Annotated Bibliography: Risks and Benefits of Salmonid Hatcheries

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Note: This bibliography is not intended to be complete or comprehensive. The following references are our attempt to provide a broad-brush and objective view of the issues concerning the risks and benefits of salmonid hatchery programs in Washington State. Undoubtedly, we have omitted important studies or someone's favorite set of references. If we have, this was unintentional and most-likely caused by our desire to keep this bibliography as succinct and relevant as possible.

Hazards and Risks

Burgman, MK. (2007). *Risks and Decisions for Conservation and Environmental Management*, Cambridge University Press. 488 + xii Pages

Outlines how to conduct environmental risk assessments. Chapters include discussions on values, perception, uncertainty, hazard assessment, inference, decisions, and risk management.

Busack, CA and KP Currens. (1995). Genetic risks and hazards in hatchery operations: Fundamental concepts and issues. *American Fisheries Society Symposium* 15: 71-80

As concern over erosion of genetic diversity in fish stocks has increased over the years, so has concern about the role of hatcheries in influencing genetic change. Whereas genetic concerns regarding hatchery operations have tended to emphasize effective population size of hatchery broodstocks, now hatchery managers need to consider a more comprehensive view of genetic risk. In this paper we present some basic concepts and associated issues in such a broad view. We recognize four fundamentally different types of genetic hazards: (1) extinction, (2) loss of within-population variability, (3) loss of among-population variability, and (4) domestication. The importance of type-2 hazards in hatchery operations has long been realized, but types 3 and 4 are controversial because of a scarcity of empirical data and because consideration of them has great ramifications for hatchery operations. Precise quantification of genetic impacts in terms of fitness depression is likely to remain a difficult if not impossible task. Ultimately, incorporation of genetic concerns into hatchery operations and other aspects of fisheries management will require managers to shift their perspective from one of managing fitness to one or managing genetic diversity.

General Hatchery Reviews

Anderson, JH, KI Warheit, BE Craig, TR Seamons and AH Haukenes (2020). A review of hatchery reform science in Washington State. Final Report to the Washington Fish and Wildlife Commission, Washington Department of Fish and Wildlife**.** 168 pages. Available from https://wdfw.wa.gov/sites/default/files/publications/02121/wdfw02121_0.pdf

Written by WDFW staff following an assignment from the Fish and Wildlife Commission in June 2018 to evaluate the findings of the Hatchery Scientific Review Group (HSRG) and the "emerging science" of hatchery reform.

HSRG (2014). On the Science of Hatcheries: An updated perspective on the role of hatcheries in salmon and steelhead management in the Pacific Northwest. Available from www.hatcheryreform.us.

A summary of the Hatchery Scientific Review Group (HSRG) to date. From the documents Executive Summary: "The Hatchery Scientific Review Group (HSRG) was charged with reviewing all state, tribal, and federal hatchery programs in Puget Sound and Coastal Washington. The review used an ecosystem-based approach founded on two central premises: that harvest goals are sustainable only if they are compatible with conservation goals, and that artificially propagated fish affect the fitness and productivity of natural populations with which they interact. The intent of the project is for science to direct the process of reform. Reforms should ensure that the hatchery system matches current circumstances and management goals.

HSRG (2015). Annual Report to Congress on the Science of Hatcheries, 2015. A report on the application of up-to-date science in the management of salmon and steelhead hatcheries in the Pacific Northwest. Available from www.hatcheryreform.us.

Hatchery Scientific Review Group (HSRG) report to Congress summarizing HSRG's conclusions, principles and recommendation.

Naish, KA, JE Taylor III, PS Levin, TP Quinn, JR Winton, D Huppert and R Hilborn. (2008). An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. *Advances in Marine Biology* 53:61-194

The historical, political and scientific aspects of salmon hatchery programmes designed to enhance fishery production, or to recover endangered populations, are reviewed. We start by pointing out that the establishment of hatcheries has been a political response to societal demands for harvest and conservation; given this social context, we then critically examined the levels of activity, the biological risks, and the economic analysis associated with salmon hatchery programmes. A rigorous analysis of the impacts of hatchery programmes was hindered by the lack of standardized data on release sizes and survival rates at all ecological scales, and since hatchery programme objectives are rarely defined, it was also difficult to measure their effectiveness at meeting release objectives. Debates on the genetic effects of hatchery programmes on wild fish have been dominated by whether correct management practices can reduce negative outcomes, but we noted that there has been an absence of programmatic research approaches addressing this important issue. Competitive interactions between hatchery and wild fish were observed to be complex, but studies researching approaches to reduce these interactions at all ecological scales during the entire salmon life history have been rare, and thus are not typically considered in hatchery management. Harvesting of salmon released from fishery enhancement hatcheries likely impacts vulnerable wild populations; managers have responded to this problem by mass marking hatchery fish, so that fishing effort can be directed towards hatchery populations. However, we noted that the effectiveness of this approach is dependant on accurate marking and production of hatchery fish with high survival rates, and it is not yet clear whether selective fishing will prevent overharvest of wild populations. Finally, research demonstrating disease transmission from hatchery fish to wild populations was observed to be equivocal; evidence in this area has been constrained by the lack of effective approaches to studying the fate of pathogens in the wild. We then reviewed several approaches to studying the economic consequences of hatchery activities intended to

inform the social decisions surrounding programmes, but recognized that placing monetary value on conservation efforts or on hatcheries that mitigate cultural groups' loss of historical harvest opportunities may complicate these analyses. We noted that economic issues have rarely been included in decision making on hatchery programmes. We end by identifying existing major knowledge gaps, which, if filled, could contribute towards a fuller understanding of the role that hatchery programmes could play in meeting divergent goals. However, we also recognized that many management recommendations arising from such research may involve trade-offs between different risks, and that decisions about these trade-offs must occur within a social context. Hatcheries have played an important role in sustaining some highly endangered populations, and it is possible that reform of practices will lead to an increase in the number of successful programmes. However, a serious appraisal of the role of hatcheries in meeting broader needs is urgently warranted and should take place at the scientific, but more effectively, at the societal level.

National Research Council. (1996). *Upstream: Salmon and Society in the Pacific Northwest*. Washington DC, The National Academies Press. 452 + xx pages

Extensive summary concerning the status of salmon populations concerning the factors including environment, limits to populations, values, genetics and conservation, habitat loss and rehabilitation, dams, hatcheries, fishing, and institutional change. The hatchery discussion is on pages 302 – 323.

Withler, RE, MJ Bradford, DM Willis and C Holt (2018). Genetically based targets for enhanced contributions to Canadian Pacific Chinook salmon populations. DFO Can. Sci. Advis. Sec. Res. Doc. 2018/019.: xii + 88 p.

The Wild Salmon Policy (WSP) establishes conservation of wild Pacific salmon and their habitat as the highest priority for Pacific salmon resource management decision-making. Hatchery production in the Salmon Enhancement Program of DFO is used as a conservation tool for wild populations and can increase the availability of fish for harvest but is a risk factor to wild genetic diversity that requires management and mitigation to safeguard Pacific salmon biodiversity in Canada. We recommend use of the proportionate natural influence (PNI) and associated metrics developed by the U.S. Hatchery Scientific Review Group to evaluate and monitor the adaptive state of integrated hatchery populations, and to identify hatchery-influenced populations for WSP assessments. We develop a classification system for Canadian Pacific salmon populations that reflects the adaptive state of the population based on constituent proportions of natural- and hatchery-origin fish. Among the biological categories, increased genetic risk is associated with increasing hatchery influence and a decreasing proportion of wild fish. We modelled the population dynamics of a Chinook Salmon population including the genetic impacts on fitness from hatcheries to evaluate the use of three management measures - hatchery program size, proportion of hatchery fish marked, and proportion of marked fish selectively removed - in managing to a target PNI level. Except for populations at risk of extirpation, limiting hatchery size by scaling the size of the hatchery program to natural production is an effective way to minimize genetic risk of enhancement to wild populations. Limiting hatchery program size also limits the production of fish for harvest, resulting in a tradeoff between genetic risk and socioeconomic benefit in enhancement programs implemented for harvest augmentation. Genetic risk associated with higher levels of hatchery production can be minimized by reducing the proportions of hatchery-origin fish included in the hatchery broodstock and/or allowed to spawn in the natural environment. Manipulation of proportions of natural- and hatchery-origin fish is dependent upon some type and level of marking that allows pre-spawning differentiation of fish originating from the two spawning environments. In conservation programs, the risk of

domestication occurring at low PNI values must be balanced against the genetic and demographic risks of small population size in the absence of high proportions of hatchery-origin fish. We provide recommendations for the classification and management of enhanced populations consistent with the principles of developing explicit biological goals for hatchery-influenced populations, implementing scientifically defensible hatchery programs and using adaptive management of hatchery programs to meet objectives in a risk averse manner.

