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PERSPECTIVE

Ecological considerations for reintroducing Chinook salmon upstream of Shasta Dam

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Abstract

In this assessment, we reviewed existing literature to assess the ecological risks, benefits, and uncertainties associated with reintroducing Chinook salmon (*Oncorhynchus tshawytcha*) into the McCloud River, a tributary of the Sacramento River, California. Two source populations are being considered for reintroduction by co-managers in the basin (the Winnemem Wintu Tribe, California Department of Fish and Wildlife, and National Oceanic and Atmospheric Administration): existing winter-run Chinook salmon (WRCS) from the mainstem Sacramento River, and Chinook salmon from New Zealand (NZCS), which originated from eggs shipped from tributaries of the Sacramento River in the late 19th and early 20th century. Reintroduction has the potential to reduce extinction risks for the Sacramento River WRCS evolutionarily significant unit, which is currently listed as endangered under the U.S. Endangered Species Act. The primary ecological benefits identified were enhancement of spatial diversity and access to cold-water refuge for WRCS. Primary risks included depletion of source populations and potential disease transmission from New Zealand and the mainstem Sacramento River into the McCloud River. Predation or competition between reintroduced Chinook salmon and resident fish in the McCloud River is also possible but likely to be biologically negligible. There are many uncertainties regarding how WRCS and NZCS may interact with each other and with other species in the McCloud River, several of which may depend on Chinook salmon life history expression. The ecological risks, benefits, and uncertainties described here are important considerations for planning and implementing Chinook salmon reintroduction, along with other key considerations such as dam passage and cultural concerns.

KEYWORDS

Chinook salmon, disease, genetics, McCloud River, reintroduction, risk assessment, species interactions

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1 | INTRODUCTION

Since European settlement of western North America, many populations of Pacific salmon (*Oncorhynchus* spp.) have experienced severe decline due to multiple factors including construction of dams, habitat degradation, and other environmental changes (Anderson et al., 2014; Gregory & Bisson, 1997; Myers, 1998). Because Pacific salmon have anadromous life histories which include migration between marine and freshwater habitats, impassible migration barriers formed by large dams often result in the extirpation of populations from their historical spawning ranges unless passage options (i.e., fishways, trap-and-haul) can be provided (Keefer et al., 2021; Kock, Ferguson, et al., 2021; Zeug et al., 2011). Across their range, Pacific salmon have deep spiritual and cultural importance to Native American groups and are considered First Foods; therefore, the decline of salmon has been catastrophic for many of these communities (Blanchet et al., 2022; O'Brien, 2014; Reed & Norgaard, 2010; Willette et al., 2016). Pacific salmon also serve key ecological roles by transporting nutrients from marine to freshwater systems, and their population dynamics can influence biodiversity and ecosystem function (Brandt et al., 2024; Ruggerone et al., 2023; Schindler et al., 2003). Additionally, Pacific salmon populations support commercially and recreationally valuable fisheries, and their decline can detrimentally affect local economies (Huber & Carlson, 2015; Richerson et al., 2018). Therefore, restoring Pacific salmon to areas where they are currently extirpated has the potential to result in significant benefits if managers can address potential challenges and constraints of working in landscapes that have been dramatically altered by dams and other environmental changes (Anderson et al., 2014; Berger-Tal et al., 2020).

The Central Valley of California was once home to abundant populations of Pacific salmon including four seasonal runs of Chinook salmon *O. tshawytscha* (winter, spring, fall, and late fall runs, defined by their seasonal upstream migration timing) (Fisher, 1994; Yoshiyama et al., 2001). Chinook salmon were central to the livelihoods and cultures of Indigenous communities in the area (Fisher, 1994; Yoshiyama, 1999) (Figure 1). Following the gold rush and the establishment of California statehood in the 1840s–1850s, Central Valley Pacific salmon populations (including Chinook salmon) severely declined due to overexploitation, habitat loss, and environmental alteration (Yoshiyama, 1999). For example, Euro-American settlers harvested eggs from Chinook salmon in Sacramento River tributaries and shipped them around the world to support salmonid introductions that were popular during the late 19th century and early 20th century (Crawford & Muir, 2008). Some of these shipments were to the South Island of New Zealand, where populations of Chinook salmon (New Zealand Chinook salmon, NZCS) still persist in the wild (McDowall, 1994; Quinn et al., 1996; Yoshiyama & Fisher, 2001). Ultimately, the construction of Shasta Dam extirpated Chinook salmon from their historical habitat on the McCloud River and other headwater tributaries of the Sacramento River (Garrett, 2010). Lost access to the McCloud River and other tributaries upstream of Shasta Dam had particularly negative consequences for winter-run Chinook salmon (WRCS), which have adapted to spawn during late spring and summer, requiring cool summer stream temperatures found in these tributaries for embryo incubation. Currently, WRCS cannot move upstream of Keswick Dam (located 14 rkm downstream of Shasta Dam; Figure 1), and therefore they spawn in the mainstem Sacramento River downstream of the dam or are collected and artificially propagated at the Livingston Stone National Fish Hatchery, which is located in the tailrace of Shasta Dam (NOAA, 2024). Spawning below Keswick Dam is possible due to careful temperature regulation of water released from Shasta Dam, but during drought years, it may not be possible to provide sufficient cool water to ensure spawning success and embryo survival. As severe droughts become more frequent, the ability of managers to regulate water temperatures for WRCS below Keswick Dam may be further reduced (Hallnan et al., 2020). For this and other reasons, WRCS are considered to be highly vulnerable to environmental change given their current limitations in spatial distribution (NOAA, 2024).

