A review of hatchery reform science in Washington State

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Table of Contents

ABSTRACT

Here we review the science of hatchery reform, describing the benefits of hatcheries, the risks of hatcheries, and the major operational options available to hatchery mangers for balancing the benefit-risk trade-off. Our review is a component of a larger evaluation of the Washington Department of Fish and Wildlife's (WDFW) hatchery and fishery reform policy, adopted in 2009, that embraced the recommendations of the Hatchery Scientific Review Group (HSRG). Thus, we explicitly aim to synthesize new and emerging science available in the last ten years, towards the goal of helping inform whether a revision to the policy is warranted. We focus on Pacific salmon and steelhead hatcheries, with strong emphasis upon examples from Washington State to illustrate key concepts.

Hatchery benefits have received much less research attention than hatchery risks. The goals of hatcheries are typically classified as providing harvest opportunities or improving the conservation status of natural populations. Harvest opportunities, which are heavily subsidized by hatcheries in Washington State, provide economic benefits, sociocultural benefits, and satisfy legal obligations, including fulfilling the treaty rights of Native American Indian tribes. We provide a brief overview of these benefits, but they are not the focus of this paper. Regarding conservation, hatcheries have proven successful at preserving unique genetic lineages. Hatchery-origin fish also commonly spawn naturally in rivers throughout Washington State, both intentionally and unintentionally. Depending on the circumstances, this can have short-term conservation value to population demographics, but must be carefully weighed against long-term genetic risks. However, the evidence that hatcheries have increased the abundance of natural-origin adult salmon, a fundamental metric for evaluating population

status, is generally sparse, likely because key assumptions regarding habitat carrying capacity and hatchery operational objectives (e.g., high proportion natural-origin broodstock) are rarely met.

Hatchery risks include fishery risks, ecological risks and genetic risks. Fisheries targeting abundant hatchery runs can unintentionally increase mortality of co-mingled natural populations. We describe three factors that contribute to fisheries risks: constraints on implementing mark-selective fisheries that remove only hatchery-origin fish; an asymmetry between lost harvest opportunity and the conservation gain of curtailing fisheries; and uncertainty in the harvest benchmarks due to the frequency of naturally spawning hatchery-origin fish.

The ecological risks of hatcheries, especially competition for limited foraging resources and increasing predation on natural populations, have been recognized for some time. Retrospective analysis of population monitoring data highlight the potential for hatcheries to reduce the productivity and abundance of natural populations via ecological interactions. However, at the population or watershed scale, ecological impacts of hatcheries are difficult to separate from other factors affecting productivity and abundance, including the genetic risks of hatcheries.

Several hatchery reform measures are intended to minimize ecological interactions. These include releasing smolting rather than pre-smolt fish, volitional rather than forced releases, the use of acclimation ponds rather than direct releases, delaying releases until after the migration of threatened species that hatchery-reared fish might consume as prey, and concentrating hatchery releases geographically distant from natural populations. Isolated case studies have demonstrated the effectiveness of some of these approaches, but research on ecological interactions lags far behind the attention devoted to genetic risks of hatcheries. Importantly, research suggests the potential for ecological interactions in marine environments shared between multiple hatchery and natural populations, yet very little is known about the likelihood or magnitude of population-scale ecological impacts of hatcheries.

The major genetic risks of hatcheries include the loss of genetic diversity within and among populations, and the loss of fitness due to selection for traits favorable in the hatchery but deleterious in the wild. Despite risks of inbreeding and loss of alleles in small populations, there are several examples in which conservation hatcheries have maintained or even increased within population genetic diversity through thoughtful management. However, at larger regional scales, some hatchery practices, including a legacy of intentional transfers of eggs and broodstock between watersheds, have contributed to genetic homogenization and reduced genetic diversity among populations. Studies comparing the number of offspring produced by hatchery-origin fish and natural-origin fish when both groups spawn in the wild (relative reproductive success, RRS) have demonstrated a general pattern of lower reproductive success of hatchery-origin fish. Researchers have highlighted domestication selection as a plausible cause for the lower RRS of hatchery-origin fish, although unequivocal, empirical, population-scale evidence for a genetic basis to fitness loss remains rare.

Minimizing fitness loss by managing gene flow between a hatchery population and its companion natural population has been a fundamental focus of hatchery reform. Through a combination of regional conservation prioritization, assessing the current status of the natural population, and specifying whether or not the hatchery intentionally exchanges genetic material with the natural population, the HSRG advanced a method for setting fitness loss risk thresholds. These thresholds track the proportion of hatchery-origin fish spawning naturally (pHOS) and the proportion of natural-origin fish used in hatchery broodstock (pNOB). Importantly, these metrics are surrogates for true, realized fitness risks. However, they have strong conceptual support from genetic models, including novel exploration of existing models presented in this paper. Furthermore, recent empirical RRS research has highlighted that hatchery programs employing 100% natural origin broodstock can provide demographic conservation benefits while maintaining genetic diversity with minimal or no apparent genetic fitness loss.

While recognizing the social, political, economic and legal considerations that factor into decisions regarding hatchery policy, we reached the following conclusions regarding hatchery reform in Washington State.

Overarching themes

- Hatchery reform is but one of several factors requiring careful planning and aggressive implementation needed to achieve meaningful recovery of salmon populations
- Hatchery reform is largely aimed at reducing risk in a relative but not absolute sense
- In WDFW's hatchery system, a focus on efficiency and maximizing abundance prevents widespread implementation of risk reduction measures

HSRG Recommendations

- The principles of reducing pHOS and increasing pNOB to achieve fitness gains in wild populations are well-founded, and should be fundamental goals in any hatchery reform management action

- Program size requires more careful scrutiny and scientific justification because it affects virtually every aspect of hatchery risks
- The HSRG's phased approach to recovery has strong conceptual merit, but its implementation has resulted in an absence of stricter, conservation oriented PNI goals for many populations
- We recommend crafting a stand-alone monitoring and adaptive management plan for each hatchery program that quantifies both benefits and risks, and explicitly links hatchery performance metrics to potential operational changes

Knowledge gaps and major assumption of current hatchery management

- The absence of a landscape-level, replicated experiment prevents empirical assessment of hatchery reform effectiveness
- Hatcheries have potential for large magnitude ecological impacts on natural populations that are not well understood, not typically evaluated and not measured
- Understanding the role of life history diversity on hatchery-wild ecological interactions and ecosystem stability is a significant research need
- We recommend a more rigorous, consistent and intentional evaluation of cumulative hatchery effects across multiple hatchery programs operating within a geographic region

Overall, our review supports the fundamental concepts and approach of the HSRG, but also identifies knowledge gaps and challenges to coordinated, robust implementation of scientific principles at a statewide scale. In order to advance hatchery reform as a comprehensive program for developing scientifically defensible hatchery programs, these issues warrant dedicated, programmatic initiatives.

INTRODUCTION

Hatchery production is an integral component of salmon and steelhead management throughout the world. Towards a variety of societal goals, salmon hatcheries generally aim to increase early life survival by artificially spawning and rearing fish in a controlled, relatively benign environment subject to less dynamic conditions than natural rivers. This allows hatcheries to circumvent or reduce natural mortality experienced during the relatively vulnerable egg incubation phase and, depending on the species and hatchery program, early rearing in freshwater. In the western coterminous United States, hatcheries typically (though not always) release fish into freshwater, where they migrate downstream to rear in natural marine habitats. In Washington, Oregon and Idaho, hatcheries were first developed in the late 19th century, and have subsequently grown to approximately 500 separate programs that cumulatively release 325 million juvenile fish annually (Flagg 2015).

Hatchery production presents several potential benefits, but also poses risks to natural populations. Hatcheries were originally developed to increase abundance, enhance fisheries, and offset lost habitat. More recently, roughly in the last three decades or so, hatcheries have entered widespread use as a tool to conserve or recover threatened or endangered natural populations. Currently, most hatchery programs have the goal of either providing harvest opportunities or promoting conservation of imperiled populations. In some cases, hatcheries are used to fulfill legal obligations, including fulfilling the treaty rights of Native American Indian tribes. The risks posed by hatcheries to natural populations encompass risks of increasing fishing pressure on natural populations; ecological risks of competition, predation, disease or facility effects; and genetic risks of homogenization, reduction in adaptive evolutionary potential, and loss of population fitness through domestication.

In the Pacific Northwest, where many populations are listed as threatened or endangered under the U.S. Endangered Species Act, hatchery reform has emerged as the primary approach to balancing the benefits and risks of hatcheries. We define hatchery reform as widespread, institutionalized changes to hatchery programs intended to reduce risk to natural populations. Hatchery reform is largely synonymous with the principles and recommendations of the Hatchery Scientific Review Group (HSRG 2015), intended to minimize impacts to natural populations while maintaining sustainable fishing opportunities. However, our review additionally addresses actions that were not specific recommendations of the HSRG per se, but rather reflected decades of evolution in hatchery practices (Table 1). Hatchery reform encompasses a suite of activities from human-value driven exercises such as goal setting to on-the-ground, operational changes in breeding, rearing and release protocols.

The purpose of our paper is to review the science supporting hatchery reform as practiced in Washington State. We aim to inform fishery and hatchery managers as to the efficacy, strengths and weaknesses of specific hatchery reform activities. Our review is motivated by action of the Washington Fish and Wildlife Commission, who in June 2018, directed the Washington Department of Fish and Wildlife (WDFW) to review and update its Hatchery and Fishery Reform Policy (C-3619), originally adopted November 2009. During the review period, the Commission suspended several components of the Hatchery and Fishery Reform Policy to grant greater flexibility for hatchery production. Here we present one component of WDFW’s evaluation: a review and update on the science of hatchery reform. A parallel effort, presented elsewhere, evaluates WDFW's implementation of the 2009 Hatchery and Fishery Reform Policy.

We provide general discussion of the literature, focusing on Pacific salmon and steelhead, using specific (often unpublished) examples from Washington State to illustrate key concepts. Hatchery production of Chinook salmon, coho salmon and steelhead trout in Washington is among the highest in the world, therefore, lessons learned in Washington can be applied elsewhere. Our review emphasizes conceptual and technical limits to our current understanding of hatchery risks and the degree to which hatchery studies can, and are used to, guide hatchery management at the watershed and regional scale.

Hatchery production and hatchery reform inherently represents a risk-benefit trade-off, and so our review begins by reviewing the benefits and risks of hatcheries. We then review the major components of hatchery reform, focusing on goal setting, broodstock management, release number, rearing strategies, release strategies, disease, and adaptive management. The discussion of hatchery reform aims to describe the scientific support and assess the efficacy of each action. We next briefly summarize emerging science newly available in the last ten years, and close the paper with a series of conclusions.

BENEFITS OF HATCHERIES

Here we review the goals of salmon and steelhead hatcheries, and whether or not they are meeting those goals. We describe, and where possible, quantify the benefits that hatcheries aim to provide to humans and ecosystems of Washington State. The vast majority of hatchery programs are classified as having one of two goals: increasing fishing and harvest opportunities, or promoting the conservation of natural populations. These hatchery goals are often intertwined with complex treaty, legal, mitigation, or political obligations, which we review briefly. However, our primary focus is on the biological outcome (fishing, conservation) rather than the regulatory instruments. We briefly discuss a third goal, research and education, though it is a component of only a small minority of the hatchery programs operating in Washington State.

Harvest benefits

A primary purpose of hatchery programs is to provide harvest opportunities. Thus, a reasonable question is how many people participate in hatchery-subsidized fisheries in Washington State, and what are the benefits that human communities derive from these fisheries? Here we review information on economic, social, and cultural benefits of fisheries supported by hatcheries.

It is difficult to precisely separate the incremental, added benefits of hatcheries to fisheries that also encounter naturally spawned, or wild fish (Naish et al. 2008). However, in Washington State, most (though not all) salmon and steelhead fisheries target hatchery produced fish. Although there are exceptions, most salmon and steelhead fisheries are heavily subsidized by hatchery production, and would not exist without hatchery production, at least at the scale they are currently implemented. Thus, a general, statewide review of salmon and steelhead fisheries, despite the difficulty of separating hatchery catch, provides a meaningful description of hatchery-derived benefits. We provide economic dollar values as stated in the relevant reports and did not convert them to common dollars accounting for inflation.

Economic benefits

In 2006, non-treaty commercial salmon fisheries in Washington generated a gross revenue of $7 M, which represents harvest and seafood revenue minus fishing and processing costs (TCW Economics 2008). The 2006 economic impacts of non-treaty commercial salmon fisheries was estimated at $21 M and 507 jobs, which includes the direct personal income and secondary, indirect benefits to local economies of the persons employed in the fishing industry spending their earnings (TCW Economics 2008). Wegge (2008) estimated the direct plus indirect economic impacts of Washington's 120 salmon and steelhead hatchery programs; across the Puget Sound, Washington Coast, and Lower Columbia regions, the total contribution of non-treaty commercial fisheries to personal income was approximately $14 M.

The 2006 total economic impact (again, direct and indirect personal income) of all Washington State recreational fisheries, not just salmon and steelhead, was estimated at $393 M (TCW Economics 2008). Salmon and steelhead fisheries totaled 39% across all recreational fisheries of a different metric, net economic value (described below under *Social and cultural* section), so we suggest a coarse economic impact of $153 M for Washington's recreational salmon and steelhead fisheries. Furthermore, Wegge (2009) estimated the economic impact of

Washington's hatcheries to salmon and steelhead recreational fisheries in Puget Sound, Washington Coast and Lower Columbia at $54 M.

Another approach to assessing the economics of hatchery programs are cost-benefit analyses, but these are generally rare. Naish et al. (2008) noted that hatcheries are generally not subjected to standard economic cost-benefit analyses because they offer multi-dimensional benefits to social, cultural, and political values, and thus are not strictly held to an expectation of financial profitability. Furthermore, it is difficult to quantify the possible negative impacts of hatchery production on wild populations, which would tend to erode economic benefits (Naish et al. 2008). However, the lack of cost-benefit analyses is likely an issue of political will rather than technical obstacles because this approach is commonly employed for other complex environmental policies, such as regulating air quality (U.S. EPA 2011).

Social and cultural benefits

We define the social and cultural value of fisheries as the personal identity, emotional satisfaction, and psychological well-being derived from opportunities to catch fish. Participation provides some sense of the social importance of Washington's salmon and steelhead fisheries. In Washington State, USFWS (2014) estimated that 330,000 people fished for salmon in freshwater, and 239,000 people fished for steelhead in freshwater, and 237,000 people fished for salmon in saltwater during 2011. There is an unreported degree of overlap in the individuals participating in these fisheries, and most (> 80%) were Washington residents. From the 2008-2009 to the 2017-2018 fishing seasons, WDFW issued an average of 602,319 catch record cards, which are required to fish for salmon, steelhead, sturgeon and halibut (Kraig and Scalici 2019). For comparison, the population of Washington State was 6.8 M in 2011 and 7.4 M in 2018 (Washington State Office of Financial Management). The social value of recreational fisheries can also be estimated as net economic value, which represents anglers' willingness to pay for fishing trips, over and above their true out-of-pocket costs. TCW Economics (2008) estimated that the net economic value of Washington's non-treaty salmon fisheries as $129 M, and Washington's non-treaty steelhead fisheries as $51 M.

Similar to other threatened and endangered species, salmon and steelhead also have a non-use or non-consumptive economic value to humans (Wallmo and Lew 2012). Non-use values include the *existence* value of knowing sustainable populations occupy a species' native habitat and a *bequest* value to the current generation of knowing conservation will allow a species to persist for future generations (Loomis and White 1996). The values are typically estimated using surveys that quantify the public's willingness to pay for the expectation of achieving future, improved population status. Studies of salmon and steelhead have reported non-use values of $42 M annually to Pacific Northwestern residents for doubling of Columbia River salmon runs (Olsen et al. 1991) and $138 M annually to Washington residents for restoration of Elwha River salmon runs following the removal of two dams (Loomis 1996). The Washington Department of Ecology has used Layton et al.'s (1999) study to estimate the benefits of improving anadromous fish population status. To the extent that hatchery programs place sustainable, natural salmon populations at risk or impede progress towards salmon recovery (see risks section below), hatchery production would tend to undermine non-use economic values. What is not clear is the non-use value of salmon populations demographically subsidized by hatchery production (a frequent situation across Washington, see Appendix 1), and how this compares to the non-use value of truly wild populations sustained only by natural habitat.

Treaty rights and tribal values

In the mid-19th century, Native American Indian tribes signed treaties with the U.S. government reserving the right to fish in traditional areas, alongside other rights, in return for ceding lands across the Pacific Northwest. A series of court cases reaffirmed these fishing rights, and provided additional clarity on the meaningful exercise of treaty rights (Blumm 2017). Notably, in a 1980 U.S. District Court decision, Judge William Orrick ruled that hatchery-produced fish were included in the treaty share of harvest, in part because hatcheries had become the primary means of compensating for salmon habitat loss due to dams and other land development activities (Blumm 2017). Although a thorough review of relevant case law is beyond the scope of this paper, hatcheries present one means by which U.S. and state governments can fulfill treaty obligations.

Salmon and salmon fishing opportunities have immeasurable social and cultural value to Native American Indian tribes. Salmon are intricately intertwined with history of humans in North America (Sutton 2017). Salmon remain essential to food security, culture and spirituality of Native American tribes in the present (Quaempts et al. 2018). Furthermore, the experience of capturing salmon is an inalienable component of tribal identity (Wilkinson 2000), and fishing has sustained tribal communities and economies throughout Washington State and the greater Northwest region. Indeed, in a 1905 court case affirming treaty fishing rights, the U.S. Supreme

Court rendered an opinion that fishing rights “were not much less necessary to the existence of the Indians than the atmosphere they breathed” (U.S. vs. Winans, 198 U.S. 371).

Mitigation

Many Pacific salmonid hatcheries were built or financially supported by Public Utility Districts, the Federal Columbia River Hydropower System, or private hydropower companies as part of legal requirements (e.g., Federal Energy Regulatory Commission) to mitigate for loss of spawning habitat due to dam construction. Most of the salmon hatcheries on the Columbia River and tributaries are legally or financially associated with hydropower obligations. Mitigation hatchery programs associated with hydropower were often established long before recognition of hatchery risks, focused on production rather than conservation of natural populations, and translocated hatchery stocks to distant sub-basins, substantially altering historical patterns of life history diversity and population structure. Much of the realized benefits of these hatcheries is through harvest, and hatchery release goals are set through production-oriented treaties, policies, and acts such as Mitchell Act and US v Oregon. Thus, we consider mitigation hatcheries legally tied to hydropower to be a subset of the more general goal of providing harvest opportunities.

Some hatchery programs also have a less formal or direct association with mitigation. Industrial, commercial, residential development has resulted in the ongoing degradation and loss of salmon habitat, a problem that is particularly acute where human populations are concentrated (Northwest Indian Fisheries Commission 2016). In these regions, especially in Puget Sound, production-oriented, harvest enhancement hatchery programs are implicitly acknowledged by fishery and hatchery managers as intended to compensate for habitat loss. However, rarely is this goal formally or explicitly described in regulatory documents (e.g., Hatchery Genetic Management Plans, HGMPs), which tend to adopt the more general “harvest enhancement” objective. Mitigation is perhaps not the reason these hatchery programs were initiated many decades ago, but managers generally view mitigation for degraded habitat as fundamental justification for continuing hatchery programs in the present.

Conservation benefits

Population conservation

Hatcheries are also employed as a tool to improve the conservation status of threatened or endangered natural salmon populations. Indeed, of the 159 separate hatchery programs currently operated by WDFW, 35 of them have a goal of conservation (Murdoch et al. 2019). Conservation hatchery programs may have a variety of more focused, practical objectives including preventing extinction of a unique genetic lineage, reintroduction to habitat from which the species had been extirpated, or increasing the abundance of an extant population. One can generally view these three objectives as a spectrum of hatchery intervention urgency, with goals of progressively higher conservation status of the target population: managers are likely to first ensure population persistence (prevent extirpation), and subsequently increase the spatial distribution (reintroduction) and then increase abundance of natural salmon runs. We review hatchery programs along this spectrum.

Several case studies demonstrate that hatcheries can have significant conservation benefit towards preventing population extinction. Hatchery intervention rescued sockeye salmon in Redfish Lake, Idaho from the brink of extinction, and made progress rebuilding the run (Kline and Flagg 2014) with relatively little inbreeding attributable to captive breeding (Kalinowski et al. 2012). Supplementation programs for Hood Canal summer chum salmon (Kostow 2012; Small et al. 2014) and North Fork Stillaguamish Chinook salmon (Eldridge and Killebrew 2007) preserved a unique lineage while maintaining genetic diversity. Hatchery managers avoided non-local releases in perpetuating Elwha River Chinook salmon following construction of dams that blocked the vast majority of habitat (Brannon and Hershberger 1984), and the population currently represents a unique genetic lineage (Ruckelshaus et al. 2006).

Hatchery programs are also often used to reintroduce species to areas from which they had been extirpated. In reviewing salmon reintrodutions, Anderson et al (2014) reported no clear examples by which hatchery approaches established a self-sustaining natural population, noting that hatchery releases are ongoing in many cases, so it is unclear if natural spawning would persist without supplementation. However, several recent examples exhibiting more promising results merit mention. First, summer chum salmon were reintroduced to Chimacum Creek (eastern Strait of Juan de Fuca) from nearby Salmon Creek, and natural-origin adult abundance appears stable for two generations (2008 - 2017) following termination of hatchery releases in 2003 (Kostow 2012; PNPTT and WDFW 2014; WDFW unpublished data). Initial results from the Elwha River indicate that transplanting predominantly hatchery-origin adult coho salmon accelerated the spatial expansion of natural spawning following dam removal (Liermann et al. 2017). A large coho reintroduction program in the Columbia River Basin has initiated signficant natural spawning by the species, and supplementation is ongoing (Galbreath et al. 2014), with some evidence for adaptive evolution of hatchery broodstock (Campbell et al. 2017).

Increasing abundance of extant populations is another objective of conservation hatcheries. Sharma (2006) concluded that coho salmon supplementation on the Clearwater River increased total return to the river and spawner to spawner reproductive efficiency of the aggregate hatchery plus natural population, primarily because natural-origin adult returns were insufficient to reach juvenile carrying capacity. Fast et al. (2015) reported that Yakima River spring Chinook supplementation increased total harvest, redd counts and spatial distribution while maintaining relatively stable natural-origin returns. Importantly, both hatchery programs were relatively early generation (i.e, new) and used entirely natural-origin broodstock.

Hatchery-origin fish frequently spawn naturally in the river (Appendix 1, Table 4). This can provide a conservation benefit to low abundance natural populations by spatially or numerically expanding the utilitization of natural habitat, and maintaining some minimum number of naturally spawning fish. However, this benefit must be carefully balanced against the longer term risk of fitness decline (detailed in subsequent sections). In naturally spawning popuations receiving a large demographic subsidy from hatchery-origin fish (high proportion of hatchery-origin spawners, pHOS), transitioning to demographic independence appears to be a major hurdle to recovery.

Indeed, improving conservation status requires a different and more strict criterion than increasing the number of naturally spawning fish: increasing the number of natural-origin fish (NWFSC 2015). Thus, increasing natural population abundance via hatchery production requires, at a minimum, three generations to yield conservation benefits. In the first generation, fish spawned in the hatchery are released as juveniles. In the second generation, these hatchery-origin fish return as adults, and increase the abundance of fish spawning naturally in the river. In the third generation, a demographic benefit is characterized as increased natural-origin abundance due to the naturally spawning hatchery-origin fish in generation two. Thus, the ultimate conservation goal is increasing natural-origin adult abundance (in generation three and thereafter), not placing hatchery-origin fish on the natural spawning grounds (generation two). Therein lies a crucial assumption: prior to supplementation, the population is below carrying capacity such that the additional hatchery-origin spawners in generation two yields a net increase in natural-origin adults in generation three (Cuenco 1994). Alternatively, if the additional hatchery-origin spawners in generation two exceed carrying capacity, there may be no net increase in generation three natural-origin abundance due to a decrease in per capita population productivity caused by density dependent processes.

Multi-generational examinations of the demographic benefit provided by conservation hatcheries are relatively rare. In Johnson Creek, Idaho, spring Chinook salmon spawned in the hatchery (generation one), produced 2.5 times more natural-origin grandoffspring (generation three) than fish spawning naturally in generation one (Janowitz-Koch et al. 2019). Key features of this hatchery program include its relatively small size (≤ 40 pairs spawned annually) and use of 100% natural origin broodstock (Janowitz-Koch et al. 2019). In the Hamma Hamma River, Washington, in the period after steelhead supplementation stopped during which only natural-origin fish returned to the river (generation three), natural-origin abundance (mean = 26 redds) increased from the period prior to when supplementation began (mean = 10 redds, Berejikian and Van Doornik 2018). This hatchery program excavated fertilized embryos from naturally produced redds, and similar to the Johnson Creek study, was relatively small in size (≤ 25 redds excavated annually).

Two additional studies, both within the interior Columbia River Basin, provide a more comprehensive synthesis of conservation hatchery benefits to increasing abundance. Scheuerell et al. (2015) examined 43 years of data from 22 Snake River spring/summer Chinook salmon populations, 12 of which were supplemented, to determine if the density of natural-origin adults in generation three increased after hatchery-origin adults spawned naturally in generation two. The authors found a relatively small supplementation effect size. On average, supplemented populations had 0 – 8% greater natural-origin abundance than non-supplemented years (Scheuerell et al. 2015). Across all 12 supplemented populations, the overall effect size was 3.3 %, with a 95% credible interval of -8% - 15%, and a 73% probability that the effect size was positive rather than negative (Scheuerell et al. 2015). Venditti et al. (2018) examined 13 supplemented and 14 reference Chinook salmon populations before, during and after supplementation (22 years total) in the Salmon and Clearwater basins in Idaho. Most importantly, while the presence of hatchery-origin spawners increased total abundance of naturally spawning fish during supplementation (generation two), abundance generally decreased to pre-supplementaton levels after supplementation had ceased (generation three), indicating no net gain in natural-origin spawners (Venditti et al. 2018).

We conclude that evidence for population conservation benefits of hatchery programs varies according to the spectrum of intervention urgency. In multiple situations, hatcheries have proven successful at preventing population extinctions and preserving unique genetic lineages. Hatchery-based reintroductions have promoted natural spawning in previously unoccupied habitat, yet we found only a single example in which natural reproduction was sustained for multiple generations following termination of hatchery releases (Chimacum Creek summer chum salmon). Lastly, although two individual hatchery case studies provide evidence for increased natural-origin abundance (Berejikian and Van Doornik 2018; Janowitz-Koch et al. 2019), two broader synthetic investigations suggest extremely limited or minimal conservation benefits to natural-origin abundance (Scheuerell et al. 2015; Venditti et al. 2018).

We postulate that the lack of evidence for increasing natural-origin abundance through supplementation is related to two factors. First, rarely are the primary factors contributing to a population decline addressed (e.g., degraded or inaccessible habitat). We suggest a more careful examination of the ecological conditions required for hatcheries to successfully boost natural-origin abundance, primarily that pre-supplementation abundance is well below habitat carrying capacity. Under this circumstances, a hatchery program might help the population cross an abundance threshold for avoidance of depensation effects (Liermann and Hilborn 2001) or increase the rate of numerical population expansion toward carrying capacity. However, it is unclear whether these conditions are met or even evaluated in the majority of conservation hatchery programs. Second, conservation programs rarely achieve operational targets (e.g., exclusively or high percentage of natural-origin broodstock, see Table 4).

Ecosystem benefits

Pacific salmon are well recognized as keystone species providing energy and nutrient subsidies, either directly or indirectly, to freshwater and terrestrial ecosystems, supporting a host of mammalian, avian, amphibian and resident fish species (Willson and Halupka 1995; Cederholm et al. 1999; Gende et al. 2002). More recent attention has focused on the role of Chinook salmon in marine ecosystems, especially as the preferred prey for fish eating, endangered Southern Resident Killer Whales (Ford and Ellis 2006). To the extent that hatchery-produced salmon serve as prey for threatened species or provide nutrient subsidies to degraded habitats, hatcheries might provide ecosystem-level conservation benefits. Over much of their history, hatchery programs have rarely identified ecosystem services as explicit goals. However, hatchery managers have recently proposed increasing hatchery production in order to provide additional prey for killer whales (WDFW 2019).

To our knowledge, the ecosystem services provided by salmon hatcheries, as separate from those provided by natural populations, have not been evaluated in the literature. However, we make several general observations. Any salmon that return directly to hatchery facilities do not provide an energy subsidy to aquatic systems, and thus manual carcass transport from hatchery facilities to target streams is frequently employed as a nutrient enhancement strategy. Many hatchery-origin fish do spawn naturally in the river (Appendix 1), thereby contributing to nutrient enhancement, though this also tends to present genetic risks to sympatric natural salmon populations (described in genetic risks section). Finally, proposals to increase hatchery production for the benefit of killer whales implicitly assume 1) marine rearing habitats have sufficient capacity to support additional salmon, 2) hatchery stocks identified for increased production are accessible as prey to killer whales in time and space.

