Review of potential benefits and risks of hatchery supplementation for salmonid populations of conservation concern with focus on Interior Fraser River Steelhead (*Oncorhynchus mykiss*)

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i

Executive Summary

Report objectives.

Since 2000, the abundance of Interior Fraser River steelhead (*Oncorhynchus mykiss*) spawners has declined from thousands to dozens. As a result, some members of the public have advocated for conservation intervention via hatchery supplementation. This report reviews literature on hatchery supplementation of anadromous salmonids, focusing on B.C. Interior Fraser River steelhead and the hypothesized risks faced by natural origin fish following the propagation and presence of hatchery origin fish. We examined available evidence concerning each hypothesis, and identified ways that hatchery managers can reduce unintended negative consequences of supplementation. To inform how a hatchery might affect the natural origin steelhead population, we also developed population dynamics models to predict long-term outcomes under various hatchery supplementation scenarios, accounting for genetic and ecological interactions between natural and hatchery origin fish.

Summary of literature review.

- **Ecological effects of hatchery supplementation.** We reviewed literature associated with the ecological risks of hatchery supplementation, focusing on four hypotheses: E1) the release of hatchery-origin (HOR) juveniles may negatively affect natural origin (NOR) conspecifics in rearing streams via competition; E2) HOR juveniles may not go to sea, increasing the abundance of the resident population of *O. mykiss* and the number of competitors faced by NOR juveniles; E3) the offspring of HOR adults reared in the wild (i.e., first-generation NOR fish) are not effective replacements of NOR juveniles (in terms of, e.g., habitat use); and E4) the increased combined abundance of HOR and NOR fish may attract predators and increase NOR mortality. Evidence suggests that HOR fish can negatively impact NOR juveniles through competition, but hatchery practices can mitigate this risk (e.g., integrating locally sourced NOR broodstock and producing age-2 HOR smolts of similar size to age-2 NOR juveniles). Managers can reduce NOR-HOR competition by volitionally releasing HOR from acclimation ponds downstream of important rearing habitats. Considering hypothesis E3, the literature suggests that there is a low risk of HOR fish out-competing and replacing NOR conspecifics. To mitigate the risk, managers can minimize competition by restricting HOR adults' access to natural spawning areas. Considering E4, the hypothesized risk of increased predation, the low abundance of HOR steelhead relative to other salmonids means that there is not likely a strong predator response to supplementation. Additional research on residualized rainbow trout is needed for a comprehensive assessment of their impact on predation.

- **Fishery mortality risks of hatchery supplementation.** We assessed a single fishery-related hypothesis: F1) the risk of increased angler attraction to the combined HOR and NOR steelhead population. There is a risk that successful hatchery production may increase fishing effort on the NOR-HOR complex, and anglers may favor the selection of younger/slower growing NOR fish. If harvest of HOR adults is controlled with a selective fishery that removes only visibly marked fish (e.g., hatchery fish with an adipose fin clip), there is also risk that a catch-and-release fishery could incur incidental mortality on NOR steelhead. While studies on incidental mortality rates for caught and released NOR steelhead generally indicate low mortality, these depend on

capture gear, water temperature, and handling methods. However, our review suggests that even with the establishment of new recreational and Indigenous fisheries for HOR steelhead, the associated fishing effort is expected to be limited, minimizing the likelihood of incidental mortality rates reaching levels that would be detrimental to population recovery potential.

- **Genetic and epigenetic risks of hatchery supplementation.** Considering genetic and epigenetic risks of hatchery supplementation, we addressed three hypotheses: G1) inbreeding depression causes loss of genetic variation, reductions in effective population size, and lower recruits per spawner; G2) domestication selection within hatcheries can rapidly alter fitness-related traits in HOR fish; and G3) epigenetic changes caused by differences in the hatchery and natural environments lower the fitness of HOR fish and may be transmitted to the NOR population. Steelhead spawning aggregations mean that naturally, some inbreeding is inevitable in the population. Hatchery programs amplify the genetic influence of a few NOR fish, and can therefore lower genetic diversity and effective population size. On the other hand, hatcheries can increase spawner abundance and therefore stabilize or increase effective population size, depending on the details of the hatchery program. Considering G2, there are many studies showing reduced early life survival of HOR fish compared to NOR conspecifics due to non-random breeding and domestication selection within the hatchery leading to genetic changes. Even over short timespans, there is evidence that hatchery environments induce epigenetic changes associated with growth, migration timing, and other factors. Whether epigenetic changes are consistently stable through life and transmitted to progeny remains uncertain. To mitigate the genetic and epigenetic risks associated with hatchery production, managers can conduct ongoing research on fitness-related trait differences between HOR and NOR populations and adapt hatchery practices to reduce domestication selection and epigenetic change, typically by mimicking natural processes during rearing. Minimizing interbreeding between NOR and HOR adults is also recommended (e.g., by prioritizing NOR fish for broodstock and selectively removing HOR individuals on natural spawning grounds).

Summary of population modelling. We conducted population modelling to assess the conditions under which hatchery supplementation might improve or worsen the abundance of the Thompson River population of NOR Interior Fraser steelhead. Using parameter values based on previous studies for this population, we first modelled hatchery supplementation using a relatively simple Beverton-Holt (BH) production model. We then built on this simple model using the commonly applied All-H Analyzer (AHA), which models intergenerational fitness consequences arising from NOR-HOR interbreeding. Using plausible values for fitness-related functions, and choosing parameters that recreated the past two decades of Thompson River steelhead escapement data, the AHA model was able to replicate most of the results in the Beverton-Holt production model and expanded on the simpler model's results by demonstrating plausible erosion of fitness over time under different hatchery conditions.

Both models found that the abundance of NOR spawners could improve under a small, all-NOR-broodstock hatchery program, but the increase in abundance from hatchery supplementation was relatively small compared to the increase expected if ecological conditions (e.g., those affecting marine survival) improved. If the goal of the hatchery program is to reduce the probability of extirpation, a small hatchery program can support this with minimal erosion of genetic diversity and NOR productivity; however, the program may need to include limitations on HOR-NOR interbreeding in the wild to meet genetic integration goals (e.g., proportionate natural influence levels). Importantly, while our models

suggest that NOR abundance can increase under modest hatchery programs, this success is conditional on HOR's ability to survive and reproduce. Both models identified a crucial link between hatchery performance and marine survival. When marine survival is low—typical in recent years—the risks of negative hatchery impacts increase, in part because productivity of the NOR population is limited by ocean conditions. Both models predicted that NOR population abundance declines rapidly when marine survival falls below 6%, and the population becomes non-viable below 1.7% (regardless of the hatchery program). We found that hatchery programs also fail to improve NOR spawner abundance if the relative reproductive success of HOR fish is very low to negligible, such that the act of removing NOR for broodstock only increases the risk of extirpation. Because supplementation hatchery programs are typically implemented when the population is barely viable and marine survival is low, broodstock removals have a significant negative effect on NOR spawners, even driving recruitment below replacement. However, both models were limited by not including interactions with the resident population of *O. mykiss*.

Conclusion. Hatcheries have potential to further conservation objectives. However, the literature contains numerous case studies and reports demonstrating a range of effects of hatcheries on wild spawning populations. Program design and ecological conditions, especially marine conditions, can strongly influence the success of hatchery supplementation programs for anadromous species like steelhead. This suggests that different populations may respond differently to hatchery intervention, and therefore different hatchery programs may have population-specific risks, costs and benefits. This report explores several different hypothesized hatchery impacts (both positive and negative) and the literature supporting them, including population models to explore the conditions under which a hatchery program for Interior Fraser River steelhead populations might improve conservation outcomes. Any potential hatchery program needs to consider the costs, risks and potential benefits with respect to the mandated objectives of the management agency implementing the hatchery.

Table of Contents

Introduction

Overview of the stock status of Interior Fraser River Steelhead

Over the last four decades, spawner abundance has declined precipitously in many steelhead (*Oncorhynchus mykiss*) populations in southern B.C. and the US Pacific Northwest (Kendall et al. 2017). Spawner counts for two B.C. Interior Fraser River steelhead (IFRS) populations, Thompson and Chilcotin, have declined by 80% over the last three generations to 216 and 78, respectively (COSEWIC 2020) and recent annual estimates indicate further decline (Figure 1). Both populations have been designated as endangered by COSEWIC (2020) and meet the Extreme Conservation Concern (ECC) criteria under the proposed conservation management system for B.C. steelhead (Johnston et al. 2002a).
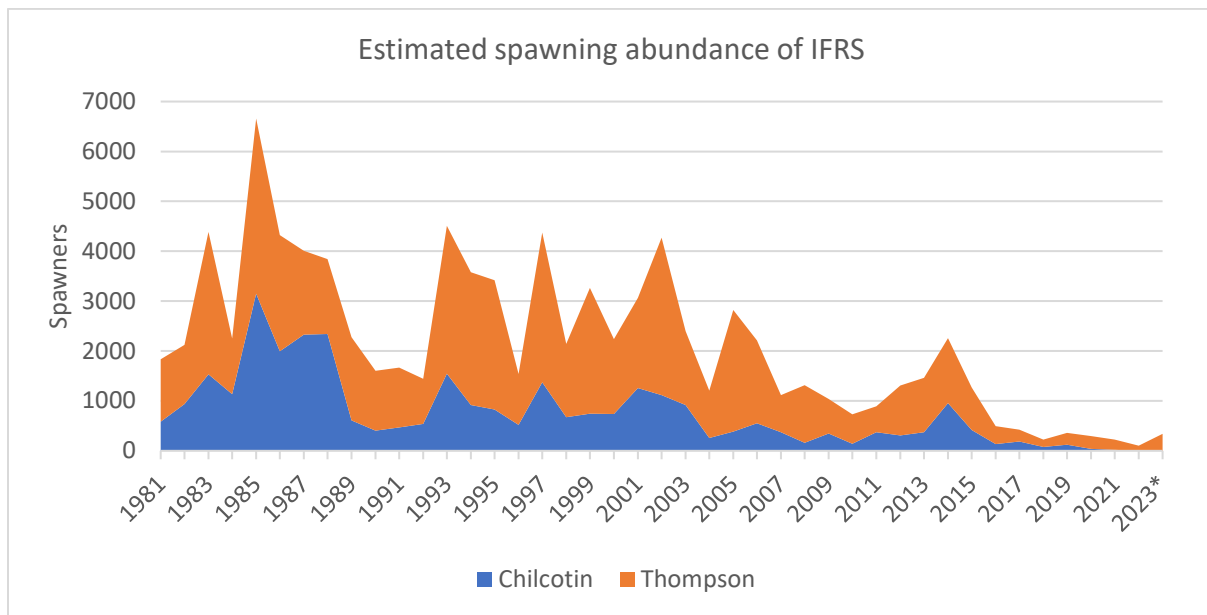
*Figure 1. Estimated spawning abundance of Interior Fraser River Steelhead (IFRS) populations of the Thompson and Chilcotin. Data obtained from B.C. Ministry of Environment (2023). *2023 estimates are based upon a test fishery so are preliminary.*

The Johnston et al.'s system uses a Beverton-Holt (BH) Spawner-Recruit model, and considers the stock's status relative to two reference point indicators. The first reference point is the Conservation Concern Threshold (CCT); spawner abundances below this point indicate the stock is overfished. CCT is defined in terms of maximum sustainable yield, approximated as 0.30-0.35*β—where β is the maximum

observed abundance under favorable environmental conditions (Johnston et al. 2002a).[1] The second reference is the limit reference point (LRP), defined as the spawner abundance where recovery to the CCT is possible within one generation; LRP is approximated as 0.10-0.15*β. If spawner abundance is below the LRP, the stock is considered to be in an Extreme Conservation Concern (ECC) regime and extraordinary management actions are required to eliminate controllable mortality and increase productivity. IFRS populations are within this ECC regime, and therefore management intervention is required to improve the stock status.

Summary of COSEWIC threat assessment

Several threats are believed to concurrently stress IFRS populations. A generalized list of threats was qualitatively evaluated in 2020 by an expert opinion consensus (see appendices A and B in COSEWIC, 2020). The two IFRS populations have similar assessed threat severity, with similar comments on the nature of each major threat (see *Table 1* in Appendix 1: Threats to Thompson and Chilcotin steelhead as identified by COSEWIC). Four threats—fishing and harvesting effects, changes to both marine and freshwater ecosystems, increased predator abundance, and effluent from agriculture—are thought to have medium to high impact on both populations. Harvest effects and ecosystem effects are both considered high impact, predator abundance medium-high impact, and effluent pollution medium impact.

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[1] These approximations from the Beverton-Holt model are insensitive to a wide range of different values of stock productivity ($\alpha > 2$). When α is below 2, the maximum sustainable yield approximations become biased upwards, and are therefore increasingly conservative under worsening survival conditions.

Table 1. High- to medium-impact threats to Thompson and Chilcotin steelhead populations, as identified and ranked by COSEWIC (2020, Appendices A and B). The hierarchical classification of threats is adopted from IUCN-CMP (Salafsky et al. 2008). A complete list of threats is given in Table A 1 (Appendix 1: Threats to Thompson and Chilcotin steelhead as identified by COSEWIC). Where threat level and comments are identical for Chilcotin and Thompson populations, they are placed in a single cell.

Threat	Description	Threat Level		Comment Summary
		Thompson	Chilcotin	
5.4	Fishing & harvesting aquatic resources	High		Fishing affects adults returning to spawning grounds from the sea and migration to the sea after spawning. Migration from the sea coincides with fisheries for one or more other Salmon species. First Nations FSC fisheries also occur on post-spawning Steelhead returning to the sea. All fish returning from sea to rivers to spawn must pass through the fishery as do fish returning to the sea post-spawning. Estimated annual mortality ranges between 15 and 25% based on simulation estimates of run timing and migration speed.
7.3	Other ecosystem modifications	High		Includes reduced ocean productivity and competition from other salmonids resulting from ocean ranching in the high seas, and offshore predation on smolts and adults. In freshwater includes riprap of stream banks, sedimentation and thermal problems due to loss of riparian vegetation and water extraction.
8.2	Problematic native species/diseases	High-Medium		The reduced population abundance of Steelhead makes predation, particularly by pinnipeds, a threat. Adults migrating to overwintering areas of Thompson River from sea, smolts migrating to sea, and smolt off-shore migration are all vulnerable. Mortality from threat is uncertain but up to 50% of smolts are lost during transit from freshwater out of Georgia Strait. Diet data indicate that Steelhead are consumed by seals in the Fraser estuary and in the Strait of Georgia and Puget Sound. In freshwater, otters, whitefish, and Bull Trout may be a predation threat. Interbreeding of Steelhead and Rainbow Trout is also an increasing threat at current abundance. Impact of sea lice on smolts and adults during migration past fish farms in northern Johnstone Strait are a current and future threat with uncertain impact.
9.3	Agricultural & forestry effluents	Medium	Low	Pollutants include runoff from agriculture and following logging and fire damage, sedimentation, pesticides both in the Thompson and lower Fraser watersheds.

Harvest, considered a high-level threat (Threat 5.4, *Table 1*), is the result of a complex mixture of bycatch in commercial net fisheries and directed harvest in freshwater recreational and First Nations Food, Social and Ceremonial (FSC) fisheries. Management agencies have pursued policies designed to reduce harvest in all these fisheries. Selective fishing methods, time and area fishing closures, and mandatory release regulations have all played a role in lowering harvest mortality from around 70% to 10-20% over the last 40 years (Levy and Parkinson 2014). Despite these decreases in fishing mortality, the populations have continued to decline and therefore other threats likely contribute to the decline of IFRS populations.

High severity threats associated with the marine environment—e.g., low productivity and high predator abundance (*Table 1*, Threats 7.3 and 8.2)—are driven by evidence of widespread declines in steelhead abundance (Kendall et al. 2017). Marine survival is spatially correlated, which suggests that local marine conditions contribute to high mortality during the first few months in the ocean (Kendall et al. 2017). This is supported by data on post-smolt growth that associates poor growth during the first summer in the ocean with poor smolt-to-adult survival (Friedland et al. 2014; Wilson et al. 2021). Research in inland seas including Puget Sound and the Georgia Basin indicate that predatory pinnipeds like harbor seals (*Phoca vitulina*) can be a significant contributor to migrating smolt mortality (Sobocinski et al. 2020; Courter et al. 2022), including steelhead (Berejikian et al. 2016) and other salmon (Thomas 2015). For IFRS, the effect of poor marine survival may be compounded by low survival during downstream migration; recent estimates indicate that 70% of Thompson River steelhead smolts die before reaching the mouth of the Fraser (Welch et al. 2008).

The threat from freshwater habitat degradation—e.g., sedimentation, loss of riparian vegetation, and pollution from agriculture—has been ranked as medium to high (*Table 1*, Threats 7.3, 9.3). Both the Provincial and Federal governments have passed legislation to protect fish from habitat degradation, including the 1985 Federal Fisheries Act,[2] the 1997 B.C. Fish Protection Act,[3] and the B.C. Forest and Range Practices Act.[4] However, the success of these regulations has been limited by the natural instability of B.C. terrain and associated landslides, severe weather events such as the 2021 flooding,[5] and continuing natural resource development. The net result is that the severity level of these threats continues to be medium-high with limited opportunities for mitigation. Considering these threats, and difficulties mitigating their effects, the 2019 Steelhead Action Plan drafted by Fisheries and Oceans Canada and the B.C. Provincial Government called for the development of a plan to selectively use hatchery production to help sustain wild populations.

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[2] https://laws-lois.justice.gc.ca/eng/acts/f-14/

[3] https://www.bclaws.gov.bc.ca/civix/document/id/complete/statreg/97021_01a

[4] https://www.bclaws.gov.bc.ca/civix/document/id/complete/statreg/02069_01

[5] https://www.tnrd.ca/services/emergency-services/2021-floods/

Objectives of this report

This report reviews the literature evaluating the use of hatcheries to restore the historical abundance of anadromous salmonids, with a focus on B.C. IFRS. Our approach was to develop a list of hypotheses that represent processes that are thought to negatively affect the success of hatchery restoration initiatives, considering literature on both steelhead and other salmonids. Each hypothesis was then evaluated in terms of the evidence supporting the hypothesis and the importance of each process in driving the demography of IFRS populations. We provide a context for these hypotheses by summarizing some of the historical information on IFRS and sympatric rainbow trout populations. We also focus on the ecological and genetic risks of supplemental hatchery production programs that are most relevant to IFRS.

Existing hatchery policy for the IFRS population

Current hatchery production of steelhead in B.C. seeks to provide improved angling opportunities rather than improving stock status per se. Steelhead streams are designated as one of "wild" or "hatchery-augmented", according to definitions in the Steelhead Stream Classification Policy fully enacted in 2007 (*Steelhead Stream Classification Policy* 2005). Because of the dangers that hatchery augmentation can pose to at-risk wild populations (e.g., Pollard 2013), this stream classification policy did not consider hatcheries as an appropriate means of improving stock status. Rather, this policy establishes regulations to keep wild and hatchery-augmented streams genetically segregated. To limit interbreeding in hatchery-augmented streams, hatchery fish can be visibly marked by clipping adipose fins, allowing for selective removal of hatchery adults before they reach natural spawning areas, thus reducing the degree of interbreeding between wild and natural conspecifics (FLNRO, 2016). However, even with these controls in place, it is presumed that there may be still significant natural spawning of those hatchery fish not captured by B.C.'s retention fishery (Pollard 2013).

While the Stream Classification policy dictates minimal hatchery intervention in wild steelhead streams, it does include protocols to create "conservation fish culture" programs. Conservation culture programs may be prescribed by a Recovery Plan to conserve a stock's within-population genetic diversity, with the stipulation that steelhead production should last a maximum of one generation. More recently, despite continued skepticism about the effectiveness of conservation hatchery programs, the 2019 Steelhead Action Plan drafted by Fisheries and Oceans Canada and the B.C. Provincial Government called for the development of a plan to selectively use hatchery production to help sustain wild populations. Skepticism about such a program is high, however, with ongoing assessments of the benefits and risks of hatcheries indicating low likelihood of success that might "put the wild [IFRS] population at higher risk for extirpation" (Rhodes and Jenkins 2021).

Policy decisions in other regions can help inform how managers can make prudent decisions while assessing hatchery programs. While some hatcheries are primarily managed to meet harvest goals, we assume that an IFRS hatchery program would focus on minimizing the risk of extirpation and increasing abundances. The goals of a hatchery program range along a spectrum depending on the severity of extinction risk, and the program's goals are expected to progress with time and population recovery. These goals include 1) preventing extirpation, 2) increasing the spatial distribution of the population via

reintroduction, and 3) increasing the abundance of natural runs (HSRG 2014; Anderson et al. 2020). Meeting any of these goals requires that the unsupplemented population is below carrying capacity.

Evidence supporting hatcheries' ability to sustain threatened populations is mixed. Although there are relatively few studies assessing the outcomes of hatchery programs over multiple generations, there is some evidence that hatcheries improve—or at least do not negatively impact—natural origin abundance. For example, a three-generation study in Johnson Creek, Idaho found that releases from a small spring Chinook hatchery program (i.e., spawning less than 40 broodstock per year, all of natural origin) were able to produce 2.5-times the grand-offspring than natural origin salmon (Janowitz-Koch et al. 2019).

Whether short-term improvements to reproduction lead to long-term increases in natural origin abundance or spatial range is less straight-forward. An analysis of 22 hatchery-supplemented populations on the Snake River basin found minimal but positive effects of supplementation on natural-origin fish density (0-8% higher in supplemented years than unsupplemented), and that variations in fish density was influenced more by interannual effects than supplementation (these interannual effects include ecological and inbreeding effects; Scheuerell et al. 2015). While hatchery programs cannot address factors that limit survival outside of early life (i.e., the life stages that occur within the hatchery; Venditti et al. 2018), hatchery programs that prevent extirpation may offer managers more time to address these factors. Considering reintroduction, there is also evidence from the Yakima River that even after 10-30 generations of hatchery legacy, hatchery coho salmon have the ability to re-establish themselves in basins from which they were historically extirpated (Bosch et al. 2007). Importantly, the benefits of some conservation hatchery programs—e.g., increasing abundance and spatial diversity of the population—may depend on continued supplementation (Venditti et al. 2018).

There are many suggested reasons as to why hatchery programs fail to improve the abundance of supplemented populations; these reasons comprise the list of hypotheses addressed in the literature review section of this report.

Life history diversity of IFRS

The species *O. mykiss* has two life histories, non-anadromous or resident (rainbow trout[6]) and anadromous (steelhead). The ecological and genetic interactions between these life-history types must be considered when establishing a hatchery program. Management measures associated with B.C. steelhead populations sometimes assume that steelhead and rainbow trout are two distinct, non-interbreeding populations (COSEWIC, 2020), but this assumption may be not entirely true (Courter et al. 2013; Kendall et al. 2015). For example, Phillis et al. (2016) found that within time scales relevant to stock management, a population can evolve migratory and/or resident life histories. Therefore, many basic population dynamics considerations—e.g., a rescue effect for the anadromous steelhead component originating from the rainbow trout population component, and the implications of competition in the freshwater life stages where both life history types coexist (Terui et al. 2023)—should

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[6] Non-anadromous and resident are typically synonymous in the *O. mykiss* life-history literature. In this review, "rainbow trout" is used only in reference to the non-anadromous life history type.

underpin discussions concerning the use of hatcheries for supplementing low abundance wild steelhead populations.

In particular, the metapopulation dynamics between rainbow trout and steelhead *O. mykiss* bear implications for hypothesized effects of hatchery stocking. Parentage studies have found that rainbow trout produce anadromous offspring that successfully reproduce (Courter et al. 2013; Kendall et al. 2015). A recent study comparing otolith microchemistry of rainbow trout and steelhead in the Thompson River watershed showed that rainbow trout mothers produce both female and male steelhead (R. Bison, pers. comm.). In contrast, steelhead mothers produce relatively few rainbow trout females, and produce a higher percentage of steelhead smolts than rainbow trout. Both rainbow trout and steelhead produce juveniles with stream-rearing life histories, resulting in overlapping habitat use by both rainbow trout and steelhead juveniles. Because steelhead can be produced by rainbow trout females, rainbow trout can contribute to the recovery of IFRS anadromous life history types. This complex metapopulation structure also creates the possibility that hatchery origin (HOR) fish could increase the abundance of rainbow trout, reducing the growth and survival rates of wild steelhead fry and parr due to competition between natural origin (NOR) fry and parr and HOR rainbow trout. There is also a risk of predation on NOR steelhead fry and parr by HOR rainbow trout (see section "Hypothesis E2: Some HOR smolts stocked in rearing streams do not migrate to the ocean, residualize, and then compete with NOR parr, reducing their growth and survival").

Any review of literature about hatcheries is complicated by the spatial extent of available river habitat for steelhead spawning and rearing, hatchery practices, and differing metrics of hatchery program success in different river systems (Brannon et al. 2004; Fraser 2008). The growing literature about how residency shapes steelhead and rainbow trout populations indicates that, depending on the location and life stage chosen for releasing hatchery-reared *O. mykiss*, competition between hatchery and wild fish may be significant (McMichael et al. 1997; Hausch and Melnychuk 2012; Kendall et al. 2015). Certainly, at least in some rivers, the relationship between environmental drivers, hatcheries, and freshwater competition is important (Brannon et al. 2004; Courter et al. 2019).

Exploratory modelling

Finally, any hatchery stocking program should have clear objectives set by decision-makers. Analysts can help inform the decision process by using observations and models to evaluate outcomes under different management actions. To investigate the potential implications of hatchery supplementation for sustaining and recovering IFRS populations we carried out some exploratory modelling of the Thompson River population using both a relatively simple Beverton-Holt model (with penalties on the hatchery component, see section "Exploratory modelling of hatchery production: simple Beverton-Holt model" and Appendix 2: Beverton-Holt stock-recruit analysis of hatchery-wild interactions in Steelhead) and using the All-H Analyzer (AHA) simulation software (HSRG 2020) which explicitly simulates genetic consequences of hatchery supplementation (see section "

Exploratory modelling of hatchery production: AHA model" and Appendix 3: All-H Analyzer Model Results). Unlike the Beverton-Holt model, the AHA model is designed to inform hatchery program rules, like the size of the hatchery program, accounting for genetic risk. However, deciding which modelling approaches, decision rules, and performance metrics are appropriate for this analysis requires input from at least program managers and community members. These latter issues are beyond the scope of the current review.

Overview of hypotheses on the effects of hatcheries on wild salmonid populations

To provide a transparent analytical framework for our review of the effects of hatcheries on wild *O. mykiss* populations, we grouped hypotheses into three distinct categories: 1) ecological, 2) fishery related, and 3) genetic and epigenetic. These hypotheses are summarized in Table 2 and systematically evaluated in subsequent sections.

Ecological hypotheses (E1-4) are related to predation, intra-specific competition, and habitat usage. The fishery related hypothesis (F1) is focused exclusively on harvest control and angling issues. The genetic and epigenetic hypotheses (G1-3) look at genetic variability, domestication, epigenetic changes, and other issues related to inheritance that arise from hatchery supplementation. The life cycle stage(s) where each hypothesized effect is most likely to be seen is shown in the life cycle diagram in
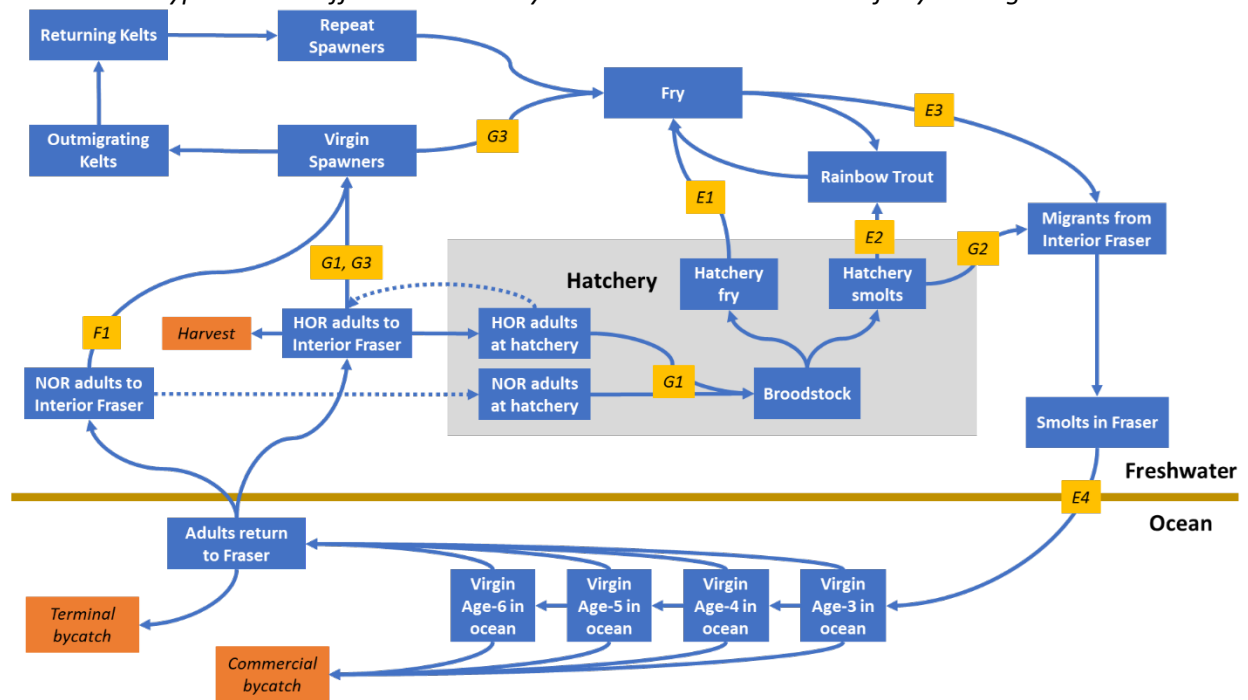
Figure 2.

Table 2. Codes and definitions used in this review of hypotheses related to the effects of hatcheries on wild populations. HOR[7]: hatchery origin, NOR: natural origin.

Code	Definition of hypothesis
	Ecological hypotheses
E1	Release of HOR juveniles in streams results in lower growth and survival of NOR juveniles.

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[7] The "HOR" and "NOR" acronyms are in common use in the Pacific Northwest salmonid literature. The "R" can stand for "recruits" or "returns" but the acronyms are often applied to describe a fish's origin at any life stage.

E2	Some HOR smolts stocked in rearing streams do not migrate to the ocean and then compete with NOR parr, reducing their growth and survival.
E3	HOR adults spawn successfully but intraspecific density-dependent competition leads to replacement rather than supplementation of the NOR juvenile population.
E4	Increased abundance of combined HOR and NOR populations (e.g., at smolting) attracts predators and increases predation mortality rates on NOR fish.
	Fishery hypothesis
F1	Anglers are attracted to the increased abundance of combined hatchery and wild population, thus increasing annual adult mortality rate/year and select for younger age/slower growth in NOR fish.
	Genetic hypotheses
G1	Inbreeding Depression: Loss of genetic variation causes reductions in effective population size and maximum recruits-per-spawner (R/S) in HOR populations spawning naturally.
G2	Domestication selection: Maladaptation of HOR fish after release into the natural environment leads to reduced survival, growth or reproduction in HOR (and NOR after HOR-NOR interbreeding). Selection for traits that were beneficial in the hatchery environment reduce maximum R/S in adult HOR spawning naturally (and in NOR fish after HOR-NOR interbreeding).
G3	Epigenetic changes that upregulate traits (e.g., growth) in HOR fish cause higher mortality in NOR fish in natural environments after HOR fish are released, possibly in the next generation if traits are carried to the offspring of naturally spawning HOR adults.
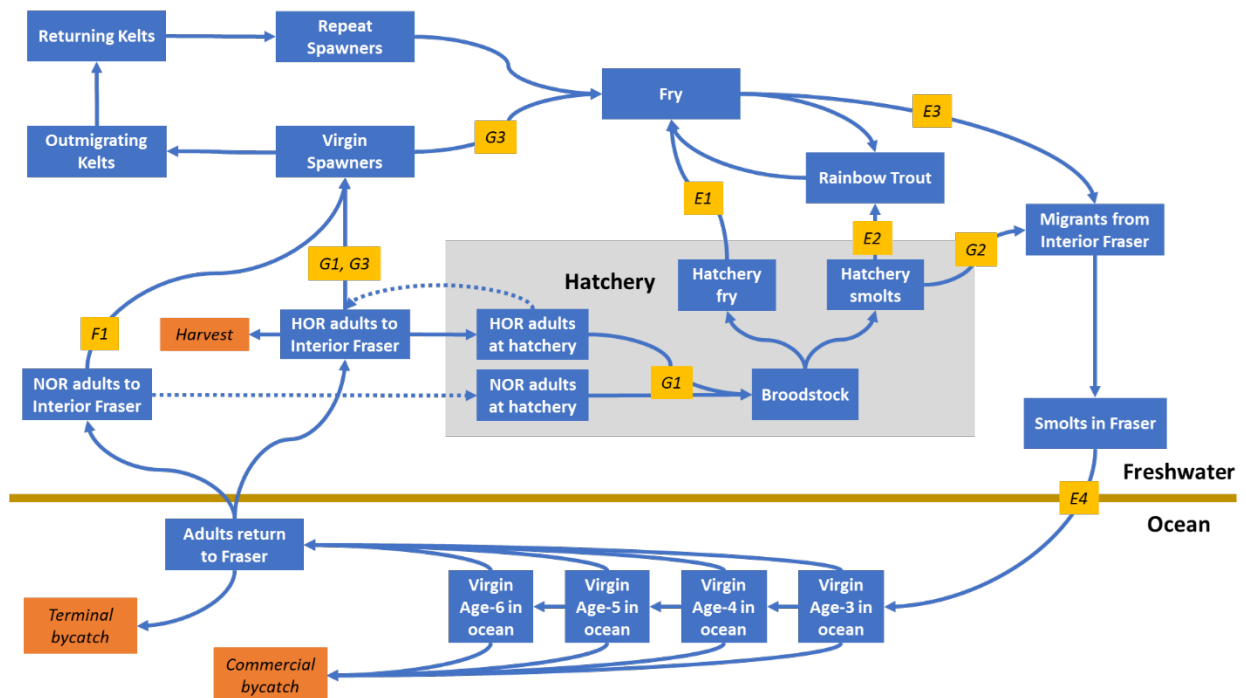
Figure 2. Graphical representation of a steelhead life cycle, including residualization to rainbow trout and production of anadromous fry from the non-anadromous parents (note that resident life history processes are not included in the models described in this report). This life cycle includes potential hatchery processes, and the stages in the life cycle where hatchery effects are hypothesized to occur are

10

indicated in yellow boxes. Abbreviations for each hypothesis are defined in Table 2*. NOR: natural origin; HOR: hatchery origin.*

Ecological effects of hatchery supplementation

Both theory and empirical data indicate that the intentional release of captive-bred native species undermines the ecological stability of fish communities, leading to greater temporal fluctuations and less taxonomic richness in rivers with intensive release of hatchery salmon (Terui et al. 2023). While HOR releases of steelhead in the Interior Fraser River could improve stock status and reduce extinction risk in the NOR population, they may also result in negative ecological effects on the NOR population due to competition and predation. We outline some key hypotheses for these ecological effects, examine the evidence in the literature, assess the risk to the IFRS population, and detail mitigation measures that could be adopted.

Hypothesis E1: Release of HOR, pre-smolt juveniles in streams results in lower growth and survival of NOR juveniles

Mechanisms and evidence of effects

Competition between populations of the same or different species occurs when interacting populations utilize a limited resource, e.g., food or space, and the fitness of at least one is reduced as a result (Birch 1957). It can be demonstrated as emergent differences in the populations' survival, growth, food consumption, habitat use and/or behaviour (Weber and Fausch 2003; Tatara and Berejikian 2012). The release of juvenile HOR steelhead into streams as fry or parr is expected to result in competition with NOR steelhead residing in the same habitat. Among juvenile steelhead, competition in freshwater can occur through direct conflict for rearing territories and through indirect depletion of food resources during the time from emergence until the transition from parr to smolt and migration downstream, i.e., smoltification. Released hatchery steelhead fry and parr exhibit similar habitat preferences and hold similarly sized territories as their wild counterparts (Tatara et al. 2008, 2009).

Several factors affect competition between juvenile steelhead of hatchery and natural origin (Tatara and Berejikian 2012). These can be grouped into 1) population factors that affect groups of competing individuals, which include fish density and duration of cohabitation; and 2) properties of competing individuals, which include relative body size, prior residence, and rearing environment effects (Tatara and Berejikian 2012). It has been suggested that the most important factor affecting competition is the combined density of HOR and NOR juvenile steelhead (Tatara and Berejikian 2012; Anderson et al. 2020). As the combined density approaches the carrying capacity of rearing streams, then performance of the NOR population may be reduced due to density dependence as per capita resource availability declines to a level where growth, survival and productivity are negatively affected (Figure 3). Indeed, intraspecific competition is the most common mechanism producing density dependence in salmonid species (Grossman and Simon 2020). Steelhead survival from fry to smolt stages has been shown to be highly density dependent (Ward and Slaney 1993), while density dependent growth has been documented across juvenile stream-rearing salmonids (Grant and Imre 2005; Grossman and Simon 2020), including steelhead (Hume and Parkinson 1987; Myrvold and Kennedy 2015). The release of HOR juveniles may thus interfere with the density dependent mechanisms that regulate wild populations, leading to reduced growth and survival of NOR juveniles (Einum and Fleming 2001; Kostow 2009; Buhle et al. 2009).

12

In addition to density, the duration of freshwater cohabitation between HOR and NOR juvenile steelhead is relevant to competition, which is expected to grow more intense and frequent the longer the two populations share the same habitat. Owing to their life history, wild steelhead have a high risk of competition as they can rear in freshwater for 1-7 years prior to smolting and migration to the ocean (though typically 2-3 years; Myers, 2018). This means that multiple wild cohorts will be present when hatchery fish are released in any given year. Most traditional steelhead hatchery programs manipulate spawning and rearing conditions to achieve rapid juvenile growth and produce yearling smolts for release (Berejikian et al. 2012), although some hatchery experiments have released steelhead as fry and parr (Bison 2009). While the choice to release parr may avoid some of the developmental deficits associated with hatchery environments, it will likely increase the duration of cohabitation.

Intraspecific density dependent effects in the open ocean are unlikely given that steelhead are solitary predators and their abundance is low relative to other salmonids, particularly HOR salmonids, in the Pacific (the combined abundance being <1% of total; NPAFC 2022; Myers 2018). Density dependent effects from interspecific competition with other salmonids are likely to have a greater impact on immature NOR steelhead in the marine environment (Cooney and Brodeur 1998; Wilson et al. 2022).

Individual factors affecting competition between juvenile steelhead of different origins can result in population-scale differences in the fitness of each population, so are no less important than density effects. Larger steelhead are expected to have a competitive advantage as they dominate agonistic pairwise contests (Abbott et al. 1985), allowing larger fish to defend territories in better habitats and thereby improve individual growth and survival. Steelhead hatchery programs aim to maximise post-release survival, which are positively related to release size (Hume and Parkinson 1987; Tipping 1997; Wilson et al. 2021). Hatchery juveniles are thus typically reared to larger sizes than same-aged NOR (Hill et al. 2006; Kostow 2009), which likely provides a significant competitive advantage over NOR juveniles, especially for hatchery fish released as parr (Tatara and Berejikian 2012). Experiments in artificial streams suggest that intraspecific interactions of wild and hatchery steelhead fry are very similar (Riley et al. 2009) but these interactions have effects on growth, survival and emigration (Tatara et al. 2011).

Prior residence of NOR juvenile steelhead in rearing habitats may offset the supposed size-based competitive advantage of HOR juveniles. Although not shown specifically in steelhead, the advantage of prior residence has been documented in coho salmon, where lab experiments have shown that intruders had to have a ≥6% length advantage to be equally matched against prior residents (Rhodes and Quinn 1998). Familiarity with the early rearing environment has also been shown to enhance the competitive ability of Chinook salmon reared in seminatural environments compared to hatchery settings (Madison et al. 2015). Since NOR juveniles are most likely resident prior to HOR releases, they will be more familiar with the habitat and will not have to overcome the greater cost of finding a new territory versus defending a territory and resources already held (Tatara and Berejikian 2012). Prior dominance in agonistic contests, e.g., when defending territories, may also confer an advantage to wild fish, as prior winning experience strongly influences competitive success (Rhodes and Quinn 1998). Paired dominance lab experiments on steelhead fry have shown that after initial dyadic contests, no subordinate individuals became dominant, despite obtaining size advantages sufficient to assume dominance in the initial contests (Abbott et al. 1985). The prior residence effect may partly explain why despite being significantly larger than the wild steelhead smolts, hatchery smolts released into Abernathy Creek, Washington, did not displace wild fish (Hill et al. 2006).

Rearing environment can also affect behavioural development and thus competitive ability of juvenile steelhead, but there is equivocal evidence for these effects favouring either NOR or HOR fish (Tatara and Berejikian 2012). Artificial hatchery rearing environments can cause phenotypic differences between hatchery and wild populations (Einum and Fleming 2001; Weber and Fausch 2003; Kostow 2009; Tatara and Berejikian 2012; and see section "Hypothesis G2: Domestication Selection: Maladaptation of HOR fish after release into the natural environment leads to reduced survival, growth or reproduction in HOR (and NOR after HOR-NOR interbreeding). Selection for traits that were beneficial in the hatchery environment reduce maximum recruits produced per spawner in adult HOR spawning naturally (and in NOR fish after HOR-NOR interbreeding)). Hatchery steelhead fry reared in habitat enriched tanks were competitively superior to those reared in conventional hatchery tanks (Berejikian et al. 2000). While this indicates a phenotypic response to exposure to natural environments, enriched hatchery environments do not improve post-release growth or survival (Tatara et al. 2009). Hatchery juveniles are generally more aggressive, attributable to genetic and environmental differences, e.g., rearing at high density (Einum and Fleming 2001; Weber and Fausch 2003; Kostow 2009; Tatara and Berejikian 2012). Increased aggressiveness may result in a temporary competitive advantage to released HOR juveniles (Kostow 2009; Tatara and Berejikian 2012), potentially compensating for prior residence effects. However, hatchery-reared juveniles show decreased responses to predators (Einum and Fleming 2001) as aggressive behaviours make HOR more visible to predators and thus lower their survival (Kostow 2009; Tatara and Berejikian 2012). In addition, the hatchery rearing environment may cause differences in feeding behaviour that results in slower growth of HOR juveniles upon release, which could result in their reduced survival (Einum and Fleming 2001; Kostow 2009; Tatara and Berejikian 2012).

