deschutes River Subbasin (above two mainstem dams), geometric mean SARs varied around 5% (migration years, 2006–2018; geometric mean SAR = 5.15%). As for wild spring/summer Chinook salmon, rates of adult return for wild summer steelhead that must pass up to four mainstem dams during out-migration contrast with the survival of fish originating in the Snake River Basin, where estimated SARs for summer steelhead were considerably lower (migration years, 2000–2018; geometric mean SAR = 1.91%; Fig. 3). These upstream/downstream contrasts among populations that experience comparable in-river (i.e., migration corridor), estuarine, and early ocean conditions highlight the cumulative negative effects, whether direct or indirect, of passage through multiple dams and reservoirs. While the population of Snake River fall Chinook Salmon may appear to be an exception to these patterns, having experienced increased returns in the past decade (averaging <9000 wild fish), it is supplemented heavily with hatchery-origin fish that constitute most spawners (Tiffan et al., 2020). Further, the relatively larger returns of fall Chinook Salmon likely result, in part, from their shorter freshwater life histories (e.g., Connor et al., 2005; Waples et al., 2017) and different ocean migration patterns (Fisher et al., 2014; Teel et al., 2015).

First-year ocean survival, and consequently recruitment success, is dictated by near-shore and broad-scale environmental conditions but is likely also be influenced by previous experience in freshwater (Budy et al., 2002; Schreck et al., 2006). Salmon and steelhead are highly vulnerable to mortality during the life stage transitioning from fresh to marine waters. During this transition, fish go through taxing physiological changes needed to effectively osmoregulate in brackish and marine

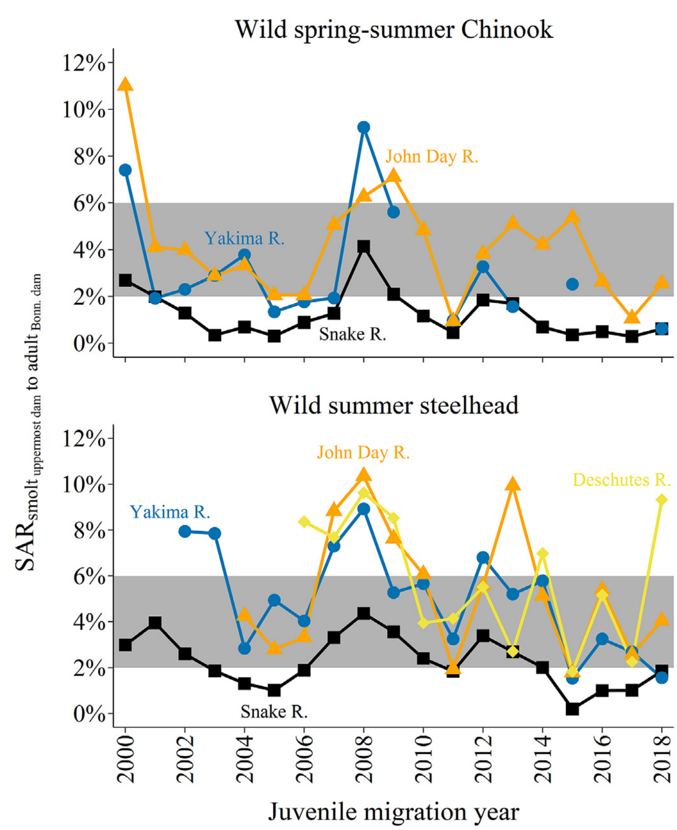

Fig. 3. Variation in smolt-to-adult returns (SARs) for wild John Day, Yakima, and Snake River spring/summer Chinook salmon (including jacks; top panel) and wild John Day, Yakima, Deschutes, and Snake River summer steelhead (bottom panel). The shaded region indicates the range of NPCC (Northwest Power and Conservation Council) SAR goals for population viability.