Research and education benefits

Some hatcheries are operated for research and education purposes. Research facilities offer opportunities to experimentally alter and evaluate spawning, rearing and release protocols. Also, some hatcheries have a “salmon in the classroom” component that offers local school groups an opportunity to learn about salmon biology, and natural resources. However, hatchery education programs must be aware that children may perceive implicit lessons regarding the role of people rather than nature in producing salmon. In general, research and education hatchery programs tend to be smaller in scale and fewer in number than harvest or conservation programs, but they present important learning and outreach opportunities.

RISKS OF HATCHERIES

There is an extensive literature on hatchery risks, especially genetics risks and fitness (Naish et al. 2008). Our purpose here is not an exhaustive review, but rather to provide background necessary to evaluate efficacy of hatchery reform actions described in the next section. Thus, we address key concepts and weight of evidence. Risks represent not only the likelihood of an adverse effect, but also its magnitude. Accordingly, where possible based on the literature, we aim to describe both the frequency of a given risk and the strength or consequences of its impact.

Fishery risks

One significant risk of hatcheries is that they subsidize and thereby intensify fisheries that incidentally encounter natural populations. Indeed, most salmon and steelhead fisheries in Washington State target abundant hatchery populations, which are typically co-mingled with natural populations that are much less abundant and less productive, often ESA-listed as threatened or endangered, leading to unintended but unavoidable impacts to the natural populations. This is the perennial problem of mixed-stock fisheries that has plagued fishery managers for decades (Wright 1981) and persists today. Salmon and steelhead fishery management is a complex web of multiple management jurisdictions and user groups, and a thorough review of harvest management is beyond the scope of this paper. However, we make three conceptual points relevant to the role that hatchery production plays in affecting harvest impacts on natural populations.

First, a common strategy to allow higher rates of harvest on hatchery populations than natural populations is to externally mark hatchery fish, often with an adipose fin clip, and employ mark-selective fisheries so hatchery-origin fish can be removed while unmarked (presumably natural-origin) fish can be returned to water. However, not all fisheries are mark selective, limiting the utility of this management tool to differentially remove hatchery-origin fish and limit fishery mortality of natural-origin salmon. Indeed, mark-selective fisheries account for a relatively small proportion of the total estimated exploitation rates on unmarked Puget Sound Chinook salmon and unmarked Washington State coho salmon (Figures 1A and 1C). Although mark-selective fisheries have yielded the desired outcome of low estimated mortality on unmarked fish, limitations to their implementation have resulted in substantial non-selective mortality on unmarked fish. Furthermore, not all unmarked fish that are released survive. Estimates of post-release survival (Bendock and Alexandersdottir 1993; Nelson et al. 2005) and encounter rates of unmarked fish are critical assumptions for estimating total harvest mortality of natural populations exposed to mark-selective fisheries targeting abundant hatchery populations. Further research on the manner in which fishery management (e.g., gear type, time and area openings) affects these metrics would improve estimates of incidental mortality in mark-selective fisheries.

Second, although Washington's salmon and steelhead fisheries typically target abundant hatchery fish, they are limited in terms of landings, fishing effort, or time and area openings by the co-mingled lower abundance natural populations. Thus, curtailing fisheries to protect weak natural populations creates a dramatic asymmetry in the conservation benefits to natural populations vs. lost harvest opportunity on hatchery populations. For example, in some cases, Puget Sound Chinook salmon total (hatchery-origin plus natural-origin) terminal run size outnumbers naturally spawning, natural-origin abundance by an order of magnitude or more (Appendix 1). In such situations, if harvest managers incrementally restrict fisheries to meet natural-origin conservation targets, they necessarily forgo a much larger harvestable abundance of hatchery-origin fish than the corresponding increase in natural-origin abundance. Hatchery production, when implemented on a large scale, amplifies this asymmetry and thus can magnify the political pressure to take advantage of abundant hatchery runs at the expense of natural populations.

Lastly, the critical analyses addressing the fishing rates and levels of harvest that natural populations can support are typically presented in harvest plans (PSIT and WDFW 2017). Harvest plans use a variety of analytical approaches, but in the case of threatened or endangered populations, they generally aim to not impede the rebuilding of the natural population. However, these harvest benchmarks are identified via retrospective analysis of population data from an era of continual, often large-scale hatchery production, complicating assessment of natural population performance. McClure et al. (2003) described the uncertainty to population status assessments created by the presence of naturally spawning hatchery-origin fish, which might “mask” the performance of natural-origin salmon (see also Johnson et al. 2012). Similarly, we suggest that naturally spawning hatchery-origin fish add considerable uncertainty to the productivity and capacity estimates required to establish harvest benchmarks. The magnitude of this issue is likely dependent on the proportional abundance of hatchery-origin natural spawners (i.e., pHOS). At least in our demographic example of Puget

Sound Chinook, consistently high pHOS values (often > 50%, Appendix 1) suggest significant harvest benchmark uncertainty due to “masking.”

Genetic risks

The genetic effects of hatchery propagation of salmonids have been reviewed numerous times (e.g., Busack and Currens 1995; Bekkevold et al. 2006; Naish et al. 2008; Glover et al. 2017), most recently by Fisheries and Oceans Canada (DFO) in a report adopting HSRG guidelines for Canadian Chinook salmon programs (Withler et al. 2018). Here, we rely extensively on these previous reviews to briefly describe the genetic risks of hatchery propagation.

Genetic changes in wild populations resulting from hatchery propagation may happen directly or indirectly. Indirect genetic changes, i.e., genetic changes in wild fish resulting from ecological interactions of hatchery and wild fish (e.g., through disease transfer, competition, predation, etc.) have been hypothesized and are certainly possible. However, to our knowledge no studies exist that explore indirect genetic changes. Indirect genetic changes are currently impossible to predict with any accuracy, so rather than speculate on all possible outcomes, we, like in previous reviews, acknowledge their possible existence, but focus exclusively on direct genetic effects. Possible direct genetic effects of hatchery propagation fall into two broad categories: reduction of diversity (within and among populations) and maladaptation (i.e., domestication). Direct genetic effects of hatchery production on wild populations occur only through interbreeding of hatchery-produced and wild fish. The outcomes of interbreeding are therefore dependent on the breeding systems (e.g., natural spawning behavior and hatchery spawning protocols), which may vary among species and among hatchery programs. Here we provide general descriptions of direct genetic risks of hatchery propagation.

Risk of reducing within-population genetic diversity

Maintaining high levels of genetic diversity is important for long-term adaptability in the face of a changing environment (Lande and Shannon 1996; Agashe 2009; Forsman and Wennersten 2016). Populations naturally lose variation at some per-generation rate, in part because they are finite in size; genetic variation is replenished by immigration from other populations (i.e., gene flow) and by mutation. Hatchery propagation carries with it a risk of increasing the rate at which diversity is lost.

Hatchery propagation may quicken the loss of genetic diversity through increasing the rate of inbreeding. Inbreeding is defined as an increase in genetic identity by descent (IBD), where gene variants on each chromosome in an individual or among individuals in a population are identical because they share a common ancestor. An increase in IBD can occur because genetically similar individuals (i.e., relatives) mate with each other more often than by chance (positive assortative mating) or because close relatives are so abundant that mating with a relative by chance is very likely. Effective population size (N_e) is a genetic metric directly related to inbreeding where inbreeding is expected to increasingly occur with a decreasing N_e. Hatchery propagation, by increasing the abundance of relatives via spawning and increasing the egg to smolt survival of only a subset of the population, may increase the variance in family size of the entire population, dramatically reducing N_e and increasing inbreeding (i.e., the Ryman-Laikre effect, Ryman and Laikre 1991).

Inbreeding effects have been demonstrated in fishes in aquaculture, but generalizations of their results to salmon and steelhead hatchery programs is equivocal and empirical evidence of inbreeding depression occurrence due to hatchery propagation is rare (Wang et al. 2002). Christie et al. (2014b) described the relationship between inbreeding and fitness, using an extensive genetically inferred pedigree of Hood River, Oregon steelhead. They estimated that inbreeding could at most explain 4% of the reduction in fitness seen in the combined wild and hatchery population. However, that assumed a worst-case scenario of hatchery fish only spawning with other hatchery fish on the spawning grounds. When a more plausible model of random mating was used, inbreeding explained less than 1% of the observed reduction in fitness in naturally produced fish.

Hatchery propagation also carries a risk of reducing within-population genetic diversity through the loss of alleles. Without input from gene flow or mutation, populations lose genetic (allelic) diversity every generation because not all adults contribute to the next generation (e.g., Dickerson et al. 2002; Seamons et al. 2007; Williamson et al. 2010; Ford et al. 2016). Variability in reproductive success, and the reduction in diversity that accompanies it, may be due to random processes (genetic drift) or selective processes. Hatchery propagation may increase the risk of losing diversity from the same hatchery activities that reduce within-individual diversity: if the subset of adults used as broodstock are not representative of all allelic diversity in the population, alleles may be lost. The smaller the sample of adults used as broodstock, the larger the chance of losing alleles. Variability in reproductive success of hatchery-produced fish will further increase the chances of reducing within-population diversity. Some empirical studies have documented inbreeding in hatchery populations (see Wang et al. 2002 for a review of inbreeding with a focus on salmonids; e.g., Naish et al. 2013) and reduced N_e due to hatchery supplementation (e.g., Christie et al. 2012b), whereas others have found little evidence for reduced genetic diversity in supplemented populations (Van Doornik et al. 2011). The likelihood and magnitude of impacts on within population diversity likely vary greatly depending on how hatchery programs are managed (Waters et al. 2015).

Among population genetic diversity

Intraspecific genetic diversity is important for metapopulation viability and stability through portfolio effects and provides substrate for evolution to occur (Greene et al. 2010; Schindler et al. 2010; Schindler et al. 2015; Braun et al. 2016). Hatchery propagation can reduce diversity among populations, making different populations genetically more similar to one another. Such genetic homogenization may reduce the fitness of all involved populations through the introduction of locally deleterious alleles or through the break-up of co-adapted gene complexes that may be local adapted. This process is termed outbreeding depression, and it is characterized by the break-up of beneficial allelic combinations through introgression and recombination.

Homogenizing gene flow among hatchery and wild populations occurs through two primary pathways. First, intentional transfers of broodstock, eggs or juveniles between river basins may result in gene flow among transferred and local stocks, a practice that was common throughout much of the 20th century. Second, some fish released from the hatchery may on their own migrate to non-natal populations (i.e., stray or fail to home), where they interbreed with local spawners. Straying of hatchery produced fish to non-natal sites is well documented and differences in stray rates among species, life histories, and populations of hatchery salmon and trout has been demonstrated (e.g., Westley et al. 2013). However, the ultimate impacts of hatcheries on maintaining or increasing genetic homogenization through straying among populations are poorly understood.

In many cases, contemporary population genetic structure and specifically a loss of regional diversity, reflects a legacy of intentional stock transfers and unintentional straying, with examples of Puget Sound coho salmon (Eldridge and Naish 2007) and Central Valley California Chinook salmon (Williamson and May 2005). However, other researchers have found no evidence for the erosion of population structure due to hatchery practices (Heggenes et al. 2011), so the level of risk likely varies according to hatchery program specifics, species life history, and natural patterns of genetic diversity. Furthermore, clear evidence of fitness loss attributable to outbreeding depression in salmon and steelhead is rare and may depend, for example, on the trait examined, the environment which the population is subjected to, or the magnitude of the genetic differences among populations (McClelland et al. 2005; McClelland and Naish 2007; Fraser et al. 2008; Dann et al. 2010; Houde et al. 2011; Côte et al. 2014; Lehnert et al. 2014).

Domestication

Hatchery propagation may lead to genetic adaptation to the hatchery environment with reduction of the fitness of hatchery-produced fish when spawning naturally, often called domestication selection (Christie et al. 2012a; White et al. 2013; Hagen et al. 2019). Fitness of wild fish may decline when they interbreed with domesticated hatchery fish. Some level of domestication selection is unavoidable because the hatchery environment is different than the natural environment. Importantly, domestication selection is likely largely or entirely unintentional in most salmon and steelhead hatchery programs operated by WDFW. In some cases, deliberate selection for earlier spawning timing (e.g., steelhead trout: Crawford 1979) was likely accompanied by unintentional domestication selection on other traits. A variety of morphological, life-history, behavioral, and physiological traits are known to have a genetic basis in salmon (Carlson and Seamons 2008), providing ample scope for inadvertent domestication selection in the hatchery.

Assessing the relative reproductive success (RRS) of hatchery-origin and natural-origin fish when spawning naturally has become a common approach to investigate impacts of domestication in hatchery salmon and trout. Most RRS studies have used genetically inferred pedigrees to compare the number of offspring (i.e., fitness) produced by hatchery-origin and natural-origin fish spawning in the wild. Currently, there is only one long-term study of RRS, which revealed, in steelhead, that there were multi-generational declines in RRS from hatchery exposure that carried over to the natural-origin offspring of hatchery-origin parents that spawned in the river (Araki et al. 2009). Many other studies have found that hatchery-origin fish are less fit than natural-origin fish when spawning in the wild (e.g., Araki et al. 2007; Williamson et al. 2010; Thériault et al. 2011; Ford et al. 2016; Janowitz-Koch et al. 2019). Two RRS studies have provided evidence that the lower fitness of hatchery-origin fish has a genetic basis (Araki et al. 2008; Ford et al. 2016), whereas two others with an appropriate study design did not (Thériault et al. 2011; Ford et al. 2012). Interpretation of RRS studies is often made difficult by the unknown degree of hatchery introgression prior to the onset of the study.

Indeed, there may be less difference between fitness of hatchery fish and wild fish if the fitness of wild fish has already been significantly reduced because many putative 'wild' fish are actually hatchery/wild "hybrids" (Willoughby and Christie 2017). However, in a review of RRS estimates associated with recently established hatchery programs, hatchery fish had much lower reproductive success than natural-origin fish and no difference in effects was found among species (Christie et al. 2014a).

Recent research effort has also been devoted to using gene expression and epigenetics approaches to better understanding the processes or mechanisms by which changes in fitness could occur. Hatchery propagation produces differences in gene expression generally, with some plausible links to specific traits (Roberge et al. 2006; Sakhrani et al. 2013; reviewed in Glover et al. 2017), even in only one generation (Christie et al. 2016). An emerging field of research is in epigenetics, which are non-DNA chemical tags on DNA that may affect gene expression. Some differential gene expression may be the result of heritable and non-heritable epigenetic processes (Ledón-Rettig et al. 2012; Verhoeven et al. 2016; Gavery and Roberts 2017; Best et al. 2018). High epigenetic variation has been shown in wild animals (Hu and Barrett 2017) and hatchery propagation has been shown to produce differences in epigenetic signatures (Le Luyer et al. 2017; Gavery et al. 2018). These fields as applied to fitness effects of hatchery propagation are still in their infancy and duration of inheritance of epigenetic mutations remains an important unanswered question.

Ecological risks

Hatchery releases can also present ecological risks, a topic that has been the focus of several previous reviews (Einum and Fleming 2001; Kostow 2009; Tatara and Berejikian 2012). Thus, rather that providing a detailed examination of ecological mechanisms or a comprehensive review of all study results, we aim to summarize the state of knowledge on the magnitude and commonplace of ecological interactions between hatchery and natural fish. We first review four important mechanisms conferring ecological risk: competition, predation, disease, and facility effects. Finally, we review population-scale retrospective analyses intended to quantify the realized impacts of hatchery programs on natural populations.

Ecological risk mechanisms

Competition- When hatchery fish are released to the natural environment, they may compete with naturally produced fish for food, rearing territories or spawning territories. If hatchery fish reduce the accessibility of these resources to naturally produced fish, they may ultimately depress the growth, survival, or productivity of natural populations. Tatara and Berejikian (2012) emphasized this outcome could result from two different ecological processes. First, biological differences between hatchery and wild fish could provide a competitive advantage to hatchery fish. Second, even without any differences between hatchery and natural fish, releasing hatchery fish into the natural environment may cause the abundance of the combined hatchery plus natural population in aggregate to (at least temporarily) exceed habitat carrying capacity, reducing the performance of a natural population due to density dependence. These two ecological processes are useful context for interpreting results and management implications of hatchery-natural ecological studies. They are also associated with spatial and temporal scale. In general, numerous small scale studies examining the competitive differences between hatchery and natural fish have provided fairly precise descriptions of ecological competition. However, larger scale studies examining the degree to which hatchery releases reduce natural population productivity due to density dependence are much less common and typically offer less precise ecological explanations for observed results (Figure 2).

A great deal of research conducted in laboratories or experimental stream channels has assessed competition between hatchery and natural fish by evaluating response variables such as levels of aggression, feeding behavior, growth and survival. Such studies have generally found sufficient ecological niche overlap between hatchery and natural fish to cause competition, and have assessed asymmetries in the competitive abilities between hatchery and natural fish (Einum and Fleming 2001; Tatara and Berejikian 2012). Some factors (often larger size, more aggressive behavior) tend to favor hatchery fish in competition, whereas other factors (often prior residence, predator avoidance behavior) tend to favor naturally produced fish. Most of these mechanistic, experimental studies have focused on salmonid life stages occuring in freshwater rather than marine habitats.

At the scale of a natural populations, three factors will primarily affect the magnitude and impact of competition between hatchery and natural fish (adatped from Taratara and Berejikian 2012). First, the number of hatchery fish released will affect the frequency of hatchery-natural encounters and determine the abundance of the combined hatchery-natural population in comparison to habitat carrying capacity, which Tatara and Berejikian (2012) argued was the “most important” factor governing hatchery-natural competiton. Second, the duration of habitat cohabitation will affect the length of exposure of natural fish to competition with hatchery-reared fish. This duration is strongly affected by the propensity of hatchery-reared fish to migrate through shared rearing environments upon their release. Lastly, the nature of the competitive interactions will be determined by species and individual traits (behavior, size, prior residence).

Although experiments examining competition mechanisms have focused on freshwater life stages, hatchery-natural competition may also occur in marine environments. Biologists have recognized the potential for density-dependent limits on productivity in marine habitats for some time (Peterman 1978). Beamish (1997) asserted that substantial expansion of hatchery production had the potential to reduce the abundance of natural populations due to finite marine carrying capacity, emphasizing that shifts in marine productivity can reduce the total (hatchery plus natural) abundance supported by the ocean. Ruggerone and Goetz (2004) suggested that indirect foraging competition with pink salmon limited the marine survival of hatchery Chinook salmon stocks in Puget Sound and the lower Strait of Georgia during periods of lower marine prey availability, providing evidence for competition and limited carrying capacity in marine habitats. Pink and chum salmon are the most numerous species in the North Pacific Ocean, and both exhibit a negative correlation between body size and total abundance, indicative of density dependent competition (Ruggerone and Irvine 2018). Cunningham et al. (2018) found a negative relationship between the survival of Yukon Chinook salmon and the number of chum salmon released from Japanese hatcheries, suggesting competition in the open Pacific Ocean as a plausible mechanism.

The frequency, magnitude and ultlimate impact of hatchery-natural competition in the marine environment likely varies according to species. We suggest significantly stronger potential for hatchery-natural competition for species with extensive use of estuaries and nearshore areas, primarily Chinook salmon subyearling migrants and chum salmon, because these areas are more limited in availability and more degraded by human activities than open ocean habitats (i.e., continental shelf or North Pacific Ocean). Hatchery and natural Chinook salmon clearly exhibit broad overlap in time and space during estuary and nearshore rearing, providing potential for competition (Rice et al. 2011). However, segregation among habitat types and exploitation of separate foraging niches, as was demonstrated for hatchery and naturally spawned Chinook salmon in the Nisqually River estuary and neashore, would tend to limit hatchery-natural competition (Davis et al. 2018).

Despite potential for competition in marine habitats, relatively little is understood regarding realized impacts of hatchery production on natural populations. This is due in large part to the logistical difficulties of sampling and making direct observations or population-scale estimates of key vital rates (e.g., survival) in these habitats. Importantly, the marine conditions or hatchery management strategies that do and do not induce competition are not understood. Population-scale retrospective studies, reviewed below, offer some insight, but lack a sufficiently detailed mechanistic information to fine-tune hatchery management for the trade-off between competion risks and hatchery benefits. Similar to freshwater habitats (e.g., Tatara and Berejikian 2012), we suggest that the strongest determinant of hatchery-natural competition in marine habitats is the combined hatchery plus natural abundance relative to marine carrying capacity , underscoring the importance of hatchery program size (number of fish released) in controlling the level and impact of competition. At the scale of the Pacific Ocean, Alaska pink salmon and Japanese chum salmon numerically dominate hatchery releases (Ruggerone and Irvine 2018). Thus, Washington's hatchery programs likely have the largest influence on marine competition in the geographically proximate habitats of Puget Sound, the Columbia River estuary, and nearshore Washington coastal habitats.

Predation- Predation is another ecological mechanism by which hatchery releases present ecological risks to natural populations. It is well established that salmonids are piscivorous and prey upon smaller bodied salmonids, and studies show that hatchery-reared yearling smolts and residuals can consume smaller, natural-origin subyearling salmonids (Naman and Sharpe 2012). Predation rate and overall impacts from hatchery predation likely vary due to spatial and temporal overlap with prey species (Naman and Sharpe 2012), predator and prey abundance (Simpson et al. 2009), and the relative sizes of predator and prey (Pearson and Fritts 1999). Salmonids that residualize in freshwater can increase the amount of time that natural-origin salmonids are exposed to direct predation by hatchery fish. Even at low levels of predation, large releases of hatchery fish can have a measureable impact on natural-origin salmonids, especially if natural populations are small (Whitsel et al. 1993; Naman and Sharpe 2012). However, overall, there are few direct assessments of predation by hatchery salmonids on natural-origin 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).

Large hatchery releases may affect the behavior of other predators in the area, resulting in short-term avian, piscine, or mammalian predator aggregations, or long-term increases in predator abundance due to increased prey availability, both of which could indirectly impact naturally produced fish. Studies show that predators will exploit hatchery-released salmonids and piscine (Collis et al. 1995; Shively et al. 1996) and avian (Wood 1985; Wood 1987b) predators will aggregate near hatchery release sites. Hatchery releases of Chinook salmon have become more synchronized over time (California: Huber and Carlson 2015; Salish Sea: Nelson et al. 2019a), possibly amplifying impacts to co-mingled naturally produced salmon. Conversely, other authors have suggested that abundant hatchery fish may buffer natural populations from predation if hatchery plus natural abundance exceeds the capacity of predators to feed. Several studies indicate that consumption of salmonids by avian (Wood 1987a; Faulkner et al. 2008) and piscine (Peterson and Deangelis 1992) predators is depensatory: as prey (salmonid) abundance increases, mortality by predation decreases. Overall, large-scale hatchery releases have the potential to significantly alter predator dynamics, but very little is known or understood regarding either short- or long-term impacts to natural populations.

Disease- Fish disease risks associated with enhancement hatchery programs were summarized by Naish et al. (2008) and included the potential for the: a) introduction of exotic pathogens, b) amplification of endemic pathogens, c) horizontal transmission between infected hatchery and their wild counterpart, d) introduction of pathogens at unusual times, e) alteration genetic factors contributing to disease resistance, f) introduction pollutants to natural systems via the effluent. An acknowledgement of fish disease risks was in the summary prepared by HSRG (2014). In that review, the HSRG expressed satisfaction with the state of surveillance of fish disease and a desire to move away from disease avoidance towards vaccination and increased preparedness for the establishment of new diseases in the face of climate change. However, the HSRG proposed few specific recommendations surrounding the management of disease risks.

To manage risk, an understanding of both the likelihood of an injurious outcome to occur and the magnitude of its impact is required. Data necessary to characterize likelihood and magnitude of impact are frequently unavailable for fish disease hazards; particularly so in the context of hatchery-wild fish interactions. For example, while pathogens may be shed by hatchery fish and contribute to an increased risk for surrounding fish populations, the pathway to characterize the impact is limited by a large data gap. In recent years, more effort has been placed in applying disease theory and epidemiological models to guide risk assessment of fish disease in free-ranging fish populations (Krkošek 2010; Ray et al. 2010; Ferguson et al. 2018). Although mathematical models can understate the complexity of nature, they provide the parameter estimates necessary to quantitatively illustrate the potential impacts of a disease hazard related to changes to production strategies of fish hatcheries. Models describing the dynamics of disease in populations incorporate an understanding of: a) the numbers of susceptible hosts, b) the mechanisms of pathogen transmission, c) the rate at which the pathogen leads to mortality, and d) the capacity of the host to form a resistance or immunity to the pathogen (Anderson and May 1979a; Anderson and May 1979b). The application of these models is more common for terrestrial diseases but have been applied to support decisions surrounding commercial fish farming activities (Werkman et al. 2011) but only a limited number of fish pathogens have the empirical data necessary to implement such models. Additionally, the impact of a changing climate will confound current understanding surrounding the impact of many infectious agents by altering their distribution and virulence (Marcogliese 2008; Karvonen et al. 2010).

The majority of infectious disease issues in hatchery production are the result of fish pathogens that are endemic to the region. Transmission of these pathogens can occur between hatchery and wild fish in either direction. The increased rearing numbers of suitable fish hosts at hatchery production facilities can serve to amplify the number of pathogens shed into the environment (Moffitt et al. 2004). Examples of pathogen amplification have been observed in salmon hatcheries on the Willamette River in Oregon. Sentinel fish placed in the effluent of hatcheries undergoing disease outbreak developed infections but infections were never observed in sentinel fish located in the hatchery inflow from these same hatcheries (Jakaitis 2014). In absolute terms, this reflects an increase in infectious particles released and risk of transmission of disease to surrounding populations, however, data surrounding fish viral diseases suggest a higher likelihood of impact caused by transmission from wild to hatchery than from hatchery to wild (Kurath and Winton 2011).

Host density is an important factor when determining transmission and persistence of a pathogen in a population as increased density increases the likelihood of interaction between infected and susceptible individuals (Arneberg et al. 1998). Models presented by Krkošek (2010) suggest that maintaining high densities of susceptible hosts, such as in marine net-pens, during periods not reflective of natural patterns of pathogen prevalence sustain sea lice infections in wild fish in areas where commercial and wild salmon interact. Compared to commercial aquaculture, there have been few efforts to characterize horizontal transmission between sympatric populations of hatchery-reared fish and wild fish. Rhodes et al. (2011) illustrated a positive relationship between higher Chinook salmon densities and *Renibacterium salmoninarum* prevalence in the nearshore areas of Puget Sound, WA. There are also data to suggest that higher fish densities in the in the hatchery environment can lead to increased virulence of pathogens (Pulkkinen et al. 2009; Sundberg et al. 2016). Finally, it is well established that high rearing density can lead to immunosuppression as would be true for any aquaculture stressor (Green and Haukenes 2015).

We discuss genetic risks elsewhere more broadly but the overall immunological response and resistance to pathogens is influenced by genetics. Hatchery-origin fish have exhibited diminished resistance to certain pathogens in some cases, possibly explaining their performed poor performance compared to their wild counterparts (Bartholomew 1998) and that local adaptation contributes to the major histocompatibility complex variation that is important for pathogen recognition by the host (Dionne et al. 2009). Genetic effects also include changes to the pathogen as a function of the hatchery environment. A recent review by Kennedy et al. (2015) summarized the potential of increasing pathogen virulence associated with hatchery practices; these include, in addition to the aforementioned host density, practices frequently used to reduce disease impacts within the hatchery (e.g. vaccination, reducing vertical transmission) that promote a new equilibrium between host and pathogen. These observations and hypotheses, while supported generally by disease theory and tested in other animal production systems, have not been empirically examined in any detail for fish pathogens.

Facility effects- Hatchery facilities often alter the physical environment, potentially impacting the quality and quantity of fish habitat. Instream structures such as weirs or water diversion dams can impede upstream or downstream fish migration, and impacts can include displaced spawning, fallback, increased injury or mortality due to handling effects, and changes to redd distribution. The diversion or withdrawal of water can impact the environment in the vicinity of the hatchery, and directly or indirectly affect natural populations. Hatchery effluents can affect nutrient levels, temperatures, invertebrates, and presumably fish populations downstream of the discharge point. In general, physical impacts of hatchery facilities are regulated by local, state, and federal environmental authorities. There is little research on the effects of hatchery facilities and hatchery activities on local water quality, invertebrates, or fish, other than compliance monitoring. Hatcheries tend to be evaluated on a case-by-case basis according to these regulations. Site-specific features related to the hatchery facility itself and the local environment (stream size, gradient, flow regime, etc.) make it very difficult to generalize about these effects but this variation does not mean that the effects are inconsequential. Effects on natural salmonid populations and other fishes can be important.

Review of population scale studies

Although the relevant ecological concepts are well described, empirical assessments of population-scale impacts to natural populations are generally rare. The most common approach is a retrospective analysis of natural population data, examining correlative relationships between a hatchery parameter, often number of juveniles released from hatcheries or number of hatchery-origin spawners, and a metric of natural population performance, often survival or productivity. These studies typically assess multiple decades of natural popuation, hatchery and environmental covariate data, with each time series represented by a single estimate each year, often in a stock-recruit (density dependent) modeling approach. Importantly, they evaluate response variables of utmost importance to understanding the impact of hatcheries on the viability (sensu McElhany et al. 2000) of threatened or endangered natural populations: population-scale abundance and productivity. However, such studies are necessarily less mechanistically descriptive than smaller scale experimental studies, due to the difficulties of isolating the outcomes of hatchery-natural ecological interactions at the scale of populations (Figure 2).