The potential for hatcheries to have negative effects on wild salmonid populations through competition has been suggested for over 30 years (e.g., Hilborn 1992). Several reviews, including those referenced above, have synthesised the results of studies documenting the effects of competition between hatchery and wild juvenile salmonids (Einum and Fleming 2001; Weber and Fausch 2003; Naish et al. 2007; Kostow 2009; Tatara and Berejikian 2012; Anderson et al. 2020). These have typically found more negative ecological effects of competition on wild populations. However, despite the extensive study of competition between HOR and NOR populations, there is still limited understanding of whether hatchery fish have competitive advantage over wild fish because of their origin and rearing history, or if competitive effects are only density dependent and associated with their release timing and location. Most studies of competition have used additive experimental designs that address the effect of releasing hatchery fish at certain densities in a specific habitat (Tatara and Berejikian 2012). Such designs make generalisation to other populations difficult as they do not provide answers about the relative competitive abilities of hatchery and wild fish due to confounding with density; these answers require use of substitutive experimental designs where density is held constant among treatments to test for differences in competitive ability between NOR and HOR juveniles (Weber and Fausch 2003; Tatara and Berejikian 2012). There is a limited body of substitutive experiments due to difficulties conducting them at large spatial and temporal scales, but when competitive ability is measured via growth rate, hatchery and wild salmonids appear to be approximately equal (Tatara and Berejikian 2012; Kennedy et al. 2022). Large-scale experiments are necessary to understand hatchery-wild ecological interactions and the realised impacts of hatchery programs, which may only become clear in future generations (Pearsons 2008; Anderson et al. 2020).

As competition-related effects from releasing hatchery-origin juveniles could result in unfavourable outcomes for NOR juveniles, there is a risk that stocking HOR juvenile steelhead into the Interior Fraser River will impact the wild steelhead population. However, the probability of the risk is heavily context specific as it will depend upon specifics of the hatchery program and the rearing habitats into which HOR juveniles are released. Hatchery programs need to be tailored to individual watersheds following comprehensive review and analysis of each program and predictions about how the hatchery and wild populations will interact (Kostow 2009). For example, if the carrying capacity of rearing habitats in the mainstem and tributaries of the Thompson and Chilcotin Rivers were markedly different, the hatchery program would need to be scaled to each river to ensure that the combined density of NOR and HOR juveniles does not result in negative density-dependent effects on the wild population. This requires that the freshwater juvenile capacity is estimated during the planning stage, e.g., using spawner-recruit data from the wild population or habitat-based assessments (Kostow 2009). Because freshwater habitats change over time, e.g., following logging and related reduction in productivity within the watershed (Wilson et al. 2022), the carrying capacity would need to be continually evaluated and the hatchery program updated. In the Thompson drainage, carrying capacity estimates were made prior to stocking (Sebastian and Yaworski, 1984) but the subsequent fry and parr stocking program met with limited success (Bison 2009).

There are various hatchery rearing and release practices that could reduce the ecological risk on wild steelhead from hatchery stocking. Most hatchery programs aim to release juveniles that are actively smolting and will promptly out-migrate. This typically involves the release of yearling smolts that have been grown in the hatchery environment to a larger size than same-age wild conspecifics. If those larger fish fail to smolt and residualize instead, there is likely to be competition with the wild population. This issue can be exacerbated if the aim of the hatchery program is population recovery rather than harvest. Recovery programs typically require locally sourced natural-origin broodstock (NOB) to maintain genetic integrity (see section "Genetic and epigenetic risks of hatchery supplementation"), but mixed natural-and-hatchery broodstock produce slower-growing juveniles compared to hatchery-only broodstock, thus making achieving smoltification thresholds more challenging (Tatara et al. 2017). One option to mitigate this is to integrate NOB and extend the hatchery rearing period to release age-2 smolts, which can result in larger juveniles that are more likely to reach the smoltification threshold, travel faster, and have higher outmigration survival than yearling smolts produced from non-local broodstock (Tatara et al. 2017). Furthermore, hatchery programs that aim to produce age-2 smolts can result in mean smolt sizes and size variability that are more similar to wild populations (Berejikian et al. 2012), therefore decreasing the ability of HOR juveniles to competitively dominate NOR juveniles (Kostow 2009).

A further strategy to reduce competition is to use acclimation ponds. In this strategy, HOR smolts are released volitionally and those individuals that do not smolt are removed before they can residualize in the rearing habitats and compete with the NOR population (Viola and Schuck 1995). The non-migrating fish can then be located in rearing habitats where there is lower risk to wild populations (Kostow 2009). If there are areas within the watershed where rearing habitats are particularly important to wild populations, it is also worth exploring whether 1) large releases of HOR juveniles can be made downstream of these areas to reduce competitive interactions with NOR juveniles, or 2) release groups

be smaller and staggered over several days to avoid HOR juvenile concentrations that would attract predators (Kostow 2009).

Hatchery programs may also seek to produce hatchery-origin fish that have behavioural characteristics similar to natural-origin fish, for example in enriched hatchery environments that result in improved foraging and reduced rates of aggression (Cogliati et al. 2022). By varying diet, density, and tank characteristics like cover and substrate complexity, wild fish surrogate programs seek to rear hatchery fish with body size and behavioural phenotypes more similar to wild fish than those produced in conventional rearing environments. However, while these conditions may improve growth and survival of HOR juveniles upon release, the desired outcome may not always be achieved and come with negative effects on the foraging and aggressive behaviour of NOR juveniles resident at release locations (Tatara et al. 2008).
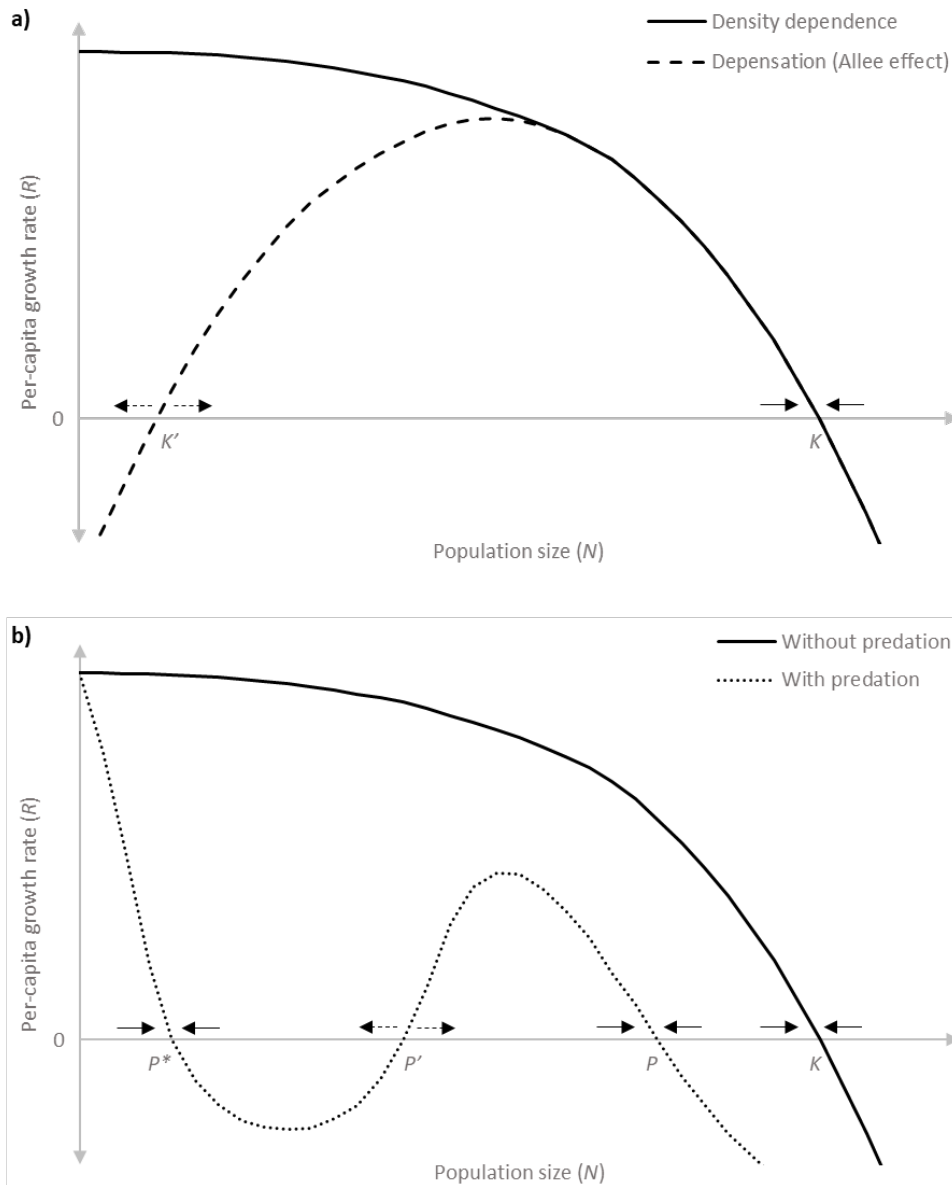
Figure 3. Density dependence represented by per-capita growth rate (R=(dN/dt)/N) as a function of population size (N). When R=0, N is at either a stable (solid arrows) or unstable (dashed arrows) equilibrium (figures adapted from Liermann and Hilborn 2001; Clark et al. 2021). a) Under compensatory density dependence R declines with increasing N, with an equilibrium at K. Depensation (also called the Allee effect or inverse density dependence) produces a positive slope as R is reduced at small N, with an unstable equilibrium at K' below which R becomes negative and the population goes towards extinction. It can be caused by mechanisms associated with small populations, including inbreeding depression or behavioural changes, e.g., reduced protection from predators. b) Predation can reduce the stable equilibrium from K to P. When the predation rate is highest at intermediate N, additional local minima emerge and a lower stable equilibrium will exist at P*. This is a 'predator pit', i.e., when N<P' the population is trapped at low numbers. In a predator pit, predators maintain prey at N<P' via density-dependent predation; whereas at N>P', predation rate decreases due to factors such as predator satiation or handling time.

Hypothesis E2: Some HOR smolts stocked in rearing streams do not migrate to the ocean, residualize, and then compete with NOR parr, reducing their growth and survival

Mechanisms and evidence of effects

Hatchery origin salmonid populations can suppress wild salmonid populations through competition between wild and hatchery origin fish that share the same habitat. Furthermore, it has been hypothesized that hatcheries may increase the rate of residualization for steelhead populations and increase the abundance of the non-anadromous population (Viola and Schuck 1995; Hausch and Melnychuk 2012). As discussed in the previous section, hatcheries can release fish at different life stages and at different locations; these may impact what habitat is being used by the hatchery fish during rearing and whether this overlaps with wild fish habitat use (Tatara et al. 2019). A temporary residualization issue occurs if HOR yearling parr do not smolt immediately after release, but instead smolt after growing in fresh water until reaching adequate size (Tatara et al. 2017). Hatchery practices often seek to release large-bodied fish and increase the likelihood of smoltification (e.g., by selecting for high growth rates and reduced age of smoltification; Berejikian et al. 2017) within only one to two years of hatchery rearing. If released after only one year of growth, slower-growing hatchery fish are likely to delay migration or residualize fully and reproduce without going to sea (Hausch and Melnychuk 2012; Tatara et al. 2019). Those that remain to grow in freshwater are likely competitors with natural conspecifics (Tatara et al. 2019).

Because it is possible that the ecological and genetic consequences of hatchery-produced residualized steelhead outweigh the potential contribution of residualized and resident fish to anadromous populations, hatchery practices are key (Tatara et al. 2019). Factors such as age and location of released fish influence migration behaviours, and hatchery practices are critical determinants of whether hatchery released fish remain in the river or emigrate to the ocean, with. For example, Hausch and Melnychuk (2012) reviewed 16 studies on residualization and concluded that releasing fish near the ocean and using hatchery origin broodstock, rather than NOB, reduced residualization. However, these mitigation strategies may conflict with conservation objectives such as maintaining genetic variability and preserving the endemic stock.

Risk to the IFRS population and potential mitigation measures

The risk of residualization in hatchery releases can be reduced by rearing fish to a modestly large size (over a longer rearing period; Tatara et al. 2019) and releasing them near the river mouth. However, this approach may be inappropriate for an IFRS hatchery program owing to the populations' use of habitat deep in the interior of B.C., such that releasing hatchery fish near the mouth of the river may not be feasible. If release near the river mouth is not possible, rearing hatchery fish for a longer time prior to release can encourage NOB-produced hatchery fish to go to sea (Tatara et al. 2017). As mentioned under E1, a further strategy is to use acclimation ponds, where HOR smolts are released volitionally and those individuals that do not smolt are removed before they can residualize (Viola and Schuck 1995).

Because IFRS and rainbow trout are a single interbreeding population (R. Bison, pers commn.), a hatchery-induced shift towards the non-anadromous life history may not necessarily be problematic for the long-term population viability of the steelhead life history component. Should marine conditions

change and a new regime emerges that is associated with a return to higher marine survival rates for anadromous steelhead, the rainbow trout population component could provide a sufficiently large "rescue" source of steelhead smolts to rebuild the anadromous population component, although this may take tens of generations (Phillis 2014; Phillis et al. 2016). Population dynamics modelling could potentially help assess the credibility of the above outlined scenarios and how alternative hatchery supplementation options could potentially attenuate the rescue effect.

Hypothesis E3: HOR adults spawn successfully but intra-specific density dependent competition leads to replacement rather than supplementation of the NOR juvenile population.

Mechanisms and evidence of effects

In addition to competition between released HOR and NOR juvenile steelhead (Hypothesis E1: Release of HOR, pre-smolt juveniles in streams results in lower growth and survival of NOR juveniles), there may be competition among HOR and NOR adults returning to the spawning grounds and subsequent competition between their offspring. Hatchery fish seldom all return to the hatchery to spawn and the majority of HOR adults may instead spawn in the streams, where they may outnumber the NOR adults (Naish et al. 2007). If the carrying capacity of the spawning grounds has been met by the NOR population, then addition of HOR spawners will reduce the productivity of both populations through density dependence. Increased competition for spawning sites can lead to NOR redds being superimposed or spawning occurring in less favourable habitat, and thus fewer NOR adults spawning successfully.

As described under Hypothesis E1: Release of HOR, pre-smolt juveniles in streams results in lower growth and survival of NOR juveniles above, competitive interactions require temporal and spatial overlap in the juveniles produced by NOR and HOR parents spawning in the wild. In contrast to HOR steelhead juveniles, which aggregate close to the hatchery in high densities compared to NOR parr (Tatara et al. 2009), the distribution of first-generation steelhead parr produced from HOR adults in Abernathy Creek in the Columbia River was similar to NOR parr (Kennedy et al. 2022). Combined with no significant difference in size between these NOR and HOR-produced parr, parr occupying the full extent of accessible and suitable habitat indicate that offspring from HOR adults are efficiently competing with NOR fish for both food and space (Kennedy et al. 2022). There is thus potential for negative competitive interactions between HOR-produced and NOR juveniles which could reduce NOR steelhead abundance.

Separate studies in Oregon have indicated that on spawning areas with high proportions of hatchery-origin steelhead adults, there were large declines in the productivity of wild steelhead (Chilcote 2003; Kostow and Zhou 2006). These productivity declines were determined to be caused by ecological rather than genetic interactions (Kostow 2009) and suggested that removal of hatchery steelhead could increase productivity of these wild populations. However, Courter et al. (2019) subsequently analysed a longer time series of stock-recruit data from the Clackamas River to contradict the findings of Kostow and Zhou (2006), instead finding that numbers of HOR spawners did not have a negative effect on NOR recruitment but that productivity was negatively affected by poor ocean conditions and low spill at the dam in the lower reaches of the Clackamas basin.

Furthermore, a long-term analysis of stock-recruit data from Hood River steelhead found that the productivity of NOR adults was not associated with the proportion of HOR adult steelhead; rather, it was

associated with pinniped predation, ocean conditions, streamflow, and the number of hatchery steelhead smolts released (Courter et al. 2022). Surprisingly, the effect of hatchery smolt releases on NOR recruitment was positive, which Courter et al. (2022) suggested was evidence that HOR smolt releases may have been insulating NOR juveniles from predation. Lister (2014) also concluded that the presence of HOR spawners did not reduce the recruitment of NOR spawners in the Columbia River. Interestingly, across three population pairs with mixed HOR-NOR spawners or all NOR spawners, HOR steelhead only contributed substantially to returning adult recruitment when NOR populations were well below carrying capacity (Lister 2014). This implies that HOR spawners do not perform as well in wild conditions and so are less likely to affect natural production in mixed populations, adding further evidence to hatchery spawners having reduced reproductive success (Christie et al. 2014).

Although the evidence that HOR spawners reduce productivity of the NOR population is equivocal, the offspring of HOR spawners that do successfully breed in streams will compete naturally with NOR juveniles via many of the same intra-specific mechanisms outlined under Hypothesis E1: Release of HOR, pre-smolt juveniles in streams results in lower growth and survival of NOR juveniles, including density dependent competition (Keeley 2003). This is expected to have a negative effect on the number of NOR juveniles in the next generation, thus reducing NOR productivity. However, unlike hatchery-reared juveniles, 'naturally produced' offspring of HOR spawners may not have the same competitive advantages as those produced in the hatchery. One such competitive factor may be size; compared to NOR steelhead, HOR steelhead produce smaller eggs (Hanson et al. 2016). Because egg size increases with female age (Quinn et al. 2011), this could be related to earlier age of maturation typical for HOR steelhead. Fry hatched from larger eggs can be of larger size than fry from smaller eggs (Beacham et al. 1985), though this size advantage does not appear to be maintained beyond the first year of growth (Thorpe et al. 1984; Jones et al. 2015). There is also some evidence that offspring of first-generation HOR steelhead grow faster than offspring of wild fish (Blouin et al. 2021). While this indicates that juveniles with HOR parents can grow faster than NOR juveniles given abundant resources, thus overcoming the initial disadvantage associated with egg size, experiments in natural environments have found no difference in growth rates between HOR fry and NOR fry (Tatara et al. 2009) or between HOR-produced parr and NOR parr (Kennedy et al. 2022). Either way, studies on brown trout, *Salmo trutta*, have shown that early growth and survival after emergence is positively correlated with egg size (Einum and Fleming 1999). If this holds in steelhead then NOR juveniles could have a competitive advantage over offspring from HOR spawners, at least during the first year of growth. In addition, it has been shown that steelhead fry from HOR adults spawning naturally in the wild do not survive well due to a mismatch between suitable river conditions and the timing of spawning by HOR adults, which due to being selectively bred for earlier returns may be several months earlier than NOR adults (Leider et al. 1990; Jones et al. 2015).

Risk to IFRS population and potential mitigation measures

Any steelhead hatchery program in the Interior Fraser will likely result in HOR adults spawning in the same spawning areas as the NOR population (Kennedy et al. 2022), so it is likely that HOR-produced juveniles and/or their offspring will compete with NOR juveniles. Here again the goal of the hatchery program is important. If for supplementation or reintroduction, then HOR-produced juveniles growing to similar sizes and showing similar spatial distributions as NOR juveniles is a positive outcome.

However, if the goal of the hatchery program is to maximize harvest while minimizing ecological risk to the wild population this is not a desirable outcome.

There are potential approaches to mitigate this ecological risk to the Interior Fraser steelhead population. If using a local NOR broodstock is not a requirement of the hatchery program, use of a hatchery-origin broodstock that returns and spawns at a different time than the wild population could both minimize the overlap between spawning adults and result in HOR-produced fry that emerge in less favourable flow and temperature conditions, minimizing risk to the NOR population. Another approach is to restrict the number of hatchery adults allowed into natural spawning areas (Kostow 2009). If 100% of hatchery-origin releases are visibly marked (e.g., by clipping with an adipose fin clip), this could be achieved by selective fishing of hatchery fish (which carries its own risks to the wild population, see Hypothesis F1: Anglers are attracted to the increased abundance of the combined HOR and NOR population, increasing annual adult mortality rate and selecting for younger age/slower growth NOR fish) or removal of hatchery adults at weirs as they migrate to spawning grounds (removal at dams is practiced in other watersheds). Other methods include decreasing the number of HOR steelhead released or locating the hatchery or release sites away from known important natural spawning areas so that the HOR adults return to habitats less likely to be used by NOR adults (Kostow 2009). It is important to note that restricting the movement of HOR adults into NOR spawning areas may not protect wild populations from negative hatchery effects due to competition between NOR and HOR-produced juvenile steelhead. Kennedy et al. (2022) only studied the spatial distribution of age-1 parr produced by HOR adults, not the spawning distribution of the HOR adults. As they discussed, juveniles can also move widely to find optimal feeding conditions (Gowan and Fausch 2002; Myrvold and Kennedy 2015).

The hatchery rearing conditions are also key to any approach to mitigate competition. Kennedy et al. (2022) suggested that the similar distributions of HOR-produced parr and NOR parr could be a result of several factors, including the HOR adult steelhead exhibiting the same spawning habitat preferences, response to distribution of suitable mates and attraction to hormone and pheromone cues as NOR steelhead (Dittman et al. 2010; Keefer and Caudill 2014), or response to olfactory signals that were present in the water source used in the hatchery. In the Kennedy et al. (2022) study, the HOR adults were raised mostly in stream water rather than well water. This suggests one approach to increasing the proportion of HOR adults that return to a specific location, i.e., the hatchery, would be to increase the strength of the olfactory signal to that location, e.g., by raising the hatchery steelhead in well water. This could in turn skew the distribution of the offspring from HOR spawners to that location.

Hypothesis E4: Increased abundance of combined hatchery/wild population attracts predators and increases predation mortality rates on wild fish

Mechanisms and evidence of effects

Systematic changes in the abundance, spatial distribution, and foraging behaviours of predator populations have been hypothesized to be drivers of systematic changes in salmonid population productivity and abundance (Chasco et al. 2017; Korman et al. 2018; Nelson et al. 2019b; Walters et al. 2020; Warnock et al. 2022). For example, several salmonid species have piscivorous life history components that prey upon smaller bodied salmonids (Warnock et al. 2022). Piscivorous hatchery-reared yearling smolts and residualized hatchery origin fish can consume smaller natural-origin

salmonids (Naman and Sharpe 2012). Vulnerable prey sizes are commonly up to one third of the body length of piscivorous salmonid species (Warnock et al. 2022). Thus population level impacts of hatchery-origin fish predation on wild salmonid juveniles can vary depending on the relative body sizes of the hatchery origin predators and wild salmonid prey in addition to their spatial and temporal overlap (Naman and Sharpe 2012). Long-term outcomes of predator-prey interactions, in general, also depend on spatial-temporal variations in predator and prey abundances (Pearsons and Fritts 1999; Simpson et al. 2009; Anderson et al. 2020).

Increased abundance of residualized hatchery produced salmonids can increase the amount of time that natural-origin salmonids are exposed to direct predation by hatchery fish (Anderson et al. 2020). Even at low levels of predation, large releases of hatchery fish can impact NOR salmonids, especially when natural populations are driven to low abundance levels (Whitsel et al. 1993; Naman and Sharpe 2012; Anderson et al. 2020). However, there exist few direct assessments of predation by HOR salmonids on NOR conspecifics, and the majority of studies did not quantify population scale impacts to natural populations, or comprehensively evaluate predation risk (Flagg et al. 2000; Naman and Sharpe 2012; Anderson et al. 2020).

In addition to conspecific predation, high concentrations of prey like juvenile salmonids can attract predators. Release of large numbers of HOR juvenile salmonids has been hypothesized to lead to short-term and long-term numerical responses of avian, piscine, and mammalian predator species (Anderson et al. 2020). For example, relatively large numbers of Artic terns and cormorant species known to eat large numbers of downstream migrant smolts have aggregated in the Lower Columbia River in the past several decades; up to 25 million smolts have been eaten annually by terns and cormorants in the Lower Columbia River, equating to up to 19% of migrating smolts (Evans et al. 2019). Avian and piscine predators have been found to aggregate near hatchery release sites and exploit released smolts (Wood 1985, 1987; Collis et al. 1995; Shively et al. 1996). Long-term increases in the abundance of salmonid predators in the North Pacific Ocean, e.g., salmon sharks and northern resident killer whales, may have been partly driven by increases in hatchery salmon abundance over the same region and period (Seitz et al. 2019).

In some instances, predation is depensatory (Wood 1987; Petersen and DeAngelis 1992; Faulkner et al. 2008). Especially when wild smolt abundance is low, if IFRS predators show a numerical response to high densities of hatchery-produced smolts, this can result in increased predation rates that prevent increases in the wild salmonid population (Figure 3). A predator pit (e.g., where wild salmon abundance is kept low due to high predation rates despite low abundance of the wild population) could thus prevent recovery of depleted wild salmonid populations (Liermann and Hilborn 2001; Warnock et al. 2022). Depensatory predation can also cause smaller less productive stocks to go extinct.

Since the 1970s, the five- to ten-fold increases in Steller sea lions (*Eumetopias jubatus*) and harbour seals and depensatory predation have been hypothesized to have prevented the recovery of some low abundance salmon and steelhead stocks via predator pits (Chasco et al. 2017; Korman et al. 2018; Walters et al. 2020) and caused the practical extinction of some of the wild steelhead populations on Vancouver Island (Mike McColloch, pers. comm.). The large increases in abundances of pinnipeds in B.C. waters since the 1970s was found to be the most significant explanatory variable of several candidate variables that could explain the large decreases in productivity of IFRS over the past few decades

(Korman et al. 2018a; Rob Bison, pers. comm.). Diet studies of harbour seals in the Strait of Georgia in the past decade have shown both juvenile and adult steelhead to be consistently present in the diets of harbour seals and possibly disproportionately high relative to the abundance of co-migrating smolts of other salmonids (Thomas et al. 2017, 2022). Sobocinski et al. (2020) found that predation by harbor seals was the predominant driver of declines in abundance and productivity in twelve Puget Sound steelhead stocks. They highlighted that in contrast to smolts of the five Pacific salmon species, steelhead smolts were particularly susceptible to predation by marine predators such as harbor seals due to 1) steelhead smolts lengths being the most preferred by harbor seals, and 2) steelhead smolts tending to migrate in the top 10 meters of the water column and "appear[ing] to be more dispersed and school less than salmon in open marine waters".

Hatchery releases of Chinook salmon have become increasingly synchronized (Huber and Carlson 2015; Nelson et al. 2019a), possibly leading to increased numerical responses of predators and amplifying predation impacts on co-mingled naturally produced salmon (Anderson et al. 2020). However, a causal linkage between an increase in pinniped abundance and the large-scale increase in hatchery-produced salmon in the North Pacific Ocean has not been established. The most credible cause of the large increases in pinniped since the 1970s was the establishment of the U.S. Marine Mammal Protection Act in 1970 and the inclusion of the protection of marine mammal species in the Canadian Fisheries Act in the early 1970s (Olesiuk 2008, 2018). These policy changes led to cessation of deliberate controls on pinniped populations on the west coast of North America in the early 1970s. Population dynamics modelling shows that following these protections, pinniped population abundances have grown to historic highs (Olesiuk 2008; Nelson 2020). In contrast to the hypothesized link between hatchery releases and depensatory predation, hatchery fish may instead serve to satiate predators. Predators are expected to prefer recently released hatchery fish (Berejikian 1995; Muir et al. 2001), which may be available in sufficient numbers to satiate predators (Furey et al. 2016; Anderson et al. 2020). Therefore elevated localized densities of hatchery fish may increase the percentage of the predator population that becomes satiated, leading to a reduction in predation rates on wild salmon that share the same habitat with HOR (Courter et al. 2022). Predator satiation might or might not override potential depensatory predation effects on rates of population increase for wild salmonids.

Increased predator abundance by itself is not sufficient evidence of higher mortality rates. Either the ratio of predators to wild salmonid prey or the number of wild salmonid prey eaten per predator will need to increase sufficiently to drive wild salmonid mortality rates up in the presence of hatchery fish (Nelson 2020; Walters et al. 2020). Large-scale hatchery releases have the potential to significantly alter predation dynamics; however very little is known or understood regarding either short- or long-term impacts to natural populations (Anderson et al. 2020).

Risk to the IFRS population and potential mitigation measures

Modifications to the stage, size and timing of release of hatchery reared salmonids have been considered and implemented to improve return rates of hatchery reared salmon and minimize impacts on wild salmonids (Bilton et al. 1982; Irvine et al. 2013; Hagen et al. 2021). Releasing hatchery juveniles at the stage when they are most likely to smolt and migrate downstream has been considered to minimize residualization and interactions between hatchery and natural origin salmonids in stream habitats (Hagen et al. 2021). Sites for release of hatchery smolts have also been chosen to avoid habitats

used by natural origin juvenile salmonids and minimize predation on and competitive interactions with wild juvenile salmonids (Anderson et al. 2020).

Hatchery supplementation of steelhead in the Thompson or Chilcotin Rivers could potentially lead to increased abundance of hatchery origin juvenile steelhead and residualization. Residualization rates in IFRS have been high since the populations declined in the 1990s and could be expected to remain high as long as marine survival rates for IFRS remain low (Levy and Parkinson 2014). Residualized rainbow trout in the Thompson and Chilcotin River systems can grow large enough to prey upon steelhead fry and parr. An increased abundance of HOR steelhead juveniles and residualized rainbow trout in streams inhabited by NOR steelhead could lead to increased predation rates on wild steelhead eggs, fry, parr and smolts. For there to be negative impacts of HOR predation on the wild population, the following conditions would need to be met:

1. As the abundance of juvenile hatchery steelhead and/or residualized rainbow trout is relatively high in some reaches of these tributaries, the net increase in juvenile hatchery fish and residualized trout abundance from hatchery releases and residualization of hatchery steelhead would need to be substantial enough to lead to increased predation rates by rainbow trout on NOR juvenile steelhead.
2. To be exposed to increased predation rates, the wild juvenile steelhead would need to remain for a sufficiently long time in the same locations as the higher density hatchery origin steelhead populations.
3. A sufficiently large percentage of the hatchery origin juvenile steelhead and rainbow trout population would need to have a sufficiently high fraction of juvenile steelhead in their diets to lead to an increase in predation rates on juvenile wild steelhead above recent and current levels.
   - The extent of residualization of HOR juvenile steelhead that would occur remains highly uncertain.
   - The extent to which the density of HOR juvenile steelhead and rainbow trout would increase in the stream reaches frequented by juvenile steelhead is highly uncertain.
   - As the availability and relative densities of invertebrate and juvenile salmonids from other salmonid species that could be prey for hatchery steelhead parr and rainbow trout could be much higher than wild juvenile steelhead in the Thompson and Chilcotin rivers, the potential for the fraction of wild juvenile steelhead in the diet of rainbow trout to increase remains highly uncertain.
   - Scenario-based population dynamics models that represented predation of hatchery origin residualized rainbow trout on juvenile steelhead could help to identify the conditions under which this could negatively impact the wild steelhead population.

A mark selective fishery for residualized hatchery produced steelhead could help to reduce the abundance of hatchery produced residualized steelhead and reduce the potential predation rates on, and competition with, natural origin juvenile steelhead. A minimum size limit set to some threshold size larger than the average size of a steelhead smolt would be needed to avoid retention of anadromous juvenile hatchery steelhead.

Predator control measures have been considered and implemented in some regions to reduce predation rates on both hatchery and wild salmonid stocks (Yurk and Trites 2000; Evans et al. 2019; Steingass et al. 2019). In the past decade, predation by Steller and California Sea Lions (*Zalophus californianus*) on returning adult salmon and steelhead in the Lower Columbia River, has been found to be fairly high, for example, up to 44% of Columbia River spring Chinook salmon and 25% of upper Willamette River steelhead[8]. Measures to reduce predation rates on returning adult salmon and steelhead by controlling sea lions via euthanasia were federally approved in 2020. Increased return rates of winter steelhead to the Upper Willamette in 2020 were attributed to the lethal control measures taken. Because pinnipeds predate numerous other steelhead populations and fish species, control measures for B.C. pinnipeds should be considered in terms of their benefit for numerous salmonid and non-salmonid species (Nelson et al. 2019b; Nelson 2020).

Increased abundance of hatchery steelhead smolts from the Thompson or Chilcotin Rivers could lead to a numerical response of estuarine and marine predators and increased predation rates on wild steelhead smolts. For there to be a negative impact the following conditions would need to be met:

1. The abundance of hatchery smolts would need to be sufficiently large to cause a short-term numerical response of at least one estuarine or marine predator species.
2. Wild steelhead smolts would need to co-migrate with the hatchery steelhead smolts.
3. The locally increased localized abundance of marine predators would need to lead to an increased predation rate on wild smolts.
4. Satiation of predators from predation on hatchery smolts and other salmonids would not reduce predation rates on wild steelhead smolts.
5. Marine predators would not be more attracted to and drawn away by highly abundant co-migrating salmonid smolts of other salmonid populations. The relative abundance of hatchery produced Thompson River hatchery smolts would be unlikely to be as high or higher than other comigrating populations of salmonid smolts in the Fraser River; in contrast, the abundance of other co-migrating wild salmonid smolts could be expected to be orders of magnitude higher than the abundance of Thompson River hatchery produced smolts. A numerical response of estuarine or marine predators to hatchery produced steelhead from the Thompson or Chilcotin Rivers would thus appear to be highly speculative.

A large biomass of both salmonid and non-salmonid species is consumed annually by pinnipeds (approximately 400,000 tons/year; Walters et al. 2020; Thomas et al. 2017; 2022), so reducing B.C. pinniped abundance through population control would likely improve marine survival for several fish species in B.C., including IFRS. Reducing the abundance of both harbour seals and Stellar sea lions in B.C. by no less than 50% of their current abundance is projected to lead to immediate increases in marine survival rates of B.C. Chinook and coho salmon populations and observable increases in abundance of both species within about five years of the implementation of a population control program (Balanced Pinniped Society 2019). Deliberate control programs for pinniped populations would be necessary to keep their abundance below 50% of current levels, and following implementation it would be necessary

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[8] https://www.dfw.state.or.us/fish/sealion/index.asp

to carefully monitor for changes in recruits per spawner and residualization rates in Chilcotin and Thompson River steelhead stocks in response to increased marine survival rates.

Fishery mortality related risks of hatchery supplementations

Hypothesis F1: Anglers are attracted to the increased abundance of the combined HOR and NOR population, increasing annual adult mortality rate and selecting for younger age/slower growth NOR fish

Mechanisms and evidence of effect

Hatchery programs are intended to produce higher fish abundance and are typically terminated if they do not. If the supplemented populations are part of a fishery, particularly an open-access fishery, higher fish abundance generally attracts higher fishing effort (Pitman et al. 2019) but this increase in fishing effort may or may not result in higher fishery-related mortality on wild fish populations. For example, in the Skeena river relative fish abundance varied by 400% between years, but the interannual variation in the number of fish captured in three tributaries only ranged between 200% and 250% (Pitman et al. 2019). The proportion of fish captured (i.e., the harvest rate) only increases if the proportional increase in fish abundance is less than the proportional increase in harvest mortality, which is usually calculated as the product of catch per unit effort and fishing effort. This is generally not the case in open access fisheries for the same reason that, in an ecological setting, high densities of prey can reduce predation mortality rate (e.g. Furey et al. 2016).
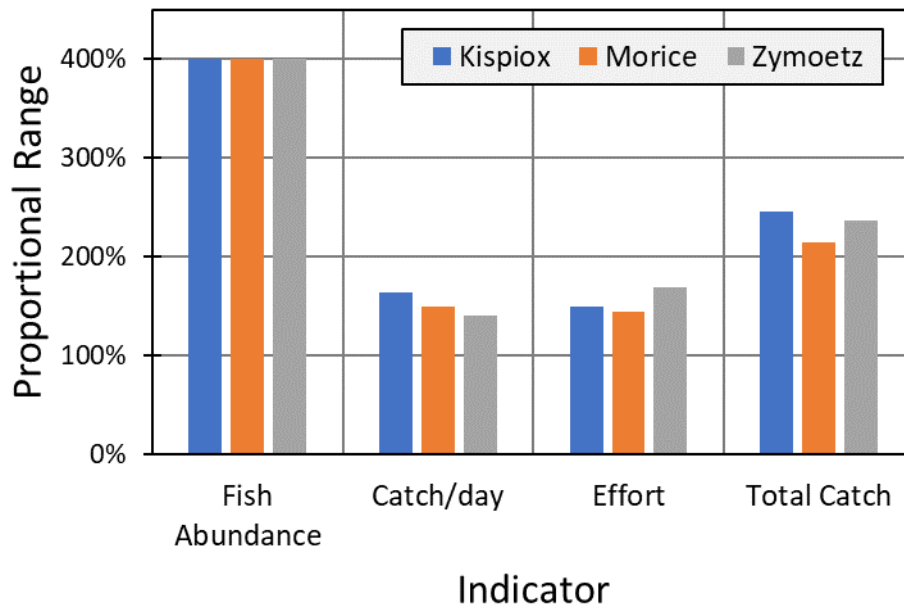
Figure 4. Relative range of four indicators for steelhead fisheries on three tributaries (the Kispiox, Morice, and Zymoetz) of the Skeena River. Data is from figures 2 and 3 in Pitman et al. (2019) for years prior to a management intervention in 2012. Relative fish abundance is a fishery-independent indicator of the number of adult steelhead entering the Skeena River each year. Relative catch/day and effort indicators represent the ends of regression line for indicator value versus fish abundance. The total catch indicator is the product of the effort and catch per day indicators.

Hatchery programs must be designed to avoid situations that increase fishing mortality on NOR populations. Hatchery programs can produce higher fishery mortality[9] on the NOR component of a steelhead population in a variety of circumstances, for example:

1. The recreational fishery on NOR fish may be open/closed depending on the presence/absence of HOR fish. This includes catch and release fisheries.
2. Effort density, and therefore fishing mortality, can be zero at very low fish densities (Cox et al. 2002). If the NOR abundance is too low to attract significant amount of effort, and adding HOR fish pushes the catch rate above a threshold, then NOR fishing mortality can increase significantly.
3. A harvest fishery on HOR fish may attract effort levels that are proportionally much higher than the increase in fish density because anglers generally prefer to harvest, rather than release, captured fish (Carter and Liese 2012; Hunt et al. 2019).

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[9] Fishing mortality includes legal harvest but for many NOR populations, mortality is a combination of post-release death and illegal harvest.

In addition to targeted recreational fisheries, IFRS are harvested as bycatch (in commercial and Indigenous fisheries) as well as a targeted Indigenous fishery (Levy and Parkinson 2014; Bison 2016). Bycatch harvest rates can be excessive in situations where:

1. A low productivity stock is harvested at a high rate as bycatch in a fishery that targets, and is managed for, optimal yield from a high productivity stock.
2. A stock is harvested as bycatch in several sequential fisheries where each has a sustainable harvest rate but the combined harvest rate for the bycatch stock is excessive (IFRS are sequential bycatch in sustainable fisheries for Nitinat chum, Lower Fraser chum and Fraser Canyon First Nations food fisheries).
3. NOR stocks are bycatch in high harvest rate fisheries for other stocks or species of HOR fish.

Directed harvest rates in many NOR populations, including IFRS, have declined to relatively low levels in the past few decades to address conservation concerns (Johnston 2013) triggered by systematic declines in stock productivity and marine survival rates (Nelson et al. 2019b; COSEWIC 2020; Sobocinski et al. 2020, 2021; Welch et al. 2021; Courter et al. 2022). In contrast, bycatch harvest rates have remained high for many populations, including IFRS (Bison 2016). A common problem is that commercial, recreational, and Indigenous fisheries could develop to harvest abundant HOR populations that are co-mingled with less abundant and less productive NOR populations (Anderson et al. 2020). Reducing effort in high-intensity but sustainable harvest on co-mingled populations is often resisted by participants in these fisheries despite their demonstrable impact on populations affected by bycatch. As a result, managers may prefer to use hatchery subsidies to maintain high levels of effort in low bycatch fisheries by increasing IFRS sustainable harvest rates.

For IFRS, hatchery augmentation may trigger an increase in directed Indigenous harvest. Harvest of IFRS has been voluntarily restricted by local First Nations (Levy and Parkinson 2014), but DFO catch allocation policy prioritizes the First Nations sector[10]. The recreational fishery on IFRS is currently closed (including catch and release) and the priority for any harvestable surplus generated by a hatchery program would presumably be First Nations harvest opportunities rather than harvest or post-release mortality associated with a recreational fishery.

High fishing mortality rates and size selective fisheries have been hypothesized to select for younger age at maturity and slower growth in exploited salmonid populations (Ricker 1981). For example, over the past century the mean body size, mean age and fecundity of numerous adult Chinook salmon populations have decreased considerably (Ricker 1981; Oke et al. 2020). Environmental change and increased competition at sea with highly abundant NOR and HOR salmon have also been hypothesized to contribute to decreases in size-at-age in some salmonid populations through reductions in the availability or quality of food resources (Oke et al. 2020).

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[10] http://waves-vagues.dfo-mpo.gc.ca/Library/240366.pdf

Risk to the IFRS population and potential mitigation measures

A common strategy used to maintain higher rates of harvest on hatchery populations is to externally mark hatchery fish, usually with an adipose fin clip, and employ mark selective fisheries so HOR fish can be harvested while unmarked (presumably NOR) fish can be returned to the water (Anderson et al. 2020). Although mark selective fisheries have yielded the desired outcome of low estimated mortality on unmarked fish in some instances, in others limitations to their implementation have resulted in substantial non-selective mortality on unmarked fish (Anderson et al. 2020). For example, due to stress and injury in the capture process, not all captured unmarked fish that are released survive to spawn (Taylor and Barnhart 1996; Nelson et al. 2005; Twardek et al. 2018). The opportunity to catch and kill hatchery fish could attract enough fishers and fishing effort such that catch and release mortality on wild fish could significantly reduce their reproductive success, population productivity and ability to recover from low abundance. However, when higher fish abundances attract additional angling effort, the newly attracted anglers are often less effective than those present at lower abundance levels and harvest rates can actually significantly decrease in a numerical response of angling effort to increased abundance (Pitman et al. 2019).

Furthermore, not all fisheries that capture a mixture of NOR and HOR fish are mark selective. For example, while mark selective fisheries for hatchery produced Chinook salmon have been in place for many years in the State of Washington and Oregon, this has not until 2023 been the case for saltwater recreational and commercial fisheries for Chinook salmon in B.C. This is despite the facts that 1) numerous but not all hatchery produced Chinook salmon in B.C. are adipose fin clipped and could allow for mark selective fisheries in B.C., and 2) many thousands of Chinook salmon originating from Washington and Oregon regularly migrate into B.C. waters and have been caught and retained annually in Canadian fisheries irrespective of whether they are marked or unmarked. Meanwhile, unmarked wild Chinook salmon stocks of Canadian origin that migrate through American waters benefit from mandatory release in the U.S. mark selective fisheries, but upon re-entering Canadian waters to return to their natal streams these same fish face the risk of retention in Canadian mark indiscriminate fisheries. Lack of consistency in the implementation of mark selective fisheries can thus limit the utility of this management tool to differentially remove HOR fish and limit fishery mortality of NOR salmonids.