In 2023, the local Winnemem Wintu Tribe (WWT; not federally recognized), California Department of Fish and Wildlife (CDFW) and National Oceanic and Atmospheric Administration (NOAA) entered into a co-management agreement, committing to a collaborative approach for reintroducing Chinook salmon to the McCloud River (NOAA, 2014; WWT, 2016; WWT et al., 2023). The co-managers' two primary objectives were: (1) to reintroduce WRCS into their historical spawning grounds in the McCloud River, and (2) to reintroduce NZCS to the McCloud River. By pursuing these objectives, the co-managers sought to achieve multiple ecological and cultural goals. The WRCS evolutionarily significant unit was federally listed as threatened under the U.S. Endangered Species Act (ESA) in 1989 and reclassified as endangered in 1994 (NOAA, 2024), in addition to being listed as endangered in the state of California in 1989 (CNDDB, 2026). State and federal agencies are therefore legally obligated to minimize factors identified as placing endangered WRCS in jeopardy. A recovery plan for WRCS and other listed salmon in California's Central Valley was published in 2014 to identify threats to the species, guide management actions, and develop

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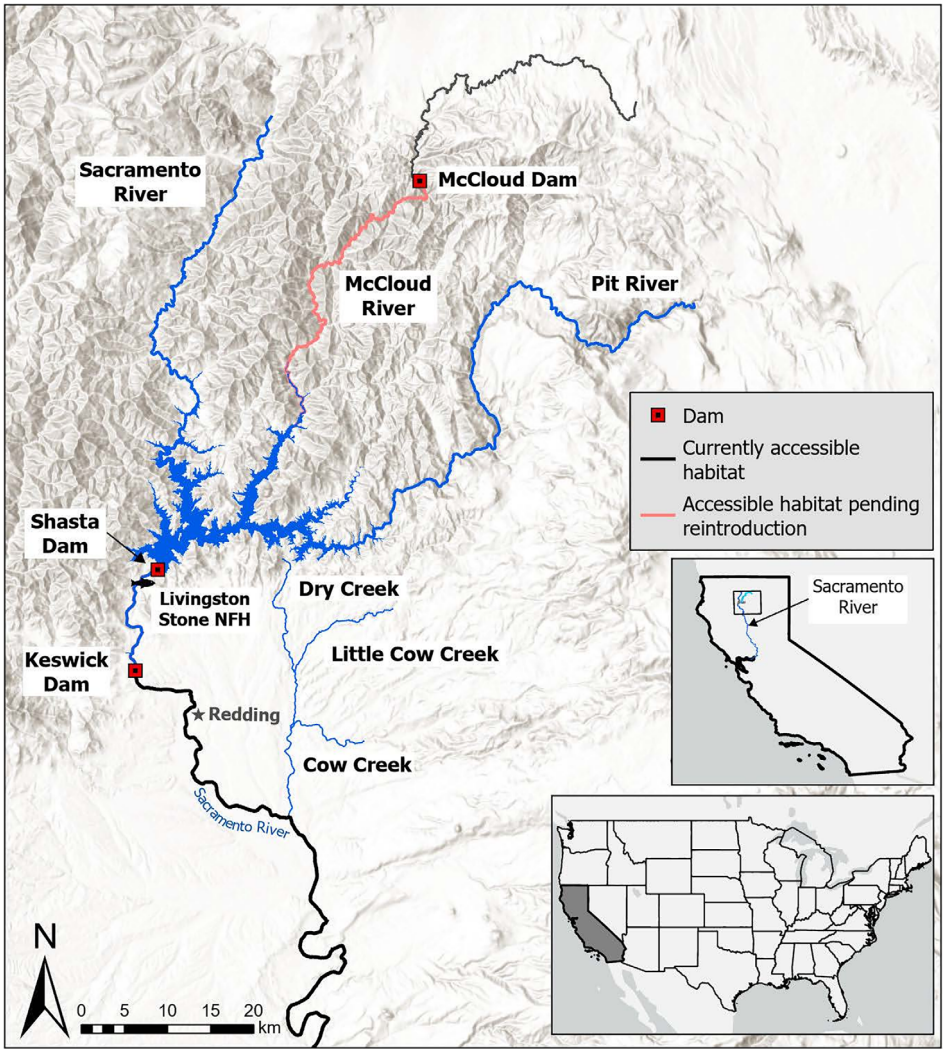


FIGURE 1 Multiple runs of Chinook salmon currently spawn in the Sacramento River below Keswick Dam but have been extirpated above the dam due to lack of passage. Reintroduction of Chinook salmon above Shasta Dam in the McCloud River could aid in the recovery of runs that are threatened with extinction, as this tributary provides relatively cool habitat year-round. Co-managers are currently exploring the possibility of reintroducing Chinook salmon to the McCloud River above Shasta Reservoir. Source populations under consideration include winter-run Chinook salmon below Keswick Dam and Chinook salmon from New Zealand that originated from Sacramento River tributaries in the late 19th Century.

objectives and delisting criteria (NOAA, 2014), and this plan identified reintroduction of WRCS to above-dam areas as a high priority for the recovery of this evolutionarily significant unit (NOAA, 2014). Reintroducing NZCS would restore the spiritual and cultural relationship between the river, the Chinook salmon, and the local Native American community (WWT, 2016). It would also provide a source population that is wild and phenotypically and genetically diverse (Quinn et al., 2001). NZCS are also considered by the Native American co-managers to be better adapted to surviving and reproducing in headwater streams, versus the WRCS that have been excluded from their historical spawning grounds (WWT, 2016).