Population-scale studies analyzing the number of juvenile hatchery fish released are generally interpreted as an assessment of the ecological (not genetic) impacts. In some cases, additional environmental co-variates provide insight and indirect examination of ecological mechanisms of hatchery impacts (e.g., competition). Levin et al. (2001) found a negative relationship between Chinook salmon hatchery releases and smolt to adult return (SAR) rate of spring/summer Chinook salmon aggegated from multiple Snake River populations during years of poor ocean productivity. The authors interpreted these results as evidence for competition for a limited forage base during early ocean rearing when prey was scarce. Levin and Williams (2002) found an interspecific negative relationship between the number of hatchery steelhead released and SAR of Chinook salmon in the Snake River Basin. This study found no relationship betweeen hatchery steehead releases and natural steelhead SAR, and did not provide analytical support for one ecological mechanism over another. A study of 15 populations of Oregon coastal coho salmon found a negative relationship between hatchery smolt releases and adult productivity (Buhle et al. 2009). However, this result is difficult to interpret as exclusively ecological because the authors' top models also included hatchery spawner density term, which might be due to genetic effects (see below). Scheuerell et al. (in review) found a negative statistical correlation between steelhead productivity (adult recruits per spawner) and steelhead hatchery releases in the Skagit River but did not evaluate ecological mechanisms. Lastly, and in contrast to the studies above documenting a negative relationship, Nelson et al. (2019b) found no relationship between the number of hatchery juvenile Chinook salmon released and adult recruits per spawner (productivity) of 20 Chinook salmon populations in Washington and British Columbia. By aggregating hatchery releases across three broad geographic regions (Strait of Georgia, Puget Sound and the Strait of Juan de Fuca), Nelson et al. (2019b) aimed to assess ecological interactions during early marine rearing.

Analyzing the abundance or proportion of hatchery-origin fish spawning naturally is another approach to empirical, population-scale studies of hatchery effects. Importantly, these studies often cannot separate ecological vs. genetic mechanisms because the hatchery metric tracks both ecological and reproductive contact. Kostow and Zhou (2006) found a negative relationship between natural productivity of Clackamas River (OR) winter steelhead and the abunance of hatchery-origin summer steelhead spawners. They concluded that the hatchery spawners caused the combined hatchery plus natural population to regularly exceed carrying capacity leading to ecological competition between hatchery and natural fish. They dismissed genetic effects because empirical genetic data indicated minimal interbreeding between the hatchery and natural populations. However, using an updated Clackamas dataset, a different model, and comparisons to neighboring populations, Courter et al (2019) subsequently contradicted the results and interpretation of Kostow and Zhou (2006, further discussion below). Buhle (2009) found that the density of hatchery-origin fish spawning naturally was negative related to adult productivity in 15 populations of Oregon coastal coho salmon. Similarly, Chilcote et al. (2011; 2013) found that the proportion of hatchery-origin fish in naturally spawning populations was negatively correlated to the intrinsic productivity parameter of the stock-recruit curve across 93 populations of naturally spawning Chinook salmon, coho salmon and steelhead from Washington, Oregon and Idaho. However, both Buhle (2009) and Chilcote (2011) evaluated the productivity of mixed hatchery plus natural spawning populations, and thus neither study can separate poor performance of hatchery fish (low fitness) from a reduction in natural-origin performance caused by genetic or ecological impacts of hatchery fish.

Lister (2013) used a unique study design to separate two different hypotheses: the hatchery-origin fish reduce natural-origin productivity versus hatchery-origin fish perform poorly in the natural environment. He found that natural-origin productivity was no different between three mixed hatchery-origin plus natural-origin spawning populations and three paired, geographically proximate reference populations composed of exclusively natural-origin spawners. The authors thus concluded that the presence of hatchery spawners did not reduce the productivity of natural-origin spawners. Interestingly, however, the hatchery fish only contributed substantially to returning adult recruitment in the population that was well below carrying capacity; they did not contribute to adult recruitment in two populations that were at or above carrying capacity.

Courter et al.'s (2019) results, in particular the direct contradiction to the earlier results of Kostow and Zhou (2006), illustrate an important point regarding assessment of population data for ecological hatchery impacts. The retrospective, empirical population data approach is subject to serial autocorrelation and the difficulty of measuring annual environmental (non-hatchery) changes in complex ecosystems. Courter et al. (2019) suggest that poor ocean survival conditions during the period of hatchery build-up and maximum hatchery production went undetected by Kostow and Zhou (2006), leading to the erroneous conclusion that hatchery fish caused the declines in natural-origin productivity. In Alaska, the opposite phenomenon was observed: production of hatchery pink salmon increased dramatically during a period of favorable ocean conditions, leading to an overall increase in fishery catch, contributing to the uncertainty regarding the value or success of hatchery production (Amoroso et al. 2017). In both cases, it is difficult to separate hatchery management from climate-scale environmental factors governing natural production because both tend to change slowly over time, limiting contrast among years.

Given these challenges, large-scale manipulative experiments assessing abrupt changes in hatchery management are crucial to understanding hatchery impacts. Notably, Jones et al. (2018) reported increased natural-origin abundance and diversified spawn timing in a coastal Oregon coho salmon population two generations after the termination of coho salmon hatchery releases. Put simply, population- or landscape-level experiments are essential to advance understanding of hatchery-wild interactions and realized impacts of hatchery programs.

Our review of ecological risks of hatcheries highlights important trade-offs according to the spatial scale of study design (Figure 1). Whereas small-scale, experimental studies can precisely describe hatchery or density effects and isolate biological processes, they are not readily scaled up to understanding how hatchery production affects the survival, productivity or abunance of natural populations. Conversely, whereas population-scale retrospective studies measure response variables of utmost importance to popualtion viability, definitively isolating hatchery effects from other biological or physical processes using statistical correlation has proven challenging (Figure 2).

Overall, despite difficulties interpreting mechanisms, empirical population scale studies point to the importance of density dependence for understanding mechanisms of hatchery-natural ecological interactions. For populations targeted for recovery, we suggest a need for rigorous evaluation of density dependent constraints on natural productivity in determining the size of hatchery programs, for both conservation and harvest purposes. Hatchery programs that regularly caused the combined hatchery and natural population to exceed carrying capacity are likely to lead to ecological competition with natural popuations. Importantly, habitat capacity constraints can fluctuate over time, especially in marine environments. Even less is understood about how hatchery releases affect predation on natural populations.

HATCHERY REFORM

Here we evaluate the widespread, institutionalized changes to hatchery programs, informed by scientific research, that are intended to reduce the risks and maintain or increase the benefits of hatchery production. We review hatchery reform actions and the rationale behind them. We further aim to assess the hatchery reform efficacy by evaluating the scientific evidence supporting each action. Empirical assessments of hatchery reform actions are rare, thus, our evaluation of hatchery reform effectiveness probes the periphery of current understanding and largely addresses concepts rather than case studies.

Since the early 2000s, "hatchery reform" has become largely synonymous with work of Hatchery Scientific Review Group (HSRG). Supported by federal actions and funding, the goal of the HSRG is to promote conservation and sustainable fisheries while mitigating risks of hatchery production. The HSRG is the primary, perhaps only entity providing guidance for operating hatcheries in a scientifically defensible manner, and their principles and recommendations were the foundation of WDFW programmatic reforms adopted in 2009 (Commission Policy C-3169). Within the scope of our review, the core, specific actionable HSRG recommendations adopted by WDFW largely addressed goal setting (biological significance and stages of recovery), broodstock management and informing hatchery program size via the All-H Analyzer model. For the most part, but not exclusively, these actionable recommendations focus on reducing genetic risk to natural populations (HSRG 2014).

However, our broader definition of hatchery reform also includes changes that were not necessarily specific recommendations of HSRG for widespread implementation (Table 1). In many cases, changes to practices such as rearing strategies, release strategies and disease management may be reflective of the long-term (decades) evolution of hatchery practices rather than more recent hatchery reform efforts *sensu* HSRG. These actions are likely consistent with HSRG general principles but often not specific HSRG recommendations per se. In some cases, these changes were likely motivated by improving hatchery efficiency, and not necessarily reducing risk to wild populations.

Our review evaluates the institutionalized reforms stemming from HSRG recommendations and a select number of broader changes associated with evolution of hatchery practices. We begin by addressing broodstock management, including setting biological significance goals and identifying phases of recovery, because these topics are core components of HSRG recommendations. We then address hatchery program size, a topic that is intertwined with all aspects of hatchery reform. We subsequently review rearing strategies, release strategies, mass marking, disease management, and adaptive management.

Broodstock management – reducing the risk of fitness loss from domestication

Broodstock management to mitigate for the potential negative effects of hatchery fish on wild salmon and steelhead populations is not a recent idea, and is not a management concept that originated with the HSRG (2014[1]). Over the past 40 years, publications (e.g., Reisenbichler and McIntyre (1977), Allendorf and Ryman (1987), Hutchings (1991), Ryman and Laikre (1991), Waples (1991), Cuenco et al. (1993), and Busack and Currens (1995)) have

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[1] Since 2004 the Hatchery Science Review Group (HSRG) has issued a series of detailed reports and two publications (Mobrand et al. 2005; Paquet et al. 2011). A large portion of this extensive work is summarized in the HSRG (2014; October 2014 update) report. For simplicity, we will limit our HSRG citation to this document, unless we are highlighting work that appears specifically in other documents.

included recommendations to manage hatchery environments, broodstock, and natural escapement, with respect to the rebuilding or maintaining the viability of wild populations. Many of these publications have highlighted the need to reduce the selective differences between the hatchery and wild environments; control the numbers of hatchery fish that spawn in the wild; incorporate wild fish as broodstock; maintain molecular diversity; or design monitoring programs. Overall, genetic risks posed by hatchery populations on wild populations include (1) among-population genetic diversity; (2) within-population genetic diversity; and (3) within-individual genetic diversity or relative fitness of individuals (Busack and Currens 1995; Waples et al. 2016). One goal of hatchery reform is to maintain adaptive genetic diversity to support diverse life history "portfolios" (sensu Schindler et al. 2010). Broodstock and escapement management are a set of tools that are designed to achieve that goal.

HSRG broodstock management guidelines

Since the early 2000s, the HSRG has provided focused work on hatchery reform by aggregating and summarizing the scientific literature, developing tools for managers to achieve hatchery reform, and by recommending management actions for hundreds of hatchery programs (HSRG 2009a; HSRG 2014 and HSRG references therein). Although broodstock and escapement management did not originate with the HSRG, and the HSRG described many other actions in addition to those related to relative fitness of hatchery and wild populations, the HSRG perspective on broodstock and escapement management has become institutionalized (e.g., WDFW Policy C-3619) and synonymous with "hatchery reform." Indeed, the HSRG website address is http://hatcheryreform.us/. Currently, broodstock and escapement management in Washington is based on the philosophy, guidelines, and recommendations of the HSRG, and at the core of the genetic components of the HSRG's "Standards and Principles" (HSRG 2014) is the model developed by Ford (2002).

Ford (2002) modeled mean relative fitness of a wild population affected by a hatchery population based on these parameters: (1) the optimal phenotypic trait values for the hatchery and wild environments, respectively, (2) phenotypic trait variance, (3) the width of the hatchery and wild fitness curves, (4) heritability of the trait, and (5) two gene flow parameters, (5a) the proportion of hatchery or broodstock spawners that are of natural-origin, and (5b) the proportion of natural spawners that are of hatchery origin. The HSRG termed parameters 5a and 5b above as pNOB (proportion of natural-origin broodstock; Equation 1) and pHOS (proportion of hatchery-origin spawners), respectively. HSRG described two forms of pHOS, one based on relative counts of hatchery-origin spawners and natural-origin spawners ($pHOS_{census}$ Equation 2), and the other where the number of hatchery-origin spawners is modified to reflect their average relative reproductive success compared with natural-origin spawners ($pHOS_{effective}$ Equation 3).

$$pNOB = \frac{NOB}{NOB + HOB} \qquad \text{Equation 1}$$

$$pHOS_{census} = \frac{HOS}{HOS + NOS} \qquad \text{Equation 2}$$

$$pHOS_{effective} = \frac{(RRS \times HOS)}{((RRS \times HOS) + NOS)}, \qquad \text{Equation 3}$$

With NOB being the natural-origin fish in the broodstock, HOB the number of hatchery-origin fish in the broodstock, HOS the number of hatchery-origin fish spawning naturally, NOS the number of natural origin fish spawning naturally, and RRS the relative reproductive success. Hatchery-origin RRS is scaled relative to natural-origin spawners, whose RRS value is, by definition, set to one. The RRS value used in Equation 3 is either defined empirically or those values established by HSRG (2014). All RRS values recommended by HSRG are less than one (i.e., hatchery-origin spawners' reproductive success is less than that natural-origin spawners), and the default value for coho and Chinook was set by HSRG (2014) at 0.80.

HSRG summarized the collective effects of pHOS and pNOB in a single statistic, Proportionate Natural Influence (PNI), defined as:

$$PNI = \frac{pNOB}{pNOB + pHOS}\text{[2]} \qquad \text{Equation 4}$$

Equation 4 is an approximation of two more-complicated equations that describe the genetic influence of the natural environment on the mean phenotypic values of wild and hatchery populations, respectively (HSRG 2009b). Equation 4 estimates the genetic risks across all phenotypes of a hatchery population to a wild population when the two populations are managed as a single entity (i.e., integrated hatchery program; see below), and where there is designed gene flow from the wild into the hatchery (pNOB) and from the hatchery into the wild (pHOS). PNI has become the primary metric and management goal for integrated hatchery programs (HSRG 2014).

The HSRG considered three integral parts of broodstock and escapement management (HSRG 2014) to manage gene flow from hatchery production into wild populations, and to

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[2] HSRG uses effective pHOS when calculating PNI. Our understanding is that the models in Ford (2002) already account for RRS (i.e., differences in the optimal phenotypes between hatchery- and natural-origin fish, and the strength of selection parameters). We consider it incorrect to use effective pHOS with the models in Ford (2002), and unless otherwise noted, we use census pHOS when discussing both pHOS and PNI.

determine target values for pHOS and PNI: (1) the design of the hatchery program; (2) the designation of the wild populations affected by a hatchery program; and (3) the stages of recovery of the wild population. First, to manage a hatchery's influence on wild populations, the hatchery should be designed as either a segregated or integrated program. The intent of a segregated program is to establish two separate populations where both pHOS and pNOB are designed to be zero, and therefore gene flow between the hatchery and wild populations is limited. This has been attempted by selecting only hatchery-origin fish as broodstock (i.e., pNOB = 0), and limiting pHOS by temporally or spatially separating hatchery and wild populations and controlling straying of hatchery-origin adults into wild populations (HSRG 2014). An integrated program attempts a nearly opposite strategy than that of a segregated program; that is, to create a single population that exists in two different environments – hatchery and wild, and to balance migration between these two environments to achieve a specific PNI. Hatchery programs with a conservation goal typically employ integrated broodstock management. Indeed, 34 of the 35 (97 %) conservation hatchery programs operated by WDFW employ integrated broodstock management, whereas only 47 of 124 (38 %) WDFW harvest hatchery programs employ the integrated approach.

Second, HSRG considered different pHOS and PNI targets for populations based on the populations' "biological significance" (HSRG 2014:24) and relevance to recovery goals. HSRG does not provide recommendations as how a population is designated as Primary (first tier; foundation for salmon recovery and restored to high or very high viability), Contributing (second tier; improvement needed and targeted for medium viability), or Stabilizing (third tier; maintain at baseline levels when considered a very low viability); that decision is made during the recovery planning process and includes co-managers of the populations (e.g., federal agencies, tribes, and WDFW)[3]. However, HSRG applies different pHOS and PNI targets based on the designation, with targeting more stringent thresholds for Primary populations compared to Contributing populations. Stabilizing populations have no pHOS or PNI target values.

Third, HSRG (2014) identified four stages or phases of recovery: Preservation, Recolonization, Local Adaptation, and Full Restoration. These phases were developed during discussions concerning the recovery of Elwha River salmonid populations following the removal of two dams (HSRG 2012). The phases of recovery are based on the current status of the population with respect to its genetic composition, and its ability to maintain a viable population in the absence of a hatchery. The objective of the Preservation phase is to retain whatever genetic diversity may have existed in the wild population before its decline. It is assumed demographically that the natural spawning population cannot be sustained without migrants from the hatchery, and that the original habitat has been degraded and suitable habitat is limited. In the most extreme sense, the hatchery is necessary to prevent the extirpation of the local population, and assumes that the hatchery population retains the genetic diversity and identity from the original wild population. According to HSRG (2014), the recolonization phase is characterized by an increase in suitable habitat, and the phase's objective is to colonize the now "underutilized" habitat. The two remaining phases (Local Adaptation and Fully Recovered) involve increasing abundance of natural-origin spawners, ecological and genetic diversity, and average relative fitness, with the Full Restoration phase

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[3] To our knowledge, the Primary, Contributing, and Stabilizing designations were established by the Lower Columbia Fish Recovery Board, and first defined in Washington Lower Columbia Salmon Recovery and Fish & Wildlife Subbasin Plan (https://www.lcfrb.gen.wa.us/). See Definitions.

characterize by a fully functional and diverse wild population existing in a fully restored and protected habitat (HSRG 2014).

HSRG broodstock management targets

HSRG established their broodstock management targets in 2009 when they applied and refined their reform principles to Columbia River Basin salmonid hatchery programs (HSRG 2009a). These management targets were based, in part, on a detailed algebraic analysis of the Ford (2002) model (HSRG 2009b). HSRG established that $PNI = 0.50$ is a fundamental target because it is a line between greater hatchery ($PNI < 0.50$) versus greater natural ($PNI > 0.50$) influence on the entire integrated hatchery-wild population. To maintain at $PNI > 0.50$, HSRG (2009b) found that in integrated populations, pNOB becomes relatively inefficient when pHOS exceeds 0.30; therefore pHOS should not exceed 0.30. In segregated populations, where $pNOB \sim 0.00$, maintaining $PNI > 0.50$ would occur if $pHOS < 0.05$[4]. HSRG (2009a) parsed the findings of HSRG (2009b) into targets specific to Primary, Contributing, and Stabilizing populations. These targets are shown in Table 2; it is important to note here that although Table 2 includes the four phases of recovery discussed above, in 2009 HSRG had not yet established these four phases and HSRG (2009a) provided only one set of pHOS and PNI targets for Primary and Contributing populations.

Canada's Department of Fisheries and Oceans (DFO) reviewed HSRG principles, including pHOS and PNI target values, for their Chinook populations (Withler et al. 2018). Although DFO

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[4] HSRG (2009b) made this determination using the more complicated equations for PNI, not the approximation shown above as Equation 4.

adopted the HSRG approach to manage the potential genetic effects of hatchery production on their wild Chinook populations by making use of pNOB, pHOS, and PNI goals, they used a different set of population designations, emphasized Canada's Wild Salmon Policy definition of a "wild" fish (DFO 2005)[5], and established different target values for pHOS and PNI than those instituted by the HSRG (Table 3).

Overall, there is similarity between the HSRG and DFO target values for pHOS and PNI. Although DFO did not establish a segregated population designation, functionally, their Wild and Wild-Stray designations are the same as HSRG's segregated populations. That is, both sets of designations are intended to represent wild populations with minimum gene flow from hatchery populations. The DFO pHOS value for the Wild designation is more restrictive than the HSRG standard for pHOS for Primary populations, although HSRG stated that their "standard[s] for segregated populations may be *insufficient* to safeguard the long-term viability of the affected naturally spawning Primary and Contributing populations" (HSRG 2014:40, emphasis added).

The PNI and pHOS targets for the DFO Integrated-Wild, Integrated-Transition, and Integrated-Hatchery populations are roughly equivalent to the Primary, Contributing, and Stabilizing population designations, but with minor differences. The pHOS target for Integrated-Wild populations (pHOS = 0.28) is based on Canada's Wild Salmon Policy and differs slightly from HSRG's target for both Primary and Contributing populations (pHOS = 0.30)[6]. The

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[5] Canada's Wild Salmon Policy (WSP) defines a fish as wild if it and both parents were born in the natural environment (DFO 2005)

[6] DFO established a pHOS = 0.28 as the target value by assuming random mating a population composed of 28% hatchery- (H), that is, pHOS = 0.28, and therefore 72% natural-origin fish (N) would result in 52% NN pairing, 40% HN pairing, and 8% HH pairings. Offspring from all these pairing would be natural-origin, but only the 52% of the offspring (from the NN pairings) would be defined as wild based on Canada's definition of a wild fish (Withler et al.

other difference between DFO and HSRG's target values addresses Contributing and Integrated-Transition populations, where DFO set pHOS to be ≤ 0.50 and HSRG set pHOS to be < 0.30, although both DFO and HSRG set PNI to be > 0.50.

Establishing broodstock management targets are useful as they provide measurable objectives. However, quantitative approaches can establish different specific target values while attempting to accomplish the same goals; compare HSRG (2009b) with Withler et al. (2018). Although considerable thought and effort was made by both DFO and HSRG to establish their targets, these targets are subjective, and "may or may not be ultimately sufficiently protective to contribute to recovery of natural populations" (RIST 2009:75).

Integrating HSRG broodstock management targets into phases of recovery and relating targets to current status of Chinook populations

In 2014, HSRG (2014) generalized the description of the four phases of recovery, originally designed for the Elwha River (HSRG 2012), but did not associate pHOS and PNI target values with the phases until 2015 (HSRG 2015). However, they applied the target values only to populations in the Local Adaptation and Fully Restored phases, leaving populations in the Preservation and Recolonization phases without targets.

In reference to the Elwha River, HSRG (2012) stated that in the Preservation and Recolonization phases the populations would rely on hatchery-origin spawners (i.e., high pHOS). We understand the demographic need to maintain natural spawning when a depressed

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2018). A value of 0.28 is the largest pHOS that would ensure that the natural spawning population was composed of greater than 50% wild fish (NN pairings).

population is in the Preservation or Recolonization phase. However, if there is a large difference between the hatchery and wild environments, hatchery-origin natural spawners would have low fitness, generating relatively few natural-origin recruits. The longer a population relies on hatchery-origin spawners (i.e., the longer pHOS remains high), the higher the probability a population may be unable to generate natural-origin recruits, even when habitat is restored. If the ultimate goal for a population is to progress from the Preservation and Recolonization phases to the Local Adaptation and Full Restoration phases, pHOS should also be limited to some extent during the Preservation phase, and especially the Recolonization phase. In other words, during the Preservation or Recolonization phases, an appropriate balance is needed between the demographic and fitness needs of the naturally spawning population.

We reviewed current designations and recovery phases for 24 Chinook integrated hatchery programs operated by WDFW, and found relatively little difference in broodstock management metrics of conservation vs. harvest hatchery programs. Our review evaluated if these programs met HSRG targets when considering or not considering the phases of recovery (Table 4). Of the 24 programs, 15 (63%) are associated with natural populations designated as Primary, five as Contributing and four as Stabilizing. Most of the programs associated with Primary populations (N = 9) are intended for Conservation, and are in either the Preservation (N = 7) or Recolonization (N = 2) phase, which means that there are no pHOS, pNOB, or PNI targets. The mean pHOS for these populations is 0.61, and one program (Kendall Creek) has a PNI = 0.0, indicating that the entire integrated population has no natural influence. The remaining six Primary populations, either in the Local Adaptation or Fully Restored phase, all are associated with harvest hatcheries, and only two programs (Eastbank – Dryden Pond summer Chinook; Priest Rapids) are meeting HSRG targets (Table 4). The pHOS for the Eastbank-Dryden (pHOS = 0.06) and Priest Rapids (pHOS = 0.08) populations compare with a mean pHOS = 0.53 for the other four Primary populations with Harvest hatchery programs, very similar to those Primary populations in the Preservation/Recolonization phase with Conservation hatcheries. In fact, the broodstock and escapement management profile for the Primary Conservation and Primary Harvest populations are very similar – mean PNIs = 0.43 and 0.51, respectively.

If the recovery phase is removed from consideration for both the Primary and Contributing programs and one applies the appropriate HSRG targets to all programs, regardless of recovery phase, only six of the 20 programs (30%) meet HSRG pHOS and PNI targets (Table 4). Of these, four of the six spawned the fewest broodstock among all programs examined, and the other two programs (Dryden, Priest Rapids) have very small ratios of broodstock to escapement abundance (B/E < 0.10) compared to most hatchery programs examined (Table 4). In fact, six of the eight programs with the smallest broodstock to escapement ratio are the six programs that meet the HSRG pHOS and PNI targets (Table 4), including a large hatchery program (Priest Rapids) paired with a very abundant natural population (Hanford Reach). These data strongly suggest that in addition to pHOS and PNI, an appropriately sized hatchery program is critical for ensuring that fitness in the natural environment is sustained in the integrated hatchery-wild population.

Genetic models informing broodstock management

Models have been developed to estimate the genetic risks of releasing captive-breed individuals to supplement wild populations, and many of these models have either focused on or included salmonids (Waples and Do 1994; Lynch and O'Hely 2001; Tufto 2001; Ford 2002; Theodorou and Couvet 2004; Goodman 2005; Baskett and Waples 2013). Although these models may differ in their theoretical basis, mathematical construction, parameters, and assumptions, they all suggest that gene flow from the hatchery population will have negative effects on the average fitness or genetic diversity of the wild populations, despite the potential for a short-term demographic benefit.

It is beyond the scope of this review to include descriptions and comparisons of all models that are relevant to the supplementation of salmonid populations, but in this section we will provide a more detailed look at the Ford (2002) model, because of its relevance to hatchery reform practices, and to help evaluate the efficacy of HSRG broodstock and escapement management principles, and the pHOS and PNI targets. We will also provide here a brief discussion of the Baskett and Waples (2013) model, as a comparison to Ford (2002) model.

Ford model- The complete Ford model (Ford 2002) is a relatively simple deterministic model divided into two parts: (1) a phenotypic model focused on hatchery and wild phenotypes and their related genetic fitness effects, making use of six parameters, discussed above in a previous section, and (2) a demographic model that adds hatchery and wild population sizes, carrying capacities, and growth rates to elements of the phenotypic model.

Since the HSRG (2014) used only the phenotypic model of Ford (2002), we will focus on that model here, and explore the relationships among pHOS, pNOB, PNI and fitness, as they relate to HSRG broodstock and escapement management principles and targets. In using the Ford model as a tool, either directly or as part of an application such as the AHA model (HSRG 2017), hatchery managers estimate the relative fitness cost to the wild population associated with specific pHOS, pNOB, and PNI regimes. Although management actions are specific to pHOS and pNOB, when making management decisions based on the model, and in the absence of empirical data, managers make assumptions about: selection strength (weak versus strong); differences in fitness associated with hatchery and wild phenotypic trait optima (optima near versus far apart); and heritability of that phenotypic trait (small versus large portion of the phenotypic variance attributed to additive genetic variance).

Depending on model assumptions, the fitness loss in the wild population can range from being negligible to extreme, and there is considerable variability in fitness loss associated with selection strength and trait optima differences given a range of pHOS and pNOB values and heritabilities. For example, Figure 3 shows the change in the mean relative fitness of fish in the wild environment through 20 generations for different levels of "hatchery effect"[7]. In all cases, mean relative fitness declines with time, although in some cases that decline can be negligible (Figure 3, upper left). As the hatchery effect increases, mean relative fitness declines, and the magnitude of that decline is related to pHOS, pNOB, and PNI. Although mean relative fitness responds to changes in PNI, the magnitude of that response is more sensitive to changes in pHOS than it is in pNOB. In Figure 3, we provide four different pHOS – pNOB combinations,

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[7] Combination of selection strength and optimal phenotype difference, defined in Appendix 2.

with PNIs equal to 0.11, 0.50, 0.50, and 0.89, respectively. As expected, with a PNI = 0.11 (pHOS = 0.8 and pNOB = 0.1) the magnitude of the mean fitness decline is the largest. Increasing pNOB to 0.8, keeping pHOS fixed at 0.8 (PNI = 0.5), results in a fitness benefit – an increase in mean relative fitness, compared with the PNI = 0.11 curve. However, you get a larger fitness benefit – an even larger increase in mean relative fitness, when you decrease pHOS to 0.1 while keeping pNOB = 0.1, also resulting in a PNI = 0.5. That is, although in both scenarios PNI = 0.5, there is larger fitness benefit when you decrease pHOS than when you increase pNOB, although you get the largest fitness benefit when you do both (Figure 3).

Given the range of potential mean relative fitness associated with different hatchery effects (Appendix 2) and heritabilities (heritability data not shown), comparing different pHOS and pNOB broodstock management combinations is cumbersome. However, using the Ford model, change in fitness is log-linear across the range of parameter values (Craig Busack, personal communication 2019). This means that you can directly compare different broodstock and escapement management options across parameter space, to determine which management option provides the lowest risk of fitness loss to the wild population. This technique has the potential to help hatchery managers decide between competing management options, without needing to make assumptions about selection strength, optimal phenotype differences, or heritabilities. Although this technique can be used to compare any combination of management options; we limited this comparison here to assess the relative fitness effects resulting from decreasing pHOS versus increasing pNOB across, across a broad range of parameter values (Appendix 3). The results from this analysis is consistent with but generalizes the results summarized above and with Figure 3: decreasing pHOS provides greater fitness gain than increasing pNOB, regardless of selection strength, optimal phenotype differences, and heritabilities.