Hatchery production of IFRS could potentially result in moderate to high numbers, e.g., up to thousands, of hatchery steelhead returning. If sufficiently large returns of hatchery steelhead resulted, recreational fisheries for hatchery steelhead could potentially be re-established. Such fisheries could allow the mark selective retention of hatchery produced steelhead. Alternatively, a catch-and-release fishery could be permitted for adult steelhead, i.e., with no retention of either hatchery or wild steelhead should the assessed abundance of hatchery and wild fish exceed some minimum agreed benchmark level. In either case, it is likely that increased abundance of the combined adult wild and hatchery steelhead populations and recreational fishery openings would attract angling effort (Pitman et al. 2019). A retention fishery for hatchery steelhead could potentially attract a higher level of angling effort than a catch-and-release fishery and result in increased incidental fishing mortality rates in wild steelhead. And even with the release of natural origin steelhead, this could still lead to increased mortality rates on natural origin steelhead due to incidental mortality caused by the capture and release of wild steelhead. Studies have shown that incidental mortality rates for caught and released steelhead have been relatively low (Nelson et al. 2005; Twardek et al. 2018). Due to long holding times in the natal river prior

to spawning, individual summer steelhead have been known to be captured multiple times in catch-and-release recreational fisheries. Nelson et al.'s (2005) findings did not support the hypothesis that the chance of successful spawning was significantly reduced in steelhead caught and released two or more times. Studies on Atlantic salmon (e.g., Richard et al. 2014) suggest possible sublethal and lethal consequences of repeat capture and release. However, the results could be different for summer steelhead where water temperatures may be considerably warmer than those during Nelson et al.'s (2005) study on winter steelhead. Increased mortality rates from increased recreational fishing effort could negatively impact the recovery of wild Interior Fraser steelhead populations. But without careful analysis, is not possible to predict the level of increase in incidental mortality that could negatively impact population recovery.

Population dynamics modelling of IFRS could address the potential short-term and long-term effects on the chance of recovery of the wild steelhead population under two levers of management control: hatchery production and different scenarios for how mark selective fisheries might reduce the abundance of naturally spawning HOR adults. Estimating plausible post-release survival requires accounting for the conditions of capture, e.g., river temperatures, gear used (Taylor and Barnhart 1996; Nelson et al. 2005; Twardek et al. 2018) and encounter rates of unmarked fish. These will help to inform how total harvest mortality of natural populations and population recovery rates could respond to mark selective fisheries that target hatchery populations. However, we note that fisheries management is to prioritize first stock conservation, then Indigenous fisheries, then the interests of other groups (*R. v. Sparrow* 1990).

Genetic and epigenetic risks of hatchery supplementation

Hypothesis G1: Inbreeding Depression: Loss of genetic variation causes reductions in effective population size and maximum recruits per spawner

Mechanisms and evidence of effects

A primary genetic risk of a hatchery program is loss of genetic diversity, e.g., via inbreeding. Inbreeding occurs when individuals that are closely related, typically through shared ancestry, mate and reproduce. This can lead to inbreeding depression, where genetic diversity loss reduces fitness via loss of heterozygosity[11] and accumulation of expressed detrimental recessive alleles (Hedrick and Garcia-Dorado 2016). Overall, inbreeding depression has been well documented across many taxa, and can lead to lowered population productivity and increased extinction risk (Hedrick and Garcia-Dorado 2016). Given the use of hatcheries for population conservation, this risk is an important consideration for any hatchery program.

There are some concerns that a hatchery could reduce the genetic diversity in the wild IFRS population, e.g., through the Ryman-Laikre effect, which occurs when 1) genotypes from relatively few adults (i.e., the hatchery broodstock) are amplified in wild spawning HOR fish and 2) egg-smolt survival rates are much higher in hatchery produced fish. In other words, because the abundant HOR spawners contain the genetic diversity from only a few hatchery-spawned parents, their progeny will have less potential genetic diversity than the progeny of NOR adults. Unless the hatchery contribution to spawning in the wild is very low or hatchery populations are highly productive (Waples et al. 2016), amplifying the progeny of broodstock reduces the effective population size of the population (Ryman and Laikre 1991; Christie et al. 2012b; Hagen et al. 2021).

Ryman and Laikre (1991) present the idea of an effective population size given by the following equation:

$$\frac{1}{N_e} = \frac{x^2}{N_c} + \frac{(1-x)^2}{N_w}$$

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[11] Heterozygosity occurs when an individual inherits different versions of a gene from each parent. Animals typically have two sets of chromosomes, one from each parent, and the genes may match or differ between parents. More closely related parents are more likely to have the same genes as each other, thus reducing heterozygosity and increasing the chance that both parents' chromosomes have a detrimental version of some fitness-related gene (Charlesworth and Charlesworth 1999).

Where N_e is effective[12] population size, N_c is the effective number of parents in the hatchery and N_w is the effective number of wild parents. The relative contribution of offspring from the captive parents is x and $(1-x)$ is the contribution of the wild fish. Note that the larger N_w is relative to N_c the more the effective population size is dominated by wild fish. As the effective population size and genetic diversity decrease, the risk of inbreeding and inbreeding depression grows more likely. There have been some studies focusing on how small populations have to be relative to hatchery programs for inbreeding to be problematic; these make it clear that the potential outcomes depend on the attributes of both the wild population and hatchery program (Waples et al. 2016).

There exist some questions about how small the effective population size would have to be before issues of inbreeding arise from the initiation of a hatchery program. It remains unclear how much reduction in genetic variability is considered a conservation problem, as genetic loss may not translate to fitness loss. It is also difficult to estimate the relationships between inbreeding, effective population size, the proportion of HOR fish in the population, and population productivity (e.g., measured via recruits per spawner). While there has been some directed research on whether hatcheries affect the abundance and biomass of conspecific NOR populations, many of these studies struggle to identify mechanisms of lowered productivity (e.g., Pearsons and Temple 2010). It is often difficult to isolate a single cause for changes in population biomass: environmental conditions, harvesting, and other variables can be difficult to control for when looking for inbreeding consequences of hatcheries on NOR productivity (Waples et al. 2016).

Despite these difficulties, the genetic implications of hatchery production have been extensively reviewed in salmonids and it is not clear whether hatcheries always reduce genetic variability. Considering steelhead, a study of five supplemented rivers in B.C. failed to identify significant impacts of hatchery supplementation on the genetic structure of steelhead populations when native NOR are used for broodstock. This was perhaps due to low interbreeding between HOR and NOR populations in the wild (Gow et al. 2011). Heggenes et al. (2006) looked at genetic diversity before and after the establishment of a conservation hatchery in a steelhead population in the Kitimat River in B.C., and concluded that under its hatchery practices, there was little reduction in genetic variability or change in genetic structure. However, there may have been a reduction in rare alleles (perhaps evidence for "purifying selection" which can occur following inbreeding; Hedrick and Garcia-Dorado 2016).

Considering other salmonids, there has been some work looking at inbreeding depression in wild endangered salmon. Rollinson et al. (2014) found that inbreeding depression happened in some hatchery-supplemented Atlantic salmon streams in Nova Scotia where the NOR spawning population was low (approximately 200 spawners). But Hedrick et al. (2000) estimated effective population size from microsatellites and found that the Sacramento winter-run Chinook stock's effective population size stabilized. This is also the case in other Chinook hatchery programs. Over four generations of a Chinook hatchery program in the upper Yakima River, there were similar rates of inbreeding in a NOR population

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[12] In contrast to census abundance, "effective" abundance accounts for sex ratio and other factors that reduce the genetic diversity of breeding individuals from that of an ideal population (i.e., a population with stable abundance, equal sex ratio, and random mating).

supplemented with an all-NOR broodstock hatchery and a genetically isolated NOR population, despite different effective population sizes (Waters et al. 2020). Here, DNA sequencing found that inbreeding increased sharply in both the integrated and segregated populations following hatchery supplementation, but then declined in the fourth generation. Moreover, the amount of inbreeding was not significantly related to any fitness-related trait except for spawning timing in the integrated population (Waters et al. 2020).

Great care needs to be taken in evaluating these results due to the variation in-population sizes, species, and hatchery program—hatchery practices and fisheries management are essential to understanding the genetic effects of hatcheries on NOR populations (Brannon et al. 2004). Brannon et al. point out that when considering genetic variability, it is important to define what about genetic diversity is important (e.g., neutral genetic variation is different from the frequency of notable, fitness-relevant alleles). Some amount of inbreeding is also expected in natural populations; even without hatchery supplementation, inbreeding may be common in salmonids because they only spawn in their natal streams with fish that are likely related. For example, Waters et al. found a high degree of interbreeding even in a genetically segregated, all-wild Chinook population (2020).

Risk to the IFRS population and potential mitigation measures

Prior to any hatchery implementation, a clear definition of what level of inbreeding is cause for concern and quantitative measures should be developed to evaluate if inbreeding depression is happening, and, if it is, to assess whether the loss of genetic diversity impacts fitness. For example, managers could use microsatellite data and DNA analysis to estimate genetic variation at fitness-relevant alleles (Heggenes et al. 2006). Using wild brood can mitigate against inbreeding depressions, as can any actions that reduce the prevalence of HOR spawners in natural spawning areas (e.g., mark selective fisheries).

Unlike salmon, however, residual steelhead present important considerations for any supplementation program. The NOR population is divided into residual and anadromous subpopulations, each of which may be genetically segregated with distinct genotypes. As a result, there may be more genetic diversity in the population complex as a whole than what is in the anadromous component and the wild population may be large with relatively low potential for inbreeding. If low marine survival is causing the rainbow trout life history to be much more common than the steelhead life history, then a hatchery program may have complex implications for the abundance of steelhead spawners. To further mitigate the risk of hatcheries on genetic diversity, implementing measures to protect both life history types should be considered.

Managers have to make difficult choices about the cost of information (especially given the high cost of genotyping and genetic research), the possibility of adaptive management, and the risks of action versus the risks of inaction. Where possible, it may be worth treating hatchery implementation as an experiment. If loss of genetic variability is considered an important concern for a prospective hatchery program, constructing a cladogram from genetic analysis of the subpopulations is likely to be beneficial. Establishing a baseline of genetic diversity prior to starting hatchery operations is vital, then managers can take annual samples of, e.g. microsatellite data, assess changes in genetic variation, and modify the hatchery program to see how much it impacts genetic structure in the population over time. This way, changes in genetic diversity can be used to learn how to manage the hatchery to reduce risk. Importantly, changes in genetic variability and genetic structure should be empirically measured for

both the steelhead and rainbow trout populations to minimize unintended consequences on the residual population.

Hypothesis G2: Domestication Selection: Maladaptation of HOR fish after release into the natural environment leads to reduced survival, growth or reproduction in HOR (and NOR after HOR-NOR interbreeding). Selection for traits that were beneficial in the hatchery environment reduce maximum recruits produced per spawner in adult HOR spawning naturally (and in NOR fish after HOR-NOR interbreeding)

Mechanisms and evidence of effects

Hatchery supplementation can reduce genetic diversity in the wild-spawning population, reduce within- and across-population diversity, and can reduce the prevalence of adaptive traits as a result of domestication within hatcheries (Naish et al. 2007; Hayes et al. 2013; HSRG 2014). In addition to loss of genetic diversity from hatchery activity, there may also be fitness consequences to hatchery supplementation as a result of domestication selection. In hatcheries where broodstock are selected non-randomly, where hatchery fish adapt to the hatchery environment, or where hatchery conditions do not subject the same selective pressures as those experienced by wild-rearing fish, hatchery origin fish may exhibit a different phenotype than that selected for in the wild (Busack and Currens 1995; Araki et al. 2008; Hayes et al. 2013). Even in first-generation hatchery fish (i.e., those from natural broodstock parents), relative reproductive success can be lower than that of natural conspecifics (Schroder et al. 2008; Chilcote et al. 2011; Christie et al. 2014). This can have implications for wild-spawning populations when mixed spawning of hatchery- and wild-origin fish reduce population-wide productivity. Differences in fitness persist even when hatchery and natural origin juveniles are reared in a common environment, suggesting that performance differences are a function of genetic or epigenetic factors, not just rearing environment (Hayes et al. 2013). If traits such as growth rate or outmigration rate have a genetic basis that differs between HOR and NOR populations (via domestication or post-release selection; Reisenbichler et al. 2004; Hayes et al. 2012), there may be long-term productivity consequences of interbreeding. However, research into the genetic underpinning of fitness-linked traits like reproductive success and migration timing is ongoing (e.g. Prince et al. 2017; Waples and Lindley 2018; Ford et al. 2020).

Risk to the IFRS population and potential mitigation measures

While these risks can undermine conservation outcomes of hatchery supplementation programs, in-hatchery practices can help to mitigate each of fishery, ecological, and genetic risks. For example, ecological interactions and disease transmission in the wild may be minimized by releasing hatchery fish during periods of the year when few native juveniles are present. Mark-selective fisheries can target hatchery origin adults when hatchery releases are externally marked and fishing methods selective (HSRG 2014), but their ability to reduce the HORs' genetic contribution to the next generation depends on the effectiveness of marking programs (Naish et al. 2007). In addition to minimizing the abundance of HOR spawning in the wild, loss of genetic diversity can also be mitigated against by integrating a high proportion of NOR fish into the broodstock.

To inform hatchery program planning, managers should consider life cycle models to assess plausible long-term fitness consequences of different hatchery programs. For example, managers could develop scenarios using the All-H Analyser (AHA) modelling tool (HSRG 2020). Given assumptions about population fitness and how it is influenced by long-term patterns of natural and domesticating selection, AHA projects long-term effects of different hatchery and selective harvest management strategies on the phenotype and fitness of wild and hatchery produced fish. As part of their review of hatchery supplemented salmonid populations in the Columbia Basin, the HSRG created and applied the AHA model to evaluate management options given assumptions about habitat, hydrology, harvest, and hatchery programs (Paquet et al. 2011). This tool has been used extensively to evaluate hatchery and fishery management options for the Columbia River salmon and steelhead stocks (Paquet et al. 2011; HSRG 2014), and has been extended to investigate how hatchery practices, in tandem with selective harvest of marked hatchery fish, can meet population and genetic targets in western British Columbia (Withler et al. 2018); see the section, "

Exploratory modelling of hatchery production: AHA model".

Clearly hatchery practices can mitigate many of the risks from domestication selection. However, a more thorough understanding of the population structure is important for both management and life cycle modelling. If steelhead and rainbow trout are one interbreeding population in the interior of B.C., then it is likely that rainbow trout should be included in the broodstock and as a contributing source of genetics for the overall population. However, if the program goal is to increase the number of steelhead spawners, trying to include the full population in the broodstock could counteract selecting for and enhancing the steelhead component.

Hypothesis G3: Epigenetic changes that upregulate traits (e.g., growth) in HOR fish cause higher mortality in NOR fish in natural environments after HOR fish are released, possibly in the next generation if traits are carried to the offspring of naturally spawning HOR adults

Mechanisms and evidence of effects

In addition to genetic change, there is also potential for epigenetic differences to emerge between NOR and HOR fish. Epigenetics involves changes to DNA transcription (i.e., turning the expression of certain genes on or off) without altering the DNA sequence itself. Mechanisms of epigenetic change include methylation and demethylation, the addition or removal of a methyl (CH_3) group to DNA (these methyl groups, if present, physically prevent transcription of the gene it is attached to). For example, a gene that is linked to high growth rate may only be activated (de-methylated) in some environments, such as hatcheries, in response to environment cues, like abundant food. Some epigenetic changes persist for the life of the organism even if the environment changes (e.g., after release from the hatchery into a low-food environment). In some cases, methylation can even be passed via eggs and milt to progeny. For example, if the post-release hatchery fish does not turn off genes related to high growth rate in response to the change in environment (i.e., lower food availability), the modified gene expression may be harmful. Further, if the epigenetic "on" marker is passed to the eggs or milt, the wild offspring of the hatchery fish may also have the "high growth" gene turned on. This can therefore lead to poor performance of hatchery fish after release and poor performance of their progeny that are spawned in natural streams.

Even within one generation of hatchery rearing, fitness differences between hatchery and naturally reared fish can emerge without evidence of genome-wide genetic changes (Christie et al. 2012a). Because epigenetic processes do not involve changes to DNA sequences, they differ fundamentally from genetic selection that acts to change the frequency of alternative DNA sequences in a population. Epigenetic processes have the potential to produce large changes in important characteristics, such as growth rate, in a much shorter period than genetic selection. These changes can also be plastic throughout an individual's lifetime, adapting to different environmental cues. Only if epigenetic changes are permanent over an individual's lifetime and heritable should we expect a loss in NOR productivity as a result of epigenetic changes from hatchery rearing and HOR-NOR interbreeding. A potential explanation for observed fitness differences between natural and hatchery-reared fish, then, lies in developmental plasticity as a result of epigenetic changes. Because environmental conditions differ between hatchery and wild-reared fish (e.g., temperature, feeding conditions, predator presence, rearing density, and water quality), stress-induced epigenetic changes during development could result

36

in disparities in the fitness of adults (Jonsson and Jonsson 2014). Epigenetic changes induced by the hatchery environment are important because they provide a non-evolutionary mechanism to explain: 1) poor survival of hatchery smolts without evolution of maladaptive traits and 2) the presence of maladaptive traits in the progeny of HOR spawning in the wild.

However, our understanding of the epigenetic processes related to hatchery rearing is relatively recent. When comparing hatchery-reared and wild fish, epigenetic changes are seen in a few key genome regions, even when comparing hatchery programs across wide geographic distances (Le Luyer et al. 2017; Koch et al. 2023; but see a contrasting study by Blouin et al. 2010). These genome regions with high rates of epigenetic change contain genes that are linked to stress and immunity responses, embryonic development, liver function, growth, smoltification, and spawn timing (Gavery et al. 2018; Christensen et al. 2021; Nilsson et al. 2021; Koch et al. 2023). Epigenetic modifications in these regions may also influence residency patterns in supplemented steelhead and rainbow trout populations (Kendall et al. 2015; Baerwald et al. 2016).

There are several limitations to our current understanding of how observed epigenetic differences might impact larger population dynamics and fitness in steelhead. Although there is overlap in which genome regions tend to be differently methylated in hatchery- and naturally-reared salmonids, the change is not uniform—hatchery and wild-reared fish are not consistently hyper- or hypo-methylated in modified gene regions (Koch et al. 2023). Due to the complexities of gene expression, if a genome region becomes methylated or demethylated it may not necessarily result in altered phenotype (Leitwein et al. 2021; Christensen et al. 2021; Koch et al. 2023). Similarly, lack of methylation does not definitively prove that there has been no epigenetic modification at that region (Blouin et al. 2010), as different environmental cues experienced in the hatchery and wild environment may cause methylation and subsequent demethylation of the same genes.

Ultimately, even if epigenetic regulation triggers a phenotypic change, epigenetic changes may not persist within an individual's lifetime, let alone between generations. Some salmonids maintain epigenetic markers of rearing environment after oceanic migration (Leitwein et al. 2021); this creates the possibility for some heritable epigenetic changes to establish in the wild population when hatchery reared fish interbreed with the natural population. Epigenetic differences between the sperm cells of hatchery and naturally reared fish suggest that epigenetic markers acquired during rearing may be heritable to progeny spawned in the wild (Ford et al. 2016; Nilsson et al. 2021); however, the methylation differences that emerge in early life may be 'overwritten' by adulthood as a result of ongoing epigenetic change through life (Gavery et al. 2018). There are to date no studies we are aware of that examine epigenetic modifications in steelhead egg cells, despite the likely importance of maternal effects on developmental plasticity.

Risk to the IFRS population and potential mitigation measures

There is a high degree of uncertainty over whether epigenetic changes in gene expression associated with hatchery rearing will result in lower productivity of wild-reared fish. While there is evidence for consistent epigenetic differences between wild and hatchery reared steelhead, these outcomes do not necessarily result in lower fitness of the HOR subpopulation, particularly when the epigenetic changes are later undone (e.g., when a gene that was methylated in the hatchery is demethylated after release, this reverts the epigenetic change and may subsequently revert the altered phenotype and its fitness

consequences). Moreover, even if epigenetic changes persist to adulthood, it is unclear whether methylation patterns will be transmitted to wild reared offspring of hatchery origin parents.

To lower the risk of epigenetic changes to the genome as a result of hatchery rearing, the hatchery environment can be enhanced to be more similar to nature, e.g., by ensuring food types and abundance conform to those typical in the wild, by lowering rearing densities, and by providing tank cover and complex habitat structures (Self et al. 2018). For example, the Wild Fish Surrogate Program at Oregon State University seeks to develop techniques to produce more wild-like fish from hatcheries, such that these fish are better stand-ins for wild fish in cases where wild abundance is too low to meet research needs (Cogliati et al. 2023). Although surrogate fish have more wild-like phenotypes than fish from conventional hatchery rearing environments, their phenotypes are not always intermediate and it is yet unclear the extent to which the modified hatchery rearing environment reduces plausible epigenetic consequences of hatchery production.

Exploratory modelling of hatchery production: simple Beverton-Holt model

Modelling production over different levels of marine survival

A simple model that includes a density dependent egg-smolt phase, followed by a density-independent smolt-adult phase, can help us understand the mechanisms that drive the extreme variation in steelhead population abundance (Appendix 2: Beverton-Holt stock-recruit analysis of hatchery-wild interactions in Steelhead). Strong density dependence at the egg-smolt stage means that juvenile abundances can be relatively stable across a wide range of spawner abundance because egg-smolt survival is lower at high egg density (Ward 2000; Decker et al. 2015, Figure 5). In contrast, adult abundance is driven by highly-variable, density independent marine survival (Figure 6).
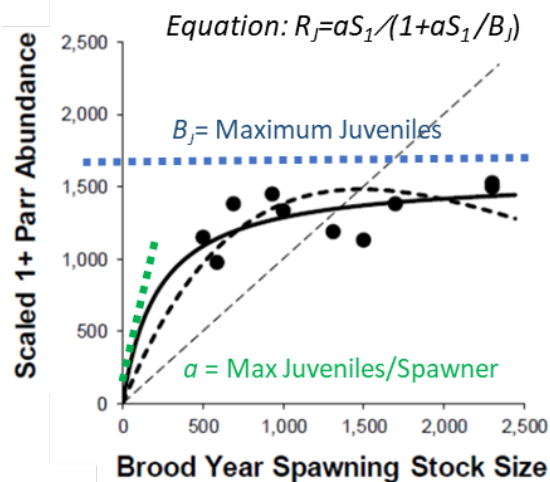
Figure 5. Reproduction of Decker et al. (2015; Figure 7d). Juvenile recruitment curves (BH solid line & equation, Ricker dashed line) for the Thompson River steelhead/rainbow population. Spawning stock abundance only includes steelhead. S_1=Female Spawner Abundance in Generation 1, R_J=Smolt Recruits, B_J=maximum smolt abundance at large S_1, $a= R_J/S_1$ at low spawner abundance. Approximate values for B_J and a have been added.
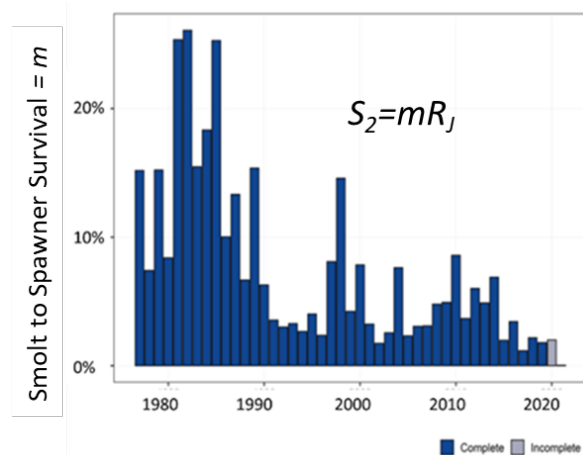
Figure 6. Smolt to adult survival for Keogh River steelhead. S_2=Spawner Abundance in Generation 2, and m=Smolt to Spawner Survival.

The data in Figure 5 and Figure 6 can be used to understand why adult abundance varies. We observe very large fluctuations in spawner abundance because m can vary by about 20x through a combination of decade long trends and year to year fluctuations (Figure 6). In each generation, the population moves toward a stable equilibrium where $R_A=S$ but equilibrium is never observed because m, and to a lesser degree a and B_J, are constantly changing. Instead, the population tracks a constantly changing replacement abundance (R_R) but never reaches equilibrium.

This type of time variation in recruitment parameters, which results in non-stationary R vs S curves, are observed in steelhead populations (e.g. Wilson et al. 2022) and many other fish species (Szuwalski et al. 2015).

Understanding what is happening to smolt abundance and egg-smolt survival in Figure 6 is the key to understanding how the population may respond to the increased mortality stress represented by low marine survival. For the parameter values that approximate Thompson River observations, R_R for smolts declines slowly across a wide range of marine survivals (i.e. >7%) but then declines rapidly when marine survival falls below 6% before the population becomes non-viable at $m < 1.7\%$ (Figure 7).

The hypothesized effects of hatchery supplementation can be modeled in terms of their effects on a and B_J. For a given value of m, positive changes in either parameter produce a positive response in smolt replacement abundance (i.e., R_R) and vice versa for negative changes in a or B_J. Hatchery supplementation increases both smolts/female spawner (i.e., the a parameter) and maximum smolt abundance (i.e., the B_J parameter) of the combined hatchery/wild population (Appendix 2: Beverton-Holt stock-recruit analysis of hatchery-wild interactions in Steelhead). However, if wild fish are viewed as an independent population[13], the opposite occurs. For example, if wild fish are removed from the population to be used for hatchery broodstock, then wild smolts/female spawner must be lower, and if hatchery juveniles compete with wild juveniles, then the capacity of the habitat available for wild fish (i.e. B_J) is lower (Appendix 2: Beverton-Holt stock-recruit analysis of hatchery-wild interactions in Steelhead).

The risks to the wild population are amplified by lower marine survival. When marine survival is high, small changes in a or B_J have little effect on the viability of the wild population; the population responded more acutely to the increase in mortality stress when marine survival rate dropped below 7%. Recent estimates of marine survival are lower than this 7% threshold (see Keogh estimates in Figure 7 and Kendall et al. 2017), suggesting that hatchery supplementation risks would be relatively high compared to years with higher marine survival.

See Appendix 2: Beverton-Holt stock-recruit analysis of hatchery-wild interactions in Steelhead for further details on a stock-recruit analysis of hatchery-wild interactions in steelhead.

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[13]For example, under the US Endangered Species Act, hatchery fish are only considered to be part of a conservation unit if the hatchery program is designed to restore reproduction of natural origin fish https://www.federalregister.gov/documents/2005/06/28/05-12349/policy-on-the-consideration-of-hatchery-origin-fish-in-endangered-species-act-listing-determinations see also https://www.pac.dfo-mpo.gc.ca/fm-gp/salmon-saumon/wsp-pss/policy-politique-eng.html#policy
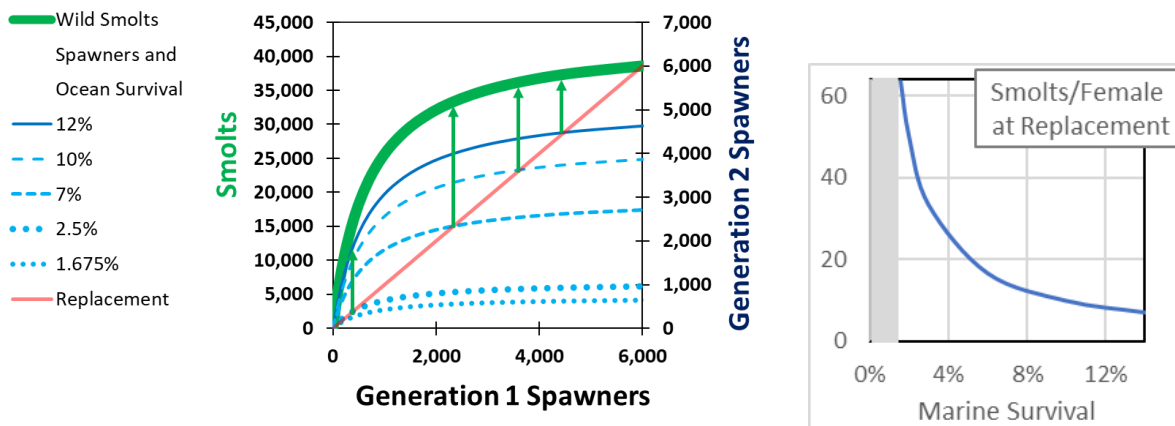
Figure 7. Smolt abundance (green line), and Generation 2 (G2) spawner abundance (blue lines) versus G1 spawner abundance, over a range of marine survivals. The red line represents replacement, where G2 = G1 spawner abundance. Smolt abundance at equilibrium is represented by the tips of the green arrows. The blue lines represent the same equation ($S_2 = m(aS_1/(1 + aS_1/B_J))$), where m is Marine Survival, a= 60 smolts/female and B=40,000 smolts. Details of the derivation of the equation parameters are given in Appendix 2: Beverton-Holt stock-recruit analysis of hatchery-wild interactions in Steelhead. The inset shows that smolts/female at replacement increases as a compensatory response to lower marine survival until it reaches the maximum value of smolts/female (60) and the population is no longer viable (grey area).

Exploratory modelling of hatchery production: AHA model

While the analysis above explores how the hypothesized effects of hatchery supplementation can affect the *a* and *B* parameters applied in a BH model, this modelling approach is limited by its handling of inter-generational productivity loss. In this simple BH model, these productivity losses are fixed and deterministic—ignoring inter-generational loss of fitness as a result of cumulative genetic effects. Moreover, changes to *a* and *B* were not derived quantitatively.

To more realistically capture genetic consequences of the hatchery program, we applied the All-H Analyzer model (AHA), a commonly applied and quantitative modelling approach that simulates how fitness effects of domestication manifest over a 100-generation timespan (Paquet et al. 2011; HSRG 2020). The AHA model has several advantages over the simpler BH modelling approach documented above and in Appendix 2: Beverton-Holt stock-recruit analysis of hatchery-wild interactions in Steelhead. First, the AHA model explicitly addresses fitness consequences that accumulate through generations via drift in fitness-related phenotypic traits (cf. Ford 2002). By explicitly modelling natural selection in wild spawning areas as well as domestication selection in the hatchery—both as functions of the ratio of HOR:NOR spawners in the environment—AHA more realistically captures long-term genetic consequences of different hatchery practices on NOR productivity. The AHA model therefore allows for evaluation of hatchery programs that differ in terms of the size of broodstock collected for supplementation and the abundance of HOR spawners allowed on hatchery grounds. Similar to the above modelling framework, AHA incorporates density dependent production of NOR fish on natural spawning grounds via a three-stage BH model, allowing for fitness consequences that are more significant in early life than later stages. Additionally, the AHA framework provides a useful metric of long-term fitness loss, proportionate natural influence (pNI):

$$pNI = \frac{pNOB}{pNOB + pHOS}$$

where pNOB is the proportion of natural origin fish in the broodstock, and pHOS is the proportion of hatchery origin fish spawning in natural areas. pNI is considered a useful approximation for the equilibrium distance between a population's current phenotypic trait and the trait with maximum fitness, which gives general guidance about the direction of the hatchery program in terms of fitness consequences. This metric is useful for setting targets and assessing the relative genetic risk of a hatchery program on the NOR population.

Applications of the AHA model in B.C. and elsewhere

Over the past decade, management agencies in B.C. have been building capacity to use the AHA model to inform hatchery program goals and management practices. We are aware of at least two applications of AHA in B.C., both to improve the management of Chinook hatchery programs. First, DFO researchers used the AHA model to develop genetic guidelines and quantitative benchmarks to assess hatchery influence on wild populations (Withler et al. 2018). This work identified quantitative benchmarks for pNI that relate to different biological status categories, and identified what information is needed to inform this. They found that pNI outcomes could be maximized by minimizing the size of the hatchery program, manipulating broodstock composition, and selectively harvesting HOR returns to natural spawning

areas. This report concluded with five biological categories of populations differentiated by the level of hatchery supplementation, each with targets for the proportion of HOR spawners in the wild (pHOS), proportion of NOR broodstock, and the pNI associated with these combinations (

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Table 3. Proposed designations for individual Chinook salmon populations that vary in the degree of influence of integrated hatchery programs and the proposed genetic guidelines for hatchery management. Modified from Withler et al. 2018. pHOS refers to the proportion of hatchery origin spawners counted at census; it does not account for relative reproductive success. pNOB: proportion of natural-origin broodstock, pNI: proportionate natural influence.

Category	pHOS (census)	pNOB	pNI	Definition
Wild	≤ 0.03	N/A	N/A	Designated wild[14] populations that do not have hatchery programs (for at least two generations); strays from out-of-basin hatchery production are limited to <3% per year.
Wild-stray influenced	> 0.03	N/A	N/A	Population receives strays from an out-of-basin hatchery. A very large fraction of fish are wild but gene flow modelling suggests a long-term decline in pNI as the pHOS increases.
Integrated wild	≤ 0.23	≥ 0.77	≥ 0.80	Hatchery production is managed to keep wild fish ≥50% of the spawning population.
Integrated-transition	≤ 0.53	≥ 0.47, < 0.77	≥ 0.5, < 0.80	pNI ≥ 0.5 ensures natural-origin influence predominate but wild fish are in the minority.
Integrated-hatchery	> 0.53	< 0.47	< 0.5	Net gene flow from hatchery environment and most fish are hatchery origin. Few fish are wild.

Then, in 2019, members of the Pacific Salmon Commission and DFO's Salmonid Enhancement Program were trained on and applied the AHA model to aid management of West Coast Vancouver Island Chinook hatcheries (Ramshaw and Mahoney 2019). This work supported integrated planning of the hatchery program, including identifying populations where there is potential to improve harvest value and minimize negative interactions between wild and hatchery populations. To our knowledge, there has been no application of the AHA tool to assess Canadian steelhead populations.

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[14] Under Canada's Wild Salmon Policy (DFO 2005), a fish is wild if they and both their parents were born in the wild.

Beyond British Columbia, the Washington Department of Fish and Wildlife (WDFW) has recently applied the AHA model in their assessment of 15 steelhead hatchery programs in the state (Marston and Huff 2022). The goal of these hatchery programs is primarily to create harvest opportunities, and many programs seek to genetically segregate hatchery fish from natural origin conspecifics. Following the implementation of the 2008 State-wide Steelhead Management Plan, the state has set allowable levels of genetic integration (via targets for the maximum proportion of hatchery-origin fish on spawning grounds, pHOS, and geneflow within the hatchery). For integrated NOR-HOR populations, WDFW applied the AHA model to recommend maximum smolt release sizes that meet policy requirements. In cases where the NOR population is not meeting production targets, WDFW recommends a reduction in the hatchery program. In addition to specific recommendations for each hatchery program, the report authors identified general recommendations (e.g., taking a maximum of 30% of NOR returns for broodstock, allowing volitional juvenile release, and establishing selective HOR fishing that ensures meaningful harvest opportunities at high rates).

Other applicable modelling approaches that assess the long-term outcomes of hatchery supplementation often assume genetic segregation (e.g., the Proportion Effective Hatchery Contribution; Warheit 2014; and Hoffmann's Demographic Geneflow Model; Hoffmann 2014), or are focused primarily on ecological effects (e.g., Pearson and Busack's Predation, Competition, and Disease model; Pearsons and Busack 2012). Additionally, most AHA applications focus on providing advice to existing hatchery programs with respect to targets set in policy documents (c.f. Marston and Huff 2022).

Our goal is not to assess a particular hatchery program, but to ask a broader question: under which conditions would a hatchery program increase the abundance of NOR fish in the IFRS population? We assess long-term population outcomes in terms of genetic risk, abundance, and productivity under alternative hatchery program scenarios, but do not prescribe any particular scenario. A summary of the results is presented below. See Appendix 3: All-H Analyzer Model Results for more details on our application of the AHA model to IFRS.

Hatchery scenarios modelled with the AHA framework

Unlike the simpler BH model in the previous section, which explored only one plausible outcome of hatchery supplementation in terms of loss of productivity, the AHA model quantifies changes to the a and B parameters that result from a specific hatchery program. By calculating the genetic outcomes that arise when there is interbreeding between HOR and NOR populations, AHA can be used to compare specific hatchery programs in terms of their relative long-term effects on the NOR population. Therefore, we can use the AHA model to compare different types of hatchery programs, not just the presence or absence of a program as per the last section.

To assess how different hatchery practices affect the status of the IFRS population along these metrics, we assume that hatchery program managers have three major "levers" of hatchery management. First, managers can modify the number of NOR fish taken for broodstock. Second, managers may limit the percent of NOR returns taken for broodstock. Finally, we consider a scenario where a manager could visibly mark all hatchery releases and implement a mark-selective fishery program.

We consider three plausible hatchery programs as management scenarios to be simulated with AHA:

1. "Status quo": Using parameter estimates considered representative of the current IFRS population (Table A 3), this scenario projects the system without a hatchery program. No fish are taken for broodstock, no HOR fish are reared or released, and all NOR returns are allowed to spawn naturally without any freshwater fishery-related mortality.
2. "Hatchery without selective harvest on HOR": In this scenario, we simulate a minimal hatchery which takes in 10 NOR fish for broodstock (up to a maximum of 10% of the returning NOR spawners). All fish reared in the hatchery that survive to smolt stage are released and assumed to migrate to sea, where they experience 50% the marine survival of NOR conspecifics. Like scenario 1, there is no freshwater fishery mortality.
3. "Hatchery with selective harvest on HOR": This scenario is identical to scenario two in terms of hatchery production, and differs only by including a freshwater selective fishery for HOR returns. This scenario assumes that hatchery releases are visibly marked (e.g., with an adipose fin clip) and that a selective fishery would develop with the ability to remove 60% of returning HOR adults before they spawn on natural spawning grounds. We assume 0% incidental mortality on NOR adults from this selective fishery.

While there are currently no hatchery program rules in place to inform management of the IFRS population, we assumed that the hatchery program would be a semi-integrated program in which only NOR adults are taken in for broodstock (i.e., 100% natural origin broodstock, NOB; following the *Steelhead Stream Classification Policy* 2005), and that anadromous HOR adults returning to their natal rivers would be allowed to spawn naturally. Because we assume that the hatchery program would exclusively use NOR for broodstock, we assume that the IFRS population would be classified as one of the three integrated types in

, most likely the "integrated wild population" type (with a target pNI of at least 0.8).

The final management lever—selective harvest—can reduce the prevalence of HOR spawners in natural spawning grounds and limit NOR-HOR interbreeding. Selective removal is only possible when the hatchery releases visibly marked individuals (e.g., via an adipose fin clip). We therefore include scenarios with 0% selective removal rate on HOR returning adults, and scenarios with 60% selective harvest (considered the maximum feasible removal rate; Rob Bison, pers. comm) to assess whether hatchery program goals may be better met if adult hatchery fish are removed by a selective fishery.

Metrics to compare hatchery programs

To have a quantitative means of comparing the hatchery programs described above, the AHA model reported several metrics related to population abundance, productivity, and genetic integrity under a given hatchery scenario.

The first metric we consider is NOR spawner abundance. We define a NOR fish as any fish spawned in the wild (unlike the definition of "wild" according to Canada's Wild Salmon Policy, which defines a wild fish as one spawned in the wild from NOR parents). In recent decades, IFRS NOR abundance has been declining (Figure 1), and hatchery supplementation should increase or at least stabilize the population of

naturally spawned steelhead to be considered successful. We therefore compare NOR abundance under several plausible hatchery management scenarios as well as under the status-quo, no supplementation with hatchery production.

Second, we consider several outcomes that reflect population productivity. Because the AHA model explicitly calculates loss of fitness and productivity with increasing integration of domesticated HOR fish (unlike simpler approaches like the BH modelling above), we can track loss in both of the a and B BH parameters as a function of interbreeding between the NOR and HOR populations. Long-term expected fitness loss can also be summarized with pNI, reported for each hatchery scenario in the text below. In reporting results from the AHA model, we either show timeseries of results (demonstrating the change in metrics over subsequent generations of hatchery integration), or the expected long-term result of the hatchery program (i.e., at the 100th generation).

Generating pessimistic scenarios with AHA

We also explored what conditions would be required to see NOR abundance declines under hatchery supplementation. Results of the base case scenarios suggested that a modest hatchery program could be expected to improve the long-term abundance of NOR spawners. However, we found that NOR population abundance can decline by changing the values of two key parameters in the AHA model: the relative reproductive success of HOR in the wild (RRS), and the relative marine survival rate of HOR versus NOR.

AHA model results: NOR spawner abundance

NOR spawner abundance under base case scenarios

First, we consider how different hatchery programs influence the abundance of NOR spawners returning after 100 generations of hatchery supplementation (we chose 100 generations to represent the long-term equilibrium of the hatchery system, according to AHA model assumptions of long-term dynamics). When varying both the NOB abundance and the maximum % of NOR returns to be integrated as broodstock, we expect to have greater NOR abundance with a larger hatchery program (Figure 8, Figure 9). If a mark-selective fishery is implemented with a removal rate of 60%, we see lower NOR abundance compared to the no-harvest case throughout the time series.

Interestingly, our results demonstrate that even if a significant hatchery program were established (i.e., with up to 100 NOR fish taken for broodstock in each year), this would not be able to recover the NOR population to historical abundances. The maximum simulated hatchery program would only produce ~660 NOR spawners, compared to historical abundances in the low 2,000s (see Figure 1). Similar to results under the simpler BH model, marine survival is highly influential here; only in simulations with marine survival surpassing 3% does the AHA model predict NOR abundance approaching or surpassing 2,000 individuals (Figure 8, and Figure 11). Because the population appears to be dropping, to recreate current low abundance of the NOR spawner population we assumed smolt-adult return rate (SAR) of NOR fish was only 1.75% in our base case scenarios, with HOR SAR assumed to be only half this value (e.g. Melnychuk et al. 2014). We found that this low SAR is likely to limit the benefits of the hatchery

program, and the AHA model predicted that supplementation can only slightly increase NOR abundance when a population is experiencing low marine survival and the benefit of the hatchery program declines as marine survival of NOR fish improves (Figure 11). These results reflect those from the simpler BH model (e.g., Figure 7).

NOR spawner abundance under pessimistic hatchery scenarios

First, considering RRS, we assumed a default RRS of 0.4 (within the range observed for steelhead reported in Christie et al. 2014). When we lowered the RRS from our default assumption of 0.4, the benefits of the hatchery program on NOR abundance declined. AHA predicted that when RRS drops to very low values (i.e., 3% or lower), no hatchery program of any size can increase the abundance of NOR spawners compared to a non-supplemented case (Figure 12).

