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IN THE UNITED STATES DISTRICT COURT
DISTRICT OF OREGON
PORTLAND DIVISION

NATIONAL WILDLIFE FEDERATION, *et al.*,
Plaintiffs,
and
STATE OF OREGON,
Intervenor-Plaintiff,
v.
NATIONAL MARINE FISHERIES SERVICE,
et al.,
Defendants,
and
NORTHWEST RIVERPARTNERS, *et al.*,
Intervenor-Defendants.

Case No.: 3:01-CV-00640-SI

SUPPLEMENTAL FILING
OF WARM SPRINGS,
UMATILLA AND
YAKAMA TRIBES;
REFERENCES TO
SCIENTIFIC LITERATURE
DEMONSTRATING
BENEFITS OF ARTIFICIAL
PRODUCTION TO
“WILD/NATURAL”
POPULATIONS

JUNE 23, 2015, SUMMARY
JUDGMENT HEARING

During the oral argument offered by John Ogan, counsel for the Confederated Tribes of the Warm Springs Reservation of Oregon, his Honor inquired if there was scientific support for

the proposition that artificial production strategies (“hatcheries”) can provide positive benefits to wild or natural ESA listed salmon and steelhead populations. Counsel responded positively but only anecdotally, and offered to supply the Court with references to specific scientific studies and reports in a supplemental filing. The Court accepted the offer.

Exhibit 1 is a bibliography of scientific literature that the Amicus Lower River Tribes submit illustrates that there is ample scientific literature supporting the use of artificial production and benefits to “natural” populations and/or ecological health of a system used by such populations. An abstract is provided for each study, and the Court may follow the citations to the literature should it desire to review the entire study and report.

Exhibit 2 is a full copy of a scientific study published in 2012 regarding spring chinook populations and artificial production entitled: *“Supportive breeding boosts natural population abundance with minimal negative effects on fitness on a wild population of Chinook salmon.”* This study was conducted on tributaries to the Salmon River in Idaho. Those following this work often refer to it as the “Johnson Creek supplementation study.” The tribes recommend that the Court review this contemporary study in the “FCRPS BiOp area” fully when time permits.

Respectfully submitted.

DATED this 2nd day of July, 2015.

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CERTIFICATE OF SERVICE

I hereby certify that on July 2, 2015, I electronically filed the foregoing document with the Clerk of the Court using the CM/ECF system which will send notification of such filing to all parties in this matter who are registered with the Court's CM/ECF filing system.

DATED this 2nd day of July, 2015.

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Bibliography in Support of Supplementation Science

Compiled by:
Bill Bosch, Yakama Nation Fisheries – Yakima Klickitat Fisheries Project
Peter Galbreath, Columbia River Inter-Tribal Fish Commission

Current Revision, June, 2015

Purpose: The primary purpose of this bibliography is to present publications or studies that support the theory that supplementation (as defined by RASP 1992) techniques can be used to maintain or increase natural production, while maintaining the long-term fitness of the wild and native salmonid populations and keeping adverse genetic and ecological impacts within acceptable limits.

Note: The term “abstract” is used here to denote an abstract as published by the authors. The term “synopsis” is used when compilers of this bibliography summarized publications, generally using sentences taken directly from the publications.

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Can supplementation maintain or increase natural production?

Araki, H., W. R. Ardren, E. Olsen, B. Cooper, and M. S. Blouin. 2007. Reproductive success of captive-bred steelhead trout in the wild: evaluation of three hatchery programs in the Hood River. *Conservation Biology* 21 (1), 181-190.