environments. The success of this transition, and the ability of a migrant to survive during later life stages, is dependent on timing and the capacity of a fish (i.e., condition) to adapt to a new environment. Effective transition is likely made more difficult by the impacts of hydroelectric dams during out-migration to the ocean. For example, the condition of these fishes can be compromised by mechanical injury and stress during passage through bypass systems and turbines, with substantial delay in migration. Rates of migration are further reduced in reservoirs between dams, as discharge through the larger cross-sectional area of a run-of-the river reservoir (i.e., water surface elevation raised by dam and consequent widening) results in lower velocity, which slows out-migration (Dreher et al., 2000). Slowed outmigration may increase exposure to predation, competition, and elevated temperatures, thus increasing energetic costs and propensity for disease, and result in poorly timed estuary arrival. All these factors can constrain the survival of out-migrating smolts and likely influence mortality in subsequent life stages (Williams, 1989, 2001; Kareiva et al., 2000; Budy et al., 2002; Wilson, 2003; Muir et al., 2006). For example, conditions for growth in fresh water, migration timing, and the degree of overlap with high-quality prey in near-shore coastal habitats influence individual survival and annual SARs for Columbia River Basin steelhead (Wilson et al., 2021). Further, Snake River salmon and steelhead that may be compromised physiologically due to hydrosystem experience then must transition to the ocean, where they compete for food while avoiding predators. Research surrounding these ecological mechanisms provide evidence that Snake River spring/summer Chinook Salmon and summer steelhead experience delayed mortality in the ocean because of migration experience through the CRS.

The influence of freshwater factors on marine survival of anadromous species remains contentious and alternative perspectives exist (e.g., Schaller et al., 1999; Zabel and Williams, 2000; Schaller et al., 2000; Faulkner et al., 2019, Storch et al., 2020). For example, Welch et al. (2020) suggested that most variation in life-cycle survival can be explained by marine effects common among populations of Chinook Salmon throughout the west coast of North America (but see Kope and Botsford, 1990; ISAB, 2021). The authors argued that freshwater factors–including the number of dams encountered during migration–generally have little bearing on SARs. Nonetheless, as discussed above, an expansive body of evidence based on research and analyses across decades supports the role of freshwater factors as important determinants of life-cycle survival, and effects of these drivers can manifest during early ocean experience (i.e., delayed, or latent effects; Budy et al., 2002; Schreck et al., 2006; Schaller et al., 2007; Petrosky and Schaller, 2010; Marmorek et al., 2011; Haeseker et al., 2012; Schaller et al., 2014a).

3.4. Responses to breaching Lower Snake River dams

Breach of the four LSR dams would likely increase long-term survival and recovery of anadromous species that pass mainstem dams. Actions that include breach of the four LSR dams have been predicted to yield the highest improvements in survival for Snake River species (NOAA, 2000, 2020a,b). That conclusion is supported by extensive evidence from a peer-reviewed, interagency process established in the 1990s. The Plan for Analyzing and Testing Hypotheses (PATH) summarized available empirical evidence, analyzed retrospectively patterns of life-cycle survival, and conducted prospective analyses under a range of potential future scenarios. These analyses suggested options that include dam breach are most likely to precipitate the recovery of Snake River salmon and steelhead (Marmorek et al., 1998; Peters and Marmorek, 2001). The body of evidence that has accrued since the PATH process has reaffirmed the major adverse effects of mainstem CRS dams on Snake River salmon and steelhead populations (e.g., Williams, 1989; Williams, 2001; Nemeth and Kiefer, 1999; Kareiva et al., 2000; Wilson, 2003; Harrison, 2011; Schaller et al., 2014a; Petrosky et al., 2020).

Substantial evidence from multiple analytical approaches have demonstrated consistently latent effects (i.e., delayed hydrosystem mortality) on Snake River Chinook Salmon over varying ocean conditions (Williams et al., 2005; Buchanan et al., 2011; Marmorek et al., 2011; Schaller et al., 2014a; Petrosky et al., 2020). In 2020, at the request of agencies within the U.S. Federal Government, members of the Comparative Survival (CSS) conducted model simulations to inform the Columbia River Systems Operations (CRSO) Environmental Impact Statement (EIS; CRSO, 2020). The CSS applied empirical statistical models–that inherently capture latent effects–to assess the efficacy of alternatives to mitigate negative effects of the CRS, including options that incorporate dam breach.