Second, considering the influence of relative HOR marine survival on hatchery outcomes, we found that as the SAR of HOR releases decreases, so too does the benefit to NOR abundance from the hatchery. In an extreme case, when we drop HOR SAR to 7% or less that of NOR, NOR abundance was worse than when no hatchery is implemented (Figure 13). In these cases, the benefit to early life survival in the hatchery is not enough to overcome the poor survival and reproductive potential of post-release HOR, such that the collection of NOR for broodstock results in long-term population decline.

Figure 8. Abundance of natural origin returns (NOR) following 100 generations of a hatchery supplementation program, where the program varies in terms of the maximum number of broodstock taken into the hatchery (y-axis) and the maximum percent of the NOR returns represented by broodstock take (x-axis). The points in the lower left corner represent scenario 1 (status-quo, where no hatchery is initiated) and scenario 2 (a hatchery with up to 10 NOR (up to 10% of the NOR return abundance) taken for broodstock). Values on the isopleth represent NOR abundance; darker colors occur in areas with higher NOR abundance.
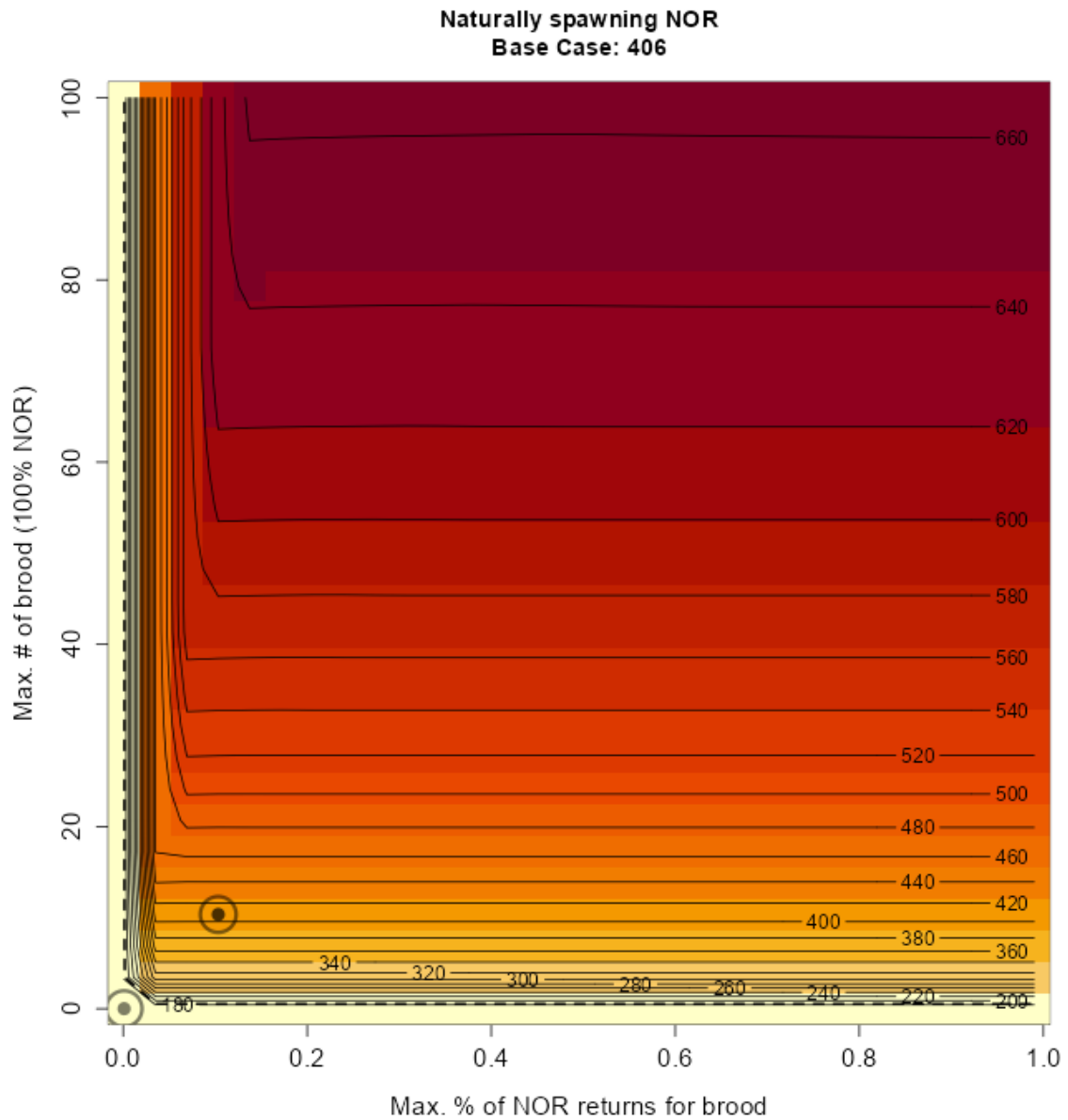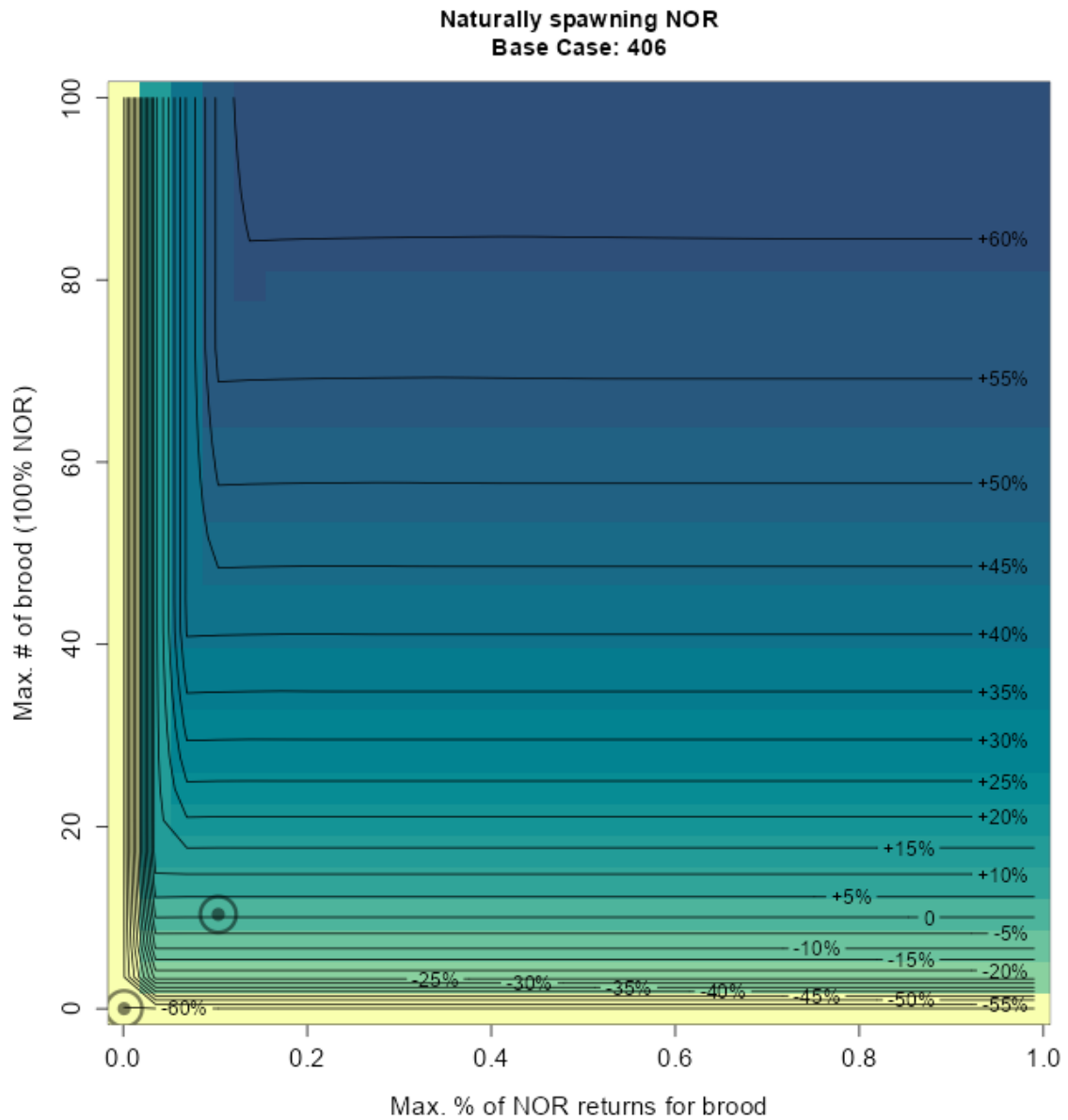
Figure 9. Abundance of natural origin returns (NOR) following 100 generations of a hatchery supplementation program, where the program varies in terms of the maximum number of broodstock taken into the hatchery (y-axis) and the maximum percent of the NOR returns represented by broodstock take (x-axis). The points in the lower left corner represent scenario 1 (status-quo, where no hatchery is initiated) and scenario 2 (a hatchery with up to 10 NOR (up to 10% of the NOR return abundance) taken for broodstock). Values on the isopleth represent % difference from the status-quo; darker colors occur where the hatchery would result in higher NOR abundance than the status-quo.

49
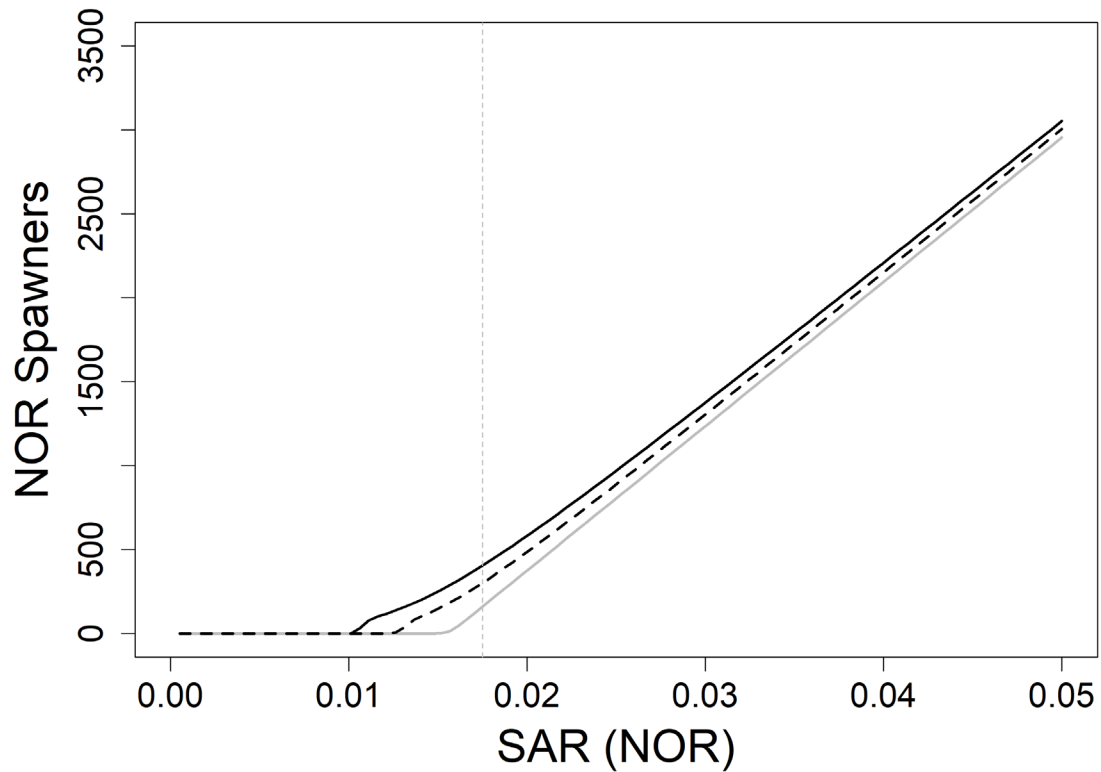
Figure 10. The relationship between smolt-adult return rate of NOR adults (SAR (NOR)) and the abundance of natural origin returns (NOR) at the 100th generation of a hatchery supplementation program (scenario 2, 10 NOR for broodstock or up to 10% of the NOR returning abundance). The grey line represents expected outcomes under the status-quo management scenario, in which no hatchery program is implemented, and no loss in fitness is expected. The solid black line shows scenario two (which breeds 10 NOR in each generation, with 0% selective harvest on HOR returns), while the dashed black line shows scenario three (10 NOR in each generation, with 60% selective harvest on HOR returns).The vertical dashed line represents the NOR smolt-to-adult return rate assumed in base case scenarios (see Table A 3).
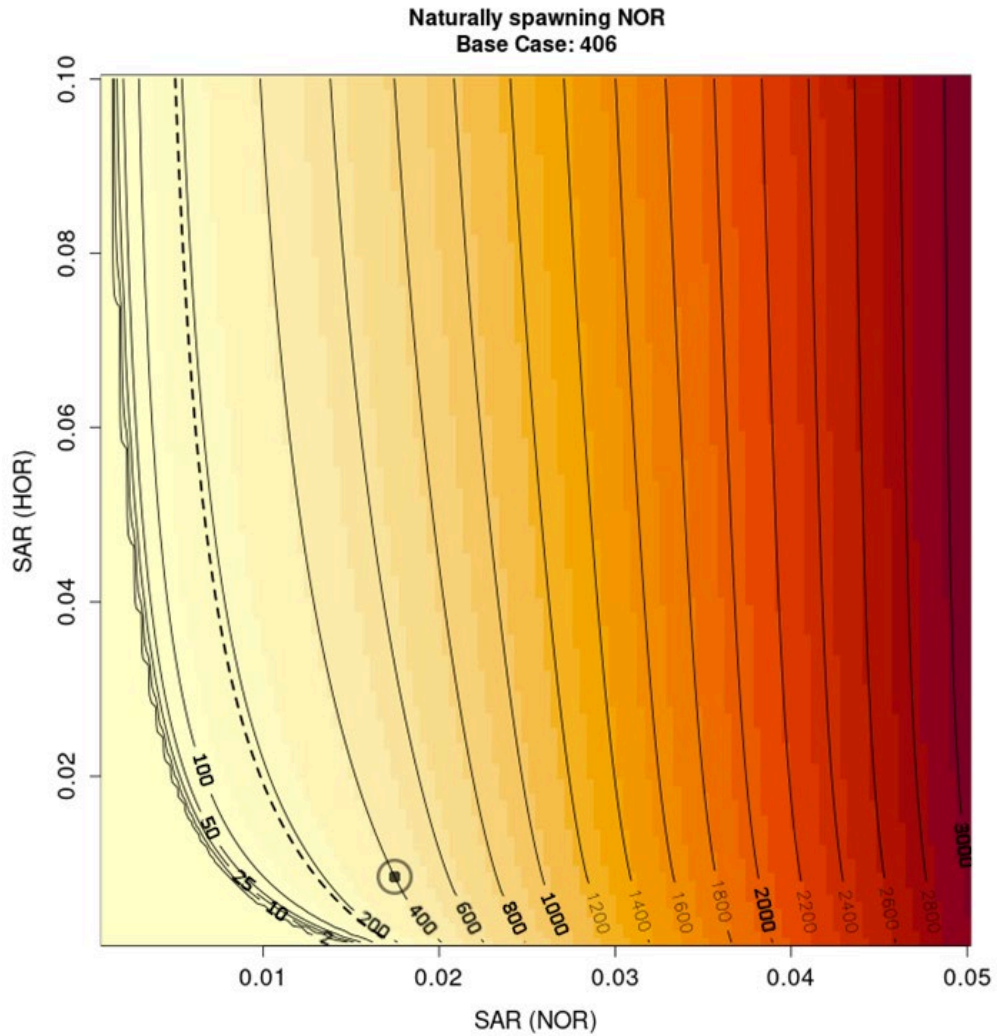
Figure 11. Sensitivity of the abundance of NOR spawners in the 100th generation to assumptions of NOR and HOR marine survival rates for scenario 2, a minimal hatchery (10 NOB, maximum 10% of the NOR returns) with 0% selective harvest mortality on HOR returns. The black point represents the base case assumption of marine survival rates, and the value in the title shows NOR abundance under those assumed values. The dashed line shows abundance under the non-supplemented base case 1. Values on the isopleth represent NOR abundance; darker colors occur in areas with higher NOR abundance.
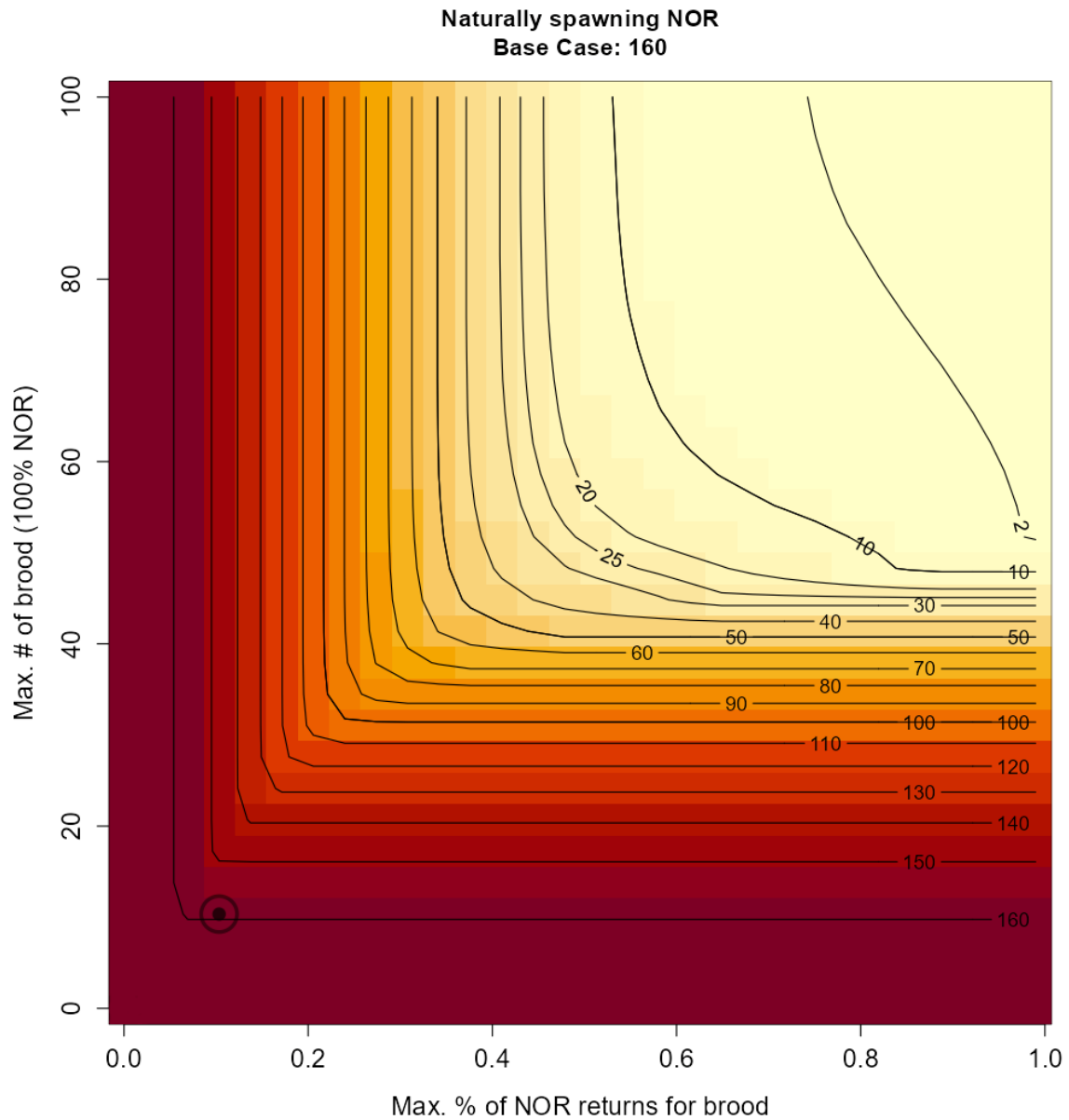
Figure 12. Results of exploratory modelling of pessimistic hatchery scenarios, showing the abundance of NOR spawners in the 100th generation to assumptions of different hatchery programs. Unlike Figure 8, this is a pessimistic case where the relative reproductive success (RRS) of HOR compared to NOR spawners is arbitrarily set at 0.03 (compared to 0.4 in the base case; 0.03 is selected to generate negative outcomes of a hatchery program under this parameterization). The black point represents the base case assumption of marine survival rates, and the value in the title shows NOR abundance under those assumed values. Values on the isopleth represent NOR abundance; darker colors occur in areas with higher NOR abundance.
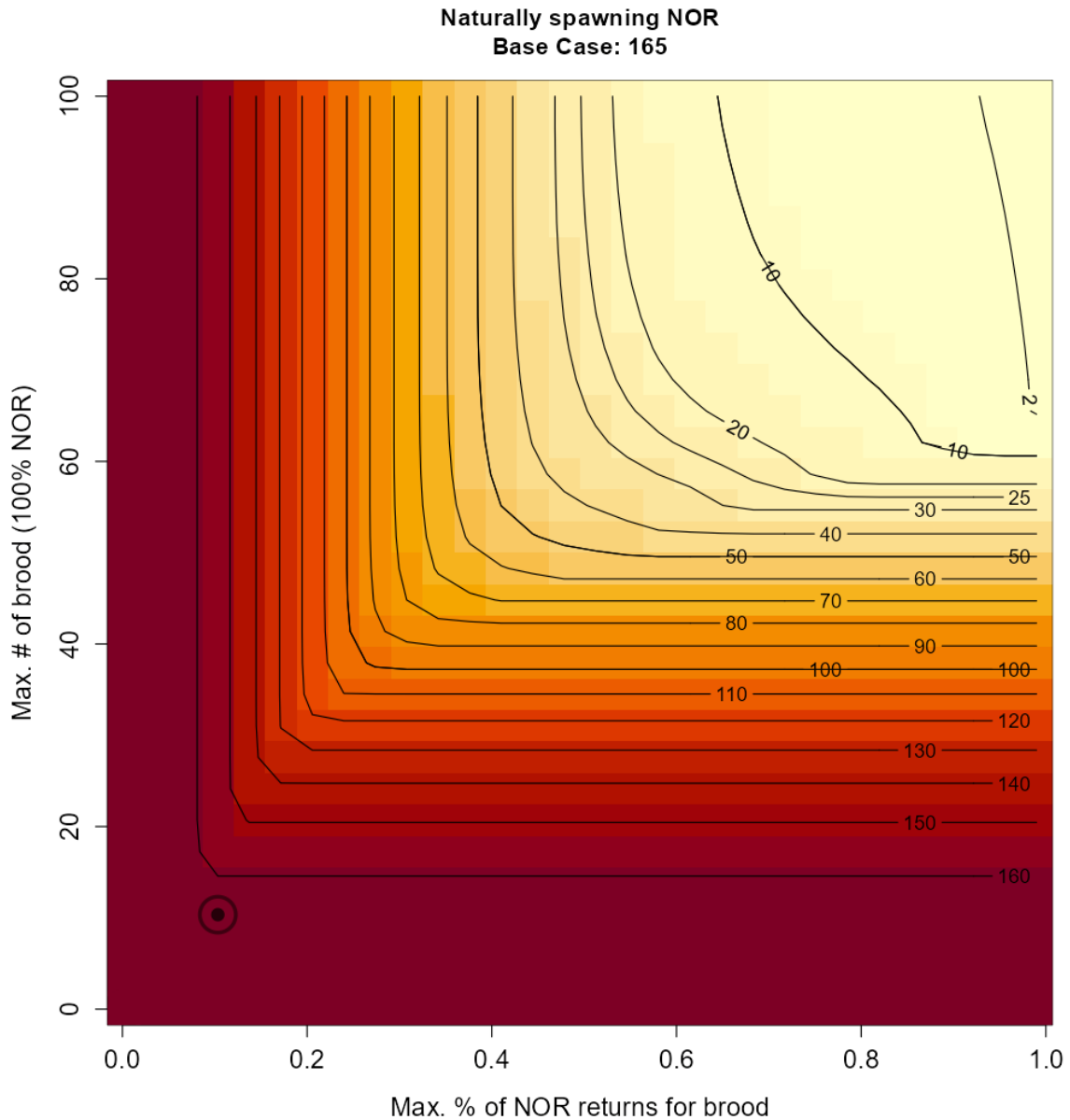
Figure 13. Results of exploratory modelling of pessimistic hatchery scenarios, showing the abundance of NOR spawners in the 100th generation to assumptions of different hatchery programs. Unlike Figure 8, this is a pessimistic case where smolt-adult return rate (SAR) of HOR compared to NOR spawners is arbitrarily set at 0.04 (compared to 0.5 in the base case; 0.04 is shown to demonstrate the negative outcomes of a hatchery program under this parameterization). The black point represents the base case assumption of marine survival rates, and the value in the title shows NOR abundance under those assumed values. Values on the isopleth represent NOR abundance; darker colors occur in areas with higher NOR abundance.

Fitness-adjusted productivity and capacity BH parameters under the base case

Under both hatchery supplemented scenarios (i.e., scenarios 2 and 3), fitness-adjusted productivity and capacity is expected to decline throughout the 100-generation timeseries (Figure 14). Scenario 2 and 3 are expected to result in an immediate drop in fitness that eventually stabilizes—this is because in the first generation when HOR adults reach natural spawning grounds, HOR spawners greatly outnumber NOR. Then, abundant HOR spawners reproduce in the wild. Their offspring, now considered NOR fish as they are reared in the wild, contribute to the NOR spawning population in the next year. This subsequent increase in NOR stabilizes the loss in fitness over time. pNI also begins low—reflecting the initial "boom" of HOR spawners—and then stabilizes over generations as NOR abundance increases (Figure 15). In scenarios where a mark-selective fishery is implemented that removes 60% of returning HOR adults, the proportion of HOR fish spawning naturally declines resulting in higher pNI and less intergenerational fitness loss compared to scenario 2 results.

We show a more exhaustive set of results in Appendix 3: All-H Analyzer Model Results.
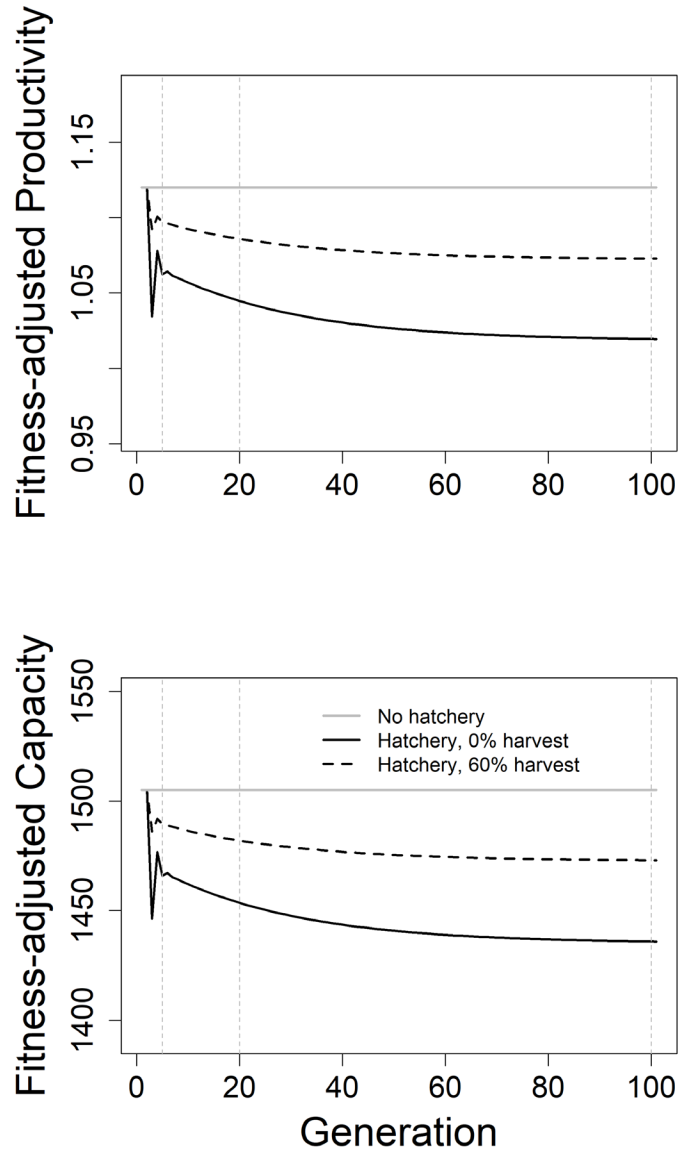
Figure 14. Losses in fitness-adjusted productivity and capacity of the naturally spawning population (NOR and HOR combined) as projected by the AHA model over 100 generations of alternative hatchery supplementation programs. As fitness of the naturally spawning population drops—as a result of introgression of hatchery fish—it is expected that the population's productivity and capacity will decline. The grey line represents expected outcomes under status-quo management scenario, in which no hatchery program is implemented, and no loss in fitness is expected. The solid black line shows scenario two (which breeds 10 NOB in each generation, with 0% selective harvest on HOR returns), while the dashed black line shows scenario three (10 NOB in each generation, with 60% selective harvest on HOR returns). Vertical lines indicate the 5th, 20th, and 100th generation simulated.
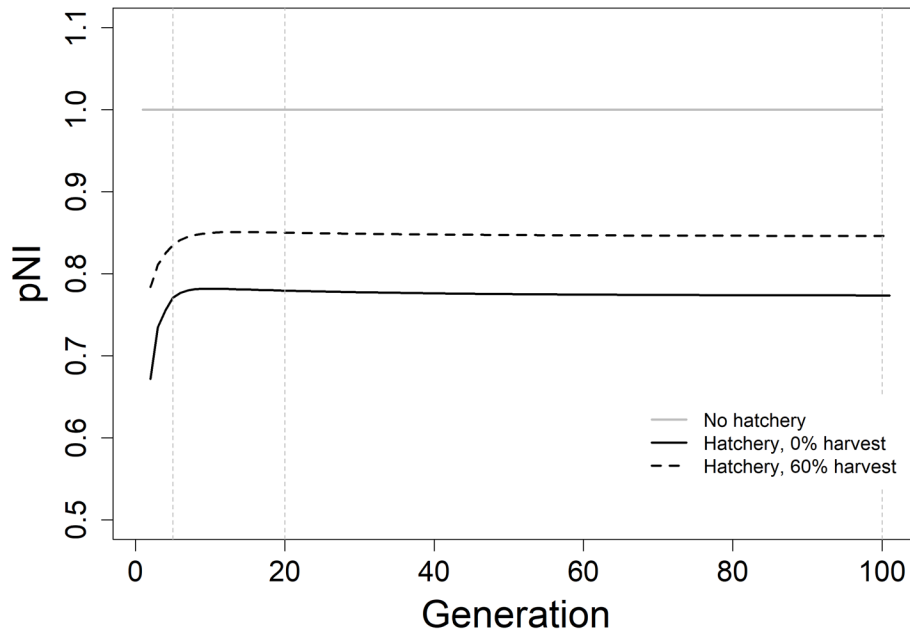
Figure 15. AHA-projected proportionate natural influence (pNI) for the IFRS population under three hatchery supplementation scenarios over 100 generations. pNI is calculated as a function of the composition of broodstock and naturally spawning fish (see text for equation). The grey line represents the status-quo management scenario, in which no hatchery program is implemented. The solid black line shows scenario two (10 NOB in each generation, with 0% selective harvest on HOR returns), while the dashed black line shows scenario three (10 NOB in each generation, with 60% selective harvest on HOR returns). Vertical lines indicate the 5th, 20th, and 100th generation simulated.

Summary

Status of the IFRS populations

Since the 1980s, Interior Fraser River Steelhead populations have experienced marked long-term declines in abundance from thousands to dozens of spawners (COSEWIC 2020). The imperiled conservation status of IFRS has required the implementation of new conservation measures to prevent further decline and promote stock recovery. Reductions in both targeted and incidental harvest of NOR steelhead have produced no signs of population recovery. COSEWIC deliberations have identified several ongoing threats including: continued incidental mortality on returning adult steelhead in commercial and Indigenous fisheries that target more abundant salmon species; increased predation rates from increased abundances of marine mammals, especially pinnipeds, that prey on steelhead smolts and adults; compromised habitat quality in freshwater due to agriculture and increased frequency and magnitude of forest fires; and increased stream temperatures and low summertime flows and extreme floods due to climate change (COSEWIC 2020). Beyond attempts to further reduce incidental mortality rates in fisheries and prevent human activities that cause damage to the spawning and rearing habitats of steelhead, there are no obvious, universally-accepted approaches that could be taken to prevent further decline and promote stock recovery.

Recently, there have been highly polarized debates between community-based groups over whether new steelhead hatchery programs should be initiated as a response to the Extreme Conservation Concern status of high-profile stocks such as Thompson River steelhead. This review was developed in response to this debate in order to summarize what the literature says about the potential risks and benefits of using hatcheries for conservation purposes, with specific focus on the imperiled status of IFRS. In Canada and elsewhere, hatchery production of salmonids has been implemented for several decades to provide harvest opportunities, to compensate for environmental damage (mainly hydropower), and to aid the recovery of depleted wild populations (Naish et al. 2007; Paquet et al. 2011). While conservation hatcheries are no longer used to augment low-abundance steelhead populations (B.C. FLRO 2016), Fisheries and Oceans Canada has been reconsidering expanding the use of hatcheries for conservation purposes, including for IFRS populations. Given the imperiled status of a growing number of wild populations of steelhead in B.C., the B.C. Government had recently reconsidered the use of hatcheries for the conservation of depleted wild stocks of steelhead in a recent Action Plan. However, this plan concluded that, "significant evidence from other jurisdictions as well as B.C.'s experience using hatcheries confirm that attempting to rebuild wild IFS using a hatchery program will likely be unsuccessful at this time and put the wild IFS population at higher risk for extirpation" (Rhodes and Jenkins 2021; but we note that in that report they do not document the literature that formed the basis of this conclusion and we are not certain if our review included the same information as theirs). We were thus tasked in 2022 with providing an independent review of literature associated with the potential benefits and negative effects of hatchery production on wild salmonid stocks with a particular focus on the potential use of hatchery supplementation to promote the recovery of IFRS populations.

Summary of findings regarding hypothesized risks of hatchery supplementation

We provide below summaries of review results for each alternative hypothesis on effects of hatchery supplementation on salmonid populations and offer considerations with respect to the question of using hatchery supplementation for Interior Fraser steelhead.

Hypotheses E1 and E2: Release of HOR juveniles in streams results in lower growth and survival of NOR juveniles; some HOR smolts stocked in rearing streams do not migrate to the ocean, residualize, and then compete with NOR parr

Release of hatchery produced steelhead may negatively impact the NOR steelhead population through density dependent competition between juveniles, with the risk to the NOR population increasing with duration of cohabitation with HOR juveniles following release. However, prior residence in rearing habitats by NOR juveniles may offset the size-based advantages that HOR juveniles typically acquire. If a hatchery program is initiated for IFRS, there are some practices that may reduce the risk of density-dependent competition between HOR and NOR juveniles. A program that integrates locally sourced NOR for broodstock (if available) and aims to produce age-2 HOR smolts that are of similar size to age-2 NOR juveniles will be more likely to out-migrate upon release, thus reducing cohabitation. To further reduce the risk to the NOR population, hatchery fish could be held in acclimation ponds that allow volitional migration, such that non-migrating HOR juveniles may be removed before entering the river and potentially released downstream of rearing habitats known to be important to the wild population. Given current numbers of spawning adults are extremely low relative to historical averages, it is unlikely that rearing habitats are close to carrying capacity. However, the extent to which HOR and NOR fish fill habitat capacity should be regularly assessed if hatchery production results in increased IFRS abundance and, if rearing capacity is reached, the scale of future HOR releases reduced.

Hypothesis E3: HOR adults spawn successfully but intra-specific density dependent competition leads to replacement rather than supplementation of the NOR juvenile population

HOR-produced juveniles that grow to similar sizes and show similar spatial distributions to NOR juveniles are desirable for a hatchery program aimed at population recovery. While HOR adults do not appear to perform as successfully as NOR spawners, juveniles produced by HOR spawners may compete efficiently with NOR juveniles. Such 'naturally produced' offspring of HOR may not have the same competitive advantages as those produced in the hatchery (e.g., larger size, more aggression). HOR-produced juveniles that grow to similar sizes and show similar spatial distributions to NOR juveniles are desirable for a hatchery program aimed at population recovery. While the risk of HOR-produced juveniles replacing rather than supplementing NOR juveniles can thus be considered relatively low, there are some practices to reduce risk of replacement should a hatchery program be initiated for IFRS. These practices focus on restricting HOR adult access to natural spawning areas either in time or space such that HOR spawning success is lowered relative to NOR spawners.

Hypothesis E4: Increased abundance of combined hatchery/wild population attracts predators and increases predation mortality rates on wild fish

Hatchery production of IFRS could potentially increase predation rates on juvenile IFRS through unintended increases in the abundance of residualized rainbow trout in juvenile IFRS rearing areas. While the timing and location of release of hatchery smolts could be aimed at minimizing residualization of hatchery produced juvenile steelhead, it is fairly common for a percentage of hatchery smolts released to residualize and remain through to maturation in freshwater (e.g., as commonly happens with hatchery summer steelhead smolts in the South Santiam River, Ryan Hogan, pers. commn). Increased abundance of residualized rainbow trout however may not necessarily increase predation rates on natural origin juvenile IFRS, especially when other preferred prey species may be much higher in abundance than natural origin juvenile steelhead in the stream reaches where residualized fish are present. Should hatchery production of IFRS be implemented, predation risk could be assessed by implementing sampling studies to assess the rate of residualization of hatchery origin steelhead, the preferred habitats of residualized rainbow trout, and their diets. Numerical or functional responses of other species of predators to hatchery production of IFRS are unlikely due to the relatively low abundance of HOR IFRS compared to other salmonid species in the freshwater, estuarine and marine habitats that would be used by both HOR and NOR IFRS.

Hypothesis F1: Anglers are attracted to the increased abundance of the combined HOR and NOR population, increasing annual adult mortality rate and selecting for younger age/slower growth NOR fish

Should hatchery production be successful in producing sufficient abundances of hatchery origin steelhead to create new mark selective recreational and Indigenous fisheries for hatchery steelhead, fishing effort could increase in river reaches inhabited by mature IFRS and incidental mortality rates on natural origin IFRS could potentially increase. Available studies on incidental mortality rates on caught and released steelhead and Atlantic salmon (Nelson et al. 2005; Richard et al. 2014; Twardek et al. 2018), however, mostly indicate that incidental mortality rates on released fish are typically very low, though may vary depending on gear of capture, river water temperature, and how the fish are handled prior to their release. Incidental mortality rates of natural origin fish associated with increases in fishing effort from hatchery production may be more significant when hatchery production supports substantial commercial and Indigenous fisheries that target hatchery produced fish. Given that any new recreational and Indigenous fisheries that may be established for hatchery produced IFRS are likely to be relatively small in scale and with limited amounts of fishing effort, it is thus unlikely that associated incidental fishing mortality rates on IFRS could increase to levels that negatively impact population recovery potential.

Hypothesis G1: Inbreeding depression: Loss of genetic variation causes reductions in effective population size and maximum recruits per spawner

Assuming that native NOR brood stock will be used exclusively in any hatchery programs, two key genetic risks as a result of hatchery supplementation include reductions to 1) the effective population size and genetic diversity of the wild population, and 2) fitness of the population (via two mechanisms:

domestication of HOR fish and their NOR progeny, and epigenetic changes to gene expression). First, considering genetic diversity and effective population size of the wild population, hatchery programs risk amplifying the genetic contribution of relatively few NOR fish (i.e. those taken for broodstock) by improving the egg-to-smolt survival only for the offspring of broodstock. This is hypothesized to reduce the maximum number of recruits per spawner via an inbreeding depression, but inbreeding rates can be high in natural populations and mitigated by using NOR broodstock. In some cases, hatcheries may stabilize or even increase effective population size. Rainbow trout considerations are also key, as rainbow trout and steelhead comprise an interbreeding population and there is likely a large wild population of resident *O. mykiss* that contains broad genetic diversity. Should any hatchery program should implemented, the residualized population should also be monitored so that its genetic diversity may be preserved as much as possible. Managers should assess baseline genetic diversity before implementing a hatchery program, and track changes to heterozygosity and fitness.

Hypotheses G2 and G3: Domestication selection and epigenetic changes that upregulate traits (e.g., growth) in HOR fish cause higher mortality of HOR fish and NOR fish after interbreeding in natural environments

Differences between natural and hatchery rearing environments result in different selective pressures and potentially different gene expression between natural and hatchery environments. In the hatchery, various processes including non-random selection of broodstock and adaptation of fish to the hatchery environment may impact which phenotypes are expressed in HOR fish (e.g., higher growth rates may be advantageous and highly expressed in hatcheries but not advantageous in nature). If HOR fish produce progeny with the traits that are useful in a hatchery but a disadvantage in the wild, HOR-NOR interbreeding could introduce maladaptive traits into the NOR population and lower NOR fitness. This may arise through changes in gene frequency, via domestication selection, or in gene expression, via epigenetic change. HOR and NOR fish often have different epigenetic markers, typically in genome regions associated with growth, freshwater residency, migration timing, smoltification, and metabolism. Yet research investigating methylation patterns are not consistent, and it is not evident that epigenetic changes that occur in freshwater hatchery rearing are maintained through subsequent life stages or passed to progeny. Given the relatively new field of epigenetic research, there is still a great deal of uncertainty about how hatchery rearing influences gene expression in one or multiple generations. However, managers can cater programs to minimize fitness loss. If phenotypic differences are identified between HOR and NOR fish, hatchery practices may be adapted to counteract the domestication selection. For example, hatchery releases could be timed such that outmigration better mimics NOR movements (but in a way that still minimizes the risk of negative ecological interactions between natural and hatchery conspecifics). Further, if only NOR are used for broodstock and if HOR are removed before spawning in the wild, these actions can further reduce the risk of domestication affecting the fitness of wild spawning populations.

Summary of modelling results

To complement our literature review, we also performed two modelling exercises to identify how a hatchery program might benefit the naturally spawning IFRS populations. First, we applied a Beverton-

Holt production model to simulate juvenile recruitment under different marine survival and hatchery supplementation scenarios. This model assumed that hatchery supplementation decreased productivity of the population by a fixed "discount" factor, a relatively simple approach to assessing how hatchery domestication impacts supplemented wild populations. To overcome this limitation, we then built a population model based on the All-H Analyzer (AHA) software, which explicitly calculates the loss in productivity resulting from interbreeding between hatchery and natural origin fish. The AHA model was also used to assess long-term outcomes of an IFRS hatchery program under different marine survival and broodstock collection rules.