Finally, the mean relative fitness associated with HSRG's Primary and Contributing population pHOS and PNI target values (Table 2) is a function of all the parameters of the Ford (2002) model. In presenting the long-term fitness effects of specific pHOS and PNI values HSRG (2014: Table 3-2) stated that they were assuming "high heritability, strong selection, equal phenotypic variance, and differing phenotypic optima for the natural and hatchery population" (HSRG 2014: 38). Figure 4 shows the fitness consequences of different hatchery effects on the HSRG Primary and Contributing population targets, keeping constant heritability (0.3). The prediction of more favorable consequences of the Primary population targets, compared with those of the Contributing population targets, depends on the hatchery effects. For each hatchery effect the Primary population targets always result in higher mean relative fitness, as expected. However, a Contributing population managed under HSRG standards operating in an environment with a moderate-large hatchery effect, for example, will have higher fitness than a Primary population managed under HSRG standards operating in an environment with a large hatchery effect.

The set of analyses discussed in the section do not suggest any particular set of pHOS or PNI target values, nor do they imply that the Ford model can be used to select a set of target values. Instead, the Ford model is a heuristic tool, and our application of the tool supports the idea that decreasing pHOS and increasing pNOB provide fitness benefits to wild populations. Furthermore, we also find that decreasing pHOS provides greater fitness benefit than decreasing pNOB, regardless of hatchery effect or heritability, but, doing both provides the most fitness benefit. These results are wholly consistent with nearly two decades of work by the HSRG (2014, 2015).

Ford (2002) -based demographic model – The Ford (2002) phenotypic model provides an estimate of wild fitness loss as a result of hatchery-wild interactions. Understanding fitness loss is an important component to assessing the risk of hatchery programs to wild populations. A more complete understanding of that risk would include how hatchery programs affect the size and recruitment of wild populations. Although Ford (2002) provided a demographic model, as discussed above, we applied an implementation of that model, based on Busack (2019, unpublished R-script), and used that model to assess how pHOS, pNOB, and broodstock size affects the abundance and fitness of the wild population. This demographic model is an extension of the Ford phenotypic model, where the wild and hatchery fitness values, following each iteration (generation) of the model, are used as parameters in population recruit functions. The technical details of our model, as well our application of the model, are in Appendix 4. Here we present a brief discussion of the results and how these results could be interpreted in terms of hatchery reform.

As with the Ford phenotypic model, this demographic model should not be used directly to design management actions, nor should it be used to make predictions about the future state of a population. However, given a set of assumptions and model parameters, the model suggests that: (1) managing an integrated hatchery population with relatively high pHOS and low pNOB can result in a situation similar to that of the Kendall Creek hatchery and the NF Nooksack spring Chinook population today – a natural spawning population dominated by hatchery-origin spawners, low natural recruitment and fitness, and a domesticated hatchery population with high fitness in the hatchery, but near zero fitness in the wild; (2) it is difficult to reverse the situation described in #1, but if possible, given the caveats described in Appendix 4, it would require a decrease in hatchery production and an extremely low pHOS; (3) increasing pNOB may provide a demographic boost to the natural spawning population, but increasing pNOB may be constrained if recruitment from the natural spawning population is low, and high pNOB may decrease recruitment from the hatchery population by decreasing hatchery fitness; (4) an initial demographic boost may result following the establishment of the hatchery, but in both examples discussed in Appendix 4 (Figures A4-1, A4-2) the boost was short in duration; and (5) as with the Ford phenotypic model, the demographic model suggests that reducing pHOS produces greater natural recruitment, recruit per spawner, and wild fitness than increasing pNOB (Appendix Figure A4-3).

Baskett and Waples model – The Baskett and Waples (2013) model (henceforth, the BW model) differs in several respects from the Ford models, including our demographic implementation of the Ford Model. The BW model makes use of the full salmonid life cycle, including reproduction; hatchery release; density dependent mortality during outmigration; ocean survivorship and harvest; return migration survivorship; hatchery and natural selection; and the genetic component of the model allows for mutation and change in genetic variance. The model does not track whether an individual selected for broodstock is of hatchery- or natural-origin (i.e., it does not include pNOB as a parameter), but all adult individuals not selected for broodstock spawn in the wild, and pHOS is included as a parameter. However, the model does include the percent of fish that are removed from the wild for broodstock, a parameter not included in the Ford demographic model, but is included in our demographic model, is considered in the Withler et al. (2018) treatment of the HSRG approach to hatchery reform, and is also included in effective population size models relevant to hatchery supplementation (e.g., Ryman and Laikre 1991; Waples et al. 2016). As with the Ford model, the BW model assumes a single but separate fitness optima for hatchery and wild environments, but unlike the Ford model, the BW model includes assortative mating based on similarities in the trait under selection. That is, the model uses a single trait for both mating and for fitness.

The BW model shows that the effects of hatchery supplementation on wild fitness and demographics depends on when during the life cycle selection and density dependent mortality occur. If selection in the hatchery occurs after spawning, but before the juvenile fish are released into the natural environment (i.e., in the hatchery), when those fish return as adults and are not used as broodstock, they have the potential to stray and have a negative effect on the wild population because their fitness in the wild is less than that of the wild population. However, if selection is weak, the fitness in the wild population stays high, wild population size increases relative to baseline, and pHOS remains low (Baskett and Waples 2013). But, as trait optima differences between the hatchery and wild environments increases (i.e., larger hatchery effect, as described for the Ford model in Appendix 2), the fitness and size of the wild population declines, and pHOS increases to the point where there are no natural-origin fish that spawn naturally. These results are similar to the fitness results from the Ford model (Figure 3).

If selection occurs after release, just before or at reproduction when the fish return as adults, for large or small trait optima differences (large or small hatchery effect), the fitness of the wild population remains high, either because there is little fitness difference between the hatchery- and natural-origin spawners (small hatchery effect), or if there is a large hatchery effect, the hatchery-origin fish are maladapted to the wild environment, and die before reproduction or otherwise don't reproduce. Hatchery supplementation may provide a boost to population size if there are no large density dependent effects during outmigration, and if there is weak selection. However, wild fitness declines, pHOS increases, and population size declines below baseline if there is a moderate hatchery effect, resulting in natural spawning of hatchery-origin fish with lower fitness.

By their nature, hatchery environments are different from the wild environment, and rarely are hatcheries designed to resemble the wild environment. However, if hatcheries are too different than the wild environment, hatchery managers risk producing fish that are too maladapted to the wild environment resulting in an insufficient number of fish that survive for fisheries and for broodstock. Therefore, it is likely that in most hatcheries, the differences in hatchery and wild trait optima may be somewhere in that intermediate zone, where there are risks to the wild population, if pHOS cannot be controlled, regardless of when selections occurs relative to reproduction.

The BW model is useful in that it identifies parameters that may be most important in understanding when and how a hatchery program may negatively affect the demographics and fitness of wild populations. However, the mathematical foundation of the model is complicated, and currently there are no applications or scripts available to critically evaluate the model. Finally, pNOB is an important component when managing the risks of hatchery programs on wild populations. An application or script of the BW model that includes pNOB would be advantageous.

Controlling pHOS

The ability to control pHOS via removal of hatchery-origin fish is a fundamental, essential requirement of effective broodstock management. Here we review the tools commonly used to control pHOS.

Weirs, or channel-spanning (often temporary) structures used to capture adult salmonids during their upstream migration, are a potential tool for controlling pHOS. The ability to control pHOS via weirs is dependent on their catch efficiency. Within Washington, examples of low capture efficiency from Forks Creek (Seamons et al. 2012), the Elwha River (Anderson et al. 2015), and the Nisqually River (Nisqually Chinook Work Group 2017) suggest weirs are extremely difficult to implement effectively, especially on larger rivers and for species that often spawn during periods of high river flow. Weirs are a major component of efforts to control pHOS in the Lower Columbia River region. Across six Lower Columbia tributaries, Wilson et al (2019) reported that the ability to reduce Chinook salmon pHOS varied by river system, ranging from a 35-48% reduction in the Kalama River, to a 1-12% reduction in the Grays River (Wilson et al. 2019). Despite trends toward lower pHOS values, most rivers were not meeting pHOS goals due to a host of factors including low weir catch efficiency, spawning below weir sites, and unmarked hatchery-origin fish (Wilson et al. 2019). The Lower Columbia assessment also noted unintended, negative impacts of weirs including delayed migration and a downstream shift in spawning distribution (Wilson et al. 2019). In contrast to the above cases, weirs deployed on four small tributaries of the Snake River in southeastern Washington were fairly effective at removing hatchery-origin fish, as most annual estimates of pHOS across multiple years were < 5% (Herr et al. 2019).

Thus, the overall picture is that the effectiveness of weirs at controlling pHOS is highly dependent on river conditions, site specifics and operational details. Despite apparent successes in SE Washington, most examples from Washington failed to achieve project goals and weirs have not proven consistently effective at controlling pHOS at a widespread scale. Weirs are labor, equipment, and cost intensive; the difficulty of implementation scales with river size and discharge variability. While it may be possible to control pHOS in some creeks or smaller rivers with weirs, success depends on a significant investment in design, engineering, and operational expertise. Should weirs occupy an essential role in hatchery reform, a critical review of design features and river conditions affecting catch efficiency is warranted.

Dams are another potential means for removing hatchery-origin fish to control pHOS, likely with a higher efficiency compared to temporary weirs due to structural permanency. However, depending on size and structure, dams present their own challenges, notably designing effective fishways or infrastructure for trapping and hauling fish, as well as altering the quality and quantity of salmon habitat. Ineffective trapping facilities at dams can lead to migration delay and a redistribution of spawners to more downstream locations (Murauskas et al. 2014). Similar to weirs, the potential for dams to control pHOS is highly context dependent, contingent on an effective trapping design, and a location where removal of hatchery-origin fish meets management objectives.

Mark-selective fisheries are another tool for controlling pHOS. Mark-selective fisheries can clearly create a higher exploitation rate on marked compared to unmarked fish (Figure 1). However, we could not find any quantitative assessment of the ability of mark-selective fisheries to control pHOS on the spawning grounds. We suggest that a robust evaluation of the extent and context in which mark-selective fisheries can effectively reduce pHOS is a significant informational need to advance hatchery reform.

A final option for controlling pHOS is reducing program size, or the number of juvenile hatchery fish released. We address program size in greater detail below.

Broodstock and escapement management – within population genetic diversity

The degree to which within or among population diversity is lost depends to some degree on how the hatchery program is conducted. Depending on broodstock management approach (i.e., integrated vs. segregated), spawner number (i.e., program size), mating scheme, and other program protocols, hatchery programs may have large or small effects on genetic diversity, or, under some conditions, diversity may be unaffected or even increase (e.g., Berejikian and Van Doornik 2018). Recognizing this, HSRG (2004) made recommendations for broad changes to hatchery program protocols to minimize these risks.

In order to reduce the risk of inbreeding and maximize N_e, the HSRG (2004) recommended that all hatchery programs use single family pairing (one male spawned with one female) or factorial mating (systematically spawning multiple males with multiple females) spawning protocols and to avoid selective breeding (HSRG 2004). These broad strategies encompass many more specific spawning protocols used to achieve the goal of maintaining genetic diversity (Fisch et al. 2015). To our knowledge, all WDFW salmon and steelhead programs currently employ single family pairing, factorial mating spawning designs, or one of the more complex strategies described in Fisch et al. (2015). However, systematic monitoring of hatchery programs has not occurred, so the success of these changes in maintaining levels of genetic diversity is unknown.

Broodstock management and program size will also affect within population genetic diversity. In perhaps the best available comparison of integrated and segregated hatchery management strategies, Waters et al. (2015) showed in Yakima River spring Chinook salmon that effective number of breeders (N_b, an N_e analogue) was higher in the integrated hatchery line than the segregated hatchery line. Furthermore, because large populations tend to retain more genetic diversity than small populations (Allendorf et al. 2013), it follows that hatchery programs spawning a larger number of fish will tend to conserve more genetic diversity than a hatchery program spawning fewer fish. Thus, the risk of losing within population genetic diversity is perhaps the only hatchery risk (ecological or genetic) that is reduced as hatchery program size increases. Hatchery managers can also maximize retention of genetic diversity by taking steps to equalize family sizes and minimizing the number of generations of hatchery propagation (Fisch et al. 2015).

Program size

Hatchery program size or release number refers to the total number of juvenile fish released from the hatchery on an annual basis. Release number, which in turn will regulate the number of returning adult hatchery-origin fish, is the hatchery program attribute that has single greatest influence on determining genetic and ecological risks posed to natural populations. For most hatchery risks, larger hatchery programs releasing more fish will confer greater risks than smaller ones. Some hatchery risks can be expressed as proportions (e.g., pHOS), and as program size increases, the absolute number of hatchery-origin fish posing risks to natural populations increases, amplifying impacts. For example, notwithstanding integrated conservation hatchery programs, hatchery-origin fish straying to the natural spawning grounds presents genetic risks to the natural population; for a given stray rate, as hatchery program size increases, the total number of hatchery-origin strays also increases. Here we review some general patterns of hatchery program size and the analytical tools used to determine hatchery program size.

Trends in total releases give some perspective on the scale of total hatchery production, if not the size of individual hatchery programs (Figure 5). Chinook and coho salmon production has been dominated by releases into the Washington portion of the Salish Sea (Hood Canal, Strait of Juan de Fuca and Puget Sound) and Columbia River, with much smaller release numbers into the Washington coast. Chinook salmon hatchery production generally increased through the 1970s, peaked in the late 1980s (200-250 million), and subsequently declined (currently approximately 170 million; Figure 5). Hatchery production of coho salmon has always been lower than Chinook salmon, it peaked earlier in time (early 1980s, > 100 million), and it has also declined more than Chinook salmon production (approximately 35 million currently, Figure 5). We suspect that the declines in Chinook and coho hatchery production were due to a combination of budget cuts, reductions in program size and a trend towards releasing larger sized fish. Steelhead hatchery releases (approximately 15 million currently) are much lower than either coho or Chinook salmon, are dominated numerically by the Columbia River and have remained relatively stable, with only modest declines from the late 1980s to present (Figure 5).

In general, hatchery programs intended for conservation tend to release fewer fish than hatchery programs intended to provide harvest opportunities. Indeed, among 24 WDFW Chinook salmon hatchery programs described by Table 4, the median conservation program size is 212,500 juveniles, much smaller than the median harvest program size of 1,750,000 juveniles. Studies of relatively small hatchery programs have demonstrated conservation benefits and no or minimal genetic risks. For example, Berejikian and Van Doornik's (2018) study released < 3,250 juvenile and < 250 adult hatchery-reared steelhead annually, whereas Janowitz-Koch et al.'s (2019) study spawned ≤40 pairs of adult Chinook salmon annually. One would expect greater risks for harvest enhancement programs that often spawn and release an order of magnitude or more fish than these conservation programs but they have received less attention in the literature regarding risk assessment. Evaluating risks posed by larger programs (e.g., Fast et al. 2015) is logistically more challenging but important to understand how genetic and ecological impacts scale with program size, as well as hatchery spawning and rearing protocols.

Determining hatchery program size to meet conservation objectives is a critical aspect for both conservation programs and harvest programs, and several analytical tools are available. The "All H Analyzer" or AHA model (HSRG 2017) is the analytical tool with the most widespread application for informing program size. AHA models reproductive exchange among a natural population and associated hatchery population, using the Ford (2002) model to predict fitness reductions in the natural population. Natural population dynamics follow a Beverton-Holt productivity model, thereby accounting for density-dependent capacity constraints of the natural habitat. The model permits fairly detailed demographic accounting of broodstock management, natural and hatchery harvest rates, straying, and hatchery survival. A roll-up function allows assessment of multiple populations simultaneously. Overall, the intent of the model is to allow users to explore various management scenarios and in achieving harvest and conservation objectives.

Previous review of AHA emphasized its limitations for fine-tuning hatchery management strategies (RIST 2009). More specifically, “the AHA model is useful as a heuristic tool for exploring a broad range of scenarios, but should not be used to quantitatively predict the outcomes of specific management alternatives” (RIST 2009). This guidance arose from uncertainty surrounding the Ford (2002) model approach for the fitness function and a lack of available population data, precluding “confident parameterization” (RIST 2009). Furthermore, AHA only addresses genetic fitness risks, it does not model or assess ecological risks of hatchery production (HSRG 2017). These observations indicate that AHA lacks the predictive precision needed for a hatchery program-by-program determination of release number in order to keep hatchery impacts on natural populations within acceptable limits.

A model of gene flow and empirical assessment of proportion effective hatchery contribution (PEHC) were used to assess genetic risks and justify program size of segregated early winter hatchery steelhead programs in Puget Sound. These approaches were employed because the species’ iteroparous life history precludes examination of hatchery marks on post-spawned carcasses as a means of tracking demographic exchange between hatchery and natural populations. The gene flow model examines temporal overlap in spawn timing between the hatchery and natural population, using release number and assumptions of hatchery stray rates and survival, to estimate the rate at which hatchery-origin steelhead spawn with natural-origin steelhead (Hoffmann 2017). The empirical PEHC estimate examined levels of hatchery-natural introgressive hybridization in watersheds with known steelhead hatchery release histories (Warheit 2014); some hatchery programs were subsequently reduced in size or eliminated to meet conservation objectives based in part on the empirical PEHC estimates.

Pearsons and Busack (2012) developed the Predation, Competition, and Disease (PCD) Risk 1 model to assess ecological risks according to a host of factors, including hatchery release number. The individual-based model predicts the outcomes of hatchery-natural encounters, tracking mortality rates of the natural-origin fish due to direct predation by hatchery-origin fish, starvation due to competition with hatchery-origin fish, and disease transfer from hatchery-origin fish. The model is fairly detailed in its bioenergetics assessment of competition and predation; some input parameters are readily measured and more or less under the control of hatchery managers (release number, size of fish released), whereas other parameters are abstractions that are not directly quantified in most monitoring programs (hatchery-natural encounter rate). PCD addresses competition and direct predation by hatchery fish occurring in freshwater; it excludes estuary, nearshore marine, and ocean habitats and indirect predation effects. Its value is as a heuristic tool, not a comprehensive quantification of hatchery impacts (Pearsons and Busack 2012), similar to AHA.

Given the outsized importance of hatchery program size for conferring both ecological and genetic risks, we suggest a rigorous justification for program size is essential for implementing scientifically defensible hatchery programs. Some analytical tools such as AHA and PCD are available, but they are generally geared towards coarse assessments, not identifying the specific release number that meets conservation (and harvest) objectives. Of critical importance is an empirical assessment of habitat carrying capacity, whether or not hatchery releases cause the aggregate hatchery plus natural abundance to exceed carrying capacity at least temporarily, and the likely biological consequences for natural populations. Given the availability of population monitoring data, with decades-long population abundance time series commonly available and the widespread use of juvenile traps to estimate freshwater smolt abundance, assessing carrying capacity via fitting stock-recruit curves should be an achievable exercise. Summation of rearing habitat across different habitat types, given estimates of rearing densities, offers an alternative approach for estimating carrying capacity (Beechie et al. 1994; Beechie et al. 2015).

We also strongly suggest that justification for hatchery program size should consider aggregate effects of multiple hatchery programs operating within a geographic region. Particularly during the early marine phase, juvenile salmonids from multiple hatchery and natural populations likely share common rearing habitats, potentially leading to aggregate ecological effects across multiple hatchery programs. Similarly, genetic risks are not limited only to demographic exchange only amongst hatchery and natural populations in the same river system, as the total number of hatchery releases in a geographic region such as Puget Sound will affect homogenization through straying.

Rearing strategies

Program size (or release number), rearing strategies, and release strategies are intertwined in that all three aspects determine how, where, and when fish are reared and released. Many of the reforms associated with rearing and release strategies result from a long-term evolution of hatchery practices intended to improve hatchery program efficiency and post-release survival (Table 1); some of these reforms also minimize genetic and ecological risks. Hatchery programs face the challenge of balancing program efficiency and risk minimization (Larsen et al. 2013; Berejikian et al. 2017; Harstad et al. 2018) as they work to achieve annual program goals.

Rearing strategies refer to the methods hatcheries employ to raise fish, and include aspects of the rearing environment such as water source, type of rearing structure, growth regime, rearing density, and the size-at- age of fish when they are released (Harstad et al. 2018; Larsen et al. 2019). "Natural" growth regimes attempt to create rearing conditions similar to those in the natural environment including seasonal fluctuations in temperatures and food availability, and typically rear fish at lower densities than in standard hatchery protocols. These growth regimes can be achieved by modulating temperature and feeding profiles in the hatchery facility (Berejikian et al. 2011; 2013; Berejikian et al. 2017) or transferring fish to acclimation ponds to increase exposure to natural environmental fluctuations (Harstad et al. 2018). When access to acclimation facilities is limited, hatcheries might also pipe in (cold) surface water from the release site location to mimic more natural, ambient conditions (Dittman et al. 2015).

Natural growth regimes can reduce the extent to which hatcheries alter maturation schedules, such as precocial male maturation. Results from a spring Chinook hatchery in the Hood River, WA, demonstrated significantly lower early male maturation rates (14% vs. 45% average: Spangenberg et al. 2014), faster downstream migration, and increased smolt to adult survival for fish reared under natural growth regimes in the hatchery (Beckman et al. 2017). Similarly, summer Chinook yearlings (Columbia River, WA) reared for extended periods in acclimation ponds exhibited reduced rates of early male maturation, increased smolt to adult survival, and increased life history diversity in returning adults (Harstad et al. 2018). Larsen et al. (2013) also reported reduced early male maturation rates due to natural growth regimes in a spring Chinook population in the Yakima River (20% compared to 41%), yet fish reared on the natural growth regime were smaller at release and had poorer post-release survival, which the authors attributed to size selective mortality. A steelhead natural growth regime program in the Methow River raised age-2 smolts that were larger, of more uniform size, migrated as quickly or more quickly, and survived as well or better than corresponding age-1 smolts reared on a standard growth profile (Tatara et al. 2017; Tatara et al. 2019). However, although the age-2 fish program produced fewer undersized fish than the age-1 smolt program, there was an increased number of precocious males, resulting in near equivalent residualism risks for both rearing regimes (Tatara et al. 2019). The Larsen (2013) and Tatara (2017; 2019) studies highlight the possible trade-offs hatchery managers face when balancing program efficiency and risk minimization, and exemplify the need to tailor rearing regimes to the species, stock, and location.

Results from a small-scale winter steelhead conservation program in Hood Canal and a production-level summer steelhead supplementation program in the Methow River basin show that steelhead raised under natural growth regimes can minimize selection for body size and growth rate (Berejikian et al. 2011; Berejikian et al. 2017; Tatara et al. 2017; Tatara et al. 2019). Berejikian and Van Doornik 2018 attributed the demographic boost and minimal genetic cost of steelhead supplementation in the Hamma Hamma River, at least in part, to natural rearing conditions which included eyed eggs collected from natural redds, low rearing densities, and natural feeding profiles. Other studies (coho, steelhead) have also reported faster outmigration, improved survival and adult returns for fish reared in low densities (Fuss and Byrne 2002; Kavanagh and Olson 2014). However, in both these studies, the increase in adult survival was not enough to make up for the loss in overall production due to the lower rearing densities, suggesting the utility of this strategy may work best for small, scale conservation programs (Fuss and Byrne 2002; Kavanagh and Olson 2014).

Recent research clearly demonstrates that rearing strategies that mimic natural rearing and growth conditions can provide survival benefits while also reducing negative genetic and ecological effects. However, the bulk of the research to date has focused on smaller scale hatchery programs with a conservation goal and two specific life history forms: yearling Chinook and age-1 or age-2 steelhead. There is a major gap in understanding how growth regimes in production-oriented, high efficiency hatchery programs intended to provide harvest opportunities affect genetic and ecological risks.

Release strategies

Release strategies refer to the practices associated with physically releasing hatchery fish into the natural environment such as where, when, and how fish are released, and the characteristics of the released fish such as age and size-at-release. Here we focus on release location, acclimation, volitional releases, and release timing.

Release location affects both genetic and ecological risks. Washington hatcheries have generally decreased out-of-basin releases and inter-basin transfers over time (data not shown), reducing the genetic risks of ongoing regional homogenization relative to previous decades when this practice was common. Regarding ecological risks, Naman and Sharpe (2012) reported lower predation rates of hatchery steelhead on naturally spawned juvenile Chinook when releases occurred downstream from Chinook spawning habitat. Hausch and Melnychuk (2012) concluded that residualism rates, and hence the opportunity for ecological interactions with natural-origin fish, were lower with shorter distances between the release site and an estuary or large river confluence;

Concentrating hatchery releases in non-native locations where no historic population was present has become a common strategy for reducing genetic and ecological risks (Appendix 1). Many of these stocks were developed in a previous era when inter-basin hatchery transfers were common but are now established hatchery runs largely perpetuated with local returns. However, we are not aware of studies directly evaluating the effectiveness of the non-natural hatchery stock strategy at reducing genetic and ecological risks. We suggest that geographic distance likely interacts with program size to determine impacts such as recipient stray rates in natural populations and competition in shared estuarine and marine rearing habitats.

Acclimation ponds are satellite rearing and release locations commonly used in conservation programs to encourage adult spawning throughout the area where more natural spawning is desired, while minimizing out-of-basin straying (Flagg et al. 2000; Dittman et al. 2010). In ten years of paired summer steelhead releases into the Grande Ronde, OR, acclimated fish had 33% higher smolt-to-adult survival and a 42% lower stray rate index than direct-released fish (Clarke et al. 2010). Some studies suggest that a longer period of acclimation can more significantly improve survival than a shorter period (Clarke et al. 2012; Harstad et al. 2018), and can have other benefits like increased adult life history diversity and reduced early male maturation (Harstad et al. 2018). Although acclimation ponds can effectively reduce out-of-basin straying, acclimation may have limited utility attracting returning adults to spawn in specific desired reaches (Dittman et al. 2010), depending on the location of the facility, habitat quality in the surrounding area, and other factors (Garcia et al. 2004; Dittman et al. 2015). Both large scale analysis of CWT recoveries (Candy and Beacham 2000) and smaller, basin-scale studies show that stray rate increases as distance between release site and the hatchery rearing facility increases (Westley et al. 2013). Even fish that are spawned and released from their natal hatchery, but reared or acclimated off-site, will stray at greater rates than fish who spend their entire rearing history on-site (Candy and Beacham 2000).

Acclimation ponds also have relevance to ecological interactions. Rosenburger et al. (2013) found that acclimation resulted in fast migration rates, earlier date of dam passage, and improved juvenile survival for subyearling fall Chinook in the Snake River basin. As a result, acclimation reduced migratory overlap between hatchery-origin and natural-origin fish, providing indirect evidence of reduced ecological interactions with natural fish. However, in another study of subyearling fall Chinook, Clarke et al. (2016) found no difference in travel times or juvenile survival for acclimated fish in the Umatilla River basin, and reported reduced survival to adulthood, compared to fish released directly into the river. Acclimation may be less effective for subyearling releases, or the timing of acclimation for subyearling releases may be more difficult to match with the imprinting process (Clarke et al. 2016). Overall, there is empirical evidence that acclimation can be effective at reducing ecological and genetic interactions, although the magnitude of the reduction varies.

Another strategy is volitional releases, which allow fish to emigrate from hatchery facilities into the river of their own accord rather than forcing them out. Volitional releases can effectively retain non-migrants and reduce residualism (Viola and Schuck 1995; Hausch and Melnychuk 2012), and produce fish that migrate more quickly and have higher survival than forced releases of non-migrants (Snow et al. 2013; Tatara et al. 2017). However, studies from Clarke et al. (2011) and Johnson et al. (2015) found that volitional releases did not confer clear benefits to survival or homing. Recent work on summer steelhead in the Methow River suggests that volitional releases can effectively isolate and prevent release of undersized parr residuals, but have limited utility retaining precocious males (Tatara et al. 2019). Volitional release strategies are included in many Hatchery Genetic Management Plans, but specific methods such as water draw down rate, maximum velocities, and length of the release period are not standardized and formal guidance is lacking to non-existent. This shortcoming prevents accurate, widespread assessment of a volitional release strategy as a risk reduction measure.

The timing of hatchery releases is intertwined with growth and rearing regimes. In Puget Sound, Chinook salmon have been released progressively later and at larger sizes over the last sixty years (Nelson et al. 2019a). We suspect the same is true for coho salmon and steelhead trout, and in other areas of the Washington State, as WDFW hatcheries have generally transitioned away from releasing fry (non-smolting fish), and instead rear and release fish at the age and size at which they are actively smolting (data not shown). Although it is difficult to confidently ascribe the intent of these changes, they are likely related to efforts to both improve hatchery efficiency (i.e., increase survival) and reduce ecological interactions with natural populations.