Several important findings arose from the CSS analyses of the mitigation options, termed Multiple Objective Alternatives (MOs; McCann et al., 2019; FPC, 2020). First, MO3 (breach the four LSR dams and spill to 120% tailrace total dissolved gas [TDG] at dams in the lower Columbia River) and MO34 (breach the four LSR dams and spill to 125% tailrace TDG at dams in the lower Columbia River) are projected to result in the SARs closer to the regional goal (i.e., mean = 4%). Other alternatives examined–that did not include breaching the four LSR dams–are predicted to result, on average, in SARs below the regional goal (range: ~1%–~3%), indicating risk of further population decline under those management options. Consistent with prior findings from the PATH process, these analyses suggest alternatives that included dam breach may have the lowest probability of producing extremely low SARs (i.e., <1%) as well as the greatest probability of SARs >2% (Fig. 4).

What do these model-predicted SARs imply about the prospects for the recovery of Snake River salmon and steelhead? In general, and for Snake River Chinook Salmon in particular, prior CSS analyses found that SARs <1% consistently led to decreased abundance in the following generation, whereas SARs ≥2% commonly allowed for some generational increase in abundance. Specifically, there exists a strong positive relationship between SARs and population productivity (McCann et al., 2017). Increases in frequency of very low SARs, as CSS simulations portend, and consequently inadequate return abundances and critically

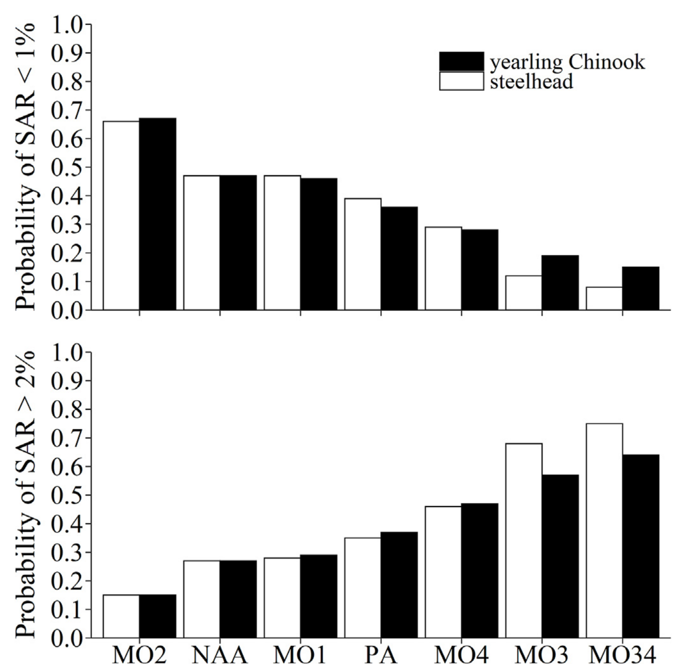

Fig. 4. Probabilities of smolt-to-adult returns (SARs) <1% (top panel) and probabilities of SARs >2% (bottom panel) for yearling spring/summer Chinook Salmon and steelhead for different management options (No-action Alternative [NAA] and Multiple Objective Alternatives [MOs]) prescribed during the CRSO EIS (Columbia River Systems Operations, Environmental Impact Statement) process (McCann et al., 2019; FPC, 2020). The dam breach alternatives are MO3 and MO34, and non-breach alternatives are MO2, NAA, MO1, PA (i.e., preferred alternative adopted by the Federal Agencies) and MO4.

low productivity on spawning grounds creates high risk for populations of salmon and steelhead, and can result in high probabilities of population extirpation and ultimately species extinction (McElhany et al., 2000; CSSOC, 2017; ISAB, 2007a; McCann et al., 2019). However, CSS simulations indicate that these low rates of adult return could be improved substantially by (1) breach of the four LSR dams and (2) maximizing spill at the lower Columbia River dams (McCann et al., 2017). Likewise, analyses conducted by NOAA Fisheries suggest operations that include breach of the four LSR dams are likely to promote the greatest relative increase in SARs and escapements (Nemeth and Kiefer, 1999; Pinit, 1999; Kareiva et al., 2000; NOAA, 2020a). These predictions, generated from two different modeling frameworks, as well as the strong positive relation between SARs and productivity, support the argument that some combination of breach and enhanced spill are the most likely actions to allow recovery of Snake River salmon and steelhead. The argument is substantiated further by the agreement among results of the modeling conducted by the CSS and those from the PATH process, carried-out over two decades earlier; both indicating strongly that breach of the four LSR dams will likely be necessary to achieve sustainable Snake River salmon and steelhead populations. It is notable that, despite the time between which PATH and CSS analyses were conducted, and the fact that CSS analyses incorporate considerably longer empirical time series, outcomes remain consistent. This consistency suggests that the projections incorporating the influence of dam breach are robust to environmental variation and measurement uncertainty.