Comparison of predictions from the AHA and simpler BH models

Comparing the simple BH model predictions with those from the AHA model, we find some results are robust to which model is chosen for simulation. For example, both models highlight the importance of marine survival, and the likely reality that a hatchery program alone will not be able to recover the IFRS population to historically observed levels (i.e., in the order of thousands of NOR spawners). Both models highlight that recovery is limited when NOR marine survival rates are low (and both models show non-viable population when NOR marine survival drops below 1.7%). Nevertheless, both models predict that NOR abundance can increase over current levels with the implementation of a modest hatchery program, with the maximum abundance limited by NOR marine survival. Under both models, hatcheries reduce the abundance of NOR spawners only when marine conditions are very poor for HOR fish or when HOR fish cannot effectively breed in nature.

However, there are key differences between the two models that influence their interpretation. The most significant difference between the models is the presence of erosion of fitness in the AHA model. The simpler BH model can project long-term abundance under a given set of a and B parameters, instead assuming that these are fixed over time. In the AHA model, fitness loss can be explicitly modelled as a gradual change resulting from a multi-generational hatchery program (i.e., where fitness loss is influenced by, e.g., broodstock collection practices and the composition of spawners in the wild). In the simpler BH model, fitness loss is based on assumed values that remain static over time, not changing in response to the hatchery program and cumulative genetic loss. Because of these differences, the AHA model more explicitly incorporates knowledge about the propagation of unfit traits in a population (cf. Ford 2002). Managers interested in the genetic effects of hatchery programs should consider the use of genetically-informed indicators that arise from the AHA model, like proportionate natural influence (pNI; Withler et al. 2018).

Under the right conditions (e.g., if the hatchery program is large enough that a majority of spawners in the wild are HOR, leading to loss of fitness from domestication selection), the genetic consequences of a hatchery program may cause worse outcomes for the NOR population compared to an unsupplemented case. We generated such pessimistic scenarios in our AHA model, finding that low survival or reproductive ability in HOR can result in a hatchery reducing the NOR abundance in the long term. We note that if we had simulated a more hatchery-dominant system (i.e., a hatchery which incorporates both HOR and NOR broodstock, such that there is genetic mixing in both hatchery and wild environments), the differences in predictions generated by the simpler BH versus the AHA model would be more pronounced.

Limitations of this report

Compiling this report has been extraordinarily challenging for a number of reasons. Firstly, there exists a vast and growing literature evaluating the potential effects on wild salmonid populations of using hatchery production either for conservation or fishery enhancement purposes. There are literally hundreds of papers addressing various aspects of the hatchery question which date back to at least the early 1990s (e.g., Waples 1991). Even early studies identified numerous potential short- and long-term morphological, phenotypical, behavioural, and genetic changes in hatchery origin salmonid populations. An increasing number of papers are thorough, high-level reviews (e.g., Brannon et al. 2004; Anderson et al. 2020; Terui et al. 2023). To address the enormity and vast wealth of literature, we focused on papers that were either thorough reviews of the subject (e.g., Brannon et al. 2004; Anderson et al. 2020; Terui et al. 2023) based on rigorous empirical studies (e.g., provided an empirical study of a single population over several years, c.f. Courter et al. 2022) or meta-analyses of several different populations (e.g., Hagen et al. 2021). In our review of these papers, we formulated a set of alternative hypotheses to characterize a fixed set of alternative potential ecological, fishery, and genetic effects of hatchery production on wild salmonid populations that have been found to be common and recurring themes in the literature.

Studies have generally concluded that, when first generation hatchery adults from local broodstock return to spawn naturally, their production of smolts per spawner is generally lower than that of natural origin populations of the same species spawning in the same streams. Concern has been raised about introgression and potential reductions in genetic variation within populations, reductions in effective population size, acquisition of domestication attributes, reductions in reproductive success, negative epigenetic changes and reduced fitness when hatchery origin spawners have spawned naturally and crossbred with natural origin spawners (e.g., Araki et al. 2007b, 2007a; Machado-Schiaffino et al. 2007; Christie et al. 2012; Le Luyer et al. 2017; Hagen et al. 2021). Concerns have also been raised about reductions in growth and survival rates in juvenile salmonids of natural origin that have experienced the added competition and possible predation from juvenile salmonids of hatchery origin (e.g., Naman and Sharpe 2012; Tatara and Berejikian 2012). In addition, concerns have also been raised about fisheries for hatchery produced salmonids that may intercept and cause increased incidental fishing mortality rates in natural origin salmonid populations (e.g., Anderson et al. 2020). This is a large body of literature to summarize in this report.

In addition to the challenge of reviewing a large body of literature, our review was complicated by the challenge of accurately representing alternative viewpoints on the scientific credibility and likelihood of realization of hypothesized hatchery driven processes. For a given hypothesized effect, there are commonly different conclusions reached between different papers on whether the hypothesized effect remained credible or not, had been realized in a given case study or had actually failed to emerge as some experts had predicted. In our review we attempted to include papers that fell across the wide spectrum of viewpoints and sought to understand apparent discrepancies in findings between different studies especially when they were markedly divergent.

For example, earlier papers that evaluated the potential effects of hatchery production on the NOR population of steelhead in the Hood River estimated that hatchery production appeared to negatively effect the fitness, effective population size and reproductive success of the NOR steelhead population

(e.g., Araki et al. 2007b, 2007a; Christie et al. 2012). Other studies have similarly reported negative associations between measures of hatchery production and effective number of breeders for example in meta-analyses of multiple river systems that have both natural and hatchery production (e.g., Hagen et al. 2021). While such studies are frequently cited as evidence of negative impacts in assessments of the potential effects of hatchery production on wild populations, more recent research on the same populations have questioned these earlier findings (e.g., Courter et al. 2019, 2022). For example, a recent study found no significant negative association between stock productivity and the proportion of hatchery origin spawners, pNI, and hatchery release amounts in a 27-year time series of brood year productivity of Hood River steelhead; rather, a significant positive association was found (Courter et al. 2022). Here, the authors emphasized in their discussion that tests of hypotheses that predict negative effects on wild populations need to go beyond just taking short-term samples to assess potential fitness effects. They sought to identify plausible mechanisms to help explain previous findings that HOR spawners had lower average reproductive success than NOR fish within the same tributaries (e.g., pointing to research that found HOR spawners were more prone to choosing inferior spawning sites than NOR spawners). The authors argued that the most informative approach to assessing negative effects of hatchery production on wild fish are expected to emerge from rigorous statistical analyses, assessing decades long datasets of hatchery production and annual population productivity and including appropriate covariates and measures of stock productivity (e.g., derived from stock-recruit data). Other examples where hatcheries have had a neutral or positive effect include those where hatchery stocking has been an integral part of a recovery plan or recommended as a part of future recovery (Kline and Flagg 2014; Kozfkay et al. 2019; Kendall et al. 2023), while other examples suggest hatcheries have no effect (Venditti et al. 2018).

Reflecting discrepancies in different studies of hatchery effects on NOR fish, we also found a diversity of viewpoints in broader review papers, ranging from strongly against to cautiously in favour of hatchery supplementation. Some reviews caution against further use of hatcheries for conservation production (e.g., Terui et al. 2023); others are cautiously positive and emphasize trade-offs between potential benefits and risks of hatchery programs while acknowledging unresolved uncertainties (e.g., Anderson et al. 2020). More positive reviews also tended to discuss how further research can address uncertainties and how the implementation of hatchery measures to mitigate potential negative effects (e.g., Brannon et al. 2004; Hagen et al. 2021), e.g., "discontinue or modify programs if risks outweigh benefits" (Paquet et al. 2011).

Considering limits to our exploratory modelling of hatchery supplementation, the greatest gap is lack of life history diversity. Neither the BH nor AHA models incorporated rainbow trout populations and their interactions with naturally spawning IFRS, despite the potential for resident populations to offset the negative impacts of poor marine survival on the IFRS population. In future research, given adequate information about the status of the resident population and realistic rates of residualization/anadromization, resident contributions could be included in a modelling framework. For example, the AHA model could be parameterized with a second NOR population, representing resident spawners, which interbreeds with anadromous NOR and HOR also spawning in the wild. Similarly, the simple BH model could be modified such that productivity includes the contribution of rainbow trout to the anadromous population. In both model frameworks, habitat capacity could be adjusted to account for resident cohabitants.

When assessing how a steelhead hatchery might be designed to minimize failure, it is valuable to review past attempts in B.C. Hatchery production has previously been implemented in the Thompson River watershed (Bison 2009), but was halted after return rates of adult HOR steelhead appeared to be relatively small. In this hatchery, incubated eggs were taken from NOR brood stock and released as HOR fry or parr into streams where wild steelhead parr were known to rear. It appeared that survival rates of hatchery origin parr were relatively low and the sparse return of hatchery origin adults indicated that downstream and marine survival rates of hatchery origin steelhead were too low to justify further attempts at hatchery production (Rob Bison, pers comm.; Bison 2009). Should new attempts at hatchery production be considered for IFRS steelhead and other B.C. steelhead populations, it is valuable to undertake a careful review of previous practice and conditions associated with the failures of previous attempts (e.g., Ward 2006; Bison 2009). For example, rearing hatchery fish to the smolt stage could result in a much higher hatchery smolt-to-egg ratio (and a higher abundance of returning HOR adults) than rearing only to parr stage. The very low smolt-adult survival rates of NOR IFRS and lower marine survival rates typical of HOR steelhead, together with other possible negative effects such as domestication and introgression, make it difficult to predict whether hatchery production of smolt-stage steelhead could significantly increase the total number of returning adult steelhead to the Interior Fraser river to help facilitate population recovery.

Suggested future research

Genetic diversity of steelhead populations: Genetic variation of the subpopulations of steelhead and rainbow trout life history types in the IFRS population is not well described. Future genetic studies should seek to estimate and quantify genetic variation and relatedness between subpopulations, with the goal of assessing how hatchery supplementation could change genetic structure. As hatchery practices can strongly influence the extent to which genetic diversity is degraded from supplementation, it is important to quantify how broodstock selection and propagation impacts IFRS diversity and fitness. While modelling tools like the All-H Analyzer can project long-term changes to fitness and phenotype resulting from interbreeding between natural and hatchery-domesticated fish, only with a baseline understanding of current genetic diversity in the population can we measure progress towards defined genetic diversity goals.

In addition to quantifying genetic variation, there is also a need for research investigating the current absolute and effective population sizes of the IFRS population based on samples of the genomes of sympatric rainbow trout and steelhead life history types. Tracking changes to absolute and effective population sizes of Interior Fraser steelhead in key tributaries including those of the Thompson and Chilcotin rivers (either with or without supplementation) will be essential for monitoring potential changes to population status and the appropriateness of implementing further conservation measures. Reducing residualization rates of steelhead released from hatcheries can come with a cost to genetic variation in the population (Kendall et al. 2015)—we need an estimate of baseline genetic diversity to understand the trade-offs between lowering residualization rates versus maintaining high genetic diversity. With a better understanding of the genetic underpinnings of life history diversity, hatchery programs could be fine-tuned to select for individuals with steelhead-type genes.

Rainbow trout population assessment: The capacity for the rainbow trout population to serve as a rescue population has implications for hatchery program management. The non-anadromous and anadromous life history strategies may be differentially selected based on freshwater versus marine survival rates. If, for example, rainbow trout population abundance is high while steelhead populations decline, it is possible that the continued production of steelhead adults by rainbow trout adults could enable eventual recovery of the steelhead offspring. In this way, if both abundance of the rainbow trout subpopulation and the rates of steelhead production by rainbow trout mothers remain non-negligible, the hatchery program may not be necessary to see recovery of the steelhead population component. A few questions thus arise: Which fisheries management options affecting the rainbow trout stock could enhance its potential to serve as rescue source for the anadromous life history type? Are there ways to reduce risk, and maximize benefits, using adaptive management tools? On one hand, the resident population may offer a population rescue effect if marine survival is very poor. This population may also serve as a genetic "vault", preserving genetic diversity that might be eroded by a hatchery program. On the other hand, the resident population may have an overall net negative impact on steelhead. This could arise if the negative effects of cannibalism, predation, and competition from the resident population outweighs their contribution to the genetic diversity and abundance of anadromous fish.

Marine survival assessment: Hatchery supplementation increases early life survival from egg to smolt—however, survival in later life stages may prove more important to overall population health of interior Fraser steelhead. It may be the case that lowered marine survival rates can explain recent declines in the steelhead population. If research indicates that marine survival exerts more influence on population health than pre-ocean entry survival, steps could be taken to improve marine conditions in tandem with changes to hatchery practices. Notably, any improvements to marine conditions for natural-origin fish would also benefit the survival of hatchery-released fish, thus improving the efficiency of the hatchery program while reducing the need for supplementation.

Habitat assessment: Many of the potentially harmful ecological impacts of hatchery steelhead on wild conspecifics arise from shared habitat use during freshwater life stages, particularly in the juvenile stage. Because hatchery fish release sites can be selected from within the river system (albeit with implications for residualization rates; Hausch and Melnychuk 2012), it would be useful to map out current habitat use of wild steelhead and rainbow trout juveniles in rivers with hatchery programs. Techniques like species distribution mapping could identify areas of connected, suitable, but unoccupied habitats. Selectively releasing hatchery fish in unoccupied regions would reduce density-dependent mortality in natural fish.

Acknowledgements

Appendix 1: Threats to Thompson and Chilcotin steelhead as identified by COSEWIC

Table A 1. Threats to Thompson and Chilcotin Steelhead as identified and ranked by COSEWIC (2020, Appendices A and B). The Classification of Threats is adopted from IUCN-CMP, Salafsky et al. 2008. Major categories (whole number, shaded cells) are a complete list. Minor categories that are "Not Applicable" are not included. Threat Level and Comments that are identical for Chilcotin and Thompson populations are placed in a single cell.

Threat	Description	Threat Level		Comments	
		Thompson	Chilcotin	Thompson	Chilcotin
1	Residential & commercial development	Not Applicable		Threats from human settlements or other non-agricultural land uses with a substantial footprint. Includes any physical modification of habitat.	
2	Agriculture & aquaculture	Negligible		Threats from farming and ranching as a result of agricultural expansion and intensification, including silviculture, mariculture, and aquaculture	
2.3	Livestock farming & ranching	Negligible		The consensus was that a small amount of trampling occurred in the rivers with severity near the low end of the range.	The consensus was that because the rivers were large they would be less accessible and any trampling would be negligible.
3	Energy production & mining	Not Applicable		Threats from production of non-biological resources. There are no energy production and mining threats in this DU.	
4	Transportation & service corridors	Negligible		Threats from long, narrow transport corridors and the vehicles that use them including associated wildlife mortality	
4.2	Utility & service lines	Negligible		Includes current maintenance work along pipeline where it crosses streams. Future development of the Trans Mtn Pipeline will include many stream crossings and disruption and would be scored here.	
4.3	Shipping lanes	Negligible		Includes dredging in the lower Fraser River for channel maintenance. All adult and smolt Steelhead traverse the area and would be affected. Effects were unknown but it was felt that with proper mitigation they would be negligible as fish move through the area rapidly.	
5	Biological resource use	HIGH		Threats from consumptive use of "wild" biological resources including both deliberate and unintentional harvesting effects; also persecution or control of specific species	

5.4	Fishing & harvesting aquatic resources	HIGH	Fishing affects adults returning to spawning grounds from the sea (late Aug. to late November) and migration to the sea after spawning (1 year)., Migration from the sea coincides with fisheries for one or more other Salmon species. First Nations fisheries also occur on post-spawning Steelhead returning to the sea. All fish returning from sea to rivers to spawn must pass through the fishery as do fish returning to the sea post-spawning. Mortality cannot be estimated directly but is based on simulation estimates of run timing and migration speed of returning Steelhead and timing of the Salmon fisheries. Fisheries are planned to occur annually in a similar manner to the past for the next 10 years. Estimated annual mortality ranges between 15 and 25% based on the simulator but varies depending on the timing of fisheries and Steelhead migration. The fisheries appear to have an impact on a population that has been in decline for decades. Includes direct FSC harvest and catch and release mortality from sport fisheries, bycatch in other fisheries (uncertain), and illegal harvest between ocean and spawning grounds (uncertain). Direct and incidental lethal scientific collecting also scored here., Recent data indicate an additional 10% mortality in the Nicola and 5% in the Coldwater. General agreement that severity exceeded 30% but considerable uncertainty about higher levels., However, low population effects increase the extinction risk. Suggestion that properly enforced mitigations could lead to significant reductions in mortality.
6	Human intrusions & disturbance	Negligible	Threats from human activities that alter, destroy, and disturb habitats and species associated with non-consumptive uses of biological resources.
6.1	Recreational activities	Negligible	Threat affects alevin emergence and fry growth (mid-June to early July) in rearing streams. A small percentage or rearing areas are affected by physical disturbance from human activity (gold panning, horse, bike, jetboats, and ATV in rearing habitat, beach parties, music festivals). Mortality from physical disturbance of the spawning and rearing habitat is difficult to assess, likely small. Timing is typically following emergence and doesn't directly affect redds and eggs. These activities are an annual occurrence expected to proceed for the next 10 years.
7	Natural system modifications	HIGH	Threats from actions that convert or degrade habitat in service of "managing" natural or semi-natural systems, often to improve human welfare

7.1	Fire & fire suppression	Negligible	Includes water withdrawal for fire suppression. Removal of water from some or all of the streams in the DU to assist in suppression of forest fires potentially affects all life history stages depending on the timing and severity of the forest fire season. Scope and severity are dependent on local terrestrial habitat and fire history, but the impact is negligible as not expecting multiple fires in one location.	
7.2	Dams & water management/use	Low	Threat expected to affect alevin emergence and growth (mid-June to early July), and Juvenile growth in tributaries (zero to 2-3 years). Affects all the Nicola and Coldwater and at least half of the Bonaparte and Deadman.	Threat expected to affect alevin emergence and growth (mid-June to early July), and Juvenile growth in tributaries (zero to 2-3 years). Direct mortality from reduced water availability (due to withdrawal) is difficult to assess but felt to be less than 10%. Water management activities are an annual occurrence expected to proceed similarly or become more serious over the next 10 years. Issues include over allocation of stream flows to agriculture, industry and municipal requirements, unregulated and poorly monitored groundwater pumping, poor control of stream levels during spawning or incubation periods, and alteration of natural flow patterns by storage facilities. The Elkin, Chilco, and Chilcotin rivers are thought to be most affected but possibly also Little Chilcotin (needs verification). Any future run of the river hydro development would be included here.

7.3	Other ecosystem modifications	HIGH	Includes reduced ocean productivity and competition from other salmonids resulting from ocean ranching in the high seas, and offshore predation on smolts and adults. In freshwater includes riprap of stream banks, sedimentation, and thermal problems due to loss of riparian vegetation and water extraction. Severity felt to be towards the higher end of the range.	Includes reduced ocean productivity and competition from other salmonids resulting from ocean ranching in the high seas, and offshore predation on smolts and adults. In freshwater includes sedimentation and thermal problems due to loss of riparian vegetation from logging and water extraction. However, the lakes in the watershed buffer the temperature and sedimentation to some degree.
8	**Invasive & other problematic species & genes**	**HIGH**	**Threats from non-native and native plants, animals, pathogens/microbes, or genetic materials that have or are predicted to have harmful effects on biodiversity following their introduction, spread and/or increase in abundance.**	
8.1	Invasive non-native/alien species/diseases	Not Applicable	Invasive species can affect the deposited eggs, newly hatched alevins, and fry rearing in the tributaries, and even juveniles and migrating smolts. Depending on the species of invader a substantial proportion of the population could be affected, and mortality depends on the species and its biological proclivities that may be simply predation or food competition but could include habitat alteration and disturbance of the substrate and could be significant. Once established invasive species would have annual impact for the next 10 years. Currently no Invasives in the DU are impacting Steelhead or resident Rainbow Trout. However, migrating smolts may be affected to limited degree by established species in the lower Fraser River.	

8.2	Problematic native species/diseases	HIGH	The reduced population abundance of Steelhead makes predation particularly by pinnipeds in the inshore as well as by Harbor Porpoises and White-sided Dolphins in the offshore a threat. Adults migrating to overwintering areas of Thompson River from sea (late Aug. to late Nov.), smolts migrating to sea (mid- April to mid-May, once they have smolted after 2 or 3 years), and smolt off-shore migration (June to September) are all vulnerable. Mortality from threat is uncertain but up to 50% of smolts are lost during transit from freshwater out of Georgia Strait. Diet data indicate that Steelhead are consumed by seals in the Fraser estuary and in the Strait of Georgia and Puget Sound. In freshwater, otters, whitefish, and Bull Trout may be a predation threat at current reduced abundance. Interbreeding of Steelhead and resident Rainbow Trout is also an increasing threat at current abundance. Impact of sea lice on smolts and adults during migration past fish farms in northern Johnstone Strait are a current and future threat with uncertain impact.
8.3	Introduced genetic material	Unknown	Not applicable to this DU but any future hatchery introductions would be considered here.
9	Pollution	Low	Threats from introduction of exotic and/or excess materials or energy from point and nonpoint sources.
9.1	Domestic & urban waste water	Negligible	Affects all life stages as smolts and adults pass through the Thompson, Chilcotin and lower Fraser. In particular, the area around the lower Fraser River is heavily populated and it drains about one quarter of the British Columbia land area. It has been heavily inundated by various pollutants including sewage, discharge from treatment plants, leaking septic, oil or sediment from roads, domestic fertilizers and pesticides, and road salt. As well, elevated fecal coliform and turbidity in the lower river and its estuary occur, particularly during the spring freshet when Steelhead and Salmon smolts from the Interior Fraser are undertaking their seaward migration. The extent to which Steelhead utilize estuarine habitats in the lower Fraser River is not well understood but it appears that they rapidly transit out of the Strait of Georgia. Pollution potentially affects the entire population, but the impacts appear to be minimal.

9.2	Industrial & military effluents	Negligible		Affects smolts and adults migrating through the Thompson and lower Fraser rivers. Industrial and military effluents such as mine and mill waste that result in elevated levels of aluminum, iron, zinc have differing effects depending on time of year and extent of exposure. All Steelhead in the area of the spill or effluent would be affected. An annual occurrence as smolts and adults transit the lower reaches of the Fraser River. Steelhead are exposed to industrial effluents in freshwater, the Fraser estuary, and Strait of Georgia. There is also the possibility of contaminant spills from train derailments into the tributaries or Thompson River proper. Estimating direct effects of the pollutants is difficult but consensus was that they were slight.	Affects smolts and adults migrating through the Chilcotin and lower Fraser rivers. Industrial and military effluents such as mine and mill waste that result in elevated levels of aluminum, iron, zinc have differing effects depending on time of year and extent of exposure. All Steelhead in the area of the spill or effluent would be affected. An annual occurrence as smolts and adults transit the lower reaches of the Fraser River, Steelhead are exposed to industrial effluents in freshwater, the Fraser estuary, and Strait of Georgia. Estimating direct effects of the pollutants is difficult but consensus
9.3	Agricultural & forestry effluents	Medium	Negligible	All life history stages potentially impacted by this threat. Pollutants include agricultural runoff, sedimentation, pesticides both in the Thompson and lower Fraser watersheds. The Bonaparte, Nicola and some of its tributaries have been particularly affected by runoff following logging and fire damage contributing to soil erosion and siltation. Loss of pool/riffle and habitat complexity. Conversion of lower Coldwater to agriculture and ranching reduced carrying capacity significantly. The entire population is potentially exposed to the pollutants and the effects were rated as moderate.	
10	Geological events	Negligible		Threats from catastrophic geological events.	

10.3	Avalanches/landslides	Negligible	The rapid and extensive removal of dead and dying trees will have significant impacts in the watersheds with increased potential for landslides depending on the local terrain. Typically result in downstream turbidity and potentially result in changes in the stream bed as waters circumnavigate the blockage. Depending on the timing of the landslide's effects could occur on various life history stages but eggs, alevins and juveniles would be most affected. Depending on the timing of the landslide's effects could occur on various life history stages but eggs, alevins and juveniles would be most affected.	
11	Climate change & severe weather	Unknown	Threats from long-term climatic changes that may be linked to global warming and other severe climatic/weather events that are outside of the natural range of variation, or potentially can wipe out a vulnerable species or habitat.	
11.1	Habitat shifting & alteration		Evidence of earlier and larger spring freshets, pine beetle infestation, higher summer air and stream temperatures. Changes in hydrographs caused by a variety of factors (e.g., snow melt, rain on snow, etc.).	
11.2	Droughts		Increasing number of years with reduced precipitation resulting in contraction in available rearing habitat.	Little evidence of drought in the Chilcotin relative to the Thompson watersheds. Buffering by the lakes at the head of the watershed.
11.3	Temperature extremes		Increases in either or both marine and freshwater temperatures.	Increases in either or both marine and freshwater temperatures. Freshwater temperatures buffered by the lakes.
11.4	Storms & flooding		Increase in winter precipitation resulting in rapid runoff, scouring of some streambeds and loss of eggs, flooding in some areas especially where widespread removal of dead trees has occurred.	Storm effects are less pronounced than in the Thompson due to the buffering effect of the lakes that stabilize discharge and minimize flooding risk.

Appendix 2: Beverton-Holt stock-recruit analysis of hatchery-wild interactions in Steelhead

Choice of a model to represent capacity for stream-rearing salmonids

To develop a production model for the IFRS population, we first selected which of the Ricker or Beverton-Holt (BH) models of the stock-recruit relationship would be appropriate for modelling hatchery supplementation of NOR steelhead in the Interior Fraser River. Adkison (2022) has summarized the difference in in the theoretical basis for the Beverton-Holt vs Ricker stock recruitment relationships:

> "*These forms can be derived (Quinn and Deriso 1999) by assuming that the instantaneous mortality rate on the offspring is either proportional to the number of parents (Ricker) or to the number of siblings (Beverton-Holt). Since the mortality rate would decrease over time as siblings died, the effect of density-dependence is not as strong in the Beverton-Holt as in the Ricker. Thus, in the Beverton-Holt model, total recruitment asymptotes to a maximum as the number of spawners increases, whereas in the Ricker, the more intense density-dependence results in an actual decrease in recruitment from the maximum at very high numbers of spawners.*"

This difference implies a fundamental difference in behavior when variance in spawners and recruits are both high from a combination of high observation and high process error. With high variance and low contrast on the horizontal axis, the best BH fit is a horizontal line through the centroid with an arbitrarily high initial slope (i.e., at typical densities, slope=0 and recruits are independent of spawners). In contrast, maximum recruits ("capacity") for the Ricker fit to many data sets is achieved at an intermediate spawner density. Extrapolation to high spawner densities (e.g., under a high marine survival regime) is often predicted to produce substantially lower smolt production (Ricker 1954).

For stream-rearing salmonids, ecological interactions among juveniles (mainly territorial behavior) suggests that a BH is more appropriate because individuals die or move if they cannot defend a territory, and winners do not suffer at high densities because subordinates give up (see, for example, Kelly-Quinn and Bracken 1989; Elliott 1990; Keeley 2001, 2003).

For non-stream rearing salmonids that migrate immediately after emerging from the gravel, intraspecific crowding interactions are mainly among adults and the Ricker relationship is probably more appropriate. Egg survival can be disproportionally low at high densities because of ecological interactions such as disease outbreaks, or digging up of eggs deposited earlier. Note that this type of interaction can also occur in stream salmonids but only in small streams with very high egg densities (e.g., Elliott 1989; note very high egg densities up to 100 eggs/m^2 in this study; see also discussion in section 4.7 of Milner et al. 2003).

For our analysis, we preferred not to use the Ricker stock-recruit relationship because the maximum number of smolts (i.e., "capacity") is poorly defined, especially when ocean survival is density independent and varies widely. Furthermore, the unfished equilibrium for Ricker will not generally correspond to maximum smolt production as the relationship becomes more hump-shaped.

Optimum Spawning Abundance

A key first step in evaluating the need for hatchery intervention is to establish the status of the stock relative to an agreed management reference point. B.C. steelhead stocks are evaluated using methodology described in Johnston et al. (2000; 2002).

Reference Points: Fixed Adult Recruit Capacity

Steelhead are assumed to follow a BH stock recruit curve[1]:

$$R_A = aS/(1 + aS/B_A) \qquad\qquad (A2.1)$$

In this form, S is spawner abundance, R_A is adult recruit abundance, a is maximum recruits/spawner as S approaches zero, and B_A is maximum adult recruits (i.e. adult capacity) at very high spawner abundance. Variation in a produces a family of R_A versus S relationships (Figure A 1) that describe the expected R_A across a range of S and a values.

Optimum spawner abundance for each curve in Figure A 1a can be defined in terms of a "Conservation Concern" Limit Reference Point (abundance at Maximum Sustained Yield, S_{MSY}; Johnston et al. 2000; 2002). The reference point, S_{MSY}, varies with stock productivity (Figure A 1b, green line) but as noted by Johnston et al. (2000; 2002), a single, a-independent, spawner abundance reference point of $0.3B_A$ is close to optimal across a wide range of a values (compare Figure A 1c versus d). This a-independent target for S can be defined in terms of a single parameter ($0.3B$), gives high yield when a is high, and is conservative (protecting the spawning stock) when a is low. This analysis suggests that an optimum escapement goal (S_{opt}) can be defined in terms of habitat capacity (B) alone without having to estimate stock productivity (a). A Ricker R_A vs S relationship does not have this characteristic (Johnston et al. 2002).

Reference Points: Variable Marine Survival Rates

Life history considerations indicate that steelhead stock recruit curves should be expressed in terms of a density-dependent smolt vs spawner relationship (Equation A2.2) followed by density-independent marine survival (Equation A2.3):

$$R_J = a_J S/\left(1 + a_J S/B_J\right) \qquad\qquad (A2.2)$$

$$R_A = mR_J = ma_J S/\left(1 + ma_J S/mB_J\right) \qquad\qquad (A2.3)$$

where R_J is smolt (juvenile) abundance, a_J is juvenile stock productivity expressed as maximum smolts/spawner, m is marine survival rate, and B_J is smolt capacity. Adult capacity (B_A) is the product of m and B_J. Adult stock productivity (a_A) is the product of m and a_J. Variation in the product ma_J produces a family of R_A versus S relationships (Figure A 2) that describe the expected R_A across a range of S and m values, where $a_A=ma_J$ is the maximum R_A/S as S approaches zero.

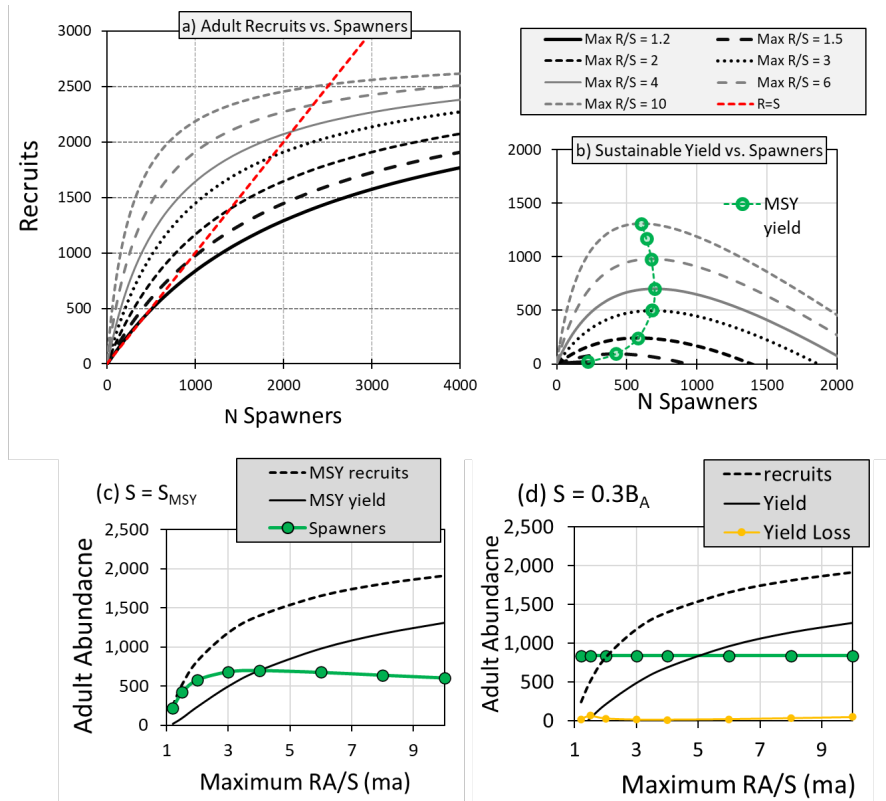[1] Symbols apply to this appendix only.

Figure A 1. Panel a) Adult recruits (R_A) versus spawners (S) curves that share a common maximum adult recruits (B_A parameter) but vary in stock productivity (a parameter). Stock productivity is the maximum R_A/S as S approaches zero. Panel b) The corresponding sustainable yield curves with MSY highlighted in green. Panel c) MSY spawners, recruits and yields for the curves in Panel a. Panel d) Spawners, recruits, and yields for a target escapement of $0.3B_A$. Yield losses are in comparison to MSY_{yield}. For a < 2, yield = 0 because $0.3B_A > S_e$ (unfished equilibrium). Yield losses are small because MSY_{yield} is small. For maximum a > 2, yield losses are small because S_{MSY} is approximately equal to $0.3maB_J$.

In contrast to the fixed B_A case (Figure A 1a), the curves in Figure A 2a do not share a common B_A because both smolt production and adult recruits per smolt increase with *m*. As a result, MSY_{yield}, continues to increase with adult stock productivity (ma_J) until *m* = 100% (Figure A 2b). The net result is that over a max R_A/S range of 2 to 10, the unfished equilibrium abundance increases by 1.8x in for the single step model (Figure A 1a), and 8.6x for the 2-step model (Figure A 2a). However, a fixed escapement goal of m_mB_J (where m_m is median marine survival) still protects the stock under poor marine survival while producing yields of >80% of MSY when marine survival is high.
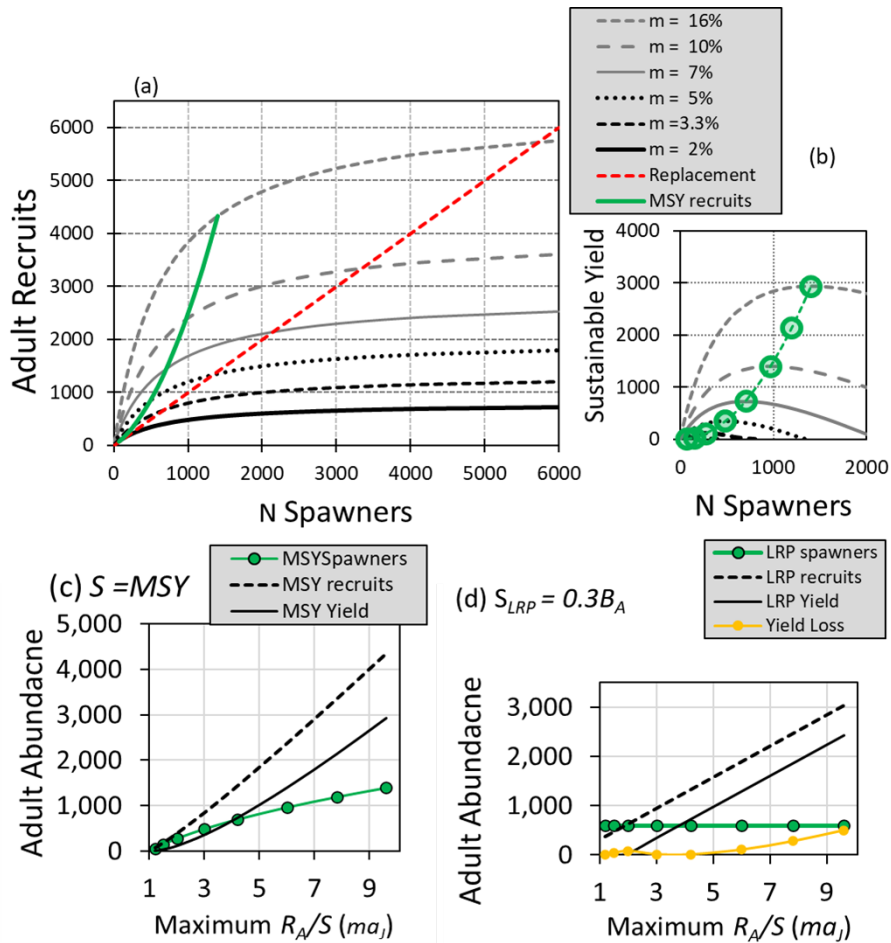
Figure A 2. Panel a) Adult recruits (RA) versus spawners (S) for a range of hypothetical curves that share a common a_JB_J but vary in m. Freshwater productivity (a_J = 60 smolts per female) and smolt capacity (B_J = 40,000 smolts) are the same for all curves. Maximum $R_A/S = ma_J$ as S approaches zero. Panel b) The corresponding sustainable yield curves with MSY highlighted in green. Panel c) MSY spawners, recruits and yields for the curves in Panel a. Panel d) Expected spawners, recruits, and yields for an ma_J-independent Limit Reference Point (LRP) policy where target S = LRP = $0.3B_A$ = $0.3mmB_J$ where mm, median marine survival, is 0.07. Yield losses are in comparison to MSY$_{yield}$. For maximum $R_A/S < 2$, yield = 0 because the LRP is greater than the unfished equilibrium but the yield losses are small because MSY$_{yield}$ is small. For maximum $R_A/S > 2$, yield losses are small because S_{MSY} is approximately equal to $0.3ma_JB_J$.

Estimating Smolt Capacity and Marine Survival

The analysis presented in Figure A 2 provides insight into the processes that produce the very wide range in steelhead adult abundance, such as that observed in Figure 1, under a variable marine survival regime, such as that observed in Figure 6. In addition, Figure A 2d suggests that effective management requires estimates of both m and B_J.

Smolt capacity (B_J in Equation A2.2) can be approximated as the smolt abundance produced by high spawner abundance but is generally inferred rather than measured directly. Direct measurement by trapping migrating spawners and smolts, especially the long time series from the Keogh River, indicates that capacity can vary with factors such as nutrient concentrations and physical habitat quality, but is relatively stable within a defined habitat regime (Ward 2000).

Smolt capacity can also be estimated as $R_J = R_A /m$ when m is high. Estimates of m must be consistent with R_A, both including or not including factors such as harvest mortality, and prespawn mortality.

Estimates of m often involve counting smolts and adults, so this may not seem particularly useful but there are several situations that do not depend on complete smolt counts:
1. m is estimated from a sub-stock (e.g., trap on a tributary)
2. m is derived from hatchery or wild tag-return data
3. m is measured in other populations with similar demography
   a. m is available in a stock with similar adult time dynamics
   b. bounds can be placed on m, e.g., 8% < m < 16% narrows the range of smolt abundance to a factor of 2, which may be adequate for many management applications
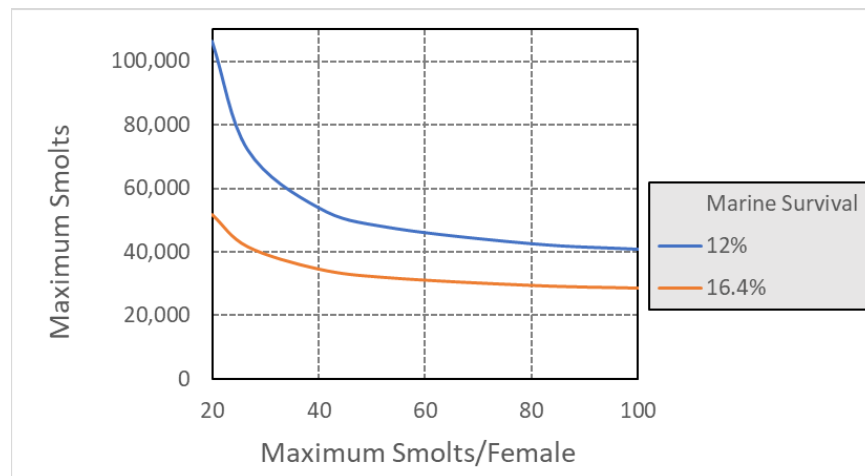

Figure A 3. Smolt capacities for the Thompson steelhead stock (B_J in Equation A2.1) across a range of smolt productivity (a_J in Equation A2.3) at two marine survival rates. Observed recruits and spawners are averaged across the 1978 to 1987 brood years. Lines represent combinations of parameters that predict recruit abundance equal to what has been observed. 16.4% is the average marine survival for Keogh River steelhead for smolt years 1980-89 and 12% is an arbitrary alternative for comparison.

A key outcome of this line of reasoning is that it can provide an estimate of juvenile capacity. For the Thompson steelhead stock, we used two data sets that provided a time series of spawners and the resulting adult pre-fishery recruits (Korman et al. 2018), and a contemporary time series of marine survival of steelhead in the Keogh River (Ratzburg 2022) combined with evidence for a correlation in marine survival between the Keogh River and other rivers entering Georgia Strait (Kendall et al. 2017).

The analytic solutions for these data (Figure A 3) suggest that the Thompson smolt capacity is in the range of 30-60 thousand smolts, possibly higher, but probably not lower given recent estimates of marine survival are typically lower than those in the 1980s (Kendall et al. 2017). The highest values of capacity are generated by combinations of parameters (low m, low a). that are associated with lower stock productivity. In the Keogh River, the intercept of $\ln(R/S)$ versus S indicates that a_J ranges from 50-150 smolts/female (McCubbing et al. 2012) and on 5 of 40 brood years, smolts/wild female are > 100 (Ratzburg 2022). Thompson females carry more eggs, but in the Keogh River, almost all male juveniles smolt (i.e., adult sex ratio ~1:1) whereas, in the Thompson half of all male juveniles do not seem to leave freshwater (i.e., adult sex ratio ~2:1 F:M; Morris 2002; Bison 2009). In addition, some Thompson River tributaries support rainbow trout populations that will compete with steelhead juveniles and therefore reduce the tendency of steelhead to produce higher smolts/female at low steelhead spawner abundance (Morris 2002).