Abstract: Population supplementation programs that release captive-bred offspring into the wild to boost the size of endangered populations are now in place for many species. The use of hatcheries for supplementing salmonid populations has become particularly popular. Nevertheless, whether such programs actually increase the size of wild populations remains unclear, and predictions that supplementation fish drag down the fitness of wild fish remain untested. To address these issues, we performed DNA-based parentage analyses on almost complete samples of anadromous steelhead (*Oncorhynchus mykiss*) in the Hood River in Oregon (U.S.A.). Steelhead from a supplementation hatchery (reared in a supplementation hatchery and then allowed to spawn naturally in the wild) had reproductive success indistinguishable from that of wild fish. In contrast, fish from a traditional hatchery (nonlocal origin, multiple generations in hatcheries) breeding in the same river showed significantly lower fitness than wild fish. In addition, crosses between wild fish and supplementation fish were as reproductively successful as those between wild parents. Thus, there was no sign that supplementation fish drag down the fitness of wild fish by breeding with them for a single generation. On the other hand, crosses between hatchery fish of either type (traditional or supplementation) were less fit than expected, suggesting a possible interaction effect. These are the first data to show that a supplementation program with native brood stock can provide a single-generation boost to the size of a natural steelhead population without obvious short-term fitness costs. The long-term effects of population supplementation remain untested.

Bailey, M.M., and J.D. Zydlewski. 2013. To stock or not to stock? Assessing the restoration potential of a remnant American Shad spawning run with hatchery supplementation. *North American Journal of Fisheries Management*, 33:459-467.

Abstract: Hatchery supplementation has been widely used as a restoration technique for American Shad *Alosa sapidissima* on the East Coast of the USA, but results have been equivocal. In the Penobscot River, Maine, dam removals and other improvements to fish passage will likely reestablish access to the majority of this species' historic spawning habitat. Additional efforts being considered include the stocking of larval American Shad. The decision about whether to stock a river system undergoing restoration should be made after evaluating the probability of natural recolonization and examining the costs and benefits of potentially accelerating recovery using a stocking program. However, appropriate evaluation can be confounded by a dearth of information about the starting population size and age structure of the remnant American Shad spawning run in the river. We used the Penobscot River as a case study to assess the theoretical sensitivity of recovery time to either scenario (stocking or not) by building a deterministic model of an American Shad population. This model is based on the best available estimates of size at age, fecundity, rate of iteroparity, and recruitment. Density dependence was imposed, such that the population reached a plateau at an arbitrary recovery goal of 633,000 spawning adults. Stocking had a strong accelerating effect on the time to modeled recovery (as measured by the time to reach 50% of the recovery goal) in the base model, but stocking had diminishing effects with larger population sizes. There is a diminishing return to stocking when the starting population is modestly increased. With a low starting population (a spawning run of 1,000), supplementation with 12 million larvae annually accelerated modeled recovery by 12 years. Only a 2-year acceleration was observed if the starting population was 15,000. Such a heuristic model may aid managers in assessing the costs and benefits of stocking by incorporating a structured decision framework.

Baumsteiger, J., D. M. Hand, D. E. Olson, R. Spateholts, G. FitzGerald, and W. R. Ardren. 2008.

Use of Parentage analysis to Determine Reproductive Success of Hatchery-Origin Spring Chinook Salmon Outplanted into Shitike Creek, Oregon. *North American Journal of Fisheries Management*, 28:1472-1485.

Abstract: Removal of fish passage barriers provides Pacific salmon *Oncorhynchus* spp. and steelhead *O. mykiss* the opportunity to recolonize previously accessible habitat, though the time scale of natural recolonization may not be sufficient for management or conservation goals. One strategy for accelerating recolonization is to outplant hatchery-origin adults into newly restored habitats. In this paper, we describe how genetic parentage analysis was used to determine the reproductive success of adult stream-type spring Chinook salmon *O. tshawytscha* taken from two localized hatchery stocks and outplanted into a stream. We defined reproductive success as the production of migratory juveniles. In 2002 and 2003, 83 and 265 adult hatchery salmon, respectively, were outplanted into Shitike Creek, Oregon, a tributary to the Deschutes River. Using 11 microsatellite markers, 799 and 827 migratory juveniles from the two brood years were genotyped and matched back to potential outplanted parents using genetic parentage analyses. Successful spawning of outplant-outplant, outplant-wild, and wild-wild fish occurred in Shitike Creek in both years. Adults outplanted in 2002 showed far fewer matches (18%) to sampled juveniles than those from 2003 (88%). Additionally, only 1% of juveniles had both parents identified as outplants in 2002, compared with almost 61% in 2003. Differences in the number of females outplanted each year appeared to account for the differential productivity. The number of offspring attributed to an individual outplant was variable, ranging from 1 to more than 10. Multiple outplant \times outplant matings were identified for each sex as males mated with up to seven females and females mated with up to four males. This study shows that, under the right conditions, outplanted adult hatchery fish taken from localized hatchery stocks can contribute to the overall juvenile production in a natural stream.