3.5. *Impacts to other life stages*

In addition to the effects described above, constrained flows resulting from the presence of the four LSR dams increases water temperatures by augmenting surface area and thus irradiation (TU, 2021), and inundate approximately 224 river km of spawning and rearing habitat for fall Chinook Salmon. Removal of the LSR dams would likely help rehabilitate river habitat and promote the eventual expansion of this sub-species. Warming of the river above critical levels from June to mid-September also reduces survival and reproduction of adult salmon (USEPA, 2020). Elevated water temperatures negatively affect migrating Sockeye Salmon, steelhead and fall Chinook Salmon that return to spawn in the Snake River. For example, during the summer drought of 2015, 96% of endangered adult Snake River Sockeye Salmon died during their upriver migration through the lower Columbia and Snake rivers from the effects of elevated water temperatures and low flows (TU, 2021). Those constraints were likely exacerbated by the presence of mainstem dams and their associated reservoirs. Resources to mitigate thermal extremes in the LSR and protect migrating salmon and steelhead are limited; there are no additional options to cool substantially the river in its current configuration (FPC, 2015; Cannamela et al., 2019). The deleterious conditions faced by migrating adult salmon in 2015 will undoubtedly become more frequent as the climate continues to warm and low-flow events become increasingly common (ISABb, 2007; NOAA, 2017b; Isaak et al., 2018).

4. Other native anadromous & potamodromous fish species

4.1. *Bull Trout*

The mainstem Columbia and lower Snake rivers, and some of their tributary subbasins, have been designated as critical habitats for migratory Bull Trout by the U.S. Fish and Wildlife Service (USFWS; USFWS, 2010). The designation recognizes that Bull Trout range from small headwater streams used for spawning and rearing, to downstream mainstem portions of rivers for rearing, foraging, migration, and overwintering.

Throughout its distribution, Bull Trout exhibit a continuum of life histories involving migrations, spawning, rearing, and foraging over broad ranges in space and time. Connectivity between tributaries and within the mainstem Columbia and Snake rivers is essential to maintain genetic exchange among core populations, to support resiliency against environmental and anthropogenic perturbations and ensure a high likelihood of population viability and recovery. Maintaining corridors among habitats provides opportunities for Bull Trout to disperse, by eliminating barriers to migration and improving habitats in migration corridors–a process essential to maintaining genetic diversity and supporting persistence of local- and meta-populations (Schaller et al., 2014b). Uninhibited dispersal will almost certainly become even more critical for the cold-water adapted Bull Trout as the frequency of elevated temperatures increases from climate change (Rieman et al., 2007; Eby et al., 2014).

Starcevich et al. (2012) and Barrows et al. (2016) determined that Bull Trout enter the mainstem Columbia and Snake rivers and move extensively, interacting with mainstem dams and reservoirs. The authors observed that these movements and interactions occur at all times of the year, across large spatial extents (8–240 km). Their syntheses indicate that Bull Trout can be exposed to various anthropogenic impacts in the mainstem corridors within the Columbia or lower Snake rivers, and some of these conditions may impede overwinter foraging, migration, and access to habitat. The USFWS recovery plan (USFWS, 2015) supports removing impediments to these life-history processes to ensure an adequate number of sufficiently large, genetically diverse populations exist to withstand catastrophic events. Connectivity–both within mainstem habitats and between mainstem and subbasin habitats–is essential to the recovery of Bull Trout. A dramatic illustration of this can be seen in the Elwha River, where Bull Trout resumed extensive migrations (∼168 km) soon after dam removals (Brenkman et al., 2019).

4.2. *White Sturgeon*

The population of White Sturgeon in LSR has been fragmented by hydrosystem development, and although not at immediate risk of extinction (Hildebrand et al., 2016), it does suffer from limited recruitment and intermittent recruitment failure (Parsley et al., 2002). Recruitment in some reaches is constrained by changes in physical habitat, including variation in the distribution of sediment, shifts in flow and thermal regimes below dams and trapping of contaminated sediments in reservoirs (Parsley et al., 2002). As a result, recreational harvest bans have been implemented to prevent extirpation (Beamesderfer and Anders, 2013).