Genetics

Araki, H, B Cooper and MS Blouin. (2007). Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. *Science* 318(5847): 100-103 DOI: 10.1126/science.1145621

Captive breeding is used to supplement populations of many species that are declining in the wild. The suitability of and long-term species survival from such programs remain largely untested, however. We measured lifetime reproductive success of the first two generations of steelhead trout that were reared in captivity and bred in the wild after they were released. By reconstructing a three-generation pedigree with microsatellite markers, we show that genetic effects of domestication reduce subsequent reproductive capabilities by similar to 40% per captive-reared generation when fish are moved to natural environments. These results suggest that even a few generations of domestication may have negative effects on natural reproduction in the wild and that the repeated use of captive-reared parents to supplement wild populations should be carefully reconsidered.

Araki, H, B Cooper and MS Blouin. (2009). Carry-over effect of captive breeding reduces reproductive fitness of wild-born descendants in the wild. *Biology Letters* 5(5): 621-624 DOI: 10.1098/rsbl.2009.0315

Supplementation of wild populations with captive-bred organisms is a common practice for conservation of threatened wild populations. Yet it is largely unknown whether such programmes actually help population size recovery. While a negative genetic effect of captive breeding that decreases fitness of captive-bred organisms has been detected, there is no direct evidence for a carry-over effect of captive breeding in their wild-born descendants, which would drag down the fitness of the wild population in subsequent generations. In this study, we use genetic parentage assignments to reconstruct a pedigree and estimate reproductive fitness of the wild-born descendants of captive-bred parents in a supplemented population of steelhead trout (*Oncorhynchus mykiss*). The estimated fitness varied among years, but overall relative reproductive fitness was only 37 per cent in wild-born fish from two captive-bred parents and 87 per cent in those from one captive-bred and one wild parent (relative to those from two wild parents). Our results suggest a significant carry-over effect of captive breeding, which has negative influence on the size of the wild population in the generation after supplementation. In this population, the population fitness could have been 8 per cent higher if there was no carry-over effect during the study period.

Christie, MR, MJ Ford and MS Blouin. (2014). On the reproductive success of early-generation hatchery fish in the wild. *Evolutionary Applications* DOI: 10.1111/eva.12183

Large numbers of hatchery salmon spawn in wild populations each year. Hatchery fish with multiple generations of hatchery ancestry often have heritably lower reproductive success than wild fish and may reduce the fitness of an entire population. Whether this reduced fitness also occurs for hatchery fish created with local- and predominantly wild-origin parents remains controversial. Here, we review recent studies on the reproductive success of such early-

generation' hatchery fish that spawn in the wild. Combining 51 estimates from six studies on four salmon species, we found that (i) early-generation hatchery fish averaged only half the reproductive success of their wild-origin counterparts when spawning in the wild, (ii) the reduction in reproductive success was more severe for males than for females, and (iii) all species showed reduced fitness due to hatchery rearing. We review commonalities among studies that point to possible mechanisms (e.g., environmental versus genetic effects). Furthermore, we illustrate that sample sizes typical of these studies result in low statistical power to detect fitness differences unless the differences are substantial. This review demonstrates that reduced fitness of early-generation hatchery fish may be a general phenomenon. Future research should focus on determining the causes of those fitness reductions and whether they lead to long-term reductions in the fitness of wild populations.

Courter, I, T Chance, R Gerstenberger, M Roes, S Gibbs and A Spidle. (2022). Hatchery propagation did not reduce natural steelhead productivity relative to habitat conditions and predation in a mid-Columbia River subbasin. *Canadian Journal of Fisheries and Aquatic Sciences* DOI: 10.1139/cjfas-2021-0351

For over 150 years, hatchery-origin anadromous salmon and trout have been reared and released throughout the Pacific Northwest to mitigate for lost habitat and sustain harvest opportunity. Some studies demonstrate that introgression of hatchery and naturally produced fish may constrain conservation efforts through maladaptive genetic processes. However, empirical demonstrations of the influence of these genetic interactions on population productivity are lacking, making it difficult to assess their importance relative to other drivers of productivity. We estimated the effect of the proportion of hatchery-origin spawners (pHOS), proportionate natural influence (PNI), and hatchery fish releases on natural adult winter steelhead recruitment in the Hood River, Oregon, over a 27-year period of record. Adult winter steelhead productivity was not associated with pHOS and PNI. However, natural winter steelhead productivity was positively associated with ocean conditions, stream flow, and hatchery fish release numbers, while negatively associated with pinniped abundance. Our analysis highlights the importance of quantifying the influence of hatchery programs on fish production relative to environmental factors known to affect natural-origin anadromous fish recruitment.

Courter, I, T Chance, R Gerstenberger, M Roes, S Gibbs and A Spidle. (2023). Response to comment on Courter et al. (2022). *Canadian Journal of Fisheries and Aquatic Sciences* DOI: 10.1139/cjfas-2022-0234

Response to Falcy (2023) comments on Courter et al. (2022)

Falcy, MR. (2023). Inferring hatchery effects using spawner-recruit data: comment on Courter et al. (2022). *Canadian Journal of Fisheries and Aquatic Sciences* DOI: 10.1139/cjfas-2022-0158

Comments on Courter et al. (2022)

Ford, MJ. (2002). Selection in captivity during supportive breeding may reduce fitness in the wild. *Conservation Biology* 16(3): 815-825 DOI: 10.1046/j.1523-1739.2002.00257.x

I used a quantitative genetic model to explore the effects of selection on the fitness of a wild population subject to supportive breeding. Supportive breeding is the boosting of a wild population's size by breeding part of the population in captivity and releasing the captive progeny back into the wild. The model assumes that a single trait is under selection with

different optimum trait values in the captive and wild environments. The model shows that when the captive population is closed to gene flow from the wild population, even low levels of gene flow from the captive population to the wild population will shift the wild population's mean phenotype so that it approaches the optimal phenotype in captivity. If the captive population receives gene flow from the wild, the shift in the wild population's mean phenotype becomes less pronounced but can still be substantial. The approach to the new mean phenotype can occur in less than 50 generations. The fitness consequences of the phenotypic shift depend on the details of the model, but a>30% decline in fitness can occur over a broad range of parameter values. The rate of gene flow between the two environments, and hence the outcome of the model, is sensitive to the wild environment's carrying capacity and the population growth rate it can support. The results have two important implications for conservation efforts. First, they show that selection in captivity may significantly reduce a wild population's fitness during supportive breeding and that even continually introducing wild individuals into the captive population will not eliminate this effect entirely. Second, the sensitivity of the model's outcome to the wild environment's quality suggests that conserving or restoring a population's habitat is important for preventing fitness loss during supportive breeding.

Ford, MJ, AR Murdoch, MS Hughes, TR Seamons and ES LaHood. (2016). Broodstock History Strongly Influences Natural Spawning Success in Hatchery Steelhead (*Oncorhynchus mykiss*). *Plos One* 11(10): e0164801 DOI: 10.1371/journal.pone.0164801

We used genetic parentage analysis of 6200 potential parents and 5497 juvenile offspring to evaluate the relative reproductive success of hatchery and natural steelhead (*Onchorhynchus mykiss*) when spawning in the wild between 2008 and 2011 in the Wenatchee River, Washington. Hatchery fish originating from two prior generation hatchery parents had <20% of the reproductive success of natural origin spawners. In contrast, hatchery females originating from a cross between two natural origin parents of the prior generation had equivalent or better reproductive success than natural origin females. Males originating from such a cross had reproductive success of 26-93% that of natural males. The reproductive success of hatchery females and males from crosses consisting of one natural origin fish and one hatchery origin fish was 24-54% that of natural fish. The strong influence of hatchery broodstock origin on reproductive success confirms similar results from a previous study of a different population of the same species and suggests a genetic basis for the low reproductive success of hatchery steelhead, although environmental factors cannot be entirely ruled out. In addition to broodstock origin, fish size, return time, age, and spawning location were significant predictors of reproductive success. Our results indicate that incorporating natural fish into hatchery broodstock is clearly beneficial for improving subsequent natural spawning success, even in a population that has a decades-long history of hatchery releases, as is the case in the Wenatchee River.