Significant challenges are associated with establishing naturally reproducing Chinook salmon populations in the McCloud River. Currently there are no upstream passage options available to adults, and downstream passage for juveniles is limited to (1) volitional passage through Shasta Reservoir, Shasta Dam, Keswick Reservoir, and Keswick Dam, or (2) experimental trapping in the lower reaches of the McCloud River followed by transport downstream of Keswick Dam. Multiple acoustic telemetry studies have been conducted to evaluate reservoir and dam passage survival for juvenile Chinook salmon released in the McCloud River. In one study, which occurred during a period of exceptionally high river flows and dam discharges, 70% of fish survived downstream passage through Shasta Reservoir and were detected at Shasta Dam (Plumb et al., 2019). However, in the other two studies, only 1% and 10% of released fish survived the reservoir and were detected at Shasta Dam (Plumb et al., 2019; Stockwell et al., 2026). Limited downstream passage through Shasta Reservoir is likely due to several factors including predation by piscivorous fish (e.g. bass *Micropterus* spp., brown trout *Salmo trutta*, and rainbow trout *O. mykiss*), which are abundant in Shasta Reservoir (Johnson et al., 2026), as well as environmental factors such as reservoir size and complexity, thermal stratification, warm water temperatures, and lack of hydraulic cues (Clancey et al., 2017; Stockwell et al., 2026). Based on these observations of low reservoir passage success, it

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will likely be necessary to develop passage alternatives focused on collecting downstream migrants prior to reservoir entry. However, experimental juvenile trapping efforts in the McCloud River and at the head of Shasta Reservoir have experienced low collection efficiency and may be hampered by predation and water conditions (Claire et al., 2025; Townsend, 2024).

Despite the challenges of providing passage, significant progress has been made toward Chinook salmon reintroduction in recent years. In 2022, a severe drought year, water temperatures below Keswick Dam were expected to exceed thermal tolerance for WRCS eggs and significantly reduce survival. To minimize mortality for this sensitive population, co-managers initiated experimental streamside incubation and releases of WRCS in the McCloud River. Some juveniles produced from these efforts were collected and transported downstream of Keswick Dam (Townsend, 2024). Streamside incubation and rearing in the McCloud River has continued each year since 2022, and at the time of this writing, these efforts have already resulted in the return of two WRCS age 2 jacks (early-returning males) to Keswick Dam in 2025 (K. Dunham, personal communication, 12 December 2025). Simultaneously with experimental releases, co-managers are working to identify long-term adult and juvenile passage solutions that circumvent Shasta Reservoir prior to scaling up WRCS reintroduction and potentially initiating NZCS reintroduction so that the reintroduced populations can be sustained via natural production (Anchor QEA & HDR Engineering, 2026). The reintroduction of Chinook salmon to the McCloud River is presently in its early stages, with only a single life stage (juveniles) present at the reintroduction site at the time of this writing. At more advanced stages of the reintroduction, return and successful spawning of adults may be achieved, resulting in full completion of the life cycle. Ultimately, reintroduction may result in increasing abundance of target populations, and the fulfillment of conservation objectives set by managers.

Risks of reintroductions can be associated with failure to achieve objectives and associated benefits, and/or unintended damage to population or ecosystem health (IUCN/SSC, 2013). Identifying these risks can aid reintroduction planning (Anderson et al., 2014; Karasov-Olson et al., 2021; USFWS, 2024) and does not necessarily imply that the reintroduction should be abandoned, as in many cases the risk of no action may exceed the risk of reintroducing a species under threat of extinction (NISC, 2024). Risk assessments have previously been conducted to support reintroduction of salmonids to areas from which they were extirpated. For example, Hardiman et al. (2017) conducted a formal risk assessment prior to the reintroduction of anadromous salmon upstream of Chief Joseph Dam and Grand Coulee Dam in the upper Columbia River in northeast Washington. This assessment provided information on potential donor sources, risk of pathogen spread, considerations for potential species interactions, and alternative reintroduction strategies. Since this assessment, substantial progress has been made toward implementing reintroduction of Chinook salmon and sockeye salmon (*O. nerka*), which has the potential to result in numerous socioeconomic and ecological benefits (Baldwin et al., 2022; U.S. Columbia Basin Tribes & Canadian First Nations, 2014; UCUT, 2022). A similar framework was developed to support bull trout (*Salvelinus confluentus*) introduction in northeastern Washington in collaboration with the Kalispel Indian Community (Hardiman et al., 2022). Other assessments have examined specific categories of ecological risks and benefits, for example, Meek et al. (2014) identified genetic considerations associated with steelhead reintroduction in the San Joaquin River (Meek et al., 2014). Overall, such evaluations can allow managers to make informed decisions, ultimately enhancing the success of reintroduction efforts (Anderson et al., 2014).