Berejikian, B. A., T. Johnson, R.S. Endicott, and J. Lee-Waltermire. 2008. Increases in Steelhead Redd Abundance Resulting from Two Conservation Hatchery Strategies in the Hamma Hamma River, WA. *Canadian Journal of Fisheries and Aquatic Sciences*, 65:754-764.

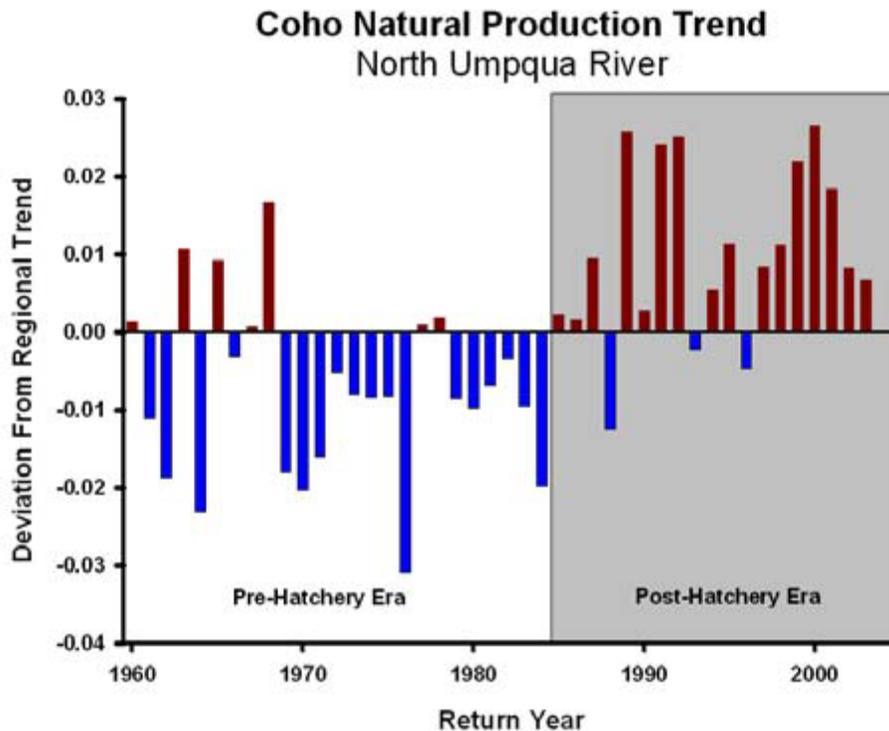
Abstract: Conservation hatcheries for anadromous salmonids that aim to increase production and minimizing genetic, ecological, and demographic risks have not been experimentally tested for their ability to increase number of adults spawning in the natural environment. The conservation hatchery program for steelhead (i.e., sea-run rainbow trout, *Oncorhynchus mykiss*) evaluated in this study caused an increase in the number of redds in the supplemented Hamma Hamma River compared with the presupplementation period. Three control populations (nonsupplemented) either remained stable or declined over the same period. The increase in redds from hatchery-produced spawners did not reduce the redd production from natural-origin spawners. The strategy of rearing and releasing adult steelhead accounted for the greatest proportion of redd abundance increases. Environmentally induced differences in spawn timing between the adult release group and anadromous adults of hatchery and natural origin may explain why the adult release group and anadromous adults assortatively formed pairing combinations on the spawning grounds. Although captive reared adults produced the majority of redds in years they were released in substantial numbers, uncertainty regarding the relative reproductive success of this strategy suggests caution in recommending one strategy over the other. A demographic boost to the naturally spawning population was effected while managing to minimize negative ecological consequences.

Caroffino, D. C, L. M. Miller, A. R. Kapucinski, and J. J. Ostazeski. 2008. Stocking success of local-origin fry and impact of hatchery ancestry: monitoring a new steelhead (*Oncorhynchus mykiss*) stocking program in a Minnesota tributary to Lake Superior. *Canadian Journal of Fisheries and Aquatic Sciences* 65:309-318.