Hess, MA, CD Rabe, JL Vogel, JJ Stephenson, DD Nelson and SR Narum. (2012). Supportive breeding boosts natural population abundance with minimal negative impacts on fitness of a wild population of Chinook salmon. *Molecular Ecology* 21(21): 5236-5250 DOI: 10.1111/mec.12046

While supportive breeding programmes strive to minimize negative genetic impacts to populations, case studies have found evidence for reduced fitness of artificially produced individuals when they reproduce in the wild. Pedigrees of two complete generations were tracked with molecular markers to investigate differences in reproductive success (RS) of wild and hatchery-reared Chinook salmon spawning in the natural environment to address questions regarding the demographic and genetic impacts of supplementation to a natural population.

Results show a demographic boost to the population from supplementation. On average, fish taken into the hatchery produced 4.7 times more adult offspring, and 1.3 times more adult grand-offspring than naturally reproducing fish. Of the wild and hatchery fish that successfully reproduced, we found no significant differences in RS between any comparisons, but hatchery-reared males typically had lower RS values than wild males. Mean relative reproductive success (RRS) for hatchery F1 females and males was 1.11 (P=0.84) and 0.89 (P=0.56), respectively. RRS of hatchery-reared fish (H) that mated in the wild with either hatchery or wild-origin (W) fish was generally equivalent to WxW matings. Mean RRS of HxW and HxH matings was 1.07 (P=0.92) and 0.94 (P=0.95), respectively. We conclude that fish chosen for hatchery rearing did not have a detectable negative impact on the fitness of wild fish by mating with them for a single generation. Results suggest that supplementation following similar management practices (e.g. 100% local, wild-origin brood stock) can successfully boost population size with minimal impacts on the fitness of salmon in the wild.

Janowitz-Koch, I, C Rabe, R Kinzer, D Nelson, MA Hess and SR Narum. (2019). Long-term evaluation of fitness and demographic effects of a Chinook Salmon supplementation program. *Evolutionary Applications* 12: 456-469 DOI: doi:10.1111/eva.12725

While the goal of supplementation programs is to provide positive, population-level effects for species of conservation concern, these programs can also present an inherent fitness risk when captive-born individuals are fully integrated into the natural population. In order to evaluate the long-term effects of a supplementation program and estimate the demographic and phenotypic factors influencing the fitness of a threatened population of Chinook Salmon (*Oncorhynchus tshawytscha*), we genotyped tissue samples spanning a 19-year period (1998-2016) to generate pedigrees from adult fish returning to Johnson Creek, Idaho, USA. We expanded upon previous estimates of relative reproductive success (RRS) to include grand-parentage analyses and used generalized linear models to determine whether origin (hatchery or natural) or phenotypic traits (timing of arrival to spawning grounds, body length, and age) significantly predicted reproductive success (RS) across multiple years. Our results provide evidence that this supplementation program with 100% natural-origin broodstock provided a long-term demographic boost to the population (mean of 4.56 times in the first generation and mean of 2.52 times in the second generation). Overall, when spawning in nature, hatchery-origin fish demonstrated a trend toward lower RS compared to natural-origin fish (p < 0.05). However, when hatchery-origin fish successfully spawned with natural-origin fish, they had similar RS compared to natural by natural crosses (first-generation mean hatchery by natural cross RRS = 1.11 females, 1.13 males; second-generation mean hatchery by natural cross RRS = 1.03 females, 1.08 males). While origin, return year, and body length were significant predictors of fitness for both males and females (p < 0.05), return day was significant for males but not females (p > 0.05). These results indicate that supplementation programs that reduce the potential for genetic adaptation to captivity can be effective at increasing population abundance while limiting long-term fitness effects on wild populations.

Koch, IJ, TR Seamons, PF Galbreath, HM Nuetzel, AP Matala, KI Warheit, DE Fast, MV Johnston, CR Strom, SR Narum and WJ Bosch. (2022). Effects of Supplementation in Upper Yakima River Chinook Salmon. *Transactions of the American Fisheries Society* 151(3): 373-388 DOI: 10.1002/tafs.10354

To promote recovery of natural salmonid populations, managers are utilizing hatchery supplementation programs to increase abundance of spawners on the spawning grounds. However, studies have provided evidence that captive breeding can result in domestication, demonstrated by lower fitness of hatchery-origin compared with natural-origin fish. Supplementation programs, therefore, typically use natural-origin broodstock in an effort to

minimize long-term negative fitness impacts. Here we evaluated the upper Yakima River spring supplementation program for Chinook Salmon *Oncorhynchus tshawytscha*, which has broodstock comprised exclusively of unmarked fish presumed to be of natural-origin. Using 5 years of spawner data, we tested for effects of hatchery breeding and rearing on total adult returns and their individual reproductive success when spawning naturally. Our study revealed that supplementation increased overall abundance of fish spawning naturally on the spawning grounds. However, on average, compared with natural-origin spawners, hatchery-origin fish had reduced reproductive success, which also translated to reduced reproductive success in three out of five return years for natural-origin fish that spawned with hatchery-origin fish. As expected, body length and return timing were also significant predictors of reproductive success. However, more generations of data are needed to establish the extent to which reduced reproductive success is passed on to naturally produced progeny.

Thériault, V, GR Moyer, LS Jackson, MS Blouin and MA Banks. (2011). Reduced reproductive success of hatchery coho salmon in the wild: insights into most likely mechanisms. *Molecular Ecology* 20(9): 1860-1869 DOI: 10.1111/j.1365-294X.2011.05058.x

Supplementation of wild salmonids with captive-bred fish is a common practice for both commercial and conservation purposes. However, evidence for lower fitness of captive reared fish relative to wild fish has accumulated in recent years, diminishing the apparent effectiveness of supplementation as a management tool. To date, the mechanism(s) responsible for these fitness declines remain unknown. In this study, we showed with molecular parentage analysis that hatchery coho salmon (*Oncorhynchus kisutch*) had lower reproductive success than wild fish once they reproduced in the wild. This effect was more pronounced in males than in same-aged females. Hatchery spawned fish that were released as unfed fry (age 0), as well as hatchery fish raised for one year in the hatchery (released as smolts, age 1), both experienced lower lifetime reproductive success (RS) than wild fish. However, the subset of hatchery males that returned as 2-year olds (jacks) did not exhibit the same fitness decrease as males that returned as 3-year olds. Thus, we report three lines of evidence pointing to the absence of sexual selection in the hatchery as a contributing mechanism for fitness declines of hatchery fish in the wild: (i) hatchery fish released as unfed fry that survived to adulthood still had low RS relative to wild fish, (ii) age-3 male hatchery fish consistently showed a lower relative RS than female hatchery fish (suggesting a role for sexual selection), and (iii) age-2 jacks, which use a sneaker mating strategy, did not show the same declines as 3-year olds, which compete differently for females (again, implicating sexual selection).

Waters, CD, JJ Hard, MSO Brieuc, DE Fast, KI Warheit, RS Waples, CM Knudsen, WJ Bosch and KA Naish. (2015). Effectiveness of managed gene flow in reducing genetic divergence associated with captive breeding. *Evolutionary Applications* 8(10): 956-971 DOI: 10.1111/eva.12331

Captive breeding has the potential to rebuild depressed populations. However, associated genetic changes may decrease restoration success and negatively affect the adaptive potential of the entire population. Thus, approaches that minimize genetic risks should be tested in a comparative framework over multiple generations. Genetic diversity in two captive-reared lines of a species of conservation interest, Chinook salmon (*Oncorhynchus tshawytscha*), was surveyed across three generations using genome-wide approaches. Genetic divergence from the source population was minimal in an integrated line, which implemented managed gene flow by using only naturally-born adults as captive broodstock, but significant in a segregated line, which bred only captive-origin individuals. Estimates of effective number of breeders revealed that the rapid divergence observed in the latter was largely attributable to genetic drift. Three independent tests for signatures of adaptive divergence also identified temporal change within

the segregated line, possibly indicating domestication selection. The results empirically demonstrate that using managed gene flow for propagating a captive-reared population reduces genetic divergence over the short term compared to one that relies solely on captive-origin parents. These findings complement existing studies of captive breeding, which typically focus on a single management strategy and examine the fitness of one or two generations.