2 | ECOLOGICAL CONSIDERATIONS FOR REINTRODUCTION

In this work, we reviewed existing literature to identify key ecological benefits, risks, and uncertainties associated with Chinook salmon reintroduction to the McCloud River. We evaluated these considerations for reintroduced individuals and their progeny (hereafter "target populations"), the original populations from which reintroduced individuals will be sourced ("source populations"), and the ecosystem in which reintroduction will occur ("recipient ecosystem"). Considerations were identified for both WRCS and NZCS target and source populations, and for the recipient ecosystem, defined as the McCloud River below McCloud Dam (Figure 1). Rather than exhaustively review all potential ecological considerations, we focused this assessment on considerations that are high priorities for Pacific salmon reintroductions (Anderson et al., 2014), including population viability, disease, and species interactions, and that are likely to be relevant to managers of salmon in the McCloud River (Table 1). The purpose of this review is to summarize critical scientific information that could ultimately be used to inform management decisions. For example, information synthesized here could be used in conjunction with expert opinion to systematically rank the risks versus benefits of different reintroduction strategies.

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TABLE 1 Categories of ecological considerations considered for review in this work.

Population or ecosystem of interest	Population viability	Disease	Species interactions
New Zealand Chinook salmon (NZCS) source population	Reviewed in this work.	Not reviewed, disease transmission to NZCS source population is unlikely.	Not reviewed, removal of NZCS is not likely to affect species interactions in source ecosystem.
WRCS source population	Reviewed in this work.	Reviewed in this work.	Not reviewed, removal of WRCS is not likely to affect species interactions in source ecosystem.
NZCS target population	Reviewed the limited information available.	Reviewed in this work.	Reviewed in this work.
WRCS target population	Reviewed in this work.	Reviewed in this work.	Reviewed in this work.
Target Ecosystem (McCloud River)	Not reviewed in this work as there are no other Endangered Species Act-listed species in the McCloud River.	Reviewed in this work.	Reviewed in this work.

Note: Categories for potential inclusion were identified based on existing frameworks (Anderson et al., 2014; Karasov-Olson et al., 2021). Categories were selected for inclusion in the review based on the authors' assessment of relevance to management decisions, and the availability of published literature.

2.1 | Population viability

Population viability, defined as the ability of a population to sustain itself over time, depends on multiple variables including spatial structure, ecological and genetic diversity, and abundance (Lindley et al., 2007; McElhany et al., 2000). We assessed the population viability benefits, risks, and uncertainties associated with reintroducing WRCS and NZCS into the McCloud River for WRCS source and target populations, and NZCS source populations (Table 1).

2.1.1 | Benefits

Benefits to WRCS Source & Target Populations

Reintroduction to the McCloud River has the potential to afford many benefits to WRCS population viability (Anderson et al., 2014; NOAA, 2014). In their current distribution below Keswick Dam, WRCS exist as a single spawning population with limited spatial structure, low genetic diversity (Banks et al., 2000; Clemento et al., 2014; Hugentobler, 2023; Meek et al., 2020), and high vulnerability to environmental change and catastrophic events (Crozier et al., 2019; NOAA, 2014, 2024). WRCS are at high risk of extinction, and hatchery supplementation has increased in recent years to compensate for the effects of adverse environmental conditions that reduce natural production (NOAA, 2024). The increased spatial structure provided by reintroduction could buffer the impacts of catastrophic events, and access to cold, spring-fed spawning and rearing habitat could provide refuge from adverse environmental conditions such as the multi-year drought that resulted in less than 5% egg-to-fry survival for WRCS below Keswick Dam during 2014–2015 (Voss & Poytress, 2017).

Restoring Pacific salmon to their historical habitats has in some cases resulted in enhanced ecological diversity and local genetic adaptation. For example, following dam removal in the Elwha River (Washington, USA), the previously extirpated summer-run steelhead (*O. mykiss*) life history began to re-emerge (Pess et al., 2024). In the Wenatchee River basin, coho salmon (*O. kisutch*) populations have begun showing signs of local phenotypic and genomic adaptation since reintroduction efforts commenced in the late 1990s (Horn et al., 2020; Horn et al., 2025). Similarly, reintroduction in the McCloud River has the potential to enhance life history and genetic diversity for WRCS, thereby improving population viability.

2.1.2 | Risks

Risks to WRCS source population

Although establishing a viable target population of WRCS in the McCloud River has the potential to benefit the existing WRCS population below Keswick Dam in the long term, removal of individuals or gametes from

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the WRCS source population has the potential to negatively affect viability in the short term. Source population viability for WRCS could be affected by depleting population abundance or by accelerating loss of genetic diversity (Frankham et al., 2002). Experimental reintroduction in the McCloud River is being carried out using eyed eggs collected at the Livingston Stone National Fish Hatchery (Townsend, 2024) and, in this way, managers are able to carefully control the proportion of gametes removed from each parent in the source population. However, providing adult passage into the McCloud River would completely remove some individuals from the potential population of spawners below Keswick Dam. If survival is low or downstream passage is unavailable for juveniles produced in the McCloud River, reintroduction has the potential to become a population sink and further reduce the already low genetic diversity observed in the population downstream of Keswick Dam (Banks et al., 2000; Clemento et al., 2014; Hugentobler, 2023; Meek et al., 2020).

Risks to NZCS source populations

Compared to WRCS, NZCS populations exhibit higher genetic, spatial, and ecological diversity (Hugentobler, 2023; Quinn et al., 2011). However, the abundance of NZCS has declined in recent years, likely due to dam construction, excessive harvest, and habitat degradation, and they are now at critically low population levels (Closs, 2024). Removing individuals or gametes from the NZCS source population for reintroduction into the McCloud River could therefore risk reducing NZCS abundance and population viability. Impacts on a single population could be mitigated by sourcing from multiple NZCS populations; however, NZCS populations differ in life history traits (Kinnison et al., 1998; Kinnison et al., 2011; Quinn et al., 2001; Quinn et al., 2011), exhibit genetic differentiation, and show no evidence of admixture (Hugentobler, 2023), and it is unknown how fitness would be affected by mixing NZCS source populations.