Abstract: The inception of a hatchery program to rebuild a naturalized steelhead (*Oncorhynchus mykiss*) population in Minnesota waters of Lake Superior gave us the rare opportunity to monitor the success of fry stocking and determine if hatchery ancestry can reduce fitness of stocked fish in the early generations of a stocking program. Through genetic monitoring of two year classes, we determined that hatchery adults produced 1.3-6.2 times as many age-2 juveniles per female than naturally spawning fish. Survival of stocked fry of parents born in a hatchery relative to those of parents born in the wild was 70% in paired-stocking comparisons. These results suggest that stocking local-origin fry can increase the short-term abundance of depleted populations and that fish with no hatchery history are a better source for supplemental stocking. Additionally, sampling small numbers of adults for broodstock created genetically distinct groups, which could potentially cause long-term genetic change in the population. Genetic monitoring of adults will be essential to determining whether differences observed persist through the life cycle of the stocked fish.

Cramer, S. P., N. K. Ackerman, and J. B. Lando. 2005. Viability of Oregon Coastal Coho: Comments on Oregon's 2005 Assessment. Report to Oregon Forest Industries Council and Douglas County. S.P. Cramer & Associates, Inc. Gresham, OR.

Synopsis: Review of data set dating back to 1958. Hatchery fish were virtually non-existent in the North Umpqua for the first 24 years of data, 1958-1981, and composed an average 76% of natural spawners after 1982. The North Umpqua showed a highly significant increase in natural production after 1982. Since 1985, when substantial returns from naturally spawning hatchery coho began, the trend in natural production of coho from the North Umpqua consistently out-performed the regional trend in natural production (see figure). This difference clearly indicates that hatchery fish were successfully reproducing and having a detectable positive influence on natural production.



Fast, D.E., W.J. Bosch, M.V. Johnston, C.R. Strom, C.M. Knudsen, A.L. Fritts, G.M. Temple, T.N. Pearsons, D.A. Larsen, A.H. Dittman, and D. May. 2015. A Synthesis of Findings from an Integrated Hatchery Program after Three Generations of Spawning in the Natural Environment. *North American Journal of Aquaculture* 77:377-395.

Abstract: The Cle Elum Supplementation and Research Facility in the Yakima River basin, Washington, is an integrated spring Chinook Salmon *Oncorhynchus tshawytscha* hatchery program designed to test whether artificial propagation can increase natural production and harvest opportunities while keeping ecological and genetic impacts within acceptable limits. Only natural-origin (naturally spawned) fish are used for hatchery broodstock. Spawning, incubation, and early rearing occur at a central facility; presmolts are transferred for final rearing, acclimation, and volitional release at sites adjacent to natural spawning areas, where returning adults can spawn with natural-origin fish. The first wild broodstock were collected in 1997, and age-4 adults have returned to the Yakima River since 2001. An unsupplemented population in the adjacent Naches River watershed provides a reference for evaluating environmental influences. The program has been comprehensively monitored from its inception. A synthesis of findings, many already published, is as follows: supplementation increased the harvest, redd counts, and spatial distribution of spawners; natural-origin returns were maintained; straying to nontarget systems was negligible; natural-origin females had slightly higher breeding success (production of surviving fry) in an artificial spawning channel, while the behavior and breeding success of natural- and hatchery-origin males were similar; hatchery-origin fish showed differences in morphometric and life history traits; high rates of hatchery

age-2 (minijack) production were reported, but the observed proportions of out-migrating juvenile and adult (ages 4 and 5) returning males were comparable for hatchery- and natural-origin fish; hatchery smolts did not affect the levels of pathogens in natural smolts; and the ecological interactions attributed to the program were within adopted guidelines. Continued study is required to assess the long-term impacts on natural production and productivity.

Fitzsimons, J.D., A. Dalton, B. MacVeigh, M. Heaton, C. Wilson, and D.C. Honeyfield. 2013. Use of Stable Isotopes to Identify Redds of Putative Hatchery and Wild Atlantic Salmon and Evaluate Their Spawning Habitat and Egg Thiamine Status in a Lake Ontario Tributary. *North American Journal of Fisheries Management* 33:741-753.