Scientists have quantified the minimum viable population size necessary for 36 populations of White Sturgeon in the U.S. Pacific Northwest and Canada. In doing so, the researchers determined the minimum length of free-flowing river required to support growing (reproducing, self-sustaining) populations. Both model-based and purely empirical approaches suggested consistent annual recruitment was characteristic of all healthy populations, for which age structure is dominated by younger fish (Jager et al., 2010).

Population viability analysis (PVA) of White Sturgeon suggests that much less free-flowing habitat is required where adults can reproduce in all years. However, in reaches where recruitment has been possible only in years where precipitation is above average, >70 km of free-flowing habitat was required to support viability (Jager et al., 2010). Further, PVA simulations suggested that reconnection will be less effective if other problems, such as poor water quality or overfishing, are not also addressed (Jager, 2006; Jager et al., 2007). Many White Sturgeon populations with poor recruitment appear to fall below a threshold amount of required spawning and rearing habitat; notable examples of this are the populations inhabiting the short reservoir segments of the LSR (Jager et al. 2001, 2010; Beamesderfer and Anders, 2013). In the absence of other limiting factors, model results suggest that the long-term likelihood of persistence is very high in free-flowing reaches >200 km in length (Jager et al., 2010). Dam removal would allow White Sturgeon to move freely among habitats to maximize growth, survival, and reproduction.

Sampling targeted specifically at age-0 White Sturgeon has shown little or no recruitment has occurred in Ice Harbor or Little Goose reservoirs from 1997 to 2005 (Chapman and Weaver, 2007). Whereas some age-0 White Sturgeon have been observed regularly in Lower Granite Reservoir, those juveniles likely originated from the population that resides upstream in the free-flowing portion of the Snake River in Hells Canyon (Parsley and Kappenman, 2000). Thus, there is compelling evidence that very limited recruitment takes place in the area impacted by the four Lower Snake River dams. There, populations of White Sturgeon are small (reservoir estimates of abundance from the mid-1990s were 4830, 4262 and 6492 fish >54 cm FL for Ice Harbor, Lower Monumental and Little Goose dams, respectively; Hildebrand et al., 2016) and dominated by older individuals (as indexed by length), consistent with poor spawning success and recruitment (Beamesderfer and Anders, 2013). This is due, in part, to impoundment and backwater effects from the dams that make the remainder of LSR unsuitable for spawning given low current velocities, reduced hydraulic complexity and substrate infilling by fines (Jager et al., 2002; Parsley et al., 2002; Koch et al., 2006; Paragamian et al., 2009; McAdam, 2011, 2012, 2015; Hildebrand et al., 2016; Hatten et al., 2018). For example, reduced flows have restricted spawning and egg incubation to areas located within 7 km downstream of each of the four LSR dams (Parsley and Kappenman, 2000). Given White Sturgeon are broadcast spawners that rely on sufficient flow and velocity for successful recruitment (Stevens and Miller, 1970; Kohlhorst et al., 1991; Parsley and Beckman, 1994; Fish, 2010), these types of reservoir effects present a notable detriment. Without recruitment, the populations cannot persist.

The LSR dams present barriers to upstream movement of White Sturgeon and very little upstream passage by juveniles or adults occurs beyond any of the LSR dams. Fishway designs that provide passage for adult salmon are inappropriate for sturgeon (Parsley et al., 2007; Jager et al., 2016). In over 17 years, counters at LSR dam fishways reported 20 White Sturgeon at Ice Harbor, 2 at Little Goose, 1 at Lower Monumental and 2 at Lower Granite dams (U.S. Army Corps of Engineers, unpublished data, 1998–2014). While some age-0 White Sturgeon pass downstream at the dams, it is likely restricted to older juveniles and some adult fish that pass through open spillways or turbines, as has been shown to occur at The Dalles Dam in the lower Columbia River (Parsley et al., 2007). Moreover, the Lower Snake populations are not fully isolated, receiving immigrants from upstream populations. Thus, with a stable (or viable) population above Lower Granite Dam, up- and down-stream (i.e., LSR) populations should effectively seed one-another if the dams were removed.

Finally, sediment characteristics and habitat suitability for sturgeon spawners and benthic prey would likely improve with dam removal (Hart et al., 2002). Work by Hatten et al. (2018) shows that reducing embeddedness and increasing habitat diversity by converting reservoirs back to rivers should produce conditions favorable to successful White Sturgeon recruitment.