The estimates in Figure A 3 can be compared with estimates based on habitat inventory and on field surveys of juvenile population densities. Juvenile survey data suggests that the maximum smolt abundances are 102,280 under the BH model and 96,261 under Ricker (see Table 11 in Decker et al. 2015), which are somewhat higher than the Figure A 3 estimates. Habitat-based assessments are still higher, in the range of 300,000 for the Thompson Drainage (Riley et al. 1998). As discussed by Decker et al. (2015, see their Section 4.2.4), steelhead and rainbow trout cannot be distinguished as juveniles, and therefore juvenile density data produce inflated estimates of smolt production. This may also be part of the underlying cause of the relatively flat relationship between counts of juveniles and spawners in the Decker et al. data (Figure A 4).
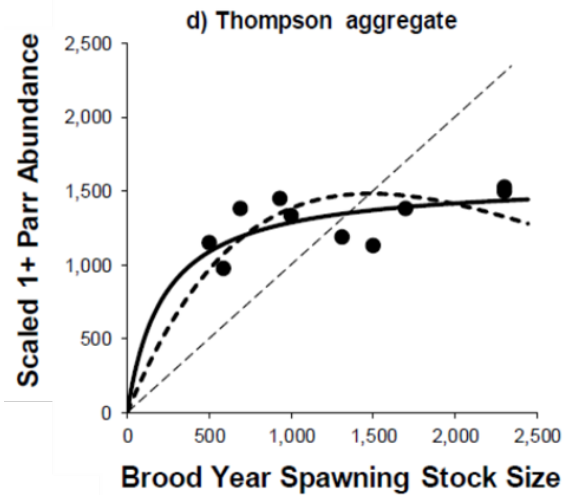
Figure A 4. Reproduction of Decker et al. (2015; Figure 7d). Juvenile recruitment curves (BH solid line, Ricker dashed) for the Thompson steelhead/rainbow population. Spawning stock abundance only includes steelhead.

Demographic Effects of Marine Survival

A key characteristic of steelhead demography is the sensitivity of adult abundance and replacement abundance to changes in marine survival. Smolt numbers at a given spawner abundance are independent of marine survival but adult recruits are directly proportional marine survival (Equation A2.3). The net result is that, as marine survival declines, adult abundance drops rapidly while smolt abundance drops much more slowly, before declining rapidly to zero as marine survival approaches a tipping point (Figure 7).

Most of the general patterns above are independent of the parameters *a, B* and *m*. Capacity is a scalar that can take on a range of values, expressed as percent of a referenced maximum value. By definition, maximum smolts/female multiplied by marine survival must be >1 at replacement and therefore smolt productivity (a_J) determines the point on the marine survival axis where spawners do not replace themselves. As a result, the resilience[2] of the population to changes in marine survival depends on a_J, even though an a_J-independent LRP performs well (Figure A 2).

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[2] Resilience is a measure of how rapidly a population can recover from a one-time mortality event or, alternatively, the ability to maintain current abundance in the face of additional chronic mortality stress (such as harvest or habitat degradation).
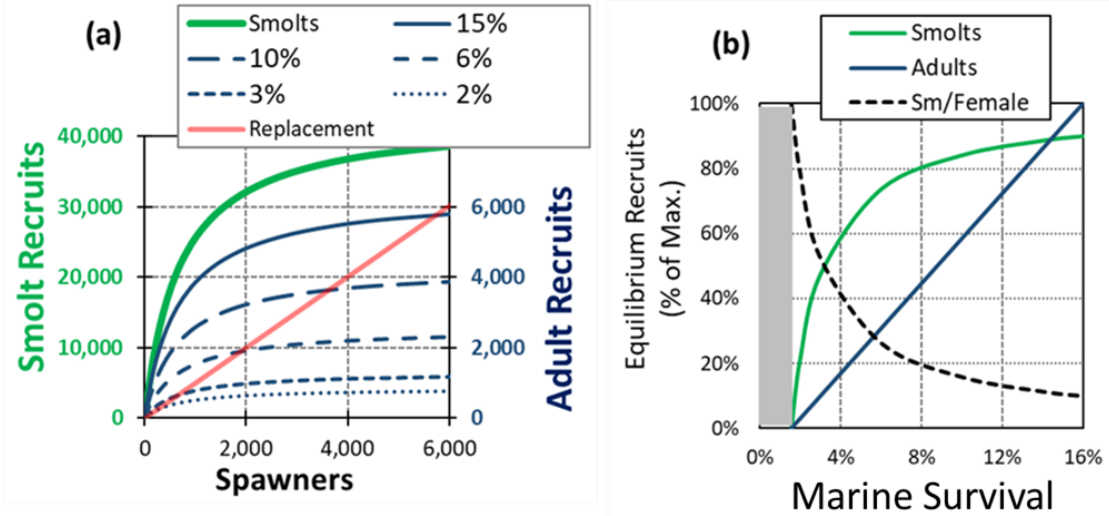
Figure A 5. Panel a) Smolt (green) and pre-fishery adult recruit abundance (blue) as a function of spawner abundance across a range of marine survivals. Smolt abundance is independent of marine survival. Beverton-Holt parameters are intended to approximate those of the Thompson aggregate stock smolts (a=60 smolts/female, B=40,000). Panel b) Replacement abundance of smolts and recruits as functions of marine survival. Capacities are 40,000 for smolts, 6,200 for adults, 60 for smolts/female. The grey rectangle indicates marine survivals where spawners do not replace themselves.

Hatchery Supplementation Analysis

The stock recruit framework in Figure A 1 to Figure A 5 can be used to illustrate the processes that affect the effectiveness of alternative hatchery management programs. This comparison is for illustrative purposes only because, although the survival and capacity parameters are intended to represent the Thompson steelhead, these parameters are based on expert opinion, not a quantified review of available information. A strategy would also include rules that limit the source and number of adults for hatchery broodstock. In this example, the rule is the lesser of 10 NOR females or 50% of NOR females. These hatchery management rules are intended to reflect a hatchery supplementation strategy that favors natural smolt production.

Background

Pollard (2013) categorized hatchery program goals as either conservation ("hatchery supplementation") or sport fisheries enhancement ("hatchery augmentation"). B.C. maintains augmentation hatchery programs in 16 steams but there are currently no supplementation programs (FLNRO 2016) because managers believe that:

> *"There are currently no known effective methods to rebuild depressed populations of wild steelhead other than reducing human-induced mortality and restoring habitat, depending on the mechanism and source responsible the decline and ongoing depressed state. Research in B.C. and elsewhere has shown that hatchery supplementation does not rebuild wild stocks, … Research has also shown that hatchery stocking can reduce the productivity of wild steelhead populations, with the negative impacts increasing with the proportion of the total population that is of hatchery origin. Thus, hatchery augmentation should only be used in special circumstances where impacts on wild populations can be avoided or mitigated for"* (FLNRO 2016, p14).

And for the Interior Fraser River Steelhead populations:

> *"Significant evidence from other jurisdictions as well as B.C.'s experience using hatcheries confirm that attempting to rebuild wild IFS using a hatchery program will likely be unsuccessful at this time and put the wild IFS population at higher risk for extirpation."* (Rhodes and Jenkins 2021, p23)*.

Despite this pessimism, captive breeding programs analogous to Pollard's hatchery supplementation category continue to be an integral part of the recovery strategy for some endangered populations (e.g., Fraser 2008; Kline and Flagg 2014). The purpose of this analysis is to illustrate the factors that would influence the success or failure of a supplementary hatchery strategy for the Thompson steelhead population.

Thompson Steelhead Analysis

The most optimistic assumption concerning the effectiveness of hatchery supplementation is to assume that growth, survival, and reproduction of hatchery origin recruits (HOR) in the natural environment are the same as their natural origin (NOR) counterparts including the survival of HOR to spawning as well as

production of progeny in following generations (Figure A 6a, b). The calculations assume that half of male juveniles residualize, but female juveniles all become smolts.

The obvious appeal of hatchery supplementation is based on the expectation of a large difference in generation 1 (Gen1) smolts/female for NOR (60) versus HOR (3000) in a typical hatchery program (

Table A 2). Assuming the release of smolt-sized HOR juveniles and that NOR and HOR smolt-to-adult return is identical, this strategy produces a 50-fold increase in smolt production/female.

Table A 2. A comparison of smolt production efficacy for hatchery and natural steelhead.

Hatchery (HOR)		Natural (NOR)	
Fecundity	10,000	Bha_w	60
All hatchery smolts/egg	0.4	BHB_w	40,000
Female smolts/egg	0.2	F:M Ratio in steelhead adults	2:1
Female smolts/female	2000	Female smolts/female	40
Male and female smolts/female	3000	All smolts/female	60
Hatchery Discount		**HOR:NOR smolt production ratio**	**50:1**
Gen1 smolt-adult survival	50%		25:1
Gen2 egg-smolt survival	40%		10:1

A more realistic assessment of hatchery supplementation can be modeled using "discounts" of hatchery spawners based on the number of returning adults and the number of NOR smolts produced in the next generation (e.g., (Milot et al. 2013). We can place these effects into 3 categories:

1. **Gen1 Adult Production**: Hatchery production of returning adults can be directly discounted for lower smolt-adult return ratios using a simple multiplier of adults/smolt.

2. **Gen2 Smolt Production**: Incorporation of next generation effects (genetic domestication of hatchery spawners, poor choice of spawning site, concentration near release point) can also be visualized as a simple multiplier of hatchery recruits to express HOR recruits in terms of "NOR equivalents".

3. **GenX+ Smolt and Adult Production**: Ongoing selection for traits that offer an advantage in hatchery environments (e.g., boldness; Biro et al. 2006; Biro and Post 2008; Biro and Stamps 2008; Thompson et al. 2018) but a disadvantage in a wild environment will depend on the relative strength of selection in the two environments and the proportion of the gene pool that is recycled through the hatchery (see section "Hypothesis G2: Domestication Selection: Maladaptation of HOR fish after release into the natural environment leads to reduced survival, growth or reproduction in HOR (and NOR after HOR-NOR interbreeding). Selection for traits that were beneficial in the hatchery environment reduce maximum recruits produced per spawner in adult HOR spawning naturally (and in NOR fish after HOR-NOR interbreeding). These effects are easier to model in a time-series framework, rather than a single generation. The relevant

parameters involve estimating heritability and relative fitness that are notoriously difficult to estimate.

Plausible hatchery discount values (i.e., HOR smolt-adult survival 50% of NOR, smolts per adult for HOR at 40% of NOR) suggest that the benefits of hatchery supplementation operated under a minimum amount of production (e.g., taking in 10 females, up to 50% of females) would be small (maximum 400 adult equivalents, Figure A 6c) in comparison to the undiscounted situation (Maximum 2,000 adult equivalents, Figure A 6b). However only half of the reduction in adult recruits (to 1,000 adults) is observed as Gen1 returns to spawning streams, the second discount (HOR = 40% of NOR) is only observed at the smolt stage in Gen2.
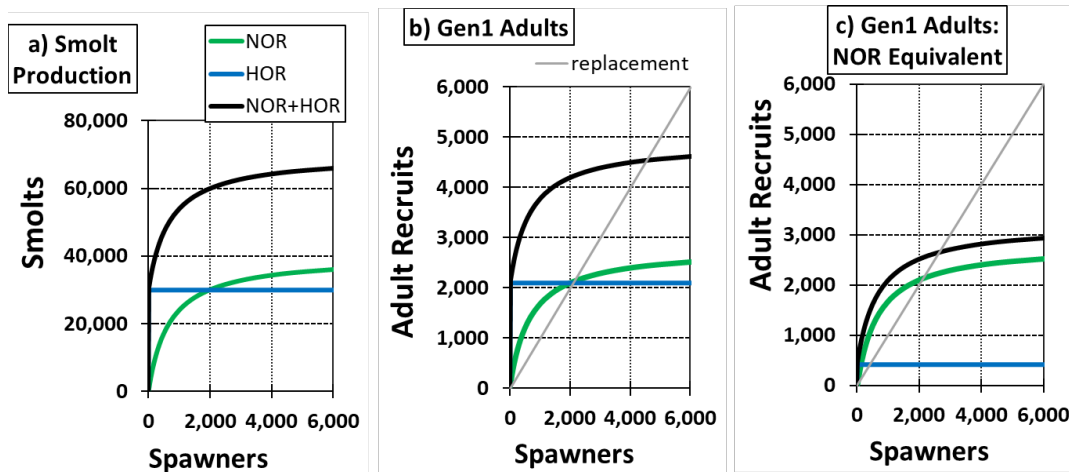

Figure A 6. Smolt (a) and adult (b) production in a system where HOR smolt performance is identical to NOR performance. (c) Adult recruits expressed as NOR equivalents in a situation where hatchery smolts survive at half the rate of wild smolts and HOR spawners produce 40% of the progeny of NOR spawners in the next generation. Table A 2 parameters, combined with a marine survival of 7%, are used in all 3 panels.

Given the hatchery discounts in Table A 2, and if adult populations are large (that which could be expected if marine survival is moderate to high, e.g. 7%, which is moderate to high), a modest hatchery program could be expanded in order to compensate for the hatchery discounts (e.g., from 10 to 50 females in the broodstock). The resulting smolt release is much larger, 150,000 vs. 30,000 (Figure A 8a versus Figure A 7a) and brings the adult equivalent abundance up to the undiscounted values (Figure A 6b versus Figure A 7c).

Supplementary hatchery programs are typically implemented at low marine survival levels when the population is barely viable. Under these conditions, broodstock removals have a more significant demographic effect because they depress the viability of the NOR segment of the population by driving recruitment below replacement (Figure A 8). Under these conditions, a much higher proportion of the Gen2 and GenX+ spawners will have experienced the hatchery environment, and therefore long-term domestication has a stronger influence on the gene pool.
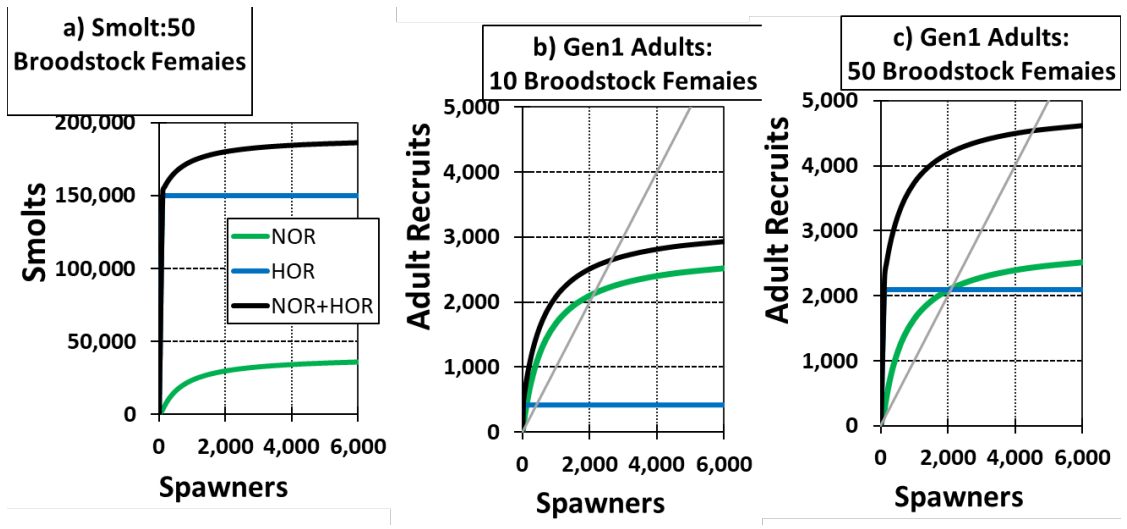
Figure A 7. The effect of increasing hatchery (HOR) production (50 instead of 10 females) on smolt abundance (panel a), and adult returns (panel c) to compensate for a reduction in hatchery survival and next general smolts/spawner. Figure A 6c and A 7b are identical. Marine survival is moderate/high (7%).
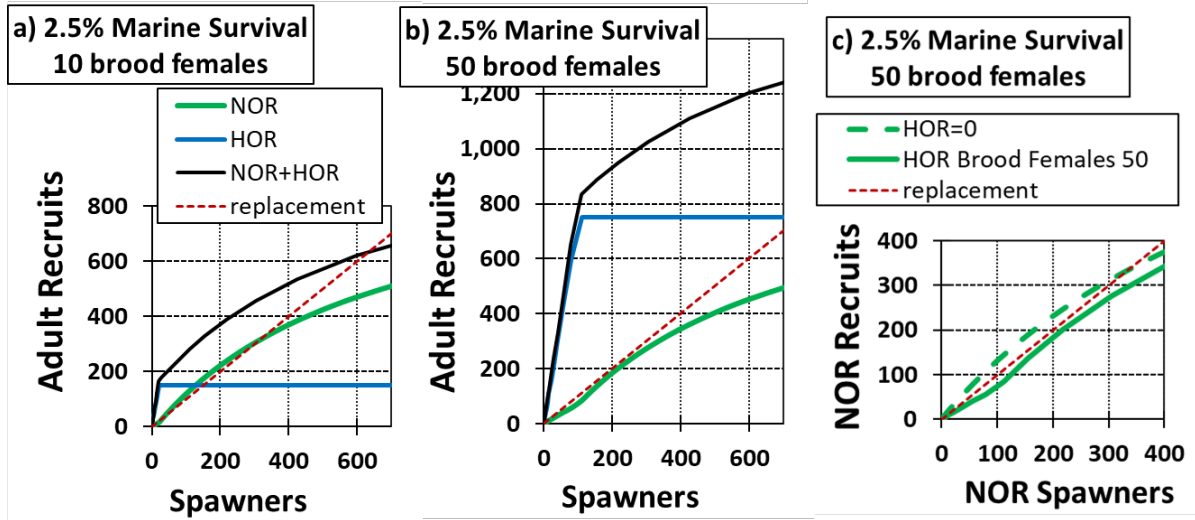
Figure A 8. At low marine survival, moving from low (panel a) to high smolt production (panel b) increases abundance (of HOR + NOR) but NOR spawners no longer replace themselves (panel c, solid green), even though the wild population is marginally viable in the absence of the hatchery program (panel c, dashed green).

Appendix 3: All-H Analyzer Model Results

A central question relevant to this hatchery review is whether hatchery supplementation of steelhead might result in a higher number of wild spawning steelhead than if the population remains wild. The modelling in Appendix 2 broadly identified which scenarios— alternative combinations of number of broodstock collected and marine survival—could result in positive or negative outcomes on the naturally spawning population. However, Appendix 2 did not account for cumulative genetic effects as a result of hatchery domestication, and the results may therefore be overly optimistic regarding long-term impacts of hatchery augmentation on NOR productivity.

To extend the analysis of Appendix 2, we also parameterized a custom version of the All-H Analyzer (AHA) model (Paquet et al. 2011; HSRG 2014, 2020), which explicitly accounts for the impacts of domestication selection and cumulative fitness loss in the natural origin (NOR) population that can arise from prolonged hatchery supplementation. As in Appendix 2, interactions between anadromous and non-anadromous *O. mykiss* are considered beyond the scope of this analysis and not considered in the model.

Introduction to the All-H Analyzer

AHA was initially published by the Hatchery Science Review Group (HSRG) in 2009 and was updated in 2020. This tool has been used extensively to evaluate hatchery and fishery management options for the Columbia River salmon and steelhead stocks (Paquet et al. 2011; HSRG 2014).

Briefly, the AHA model simulates how hatchery practices might influence fitness of the NOR population via domestication selection and interbreeding of HOR and NOR subpopulations. It simulates relative fitness of a population based on a single-locus trait. Fitness ranges from 0-1, and lower fitness populations have lower productivity as they move through juvenile life stages. To reflect different selective pressures in the hatchery and wild environments, the single-locus trait has a different optimal value in each environment – the optimal trait in the wild is favoured by natural selection, the optimal trait in the hatchery is favoured by domestication selection. In the AHA model, fitness is quantified as a normal distribution centred on the optimal trait value (Figure A 9; Ford 2002). If a population's mean trait is at the optimal value, they have a relative fitness of 1. As the mean trait moves further from the optimal, the population's fitness drops (AHA assumes that fitness can only decline to some minimum level, the fitness floor, assumed to be 0.5; (HSRG 2020).

Over generations, the trait is inherited according to trait heritability, selection, and random drift. Because domestication selection in the hatchery and natural selection in the wild are both at play, a totally segregated hatchery system (i.e., with no interbreeding of NOR and HOR) would result in each of the hatchery and naturally spawning populations converging on the optimal trait value in their environment. Whenever there is interbreeding between NOR and HOR fish, the average trait of their offspring is a function of the NOR:HOR ratio of the parent generation. However, HOR spawners in the wild are assumed to reproduce with less success than NOR conspecifics (termed relative reproductive success; Christie et al. 2014).

The population's average trait value is then used to calculate fitness, which impacts the productivity of that population. Expanding on the single-stage Beverton-Holt (BH) model described in Appendix 2: Beverton-Holt stock-recruit analysis of hatchery-wild interactions in Steelhead, the AHA model projects BH processes at each of three juvenile life transitions: adult-to-emergent fry, emergent fry-to-smolt, and smolt-to-adult transitions (Figure A 9). Fitness "loss" is distributed between these stages by down-scaling the productivity (a parameter) and capacity (B parameter) for each of these transitions. Here, we retain the AHA's default assumption of how fitness loss is distributed: 50% of loss applies at the adult-fry transition, 40% at fry-smolt, and 10% at smolt-adult. We do not assume fitness-adjusted productivity during adult stages (c.f. HRSG 2020b). For a full description of the scientific basis for this approach to fitness calculation, see the HSRG's 2009 white paper (HSRG 2009 Appendix A).

Life cycle wide productivity – converting the three-stage BH model into a single stage model

The single stage BH model defined in Appendix 2 can also be represented as a three-stage composite of BH transitions, like that required by the AHA model (Goodyear 1980; Moussalli and Hilborn 1986).

The BH equation defined in Appendix 2 represents the abundance of adult recruits, R_A, produced by S spawners as a function of marine survival rate, m; smolt capacity, B; and the maximum production of adult recruits per spawner, a_A (note that the "A" suffix has been added to indicate that this BH model represents adult-adult productivity and capacity).

$$R_A = ma_AS/(1 + a_AS/B_A) \qquad (A3.1)$$

However, the AHA model requires stage-specific values for a and B for each of the adult-to-fry, fry-to-smolt, and smolt-to-adult life stage transitions. These a and B parameters can be calculated from basic life history characteristics and from parameters defined in the adult-to-adult BH model. Adult-to-fry productivity, $a_{A \to F}$, is the product of NOR fecundity, e_{NOR}, and NOR sex ratio (sxr):

$$a_{A \to F} = e_{NOR} * sxr \qquad (A3.2a)$$

Smolt-to-adult productivity ($a_{S \to A}$) is equal to the smolt-adult return rate for NOR returns, SAR_{NOR}:

$$a_{S \to A} = SAR_{NOR} \qquad (A3.2b)$$

Fry-to-smolt productivity is calculated from observed adult to adult productivity, a_A, and the previously calculated adult-to-fry and smolt-to-adult productivity values:

$$a_{F \to S} = \frac{a_A}{a_{A \to F} * a_{S \to A}} \qquad (A3.2c)$$

To calculate stage-specific B parameters, the AHA model assumes very high capacities for the adult-to-fry and smolt-to-adult transitions (i.e., $B_{E \to F}$ and $B_{S \to A}$ are both set to $1*10^{12}$ individuals). With this assumption, AHA calculates the fry-to-smolt capacity as:

$$B_{F \to S} = \frac{1}{a_{S \to A} \left(\frac{1}{B_A} - \frac{1}{B_{S \to A}} \right)} \qquad (A3.3)$$

Then, each parameter is fitness-adjusted. In each generation g, the fitness loss in the population (f_g) is used to calculate fitness-adjusted productivity (a') and capacity (B') parameters according to the

relative fitness consequences in the adult-to-fry, fry-to-smolt, and smolt-to-adult transitions (i.e., 0.5, 0.4, and 0.1, respectively):

$$a'_{A \to F} = \left(f_g\right)^{0.5} a_{A \to F} \tag{A3.4a}$$

$$a'_{F \to S} = \left(f_g\right)^{0.4} a_{F \to S} \tag{A3.4b}$$

$$a'_{S \to A} = \left(f_g\right)^{0.1} a_{S \to A} \tag{A3.4c}$$

and

$$B'_{A \to F} = \left(f_g\right)^{0.5} B_{A \to F} \tag{A3.5a}$$

$$B'_{F \to S} = \left(f_g\right)^{0.4} B_{F \to S} \tag{A3.5b}$$

$$B'_{S \to A} = \left(f_g\right)^{0.1} B_{S \to A} \tag{A3.5c}$$

To generate recruits per spawner curves from AHA-predicted fitness-adjusted productivity and capacity terms, we converted the three-stage BH parameters into the corresponding adult-to-adult BH parameters, accounting for fitness loss. Adult to adult productivity, $a_{A \to A}$, can be calculated from the product of each stage's productivity parameters,

$$a'_{A \to A} = a'_{E \to F} * a'_{F \to S} * a'_{S \to A} \tag{A3.6}$$

and adult-to-adult capacity, $B_{A \to A}$, can be calculated as a function of adult-to-adult productivity and the productivity and capacity parameters for each stage transition:

$$B_{A \to A} = a_{A \to A} \left(\frac{a_{A \to F}}{B_{A \to F}} + \frac{a_{A \to F} * a_{F \to S}}{B_{F \to S}} + \frac{a_{A \to F} * a_{F \to S} * a_{S \to A}}{B_{S \to A}} \right)^{-1} \tag{A3.7}$$

For all results showing recruit-spawner relations projected under the AHA model (e.g., Figure A 11-A 14, Figure A 16-Figure A 17), the relationship was modelled using $a_{A \to A}$ and $B_{A \to A}$ in the 100th generation after hatchery supplementation begins.
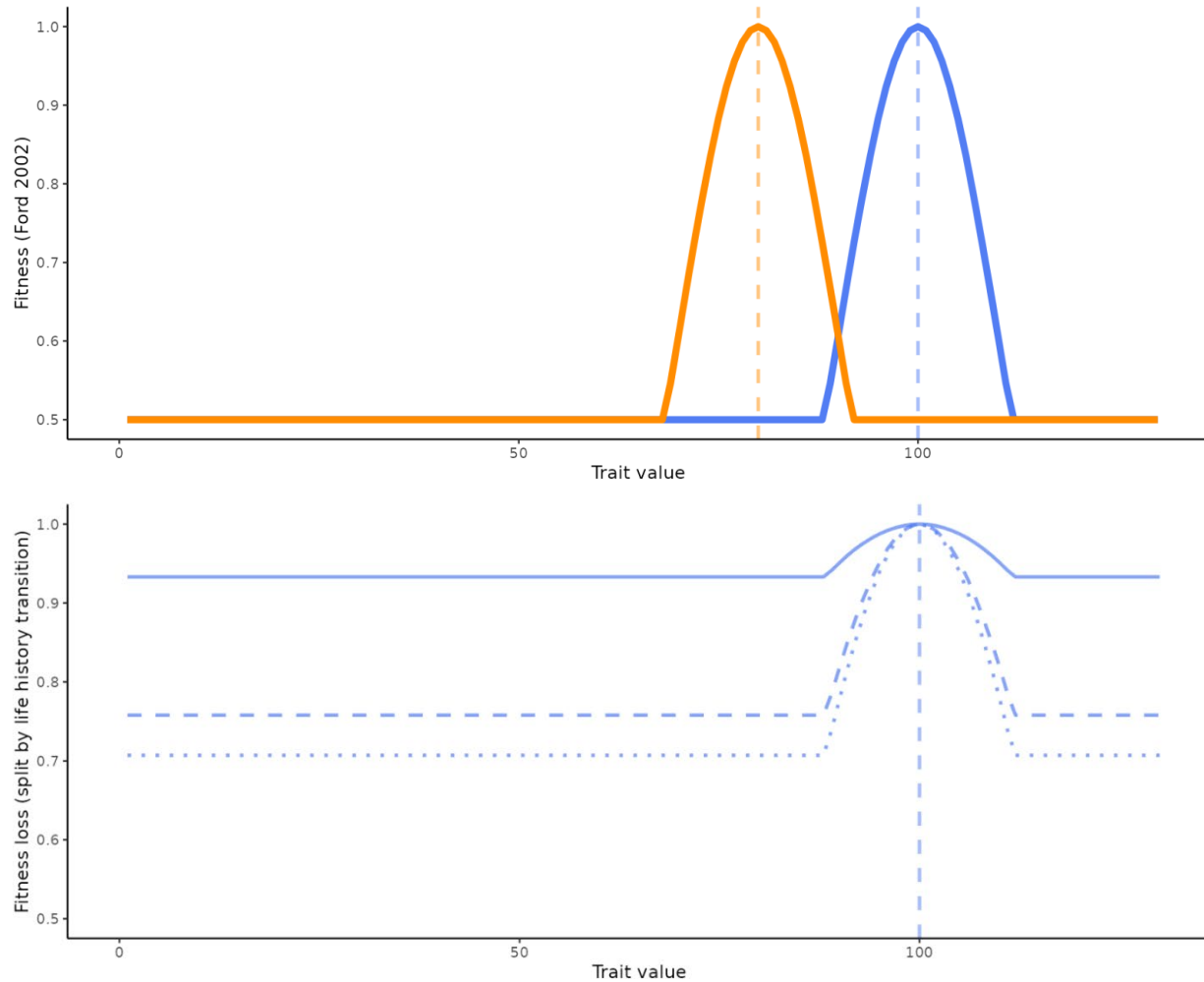
Figure A 9. Fitness of a single-locus trait as modelled by the Ford fitness equation (2002) as used in AHA. In the upper panel, fitness of the trait in a hatchery environment is shown in orange and assumed to have an optimal value of 80 (vertical dashed line); fitness in the natural environment (blue) is assumed to have an optimal value of 100 (values above and below this are less than optimal fitness). In the lower panel, we show the partitioning of fitness loss in the naturally spawned population during three transitions: egg-to-fry (dotted line); fry-to-smolt (dashed line), and smolt-to-adult (continuous line). Parameters match default values in the AHA; the same values were used to model fitness of the IFRS under a variety of hatchery scenarios. (i.e., a fitness floor of 0.5; selection strength, $\omega^2 = 3$; phenotypic variance, $\sigma^2 = 10$; with 50% of fitness loss at the egg-to-fry transition, 40% at fry-to-smolt, and 10% at smolt-to-adult).

Parameterization of AHA for IFRS

For our application of AHA to B.C. steelhead, we converted the Excel based AHA model (HSRG 2020) into an identical model in R. The purpose of translating the model into R was to allow for greater flexibility and exploration of the model, and integration of the model into a graphical Shiny interface to assist in model checking and development.

We maintained several life history parameters from the simpler BH model described in Appendix 2, with the goal of ensuring that two models' results are easily comparable. For example, we have maintained the assumption that HOR spawners in the wild have lower reproductive success than NOR conspecifics (e.g., by selecting poorer quality spawning areas; (Berntson et al. 2011; Christie et al. 2014)). Similarly, we assume that upon immediate ocean entry, hatchery released smolts will have 50% marine survival compared to NOR conspecifics. Parameters used in the three base case scenarios are shown in Table A 3.

Obtaining estimates of marine survival is difficult in low abundance wild populations since it requires tagging of juveniles before they smolt. To our knowledge, no direct estimates of marine survival are available for IFRS. However, given estimates of fecundity and estimates (or assumptions) about the freshwater survival of other life stages, we can tune the value of marine survival to result in a number of wild spawners that matches the recent estimates of around 200 spawners. This tuning indicated that a value of marine survival just under 1.8% gave around 200 spawners under the assumed fecundity, productivity, capacity, and freshwater survivals. For comparison with other populations where marine survival estimates are available, 1.8% is within range of recent estimates for Keogh River steelhead during the current regime of declining marine survival for steelhead (Kendall et al. 2017; Wilson et al. 2022). Given Keogh River steelhead exhibit strong coherence with IFRS (Korman et al. 2018; Wilson et al. 2022), this value therefore appears reasonable.

Table A 3. Hatchery and biological parameters used in the three "base case" AHA model scenarios. Values and justifications for each parameter are provided. Many parameter values—especially those related to trait heritability and fitness—are retained from the AHA model's default parameterization.

Parameter description	Value	Source/rationale
Initial values		
Initial NOR abundance	200	Based upon recent estimates of returning adults
Initial HOR abundance	0	No current hatchery program
Initial productivity of the adult NOR population	64 * NOR marine survival	Analogous to Appendix 2
Initial population capacity of the adult NOR population	86000 * NOR marine survival	BHB$_w$ from Appendix 2 (but adjusted for inclusion of males in the AHA model, unlike female-only in Appendix 2)
Initial trait value for the NOR population	100	Optimal trait value in the wild; AHA default
Marine survival parameters for the base case		
NOR marine survival	0.0175	See text for justification
HOR marine survival	0.0175 * 0.5	See text for justification; Melnychuk et al. 2014
Naturally spawning population parameters		
Fecundity in the wild	10,000	Analogous to Appendix 2
Sex ratio of wild spawners (F:M)	2:1	Analogous to Appendix 2
Relative reproductive success of HOR:NOR spawners in the wild	0.4	Analogous to Appendix 2; within range reported in Christie et al. 2014
Hatchery spawning population parameters		
Fecundity in the hatchery	10,000	Analogous to Appendix 2
Sex ratio of hatchery spawners (F:M)	2:1	Analogous to Appendix 2
Hatchery pre-spawn mortality	0.1	Analogous to Appendix 2
In-hatchery survival to release	0.4	Analogous to Appendix 2
Percent of hatchery reared fish released as smolts	100%	Assumed that hatchery program will prefer to release smolts
Fitness, trait, and inheritance parameters		
Trait value with the optimal fitness in the wild	100	AHA default
Trait value with the optimal fitness in the hatchery	80	AHA default
Selection strength (in SD units)	3	AHA default
Trait heritability	0.5	AHA default
Natural trait variation (σ^2)	10	AHA default

Relative fitness loss during the egg-fry transition	0.5	AHA default
Relative fitness loss during the fry-smolt transition	0.4	AHA default
Relative fitness loss during the smolt-adult transition	0.1	AHA default

Management scenarios modelled with AHA

To assess a variety of plausible management scenarios, we included three management levers which were allowed to vary between model runs: 1) the number of NOR fish taken for broodstock; 2) the maximum percent of NOR returns that are to be taken for broodstock (i.e., as natural origin broodstock, NOB); and 3) mark selective harvest of HOR adults before they can reach natural spawning grounds. See section "Exploratory modelling of hatchery production: AHA model" in the main text for more details.

We assume that all broodstock are used to produce the maximum number of hatchery releases possible; therefore, we do not consider policies which produce less than the maximum number of HOR releases from broodstock. Rather, we assume that all eggs collected from NOB that survive in-hatchery handling mortality are incubated until smolt stage, then all that survive to this stage are released. In this way, NOB scales linearly with the size of the hatchery releases (because handling mortality and in-hatchery survival are fixed parameters).

Measuring performance of alternative hatchery scenarios

To compare the performance of the base case scenarios, we consider four metrics of success: 1) the abundance of NOR spawners returning to wild spawning areas, 2) recruits per spawner for the wild spawning population, 3) fitness-adjusted productivity and capacity, and 4) proportionate natural influence, pNI.

To accommodate timelines typical to management decision-making while accounting for the long timespans required to assess fitness loss in supplemented populations, we assessed these metrics at three stages in time: after the 5th, 20th, and 100th generation following the beginning of the hatchery program. Because the offspring of NOB collected for the hatchery are only released after the first generation, there is a one-generation lag of hatchery returns following the initialization year. While 100 generations is a longer span than the typical time frames used for population modelling, the AHA model's main utility is to project long-term fitness consequences that compound over generations.

Following 100 generations of supplementation according to the above prescribed hatchery practices, we estimated fitness-adjusted capacity and productivity for smolt production in naturally spawning populations. These were then used as new capacity and productivity parameters in a Beverton-Holt model (i.e., to replace the hatchery discounting terms used in Appendix 2, instead reflecting the genetic legacy of interbreeding between HOR and NOR fish via AHA's predictions of long-term fitness-adjusted capacity and productivity).

Below we present timeseries plots under the baseline model, focusing on key metrics: recruits per spawner (R/S) for the wild population, the abundance of wild spawners at the 100th generation (considered analogous to at equilibrium), and proportionate natural influence, pNI:

$$pNI = \frac{pNOB}{pNOB + pHOS}$$

where *pNOB* is the proportionate natural origin fish in the broodstock, and *pHOS* is the proportion of hatchery origin fish spawning in natural areas. pNI is considered a useful approximation for the equilibrium distance between a population's current phenotypic trait and the trait with maximum fitness, and gives general guidance about the direction of the hatchery program in terms of fitness consequences; pNI is not useful as a quantitative measure of short-term dynamics. As a proportion, pNI can theoretically range from 0-1; however, in a hatchery program with an all-natural broodstock, the lowest possible value of pNI is 0.5.

Model runs to assess sensitivity

In addition to the three base cases described above, we also assessed outcomes of the AHA model under different assumptions of broodstock collection and marine survival, two key axes of uncertainty. See main text sections titled "
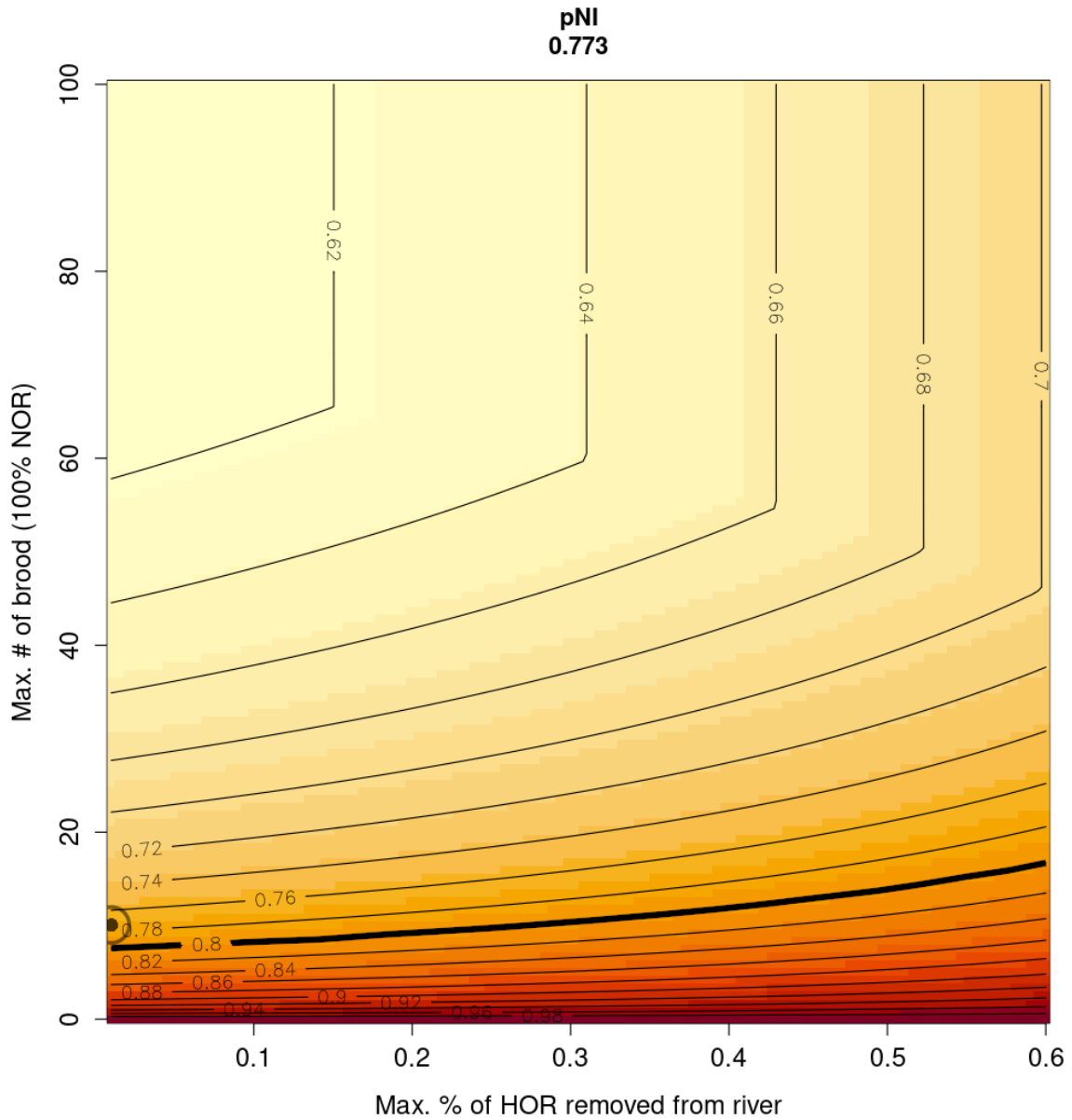
Figure A 13. Proportionate natural influence (pNI) under alternative hatchery programs; i.e., combinations of the number of natural-origin (NOR) broodstock on the y-axis, and the maximum percent of returning hatchery-origin (HOR) spawners that are removed by mark-selective fisheries on the x-axis. The thick line indicates the acceptable pNI for an integrated-wild population, 0.8 (for a Chinook population, see

). The point and value in the plot title indicate hatchery program and pNI expected under scenario 2, a hatchery with 10 broodstock and no selective removal of HOR adults. Under current model parameterization (Table A 3), with 10 NOR broodstock, removal of at least 27% of HOR returns is required to meet pNI ≥ 0.8. Darker colours represent higher pNI.

Sensitivity of results to broodstock collection rules" and "Sensitivity to marine survival assumptions ".

Model assumptions and limitations

An important secondary goal of the hatchery program may be to provide angling opportunities through augmentation. Assuming that the recreational opportunities provided by supplementation are also of interest to decision makers, we also used the AHA model to assess how many returning HOR adult steelhead might be removed by a targeted angling program. We only assess this outcome in sensitivity tests that varied the size of the hatchery program; only one of the base case scenarios assessed selective harvest of HOR adults.

The model assumes that all HOR and NOR offspring produced by the model are anadromous, and we do not consider here the rainbow trout population. In addition, we do not consider repeat spawning by kelts as incidence of repeat spawning in IFRS is very low.

Base case results

NOR spawner abundance

Under the status quo scenario, the AHA model estimated that the population would, over 100 generations, decrease from the initial abundance of 200 NOR fish in the ocean to approximately 160 NOR spawners (Figure A 10). In contrast, with a conservative hatchery program that takes 10 NOR adults to broodstock, the NOR abundance is expected to reach and stabilize just above 400 individuals by the end of the 100th generation. When there is a 60% selective harvest on HOR returns under scenario three, NOR spawners are expected to increase to just above 300 after the 100-generation timespan. These abundance estimates are an order of magnitude below historical abundances (Figure 1).

Under current model assumptions, the AHA model predicts that any hatchery program will provide improved abundance of NOR spawners over the current non-supplemented case (with absolute abundance depending on whether a selective fishery on HOR fish is in place; Figure A 10 and see Figure 8). With 0% selective harvest on returning HOR adults, the abundance of NOR spawners may increase over 200% that of the unsupplemented case.