Abstract: Both wild and hatchery Atlantic Salmon *Salmo salar* can contribute to restoration but can exhibit differences in spawning habitat selection (e.g., water depth, current speed) and egg nutritional quality (e.g., thiamine), which affect reproductive success. Hence, there is a need to be able to differentiate the spawning contribution of the two groups in the wild. As diets of wild and hatchery-reared spawners are markedly dissimilar and diet is known to influence stable isotope signature, egg stable isotope signatures offer the potential to discriminate redds of each. Using stable isotope analysis of carbon and nitrogen ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of naturally spawned Atlantic Salmon eggs, we were able to discriminate the redds of putative wild (i.e., previously stocked life stage feeding in Lake Ontario; EWSR) from putative hatchery-reared Atlantic Salmon (EHSR). Eggs of EWSR were significantly more enriched in nitrogen ($\delta^{15}\text{N}$: $15.0 \pm 0.5\text{‰}$ [mean \pm SE]) but more depleted in carbon ($\delta^{13}\text{C}$: $-26.6 \pm 0.3\text{‰}$) than eggs of EHSR ($\delta^{15}\text{N}$ = $9.8 \pm 0.6\text{‰}$; $\delta^{13}\text{C}$ = $-17.5 \pm 0.0\text{‰}$). Eggs of EHSR were indistinguishable from eggs of known hatchery Atlantic Salmon for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Using stable isotopes to discriminate redd type, few differences were found between the spawning habitat of putative wild and hatchery spawners. Similarly using the same criteria, thiamine levels in eggs of EWSR ($8,474 \pm 840$ pmol/g) were not significantly different from eggs of known wild Atlantic Salmon ($3,691 \pm 782$ pmol/g) or of eggs of EHSR ($14,865 \pm 1,050$ pmol/g), whose thiamine levels were indistinguishable from eggs of known hatchery Atlantic Salmon ($14,200 \pm 1,167$ pmol/g). Egg thiamine levels for all groups were above established mortality thresholds. Our results indicate that both hatchery and wild Atlantic Salmon can make reproductive contributions, which can be differentiated and quantified using stable isotope signatures.

Hess, M.A., C.D. Rabe, J.L. Vogel, J.L. Stephenson, D.D. Nelson, and S.R. Narum. 2012. Supportive breeding boosts natural population abundance with minimal negative impacts on fitness of a wild population of Chinook salmon. *Molecular Ecology* 21:5236-5250.

Abstract: 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 F_1 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 $W \times W$ matings. Mean RRS of $H \times W$ and $H \times H$ 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.

Kassler, T. W., D. K. Hawkins, and J. M. Tipping. 2008. Summer-Run Hatchery Steelhead Have Naturalized in the South Fork Skykomish River, Washington. *Transactions of the American Fisheries Society* 137:763-771.

Abstract: Evaluation of natural-origin, hatchery-origin, and unmarked steelhead *Oncorhynchus mykiss* from the Skykomish River drainage basin, Washington, was conducted to determine the source of unmarked steelhead that return to Sunset Falls (South Fork Skykomish River). One possible source is the large number of steelhead stocked into the Skykomish River basin from Reiter Ponds Hatchery; this hatchery stock was founded with fish from Skamania Hatchery in the Washougal River system, Washington. A microsatellite DNA analysis of 10 loci was used to evaluate unmarked samples in comparison with natural-origin samples from the North Fork Skykomish River and hatchery-origin samples from Reiter Ponds Hatchery. Results of the analyses provide evidence that the unmarked steelhead collected at Sunset Falls are more closely related to Reiter Ponds Hatchery fish than to natural-origin fish from the North Fork Skykomish River. There is evidence that unmarked steelhead at Sunset Falls are also mixing with natural-origin North Fork Skykomish River fish but to a lesser degree than with Reiter Ponds Hatchery fish. This study documents that Skamania Hatchery-origin steelhead have naturally produced offspring that are returning to spawn in a northern Puget Sound river basin.