4.3. Pacific Lamprey

Pacific Lamprey is an anadromous species of major significance to Native American communities and plays a pivotal role in freshwater and marine ecosystems (Close et al., 2002; Clemens and Wang, 2021). The species has exhibited dramatic declines in abundance, contractions in distribution and is at high risk of extirpation throughout much of the Columbia River Basin, particularly in the Snake River and middle and mid-upper Columbia River (IDFG, 2011; Wang and Schaller, 2015; WDFW, 2015; Clemens et al., 2017a; USFWS, 2019; ODFW, 2020). Further, Pacific Lamprey have been extirpated from the upper Snake River because of impoundment by the Hells Canyon Dam complex, despite having been present historically (ODFW, 2020). Threat assessments identified adult and juvenile passage at mainstem dams as the principal constraint to Snake River populations (Luzier et al., 2011; USFWS, 2019). Small effective population size–a consequence of the inability of Pacific Lamprey to reach watersheds in the upper Snake River due to passage limitations throughout the migration corridor–was identified as the second highest risk. For example, at Lower Granite Dam, daytime adult lamprey counts were <100 individuals every year of the past 22 years since lamprey counts began, versus >1000 individuals in all but 5 years at McNary Dam (Fig. 5). In coastal rivers with unobstructed passage where Pacific Lamprey are still relatively abundant, an adult abundance of 100 individuals has been documented in a 1-km reach (Brumo, 2006). Small effective population sizes occur above Lower Granite Dam despite tribes having translocated adult lamprey from the lower Columbia dams to drainages above the Snake River dams since before 2010 (e.g., Ward et al., 2012). In 13 of the past 22 years, counts at Lower Granite Dam have been <50 individuals, a status indicative of the perilous state of the species (Fig. 5; FPC, 2021).

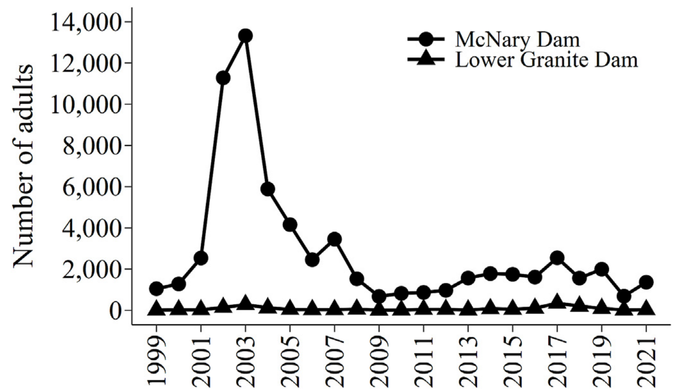

Fig. 5. Daytime adult Pacific Lamprey passage at McNary (mid-Columbia) and Lower Granite (lower Snake) dams, 1999–2021 (FPC, 2021).

5. Climate change

Global climate assessments indicate that climate change will continue to affect air temperatures, precipitation, and wind patterns in the Pacific Northwest (ISAB, 2007b; Philip et al., 2021). This has resulted in increased droughts and wildfires, and modified flow regimes; conditions that differ dramatically from those to which anadromous and potamodromous fish have evolved. Climate change will also alter Northeastern Pacific marine environments, including increased water-column stratification, altered temperature profiles and circulation patterns, increased intensity and altered timing of coastal upwelling, and a greater likelihood of hypoxia and acidification events (Bakun, 1990; ISAB, 2007b). Changes and increased variation in environmental conditions will affect the abundance, productivity, spatial structure, and diversity of Snake River anadromous and potamodromous fish species (ISAB, 2007b; Isaak et al., 2018). Therefore, climate dynamics have the potential to further reduce survival through direct and indirect effects at all life stages (NOAA, 2017b; ODFW, 2020), and any deleterious latent effects of freshwater experience in the CRS that manifest in the marine environment will presumably be magnified by ongoing climate change.