If mortality is size selective, fish released at a larger body size would survive at a higher rate than smaller fish. Although fry (≤ 45 mm) vs. smolt (≥ 70 mm or larger, depending on species) releases may create a large size contrast, the size and timing of release is likely more nuanced and complicated than simply “bigger is better.” Indeed, Snow (Snow 2015) reported that earlier, smaller-bodied releases of summer Chinook salmon had a higher smolt to adult survival rate than later, larger-bodied releases. Furthermore, recent research emphasizes flexibility in release timing to coincide with ocean conditions and nearshore food availability (Duffy et al. 2011; Irvine et al. 2013; Satterthwaite et al. 2014)

Releasing hatchery fish later in the season might also reduce predation and competition impacts on natural populations. Releasing hatchery steelhead later in the spring reduced predation on subyearling fall Chinook because Chinook were larger and had begun outmigrating themselves (Naman and Sharpe 2012). Regarding competition, releasing smolting hatchery juveniles motivated to rapidly migrate is central tenet of minimizing interactions with natural origin fish. There are some telemetry studies, predominantly with steelhead (Goetz et al. 2015; Moore et al. 2015), that assess the migration rate of smolts released from hatcheries, providing an indirect assessment of potential for competition with natural populations by characterizing overlap in time and space. However, we are not aware of studies directly evaluating the effectiveness of releasing actively smolting fish as a tool to reduce the extent and impact of competition risks. A better understanding of the migration and foraging behavior of hatchery juveniles following release would provide some assessment of competition impacts on natural populations, particularly for species such as Chinook salmon that frequently rear in estuaries and nearshore marine areas rather than rapidly migrating to the oceanic habitats.

Even under a scenario of rapid downstream migration following release from hatcheries (e.g., weeks), it seems plausible that abundant hatchery-origin fish could exclude natural-origin fish from foraging opportunities, possibly leading to latent effects on growth or survival. In other words, a short duration but high intensity competition effect, with lasting impact. Furthermore, for especially large hatchery programs, if even a small percentage (< 10 %) adopt a more protracted migration or rear for some period in lower rivers or estuaries, they might outnumber low abundance natural-origin juveniles (Appendix 1). Thus the extent to which releasing "fully smolted" hatchery fish reduces competition, and the level of hatchery-natural competition ensuing from such a strategy, are largely unknown.

Mass marking

Mass marking all fish released from a given hatchery program allows for their identification as hatchery-origin upon subsequent encounters. We consider mass marking essential to hatchery reform because it allows for a host of critical activities including mark-selective fisheries that target abundant hatchery populations, estimating demographic exchange between hatchery and natural populations (i.e., pHOS), and managing broodstock at the hatchery (i.e., controlling pNOB). Without mass marking, the abundance of hatchery-origin salmon would be confounded with natural-origin salmon.

Several mark types are available to hatchery managers. The most common mark is an adipose fin clip, and it is widely used to mass mark juveniles released from hatcheries, typically at rates exceeding 95% for given release group. An adipose clip requires only visual inspection for identification, and thus allows for mark-selective harvest when fishers are not expected to carry specialized equipment for detecting hatchery-produced fish. Coded-wire tags (CWTs) can identify hatchery-origin fish by release group, and therefore allow for relatively precise estimates of survival and straying. However, they are costlier to implement and detect than adipose fin clips, requiring both specialized detection wands and laboratory work for decoding. As a result, in large hatchery programs, only a subset typically receive CWTs; some small hatchery programs (e.g., < 250,000) may mass mark close to 100% via CWT. Thermal otolith marks are often used in conservation settings where managers wish to reduce exposure to mark-selective fisheries by not adipose clipping. Thermal otolith marks require field dissections and laboratory analysis to decode, presenting a challenge for use in broodstock management during hatchery spawning. Finally, parentage-based tagging uses genetic analysis to identify hatchery-origin fish. This approach has recently expanded greatly in the Columbia River Basin, and presents a number of advantages, including accurate, precise estimates of pHOS and stray rates (Steele et al. 2019). It is important to note that thermal otolith marks and parentage-based tagging do not allow for mark-selective fisheries on their own, and only very rarely are CWTs used for this purpose.

Disease management

In responding to endemic and exotic pathogens, the fish health community in the Pacific Northwest includes the established framework of the Pacific Northwest Fish Health Protection Committee (PNFHPC), and interactions with academic and federal scientists (Amos et al. 2014). Examples of PNFHPC contributions in reaction to a novel pathogen include a recent white paper describing Piscine orthoreovirus (PRV, Meyers 2017). In addition, "The Salmonid Disease Control Policy of the Fisheries Co-Managers of Washington State", provides guidance and agreement among co-managers to better manage risks surrounding disease. Policy goals include measures to prevent the establishment of exotic pathogens and regulated endemic pathogens, reduce the impact of salmonid fish pathogens, minimize the amplification of pathogens in the hatchery, and foster open communication surrounding fish health issues. In aggregate, these measures can reduce disease risk imposed by fish hatcheries.

Specifically, the WDFW response to infectious disease at hatcheries includes the efforts of veterinarians, pathologists, and a fully functional microbiology laboratory. However, only a small number of options are available when responding to infectious disease episodes for a variety reasons: 1) the pharmacological toolbox is small (Bowker and Trushenski 2016); 2) the regulatory environment is imposing greater restrictions on aquaculture drugs due to concerns surrounding antibiotic resistance as a human health risk (Zaman et al. 2017); 3) our delivery of medications is limited, in many cases, to feed additives that are not effective when populations are not optimally feeding at the onset of a disease episode (Ranjan et al. 2017); 4) no therapies targeted for outbreaks of specific viruses are available (Winton 2001). These difficulties in treating fish disease have prompted research on the immunology of fishes, nutritional approaches to fish health, measures to reduce chronic stress, and a focus on increased biosecurity to stop disease episodes before they start. Research on vaccines for the three important diseases identified by HSRG (2014) continues (Elliott 2017; Ma et al. 2018; Yong et al. 2019) but the promise of vaccines in controlling these diseases in a hatchery environment has yet to be fully realized. Nutritional approaches designed to enhance host resistance to disease are hampered by a lack of understanding of the physiological mechanisms that underlie their putative efficacy (Trichet 2010). While reduction of stress has been near universally acknowledged by hatchery practitioners as beneficial, the hatchery environment will always provide stressors that contribute to reduced disease resistance (Green and Haukenes 2015).

Fish health management has been improved by technical advancements to expand the list of available diagnostic tools that provide greater sensitivity and specificity when distinguishing variants of specific pathogens (Snow 2011). Reliable and efficient non-lethal sampling techniques for pathogen detection such as those developed by Elliott et al. (2015) will become more important for the surveillance of wild fish, a requirement to develop disease risk models (Williams and Moffitt 2010). As new tools develop, there is a need to define how these tools will contribute to long-term data sets surrounding fish health. For example, some hatchery populations of salmon have been screened for *Renibacterium salmoninarum* using ELISA for nearly 30 years. As new molecular tools become available and more desirable in some circumstances (see Elliott et al. 2013) the decision rubric regarding data will need to evolve and redundancy in applying methods will be required during the near term (Laurin et al. 2019). Considerable effort has been applied to characterizing and understanding risk in fish health management (Ray et al. 2010; Kurath and Winton 2011). Practices currently employed that improve rearing conditions, biosecurity, and restricting inter-basin transfers of fish reduce of risk of disease. However, disease still occurs on fish hatcheries and the impact on surrounding fish populations is uncertain. There have been examples of attempts to understand the dynamics of bacterial kidney disease and infectious hematopoetic necrosis virus in natural populations (Foote et al. 2006; Rhodes et al. 2011; Ferguson et al. 2018) but risk models are limited by a lack of information on pathogen transmission rates, threshold host densities, rates of shedding of infectious particles and environmental interactions. Among the most important strategies moving forward will be the development of a monitoring programs to better evaluate disease dynamics in the context of hatchery-wild fish interactions (Groner et al. 2016). This approach represents an expanded role and scope for fish health programs to generate data of greater use for modeling risk from existing hatchery monitoring and evaluation programs and incorporate input from fish health practitioners, fish hatchery biologists, microbiologists, fish ecologists, and epidemiological modelers. The models developed can then be applied proactively characterize disease risk in a variety of different contexts (e.g. hatchery-wild fish interactions, habitat degradation, climate change).

Adaptive management

Monitoring hatchery risk and benefits, and at the ability to modify hatchery management based on that information, is a critical element of hatchery reform. Throughout Washington, WDFW, tribal co-managers, and project partners have developed a vast monitoring infrastructure to systematically monitor key demographic metrics relevant to the HSRG broodstock management guidelines. This includes mass-marking of fish released from hatcheries, a coded wire tag program to estimate stray rates, spawning ground surveys to estimate pHOS, hatchery broodstock sampling to estimate pNOB, and abundance estimates of natural populations. Although the demographic data collection effort is vast, in many cases, there is no clear path for using that information to guide and modify hatchery management. In such cases, data are not regularly reviewed in a formal adaptive management process, nor is it clear how natural and hatchery population performance metrics would guide broodstock management, program size, rearing strategies or release strategies.

Furthermore, as a scientific community, we are not well positioned to quantify ecological risks of competition and predation in downstream shared rearing environments such as Puget Sound or the Columbia River estuary. We do not have a monitoring and adaptive management system in place to provide robust assessment of ecological risks or test assumptions of hatchery management strategies intended to reduce ecological risks. Ongoing monitoring studies (e.g., smolt traps, estuary sampling, nearshore tow netting) were not necessarily designed to quantify realized ecological impacts of hatchery fish to natural populations but with careful thought, could be adapted to suit this purpose. Monitoring of the marine food web (e.g., Puget Sound), where it has occurred, has generally not been extended to understand ecological competition between hatchery and natural populations.

Hatchery Genetic Management Plans (HGMPs) and the NOAA Biological Opinions authorizing them are the primary regulatory documents guiding hatchery management. Although, these documents provide detailed descriptions of hatchery operations, in most cases, they lack clearly articulated monitoring and evaluation plans for understanding and controlling hatchery risks. They typically mention monitoring tools useful for assessing risk (e.g., smolt traps, CWT releases) but quantifiable methods for measuring risk and numerical thresholds for either risk tolerance or program changes are relatively rare.

As emphasized by the HSRG (2015), we suggest that stand-alone monitoring and evaluation plans, inclusive of risk assessment methods, risk tolerance thresholds and an adaptive management process, are essential components of scientifically defensible hatchery programs. It is beyond the scope of our review to provide a detailed description of such plans. However, key elements would include the specifics of an individual hatchery program, opportunities to consider more general novel scientific information relevant to hatchery risks, the forum or venue in which information is delivered, and the frequency of informational review in which management changes are considered.

EMERGING SCIENCE

Here we review new, emerging scientific information available in the last ten years since WDFW adopted the hatchery and fishery reform policy in 2009. In this section, our goal is to present recent information to help determine if the HSRG principles and recommendations forming the foundation of the policy warrant reconsideration or revision. We review studies published from 2010 to present, and describe whether they generally support or generally run contrary to the HSRG approach to hatchery management. Given the importance of broodstock management to hatchery reform, we also direct the reader to the "Broodstock management – reducing the risk of fitness loss from domestication" section, which presents novel exploration of genetic models, for further perspective on the scientific validity of the HSRG recommendations.

In our literature summary, we sought to identify the most influential studies from 2010 to the present addressing a hatchery reform action, or more indirectly, informing the likelihood or magnitude of a hatchery benefit or risk. We also aimed for a diversity of scientific approaches and biological concepts, while maintaining a concise summary of recent research.

HSRG principles and the recommendations nested within them are general and not specific. For example, recommendation #7 is "size hatchery programs based on populations goals and as part of an all-H strategy" (HSRG 2015). HSRG recommendations are not prescriptive with respect to hatchery practices, but rather describe a programmatic approach to goal setting and weighing the benefits and risks of hatcheries. By contrast, science papers typically address hatchery practices and hatchery-wild interactions at a much more topically focused and finer resolution than the HSRG principles and recommendations. Due to this difference in scale, we simply cannot describe recent science papers as directly evaluating the merits of specific HSRG recommendations.

In accordance with the level of detail in HSRG recommendations, we adopted a coarse, thematic approach in our determination of whether literature from the last ten years supports or runs contrary to HSRG principles. Given a hatchery risk factor or hatchery practice identified by the HSRG as important to impacts on natural populations, did a given study support continued attention to reducing, controlling or understanding that risk factor? Or conversely, did the outcome of a particular study run contrary to predictions or assumptions (e.g., Ford model) inherent within the HSRG approach? Noting the HSRG emphasis on learning and adaptive management (principle 3, HSRG 2015), we also describe some studies as providing no value judgment on risks or benefits but rather as adding depth to our understand of mechanisms and biological processes important to hatchery-wild interactions.

Our review of the recent literature is summarized in Table 5. Modeling (Baskett and Waples 2013) and empirical studies (Christie et al. 2014a; Waters et al. 2015; Ford et al. 2016; Janowitz-Koch et al. 2019) provided strong support for the HSRG's recommendation to focus on pHOS, pNOB, and PNI in managing broodstock. A consistent observation of lower RRS of hatchery-origin fish provided basic conceptual support for fitness costs of hatchery propagation (Christie et al. 2014a), though unequivocal evidence for a genetic basis to this pattern remains rare (Araki et al. 2007; Ford et al. 2016). Studies from the Wenatchee River provide an interesting contrast between species. Whereas the lower RRS of hatchery-origin steelhead appears to have a genetic basis (Ford et al. 2016), the poor quality of natural spawning habitats used by hatchery-origin Chinook salmon emerged as a potential explanation for their lower RRS

(Hughes and Murdoch 2017), and researchers found little evidence for a genetic basis to lower RRS of hatchery-origin Chinook salmon (Ford et al. 2012). However, in this population, the fish that were most productive when spawned in the hatchery produced offspring that performed poorly in the river, emphasizing the difference between the selective environment of the hatchery compared to the river (Ford et al. 2012). Hatchery programs employing 100% natural-origin broodstock demonstrated minimal divergence from the associated natural population (Waters et al. 2015), and relatively low fitness costs (Janowitz-Koch et al. 2019). Combined, these results indicate that the Ford (2002) model-based approach adopted by the HSRG has strong scientific merit.

Considering the consistent support for HSRG broodstock principles, the scarcity of unequivocal, population scale empirical RRS evidence for a genetic basis to fitness loss merits further discussion. Case studies of Hood River (OR) steelhead (Araki et al. 2007) and Wenatchee River steelhead (Ford et al. 2016) found such evidence, whereas case studies of Wenatchee River Chinook salmon (Ford et al. 2012) and Umqua River (OR) coho salmon (Thériault et al. 2011) did not. Such studies require at least three generations of genetic information combined with census DNA sampling of adult salmon. Thus, the tremendous long-term investment in research and monitoring required to test for a genetic component to fitness loss has contributed to the scarcity of evidence for it. Furthermore, a history of interbreeding between hatchery-origin and natural-origin salmon prior to initiation of an RRS study can diminish RRS differences due to accumulated fitness loss (Willoughby and Christie 2017). Finally, notably absent from RRS studies capable of assessing heritable fitness loss are examinations of Chinook salmon hatchery programs that release juveniles as subyearlings, a major component of hatchery production in Washington State.

Major changes in hatchery management provide important opportunities to evaluate hatchery reform. Following termination of coho salmon hatchery releases in coastal Oregon, Jones et al. (2018) reported increases in natural-origin abundance and a diversification of spawn timing, suggesting hatchery program size can affect natural population performance. In the Clackamas River, OR, hatchery-origin summer steelhead were excluded above a dam beginning in 2002. Although the abundance of the natural-origin winter steelhead population appears to have increased during the hatchery exclusion period, Courter et al. (2019) found no relationship between natural-origin winter steelhead productivity and the number of hatchery-origin summer steelhead spawning above the dam from 1958 – 2015. These two studies illustrate the complexities of hatchery reform and its relationship to recovery. Whereas Jones et al.'s (2018) results underscore the potential for favorable natural population responses to major reductions in hatchery risk, Courter et al.'s (2019) study indicates hatchery reform is not a panacea in all situations. As emphasized by the HSRG, recovery will almost certainly require thoughtful integration of the many biological, physical habitat, and hatchery management factors affecting population performance.

Regarding conservation hatcheries, recent literature demonstrates that hatcheries can maintain genetic diversity and provide demographic benefits on a small scale (Berejikian and Van Doornik 2018; Janowitz-Koch et al. 2019). However, two landscape-scale assessments indicated that conservation hatcheries did not provide consistent increases in natural-origin abundance (Scheuerell et al. 2015; Venditti et al. 2018). However, neither Scheuerell et al.

(2015) nor Venditti et al. (2018) report pNOB or PNI, so the extent to which the hatchery programs under investigation utilized key hatchery reform initiatives is unclear. Regardless, these results generally support the HSRG's phased approach to recovery, though they call into question whether hatcheries have utility for progressing through the later stages of recovery when significant increases in natural-origin abundance are the goal. Combined with observations of current population demographics (Appendix 1, Table 4), it is clear that transitioning from the demographic boost provided by naturally spawning hatchery-origin fish to sustained growth of natural-origin abundance remains a major obstacle to recovery.

Hatchery-natural ecological interactions remain challenging to disentangle from other factors affecting population productivity at large spatial scales, especially in the marine environment. Ruggerone and Irvine (2018) emphasized that pink, chum and sockeye salmon numerically dominate both hatchery production and overall abundance of salmon in the Pacific Ocean, and showed some evidence of competition in the ocean. Whereas Amoroso et al. (2018) suggested that hatchery-produced pink salmon likely depressed the productivity of naturally spawning Prince William Sound pink salmon due to competition, Nelson et al. (2019b) found no relationship between the productivity of naturally spawning Chinook salmon in the Salish Sea and hatchery releases.

Recent research has also highlighted progress in understanding how rearing and release strategies can affect hatchery risks. Adopting natural growth regimes in the hatchery may reduce selection for metabolic traits that are disadvantageous in the wild (Table 5). Volitional releases can reduce residualism and thus ecological interactions with natural populations (Snow et al. 2013). Acclimation prior to release can increase the migration rate of hatchery-origin smolts, thereby reducing potential for ecological interactions with natural-origin fish (Rosenberger et al. 2013). Acclimation can also reduce stray rates to adjacent watersheds (Clarke et al. 2010), and understanding the limits of acclimation to influence spawning location (e.g., Dittman et al. 2010; Clarke et al. 2016) helps clarify its effectiveness as a risk reduction measure. Finally, exposing hatchery-origin fish to waters originating from desired spawning locations early in life, during embryonic development, provides a promising alternative to offsite acclimation for imprinting homing cues (Dittman et al. 2015).

CONCLUSIONS AND RECOMMENDATIONS

Our review focuses on fisheries biology, and we argue that decisions regarding hatchery programs should include a science-based comparison of risks and benefits. However, it is clear that other factors besides fisheries science must be considered in establishing the overarching policies that guide hatchery management. In particular, economic, social, political and legal considerations, including fulfilling treaty rights of Native American tribes, undoubtedly factor into hatchery management decisions. These values are often not comparable or even quantifiable on similar terms to the biological benefits and risks of hatcheries, adding to the challenge and complexity of hatchery management. The hatchery literature is dominated by biological studies, and we suggest a strong need for additional research on the economic, social, political, and legal value of hatcheries that will help clarify the benefit-risk trade-off. For example, carefully defining the social value of fisheries subsidized by hatcheries in comparison to wild, natural populations without fishing would help establish risk tolerance thresholds.

It is important to note that hatcheries also introduce a number of risk-risk trade-offs whereby reducing one risk simultaneously increases another risk (Waples and Drake 2004). For example, releasing smolts rather than pre-smolt fry might reduce the ecological risk of competition with natural-origin fish in shared rearing environments, but increase the risk of domestication selection due to a longer exposure to the hatchery selective environment. Similarly, curtailing fisheries targeting hatchery-origin fish to reduce incidental mortality to natural-origin fish simultaneously increases the genetic risks of high pHOS. We suggest such risk-risk tradeoffs are common in hatchery management.

The biological benefits and risks of hatcheries are highly context dependent. Freshwater and marine habitat conditions, hatchery program history, natural population history and demographics, hatchery program design, species life history, research and monitoring methods, and fishery management, among other factors, will affect the frequency and magnitude of hatchery-wild interactions. Blindly transferring research results from one hatchery study to another hatchery program without considering this context is problematic and can be misleading. Despite this complexity, here we provide some conclusions to guide hatchery management and hatchery reform. Overall, our review supports the fundamental concepts and approach of the HSRG, but also identifies knowledge gaps and challenges to coordinated, robust implementation of scientific principles at a statewide scale. In order to advance hatchery reform as a comprehensive program for developing scientifically defensible hatchery programs, these issues warrant dedicated, programmatic initiatives.

Overarching themes

Hatchery reform is but one of several factors requiring careful planning and aggressive implementation needed to achieve meaningful recovery of salmon populations. Where hatcheries were initiated in response to local or regional declines in abundance, unless the factors causing the decline in the first place are identified and addressed, hatchery reform cannot lead to recovery on its own. An expectation of rapid (1-2 generation) improvement in population status following implementation of hatchery reform, irrespective of habitat or other constraints on abundance, productivity and life history diversity, is scientifically and logically unreasonable. This idea is not new; the HSRG emphasized an “all-H strategy” or “all-H integration" as fundamental to thoughtful hatchery management. However, in our opinion, this goal has rarely been realized, and directly linking hatchery management to habitat capacity and habitat recovery plans remains a major challenge. We cannot assume failure to achieve conservation goals is the result of a flawed hatchery reform approach.

Furthermore, **hatchery reform is largely aimed at reducing risk in a relative but not absolute sense.** Hatchery operational changes such as increasing pNOB, reducing program size, or releasing smolts rather than pre-smolt fry are likely to reduce a risk factor. However, the state of the science is not sufficiently precise to confidently predict the likelihood or magnitude of the desired outcomes of these actions, such as an increases in natural population fitness due to higher PNI or survival due to reduced ecological interactions with hatchery-origin fish. If used inappropriately, modeling tools such as AHA dangerously overstate predictive precision, leading to a false sense of security that hatchery benefits and risks will meet expectations. This uncertainty underscores the need to carefully articulate risk tolerance and the level of predictive confidence required to initiate changes to hatchery programs.

In WDFW's hatchery system, a focus on efficiency and maximizing abundance prevents widespread implementation of risk reduction measures. Reform actions receiving conceptual and empirical support in the literature are difficult or impossible to implement in large-scale, production-oriented hatchery programs intended to provide harvest opportunities. Research demonstrating demographic benefits combined with low genetic costs typically results from studies on smaller-scale, conservation hatchery programs (e.g., Small et al. 2014; Berejikian and Van Doornik 2018; Janowitz-Koch et al. 2019). In small-scale programs, hatchery managers can adopt risk reduction measures such as maintaining high pNOB despite low natural population abundance or utilizing natural rearing conditions that consume more water and space than conventional rearing. Such measures become progressively more difficult, or at least more time consuming and costly, as hatchery program size increases. However, 124 of 159 WDFW hatchery programs are intended to provide harvest opportunities, many of which release very large numbers of juveniles (e.g., millions of Chinook salmon, Appendix 1, Table 4).

HSRG recommendations

Long-term empirical studies of the efficacy of hatchery reform principles are absent in Washington State. Thus, it is difficult to know with any degree of accuracy if management actions based on these reforms are achieving their intended goals. However, based on our review of the literature, results from models (e.g., Ford 2002; Baskett and Waples 2013) and empirical demographic information (e.g. Appendix 1), we provide the following conclusions regarding HSRG recommendations, chiefly regarding broodstock and escapement management practices.

The principles of reducing pHOS and increasing pNOB to achieve fitness gains in wild populations are well-founded, and should be fundamental goals in any hatchery reform management action. Reducing pHOS appears to produce a greater reduction in fitness loss than increasing pNOB, but decreasing pHOS may be more difficult to achieve. The relationship between PNI and the rate of fitness loss or increase is not well established empirically, and thus the specific pHOS, pNOB and PNI thresholds recommended by the HSRG are not associated with breakpoints in population performance, and thus are subjective. However, setting goals for PNI, pHOS and pNOB is crucial to implementing broodstock management on an institutional scale, emphasizing the value of targets for these metrics.

Program size requires more careful scrutiny and scientific justification because it affects virtually every aspect of hatchery risks. In situations where integrated population demographics are overwhelmingly dominated by hatchery production (e.g., high pHOS and low pNOB), genetically based demographic models predict that fitness and populations abundance declines are unavoidable, severe in magnitude and possibly irreversible. In some situations, reducing program size may be a more important management action than reducing pHOS or increasing pNOB when attempting to restore a natural-spawning population dominated by hatchery-origin spawners. The genetic risk of homogenization and ecological risks also scale with hatchery program size. Demographic dominance by hatchery-origin fish appears to be commonplace in Washington State (Table 4, Appendix 1), indicating risks associated with program size are pervasive.

The HSRG's phased approach to recovery has strong conceptual merit, but its implementation has resulted in an absence of stricter, conservation oriented PNI goals for many populations. The phased approach to recovery recognizes the spectrum of conservation hatchery intervention; hatcheries have proved successful at preserving a unique genetic lineage and increasing natural spawning by hatchery-origin fish, even if the evidence that hatchery programs have increased natural-origin abundance is sparse. However, HSRG recommends no PNI and pHOS goals for the first two recovery phases, preservation and recolonization. These two phases have been assigned to many populations (48 of 136 WDFW hatchery programs with phase designations, see also Table 4) without a feasible plan to reduce pHOS and increase PNI.

This situation perpetuates high pHOS and low PNI values, likely negatively affecting long-term fitness of the wild populations and restricting the potential for recovery. Assigning preservation and recolonization phases without strong scientific justification compromises conservation-oriented broodstock management goals. We recognize the complexity of recovery and the value of a recolonization approach where native genetic diversity has been lost, but assert that preservation and recolonization designations frequently confound harvest goals with conservation goals and warrant stronger scientific justification.

We recommend three changes to implementation of the HSRG's recovery phase concept. First, in order to ensure consistency between hatchery program goals and operations, harvest programs should not justify high pHOS values on the grounds of a conservation benefit to a natural population during the preservation and recolonization phases of recovery. Rather, harvest hatchery programs, including those geographically separate from populations intended for recovery, should aim to avoid impeding progress towards recovery of these populations. Second, for natural populations targeted for recovery, we recommend using the preservation designation only where a conservation hatchery is necessary to ensure population persistence, and using the recolonization designation only for populations presented with an opportunity for significant spatial expansion. In these cases, a robust assessment of natural population productivity relative to current and possible future habitat conditions is needed to ensure the scientific defensibility of these specific phase designations. Third, where conservation is the priority, we recommend developing goals for pNOB, pHOS, and PNI at least during recolonization, and carefully articulating a plan to move past the recolonization phase with measurable performance benchmarks for both the hatchery and natural population. These steps will help ensure a balance between the short term conservation benefit and the long term fitness cost of hatchery production.

Lastly, in order to improve adaptive management, **we recommend crafting a stand-alone monitoring and adaptive management plan for each hatchery program that quantifies both benefits and risks, and explicitly links hatchery performance metrics to potential operational changes.** WDFW invests considerable effort into population monitoring, yet this information does not often achieve its potential as a hatchery evaluation tool because analysis, reporting, and synthesis are typically under funded. Furthermore, for many hatchery programs, the absence of a clear framework for application of monitoring data in decision making (Murdoch et al. 2019) precludes clearly articulated risk tolerance thresholds. We suggest monitoring and adaptive management are critical not only for evaluating risks and benefits under normal operating procedures, but also assessing experimental practices (e.g., alternative spawning, rearing, and release strategies). Some risks manifest at geographic scales larger than an individual hatchery program (e.g., ecological interactions within Puget Sound); we therefore recommend a component to monitoring and adaptive management that considers information aggregated among multiple hatchery programs in a region. The importance of monitoring and adaptive management has been repeatedly emphasized by the HSRG and previous reviews of hatchery science (e.g., Naish et al. 2008; RIST 2009).

Knowledge gaps and major assumptions of current hatchery management

We argue that several major knowledge gaps and assumptions impede advancement in hatchery reform. In this section, we describe these informational needs, possible avenues for addressing them, and associated implications for scientifically defensible hatchery management.

Although **broodstock management guidelines have received strong conceptual and modeling support, the absence of a landscape-level, replicated experiment prevents empirical assessment of hatchery reform effectiveness.** The scientific community often uses surrogates to assess risk, such as relative reproductive success, theoretical models, and ecological "microcosms" that cannot be scaled to represent more encompassing hierarchical levels. These conceptual limits are not unique to hatcheries and are a feature of large ecological systems. Therefore, currently genetic-based hatchery reform activities target perceived measures of risk such as PNI. The efficacy of hatchery reform activities in improving fitness and demographics has not been tested directly. In Washington State, the absence of a watershed-scale before-after control-impact replicated experiment, similar to ongoing studies addressing habitat restoration (Bennett et al. 2016), precludes a robust evaluation of the hatchery reform effectiveness. Venditti et al.'s (2018) study in Idaho provides an excellent example for assessing the conservation benefits of hatchery programs; we suggest a similar research program is needed to evaluate the risks of hatchery programs intended to provide harvest.

Two major challenges impede an experimental approach to understanding whether or not WDFW's hatchery and fishery reform policy has worked. First, hatcheries release fish in most major river basins in Washington, providing insufficient contrast for a replicated, treatment-control landscape-level comparative approach to researching hatchery effects. We suggest that large-scale manipulative experiments that evaluate major changes in hatchery management are critical opportunities to advance hatchery reform science in Washington State. Second, not enough time has elapsed since hatchery reform was formally adopted as WDFW policy in 2009. We would expect any resulting improvements to population performance to accumulate over generations, yet many of the reform actions have been implemented gradually since 2009. Furthermore, the length of time needed to detect any improvements in population performance due to broodstock management will likely depend on the degree of fitness loss and the aggressiveness of hatchery reform measures. In other words, if high PNI can reverse 10s of generations (decades) of heritable fitness loss, it may take a similarly long time to observe improvements in population performance attributable to increased fitness.