McLean, M.L., P.T. Lofy, and J.D.M. Schwartz. 2006. Successful natural production of hatchery spring chinook salmon: A lesson from Lookingglass Creek in Eastern Oregon. Oregon Chapter AFS Meeting Presentation, March 3, 2006.

Synopsis: Reintroduction of a non-endemic hatchery spring Chinook stock from Rapid River (RR) was evaluated and various survival parameters were compared with an endemic stock from Lookingglass Creek (LCE) and other naturally produced fish from the Grand Ronde River (GRR) or other Columbia Basin tributaries (CSR). "There was no significant difference in mean adults-per-redd among the RR, LCE, or CSR. There was no significant difference in mean juveniles-per-redd between RR, LCE, and GRR. Progeny-per-parent ratios for RR were not significantly different than those estimated for GRR."

Perrier, C., F. Daverat, G. Evanno, C. Pecheyran, J-L Bagliniere, and J-M Roussel. 2011. Coupling genetic and otolith trace element analyses to identify river-born fish with hatchery pedigrees in stocked Atlantic salmon (*Salmo salar*) populations. *Canadian Journal of Fisheries and Aquatic Sciences*, 68(6): 977-987.

Abstract: This study combines otolith trace element and genetic analyses to explore the origin of individuals when hatchery-reared fish are released into wild populations. We sampled 90 juvenile Atlantic salmon (*Salmo salar*) in four rivers in Normandy (France) and in the hatchery stock. Individuals were analyzed at six microsatellite markers and their otolith elemental concentrations (14 elements) were measured using femto-second laser ablation inductively-coupled plasma mass spectrometry. Wild populations were genetically differentiated from the hatchery strain ($F_{ST} \approx 0.06$). Significant differences in elemental concentrations were found among otoliths of juveniles from the four rivers and the hatchery, allowing the identification of their geographic origin (83%–100% correct assignment). Coupling genetic and trace element analyses on the same individuals provided formal evidence that hatchery-born juveniles released into the wild can migrate to the sea and return as adults to breed on natural spawning grounds. Their progeny have pure hatchery pedigrees but have otoliths typical of river-born juveniles, meaning that they can be mistaken for hatchery-raised juveniles if only genetic data are considered. The presence of hybrids also confirmed that individuals with hatchery pedigrees can breed with wild conspecifics.

Phillips, J.L., J. Ory and A. Talbot. 2000. Anadromous salmonid recovery in the Umatilla River Basin, Oregon: A case study. *Journal of the American Water Resources Association*, Vol. 36, no. 6, pp. 1287-1308. Dec 2000.

Synopsis: The mean adult-to-adult return rate of hatchery-reared steelhead exceeded replacement and that of the naturally-spawning population. Although the smolt-to-adult survival rates of hatchery-reared fish fluctuate, salmonid escapement has increased in recent years, permitting steelhead and spring chinook harvest. Enumeration of potential spawners and observed redds reveals an increase in natural production of all supplemented species.

Plumb, J.M., C.M. Moffitt, and W.P. Connor. 2009. Hatchery Supplementation Success and the Juvenile Life-History of Wild-Reared Fall Chinook Salmon in the Lower Snake River, Idaho. AFS poster presentation, national meeting, Nashville, TN, Sept. 2009.

Synopsis: Since 1998, a fall Chinook supplementation program has been conducted in the Snake River Basin with brood captured from fish passage facilities and Lyons Ferry State Fish Hatchery. In association with hatchery releases, abundance of the wild spawning population has increased substantially. The increased release of hatchery juveniles into the river was strongly ($P < 0.0001$) related to the increase in redds 3 years later. This increase in redds was, in turn, strongly related ($P < 0.0001$) to an increase in CPUE of wild juveniles in the rearing areas. This study documents the success of hatchery supplementation with a known-origin stock to restore a wild population.

Scheuerell, M.D., E.R. Buhle, B.X. Semmens, M.J. Ford, T. Cooney, and R.W. 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.