A modified climate exacerbates risks to aquatic biota as has been shown, for example, by the mass mortality event in 2015 of returning Sockeye Salmon (Crozier et al., 2021). Thermal gradients encountered while passing dams (i.e., via fish ladders) can constrain upstream movements (Caudill et al., 2013). Warm water (≥20 °C) and low flow conditions in the Willamette River have been linked to mortality, gonadal atresia, accelerated sexual maturation and cessation of upstream migration for adult Pacific Lamprey, which may select for life histories that spawn farther downstream (Clemens et al., 2009, 2016; 2017b). Adult Pacific Lamprey migrate sooner in low flow, warm water years at Bonneville Dam (Keefer et al., 2009), presumably to avoid the negative physiological effects of warm water (Clemens et al., 2016). Generally, and across species, reducing thermal stress by providing migrants easy access to upstream refuges in headwaters and groundwater-moderated reaches will be critical for some cold-water fishes to persist under future climate regimes (Snyder et al., 2020; Jager et al., 2018).

Evaluation of the potential effects of climate change suggests that much of the tributary habitat in the Snake River Basin will remain suitable for fishes, even with a warmer climate (e.g., Isaak et al., 2018). The Snake River Basin currently contains 20% of the habitat occupied by salmon and steelhead in rivers of the Pacific Northwest; by 2080 it is forecast to contain 65% of the coldest, most climate-resilient stream habitats in the region (Fesenmyer, 2014; Isaak et al., 2018; TU, 2021; Jacobs et al., 2021). While habitat such as this exists and may provide a buffer to harmful climate effects into the future, under the current configuration of the CRS it is unclear how migratory fishes in the mainstem Snake River will access those areas without succumbing to thermal stress. Breach of the four LSR dams would improve the ability of migrating fishes to access these high-elevation, groundwater- and snowmelt-fed freshwater refuges, likely increasing survival and productivity in what will be an otherwise inhospitable future climate.

6. Other ecosystem benefits of breach

Steps to promote the life-cycle survival of migratory fishes would also benefit other species. The headwaters of the Snake River would become more productive from increased inputs of marine-derived nutrients, benefiting various aquatic and terrestrial species (Close et al., 2002; Fausch et al., 2002; Naiman and Latterell, 2005; Wipfli and Baxter, 2010; Kohler et al., 2013; Weaver et al., 2016). Rehabilitated salmon, steelhead, Bull Trout, White Sturgeon, and Pacific Lamprey fisheries would benefit those who depend on them for sustenance, culture, recreation, or commerce (Close et al., 2002; Hughes, 2015; ASA, 2019; Colvin et al., 2019). Because fisheries dependent on these species have long been lost in most places, many members of market-based economies fail to understand the importance of a subsistence-based economy to the mental and physical health of families and local communities (Colombi, 2012; Boraas and Knott, 2018; Colvin et al., 2019). However, maximizing subsistence opportunities offers substantial benefits to indigenous cultures (Wolfe and Walker, 1987; SOS, 2021; TU, 2021). In addition, and despite regulations reducing fishing opportunities for certain species, recreational fishing continues to have a substantial positive economic influence in the region (Table 1); this benefit would certainly increase if dams were breached, and harvestable abundances increased as a result.

7. Conclusions

The major factors that limit recovery of important migratory fish species are well-documented. Many analyses, representing decades of study, suggest listed populations of Snake/Columbia River Basin salmon and steelhead face seemingly insurmountable constraints to recovery owing to development and operation of the CRS (Schaller et al. 1999, 2014a; Haeseker et al., 2012; Petrosky et al., 2020). In the face of climate change, the negative impacts of dams on salmon, steelhead, Bull Trout, White Sturgeon, and Pacific Lamprey populations will be magnified, and may prevent populations from accessing thermal refuges (Torgersen et al., 2012; Isaak et al., 2018; Wang et al., 2020).