2.1.3 | Uncertainties

Beyond potential risks and benefits, several additional factors may result in either positive or negative outcomes for source or target population viability but are associated with a high degree of uncertainty. In particular, there is significant uncertainty regarding the potential genetic interactions between the WRCS and NZCS target populations. Genetic analysis indicates NZCS are descended from Central Valley Chinook salmon. However, they do not appear to be descended from WRCS but rather from both fall-run and spring-run ancestral lineages (Hugentobler, 2023; O'Malley et al., 2007). Primary areas of uncertainty include (1) the extent to which WRCS and NZCS populations would mix if they were reintroduced together in the McCloud River, and (2) if admixture occurs, whether the effects on WRCS population viability would be positive, negative, or neither.

Historically, spring-run, fall-run, and (probably) late fall-run Chinook salmon coexisted with WRCS in the McCloud River, but natural introgression among Chinook salmon runs in the Sacramento River basin prior to the construction of Shasta and Keswick dams was likely very limited due to life history timing and physical and environmental factors (Banks et al., 2000; Clemento et al., 2014; Meek et al., 2016; Meek et al., 2020). It is therefore possible that WRCS and NZCS stocks would remain reproductively isolated due to differences in behavior or spatial distribution within the McCloud River. Spatiotemporal segregation during spawning has been observed in reintroduction programs that utilize multiple source populations, such as during the reintroduction of sockeye salmon above Cle Elum Dam (Kock, Evans, et al., 2021; Matala et al., 2019). In other systems, spawning distributions are known to be influenced by release site (Kock et al., 2018) and stock of origin (Zendt et al., 2023). However, these effects can vary significantly across systems, and because NZCS have locally adapted to their new geographic distribution in the southern hemisphere, it is unknown how their spawning behaviors will manifest if reintroduced in the McCloud River, and it is difficult to predict temporal or spatial overlap with WRCS spawning. If there is overlap in spawn timing and currently available habitat in the McCloud River is not sufficient to allow for spatial segregation, it is possible that a significant degree of hybridization could occur between the WRCS and NZCS target populations (Kinziger et al., 2008; Veale & Russello, 2016). If WRCS and NZCS target populations were to genetically mix, a range of potential outcomes could occur. A low degree of mixture could have minimal effects on the WRCS target population or could even enhance population viability by improving genetic diversity (Consuegra et al., 2005; Edmands, 2007; Whiteley et al., 2015). Alternatively, a moderate or high degree of admixture could have the potential to erode the local adaptations of WRCS and possibly lead to outbreeding depression (Gharrett et al., 1999), although the effects of outbreeding are not easily predicted (Houde et al., 2011; McClelland & Naish, 2007). Careful monitoring of spatiotemporal overlap and genetic mixing between WRCS and NZCS target populations will likely be necessary to assess and mitigate any potential negative effects of admixture between the two populations in the McCloud River. Mitigating the effects of admixture could involve managing the abundance, spatial distribution, or temporal distribution of NZCS spawners relative to WRCS spawners.

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2.2 | Disease

Reintroduction could result in altered disease dynamics for both the WRCS and NZCS target populations in their new environment. Additionally, the transport of WRCS or NZCS upstream of Shasta Dam has the potential to transmit disease to the target ecosystem, resulting in potential risks for the downstream source population of WRCS as well as other aquatic species in the target ecosystem (Table 1).

2.2.1 | Benefits

Benefits to WRCS target population

In their current spatial distribution in the mainstem Sacramento River, adult and juvenile Chinook salmon may experience elevated mortality due to parasites and pathogens (Foott, 2025; Mauduit et al., 2022), although the population-level effects of disease in the basin have not been well studied (Lehman et al., 2020). Stressful environmental conditions, such as elevated temperature, can lead to enhanced susceptibility to parasites and pathogens for Chinook salmon as well as shortening the life cycles of some pathogens, leading to higher rates of transmission and/or virulence (Aihua & Buchmann, 2001; Marcogliese, 2008; Tops et al., 2006). These effects can ultimately lead to increased pathogen-associated mortality under elevated temperatures (Marcogliese, 2008; Maule et al., 1989; Ray et al., 2012; Voss & True, 2015). Environmental conditions in the McCloud River are likely to be minimally stressful, with cool water temperatures relative to below-dam conditions, especially during drought years (U.S. Bureau of Reclamation, 2014), therefore WRCS may experience reduced impacts of disease in the McCloud River. For example, temperature can strongly influence the dynamics of the myxosporean parasites *Ceratonova shasta* and *Tetracapsuloides bryosalmonae*, with warm temperatures resulting in elevated transmission and mortality for their salmonid hosts (Bruneaux et al., 2017; Ray et al., 2012). Similarly, warm water temperatures accelerate the development of the parasitic ciliate *Ichthyophthirius multifiliis* (Aihua & Buchmann, 2001), leading to elevated mortality especially under crowded conditions (Traxler et al., 1998). Previous studies indicate that access to cold water refuges has the potential to mitigate the effects of disease on salmon mortality when river conditions are stressfully warm (Chiaramonte et al., 2016); therefore the negative effects of these pathogens and others may be reduced for WRCS reintroduced to the McCloud River. As environmental change reduces the ability of managers to consistently control temperatures downstream of Keswick Dam, access to high-elevation, spring-fed streams may provide greater relative benefits for pathogen mitigation (Hallnan et al., 2020).