Disease

Chapman, JM, LA Kelly, AK Teffer, KM Miller and SJ Cooke. (2021). Disease ecology of wild fish: opportunities and challenges for linking infection metrics with behaviour, condition, and survival. *Canadian Journal of Fisheries and Aquatic Sciences* 78(8): 995-1007 DOI: 10.1139/cjfas-2020-0315

Surmounting evidence supports that infectious agents play a critical role in shaping fish physiology, behaviour, and survival. The exclusion of disease-causing agents from fisheries research has resulted in major knowledge gaps that may limit the predictive capacity of ecological models. A major barrier in wild fisheries epidemiology is the logistical constraints associated with observing disease and obtaining samples from free-ranging fish, restricting the vast majority of research to laboratory studies or aquaculture facilities. For fisheries ecologists, including infectious agents can provide greater insight into observed phenomena, particularly with respect to fish physiology (e.g., metabolism), movement (e.g., migration rates), behaviour (e.g., habitat selection), personality (e.g., bold versus shy), and survival. Here we provide a brief introduction to the current understanding of disease ecology in wild fish and describe technological advances in both epidemiology and fisheries and aquatic sciences that can be used in tandem to create comprehensive studies of disease ecology in wild fishes. Combining nonlethal sampling and molecular genetic-based identification methods with field studies creates vast opportunities for innovative study designs that have the potential to address the true complexity of aquatic ecosystems.

Kurath, G and J Winton. (2011). Complex dynamics at the interface between wild and domestic viruses of finfish. *Current Opinion in Virology* 1(1): 73-80 DOI: 10.1016/j.coviro.2011.05.010

Viral traffic occurs readily between wild and domesticated stocks of finfish because aquatic environments have greater connectivity than their terrestrial counterparts and because the global expansion and dynamic nature of intensive aquaculture provide multiple pathways of transmission and unique drivers of virus adaptation. Supported by examples from the literature, we provide reasons why viruses move from wild fish reservoirs to infect domestic fish in aquaculture more readily than 'domestic' viruses move across the interface to infect wild stocks. We also hypothesize that 'wild' viruses moving across the interface to domestic populations of finfish are more frequently associated with disease outbreaks and host switches compared to domestic viruses that cross the interface to infect wild fish.

Miller, MP and ER Vincent. (2008). Rapid natural selection for resistance to an introduced parasite of rainbow trout. *Evolutionary Applications* 1(2): 336-341 DOI: 10.1111/j.1752-4571.2008.00018.x

Introduced species and infectious diseases both independently pose challenges for the preservation of existing biodiversity. However, native species or disease hosts are by no means 'unarmed' when faced with novel environmental challenges, provided that adequate adaptive genetic variation exists to mount effective evolutionary responses. In this study, we examined the consequences of the recently introduced parasite and causative agent of whirling disease

(*Myxobolus cerebralis*) in a wild rainbow trout (*Oncorhynchus mykiss*) population from Harrison Lake, Montana (USA). Consistent with the parasite's age-specific effects, juvenile rainbow trout recruitment into Harrison Lake was substantially reduced following parasite detection in 1995. However, experimental data suggest that natural selection has rapidly reduced whirling disease susceptibility within the population over time. The rapid observed temporal change in resistance patterns argues that the standing genetic variation for parasite resistance facilitated this process. Our findings ultimately underscore the importance of preserving genetic diversity to ensure that species of economic importance or of conservation concern have maximal chances for persistence in future changing environments.

Nekouei, O, R Vanderstichel, KH Kaukinen, K Thakur, T Ming, DA Patterson, M Trudel, C Neville and KM Miller. (2019). Comparison of infectious agents detected from hatchery and wild juvenile Coho salmon in British Columbia, 2008-2018. *Plos One* 14(9) DOI: 10.1371/journal.pone.0221956

Infectious diseases are potential contributors to decline in Coho salmon (*Oncorhynchus kisutch*) populations. Although pathogens are theoretically considered to pose higher risk in high-density rearing environments like hatcheries, there is no direct evidence that hatchery-origin Coho salmon increase the transmission of infectious agents to sympatric wild populations. This study was undertaken to compare prevalence, burden, and diversity of infectious agents between hatchery-reared and wild juvenile Coho salmon in British Columbia (BC), Canada. In total, 2,655 juvenile Coho salmon were collected between 2008 and 2018 from four regions of freshwater and saltwater in BC. High-throughput microfluidics qPCR was employed for simultaneous detection of 36 infectious agents from mixed-tissue samples (gill, brain, heart, liver, and kidney). Thirty-one agents were detected at least once, including ten with prevalence >5%. *Candidatus Brachiomonas cysticola*, *Paraneuclospora theridion*, and *Parvicapsula pseudobranchiocola* were the most prevalent agents. Diversity and burden of infectious agents were substantially higher in marine environment than in freshwater. In Mainland BC, infectious burden and diversity were significantly lower in hatchery smolts than in wild counterparts, whereas in other regions, there were no significant differences. Observed differences in freshwater were predominantly driven by three parasites, *Loma salmonae*, *Myxobolus arcticus*, and *Parvicapsula kabatai*. In saltwater, there were no consistent differences in agent prevalence between hatchery and wild fish shared among the west and east coasts of Vancouver Island. Although some agents showed differential infectious patterns between regions, annual variations likely contributed to this signal. Our findings do not support the hypothesis that hatchery smolts carry higher burdens of infectious agents than conspecific wild fish, reducing the potential risk of transfer to wild smolts at this life stage. Moreover, we provide a baseline of infectious agents in juvenile Coho salmon that will be used in future research and modeling potential correlations between infectious profiles and marine survival.

Shea, D, N Frazer, K Wadhawan, A Bateman, SR Li, KM Miller, S Short and M Krkosek. (2022). Environmental DNA dispersal from Atlantic salmon farms. *Canadian Journal of Fisheries and Aquatic Sciences* DOI: 10.1139/cjfas-2021-0216

The spatial spread of genetic material is fundamental to analyses of invasive species, species dispersal, and disease surveillance. Using a quantitative environmental DNA methodology, we assessed spatial variation in Atlantic salmon (*Salmo salar*) eDNA concentration, originating from four active salmon farms, along ~55 km of narrow channels in British Columbia, Canada. We evaluated eDNA from 36 and 47 seawater samples collected at 2 and 8 m depths, respectively, at 0.3 – 3 km intervals along the channels. We fitted a Laplace dispersal kernel to eDNA data separately for 2 and 8 m depths. The model estimates that 95% of eDNA spread at 2 m depth was within 1.6 km upstream and 3.2 km downstream from farms relative to a prevailing current,

and this was expanded at 8 m (1.8 km upstream; 3.7 km downstream). Our modeling results were robust to multiple sources of simulated uncertainty associated with sampling regime and variable eDNA shedding rates. Our results provide a benchmark for the spatial spread of biological material such as pathogens or eDNA from invasive or imperilled species in a coastal marine context. This work has implications for the interpretation of eDNA data for species surveillance and predicting disease spread.

Vincent, ER. (1996). Whirling disease and wild trout: The Montana experience. *Fisheries* 21(6): 32-33

Discussion of the discovery and history of whirling disease in Montana rainbow trout.

Washington Fishery Co-Managers (2006). The Salmonid Disease Control Policy of the Fisheries Co-Managers of Washington State (Revised July 2006).

Policy Statement: It shall be the policy of the Fisheries Co-Managers of Washington State to protect free-ranging and cultured fish populations from management activities that could cause the importation, dissemination, and amplification of pathogens known to adversely affect salmonids. These management activities include, but are not limited to, the transfer of gametes, eggs, fish, carcasses, or water between watersheds. This policy sets forth the minimum fish health standards. A Co-Manager or Co-Operator may implement additional practices or measures at their facilities at their discretion. Further, acknowledging that many complex fish health situations will arise, it shall be the policy to foster open and frequent communication between Co-Managers and Co-Operators to jointly resolve these issues without endangering the health of free-ranging and cultured fish populations. Policy Goals: To prevent the importation or establishment of regulated exotic pathogens into Washington State. To prevent the introduction or establishment of regulated endemic pathogens to new watersheds within Washington State. To reduce the biological impact of specific pathogens known to adversely impact salmonids. To minimize the amplification of pathogens that can adversely affect both free-ranging and cultured fish populations. To foster open and frequent communications between Co-Managers and Co-Operators on fish health issues.

Watanabe, RA, JL Fryer and JS Rohovec. (1988). Molecular filtration for recovery of waterborne viruses of fish. *Applied and Environmental Microbiology* 54(6):1606-1609. DOI: 10.1128/aem.54.6.1606-1609.1988

The effectiveness of tangential flow filtration (TFF) for the recovery of *infectious hematopoietic necrosis virus* (IHNV) and *infectious pancreatic necrosis virus* (IPNV) from large volumes of water was evaluated. In laboratory studies, virus recovery from IHNV-seeded water following concentration by TFF was approximately 13%. However, the addition of 0.1 and 1% fetal bovine serum to deionized water stabilized the virus, increasing virus recoveries to 95%. The addition of 0.03 and 0.3% beef extract resulted in IHNV recoveries of 80 and 61%, respectively. Similar results were obtained with IPNV-seeded water. Field studies using the TFF procedure were conducted with water from areas where IHNV is endemic. IHNV was detected in effluent from an adult steelhead trout (*Salmo gairdneri*) holding pond at an estimated concentration of 1 PFU/5 ml of water. It was also detected at levels of 1 PFU/50 ml in water from a 2-m-diameter circular tank containing IHNV-infected steelhead trout fry. IHNV isolated in samples taken from the Metolius River was detected by TFF at estimated levels of 1 PFU/3 liters.