Synopsis: This study 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. The study analyzed 43 years 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. As the researchers modeled the 22 populations over the course of 25 years, they found “very limited support for a supplementation effect at both the individual population and ESU levels,” the report says. In fact, there was a 16 percent to 50 percent chance that supplementation had actually “caused some decrease in densities of wild adults across the ESU.” However, when the researchers excluded two of the twelve populations – the Minam and the Wenaha rivers had some hatchery-origin adults spawning but had not been “intentionally supplemented” – supplemented populations of wild fish increased from 1 percent to 13 percent relative to non-supplemented populations. “If habitat capacity has been reduced due to long-term structural alterations, then supplementation without concomitant habitat restoration will be unlikely to provide strong conservation benefits and may simply result in displacement of natural-origin fish by hatchery fish,” the study concludes. On the other hand, if carrying capacity is reduced because of a loss of nutrients in the stream, then supplementation could provide carcasses and increase carrying capacity. “Also, it is important to note that even if supplementation does result in a modest abundance increase, there are concerns that long-term use of artificial propagation could reduce genetic fitness, contribute to ecological risks such as competition for resources, and serve as vectors for diseases or parasites,” the study says.

Schindler, D.E., R. Hilborn, B. Chasco, C.P. Boatright, T.P. Quinn, L.A. Rogers, and M.S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. *Nature*, 465:609:612.

Abstract: One of the most pervasive themes in ecology is that biological diversity stabilizes ecosystem processes and the services they provide to society, a concept that has become a common argument for biodiversity conservation. Species-rich communities are thought to produce more temporally stable ecosystem services because of the complementary or independent dynamics among species that perform similar ecosystem functions. Such variance dampening within communities is referred to as a portfolio effect and is analogous to the effects of asset diversity on the stability of financial portfolios. In ecology, these arguments have focused on the effects of species diversity on ecosystem stability but have not considered the importance of biologically relevant diversity within individual species. Current rates of population extirpation are probably at least three orders of magnitude higher than species extinction rates, so there is a pressing need to clarify how population and life history diversity affect the performance of individual species in providing important ecosystem services. Here we use five decades of data from *Oncorhynchus nerka* (sockeye salmon) in Bristol Bay, Alaska, to provide the first quantification of portfolio effects that derive from population and life history diversity in an important and heavily exploited species. Variability in annual Bristol Bay salmon returns is 2.2 times lower than it would be if the system consisted of a single homogenous population rather than the several hundred discrete populations it currently consists of. Furthermore, if it were a single homogeneous population, such increased variability would lead to ten times more frequent fisheries closures. Portfolio effects are also evident in watershed food webs, where they stabilize and extend predator access to salmon resources. Our results demonstrate the critical importance of maintaining population diversity for stabilizing ecosystem services and securing the economies and livelihoods that depend on them. The reliability of ecosystem services will erode faster than indicated by species loss alone.

Steffensen, K.D., L.A. Powell, and J.D. Koch. 2010. Assessment of Hatchery-Reared Pallid Sturgeon Survival in the Lower Missouri River. *North American Journal of Fisheries*

Management 30:671-678.

Abstract: The population of pallid sturgeon *Scaphirhynchus albus* in the lower Missouri River between Gavins Point Dam (river kilometer [rkm] 1,305.2) and the confluence with the Mississippi River (rkm 0.0) remains imperiled, little to no natural recruitment occurring. Artificial propagation and subsequent population augmentation (i.e., stocking) may be the only viable option for maintaining pallid sturgeon populations in the lower Missouri River in the near term. Because relatively little is known about the ability of hatchery-reared pallid sturgeon to survive, the objective of this study was to quantify survival estimates for hatchery-reared pallid sturgeon stocked into the lower Missouri River. We used stock–recapture data collected from 1994 to 2008 to derive survival estimates based on the Cormack–Jolly–Seber model within program MARK. Since 1994, a total of 78,244 hatchery-reared pallid sturgeon have been released and 1% of these have been recaptured. Recapture numbers by size at stocking were as follows: 48 age 0, 730 age 1, and 38 older than age 1. Stocked age-0 hatchery-reared pallid sturgeon had an estimated apparent survival rate of 0.051 (SE = 0.008), compared with 0.686 (SE = 0.117) for age-1 fish and 0.922 (SE = 0.015) for fish older than age 1. Our analysis confirms that hatchery-reared pallid sturgeon can survive in the wild and contribute to the overall population of this species.