2.2.2 | Risks

Risks to target ecosystem

Several disease-related risks to the target ecosystem may be associated with reintroduction. Unless adequate testing and biosecurity measures are taken, pathogens could potentially be introduced from New Zealand to the McCloud River and surrounding area during the reintroduction of NZCS. A detailed assessment of the risks of pathogen transport via NZCS introduction was conducted previously by Couch et al. (2026), and here we summarize key risks identified therein. The risk of transmission would likely be greatest for conspecifics (i.e., Chinook salmon) and closely related species (i.e., other salmonids) in the target ecosystem and surrounding region, but it is possible that other aquatic species could be affected by imported pathogens as well. For the purposes of this assessment, we assumed that eggs would be the life stage used for initial importation from New Zealand and that all imported eggs would be iodophor-treated to remove external parasites and pathogens according to a standard protocol (USFWS, 2004). However, even the importation of iodophor-treated eggs could potentially result in the introduction of vertically transmitted pathogens that internally infect eggs and cannot be fully removed via external disinfection. Pathogens that have been detected in the New Zealand region but not in California include infectious pancreatic necrosis virus (vertically transmitted) (Tisdall & Phipps, 1987), pilchard orthomyxovirus (vertical transmissibility unknown) (Godwin et al., 2020; Samsing et al., 2022), and New Zealand rickettsia-like organisms (NZ-RLOs) (vertical transmissibility unknown) (Brosnahan et al., 2017, 2019). A unique strain of the bacterial pathogen *Yersinia ruckeri* that differs from those present in California is also present in New Zealand (Barnes et al., 2016) (vertical transmissibility possible but not confirmed) (Glenn et al., 2015). Because publicly available reports of pathogen testing for wild and commercially farmed NZCS are limited, it is possible that additional exotic or harmful pathogens (or pathogen strains) could be imported to California via the transport of eggs from New Zealand. If no testing, quarantine, or other biosecurity measures were in place, the risk of unintentionally introducing an infectious pathogen would be relatively high. However, the risk of pathogen importation could be reduced through biosecurity measures such as disinfecting imported eggs, pathogen testing of all brood stock from which eggs are obtained, and

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quarantine and testing of juveniles following importation (Couch et al., 2026).

If adult Chinook salmon from either target population are outplanted in the McCloud River following upstream migration through the Sacramento River, there will be a risk of importing pathogens that are currently present in the Sacramento River basin but absent above Shasta Dam due to fish movement barriers. This could present a risk for Chinook salmon target populations, other native fishes, and sport fishes upstream of Shasta Dam (Figure 1), as well as for WRCS at the Livingston Stone National Fish Hatchery (which receives its source water from Shasta Reservoir) until adequate water treatment is installed at this facility. Parasites including *C. shasta* and *Parvicapsula minibicornis*, viruses including infectious hematopoietic necrosis virus (IHNV), and several opportunistic bacterial pathogens would have the potential to be transported into the McCloud River and other tributaries upstream of Shasta Dam (Mauduit et al., 2022; Voss & True, 2015).

Risks to WRCS target population & NZCS target population

C. shasta may be the pathogen most likely to affect the establishment of Chinook salmon target populations in the McCloud River, especially if it is introduced upstream of Shasta Dam. There are several unique *C. shasta* genotypes that differentially affect salmonid host species, with genotype I specifically affecting Chinook salmon (Bartholomew et al., 2022). *C. shasta* currently affects adult and juvenile WRCS in the mainstem Sacramento River and likely contributes to mortality across multiple life stages (Foott, 2025; Voss & True, 2015). *Manayunkia occidentalis*, an annelid alternate host that is required for *C. shasta* to complete its life cycle (Atkinson et al., 2020), is currently present above Shasta Dam as indicated by the presence of other genotypes of *C. shasta* (USFWS, 2001). However, the lack of information on *M. occidentalis* distribution and density makes it challenging to predict the transmission dynamics of *C. shasta* in the McCloud River. Moreover, the severity of *C. shasta* infection is highly temperature dependent (Ray et al., 2012). As such, the effects of the parasite on Chinook salmon target populations will depend heavily on the timing of freshwater life stages and environmental conditions encountered during critical life stages.

2.2.3 | Uncertainties

There is significant uncertainty regarding the susceptibility of NZCS to pathogens currently present in the Sacramento River Basin, and it is difficult to predict whether they will have enhanced, reduced, or equivalent susceptibility relative to WRCS. For example, *C. shasta* is endemic to northern California, and Chinook salmon from this region have coevolved with the parasite and developed a degree of genetic resistance (Ray et al., 2012). Some populations of salmonids that did not evolve with *C. shasta* have been shown to be highly susceptible and experience mortality at lower infectious doses than populations that have been continuously exposed to the parasite (Bartholomew, 1998). It is unknown whether NZCS have retained resistance to *C. shasta* and other endemic pathogens in the Sacramento River basin. The timing of adult and juvenile Chinook salmon migration through the Sacramento River could have a major influence on pathogen exposure, as well as on host susceptibility (i.e., due to seasonal temperature change). For example, if migration timing overlaps with high density of *C. shasta*, *T. bryosalmonae*, or *I. multifiliis* during periods of elevated water temperature in the mainstem Sacramento River, these pathogens could have a significant effect on survival. However, if migration through the mainstem is completed during periods with lower pathogen density or more favorable environmental conditions, effects of pathogens could be greatly reduced.