Ecology

Beamish, RJ, C Mahnken and CM Neville. (1997). Hatchery and wild production of Pacific salmon in relation to large-scale, natural shifts in the productivity of the marine environment. *ICES Journal of Marine Science* 54(6): 1200-1215 DOI: 10.1006/jmsc.1997.0305

> Pacific salmon have been fished extensively for at least a century and artificial production of Pacific salmon has been a management strategy to improve production for almost as long. Hatchery production is considered important because it is commonly believed that the carrying capacity for salmon in the ocean has remained more or less constant and is underutilized as a consequence of limited production of smelts in fresh water. Since the mid-1960s, there has been an increase in hatchery production, partly as a response to a desire to increase catch and partly because of improved hatchery techniques. Since the late 1970s there has been a dramatic increase in the total Pacific salmon catch. The increases in catch are now known to result from a large-scale shift in the productivity of the sub-arctic Pacific and management and enhancement actions. Environmental indices changed about 1989-1990 and may indicate that the productive regime of the 1980s has ended. This would imply that under natural conditions Pacific salmon abundance would decline. There are no clear indications of what to expect in the new regime, but it is apparent that the massive production of artificially reared Pacific salmon would not be necessary in a less productive regime. OF concern is the impact that the large numbers of artificially reared salmon will have on wild salmon stock levels. (C) 1997 International Council for the Exploration of the Sea.

Greene, C., E. Beamer, J. Chamberlin, G. Hood, M. Davis, K. Larsen, J. Anderson, R. Henderson, J. Hall, M. Pouley, T. Zackey, S. Hodgson, C. Ellings, and I. Woo. 2021. Landscape, density-dependent, and bioenergetic influences upon Chinook salmon in tidal delta habitats: comparison of four Puget Sound estuaries. ESRP Report 13-1508.

> From the Executive Summary: "With the goal of developing general biological principles characterizing rearing conditions for natural-origin (NOr) juvenile Chinook that apply to a variety of estuaries, we examined fish-habitat relationships in four representative tidal river deltas of Puget Sound: the Nooksack, Skagit, Snohomish, and Nisqually (Fig. 1). The selected systems vary in landscape features and outmigrant population attributes (e.g., proportion of natural-origin vs. hatchery-origin or HOr juveniles), and thus represent the diverse characteristics we might expect in estuarine systems inhabited by juvenile Chinook across a broad geographic range within and beyond Puget Sound. We address three issues: how does landscape structure affect juvenile Chinook salmon distribution and abundance in tidal deltas, how common are habitat limitations (i.e., density dependence), and under what conditions do fish experience growth variability and food limitation in delta wetlands? These questions underlie whether estuary habitat restoration is likely to benefit Chinook salmon populations, and thereby will facilitate recovery from listed status.

Kendall, NW, BW Nelson and J Losee. (2020). Density-dependent marine survival of hatchery-origin Chinook salmon may be associated with pink salmon. *Ecosphere* 11(4) DOI: 10.1002/ecs2.3061

> Understanding how protected species influence the population dynamics of each other is an essential part of ecosystem-based management. Chinook salmon (*Oncorhynchus tshawytscha*) are critical prey for endangered southern resident killer whales (SRKWs; *Orcinus orca*), and increasing releases of hatchery Chinook salmon has been proposed to aid SRKW recovery. We analyzed 30 yr of data and found that density-dependent survival of hatchery Chinook salmon released into the central and southern parts of the Salish Sea (Washington, USA; and British Columbia, Canada) may be associated with the presence of naturally produced pink salmon (*O*.

gorbuscha), which are highly abundant as juveniles only in even-numbered years. We first modeled hatchery Chinook salmon marine survival as a function of the numbers of juvenile Chinook released and the presence of emigrating juvenile pink salmon between 1983 and 2012. Then, we related reconstructed numbers of hatchery Chinook salmon returning to Puget Sound to the abundance of juvenile Chinook released in even (pink emigration) and odd (non-pink emigration) years from 1980 to 2010. We found that in some regions of the Salish Sea, both hatchery Chinook salmon marine survival and adult Chinook returns varied depending on the number of hatchery Chinook released and the presence of juvenile pink salmon. Specifically, in some regions survival of hatchery Chinook salmon decreased when greater numbers of juveniles were released into the Salish Sea in even years, when large numbers of pink salmon were present, but increased or remained stable when pink salmon were not present in large numbers (in odd years). This suggests lower, density-dependent survival of juvenile Salish Sea Chinook salmon during even outmigration years. Our analyses suggest that scientists and managers should further investigate potential mechanisms for density-dependent survival of hatchery Chinook salmon from Salish Sea hatcheries when designing strategies to maximize adult returns.

Levin, PS, RW Zabel and JG Williams. (2001). The road to extinction is paved with good intentions: negative association of fish hatcheries with threatened salmon. *Proceedings of the Royal Society B-Biological Sciences* 268(1472): 1153-1158 DOI: 10.1098/rspb.2001.1634

Hatchery programmes for supplementing depleted populations of fish are undergoing a worldwide expansion and have provoked concern about their ramifications for populations of wild fish. In particular, Pacific salmon are artificially propagated in enormous numbers in order to compensate for numerous human insults to their populations, yet the ecological impacts of this massive hatchery effort are poorly understood. Here we test the hypothesis that massive numbers of hatchery-raised chinook salmon reduce the marine survival of wild Snake River spring chinook, a threatened species in the USA. Based on a unique 25-year time-series, we demonstrated a strong, negative relationship between the survival of chinook salmon and the number of hatchery fish released, particularly during years of poor ocean conditions. Our results suggest that hatchery programmes that produce increasingly higher numbers of fish may hinder the recovery of depleted wild populations.

Malick, MJ, ME Moore and BA Berejikian. (2022). Higher Early Marine Mortality of Steelhead Associated with Releases of Hatchery Coho Salmon but Not Chinook Salmon. *Marine and Coastal Fisheries* 14(6) DOI: 10.1002/mcf2.10225

Understanding the drivers of mortality during critical life history periods is an important part of increasing our capacity to rebuild depressed salmonid populations. For threatened steelhead *Oncorhynchus mykiss* in Puget Sound, Washington, early marine predation has been implicated as a key source of mortality. Yet, the agents that mediate predation pressure are poorly understood. In this study, we characterize abundances of juvenile Coho Salmon *O. kisutch* and Chinook Salmon *O. tshawytscha* in Puget Sound and relate these abundance patterns to weekly steelhead survival to better understand whether pulses of hatchery-released salmonids mediate steelhead survival. We found that weekly abundances of hatchery Coho Salmon and Chinook Salmon smolts vary by several orders of magnitude across weeks, indicating that large resource pulses are available to salmonid predators. We further found that weekly steelhead survival was significantly negatively related to abundances of hatchery-released Coho Salmon but not Chinook Salmon, which had considerably smaller body sizes than both Coho Salmon and steelhead smolts. Together, our results suggest that releases of Coho Salmon into Puget Sound mediate mortality of steelhead smolts, possibly via increased predation pressure by shared predators.

Naman, SW and CS Sharpe. (2012). Predation by hatchery yearling salmonids on wild subyearling salmonids in the freshwater environment: A review of studies, two case histories, and implications for management. *Environmental Biology of Fishes* 94(1):21-28. DOI: 10.1007/s10641-011-9819-x

We conducted a literature review on predation by hatchery yearling salmonids on wild subyearling salmonids in the western United States. The review included 14 studies from the Pacific Northwest and California. In most instances, predation by hatchery yearling salmonids on wild subyearling salmonids occurred at low levels. However, when multiple factors contributing to the incidence of predation were met, localized areas of heavy predation were noted. Total prey consumed ranged from 456 to 111 000 subyearlings for the few studies in which enough information was gathered to make the estimate. We examined two of these studies in more detail: one detecting relatively low predation in four western Washington rivers and one detecting relatively high predation in the Trinity River in northern California. In the case of the rivers in western Washington, over 70% of wild subyearlings had migrated by the time hatchery steelhead were planted and those remaining had grown large enough to reduce their vulnerability to predation. In the case of the Trinity River, less than 20% of wild subyearlings had migrated by the time hatchery steelhead were planted and most were small enough to remain highly vulnerable to predation. We found that managers can effectively minimize the predation rate of hatchery yearling salmonids by reducing the spatial or temporal overlap of predator and prey. Unknown is the extent to which low predation rates, which likely occur in most places hatchery yearlings are released, might still negatively impact prey populations that are at low abundance because of other anthropogenic factors.