Many fish populations in rivers across the United States have been rehabilitated following dam removal. In the Pacific Northwest in particular, recent dam removals have precipitated substantial rebounds for salmon, steelhead, Bull Trout, Pacific Lamprey, and other fishes (Brewitt, 2016; Jolley et al., 2018; Brenkman et al., 2019; Duda et al., 2020). Here, we focus on the needs for, and potential benefits of dam breaching for fish and fisheries, yet other socioeconomic factors deserve consideration. The LSR dams and reservoirs were not designed for flood control nor as regulating reservoirs for the lower Columbia River dams, but they do play roles in hydropower generation and commercial navigation. There have been four pertinent econometric analyses regarding these two latter ecosystem services (Whitelaw and MacMullan, 2002; Mojica et al., 2016; NWEC, 2018; ECONorthwest, 2019). The dams, locks and reservoirs facilitate barge traffic from the lower Columbia River to Lewiston, Idaho, providing relatively inexpensive transportation of bulk commodities. However, the fuel taxes paid by users cover only a small fraction of the $10 million annual costs of maintaining and operating the locks and dams (Whitelaw and MacMullan, 2002; ECONorthwest, 2019). While dams provide a relatively reliable source of hydropower, it represents a very small amount compared to other sources in the Pacific Northwest (ECONorthwest, 2019). Nonetheless, NWEC (2018) compared four energy portfolios–ranging from reliance on energy efficiency, demand response, and battery storage to dependence on energy efficiency, demand response, wind, and solar–one which would maintain the four LSR dams. Given necessary infrastructure and sufficient capacity, all four of the alternative portfolios performed better than what would be achieved by maintaining operation of the LSR dams and each reduced the risk of power shortages in the region. Mojica et al. (2016) concluded that any economic benefits from operation of the four LSR dams are exceeded by the costs of keeping them.

On a global scale, it is evident that impounded rivers alter flow and sediment regimes, fragment rivers, limit fish passage, and degrade or eliminate populations of migratory fish species (Lierman et al., 2012; Turgeon et al., 2019). Dams, and the associated reservoirs, disrupt fish migrations in large North American rivers (Rinne et al., 2005). Further, loss of connectivity has disrupted fish assemblages at the catchment level in 85% of 9330 river sites of 14 European nations (Schinegger et al., 2012). In South America, dams and reservoirs limited both adult and larval fish passage and survival (Pompeu et al., 2012). Large dams threaten fish biodiversity and food security in the Amazon, Congo, and Mekong River basins (Winemiller et al., 2016). The impassable Gezhouba Dam on the Yangtze River has led to the extinction of the Yangtze River Dolphin (*Lipotes vexillifer*) and Chinese Paddlefish (*Psephurus gladius*), and decimation of the Chinese Sturgeon (*Acipenser sinensis*) and Yangtze Finless Porpoise (*Neophocaena asiaeorientalis*; Chen et al., 2020). Further, in a global assessment, He et al. (2021) found that 261 proposed dams are on 75 rivers with >500 km of free-flowing habitat. Given evidence of the detrimental effect of dams throughout the globe, it is not surprising that LSR dams would degrade populations of anadromous and potamodromous fishes, and lessons from this highly studied system could be applied to achieve conservation goals elsewhere.

The wealth of credible scientific evidence indicates clearly that breach of the four LSR dams, with adequate spill at the remaining lower Columbia River dams, is necessary to rehabilitate declining populations of Snake River salmon, steelhead, Bull Trout, White Sturgeon and Pacific Lamprey. This rehabilitation would, in turn, benefit human populations that depend on these species economically, recreationally, and culturally.

To the questions we posed above:

(1) Will breaching of the four LSR dams increase the likelihood that naturally produced populations of Snake Basin salmon and steelhead can persist into the future?

Based on a strong weight of evidence, we conclude there is a high probability that breach– more so than any other mitigative action–would precipitate the rehabilitation of imperiled salmon and steelhead populations in the Snake River Basin.

(2) Would Snake River Basin salmon and steelhead reach healthy and harvestable levels if the four LSR dams were breached?

Table 1
Economic impacts of recreational fishing in Idaho, Oregon, and Washington (ASA, 2019).

State	No. of Anglers	No. of Jobs	Economic Output
Idaho	644,300	8,750	$1.2 billion
Oregon	569,600	13,120	$1.5 billion
Washington	882,700	14,870	$2.3 billion

Although the extent of the ultimate effects of climate change on salmon and steelhead populations in the Snake River Basin remains uncertain, decades of research points to the efficacy of breach to support healthy and harvestable populations.

(3) Would other native fish species in the Snake River Basin benefit from breaching of the four LSR Dams?

Native fish communities within the Snake River Basin are diverse, representing a wide range of life-history strategies and habitat requirements. Nonetheless, many processes and mechanisms that support these communities overlap, and it appears clear that the best way to optimize these overlapping processes and mechanisms for all species is to provide a more natural river condition (i.e., via breach). That is, protection of migratory fishes would likely provide some level of "umbrella" protection (sensu Scott et al., 1993) for other fish and wildlife species across trophic levels.

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Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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