Recruits per spawner (at 20 spawners)

To compute recruits per spawner (R/S), we used the cumulative Beverton Holt parameters from the AHA model to define a Beverton Holt stock recruit curve. We looked at R/S for each generation modelled under AHA (Figure A 11, Figure A 12), and also assessed R/S at a fixed abundance of 20 NOR spawners to compare the three base case scenarios.

Under all scenarios, R/S increased recruits per spawner (R/S; calculated at 20 spawners) reached and surpassed 1. The highest R/S was projected under status-quo, without supplementation (here, R/S at 20 spawners is projected to stabilize at 1.1; Figure A 11). Because the population of NOR spawners is higher under scenarios 2 and 3 than under the status-quo case, AHA estimated that R/S at 20 spawners would decline over time and stabilize at 1.06 and 1.01 with and without a 60% harvest rate on HOR returns, respectively.

Proportionate natural influence

Under scenario 1, there is no hatchery activity and therefore no intergenerational loss of fitness and pNI remains at 1. Scenarios two and three are predicted to cause a loss of pNI to below 0.9, even after 100 generations (see Figure 15 in the main text). AHA predicted that pNI was lowest under scenario two within the first five generations of supplementation—here, there is an initial spike in the proportion of HOR adults spawning on natural spawning grounds before the NOR population has a chance to rebuild (c.f. Figure A 10). Under scenario three, where there is 60% selective harvest of HOR returns to limit the proportion of HOR spawners on natural spawning grounds, pNI is somewhat higher than scenario two and stabilizes at 0.846. Only when there are selective removals of hatchery-supplemented scenarios are projected to result in pNI values that fall within the acceptable range for an integrated hatchery program (i.e., > 0.8,

). When there are 10 fish taken for broodstock, a minimum of 27% of HOR returns must be removed to ensure a pNI higher than 0.8 (Figure A 13).

For a full discussion of projected fitness loss between the three base cases, see section: "

Exploratory modelling of hatchery production: AHA model".

Table A 4. AHA model's estimates of the abundance of natural-origin (NOR) spawners, recruits per spawner (R/S) for the NOR population when the abundance of the NOR population is 200 spawners, and proportionate natural influence (pNI). We show model projections at three generations (Gen.): 5, 20, and 100. We show results for three management scenarios: status quo, without hatchery supplementation; and two supplemented scenarios, one with 0% selective harvest on returning hatchery origin (HOR) adults, another with 60% selective harvest on HOR returning adults.

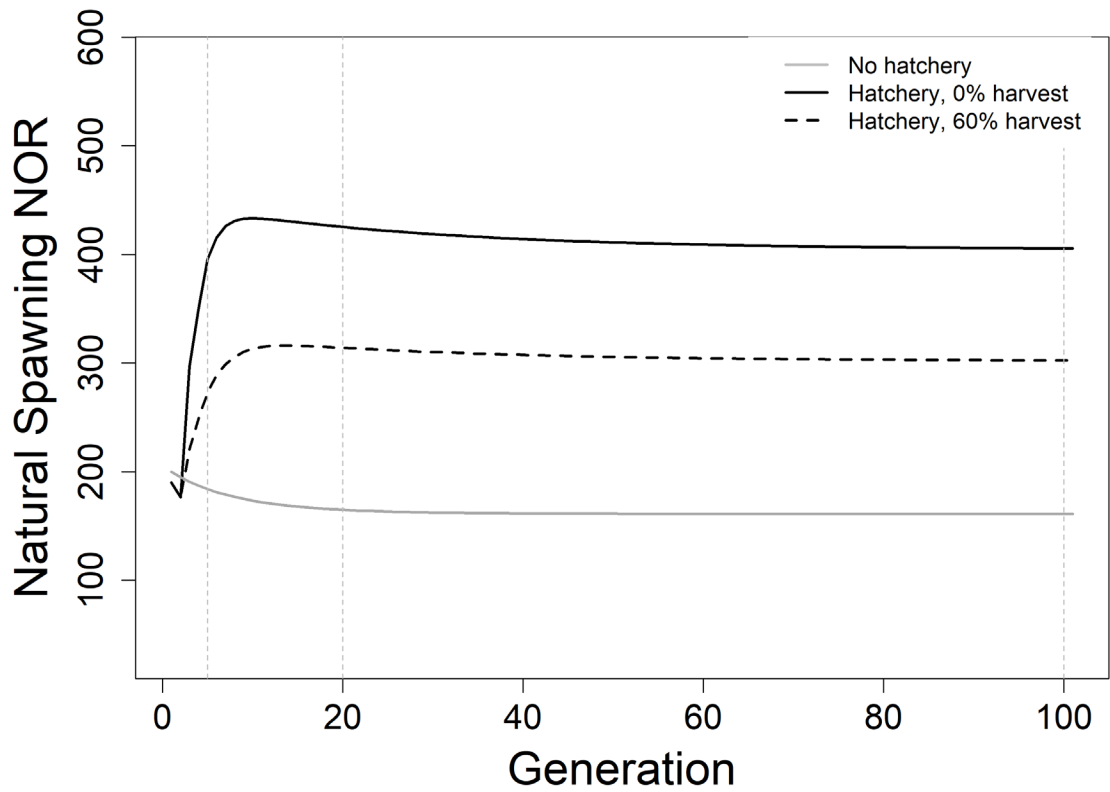| Metric	Gen.	Management scenario		
		1: Status quo	2: 10 NOB (max. 10%), 0% HOR harvest	3: 10 NOB (max 10%), 60% HOR harvest
NOR spawners	5	184	396	273
	20	165	425	314
	100	161	406	303
NOR R/S (at 20 NOR spawners)	5	1.1	1.05	1.08
	20	1.1	1.03	1.07
	100	1.1	1.01	1.06
pNI	5	1	0.77	0.835
	20	1	0.779	0.85
	100	1	0.773	0.846

Figure A 10. AHA-projected abundance of the wild spawning NOR adult population over 100 generations. The grey line represents the status-quo management scenario, in which no hatchery program is implemented. The solid black line shows scenario two (10 NOB in each generation, with 0% selective harvest on HOR returns), while the dashed black line shows scenario three (10 NOB in each generation, with 60% selective harvest on HOR returns). Vertical lines indicate the 5th, 20th, and 100th generation simulated.
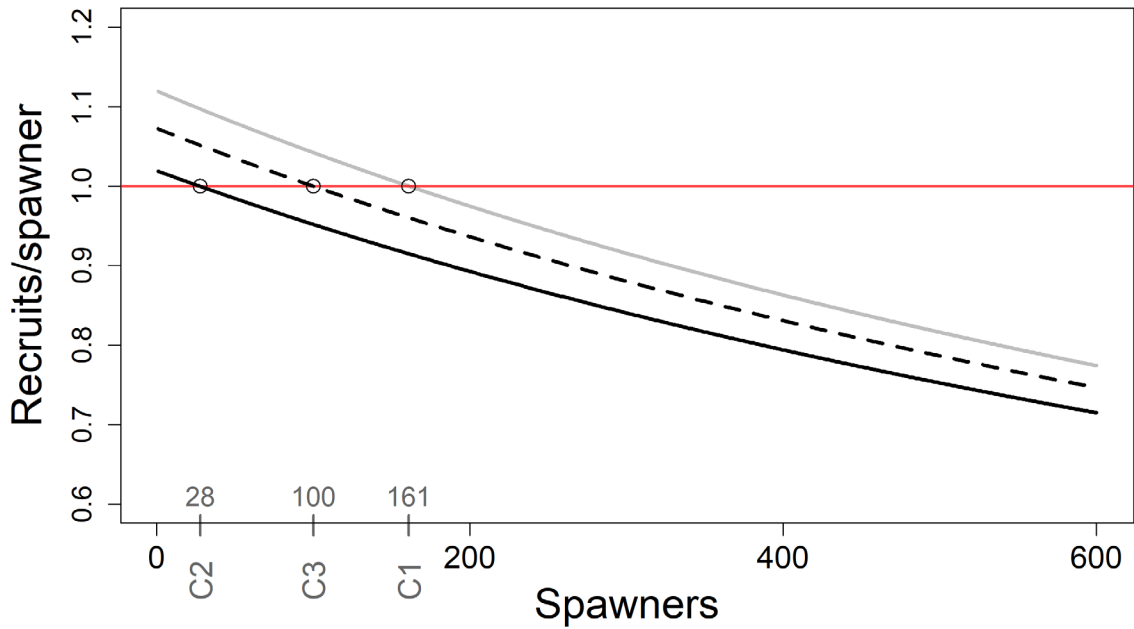
Figure A 11. Recruits per spawner for the naturally spawning NOR population (excluding HOR) at different spawner abundances after a 100-generation projection of the IFRS population using the AHA model. The grey line represents the base case scenario (case 1, C1), in which no hatchery program is implemented. The solid black line shows the curve under scenario two (C2), while the dashed black line shows the curve under scenario three (C3). The red vertical line shows where R/S = 1; the spawner abundance where the R/S curve intersects with R/S = 1 is the long-term equilibrium spawner abundance for population replacement. Equilibrium spawner abundances for each scenario (C1, C2 and C3) are shown on the X axis in grey.
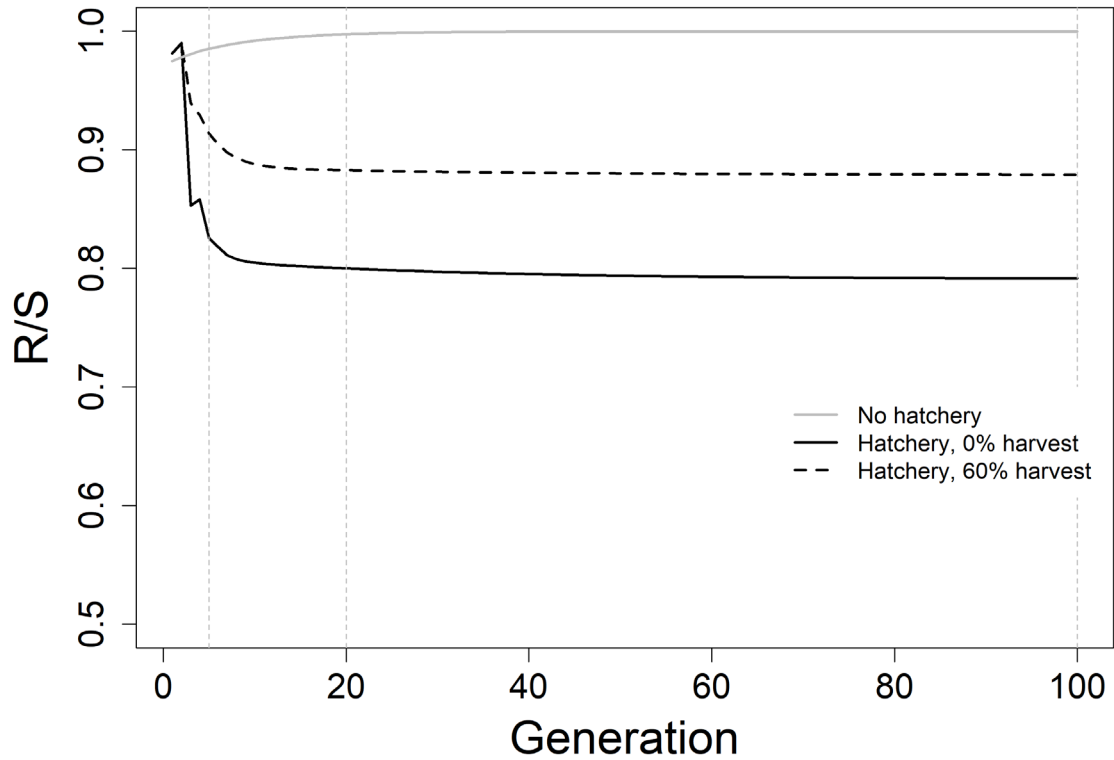
Figure A 12. AHA-projected recruits per spawner (R/S) for the NOR spawning population over 100 generations. Recruits were calculated from generation-specific productivity and capacity parameters, based on the number of NOR spawners in that generation. The grey line represents the status-quo management scenario, in which no hatchery program is implemented. The solid black line shows scenario two (10 NOB in each generation, with 0% selective harvest on HOR returns), while the dashed black line shows scenario three (10 NOB in each generation, with 60% selective harvest on HOR returns). Vertical lines indicate the 5th, 20th, and 100th generation simulated.
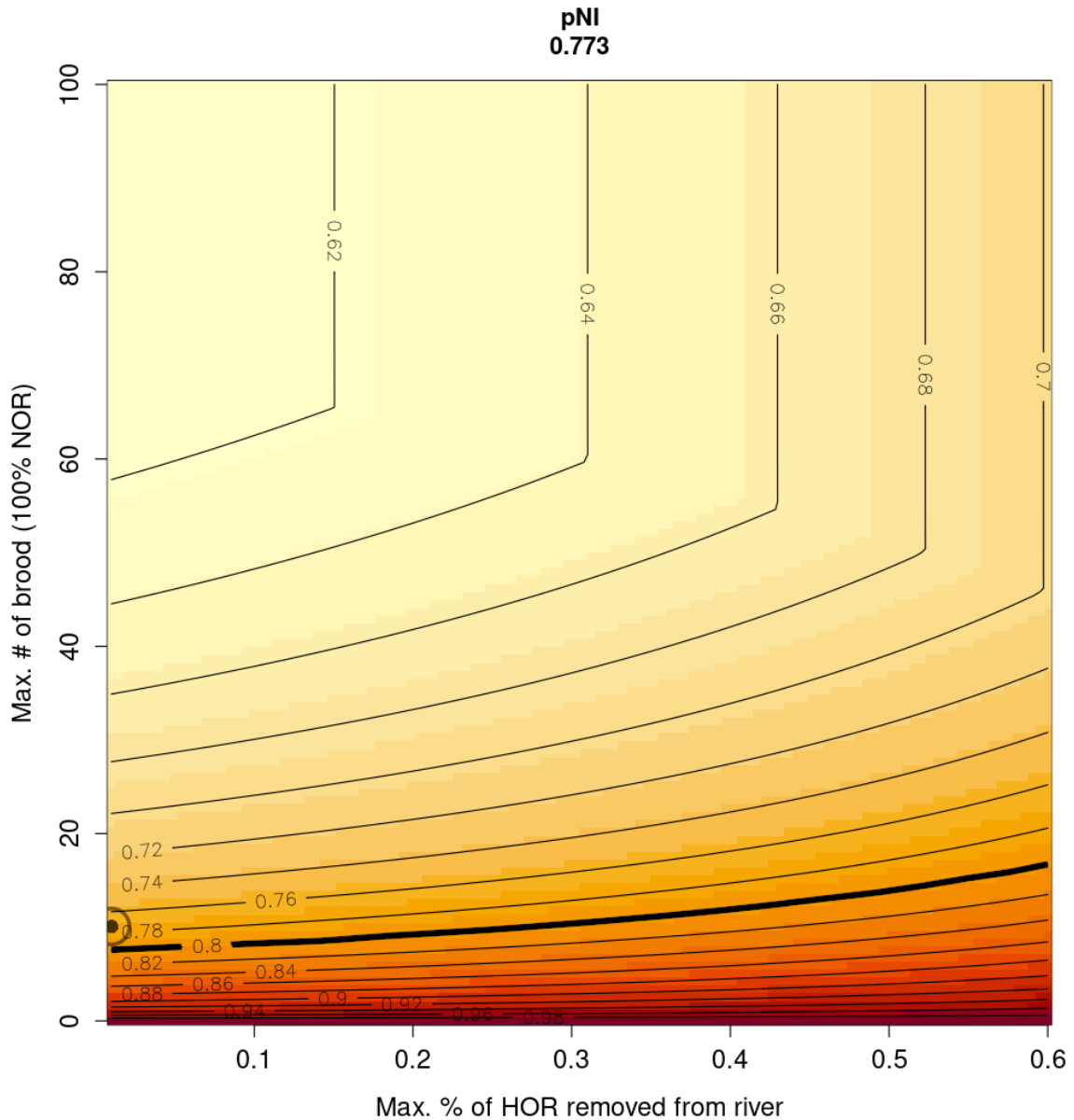
Figure A 13. Proportionate natural influence (pNI) under alternative hatchery programs; i.e., combinations of the number of natural-origin (NOR) broodstock on the y-axis, and the maximum percent of returning hatchery-origin (HOR) spawners that are removed by mark-selective fisheries on the x-axis. The thick line indicates the acceptable pNI for an integrated-wild population, 0.8 (for a Chinook population, see

). The point and value in the plot title indicate hatchery program and pNI expected under scenario 2, a hatchery with 10 broodstock and no selective removal of HOR adults. Under current model parameterization (Table A 3), with 10 NOR broodstock, removal of at least 27% of HOR returns is required to meet pNI ≥ 0.8. Darker colours represent higher pNI.

Sensitivity of results to broodstock collection rules

While the base case hatchery has a relatively small collection of NOR (10 broodstock), for sensitivity testing we allowed the maximum number of NOR broodstock (NOB) to range between 0-100 fish (assuming a 1:1 sex ratio, such that up to 50 female NOR enter the hatchery). As the abundance of the NOR population is relatively low (set to be 200 individuals in the first generation of the AHA model), it may be the case that removal of NOR for broodstock would negatively impact the productivity of the naturally spawning population. Therefore, we also included management scenarios where the proportion of NOR returns taken for broodstock ranges between 0-100% (compared to the base case, where only up to 10% of the NOR adults may be taken for broodstock).

The AHA model predicted that increasing the number of NOR collected for broodstock could result in higher NOR returns (Figure 8 and Figure 9), lower R/S (Figure A 16 and Figure A 17), and lower pNI (Figure A 18 and Figure A 19) than the base case hatchery. Overall, we found that the number of NOR collected for broodstock was more influential on all of these outcomes than the maximum percent of the total NOR returns that are collected. Only when a maximum of 20% or less of the NOR returns could be collected did abundance outcomes appear sensitive to the maximum percent rule. We found that in scenarios with a selective fishery that removes 60% of HOR, the maximum percent rule was slightly more influential on all outcomes (but not more influential than the rule dictating the maximum number of NOR collected for broodstock).

Considering harvest goals, we first considered the sensitivity of harvested abundances (under base case 3, the only scenario which includes harvest of HOR returns) to different hatchery broodstock collection rules (Figure A 20). Here, like the base case runs, we assume a selective freshwater fishery could remove 60% of HOR returns (parameterized as a fixed annual removal rate). Because the selective removal rate of 60% is likely over-optimistic, we also assessed the sensitivity of the number of HOR harvested in response to different broodstock collection and selective harvest rates (Figure A). As would be expected, the number of HOR adults harvested by a selective fishery increases with the size of the hatchery program and the rate of removal (Figure A 20 and Figure A 21).

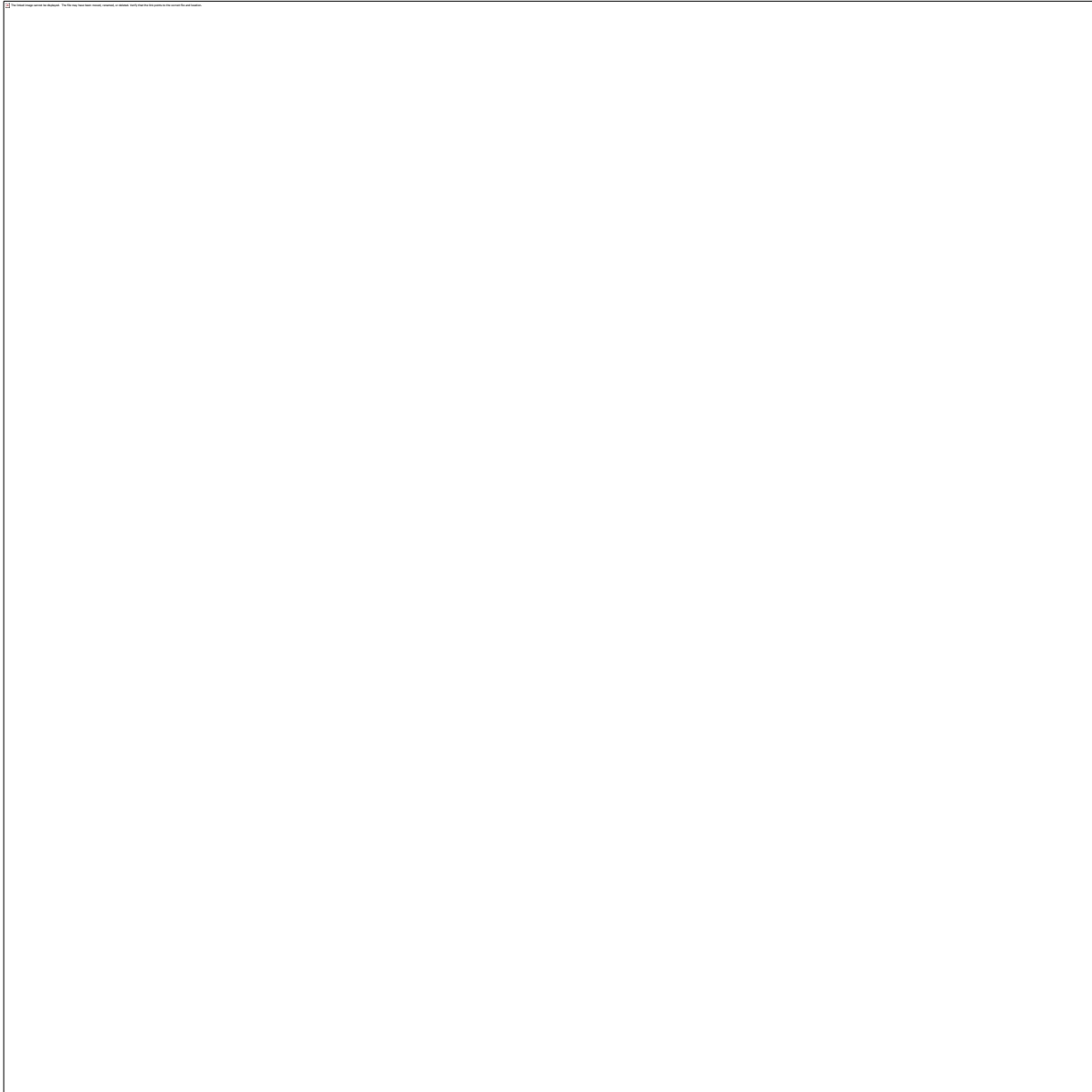Sensitivity of NOR spawner abundance to broodstock collection rules

Figure A 14. Sensitivity of the abundance of NOR spawners in the 100th generation to different hatchery rules under scenario 2, with 0% selective harvest mortality on HOR returns. The black point represents the base case assumption of hatchery practices—10 NOR taken as broodstock, or up to 10% of the NOR returns in each generation—and the value in the title shows NOR abundance under those assumed values. The dashed line shows abundance under the non-supplemented base case 1. Values on the isopleth represent NOR abundance; darker colors occur where the hatchery would result in higher NOR abundance than the status-quo.
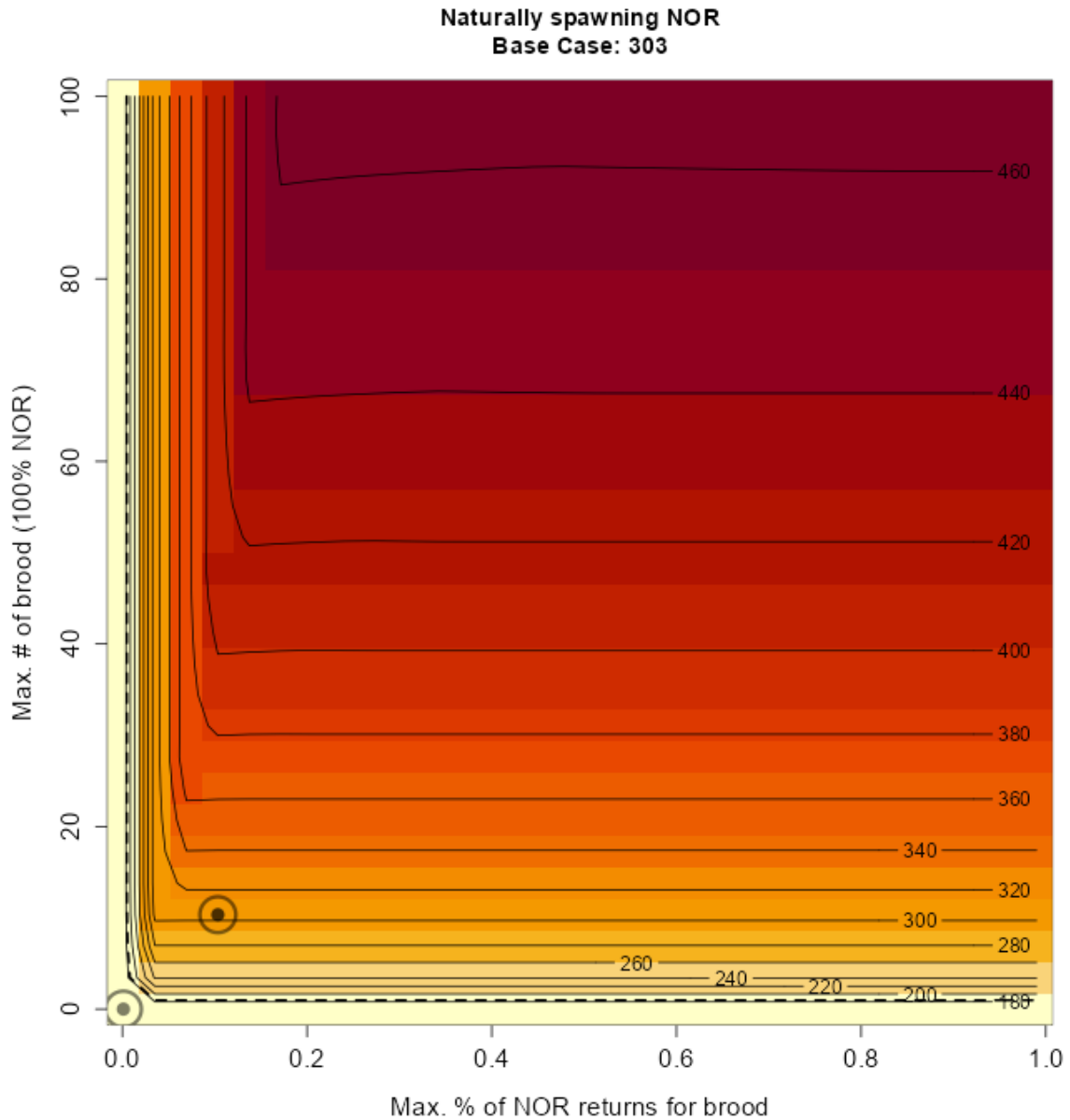
Naturally spawning NOR
Base Case: 303

Figure A 15. Sensitivity of the abundance of NOR spawners in the 100th generation to different hatchery rules under scenario 3, with 60% selective harvest mortality on HOR returns. The black point represents the base case assumption of hatchery practices—10 NOR taken as broodstock, or up to 10% of the NOR returns in each generation—and the value in the title shows NOR abundance under those assumed values. The dashed line shows abundance under the non-supplemented base case 1. Values on the isopleth represent NOR abundance; darker colors occur where the hatchery would result in higher NOR abundance.

Sensitivity of R/S (at 200 NOR spawners) to broodstock collection rules

Figure A 16. Sensitivity of recruits per spawner (at 200 NOR spawners, according to the productivity and capacity estimates in the 100th generation) to different broodstock take rules for scenario 2, with 0% selective harvest mortality on HOR returns. The black point represents the base case assumption of broodstock collection practices, and the value in the title shows R/S under those assumed values. Values on the isopleth represent R/S; darker colors occur where the hatchery would result in higher NOR abundance than the status-quo.
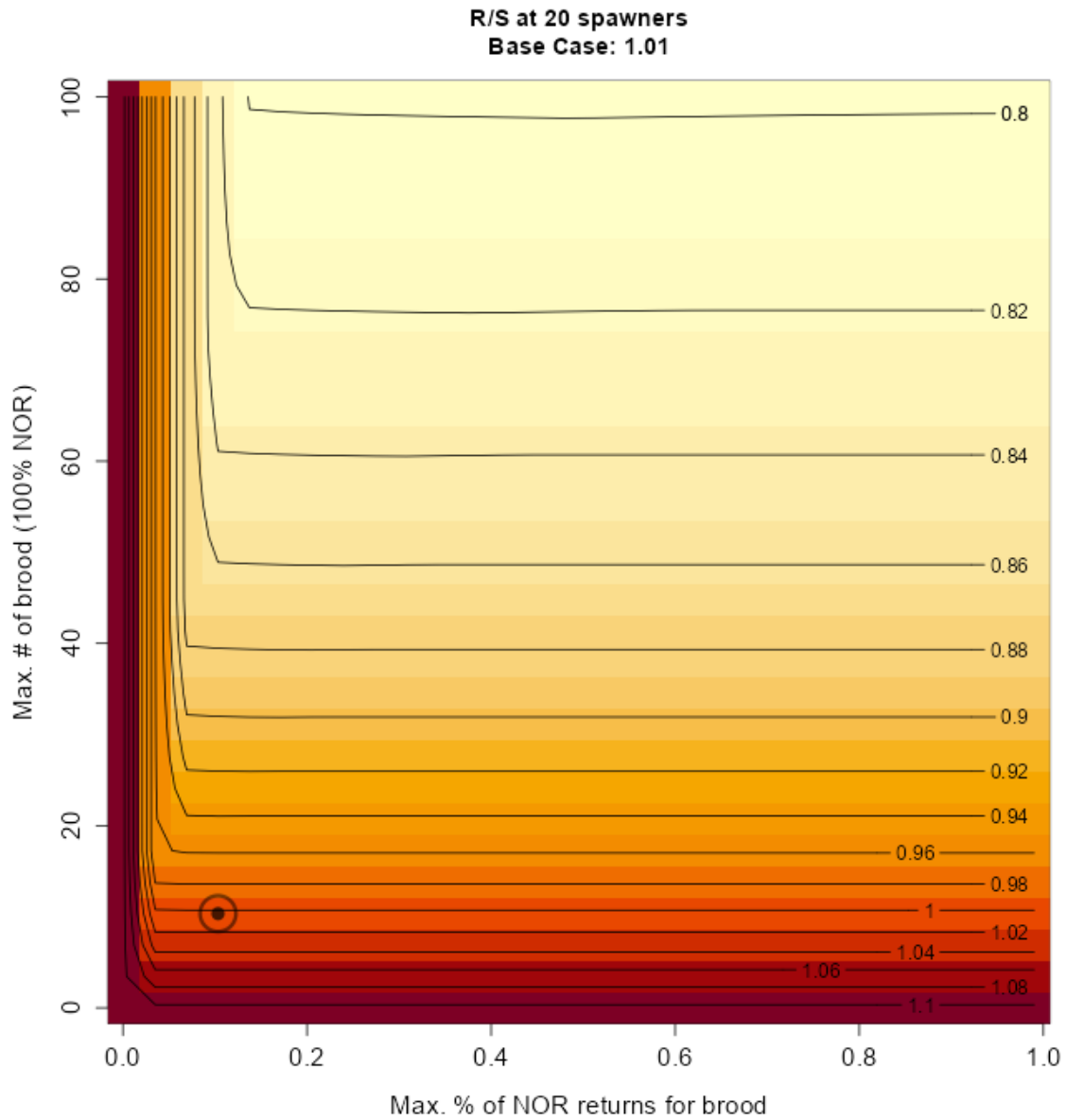
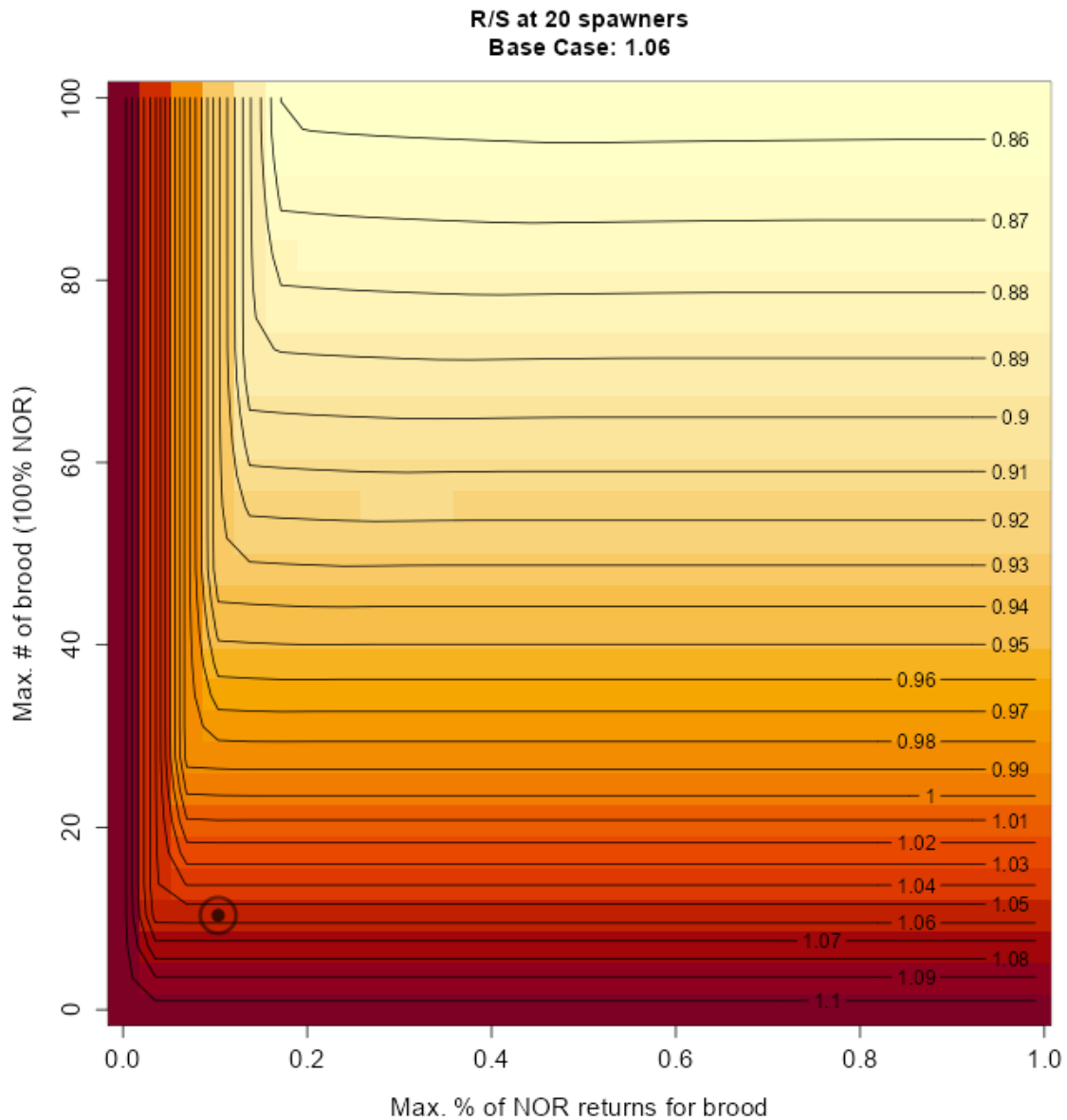*Figure A 17. Sensitivity of recruits per spawner (at 200 NOR spawners, according to the productivity and capacity estimates in the 100th generation) to different broodstock take rules for scenario 3, with 60% selective harvest mortality on HOR returns. The black point represents the base case assumption of broodstock collection practices, and the value in the title shows R/S under those assumed values.*

Sensitivity of pNI to broodstock collection rules

Figure A 18. Sensitivity of the proportionate natural influence (pNI) at the 100th generation to different broodstock take rules for scenario 2, with 0% selective harvest mortality on HOR returns. The black point represents the base case assumption of broodstock collection practices, and the value in the title shows pNI under those assumed values.
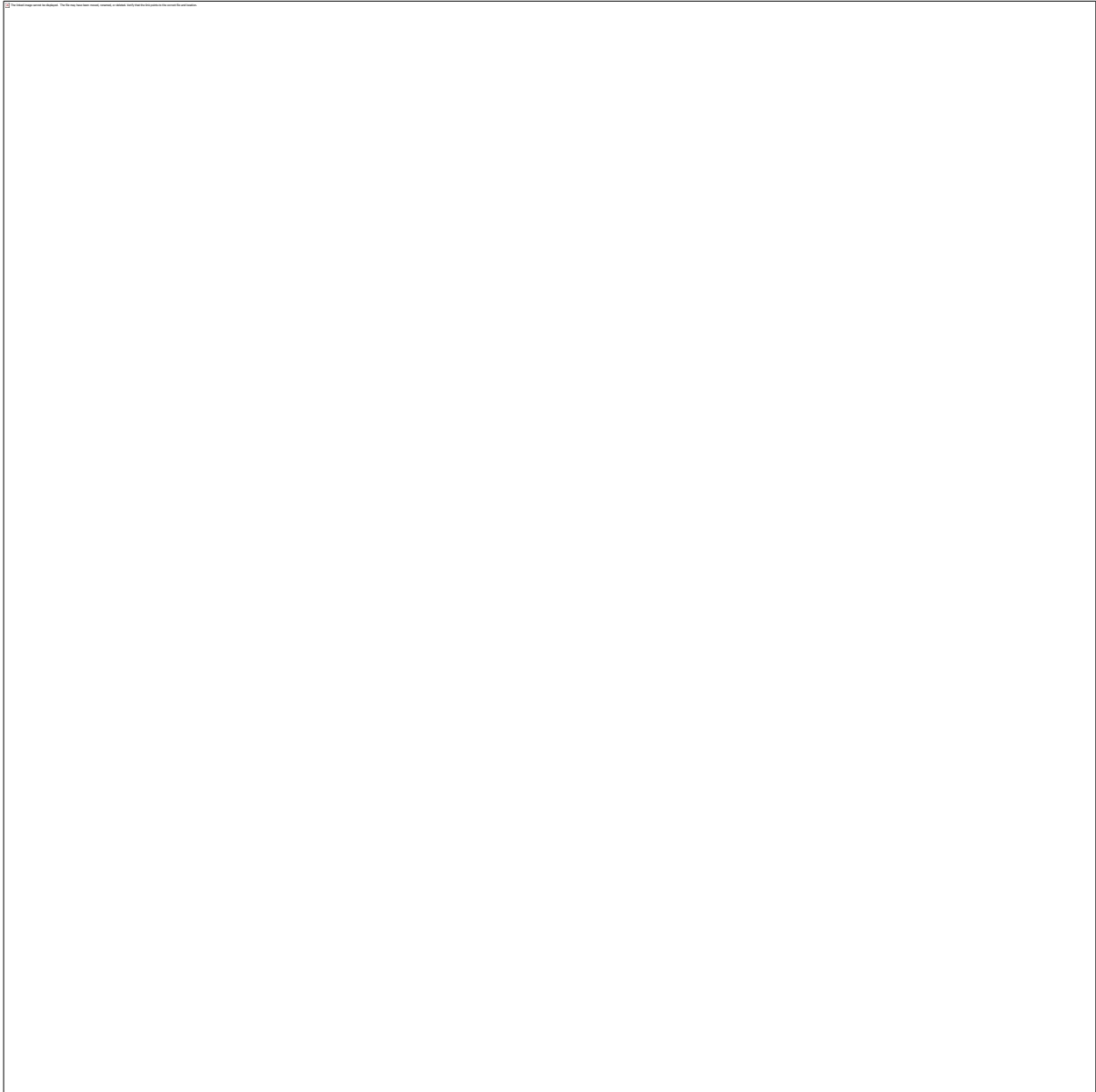
Figure A 19. Sensitivity of proportionate natural influence (pNI) in the 100th generation to different broodstock take rules for scenario 3, with 60% selective harvest mortality on HOR returns. The black point represents the base case assumption of broodstock collection practices, and the value in the title shows R/S under those assumed values.