Hatcheries have potential for large magnitude ecological impacts on natural populations that are not well understood, not typically evaluated and not measured. Genetic risks have dominated hatchery-wild interactions research and hatchery reform recommendations. However, the demographic imbalance between hatchery and natural populations alone (e.g., Appendix 1) suggests potential for population-scale competition or altered predation dynamics. Furthermore, taken in aggregate, the statewide approach to hatchery production implicitly assumes that rearing habitats shared among multiple populations in a region (e.g., Columbia River estuary, Puget Sound, nearshore coastal habitats) have sufficient rearing capacity. However, marine ecosystem carrying capacity is rarely considered in determining hatchery program size. Efforts to characterize marine carrying capacity are essential to developing hatchery management strategies that account for competition. Expectations that hatchery production is entirely additive with natural production, or that increasing the number of hatchery juveniles released will result in a commensurate increase in the number of adults caught in fisheries, preyed upon by orcas or returning to rivers, are major assumptions when such capacity limitations are unknown. Sharma (2006) provides a thoughtful example for considering carrying capacity in hatchery program evaluation. HSRG PNI targets were institutionalized by WDFW to address genetic risks, but there are no such performance targets or benchmarks for the ecological risks of competition or altering predation.

In addition to carrying capacity, **understanding the role of life history diversity on hatchery-wild ecological interactions and ecosystem stability is a significant research need**. Recent research has demonstrated that a diverse portfolio of life-histories confers long term stability among salmon population aggregates (Schindler et al. 2010), and implicated weakened diversity in a population collapse (Carlson et al. 2011). However, hatcheries have reduced the window of dates and range of body sizes at which juveniles are released over time (Huber and Carlson 2015; Nelson et al. 2019a). Unfortunately, researchers do not yet understand the ensuing consequences for marine food web dynamics. It seems plausible that a pulsed release of many similarly sized fish in a given geographic region could narrow energy flow through marine food webs, leading to boom-bust cycles for salmon, their predators and their prey, leading to ecosystem instability. This hypothesis potentially has major implications for hatchery-wild interactions but is largely untested.

In reviewing ecological considerations of carrying capacity and life history diversity, **we recommend a more rigorous, consistent and intentional evaluation of cumulative hatchery effects across multiple hatchery programs operating within a geographic region**. As implemented, hatchery reform tends to evaluate hatchery risks on a case by case basis that does not formally consider portfolio effects of population complexes or aggregate density dependent effects in shared rearing environments. Assigning the biological significance of all natural populations in a region (per HSRG recommendations), and setting hatchery program specifics accordingly, allows for some broader geographic consideration of hatchery management. However, we argue that a more explicit, quantitative cumulative assessment of all hatchery programs within a geographic region is warranted.

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DEFINITION OF TERMS

Hatchery Genetic Management Plan (HGMP): A plan describing all operational aspects of a hatchery program that provides permit coverage under the U.S. Endangered Species Act.

Hatchery-origin: Fish whose parents were spawned in a hatchery. Typically identified by a mark, often an adipose fin clip.

Integrated hatchery program: A hatchery program that aims to be genetically identical to an associated natural population though intentional natural spawning of hatchery-origin fish and hatchery spawning of natural-origin fish.

Natural or natural population: Used broadly to refer to populations inhabiting the river or natural environment. Natural populations are the targets for recovery of Evolutionary Significant Units listed as threatened or endangered under the U.S. Endangered Species Act. In many cases, natural populations have ongoing intentional or unintentional demographic exchange with a geographic proximate hatchery populations and as a result, are genetically indistinguishable from said proximate hatchery population.

Natural-origin or naturally spawned: Fish whose parents spawned in the river or natural environment. Natural-origin fish may have one or two hatchery-origin parents that spawned naturally. Natural-origin fish can and are spawned themselves in hatcheries.

Naturally spawning: Fish that reproduce in the river or natural environment, regardless of whether they are natural-origin or hatchery-origin. Hatchery-origin fish can and often do spawn naturally in the river.

Population designations: Defines the biological significance of natural populations as primary, contributing or stabilizing.

> Primary populations: Natural populations targeted for restoration to high (95-99% probability) or very high (> 99%) viability. These populations are the foundation of salmon recovery. Primary populations are typically the strongest extant populations and/or those with the best prospects for protection or restoration. These typically include populations at high or medium viability during the listing baseline.
>
> Contributing populations: Natural populations for which some improvement will be needed to achieve a stratum-wide average of medium viability (75 – 94% probability). Contributing populations might include those of low to medium significance and viability where improvements can be expected to contribute to recovery. Varying levels of improvement are identified for contributing populations. Some contributing populations are targeted for substantial improvements whereas more limited increases are identified for others.

> Stabilizing populations: Natural populations maintained at baseline levels. These are typically populations at very low viability during the listing baseline. Stabilizing populations might include those where significance is low, feasibility is low, and uncertainty is high. While stabilizing populations are not targeted for significant improvement, substantive recovery actions will typically be required to avoid further degradation.

Proportion of Hatchery Origin-Spawners (pHOS): Percent (%) of naturally spawning fish that are hatchery-origin.

Proportion of Natural Origin Broodstock (pNOB): Percent (%) of hatchery broodstock that are natural-origin.

Proportionate of Natural Influence (PNI): pNOB/(pNOB+pHOS)

Recovery: Use generically to refer to improvements in natural population status that would lead to eventual removal from the U.S. Endangered Species List. “Salmon recovery” also refers to a broad suite of habitat, hatchery, and harvest actions intended to improve salmon population status towards the goal of de-listing.

Relative reproductive success (RRS): A comparison of the number of offspring produced by hatchery-origin and natural-origin fish, often through genetic parentage analysis.

Segregated hatchery program: A hatchery program intended to be genetically distinct from natural populations by minimizing both the number of hatchery-origin fish that spawn naturally and the number natural-origin fish used as hatchery broodstock.

Wild: Reserved for cases where population traits are shaped exclusively (or nearly so) by natural selection in the wild rather than selection in the hatchery environment. We consider this term inappropriate for natural populations with continued, frequent, bi-directional demographic exchange and gene flow with hatchery populations.

TABLES

Table 1. A summary of select hatchery reform measures in Washington State.

Topic	**Hatchery reform action**	**Intended outcome**	**Source of reform**	**Degree of implementation**
Broodstock management	Specify segregated or integrated broodstock management	Manage, measure and control gene flow from hatchery programs into natural populations	HSRG	Widespread
	Selective removal of hatchery fish from river using weirs	Minimize hatchery spawning in the wild and control pHOS	HSRG; evolution of hatchery and fishery management practices	Sporadic, related to weir effectiveness
	Retention of excess broodstock at hatchery, elimination of adult recycling	Minimize hatchery spawning in the wild and control pHOS	HSRG; evolution of hatchery and fishery management practices	Unknown
	Implement mass marking of hatchery-origin fish	Differentially target hatchery-origin fish in mark selective fisheries; improve monitoring of hatchery program performance and broodstock management	HSRG emphasized; evolution of hatchery and fishery management	Widespread
	Increase implementation of mark selective fisheries	Target abundant hatchery fish in fisheries while minimizing impacts to natural-origin fish	HSRG emphasized; evolution of hatchery and fishery management	See Figure 1
Program size	Reductions in program size	Minimize genetic and ecological impacts to natural populations while meeting conservation or harvest objectives	Hatchery reform; budget cuts	Requires assessment of existing data
Rearing strategies	Adopt natural growth regimes	Minimize artificial selection for body size, growth rate; minimize residualism and	Evolution of hatchery practices	Unknown

		associated ecological interactions; maximize survival		
Release strategies	Reduce out-of-basin releases and inter-basin transfers	Minimize homogenization of population structure; promote local adaptation	HSRG emphasized, evolution of hatchery practices	Requires analysis of existing data
	Acclimation at release site	Minimize straying; increase survival and homing to intended spawning location	HSRG emphasized, evolution of hatchery practices	Requires analysis of existing data
	Volitional rather than forced releases	Minimize ecological interactions such as competition and predation; minimize residualism; increase survival	HSRG emphasized, evolution of hatchery practices	Requires analysis of existing data
	Later timed releases within a more constrained time window	Minimize ecological interactions such as competition and predation; promote rapid outmigration and increase survival	Evolution of hatchery practices	Widespread for Chinook salmon (Nelson et al. 2019a)
	Release larger, older, actively smolting fish rather than pre-smolt or fry releases	Minimize ecological interactions such as competition and predation; promote rapid outmigration and increase survival	Evolution of hatchery practices	Requires analysis of existing data
Disease management	Lower rearing densities	Minimize disease and pathogen outbreaks; improve survival	Evolution of hatchery practices	Unknown

Table 2. pHOS and PNI target values for specific hatchery broodstock management design, and population designation and status. Table is taken from HSRG (2015), except for the pHOS values for integrated programs, which are from HSRG (2014). PNI does not apply to segregated programs because by design pNOB is zero.

Natural Population		Hatchery Broodstock Management		
Designation	Status	Segregated	Integrated	
		pHOS	pHOS	PNI
Primary	Preservation	< 0.05	Not Specified	Not Specified
	Recolonization	< 0.05	Not Specified	Not Specified
	Local Adaptation	< 0.05	< 0.30	≥ 0.67
	Fully Restored	< 0.05	< 0.30	≥ 0.67
Contributing	Preservation	< 0.10	Not Specified	Not Specified
	Recolonization	< 0.10	Not Specified	Not Specified
	Local Adaptation	< 0.10	< 0.30	≥ 0.50
	Fully Restored	< 0.10	< 0.30	≥ 0.50
Stabilizing	Preservation	Current Condition	Current Condition	Current Condition
	Recolonization	Current Condition	Current Condition	Current Condition
	Local Adaptation	Current Condition	Current Condition	Current Condition
	Fully Restored	Current Condition	Current Condition	Current Condition

Table 3. Population designations, and pHOS, pNOB, and PNI target values based on Canada's Department of Fisheries and Oceans (DFO) review of HSRG principles (Withler et al. 2018). Although DFO provided both effective pHOS (pHOSeff) and census pHOS (pHOScensus), they used the pHOSeff for their calculations. pHOS values shown below are pHOSeff.

Natural Population Designation	Hatchery Broodstock Management			Comment
	PNI	pHOS	pNOB	
Wild	NA	≤ 0.03	NA	No within-basin hatchery production
Wild-Stray	NA	> 0.04	NA	No within-basin hatchery production
Integrated-Wild	≥ 0.72	≤ 0.28	≥ 0.72	Pop composed > 50% wild fish
Integrated-Transition	0.50 - 0.72	≤ 0.50	0.50 - 0.72	Greater wild than hatchery influence
Integrated-Hatchery	< 0.50	≥ 0.50	< 0.50	Gene flow from hatchery into wild

Table 4. A non-comprehensive summary of integrated Chinook hatchery programs operated by WDFW, showing the wild population Designations and Recovery Phases, and the hatchery Program Goals. For Run, Sp = Spring, Su = Summer, and F = Fall. For Designations (Design), P = Primary, C = Contributing, and S = Stabilizing. For Program Goals, C = Conservation, H = Harvest, and M = Mitigation. For the Recovery Phases, P = Preservation, R = Recolonization, LA = Local Adaptation, and FR = Fully restored. pNOB, pHOS, and PNI, Total Brood, and Escapement are for the Brood Year indicated. Total Brood is the total number of individuals spawned during that brood year. Meet HSRG – Now indicates if a hatchery program meets the HSRG target as established by HSRG (2015). Meet HSRG – Pre 2015 indicates if the hatchery program would have met the HSRG targets prior to HSRG eliminating target values for the Preservation and Recolonization Recovery Phases. Ratio B/E is the ratio of Total Brood per Escapement. Program size reflects the total number of brood year 2019 juveniles planned for release in 2020 or 2021. All data unpublished, WDFW HEAT Unit.

Hatchery	WDFW Region	Wild Population	Run	Design	Program Goal	Recovery Phase	pNOB	pHOS	PNI	Meet HSRG		Brood Year	Total Brood	Escape	Ratio B/E	Program Size
										Now	Pre 2015					
Methow-T.	2	Methow	Sp	P	C	P	0.55	0.21	0.72	Yes	Yes	2016	11	13,101	0.00	30,000
Chiwawa	2	Chiwawa	Sp	P	C	P	0.66	0.60	0.52	Yes	No	2015	109	1,836	0.06	144,000
Methow- M.	2	Methow	Sp	P	C	P	0.80	0.71	0.53	Yes	No	2015	96	1,353	0.07	133,249
Marblemount	4	Upper Skagit	Su	P	C	P	0.56	0.05	0.92	Yes	Yes	2015	90	10,706	0.01	200,000
Kendall Creek	4	NF Nooksack	Sp	P	C	P	0.00	0.77	0.00	Yes	No	2015	474	1,717	0.28	1,800,000[A]
Dungeness	6	Dungeness	Sp	P	C	P	0.25	0.75	0.25	Yes	No	2017	93	605	0.15	200,000
Elwha	6	Elwha	F	P	C	P	0.04	0.96	0.04	Yes	No	2017	1,016	1,892	0.54	2,700,000
Tucannon	1	Tucannon	Sp	P	C	R	0.79	0.67	0.54	Yes	No	2015	126	523	0.24	225,000
Lyons Ferry	1	Snake	F	P	M/C	R	0.36	0.74	0.33	Yes	No	2016	2,588	9,558	0.27	1,150,000
Dryden Pond	2	Wenatchee	Su	P	H	LA	1.00	0.06	0.94	Yes	Yes	2015	245	4,452	0.06	500,001
Washougal	5	Washougal	F	P	H	LA	0.28	0.57	0.33	No	No	2015	577	3,990	0.14	1,900,000
NF Toutle	5	Toutle	F	P	H	LA	0.17	0.70	0.20	No	No	2015	791	1,177	0.67	1,100,000
Naselle	6	Naselle	F	P[B]	H	LA	0.20	0.75	0.21	No	No	2016	1,076	2,383	0.45	2,500,000
Priest Rapids	3	Hanford Reach	F	P	H	FR	0.25	0.08	0.84	Yes	Yes	2017	5,668	73,759	0.08	7,299,543
Sol Duc	6	Sol Duc	Su	P	H	FR	0.12	0.10	0.54	No	No	2014	238	449	0.53	375,000[A]
Wallace	4	Skykomish	Su	C	H	R	0.08	0.36	0.19	Yes	No	2017	2,089	4,374	0.48	1,500,000
Lower Cowlitz	5	Cowlitz	F	C	H	LA	0.04	0.30	0.13	No	No	2015	1,691	6,060	0.28	2,400,000
Bingham Creek	6	Satsop	F	C	C	FR	0.30	0.15	0.67	Yes	Yes	2016	63	1,504	0.04	500,000
Forks Creek	6	Willapa	F	C[B]	H	LA	0.10	0.81	0.11	No	No	2016	2,306	2,995	0.77	350,000
Lake Aberdeen	6	Wynoochee	F	C	H	FR	0.18	0.00	1.00	Yes	Yes	2016	45	746	0.06	50,000
Soos Creek	4	Green/Duwamish	F	S	H	R	0.16	0.76	0.17	Yes	Yes	2017	3,250	8,357	0.39	5,500,000[A]
Issaquah	4	Sammamish	F	S	H	R	0.07	0.88	0.08	Yes	Yes	2016	1,336	1,247	1.07	3,000,000
Voights Creek	6	Puyallup	F	S	H	R	0.01	0.54	0.03	Yes	Yes	2017	1,685	2,012	0.84	1,600,000
George Adams	6	Skokomish	F	S	H	R	0.03	0.83	0.03	Yes	Yes	2016	3,483	1,342	2.60	3,900,000

[A] Includes recent increase in programs size to provide prey for Southern Resident Killer Whales (NF Nooksack: 500,000; Sol Duc: 55,000; Soos Creek: 2,000,000)

[B] Designations reflective of brood year 2016 data but Naselle recently redesignated as a Contributing population and Willapa recently redesignated as a Primary population

Table 5. Recent, emerging science on hatchery reform. Each study was classified according to whether it a) supported hatchery reform principles, b) ran contrary to hatchery reform principles, or c) was equivocal with respect to hatchery reform principals, but added depth to a hatchery-wild interaction phenomenon previously recognized as important.

Study	**Relevance to hatchery reform**	**Implications for hatchery reform**
Broodstock management		
(Hess et al. 2012; Janowitz-Koch et al. 2019)	Supports	Hatchery programs with high PNI can provide conservation benefits and limit negative fitness effects on wild fish
(Baskett and Waples 2013)	Supports	pHOS and selection in the hatchery relative to natural environment are important determinants of population fitness and demographics
(Christie et al. 2014a)	Supports	When spawning in the river, hatchery-origin fish from local or predominantly wild broodstock consistently have lower reproductive success than natural-origin fish
(Ford et al. 2016)	Supports	Evidence for genetic basis to fitness costs of hatchery propagation, replicating results of Hood Canal steelhead study (Araki et al. 2007). Increasing pNOB improves reproductive success of hatchery-origin fish spawning naturally.
(Ford et al. 2012)	Supports	Chinook salmon that were most productive when spawned in the hatchery yielded offspring that performed poorly when spawning in the river; emphasizes the difference between hatchery and river environments.
(Waters et al. 2015)	Supports	Integrated broodstock management with high pNOB and PNI limits divergence of hatchery from natural populations
(Courter et al. 2019)	Equivocal, adds depth	Abundance of adult hatchery summer steelhead not statistically correlated to wild winter steelhead productivity, contrasting earlier results of Kostow and Zhou (2006). Although wild winter steelhead do exhibit increase in abundance since roughly 2000, this trend cannot be attributed to the exclusion of hatchery adults.
(Willoughby and Christie 2017)	Supports	Duration (number of generations) of hatchery propagation affects fitness; a legacy of past gene flow from a hatchery into a natural population may minimize differences in fitness between hatchery-origin and natural-origin fish spawning naturally (upwardly bias estimates of RRS).
Program size		

(Ruggerone and Irvine 2018)	Supports	Aggregate hatchery plus natural abundance appears to approach or exceed ocean carrying capacity; the great majority of hatchery fish in the Pacific are Pink and chum salmon from Alaska, Russia, and Japan.
(Amoroso et al. 2017)	Supports	Increased pink salmon hatchery production in Prince William Sound has slightly increased MSY, but may have reduced productivity of wild populations
(Jones et al. 2018)	Supports	Increased coho salmon natural-origin abundance and diversified spawn timing two generations after termination of hatchery releases
(Scheuerell et al. 2015)	Equivocal, adds depth	Snake River spring/summer Chinook salmon conservation hatcheries did not appreciably increase natural-origin adult abundance; suggests careful evaluation of biological circumstances in which conservation hatcheries can be effective.
(Venditti et al. 2018)	Equivocal, adds depth	Snake River spring/summer Chinook salmon conservation hatcheries increased total natural spawning by adding hatchery-origin returns during supplementation, but there was no sustained increase in natural-origin abundance after supplementation was terminated; suggests careful evaluation of biological circumstances in which conservation hatcheries can be effective.
(Berejikian and Van Doornik 2018)	Supports	Increases in steelhead adult abundance and genetic diversity following a conservation hatchery characterized by excavation of naturally spawned embryos and natural rearing regimes
(Nelson et al. 2019a)	Equivocal, adds depth	No relationship between Chinook salmon population productivity and hatchery releases; emphasizes difficulty detecting hatchery-natural ecological interactions at broad spatial scales relative to other factors affecting productivity.
Rearing strategies		
(Berejikian et al. 2017; Tatara et al. 2017; Tatara et al. 2019)	Supports	Natural growth regimes in the hatchery can reduce artificial selection for body size and growth rate
(Spangenberg et al. 2014; Beckman et al. 2017; Harstad et al. 2018)	Supports	Natural growth regimes can increase smolt to adult survival, reduce early maturation rates, and may produce larger, older returning adults
(Fuss and Byrne 2002; Kavanagh and Olson 2014)	Supports	Low hatchery rearing density improves steelhead and coho adult returns
(Feldhaus et al. 2016)	Supports	Larger size at release did not result in improved survival

Release strategies		
(Snow et al. 2013)	Supports	Volitional releases reduce residualism and ecological interactions with natural populations at little cost to hatchery adult returns
(Rosenberger et al. 2013)	Supports	Offsite acclimation can increase migration rate following release, reducing potential for ecological interactions with natural-origin fish
(Clarke et al. 2010)	Supports	Offsite acclimation can improve survival and reduce out-of-basin adult stray rates
(Clarke et al. 2016)	Equivocal, adds depth	Short term (2-3 weeks) acclimation of fall Chinook did not improve adult returns or reduce stray rates
(Dittman et al. 2010)	Equivocal, adds depth	Spawning habitat quality cues may override imprinting to hatchery acclimation release sites, limiting ability to direct hatchery-origin fish to desired spawning location
(Dittman et al. 2015)	Supports	Exposing hatchery-spawned fish to waters originating from desired spawning locations early in life, during embryonic development, provides a promising alternative to offsite acclimation for imprinting homing cues
(Naman and Sharpe 2012)	Supports	Hatchery releases that minimize spatial and temporal overlap with natural populations can reduce predation rate
(Hughes and Murdoch 2017)	Equivocal, adds depth	Compared to natural-origin fish, hatchery-origin fish tended to spawn further downstream in lower quality habitats near acclimation sites, potentially explaining lower reproductive success. Emphasizes an “all-H” strategy for recovering natural populations, including protection and restoration of habitat.
Disease management		
(Rhodes et al. 2011; Ferguson et al. 2018)	Supports	Proactive disease management in hatcheries reduces potential for horizontal transmission to sympatric wild fish
(Kurath and Winton 2011)	Equivocal, adds depth	Review of the literature suggesting that, in the case of viral diseases, transmission from wild fish to fish contained in hatcheries is likely of greater impact than transmission from hatchery fish to surrounding natural populations.
(Ray et al. 2010; Hallett et al. 2012)	Supports	Proactive disease management in hatcheries reduces potential for horizontal transmission to sympatric wild fish
(Jakaitis 2014)	Supports	Illustrates the potential of fish hatcheries to amplify pathogen numbers, presumably of endemic origin. Supports efforts to secure water supplies that reduce introduction

		of endemic pathogens into a hatchery population where they can be amplified in number.

FIGURES

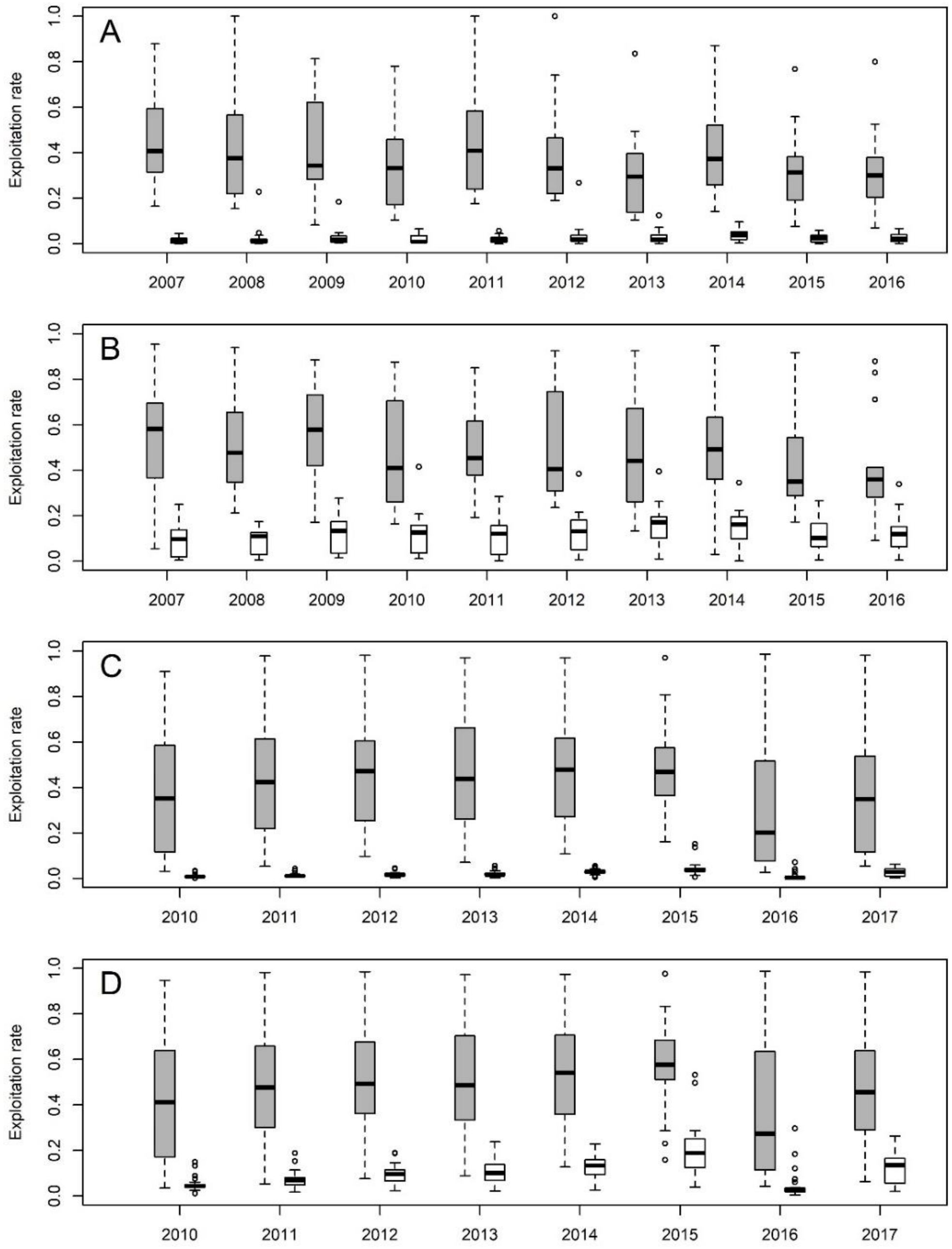

Figure 1. Estimated exploitation rates of A) unmarked Chinook salmon (N = 15 stocks), B) marked Chinook salmon (N = 15), C) unmarked coho salmon (N = 71), and D) marked coho salmon (N = 36). The gray boxes represent total exploitation rates whereas the white boxes represent the exploitation rate attributable to mark-selective fisheries. Black lines are medians, boxes are interquartile ranges, and the whiskers and points represent the remainder of the data. Estimates based on Fishery Regulation Assessment Model (WDFW unpublished). Chinook salmon stocks located in Puget Sound, coho salmon stocks from Washington State.

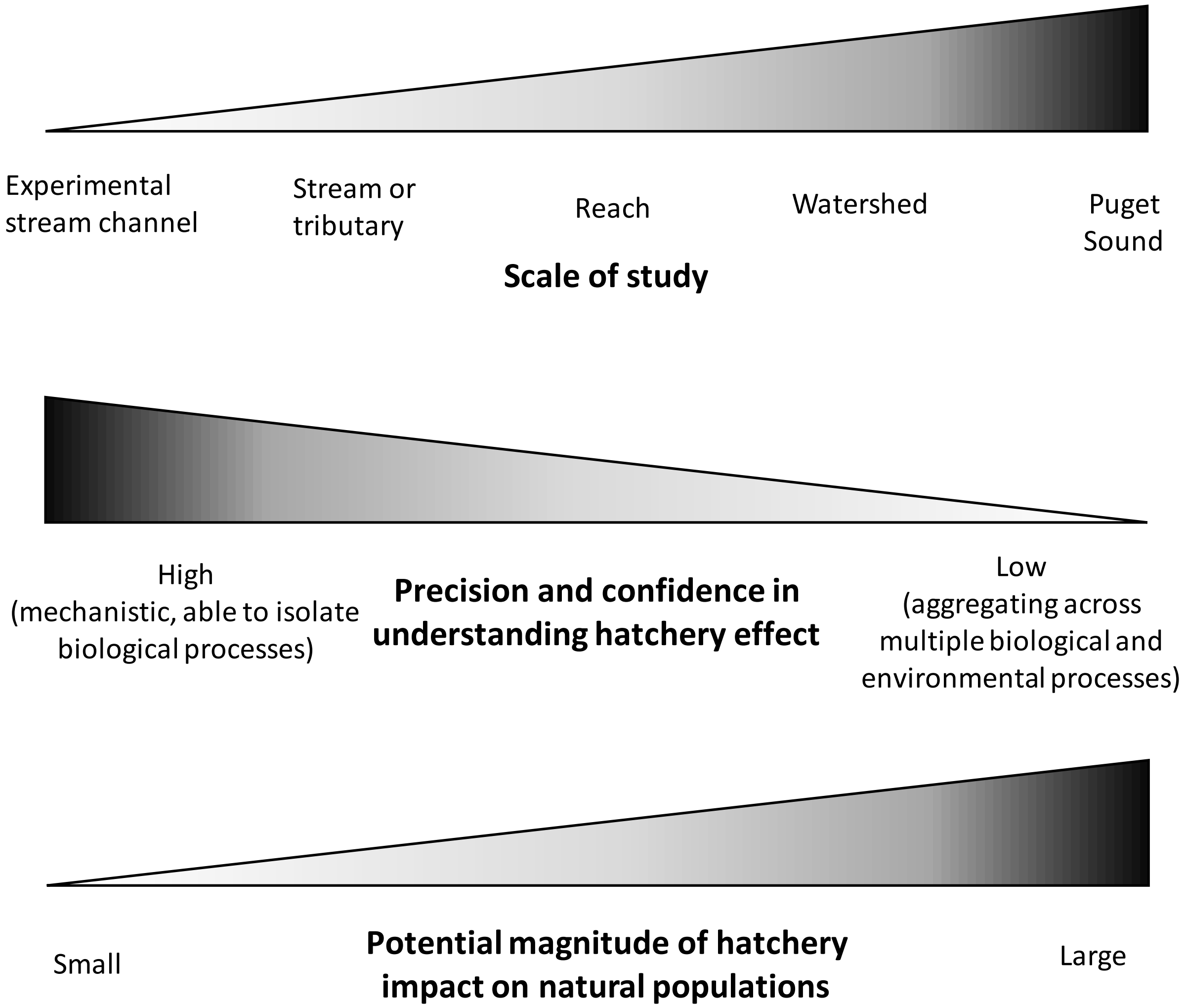

Figure 2. Trade-offs in studies of hatchery-wild interactions according to the spatial scale of investigation.