Nelson, BW, AO Shelton, JH Anderson, MJ Ford and EJ Ward. (2019). Ecological implications of changing hatchery practices for Chinook salmon in the Salish Sea. *Ecosphere* 10(11) DOI: 10.1002/ecs2.2922

For over a century, hatchery programs have been used to subsidize natural salmon populations in order to increase fisheries opportunities and, more recently, to conserve declining natural populations. While an extensive literature has described the impacts of large-scale hatchery operations on freshwater ecosystems, less attention has been given to ecosystem interactions within the marine environment. We analyzed records of hatchery-released Chinook salmon in the Salish Sea to assess temporal and spatial changes in hatchery practices since 1950, with the goal of identifying potential implications for ecosystem dynamics and conservation efforts in the region. Over the past 65 yr, we found significant changes in the size and time at which juvenile salmon are released, resulting in decreased diversity of these traits. Research suggests that predation on juvenile salmon by other fish, avian, and marine mammal species could be size-dependent, and our results indicate that current hatchery practices are releasing Chinook salmon in the size range preferred by these predators. With current marine survival rates at chronically low levels, and increasing demand for hatchery subsidies, it is important to consider how modifying existing hatchery programs intended to reduce homogenization may promote more natural marine food web dynamics, with potential benefits to both hatchery and natural Chinook populations.

Nelson, BW, CJ Walters, AW Trites and MK McAllister. (2019). Wild Chinook salmon productivity is negatively related to seal density and not related to hatchery releases in the Pacific Northwest. *Canadian Journal of Fisheries and Aquatic Sciences* 76(3): 447-462 DOI: 10.1139/cjfas-2017-0481

Predation risk and competition among conspecifics significantly affect survival of juvenile

salmon, but are rarely incorporated into models that predict recruitment in salmon populations. Using densities of harbour seals (*Phoca vitulina*) and numbers of hatchery-released Chinook salmon (*Oncorhynchus tshawytscha*) smolts as covariates in spatially structured Bayesian hierarchical stock-recruitment models, we found significant negative correlations between seal densities and productivity of Chinook salmon for 14 of 20 wild Chinook populations in the Pacific Northwest. Changes in numbers of seals since the 1970s were associated with a 74% decrease (95% CI: -85%, -64%) in maximum sustainable yield in Chinook stocks. In contrast, hatchery releases were significantly correlated with Chinook productivity in only one of 20 populations. Our findings are consistent with recent research on predator diets and bioenergetics modeling that suggest there is a relationship between harbour seal predation on juvenile Chinook and reduced marine survival in parts of the eastern Pacific. Forecasting, assessment, and recovery efforts for salmon populations of high conservation concern should thus consider including biotic factors, particularly predator-prey interactions.

Ruggerone, GT and FA Goetz. (2004). Survival of Puget Sound chinook salmon (*Oncorhynchus tshawytscha*) in response to climate-induced competition with pink salmon (*Oncorhynchus gorbuscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 61(9): 1756-1770 DOI: 10.1139/f04-112

We tested for competition between pink salmon (*Oncorhynchus gorbuscha*) and chinook salmon (*Oncorhynchus tshawytscha*) originating from rivers in the Puget Sound area using coded-wire-tagged subyearling hatchery chinook salmon. Following a 2-year life cycle, many juvenile pink salmon enter Puget Sound in even-numbered years, whereas few migrate during odd-numbered years. During 1984-1997, juvenile chinook salmon released during even-numbered years experienced 59% lower survival than those released during odd-numbered years, a trend consistent among 13 chinook salmon stocks. Lower even-numbered-year survival of chinook salmon was associated with reduced first-year growth and survival and delayed maturation. In contrast, chinook salmon released into coastal streams, where few pink salmon occur, did not exhibit an alternating-year pattern of survival, suggesting that the interaction occurred within Puget Sound and the lower Strait of Georgia. Unexpectedly, the survival pattern of Puget Sound chinook salmon was reversed prior to the 1982-1983 El Nino: chinook salmon survival was higher when they migrated with juvenile pink salmon during 1972-1983. We hypothesize that chinook salmon survival changed as a result of a shift from predation- to competition-based mortality in response to recent declines in predator and prey abundances and increases in pink salmon abundance. Alternating-year mortality accounted for most of the 50% decline in marine survival of chinook salmon between 1972-1983 and 1984-1997.

Ruggerone, GT and JR Irvine. (2018). Numbers and Biomass of Natural- and Hatchery-Origin Pink Salmon, Chum Salmon, and Sockeye Salmon in the North Pacific Ocean, 1925-2015. *Marine and Coastal Fisheries* 10(2): 152-168 DOI: 10.1002/mcf2.10023

Numerical abundance and biomass values presented here for Pink Salmon *Oncorhynchus gorbuscha*, Chum Salmon *O. keta*, and Sockeye Salmon *O. nerka* in the North Pacific Ocean span 90 years (1925-2015), representing the most comprehensive compilation of these data to date. In contrast to less populous species of salmon, these species are more abundant now than ever, averaging 665×10^6 adult salmon each year (1.32×10^6 metric tons) during 1990-2015. When immature salmon are included, recent biomass estimates approach 5×10^6 metric tons. Following an initial peak during 1934-1943, abundances were low until the 1977 regime shift benefited each species. During 1990-2015, Pink Salmon dominated adult abundance (67% of total) and biomass (48%), followed by Chum Salmon (20%, 35%) and Sockeye Salmon (13%, 17%). Alaska produced approximately 39% of all Pink Salmon, 22% of Chum Salmon, and 69% of Sockeye

Salmon, while Japan and Russia produced most of the remainder. Although production of natural-origin salmon is currently high due to generally favorable ocean conditions in northern regions, approximately 60% of Chum Salmon, 15% of Pink Salmon, and 4% of Sockeye Salmon during 1990-2015 were of hatchery origin. Alaska generated 68% and 95% of hatchery Pink Salmon and Sockeye Salmon, respectively, while Japan produced 75% of hatchery Chum Salmon. Salmon abundance in large areas of Alaska (Prince William Sound and Southeast Alaska), Russia (Sakhalin and Kuril islands), Japan, and South Korea are dominated by hatchery salmon. During 1990-2015, hatchery salmon represented approximately 40% of the total biomass of adult and immature salmon in the ocean. Density-dependent effects are apparent, and carrying capacity may have been reached in recent decades, but interaction effects between hatchery- and natural-origin salmon are difficult to quantify, in part because these fish are rarely separated in catch and escapement statistics. The following management changes are recommended: (1) mark or tag hatchery salmon so that they can be identified after release, (2) estimate hatchery- and natural-origin salmon in catches and escapement, and (3) maintain these statistics in publicly accessible databases.

Tatara, CP and BA Berejikian. (2012). Mechanisms influencing competition between hatchery and wild juvenile anadromous Pacific salmonids in fresh water and their relative competitive abilities. *Environmental Biology of Fishes* 94(1):7-19 DOI: 10.1007/s10641-011-9906-z

Avoiding negative effects of competition from released hatchery salmonids on wild fish is a primary concern for recovery efforts and fisheries management. Several factors affect competition among juvenile salmonids including: (1) whether competition is intra- or interspecific, (2) duration of freshwater cohabitation of hatchery and wild fish, (3) relative body size, (4) prior residence, (5) environmentally induced developmental differences, and (6) fish density. Intraspecific competition is expected to be greater than interspecific because of greater niche overlap between conspecific hatchery and wild fish. Competition is expected to increase with prolonged freshwater cohabitation. Hatchery smolts are often larger than wild, and larger fish are usually superior competitors. However, wild fish have the advantage of prior residence when defending territories and resources in natural streams. Hatchery-induced developmental differences are variable and can favor both hatchery and wild fish. Although all these factors influence competitive interactions, fish density of the composite population (wild + hatchery fish) in relation to habitat carrying capacity likely exerts the greatest influence. The extent of competition and relative competitive ability of wild and hatchery fish can be determined by additive and substitutive experimental designs, respectively, and the limited body of substitutive experiments suggests that the relative competitive ability of hatchery and wild fish is approximately equal when measured as growth. Conducting substitutive experiments becomes difficult as the spatial and temporal scales increase. Large-scale experiments comparing supplemented and control reaches or streams hold some promise for quantifying the effects of released hatchery fish on wild fish behavior, growth and survival.