Sensitivity of the harvest of HOR returns to broodstock collection rules
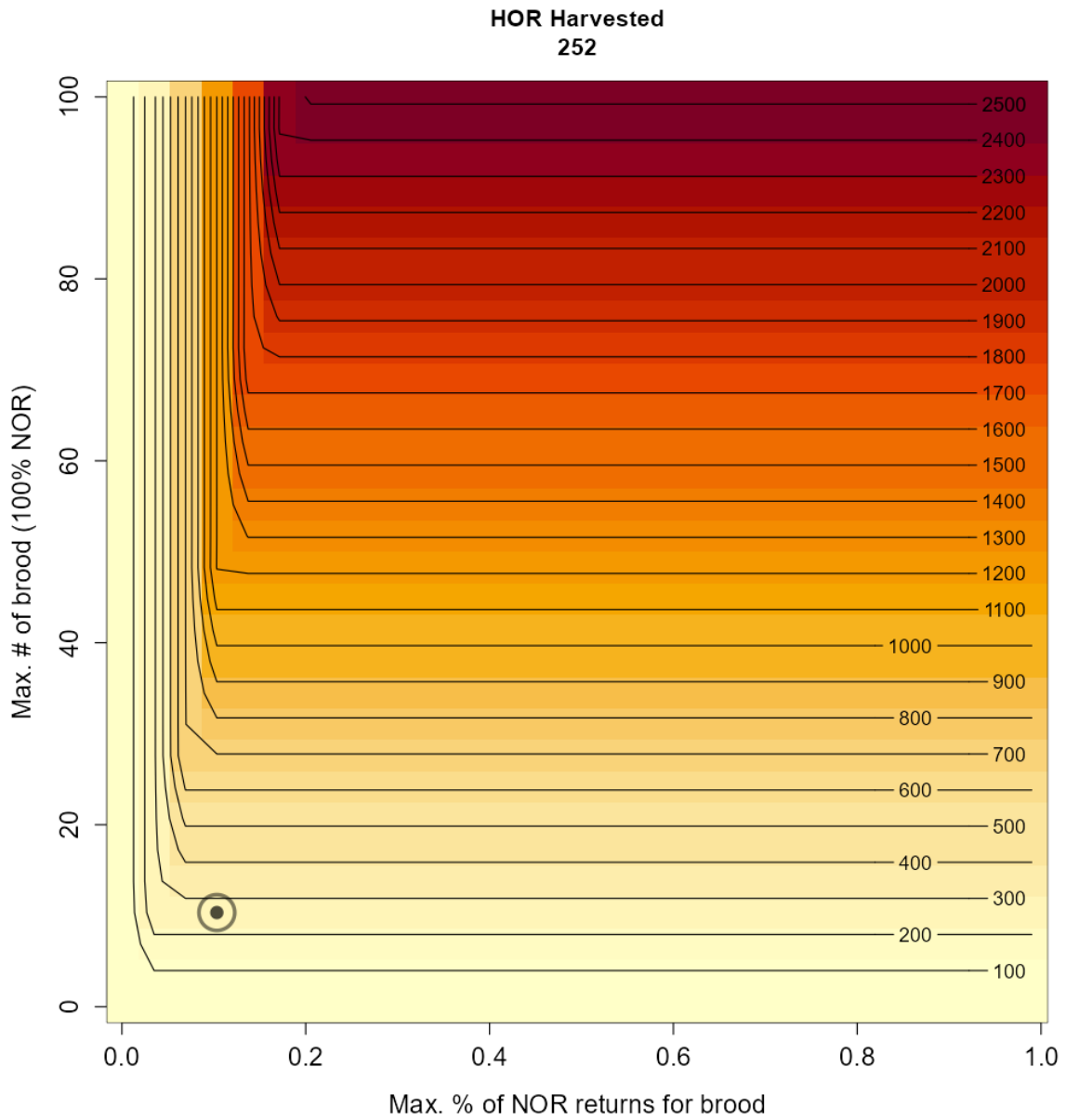
Figure A

Figure A 20. Sensitivity of the number of HOR returns harvested in the 100th generation to different broodstock take rules for scenario 3, with 60% selective harvest mortality on HOR returns. The black point represents the base case assumption of broodstock coll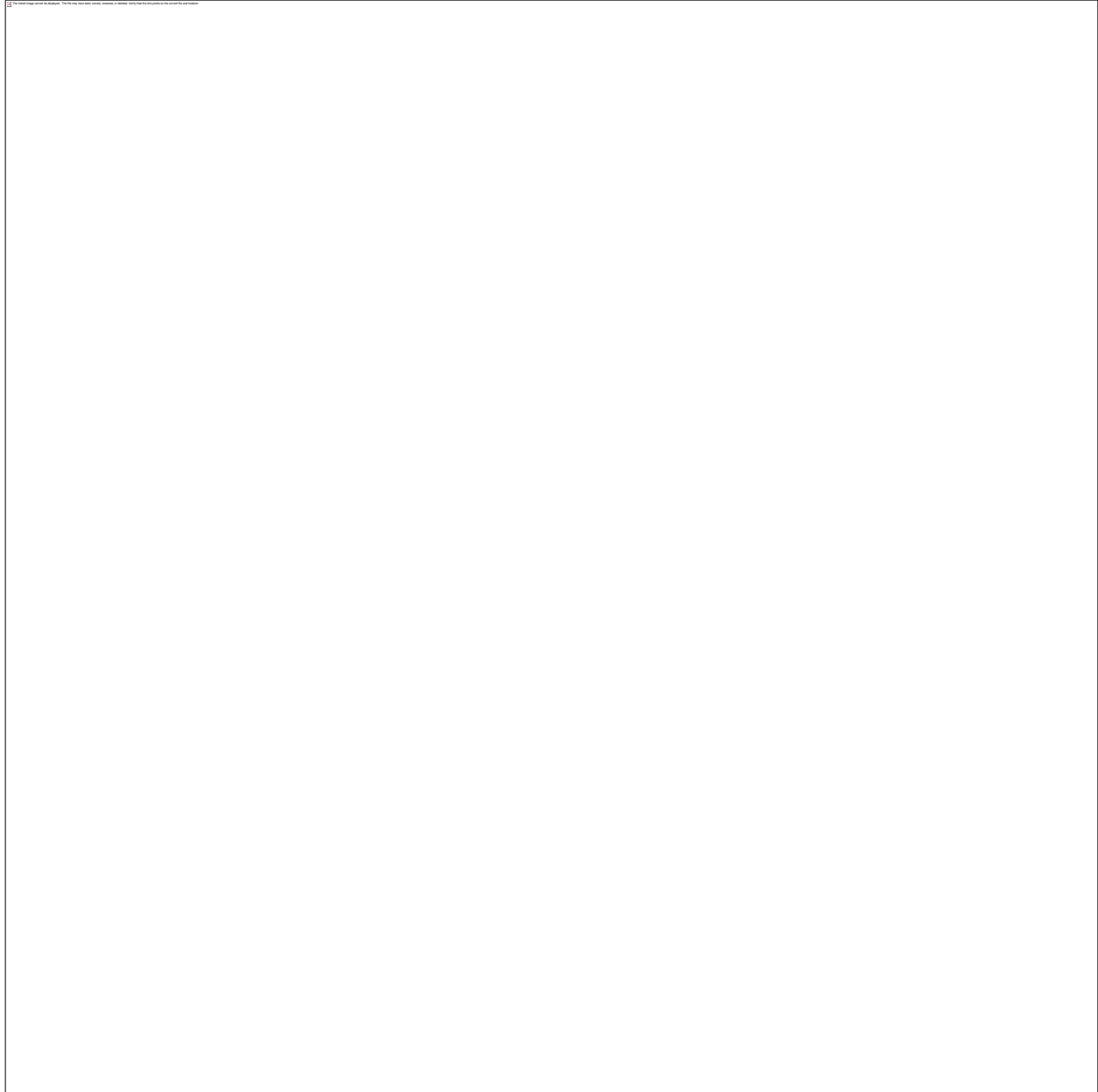ection practices, and the value in the title shows the number of HOR removed per year under the broodstock program at the black point.
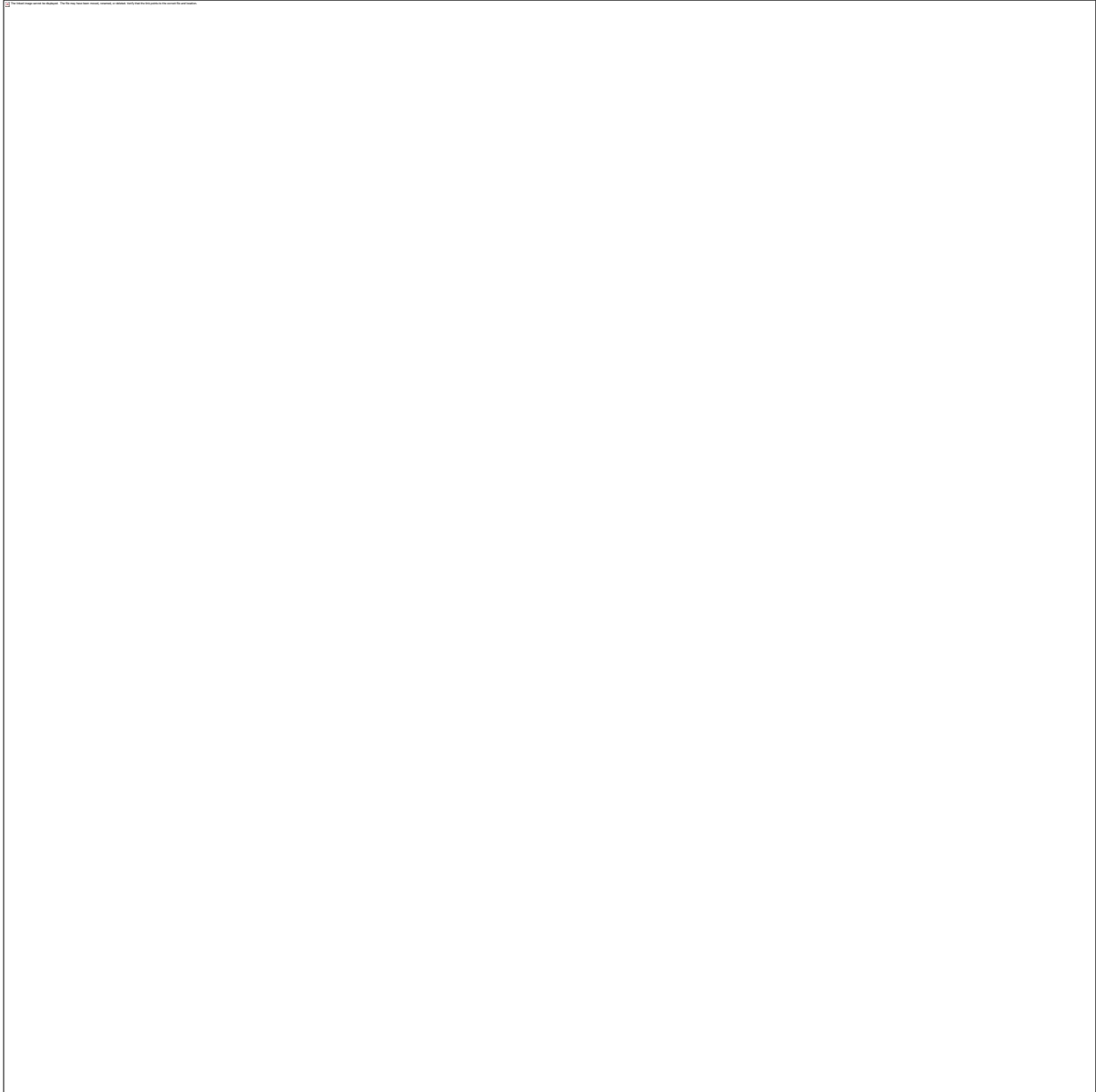
Figure A 21. Sensitivity of the number of HOR returns harvested in the 100th generation to different broodstock collection and HOR harvest rate assumptions. For reference, the point shows the combination of assumption for scenario 3, which simulates 60% selective harvest mortality on HOR returns and the collection of 10 NOR to be used as broodstock for hatchery production. The value in the title shows the number of HOR removed under those assumed values.

Sensitivity to marine survival assumptions

In addition to testing the sensitivity of outcomes to different broodstock collection scenarios, we also assessed the outcomes of different smolt-adult return (SAR) rate scenarios. In all base case model runs, we assumed that NOR marine survival rate is relatively low, 0.0175, with HOR SAR only 50% that of NOR conspecifics. To demonstrate the sensitivity of model outcomes to marine survival scenarios, we ran the AHA model for cases with NOR marine survival rates ranging from 0-0.05, and HOR marine survival rates ranging from 0-0.1. We here consider the response of three metrics to variable marine survival conditions: abundance of NOR spawners, the harvested number of returning HOR adults, R/S of the NOR population, and pNI (all in the 100th generation after hatchery supplementation begins).

Results showing projected NOR under alternative marine survival conditions are in the main text, see Figure 11 in the main text section "AHA model results: NOR spawner abundance

NOR spawner abundance". The sensitivity of R/S, pNI, and the harvested number of HOR adults are shown below. R/S was maximized when SAR for the NOR component of the population is high, but relatively insensitive to HOR, but was relatively insensitive to HOR marine survival rate (Figure A 22 and Figure A 23). We found that R/S of NOR spawners increased in simulations with high SAR (NOR), but decreased with higher survival rates of HOR (due to both increased density of spawners in natural spawning grounds and fitness-associated loss of productivity). Accordingly, scenarios with selective harvest of HOR returns resulted in higher R/S than comparable scenarios without harvest.

Considering pNI, both NOR and HOR marine survival had some influence on pNI in the 100th-generation. pNI was maximized when NOR marine survival is high and HOR marine survival low (Figure A 24 and Figure A 25).

Finally, considering HOR harvest outcomes, the harvested abundance of HOR fish was primarily sensitive to SAR (HOR), with increasing survival rates resulting in higher expected harvested abundance (Figure A 26).

Sensitivity of R/S at 20 NOR spawners to marine survival rates
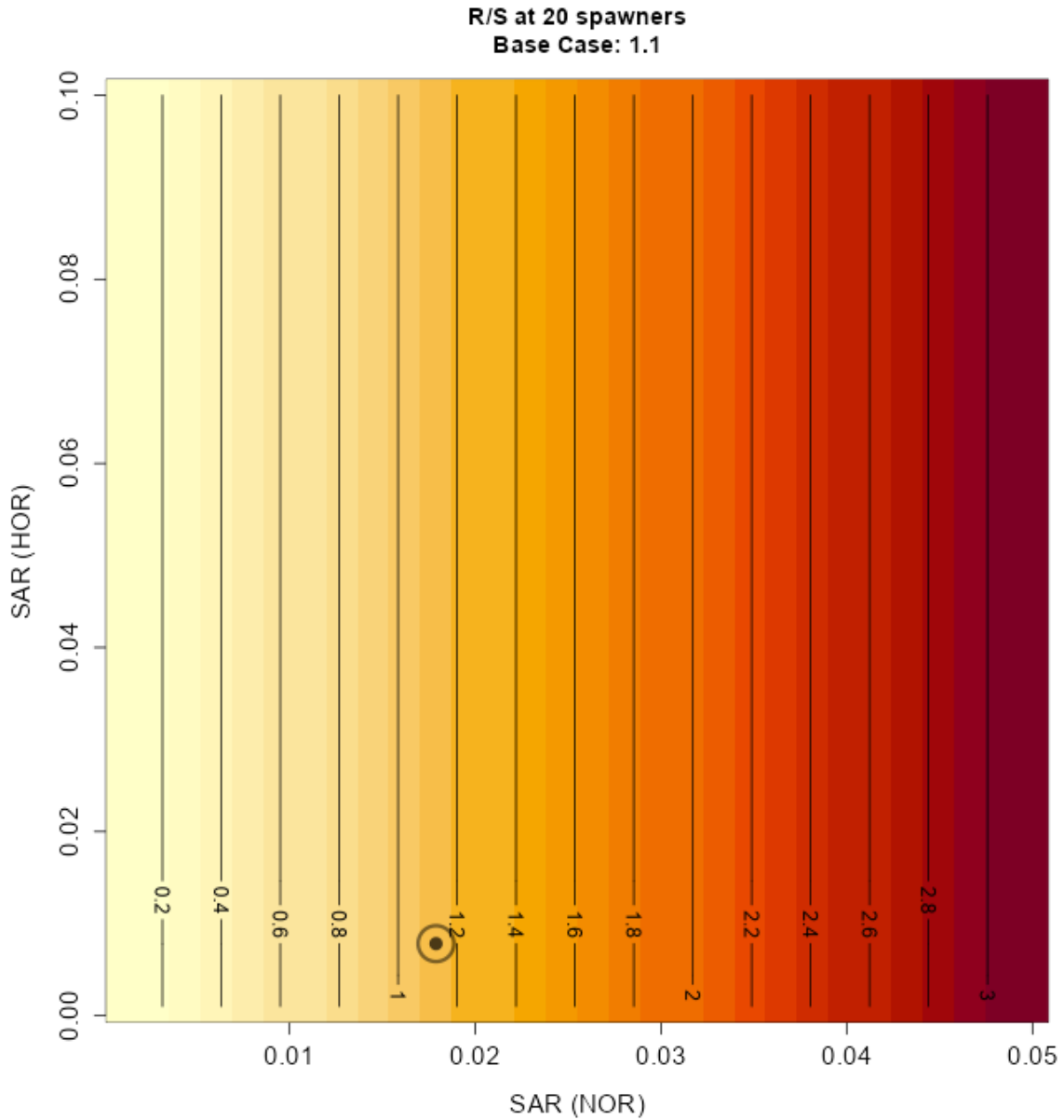
Figure A 22. Sensitivity of recruits per spawner (at 20 NOR spawners, according to the productivity and capacity estimates in the 100th generation) to assumptions of NOR and HOR marine survival rates for scenario 2, a minimal hatchery (10 NOB, maximum 10% of the NOR returns) with 0% selective harvest mortality on HOR returns. The black point represents the base case assumption of marine survival rates, and the value in the title shows R/S under those assumed values. Values on the isopleth represent expected R/S; darker colors occur in areas with higher R/S.
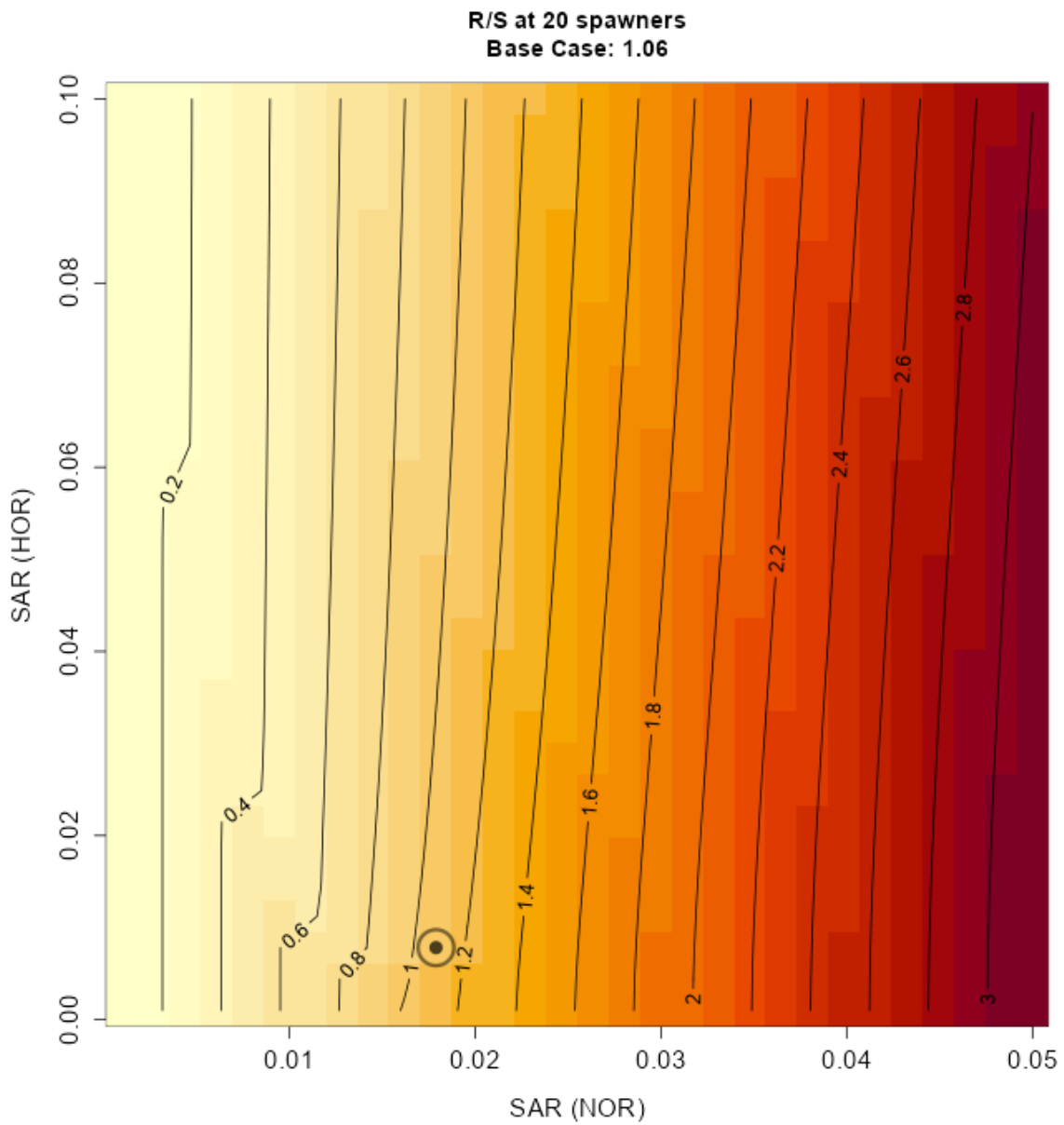
Figure A 23. Sensitivity of recruits per spawner (at 2 NOR spawners, according to the productivity and capacity estimates in the 100th generation) to assumptions of NOR and HOR marine survival rates for scenario 3, a minimal hatchery (10 NOB, maximum 10% of the NOR returns) with 60% selective harvest mortality on HOR returns. The black point represents the base case assumption of marine survival rates, and the value in the title shows R/S under those assumed values. Values on the isopleth represent expected R/S; darker colors occur in areas with higher R/S.

Sensitivity of pNI (for scenarios 2 and 3) to marine survival rates
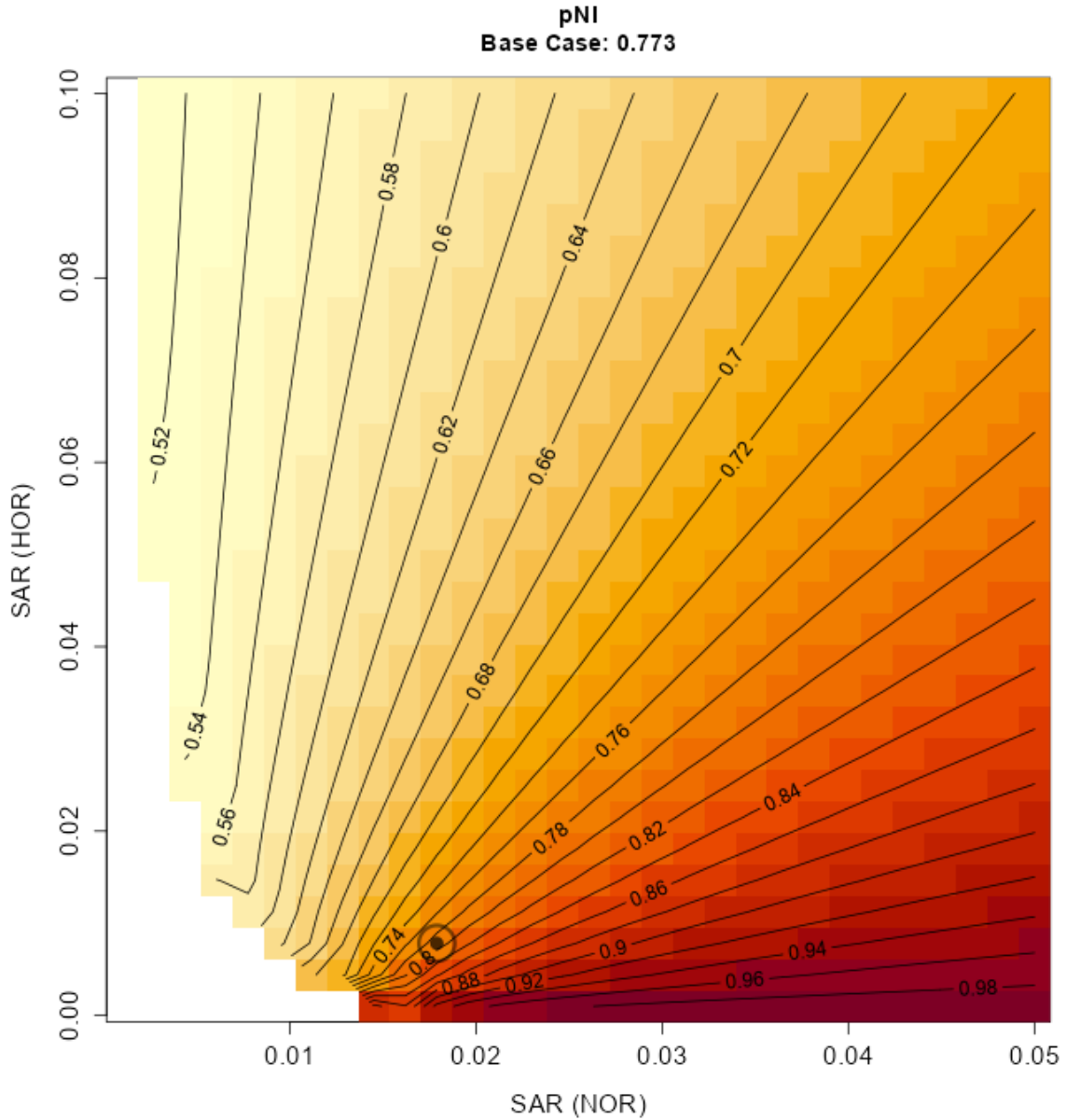
Figure A 24. Sensitivity of proportionate natural influence (pNI) in the 100th generation to assumptions of NOR and HOR marine survival rates for scenario 2, a minimal hatchery (10 NOB, maximum 10% of the NOR returns) with 0% selective harvest mortality on HOR returns. The black point represents the base case assumption of marine survival rates, and the value in the title shows pNI under those assumed values. Values on the isopleth represent expected pNI; darker colors occur in areas with higher pNI.
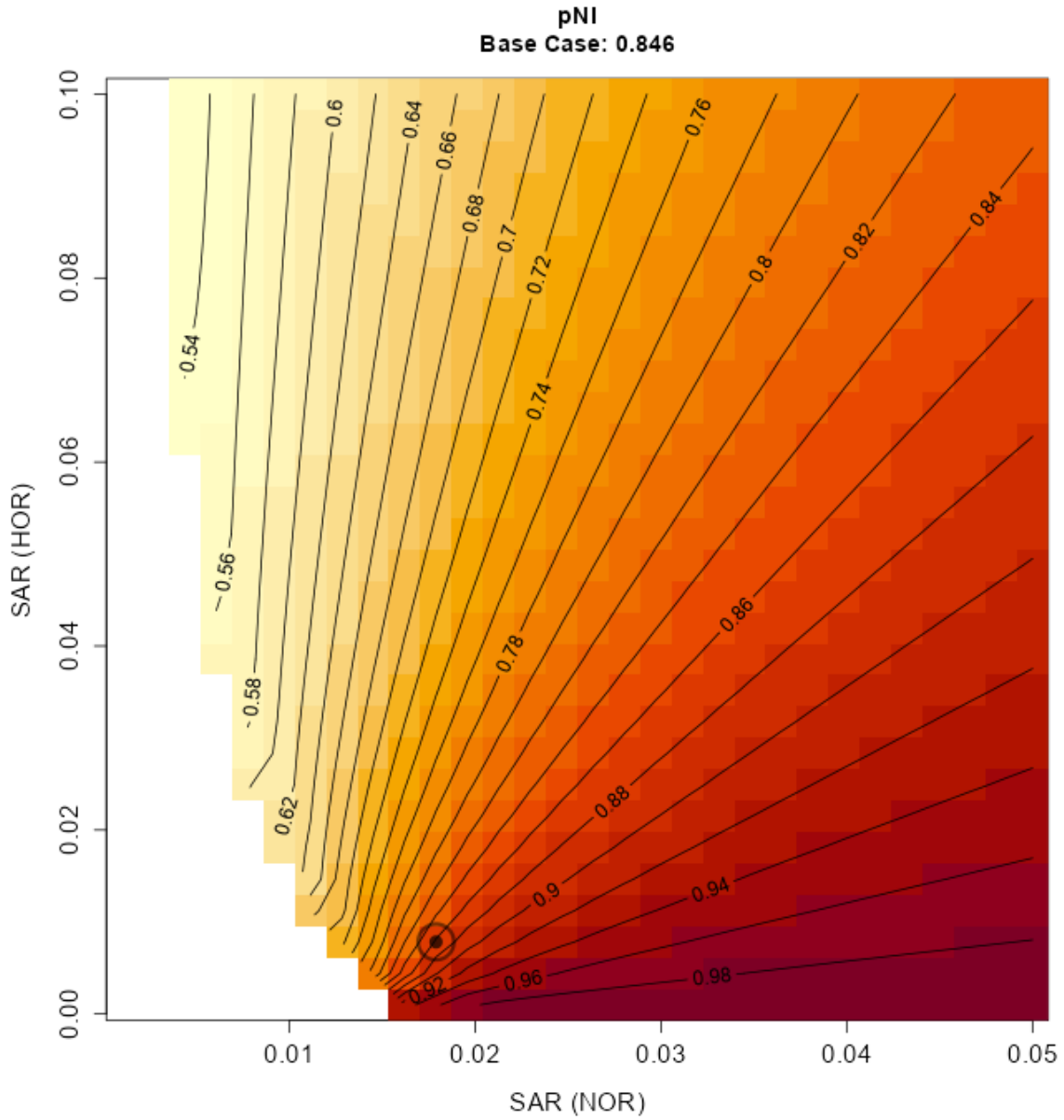
Figure A 25. Sensitivity of proportionate natural influence (pNI) in the 100th generation to assumptions of NOR and HOR marine survival rates for scenario 3, a minimal hatchery (10 NOB, maximum 10% of the NOR returns) with 60% selective harvest mortality on HOR returns. The black point represents the base case assumption of marine survival rates, and the value in the title shows pNI under those assumed values. Values on the isopleth represent expected pNI; darker colors occur in areas with higher pNI.

Sensitivity of the harvest of HOR returns to marine survival rates
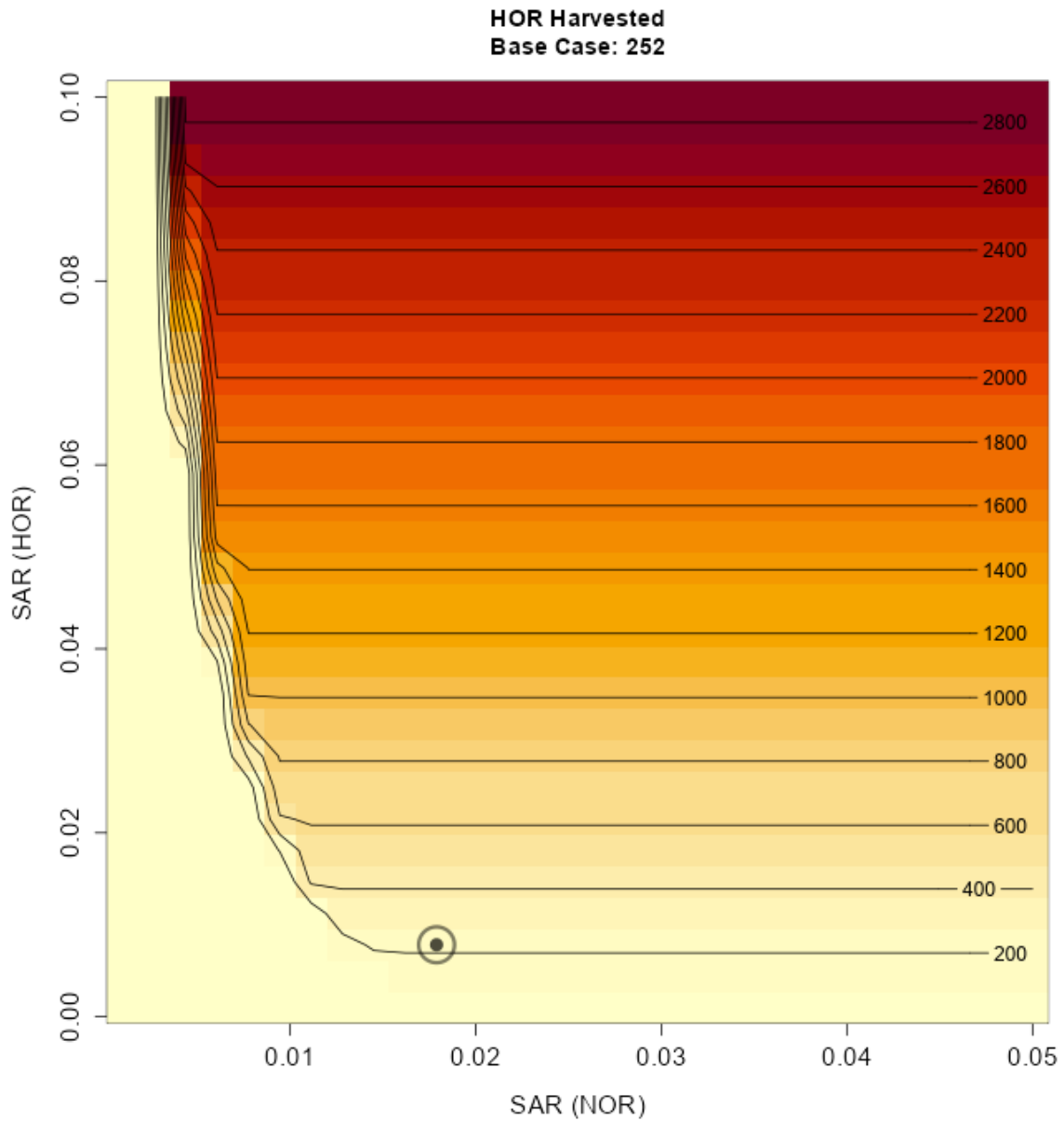
Figure A 26. Sensitivity of the number of HOR returns harvested in the 100th generation to different broodstock take rules for scenario 3, with 60% selective harvest mortality on HOR returns. The black point represents the base case assumption of broodstock collection practices, and the value in the title shows R/S under those assumed values. Values on the isopleth represent expected harvest of HOR returns; darker colors occur in areas with higher HOR harvest.

AHA Model Discussion

Summary of results

Overall, a modest hatchery program that takes 10 natural-origin (NOR) adults for broodstock is expected to provide a modest increase in the abundance of NOR spawners over several generations. The AHA model predicted that implementing a small hatchery program could result, over the long term, in NOR spawner abundances double current levels.

However, the hatchery program is projected to have a fitness consequence on the population if hatchery-origin (HOR) fish are allowed to spawn in natural spawning grounds (Figure 14 and Figure 15). Increasing the hatchery program size resulted in higher spawner abundance, but with greater fitness consequences of hatchery domestication. The fitness consequences can be reduced if limited HOR adults are allowed to spawn in the wild; this is possible if hatchery releases are marked with a visible adipose fin clip and allowed to be retained in a selective fishery (we note that we did not include incidental mortality on NOR spawners as part of the selective fishery, so scenario three which includes a selective fishery may under-estimate freshwater mortality of NOR adults).

The AHA model predicted that implementing any hatchery program is likely to reduce the recruits per spawner (R/S) of the NOR population (with less reduction in R/S with a selective HOR fishery; Figure A 11). If a hatchery program is implemented without a selective fishery, the AHA model predicted that the proportionate natural influence (pNI) would fall below acceptable levels for an integrated-wild population (i.e., 0.8;

). If a pNI target of 0.8 is required, the AHA model predicts that at least 27% of the annual HOR returns need to be removed before they are allowed to spawn (any less, and pNI drops below 0.8 under a 10-broodstock hatchery program; Figure A 13). However, we note that the pNI guidelines in Table 3 were designed to inform the management of Chinook salmon hatchery programs, and IFRS-specific pNI guidelines should be considered (perhaps after considering the genetic contribution of resident fish). Our model assumes that only NOR adults are taken for broodstock, such that interbreeding only occurs in the wild—if HOR broodstock were to be included in a hatchery program, projected pNI could be much lower than the results shown above depending on the ratio of HOR and NOR in the broodstock.

All of the AHA model results were sensitive to smolt-adult-return rate (SAR), which was a limiting factor to the productivity and abundance of NOR spawners regardless of which hatchery program, if any, was simulated. In the absence of hatchery production, spawner abundance and recruits per spawner increase linearly with marine survival (see Figure 11 and Figure A 22). Unfortunately, marine survival is both difficult to estimate (at least, difficult to estimate without age composition data) and strongly influential on the hatchery program's ability to increase NOR abundance without serious consequences for population fitness.

Model limitations

The current AHA model does not include rainbow trout or repeat spawners, so the model does not capture the complex structure of the IFRS population. Both resident and anadromous life histories co-exist in freshwater, and spawners of each type are able to produce offspring of other types. Residency

patterns arise as a function of interacting genetic, environmental, and physiological conditions, and they are highly plastic (Kendall et al. 2015). Modelling the interaction between the life history types was beyond the scope of this analysis, but we can predict broadly what types of interactions could be included in future modelling efforts.

For example, resident populations have implications for genetic diversity and exchange. Our model does not include any genetic exchange between anadromous and resident populations—because of this, we expect that the AHA model results over-estimate the genetic impact of the hatchery. This is because the resident population can serve as a gene-bank that preserves some of the NOR genetic diversity that would be eroded by hatchery supplementation. Because anadromous spawners can produce resident offspring and vice versa, if we were to include resident contributions to the anadromous NOR population, pNI and NOR abundance would likely be somewhat higher. The resident population would also stabilize the population to fluctuations in marine survival, as it is hypothesized that marine survival determines the proportion of anadromous spawners in the *O. mykiss* population, particularly in spawning habitats that are far inland (Kostow 2003). However, modelling would have to include potential negative interactions as well. For example, if there is a large breeding population of rainbow trout, they may overcrowd steelhead spawning habitat (and negatively impact NOR steelhead spawners and/or the survival of their offspring). There are also risks of juvenile competition and cannibalism that are not currently captured in the AHA model.

In addition to ignoring the resident population, the current implementation of the AHA model takes a simple, cohort-based approach. Age-structured life cycle population dynamics models are commonly used to investigate salmonid populations, and while these types of models could be developed for resident and anadromous populations, this task was outside the scope of this analysis. One potential benefit of building an age-based model that includes residualization would be that different assumptions about residualization and responses to marine conditions could be investigated. These models also allow for more accurate accounting of the genetic implications of overlapping generations. Another major benefit of such models would be their utility in management decision making.

Any discussion about hatcheries is a question of values, and any hatchery program should be carefully simulated, monitored, and evaluated according to clear and measurable objectives to ensure effectiveness. While the analysis in this appendix is a starting point for simulation modelling, managers should consider more data-informed modelling that better expresses alternative hypotheses and uncertainty. There are many tools available to study the impacts of different management actions, for example, managers could consider closed loop simulation of different hatchery and harvest strategies, adaptive management informed by simulation, and potentially "management experiments" (Walters 2001). These tools can help ensure that management outcomes favored by stakeholders are achieved. For example, one advantage of hatchery production is the increased number of returning steelhead available for recreational harvest. But any recreational harvest would have to be consistent with the laws of Canada, provincial policy, and interests of stakeholders. The above management and legal frameworks could be better accounted for in a more complicated modelling framework. However, the goal of this analysis was not to evaluate management choices but to provide an initial investigation of plausible genetic and ecological risks and potential rewards of a hatchery program.

Conclusion

While there are some genetic risks under hatchery supplementation, the AHA model predicts that the abundance of NOR fish is likely to increase under modest hatchery programs that prioritize natural broodstock. Modelling results indicate potential for hatcheries to increase the number of steelhead available for harvest and natural spawning, but these outcomes depend on the ability of hatchery fish to effectively survive marine conditions and their ability to spawn in the wild. Hatcheries do not need to result in low pNI, and there are several ways to mitigate negative genetic effects from hatcheries. Furthermore, hatcheries can improve spawner abundance and angling opportunities, but hatcheries' ability to help conservation rates depends on marine survival rates, the size of the hatchery program, and the ability to remove at least some hatchery origin fish before they reach natural spawning grounds. Particularly when SAR is low, hatcheries are projected to be less useful and improvements to marine survival can be more influential on long-term abundance estimates than the presence of a hatchery program. However, hatcheries could be used to maintain steelhead abundance during periods of low marine survival. If addressed, the limitations in our modelling are unlikely to change these conclusions.

Appendix 4: Input from Indigenous Groups

Pat Matthew, Shuswap Fishery Commission, Policy

Phone call with Murdoch McAllister

July 24, 2023.

- It was mentioned that steelhead did in the past play a critical role in the Band's sustenance. Band members in the past harvested steelhead and ate them.
- Band has been involved in the consultation process with COSEWIC's emergency listing of IFS.
- Band contributed cultural, historical and ecological information on IFS
- The Band has been involved in a few additional processes with DFO and the Province.
- Have become familiar with Prov. Biologist Rob Bison's studies on IFS and understood that Rob Bison holds also considerable scientific knowledge about IFS and has numerous theories about them.
- Familiar with protections given to IFS during Pink, Chum, and Sockeye fisheries.
- The Band's two communities have been quite involved in habitat restoration for IFS.
- The communities have had some discussions on the potential use of hatcheries for IFS.
- It is understood and appreciated that there are significant risks, uncertainties and issues associated with hatchery production
- The number of returning adults have been very low and it is understood that an unavoidable risk of serious loss could occur if all of the returning adults were to be taken into hatchery production.
- It is understood that there have been mixed reviews on hatchery production, and concerns have been expressed about further use of hatchery production for IFS
- It is understood that mortality rates of juvenile salmonids produced in hatcheries can be very high in the months following release and that for IFS research has found that marine survival rates have been very low with predation in the marine environment having had the biggest impacts with there being yet other factors adding to their survival issues at sea.
- It is understood that if freshwater survival rates are only a small part of the issue while significant impediments to survival exist in the marine phase then hatchery production might not make a lot of difference.
- It is understood that the Province's current policy stands against using hatcheries in the conservation and restoration of wild steelhead populations.
- The Band has not heard anyone countering arguments from the Province or DFO on their positions on hatchery supplementation.
- Rob Bison had identified another problem arising from hatchery production – numerous released hatchery juveniles might residualize and not go to sea.
- It is understood that steelhead interbreed with rainbow trout. Knowledge about how this works and what might occur when hatchery fish are released remains uncertain.
- Matt doesn't see the Band supporting hatchery supplementation for steelhead unless they were to see evidence that there would likely be tangible returns from it.

- On the other hand, it is recognized that some believe hatcheries could be the answer and that hatcheries have been successfully used for other salmonid populations that have previously been in trouble.
- It is understood that the issue of raising fish in a hatchery environment needs to be dealt with in an entirely clear way.
- It is recognized that hatcheries could potentially be used if a value and very good rationale for hatchery production was seen for maintaining the wild stock.
- The Band had recently got Dr. David Levy to provide a professional opinion on steelhead. It appeared that Dr. Levy had informed the band that it was mainly a survival and production issue. If fishing mortality were kept low and the survival and production issues were successfully managed and alleviated, then the fish population could be expected to increase on their own, i.e., a hatchery would not be required under these circumstances, though, if implemented in the right way, could potentially serve additional purposes.
- It is understood that an academic paper on the topic like the one UBC is preparing might not have any effect at all. It is understood that government policy on the use of hatcheries for population remediation would need to change. Hatchery programs are costly to implement and objectives of any new program would need to be made clear.
- The Band members had been active in conservation for many years for other stocks also like Interior Fraser coho salmon. They had not fished for a long time for these stocks. They had seen for many years only a couple hundred coho salmon returning annually to spawning streams. But in recent years returns had been up to a couple of thousand. If this increase holds, DFO could potentially open it up in 2024 or 2025.
- But concerns in the Band remain about potential for recovery given that drought conditions extended well into the autumn last year and are already very severe this summer.
- The Band currently runs two salmon hatcheries for conservation purposes, one on Dunn Creek and the other on Deadman Creek. These hatcheries currently produce coho salmon only. They had previously produced both coho and Chinook salmon and been used as part of the coded wire tag program.
- In one of these hatcheries there had been issues with water supply and disease. The Band has been developing a new well system to address the problem.
- It is known that there had in the past been hatchery production on the Bonaparte River for steelhead but that that had been discontinued.
- Pat recommended that I speak with people in the Chilcotin Band and also the Bands in the Nicola River area.

Murdoch McAllister had e-mailed several other Indigenous persons knowledgeable about Interior Fraser Steelhead in July 2023 to request phone calls with them. These included Mr. Urquhart, Mr. Nicklin, Mr. Sam, Mr. Ignace, Chief Antoine of the Bonaparte Band, Ms. Tina Donald, and Mr. Bennett. However, none of these latter persons were available then for a phone call.

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