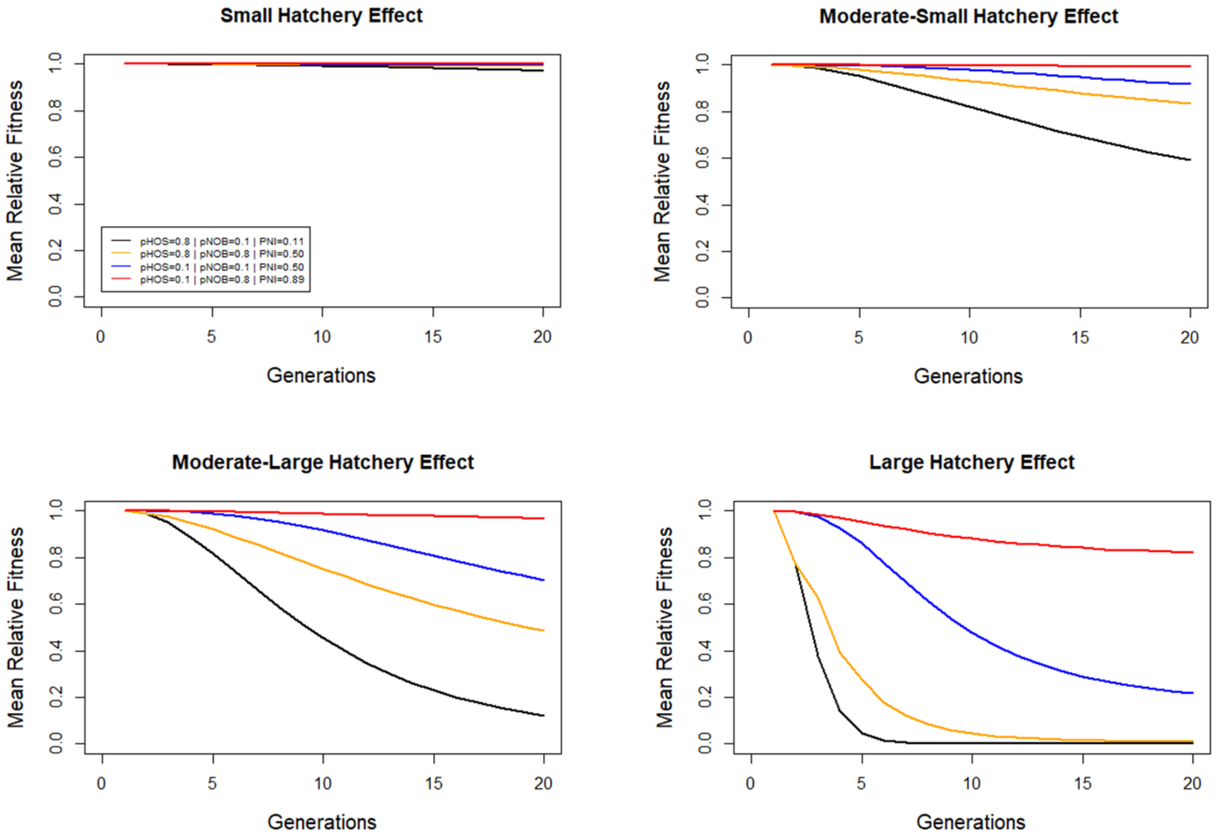

Figure 3. Mean relative fitness through 20 generations, based on Ford (2002). Mean relative fitness equal to 1.0 is maximum fitness for fish spawning in the wild. Mean relative fitness equal to 0.5 or 0.0 indicates that on average the natural spawning population has lost half or all of it fitness, respectively. Each plot shows results for the same set of pHOS and pNOB management combinations (legend upper left figure) for different hatchery effects (combination of selection strength and optimal phenotype differences; see Appendix 2). Heritability held constant at 0.3.

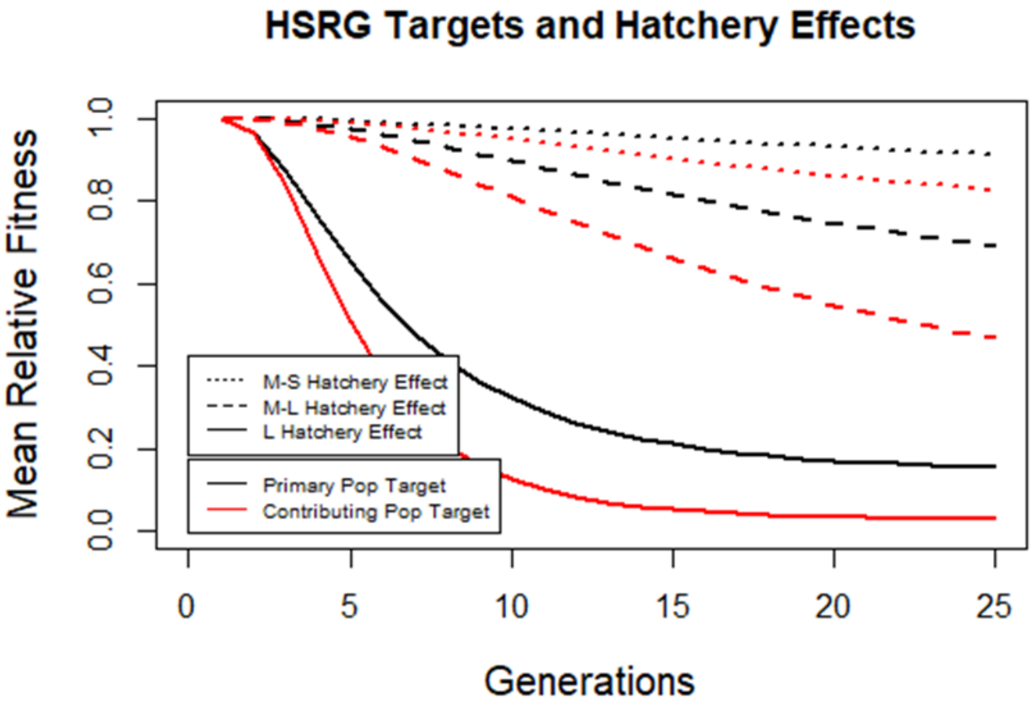

Figure 4. Mean relative fitness through 20 generations, based on Ford (2002), for three pairs of pHOS and pNOB values and hatchery effects. pHOS / pNOB values for Primary and Contributing populations are 0.30 / 0.60 and 0.30 / 0.30, respectively (Table 2). M-S, M-L, and L Hatchery Effects are Moderate-Small, Moderate-Large, and Large Hatchery Effects, respectively (Appendix 2).

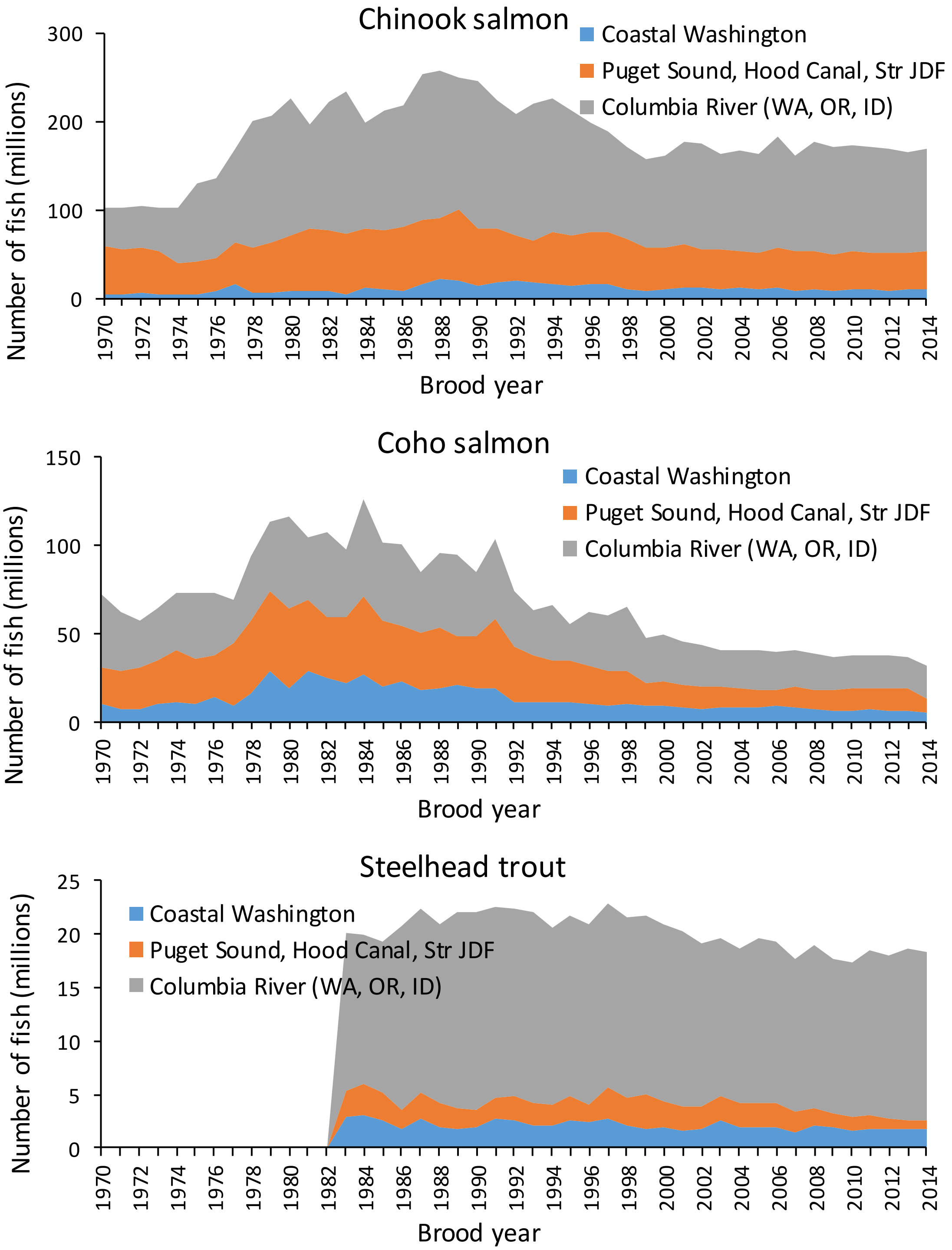

Figure 5. Trends in number of hatchery Chinook salmon, coho salmon and steelhead trout released from the Washington Coast, Hood Canal, Strait of Juan de Fuca and Puget Sound (Washington portion of the Salish Sea), and the Columbia River (inclusive of Washington, Oregon and Idaho). Data were accessed from RMIS and include releases from all sources (not just WDFW programs). RMIS steelhead data prior to 1983 are inaccurate and unreliable.

APPENDIX 1 – PUGET SOUND CHINOOK SALMON DEMOGRAHICS

Introduction

As a means to provide quantitative data underscoring our presentation of hatchery benefits, risks, and hatchery reform, here we describe population demographics of Puget Sound Chinook salmon. Our overall goal is to provide further depth to the concepts discussed in the hatchery reform science report. We provide a full accounting of adult demographics including harvest rates, total hatchery-origin plus natural-origin return to the river, total abundance of naturally spawning Chinook salmon, and the proportion of naturally spawning Chinook salmon produced in hatcheries (pHOS). We also compare watershed-scale abundance of natural-origin and hatchery-origin juvenile Chinook salmon.

We selected Puget Sound Chinook, previously identified as a distinct population segment of the species under the U.S Endangered Species Act (Myers et al. 1998; Ruckelshaus et al. 2006), for two primary reasons. First, both hatchery production and conservation efforts intended to improve natural population status consume significant tribal, federal, state, and local government resources in Puget Sound. Thus, Puget Sound exemplifies the challenge of providing hatchery benefits while minimizing risks (i.e., hatchery reform). Second, compared to species such as coho salmon and steelhead, Chinook salmon data quality tends to be higher.

Methods

We present Puget Sound Chinook salmon demographics according to the hierarchical structure of watersheds, harvest management units and natural populations. Only the Skagit and Puyallup watersheds contain multiple harvest management units, all other watersheds contain only a single management unit. Natural populations are those identified by Ruckelshaus et al. (2006). In some cases, multiple populations compose a single management unit. We also include independent hatchery stocks that are not associated with a historical population of Chinook salmon. In all cases, unless otherwise noted, numerical estimates reflect arithmetic means for the years 2012-2016.

We obtained exploitation rates, terminal run size estimates, and capacity estimates from harvest management documents and data sources. Total harvest rates across all fisheries (including terminal and pre-terminal) were based on the Fishery Resource Assessment Model validation run 6.2 (FRAM, WDFW unpublished). These estimates include the assumed adult equivalents of pre-terminal harvest of immature salmon, typically encountered in northern fisheries (Alaska and British Columbia). They also include incidental (bycatch) mortality associated with non-target salmon, such as post-release mortality of unmarked salmon in mark-selective fisheries. Because fisheries are typically constrained only by impacts to natural populations, we only present harvest rates on natural populations.

The terminal run size estimates were one of many inputs for FRAM, and represent the total hatchery-origin plus natural-origin adult return to the river, exclusive of pre-terminal fisheries. Salmon included in the terminal run size estimates might ultimately have been captured in freshwater fisheries, returned to hatcheries, or spawned naturally in the river. Freshwater capacity estimates, expressed in terms of adult Chinook salmon, were obtained from stock-recruit model fits in Management Unit Profiles (MUP) within PSIT and WDFW (2017) and Rebuilding Exploitation Rate analyses (NOAA unpublished).

Estimates of the total abundance of adult naturally spawning Chinook salmon, the proportion of naturally spawning fish that were hatchery-origin (pHOS), and the abundance of naturally spawning natural-origin salmon were obtained from WDFW's Salmon Conservation Reporting Engine (https://fortress.wa.gov/dfw/score/score/) or directly from WDFW biologists. The abundance of natural-origin juveniles was estimated in smolt traps positioned in major Puget Sound rivers. These traps are typically located downstream of most, if not all, spawning locations within a given watershed. In some cases, these traps estimate an aggregate of multiple populations. Hatchery release data were obtained from the Regional Mark Information System database (https://www.rmpc.org/). In some cases, multiple hatchery release sites were aggregated to facilitate direct comparison to natural-origin juvenile abundances.

Results and discussion

Puget Sound Chinook adult and juvenile abundances are presented in Tables A1-1 and A1-2. On average across years 2012 – 2016, approximately 216,000 adult Chinook salmon returned to river mouths and hatcheries in Puget Sound. Less than 20% of these fish (approximately 38,000) were estimated to spawn naturally in rivers; the remainder were enumerated in terminal fisheries or returns to hatchery facilities. Approximately 10% of the total adult return to Puget Sound was composed of natural-origin fish, with the remainder hatchery-origin Chinook salmon. Among natural-origin adult salmon, the majority returned to the Skagit River. Approximately 40% of the total adult return was associated with independent hatchery stocks not associated with a natural population.

Of the available capacity estimates, the Skagit watershed capacity was > 20,000, the Green and Snohomish watersheds were between 5,000 and 10,000 and all other watersheds were < 5,000. Terminal run sizes for all management units expect Skagit summer/falls and Stillaguamish approached or exceeded capacity estimates. By contrast, abundances of naturally spawning fish only approached or exceeded capacity estimates in the four of ten comparisons (Nooksack early, Skagit spring, Cedar, White spring). We note that a fishery management strategy aiming for maximum productivity would target spawning abundances less than capacity.

Hatchery-origin fish frequently spawn naturally in Puget Sound rivers, often in large numbers. Estimates of pHOS exceeded 20% in all watersheds except the Skagit. Hatchery-origin fish outnumbered natural-origin fish on the spawning grounds (i.e., pHOS > 50%) in 9 of 20 populations. Two populations inhabiting rivers without any releases of hatchery reared juveniles (Snoqualmie and Cedar) experienced pHOS > 20%.

In all watersheds except the Skagit, releases of hatchery-reared juvenile Chinook salmon outnumbered estimates of naturally produced juvenile Chinook salmon. Most Puget Sound watersheds released > 1 M hatchery-origin Chinook salmon; only Skagit, Stillaguamish, mid-Hood Canal and Dungeness watersheds released < 1 M fish.

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Table A1-1. Puget Sound Chinook demographics, Strait of Georgia and Whidbey basin MPGs. Unless otherwise noted, all values reflect arithmetic means for the years 2012-2016.

				Capacity			Adult naturally spawning abundance				Juvenile abundance	
Watershed	Management unit	Total harvest rate	Terminal Run Size (H + N)	Estimate	Ref	Natural population	Total abundance	pHOS	Natural-origin		Natural-origin	Hatchery releases
Strait of Georgia MPG												
Nooksack	Nooksack early	27 %	2,568	457	1	NF/Mid Nooksack	1,305	81 %	218		NA	1,170,079
			1,184			SF Nooksack	272	49 %	153			
	Nooksack & Samish fall	NA	36,661	NA	NA	NA	NA	NA	NA		NA	4,786,018
	San Juan Islands[A]	NA	NA	NA	NA	NA	NA	NA	NA		NA	594,567
Whidbey basin MPG												
Skagit	Skagit spring	20 %	4,865	1,683	2	Upper Sauk	1,215	2 %	1,188		3,679,258	823,530
						Suiattle	533	2 %	522			
						Cascade	301	NA	NA			
	Skagit summer/fall	40 %	14,646	22,366	2	Upper Skagit summer	10,606	4 %	10,180			
						Lower Skagit fall	2,335	5 %[B]	2,217[B]			
						Lower Sauk summer	612	8 %[C]	567[C]			
Stillaguamish	Stillaguamish	23 %	1,050	1,450	3	NF/summer	730	44 %	417		121,468	222,671
						SF/fall	98	22 %	78			
Snohomish	Snohomish	19 %	9,937	6,827	4	Skykomish summer	3,196	37 %	1,985		294,806	1,552,495
				3,588	4	Snoqualmie fall	1,061	22 %	813		61,659	0
	Tulalip Bay hatchery	NA	3,621	NA	NA	NA	NA	NA	NA		NA	2,281,362

[A] Glenwood Springs program

[B] pHOS only available in 2012, 2013 and 2015; natural-origin abundance 2014 and 2016 estimated pHOS averaged 2012, 2013 and 2015

[C] pHOS only available in 2012 and 2016; natural-origin abundance 2013 - 2015 estimated pHOS averaged 2012 and 2016

Table A1-2. Puget Sound Chinook salmon demographics, Central and South Sound, Hood Canal and Strait of Juan de Fuca MPGs. Unless otherwise noted, all values reflect arithmetic means for the years 2012-2016.

				Capacity			Adult naturally spawning abundance				Juvenile abundance	
Watershed	Management unit	Total harvest rate	Terminal Run Size (H + N)	Estimate	Ref	Natural population	Total abundance	pHOS	Natural-origin		Natural-origin	Hatchery releases
Central and South Puget Sound MPG												
Lake Washington	Lake Washington	26 %	6,779	NA[A]	NA	Sammamish	1,266	91 %	116		41,855[B]	1,691,097
				1,259	5	Cedar	1,250	30 %	913		915,091	0
Green	Green	26 %	14,295	8,971	6	Green	4,402	69 %	1,270		286,759	4,123,633
Puyallup	Puyallup fall	44 %	7,647	3,231	5	Puyallup	1,606	63 %	583		42,174	1,584,866
	White spring	19 %	3,739	954	1	White	2,180	72 %	565		7,793[C]	973,601
Nisqually	Nisqually	46 %	24,454	NA[D]	NA	Nisqually	1,585	51 %	726		103,437	3,760,382
	Mid-Sound hatchery[E]	NA	9,417	NA	NA	NA	NA	NA	NA		NA	2,117,802
	South Sound hatchery[F]	NA	16,798	NA	NA	NA	NA	NA	NA		NA	5,862,645
Hood Canal MPG												
Mid-Hood Canal	Mid-Hood Canal	23 %	358	NA[D]	NA	Mid-Hood Canal	342	NA	NA		2,886[G]	78,225[H]
Skokomish	Skokomish	58 %	30,465	NA[D]	NA	Skokomish	1,176	80%	205			4,086,004
	Hoodsport hatchery	NA	23,213	NA	NA	NA	NA	NA	NA		NA	2,753,818
Strait of Juan de Fuca MPG												
Dungeness	Dungeness	12 %		NA[D]	NA	Dungeness	291	71 %	96		54,513	194,655
Elwha	Elwha	13 %		NA[D]	NA	Elwha	2,163	95 %	112		54,200[I]	2,495,623[J]

[A] Sammamish population has never reached replacement, stock-recruit curve fitting thus unreliable (PSIT and WDFW 2017)

[B] Abundance estimate represents only Bear Creek, a tributary of the Sammamish River and only a portion of natural population

[C] White natural estimate only from 2016

[D] No stock-recruit curve fit to empirical data in PSIT and WDFW (2017) MUP

[E] Includes Grovers and Gorst hatchery programs

[F] Includes Minter, Chambers, McAllister, Deschutes and Coulter hatchery programs

[G] Abundance estimate represents only Duckabush River, one of three rivers in the Mid-Hood Canal population

[H] Hatchery releases only into Hamma Hamma River, one of three rivers in the Mid-Hood Canal population (terminated 2016)

[I] Elwha natural estimates only from 2014-2016

[J] Includes 0-372,646 annual releases into Morse Creek, an independent tributary of the Strait of Juan de Fuca (terminated 2016)

Table A1-3. Sources for capacity estimates.

Number	Stock-Recruit model	Reference
1	Beverton-Holt	Nooksack Rebuilding Exploitation Rate analysis, Sept 2017 NOAA unpublished report
2	Ricker	PSIT and WDFW 2017
3	Hockey-stick	Stillaguamish Rebuilding Exploitation Rate analysis, May 2017 NOAA unpublished report
4	Beverton-Holt	Snohomish Rebuilding Exploitation Rate analysis, Sept 2017 NOAA unpublished report
5	Beverton-Holt	PSIT and WDFW 2017
6	Beverton-Holt	Green Rebuilding Exploitation Rate analysis, Sept 2017 NOAA unpublished report

APPENDIX 2 – HATCHERY EFFECT PARAMETER DESCRIBED

For a given PNI (and pHOS, pNOB combination) there is a range of fitness-loss potential depending on what selection strength and phenotypic trait optima differences are assumed. In the figure below we provide the mean relative fitness for selection strength (omega-wild in Ford 2002) and phenotypic trait optima difference (theta in Ford 2002) combinations for four pHOS and pNOB management options.

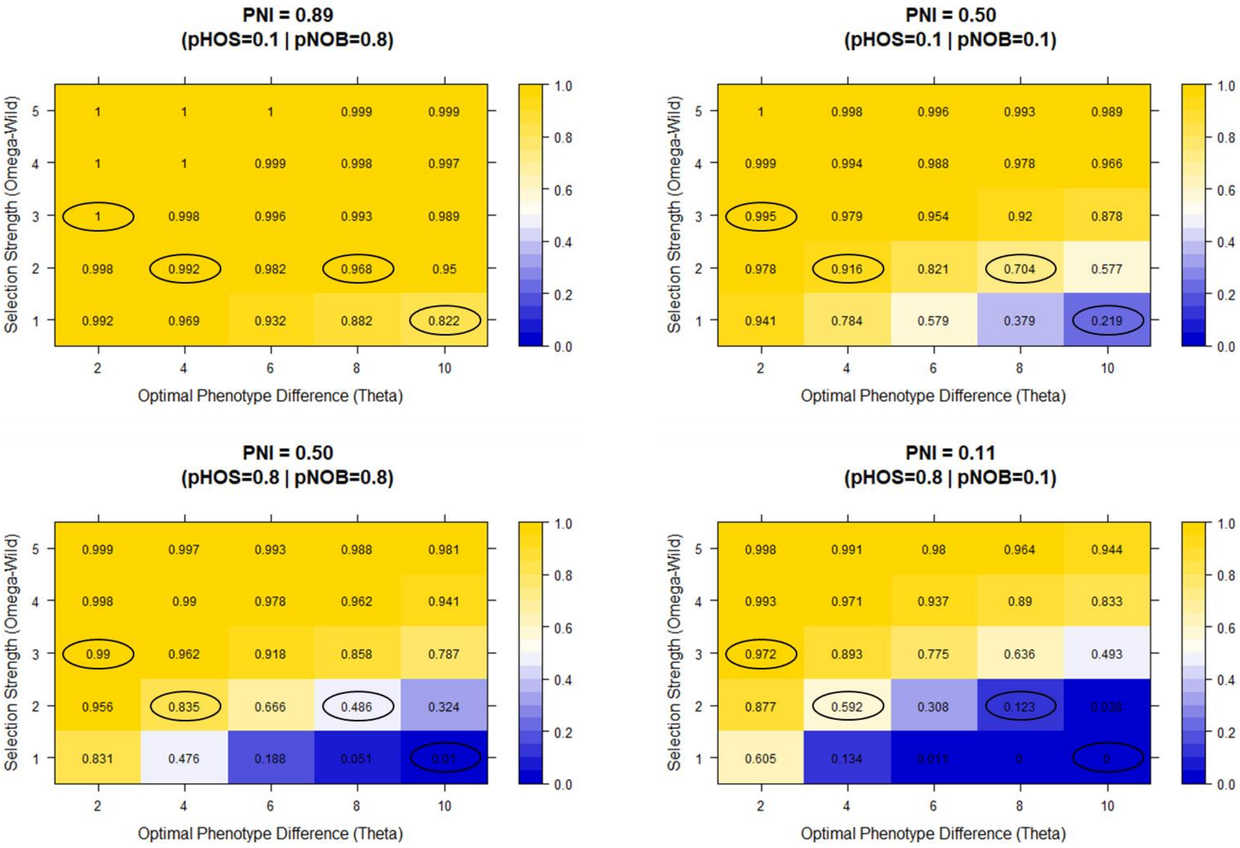

Figure A2-1. Mean relative fitness values for selection strength and phenotypic trait optima difference combinations for four pHOS and pNOB management options. Heat map ranges from a mean relative fitness 1.0 (gold) to 0.0 (blue). To simplify our discussion of fitness and selection, we designated four selection strength and trait difference combinations as small, moderate-small, moderate-large, and large hatchery effects, shown as the four ellipses left to right, respectively, in each plot.

APPENDIX 3 – COMPARISON OF pHOS and pNOB BROODSTOCK MANAGEMENT OPTIONS ACROSS A RANGE OF PARAMETER VALUES

To compare pHOS and pNOB broodstock management options across a range of parameter values, we ran the Ford model for each combination of the following parameters, for a total of 10,000 runs of the model, each run starting at generation 1 with no hatchery, and continuing through 20 generations.

- Selection strength values (omega in Ford 2002): [1, 2, 3, 4, 5]
- Difference in optimal trait values (theta): [2, 4, 6, 8, 10]
- Heritabilities: [0.2, 0.3, 0.4, 0.5]
- pHOS: [0.1 to 1.0 in 0.1 intervals]
- pNOB: [0.1 to 1.0 in 0.1 intervals]

For each run of the model, we recorded the log of mean relative wild fitness, and plotted the fitness value for specific pairs of pHOS and pNOB combinations across parameter space and compared those fitness values with other pNOB and pHOS combinations (Figure A3-1). Specifically, we compared each pHOS and pNOB combination ("New" broodstock management) to a baseline combination ("Current" broodstock management). The relationship between Current option and each New option was established by plotting, for each parameter combination, the fitness values for the Current option (x-axis) versus the fitness values for the New option (y-axis). For each comparison, the filled circles in Figure A3-1 represent specific combinations of parameter values (100 different combinations, each represented by a single filled circle) and the line is the least square regression of these points. Figure A3-1 shows four sets of comparisons; in each plot the black line is the baseline combination compared with itself. The other lines in each plot are different pHOS and pNOB combinations compared with the baseline. The further a New broodstock management line is from the black line (i.e., the shallower the line's slope), the greater the fitness gain compared with baseline. For example, in plot D, we compared the two PNI = 50 and the one PNI = 0.89 lines to the baseline PNI = 0.11 line. As with Figure 3, fitness increases with increasing PNI, but there is a greater fitness benefit when we decreased pHOS from 0.8 to 0.1 (blue line) compared with when we increased pNOB from 0.1 to 0.8 (red line), and these results are across all combinations of selection strength, optimal phenotype difference, and heritability values. The set of PNI values are the same in plots A – C, but the pHOS and pNOB values increase by a multiple of two from plots A – C. Across these three plots, the slopes of the lines remain constant, but the lines are extended as pHOS and pNOB increase.