Wood, CC. (1987). Predation of juvenile Pacific salmon by the Common Merganser (*Mergus-merganser*) on eastern Vancouver Island. I: Predation during the seaward migration. *Canadian Journal of Fisheries and Aquatic Sciences* 44(5):941-949. DOI: 10.1139/f87-112

Predation of juvenile salmonids by the common merganser (*Mergus merganser*) was investigated during the period of seaward migration in two streams where fish populations are enhanced by spawning channels and hatcheries. Observation of foraging behaviour and crop-gullet contents indicated that, during this period, mergansers foraging on freshwater reaches of the streams ate juvenile salmonids almost exclusively whereas those foraging on tidal waters rarely ate salmonids. Maximum rates of salmonid mortality were estimated by assessing

merganser abundance and the pattern of foraging activity on fresh versus tidal waters. Maximum mortality rate declined as fish abundance increased (i.e. mortality was depensatory) in all cases where the effects of prey size-selection could be ignored owing to an overwhelming abundance of one prey species. Bounds on maximum mortality rate by species for the entire migration period were computed under different hypotheses about the prey size-selection habits of mergansers; maximum mortality rate did not exceed 10% for any salmonid species over the entire seaward migration.

Wood, CC. (1987). Predation of juvenile Pacific salmon by the Common Merganser (*Mergus-merganser*) on eastern Vancouver Island. II: Predation of stream-resident juvenile salmon by merganser broods. *Canadian Journal of Fisheries and Aquatic Sciences* 44(5):950-959. DOI: 10.1139/f87-113

Predation of stream-resident juvenile salmonids by broods of the common merganser (*Mergus merganser*) was investigated in three streams on eastern Vancouver Island from 1988 to 1982. Daily fish consumption by merganser ducklings was estimated to range from 80% of body weight for ducklings at 10 d of age to 40% of body weight for those at 40 d of age. Merganser ducklings were never observed to eat juvenile salmonids on tidal waters, but did eat them on the freshwater reaches of streams studied. Typically, broods inhabited only the freshwater reaches of their natal stream while young, but spent progressively more time foraging on tidal waters as they grew older. The biomass of broods (and hence potential consumption) on fresh water was estimated by reconstructing the history of individual broods from census data. These results suggest that merganser broods consumed on the order of 82 000 - 131 800 coho salmon (*Oncorhynchus kisutch*) fry in the Big Qualicum River between June 10 and August 25. This is equivalent to 24-65% of the observed wild smolt production from this system, assuming that these fry would otherwise have survived as well as uneaten fry.

Benefits

Anderson, JH, GR Pess, RW Carmichael, MJ Ford, TD Cooney, CM Baldwin and MM McClure. (2014). Planning Pacific salmon and steelhead reintroductions aimed at long-term viability and recovery. *North American Journal of Fisheries Management* 34: 72-93 DOI: 10.1080/02755947.2013.847875

Local extirpations of Pacific salmon *Oncorhynchus* spp. and steelhead *O. mykiss*, often due to dams and other stream barriers, are common throughout the western United States. Reestablishing salmonid populations in areas they historically occupied has substantial potential to assist conservation efforts, but best practices for reintroduction are not well established. In this paper, we present a framework for planning reintroductions designed to promote the recovery of salmonids listed under the Endangered Species Act. Before implementing a plan, managers should first describe the benefits, risks, and constraints of a proposed reintroduction. We define benefits as specific biological improvements towards recovery objectives. Risks are the potential negative outcomes of reintroductions that could worsen conservation status rather than improve it. Constraints are biological factors that will determine whether the reintroduction successfully establishes a self-sustaining population. We provide guidance for selecting a recolonization strategy (natural colonization, transplanting, or hatchery releases), a source population, and a method for providing passage that will maximize the probability of conservation benefit while minimizing risks. Monitoring is necessary to determine whether the reintroduction successfully achieved the benefits and to evaluate the impacts on nontarget species or populations. Many of the benefits, especially diversity and the evolution of locally

adapted population segments, are likely to accrue over decadal time scales. Thus, we view reintroduction as a long-term approach to enhancing viability. Finally, our review of published salmonid reintroduction case studies suggests that large uncertainties remain in the success of reintroduction in establishing self-sustaining populations, particularly for programs employing active methods. Received September 10, 2012; accepted August 30, 2013

Campbell, NR, C Kamphaus, K Murdoch and SR Narum. (2017). Patterns of genomic variation in Coho salmon following reintroduction to the interior Columbia River. *Ecology and Evolution* 7(23): 10350-10360 DOI: 10.1002/ece3.3492

Coho salmon were extirpated in the mid-20th century from the interior reaches of the Columbia River but were reintroduced with relatively abundant source stocks from the lower Columbia River near the Pacific coast. Reintroduction of Coho salmon to the interior Columbia River (Wenatchee River) using lower river stocks placed selective pressures on the new colonizers due to substantial differences with their original habitat such as migration distance and navigation of six additional hydropower dams. We used restriction site-associated DNA sequencing (RAD-seq) to genotype 5,392 SNPs in reintroduced Coho salmon in the Wenatchee River over four generations to test for signals of temporal structure and adaptive variation. Temporal genetic structure among the three broodlines of reintroduced fish was evident among the initial return years (2000, 2001, and 2002) and their descendants, which indicated levels of reproductive isolation among broodlines. Signals of adaptive variation were detected from multiple outlier tests and identified candidate genes for further study. This study illustrated that genetic variation and structure of reintroduced populations are likely to reflect source stocks for multiple generations but may shift over time once established in nature.

Galbreath, PF, MA Bisbee, DW Dompier, CM Kamphaus and TH Newsome. (2014). Extirpation and Tribal Reintroduction of Coho Salmon to the Interior Columbia River Basin. *Fisheries* 39(2): 77-87 DOI: 10.1080/03632415.2013.874526

Harvest of anadromous salmonids in the Columbia River basin has been fundamental to the nutrition, economy, and cultural and religious beliefs of the regional Native American tribes. Agricultural development, dam construction, urbanization, and overharvest following colonization by European-origin settlers, however, resulted in dramatic reductions in salmon runs and negative impacts to the well-being of tribal peoples. Federal and state fishery agencies attempted to mitigate for the loss and to rebuild some salmonid populations but deemed Coho Salmon of lesser importance for upriver fisheries and allowed them to go functionally extinct. In the mid-1990s, fishery agencies of the Columbia River Treaty tribes spearheaded efforts to reestablish the extirpated Coho Salmon, beginning in the Yakima, Wenatchee, Methow, and Clearwater rivers. The programs were initiated with juveniles from composite lower Columbia River hatchery stocks, acclimated or direct released near potential spawning habitat, then were transitioned to producing juveniles with broodstock collected in-basin. Increasing numbers of fish are now returning to these rivers, a portion of which is the product of natural spawning. Results suggest that the Coho Salmon are adapting to their new environments and founding local naturalized populations.

Eldridge, WH and K Killebrew. (2008). Genetic diversity over multiple generations of supplementation: an example from Chinook salmon using microsatellite and demographic data. *Conservation Genetics* 9(1): 13-28 DOI: 10.1007/s10592-007-9298-y

We examined demographic data and microsatellite loci in a supplemented population of Chinook salmon (*Oncorhynchus tshawytscha*) seeking evidence of changes in genetic diversity or for

reduction of the effective size (Ne) arising from supplementation (i.e., the Ryman-Laikre effect). A supplementation program in the North Fork Stillaguamish River (Washington State, USA) was intended to increase abundance (N) and maintain genetic diversity in the depressed population. Since supplementation expanded in 1986, about 9% of the population has been randomly collected for broodstock. The resulting progeny are released into the wild and comprised 10-60% of all returning adults. Genotypic data were obtained at 14 microsatellite loci from adult samples collected in four years between 1985 and 2001; these data indicated that the allelic richness and expected heterozygosity did not significantly change during this period and that genetic diversity in the captive and wild progeny was similar. The inbreeding and variance Ne estimated from adult escapement between 1974 and 2004 were different for the same generation, but the ratios of effective size to census size were very similar and decreased following supplementation. The variance Ne by the temporal method increased over time, but it is difficult to draw conclusions because of necessary assumptions made during the calculations. Based on these results we conclude that: (1) genetic diversity has been maintained over multiple generations of supplementation; (2) supplementation has not contributed to a loss of genetic diversity; and (3) monitoring genetic effects of supplementation is not straightforward, but it can be useful to look at both demographic and genetic data simultaneously.