It is important to note that the method of passage (e.g., volitional passage through challenging physical and/or environmental conditions or trap-and-haul involving crowding or long transport distances) could increase stress and associated disease impacts in the Chinook salmon target populations (Colvin et al., 2018; Lusardi & Moyle, 2017). Monitoring pathogen prevalence and pathogen-associated mortality in the target populations relative to the source populations could help clarify the effects of passage-associated stress. However, pathogen surveillance and monitoring efforts in the Sacramento River basin are considered insufficient to fully understand population-level effects of disease in the system (Lehman et al., 2020). Improved pathogen monitoring has been recommended as part of a comprehensive monitoring framework for WRCS, and such monitoring could clarify some of the risks and benefits associated with Chinook salmon reintroduction in the McCloud River.

2.3 | Species interactions

Target populations of WRCS and NZCS have the potential to interact with other species in the target ecosystem, and with each other (Table 1). Removal of individuals from the source populations is unlikely to have a significant effect on species interactions, unless removal affects the persistence of these populations (see Population Viability section).

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2.3.1 | Benefits

Benefits to WRCS target population

Juvenile WRCS reintroduced into the McCloud River may be able to avoid some of the predation experienced by juveniles produced in the mainstem Sacramento River below Keswick Dam, depending on their size and timing of outmigration. Currently, juvenile WRCS are heavily predated on by warmwater fishes such as striped bass (*Morone saxatilis*), Sacramento pikeminnow (*Ptychocheilus grandis*), large-mouth bass (*M. salmoides*), and catfish (e.g. *Ictalurus* spp.), in the mainstem Sacramento River, especially at water diversion infrastructures (Lindley & Mohr, 2003; NOAA, 2014, 2024; Stompe et al., 2020; Tucker, 1998). Size-dependent mortality due to predation is often observed in systems where juvenile salmonids overlap spatially and temporally with predators (Fritts & Pearsons, 2006; Kock et al., 2019; Mensinger et al., 2025); therefore, if juvenile WRCS spend time rearing and growing in the McCloud River and undergo significant growth prior to entering the mainstem Sacramento River, they may be able to avoid some risk of predation (Sogard, 1997; Zabel & Achord, 2004). Relative predation risk will depend on the juvenile life-history strategies adopted (e.g., size at and timing of downstream migration, rearing habitats), and the environmental conditions (e.g. temperature, turbidity) encountered during rearing and migration. Chinook salmon are known to exhibit a high degree of plasticity in their life history as a result of complex interactions between genetic and environmental constraints (Bourret et al., 2016). As such, it is possible that reintroduced WRCS may evolve a dominant later outmigration strategy if it confers greater survival, though this will also be constrained by the timing and methods of juvenile collection/passage.

Diverse and abundant communities of benthic macroinvertebrates are present in the McCloud River, which have the potential to support juvenile Chinook salmon growth (Michel et al., 2026). Although the turbid nature of the river could limit drift feeding (Tippets & Moyle, 1978), it could also provide protection from predators (Gregory & Levings, 1998; Zanghi & Ioannou, 2025). The influence of turbidity on growth and predation risk will vary with its timing, magnitude, and duration, which can vary substantially across years in the target ecosystem (CDEC, 2025). The McCloud River is a spring-fed system, which typically supports more abundant macroinvertebrate communities, and thus higher growth rates for juvenile salmonids, compared to runoff-fed systems (Lusardi et al., 2021). However, research on juvenile Chinook salmon growth in this tributary is very limited, but preliminary data (Michel et al., 2026) indicate that monthly size distributions of juvenile WRCS rearing in the target ecosystem are qualitatively similar to juvenile WRCS trapped at Red Bluff Diversion Dam on the mainstem Sacramento River (Voss & Poytress, 2023). This suggests that juvenile WRCS in the McCloud River are not resource-limited relative to juvenile WRCS produced below Keswick Dam. Adult Chinook salmon that eventually return to the McCloud River also have the potential to enhance the food base for juveniles via the addition of marine derived nutrients into the system (Cederholm et al., 1999; Holtgrieve & Schindler, 2011; Merz & Moyle, 2006; Richardson et al., 2017).

2.3.2 | Risks

Risks to WRCS & NZCS target populations

Several species of introduced sport fishes are present throughout the McCloud River, including brown trout and nonnative strains of rainbow trout. Nonnative bass are also present in the lower reaches of the river. Preliminary evidence (Michel et al., 2026) suggests that some of these introduced fishes may prey on juvenile WRCS. Stable isotope analysis suggested that rainbow trout from the lower McCloud River with at least 300 mm fork length are piscivorous (Johnson et al., 2026), and brown trout are known to exhibit high rates of piscivory (Jonsson et al., 1999) and to prey on juvenile Chinook salmon in the nearby Trinity River (Alvarez & Ward, 2019). However, additional research would be needed to understand the magnitude of this potential predation and its significance for Chinook salmon population establishment in the McCloud River. It is also possible that trout and Chinook salmon may compete for food and habitat in the McCloud River as trout are highly abundant (Michel et al., 2026) and may already experience density-dependent effects on growth (Tippets & Moyle, 1978). Studies in other high-elevation streams suggest that naturally produced juvenile rainbow trout and Chinook salmon do not exhibit significant effects of interspecific competition (McMichael & Pearsons, 1998), but brown trout and Chinook salmon have been shown to compete for habitat and resources in simulated streams (Glova & Field-Dodgson, 1995). However, interspecific competition between Chinook salmon and trout has not been studied in the McCloud River, and the population-level effects of competition are difficult to predict.