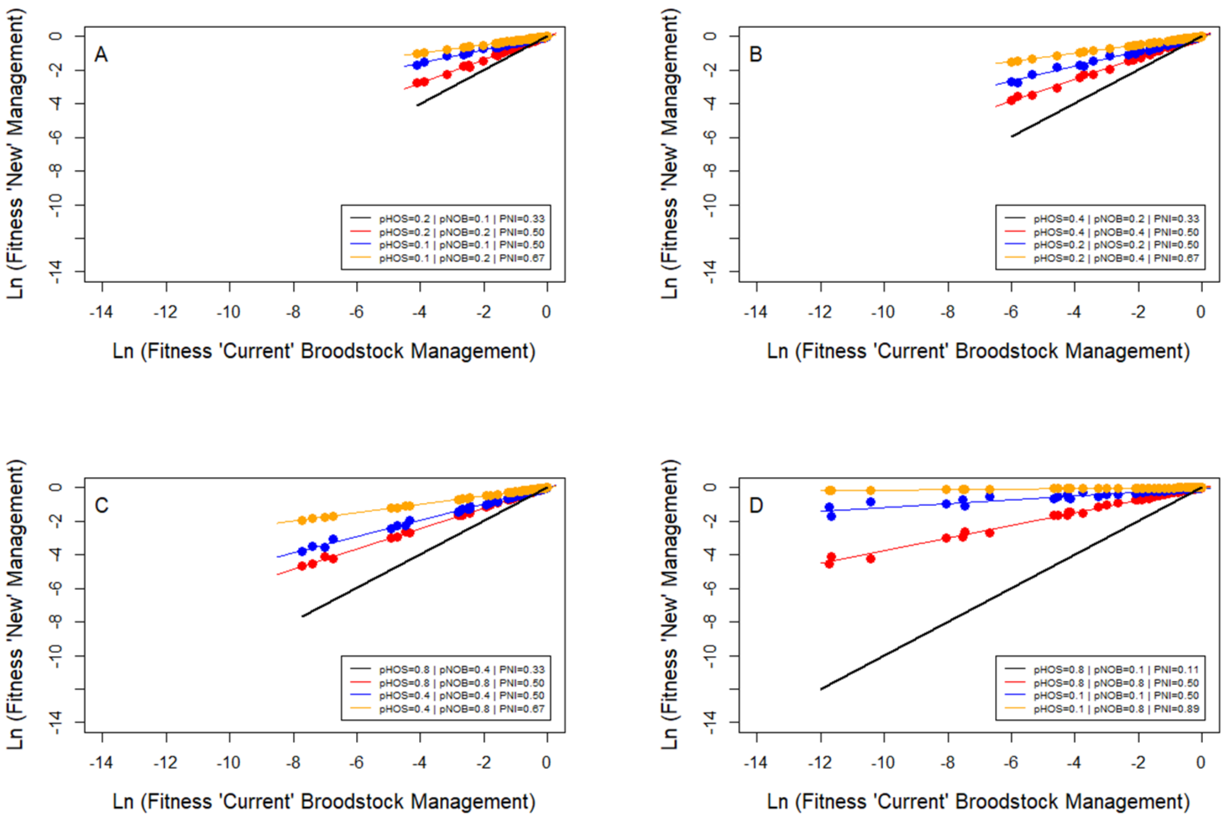

Figure A3-1. Comparison of the fitness values in the wild environment though 20 generations among the same broodstock management combinations as in Figure 3. The "Current" broodstock management combination for each plot is the black line (PNI = 0.33, with different pHOS and pNOB combinations for plots A-C, and PNI = 0.11 in plot D). The remaining three other combinations ("New" management; red, blue, and orange lines) are compared with the current combination. The black line shows the current management combination compared with itself and is indicated as a solid diagonal line. Since all three New management options result in higher fitness than the Current management option, the red, blue, and orange lines are each above the black diagonal line.

APPENDIX 4 – THE DEMOGRAPHIC MODEL

Our implementation of the Ford (2002) demographic model, based on Busack (unpublished R-script), is new and has not be rigorously tested or reviewed. We provide below a brief discussion of the salient parameters and technical details, then we provide descriptions and results from several runs of the model.

Recruitment

For wild population recruitment we used the Beverton-Holt spawner-recruit function, modified by the wild fitness value generated by the Ford (2002) model. If density dependent mortality occurs before selection we used equation (1) as the recruit function, and if density dependent mortality occurs after selection we used equation (2).

$$n_{w(t+1)} = ((n_{w(t)} r_w) / (1 + n_{w(t)}\, r_w / k_w)) W_{w(t)}\,, \tag{1}$$

$$n_{w(t+1)} = ((n_{w(t)} W_{w(t)}) r_w) / (1 + n_{w(t)}\, r_w / k_w)\,, \tag{2}$$

with $n_{w(t)} =$ wild population size in the current generation, $n_{w(t+1)} =$ wild recruitment, $k_w =$ wild carry capacity, $r_w =$ wild growth rate, and $W_{w(t)} =$ mean relative fitness in the wild. Since the fitness value ranges from 0 to 1, and rarely is fitness equal to one, including wild fitness in the recruit function usually reduces recruitment.

As we have modeled it, hatchery recruitment is not density dependent, and is designed to generate a surplus of fish beyond what is needed for broodstock and natural spawning; that is, generate a surplus of fish for whatever is the intended purpose of the hatchery (e.g., harvest). The recruitment function for the hatchery population is conditional:

If $n_{h(t)} < k_h$, we used equation (3) if density dependent mortality occurs before selection, or equation (4) if density dependent mortality occurs after selection. If $n_{h(t)} \geq k_h$, we used equation (5).

$$n_{h(t+1)} = (n_{h(t)} r_h) W_{h(t)}\,, \tag{3}$$

$$n_{h(t+1)} = (n_{h(t)} W_{h(t)}) r_h\,, \tag{4}$$

$$n_{h(t+1)} = k_h r_h W_{h(t)}\,, \tag{5}$$

with $n_{h(t)} =$ hatchery adult returns in the current generation, $n_{h(t+1)} =$ hatchery recruitment, $k_h =$ broodstock size, $r_h =$ growth rate, and $W_{h(t)} =$ mean relative fitness in the hatchery. Unless stated differently, we used the following demographic parameters in the recruit functions:

- Wild population recruitment rate (r_w): 10

- Wild population carry capacity (k_w): 1000
- Hatchery recruitment rate (r_h): 50
- Hatchery broodstock size (k_h): 300

Wild Chinook recruitment rates today are considerably less than 10 recruits per spawner. Likewise, the hatchery recruitment rate is likely less than 50 recruits per broodstock fish. Our justification for using these high growth rates was to start the wild population at a point close to carrying capacity, which was arbitrarily set to 1000 fish. The hatchery growth rate was set arbitrarily at five times the wild growth rate, but mainly for the purpose of generating a sufficient number of fish in excess of what was needed as broodstock and for pHOS. Using these parameters and the hatchery recruit function, the maximum hatchery recruitment would be 15,000 adult fish, if the number of adult hatchery returns was greater than broodstock size, and if the hatchery fitness value was equal to one.

pHOS, pNOB, and number of natural origin fish removed for broodstock

We limited the number of fish removed from the wild population to 80% of the wild population, unless that resulted in the remaining wild population to be less than 100 individuals. That is, if the wild population was less than 500 fish or fewer we limited the number of fish removed from the wild population to 20% of the wild population.

One important difference between the Ford phenotypic model and the Ford demographic model, including its implementation used here, is that in the Ford phenotypic model the hatchery and wild populations are assumed to be of infinite size, and therefore pHOS and pNOB can be set at specific, non-changing values (Ford 2002). In the demographic model we establish target pHOS and pNOB values, but the actual values change based on the dynamics of population growth and fitness.

Scenarios – Application of the demographic model

Below we present five different scenarios intended to demonstrate how pHOS and pNOB interact with broodstock size to affect hatchery and wild recruitment and abundance, and possibly the viability of wild populations. In the first scenario we start with target pNOB and pHOS values of 0.5 and 0.5 (PNI = 0.5). Our goal here was not to use as an example any existing Chinook hatchery program. Most of the hatcheries shown in Table 4 have been in operation for several decades, and the existing pHOS and pNOB values will reflect that lengthy period of production. We used this first scenario to see how the parameters interacted. In particular, we were interested in how pHOS, pNOB, interacted with recruitment, and if changes in recruitment and natural spawning size resulted in changes in pHOS and pNOB.

The second scenario differs from the first only in the target pNOB and pHOS values, which we set at 0.6 and 0.3, respectively (PNI = 0.67), the HSRG recommended target values for Primary populations. The point of this second scenario was to compare the demographic outcomes between a hatchery program with a PNI = 0.5, where the wild and hatchery selective influences are, in theory, equal (first scenario), and a hatchery program in which wild selective influences are greater than those of the hatchery environment (second scenario).

The objective for the third scenario was to see if we could recover a natural spawning population so that the natural-spawning population's fitness and recruitment would reflect more the natural environment rather than the hatchery environment; that is, a self-sustaining wild population that does not rely on recruits from hatchery production. This third scenario has three parts. We start with the situation described in the first scenario (pHOS = 0.5; pNOB = 0.5). We let that population run for 19 generations, and in the 20th generation we made the following changes:

Scenario 3A: pHOS = 0.30; pNOB = 0.6
Scenario 3B: pHOS = 0.30; pNOB = 0.6; reduce broodstock size from 300 to 100
Scenario 3C: pHOS = 0.15; pNOB = 0.6; reduce broodstock size from 300 to 100

Scenarios 1 and 2, and the parts of scenario 3 (A, B, and C) each begin with the inception of the hatchery, where, by definition, 100% of the broodstock and wild populations is of natural origin (pNOB = 1.0 and pHOS = 0.0; see Figure A4-1, upper right plot, Generation 1 – the left most portions of the red and blue lines). For all scenarios we set the hatchery effect slightly larger than Moderate-Large (difference in phenotype trait optima = 5, selection strength = 1; see Appendix 2), and heritability to 0.5.

Scenario 1 – Within a few generations of establishing the hatchery population, pNOB declined to the target value of 0.5, and was able to be held at the level through nearly 20 generations, but the decline in the number of natural-origin natural spawners eventually forced pNOB down to 0.02. Likewise, pHOS was maintained briefly at the target value 0.5, but to maintain the number of natural spawners near carrying capacity, eventually most of the natural spawners were of hatchery-origin, resulting in a pHOS = 0.975 (Figure A4-1). At the growth rate and broodstock size used in this scenario, and the high mean fitness of hatchery spawners, the hatchery population reached 15,000 recruits, of which nearly 300 would be used as broodstock, nearly 1000 spawning naturally (calculated as carrying capacity minus natural-origin spawners), and the remainder removed from the model (i.e., available for harvest or surplus at the hatchery, but not for HOS). These results are specific to the parameters we used in the model, and these parameters may or may not realistically represent a hatchery-wild system initiated 20 generations ago. However, the example demonstrates the interaction pHOS, pNOB, fitness, recruitment, and natural spawners.

Scenario 2 – The results here are strikingly different than for scenario 1 (Figure A4-2): the model stabilized with the natural spawning population composed of 70% natural-origin spawners (1-pHOS) (Figure A4-2). In addition, the total number of natural spawners was limited to 60% of the carrying capacity since the model required that pHOS be held at 0.3 if there were a sufficient number of natural-origin recruits. The number of hatchery-origin recruits declined to roughly 3500 because the fitness of hatchery spawners declined with the increased pNOB. Among the interesting results of this scenario are the relationships among a stable pNOB = 0.6, the fitness of the hatchery population, and the decline in hatchery recruitment from the 15,000 seen in scenario 1. The ability to maintain a stable pNOB = 0.6 was in part enabled by forcing a low pHOS, which maintained a relatively high wild fitness and natural recruitment. Although the high pNOB is an important component to maintain a relatively healthy wild population, the need to achieve it can limit hatchery production, which may affect harvest if that was the goal of the hatchery program.

Scenario 3 - Scenario 3A resulted in no change from the baseline conditions (scenario 1, Table A4-1), perhaps because at generation 20 pHOS was already greater than 0.3 to support a natural spawning population, and pNOB was already below 0.6 due to an insufficient number of natural-origin recruits to support a higher pNOB (see Figure A4-1). The results from Scenario 3A may be due to model constraints imposed to prevent the extirpation of the natural spawning population. Scenario 3B provided a slight improvement over baseline conditions, with increased natural recruitment, increased pNOB and decreased pHOS, increased mean fitness in the wild, but also resulted in a reduction of the number of hatchery-origin recruits, which was anticipated based on the results from Figure A4-2 (Table A4-1). Finally, Scenario 3C provided recovery for the natural spawning population by severely reducing pHOS. The number of natural spawners was reduced to below carrying capacity (865), but that number is close to the equilibrium value of 900 spawners for a wild population with the same carrying capacity and growth rate, but with no hatchery. This scenario also produced high natural recruitment, high mean fitness in the wild, but a relatively low number of hatchery recruits, leaving only approximately 500 fish after hatchery and natural spawners were removed (Table A4-1).

We highlight several caveats concerning the demographic model results. First, the model, and our implementation of the model, need peer-review, and more expansive testing across parameter space. Second, we used relatively high growth rates for both the wild and hatchery populations, and the model is sensitive to changes in these growth rates. Third, for simplicity, we presented only the results for the density dependent mortality before selection option, and the results may differ if we implemented the density dependent mortality after selection. Fourth, we assumed that we have the ability to control pHOS. With most hatchery programs we cannot control pHOS to a large extent, and we could have run the model under those conditions. Finally, recovery of the natural spawning population, as described above for Scenario C, depends on the fitness of the population, and may also be a function of a relatively high growth rate used in the model. In the model, fitness is a function of a single phenotypic trait (Ford 2002). However, regardless of whether fitness is from a single or multi-trait phenotype, the model does not account for the long-term decline and eventual absence of natural recruitment and the associated loss of alleles that may be important to fitness in the wild when the natural spawning population is composed mostly of maladapted hatchery-origin individuals. The absence of those alleles important to fitness in the wild would at best delay and may ultimately prevent population recovery.

Comparing the efficacy of improving demographic and fitness conditions in a wild population by changing broodstock size, and pNOB and/or pHOS

Our last application of the demographic model was used to compare changes in natural recruitment, recruit per spawner, fitness, and pHOS, with changes in hatchery broodstock size, and target pNOB and pHOS (Figure A4-3). We used the same combinations of pHOS and pNOB as in Figure A4-1. Each parameter combination was a separate run of the model and began with the inception of the hatchery, as in scenarios 1 and 2. We used the initial run with target pNOB = 0.1 and pHOS = 0.8 (PNI = 0.11) as baseline and compared each subsequent run to these baseline results. Decreasing pHOS alone or in combination with increasing pNOB had greater positive effects on natural recruitment, recruit per spawner, and fitness, and with a lower pHOS than increasing pNOB alone, compared with baseline (Figure A4-3). There were no differences in the results between broodstock size of 300 or 100 when pHOS alone was decreased; however, when pNOB was increased, there was greater natural recruitment, recruit per spawner, and fitness, and lower pHOS when broodstock size was 100 compared with 300 (Figure A4-3).

Table A4-1. Demographic and fitness results following Generation 70, from three alternative management scenarios, compared with conditions in Figure A4-1 (Control). The parameter values for each of the scenarios are in the upper part of the table, with the parameter values that differ from the Control in bold italic typeface. For each analysis, density dependent mortality occurred before selection and pHOS was controlled.

Scenario	**Control**	**3A**	**3B**	**3C**
Target pHOS	0.5	***0.3***	***0.3***	***0.15***
Target pNOB	0.5	***0.6***	***0.6***	***0.6***
Carrying Cap. Wild	10	10	10	10
Growth Rate Wild	1000	1000	1000	1000
Broodstock Size	300	300	***100***	***100***
Growth Rate Hatchery	50	50	50	50
Change @ Gen	Control	20	20	20
Total natural spawning	1,000	1,000	1,000	865
Natural-origin	25	25	166	735
Hatchery-origin	975	975	834	130
Natural recruitment	31	31	226	795
Hatchery recruitment	14,979	14,979	2,433	736
Mean fitness wild	0.03	0.03	0.25	0.89
Mean fitness hatchery	1.00	1.00	0.49	0.15
pHOS	0.98	0.98	0.83	0.15
pNOB	0.02	0.02	0.60	0.60

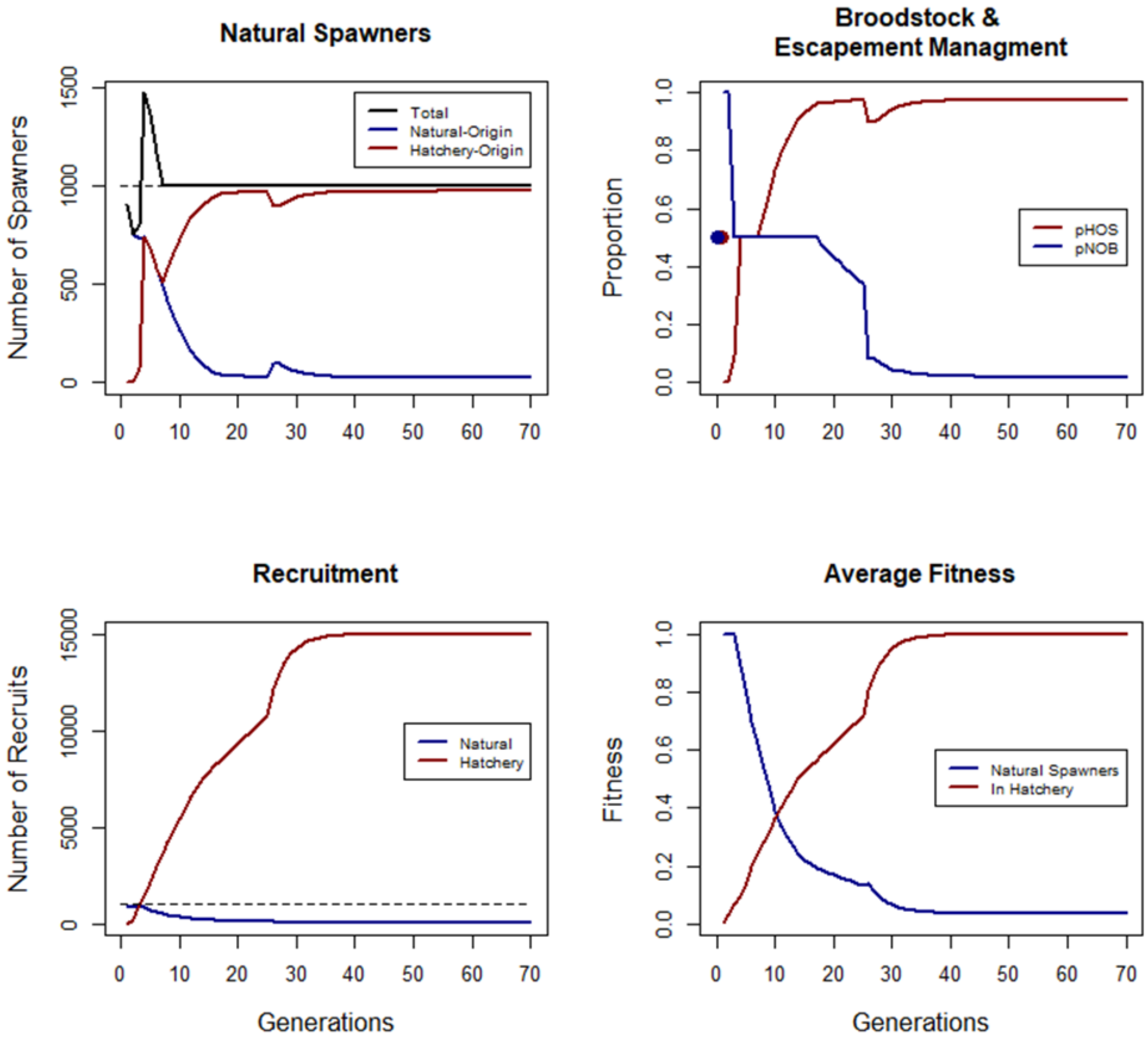

Figure A4-1. Results from an application of the demographic model using the following starting conditions: target pHOS = 0.5 and target pNOB = 0.5 (represented as the red and blue filled circles, respectively, in the upper right panel); hatchery effect slightly larger than Moderate-Large (difference in phenotype trait optima = 5, selection strength = 1; see Appendix 2); wild carrying capacity = 1000; wild growth rate = 10; broodstock size = 300; hatchery growth rate = 50; heritability = 0.5; density dependent mortality before selection; pHOS controlled; natural spawning population = 900 (Beverton-Holt equilibrium value using the above wild carrying capacity and growth rate values, and no hatchery); hatchery broodstock = 0 (model starts with no hatchery population). Natural and hatchery recruitment curves are total recruitment from the wild and hatchery environments, respectively. Dashed lines in the Natural Spawners and Recruitment panels represent the carrying capacity in the wild environment.

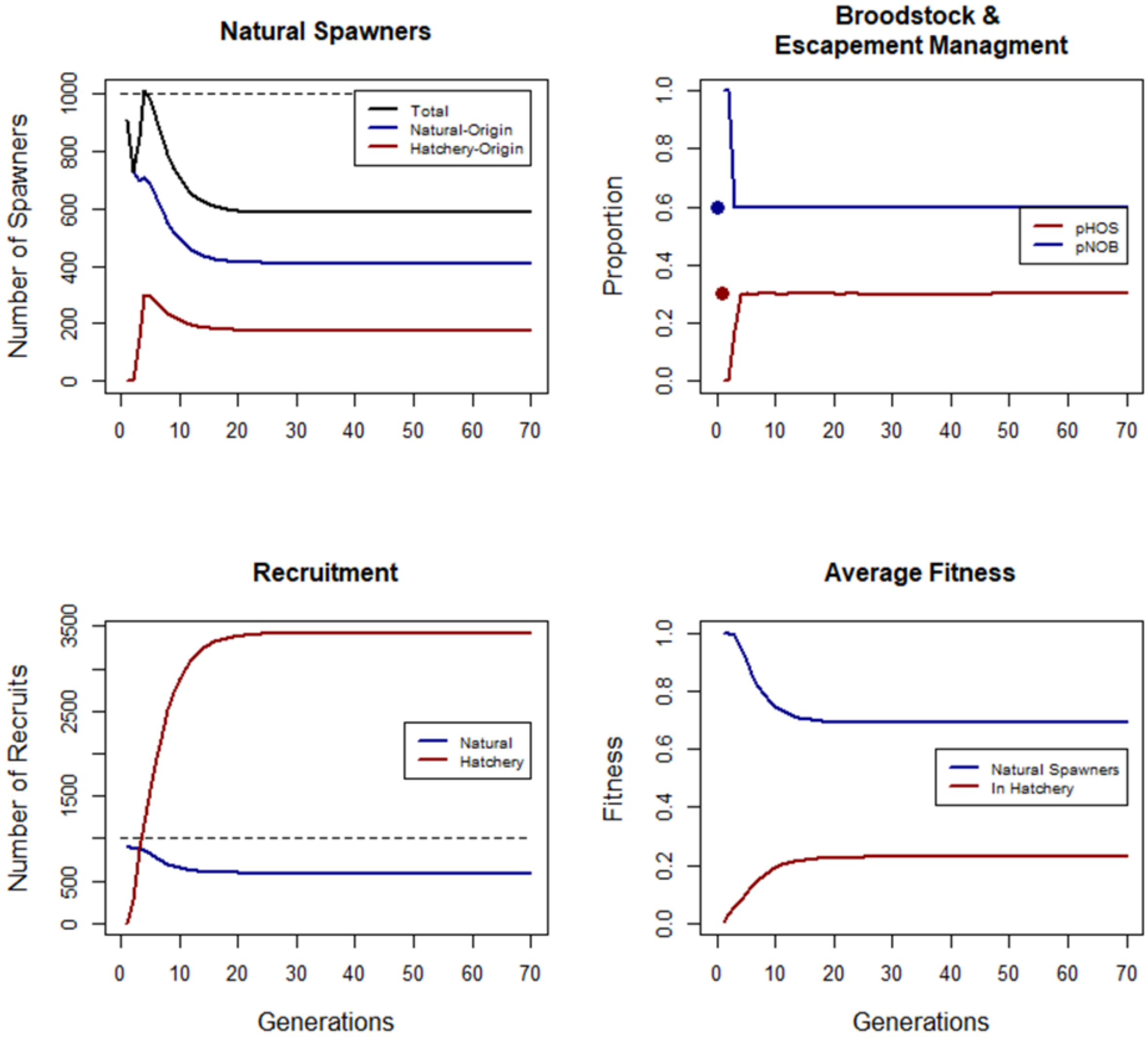

Figure A4-2. Same as Figure A4-1, except target pHOS = 0.3 and target pNOB = 0.6.

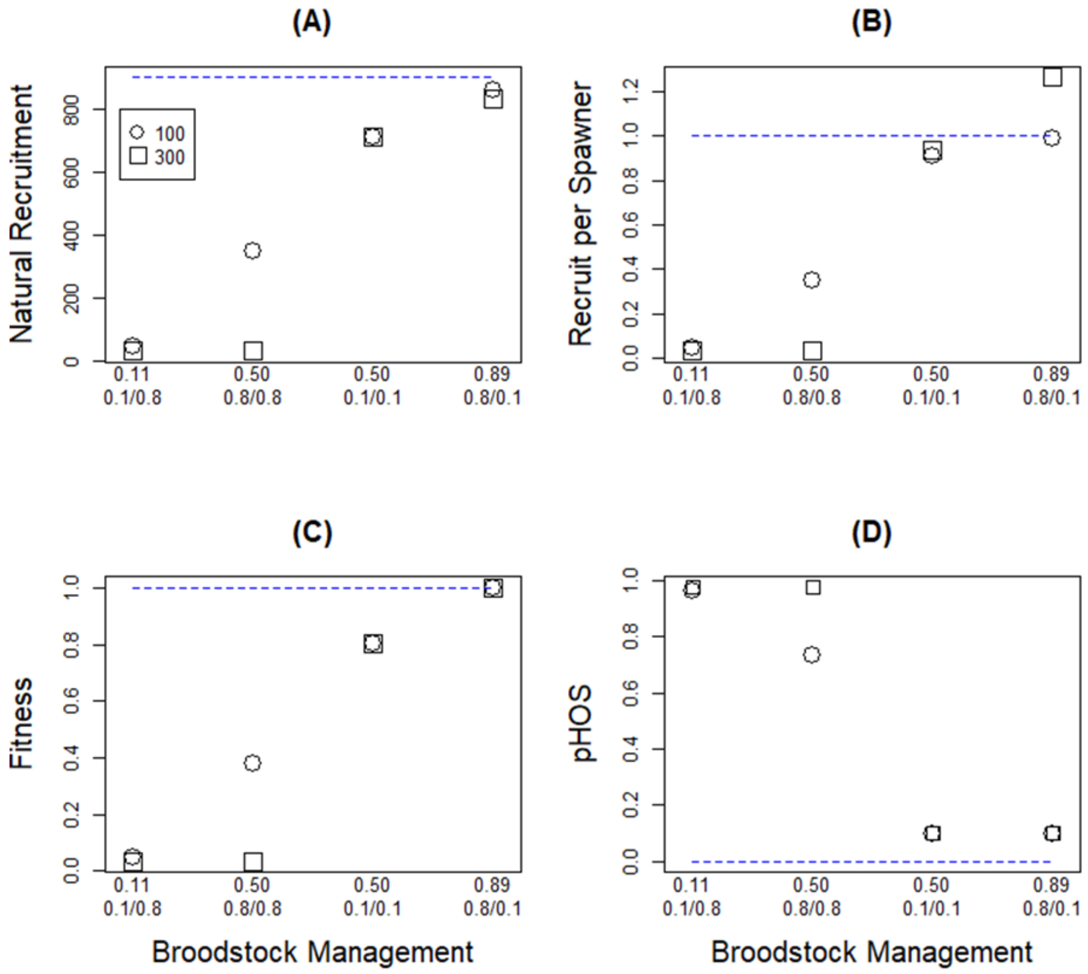

Figure A4-3. Similar to Table A4-1, demographic and fitness results following Generation 70, comparing four alternative broodstock management scenarios (x-axis). Broodstock management labels are the target values for PNI (upper value), and pNOB / pHOS (lower values, respectively). Symbols are broodstock size (legend upper left plot). Blue dashed lines are the results for a system without a hatchery. Parameter values held constant cross all four scenarios: hatchery effect slightly larger than Moderate-Large (difference in phenotype trait optima = 5, selection strength = 1; see Appendix 2); wild carrying capacity = 1000; wild growth rate = 10; hatchery growth rate = 50; heritability = 0.5; density dependent mortality before selection; pHOS controlled; natural spawning population = 900 (Beverton-Holt equilibrium value using the above wild carrying capacity and growth rate values, with no hatchery); and hatchery broodstock = 0 (model starts with no hatchery population).