Kalinowski, ST, DM Van Doornik, CC Kozfkay and RS Waples. (2012). Genetic diversity in the Snake River sockeye salmon captive broodstock program as estimated from broodstock records. *Conservation Genetics* 13(5): 1183-1193 DOI: 10.1007/s10592-012-0363-9

Snake River sockeye salmon spawning in Redfish Lake, Idaho are one of the most endangered taxa of Pacific salmon. The wild population nearly went extinct in the 1990s, and all surviving fish were incorporated into a captive broodstock program at that time. We used pedigree analysis to evaluate the effectiveness of the breeding program in retaining genetic variation from 1991 through 2008. Broodstock records document which males were crossed with which females, but fish from multiple crosses were frequently raised in the same tank so the exact pedigree of the population is unknown. Therefore, a simulation-based approach was used to estimate how much genetic diversity was retained by this breeding program. Results indicate that in 2008, after 5.5 generations of breeding, the average inbreeding coefficient was probably about 0.056. We estimated the inbreeding effective population size to be 41 over the entire program and 115 for the most recent generation. This amount of inbreeding is substantially less than has occurred in many high-profile captive breeding programs. Our results depend on several assumptions regarding the relatedness of fish in the breeding program, but simulations suggest our main results are relatively insensitive to these assumptions.

Kline, PA and TA Flagg. (2014). Putting the Red Back in Redfish Lake, 20 Years of Progress Toward Saving the Pacific Northwest's Most Endangered Salmon Population. *Fisheries* 39(11): 488-500 DOI: 10.1080/03632415.2014.966087

In November 1991, the U.S. National Marine Fisheries Service listed Snake River Sockeye Salmon (*Oncorhynchus nerka*) as endangered under the U.S. Endangered Species Act (ESA). The last known remnants of the Snake River stock return to Redfish Lake in the Sawtooth Valley in central Idaho. In the ensuing two decades since the ESA listing, many actions have been taken to conserve the population, including the initiation of a hatchery-based gene rescue program. The chief aim of this article is to describe the development and implementation of hatchery-based gene rescue activities, review present-day release strategies and associated adult returns, and describe a new effort underway to expand program production to more effectively address recolonization and local adaptation objectives. In addition, we describe achievable population triggers to allow the transition from a hatchery-based effort to a habitat-based effort that should

allow natural population recovery to proceed.

Kostow, K. (2012). Strategies for reducing the ecological risks of hatchery programs: Case studies from the Pacific Northwest. *Environmental Biology of Fishes* 94(1): 285-310 DOI: 10.1007/s10641-011-9868-1

The Pacific Northwest state and federal agencies and tribes that operate salmon and steelhead (*Oncorhynchus* sp.) hatcheries are authorized to develop and implement strategies to reduce the risks the programs pose to wild fish populations. This paper reviews five case studies from the states of Oregon and Washington, USA, where agencies and tribes have implemented or proposed programs that were intended to reduce ecological risks due to hatchery programs. The case studies are for Oregon coho salmon, Select Area terminal fisheries programs for Chinook and coho salmon in the lower Columbia River, Hood Canal chum salmon in Puget Sound Washington, Siletz River steelhead on the Oregon coast, and Okanogan River Chinook salmon in eastern Washington. The five case studies address a diversity of management objectives and species. They demonstrate some of the science and risk reduction strategies used to alleviate the ecological effects of hatcheries, and they document some of the results and outcomes of taking action. Elements of four of the case studies have been in place for nearly 20 years. The available science and the conservation ethic toward hatchery programs evolved significantly over this period, and management decisions and strategies have been influenced by public policy as well as by scientific information. Therefore the case studies also document some of the history, the evolution of ideas, the uncertainty, and the political controversy associated with the management of this risk factor. The paper concludes with six principles to help guide the development of future risk reduction programs.

Liermann, M, G Pess, M McHenry, J McMillan, M Elofson, T Bennett and R Moses. (2017). Relocation and Recolonization of Coho Salmon in Two Tributaries to the Elwha River: Implications for Management and Monitoring. *Transactions of the American Fisheries Society* 146(5): 955-966 DOI: 10.1080/00028487.2017.1317664

In 2012 the lower of two Elwha River dams was breached, restoring access of anadromous salmonids to the middle Elwha River (between the two dams), including two distinct tributaries, Indian Creek and Little River. While comparable in size, Indian Creek is considerably less steep than Little River (mean slope of 1.0% versus 3.5%, respectively) and has a warmer stream temperature regime due to its source, Lake Sutherland. During and after breaching, Coho Salmon *Oncorhynchus kisutch* were relocated to these tributaries from lower Elwha River hatcheries (below the dams) to determine if individuals from a hatchery-dominated population would successfully spawn and seed the systems with juveniles and to assess differences in recolonization between the streams. Transplantation led to immediate spawning, which resulted in levels of smolt out-migrants per stream kilometer comparable with other established Coho Salmon populations in the Pacific Northwest. During the first 2 years of the relocation, redd densities in the two systems were similar but Indian Creek produced four to five times as many smolts per kilometer as Little River. In addition, fry out-migration occurred 2 to 4 weeks earlier in Indian Creek, as predicted by the warmer incubation temperatures. In the first years of the study, there was little evidence of natural colonization of the two tributaries by adults. However, in 2016 over half of the observed adults returning to the two tributaries were not transplanted, suggesting that the progeny from the transplanted fish were returning to their natal waters. This work demonstrates that transplanting hatchery-dominated Coho Salmon adults into newly available habitat can result in immediate freshwater production that is comparable to other systems and that density and timing of juvenile out-migrants can differ dramatically based on the seeded habitat.

Small, MP, TH Johnson, C Bowman and E Martinez. (2013). Genetic assessment of a summer chum salmon metapopulation in recovery. *Evolutionary Applications* 7(2): 266-285 DOI: 10.1111/eva.12118

Programs to rebuild imperiled wild fish populations often include hatchery-born fish derived from wild populations to supplement natural spawner abundance. These programs require monitoring to determine their demographic, biological, and genetic effects. In 1990s in Washington State, the Summer Chum Salmon Conservation Initiative developed a recovery program for the threatened Hood Canal summer chum salmon Evolutionarily Significant Unit (ESU) (the metapopulation) that used in-river spawners (wild fish) for each respective supplementation broodstock in six tributaries. Returning spawners (wild-born and hatchery-born) composed subsequent broodstocks, and tributary-specific supplementation was limited to three generations. We assessed impacts of the programs on neutral genetic diversity in this metapopulation using 16 microsatellite loci and a thirty-year dataset spanning before and after supplementation, roughly eight generations. Following supplementation, differentiation among subpopulations decreased (but not significantly) and isolation by distance patterns remained unchanged. There was no decline in genetic diversity in wild-born fish, but hatchery-born fish sampled in the same spawning areas had significantly lower genetic diversity and unequal family representation. Despite potential for negative effects from supplementation programs, few were detected in wild-born fish. We hypothesize that chum salmon natural history makes them less vulnerable to negative impacts from hatchery supplementation.

Scheuerell, MD, ER Buhle, BX Semmens, MJ Ford, T Cooney and RW Carmichael. (2015). Analyzing large-scale conservation interventions with Bayesian hierarchical models: a case study of supplementing threatened Pacific salmon. *Ecology and Evolution* 5(10): 2115-2125 DOI: 10.1002/ece3.1509

Myriad human activities increasingly threaten the existence of many species. A variety of conservation interventions such as habitat restoration, protected areas, and captive breeding have been used to prevent extinctions. Evaluating the effectiveness of these interventions requires appropriate statistical methods, given the quantity and quality of available data. Historically, analysis of variance has been used with some form of predetermined before-after control-impact design to estimate the effects of large-scale experiments or conservation interventions. However, ad hoc retrospective study designs or the presence of random effects at multiple scales may preclude the use of these tools. We evaluated the effects of a large-scale supplementation program on the density of adult Chinook salmon *Oncorhynchus tshawytscha* from the Snake River basin in the northwestern United States currently listed under the U.S. Endangered Species Act. We analyzed 43years of data from 22 populations, accounting for random effects across time and space using a form of Bayesian hierarchical time-series model common in analyses of financial markets. We found that varying degrees of supplementation over a period of 25years increased the density of natural-origin adults, on average, by 0-8% relative to nonsupplementation years. Thirty-nine of the 43year effects were at least two times larger in magnitude than the mean supplementation effect, suggesting common environmental variables play a more important role in driving interannual variability in adult density. Additional residual variation in density varied considerably across the region, but there was no systematic difference between supplemented and reference populations. Our results demonstrate the power of hierarchical Bayesian models to detect the diffuse effects of management interventions and to quantitatively describe the variability of intervention success. Nevertheless, our study could not address whether ecological factors (e.g., competition) were more important than genetic considerations (e.g., inbreeding depression) in determining the response to supplementation.