2.3.3 | Uncertainties

It is possible, though unlikely, that reintroduced Chinook salmon may exhibit piscivorous behavior and prey on other native and nonnative fishes in the McCloud River. The degree of piscivory among juvenile Chinook salmon likely depends on how long they remain in the tributary

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and how large they grow during this period. Stream-reared salmonids typically do not become piscivorous until they reach approximately 270 mm fork length (Keeley & Grant, 2001). If juvenile Chinook salmon reintroduced into the McCloud River express an age-1 or age-2 outmigrant phenotype, or residualize in the tributary, it is possible that they could predate on resident fishes, but this remains an unknown until additional data are collected.

Potential interactions between WRCS and NZCS remain uncertain but could play a role in shaping the reintroduction success of each population. Uncertainty in the spawn timing of NZCS upon reintroduction and the diversity of life-history traits within the populations limit our ability to predict how they may interact. Differences in spawn timing could lead to reproductive isolation and maintenance of distinct population traits (Matala et al., 2019) or could result in productivity losses due to redd superimposition if preferred spawning habitat is the same (Baker & Hand, 2023). If distinct life-history traits are maintained, differences in emergence timing could confer a competitive advantage to earlier emergers but would be modified by temporal differences in habitat suitability and predation risk (Quinn, 2007).

3 | CONCLUSIONS

In this document, we identified key ecological considerations to inform the planning of reintroduction strategies for Chinook salmon in the McCloud River, with a focus on population viability, disease, and species interactions. Reintroduction provides opportunities to enhance WRCS population viability, for example, by providing increased spatial structure and restoring access to high-quality habitat that may buffer the effects of drought, predation, and disease. Reintroduction may also restore ecological functions in the target ecosystem, for example by returning marine-derived nutrients to the McCloud River. Several important ecological risks and areas of uncertainty were identified in this assessment, which may be addressed through additional research, monitoring, and mitigation efforts. Decisions regarding these additional efforts depend on the priorities and risk tolerances of the co-managers, as well as the feasibility and costs of such actions. For example, to mitigate the risks of importing pathogens from New Zealand, managers may choose to implement biosecurity and pathogen testing protocols (Couch et al., 2026). Genetic monitoring of NZCS and WRCS during the reintroduction process could elucidate the extent of introgression between these two target populations, clarify the relative risks and benefits of mixing, and support potential genetic management plans. Similarly, the risks and uncertainties associated with predation and competition among NZCS, WRCS, and resident fish species could be in part addressed by studying the distributions and behavior of these species in the McCloud River and developing predictive models to explore the potential effects of interactions (Peterson & Bode, 2021).

A limitation of this work is that we used only published literature to describe risks, benefits, and uncertainties and did not formally involve stakeholders or conduct expert elicitation. Expert elicitation can be a particularly effective approach for systematically identifying and ranking the risks and benefits of a proposed reintroduction (Hardiman et al., 2017; Hardiman et al., 2022; Hemming et al., 2018; Karasov-Olson et al., 2021). Such efforts can leverage professional judgment and experience to address knowledge gaps where published literature is insufficient, and they can provide a forum for enhancing stakeholder engagement (Karasov-Olson et al., 2021). For example, Hardiman et al. (2017) conducted a series of workshops to solicit information from regional experts regarding the reintroduction of anadromous salmonids above Grand Coulee Dam and Chief Joseph Dam. This approach enabled the systematic evaluation and ranking of risks associated with pathogens, genetic effects, and species interactions, as well as formally ranking potential donor sources. The synthesis of existing literature provided in this review could serve as a foundation for additional, more detailed assessments that may involve formally engaging subject matter experts and stakeholders, depending on the needs and priorities of managers and decision makers.

While this assessment focuses on ecological considerations, the success of Chinook salmon reintroduction efforts will also depend on many other variables including dam passage and ocean survival (Anderson et al., 2014). Alternatives for volitional and semi-volitional upstream and downstream fish passage at Keswick Dam and Shasta Dam are currently being explored (Anchor QEA, 2026a), but these solutions are costly and may take many years to implement; achieving passage survival sufficient to sustain populations of WRCS or NZCS in the McCloud River may be challenging (Anchor QEA, 2026b). Additionally, while a comprehensive assessment of the cultural and spiritual aspects of Chinook salmon reintroduction is beyond the scope of this review, they remain central to reintroduction planning efforts (WWT, 2016). Similarly, an assessment of the laws and policies that may constrain management of ESA-listed WRCS or importation of NZCS is beyond the scope of this review but is likely to significantly influence reintroduction decisions. However, by considering the ecological factors identified in this assessment, alongside other

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factors such as passage, cultural considerations, and policy constraints, managers may be able to avoid common pitfalls and maximize the benefits of Chinook salmon reintroduction in the McCloud River.

AUTHOR CONTRIBUTIONS

All authors were involved in the writing of this review. Tobias J. Kock, Jill M. Hardiman, and Claire E. Couch contributed to conceptualization. Claire E. Couch prepared the initial draft and generated the graphical abstract. BayLee R. Laufer generated the map for Figure 1.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

No data were generated in this study.

ETHICS STATEMENT

Not applicable.

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