Van Doornik, D.M., B.A. Berejikian, L.A. Campbell, and E.C. Volk. 2010. The effect of a supplementation program on the genetic and life history characteristics of an *Oncorhynchus mykiss* population. *Canadian Journal of Fisheries and Aquatic Sciences*, 67(9): 1449-1458.

Abstract: Conservation hatcheries, which supplement natural populations by removing adults or embryos from the natural environment and rearing and releasing parr, smolts, or adults back into their natal or ancestral streams, are increasingly being used to avoid extinction of localized populations of Pacific salmonids. We collected data before and during a steelhead (*Oncorhynchus mykiss*) supplementation program to investigate the effect that the program has had on the population's genetic diversity and effective population size and any changes to an important life history trait (residency or anadromy). We found that supplementation did not cause substantial changes in the genetic diversity or effective size of the population, most likely because a large proportion of all of the steelhead redds in the river each year were sampled to create the supplementation broodstock. Our data also showed that the captively reared fish released as adults successfully produced parr. Furthermore, we found that during supplementation, there was an increase in the proportion of *O. mykiss* with anadromous ancestry vs. resident ancestry.

Can supplementation hatcheries be managed to maintain the long-term fitness of wild/natural populations?

Anderson, J.H., P.L. Faulds, W.I. Atlas, and T.P. Quinn. 2013. Reproductive success of captively bred and naturally spawned Chinook salmon colonizing newly accessible habitat. *Evolutionary Applications* 6:165-179. doi: 10.1111/j.1752-4571.2012.00271.x.

Abstract: Captively reared animals can provide an immediate demographic boost in reintroduction programs, but may also reduce the fitness of colonizing populations. Construction of a fish

passage facility at Landsburg Diversion Dam on the Cedar River, WA, USA, provided a unique opportunity to explore this trade-off. We thoroughly sampled adult Chinook salmon (*Oncorhynchus tshawytscha*) at the onset of colonization (2003–2009), constructed a pedigree from genotypes at 10 microsatellite loci, and calculated reproductive success (RS) as the total number of returning adult offspring. Hatchery males were consistently but not significantly less productive than naturally spawned males (range in relative RS: 0.70–0.90), but the pattern for females varied between years. The sex ratio was heavily biased toward males; therefore, inclusion of the hatchery males increased the risk of a genetic fitness cost with little demographic benefit. Measurements of natural selection indicated that larger salmon had higher RS than smaller fish. Fish that arrived early to the spawning grounds tended to be more productive than later fish, although in some years, RS was maximized at intermediate dates. Our results underscore the importance of natural and sexual selection in promoting adaptation during reintroductions.

Araki, H. 2008. Hatchery Stocking for Restoring Wild Populations: A Genetic Evaluation of the Reproductive Success of Hatchery Fish vs. Wild Fish. Pp. 153-167 in K. Tsukamoto, T. Kawamura, T. Takeuchi, T. D. Beard, Jr. and M. J. Kaiser, eds. *Fisheries for Global Welfare and Environment, 5th World Fisheries Congress*.

Abstract: Potential impacts of hatchery programs on wild populations have long been discussed, and of particular interest is the reproductive success of hatchery born fish in natural environments. Here I summarize our recent studies, in which DNA fingerprinting and genetic parentage analyses were used to estimate adult-to-adult reproductive fitness of steelhead trout (*Oncorhynchus mykiss*) in the Hood River, Oregon (USA). We found: (1) Hatchery fish left fewer adult offspring per parent than wild fish, but supplementation hatchery fish (from local, wild broodstock; H_{supp}) left larger numbers of offspring than traditional hatchery fish (from nonlocal, multi-generation hatchery broodstock; H_{trad}); (2) The reproductive fitness of H_{supp} declined unexpectedly fast (~40% per generation) when H_{supp} were reused as broodstock in a hatchery, suggesting that the negative effects of hatchery rearing are cumulative and heritable; (3) Effective population size was mainly restricted by variance in reproductive success among individuals, rather than by biased sex ratio and temporal fluctuation of population sizes; (4) H_{trad} showed particularly large variance in reproductive success, indicating another negative effect of traditional programs. Our case studies suggest that using local, wild broodstock reduces negative effects of hatchery rearing, but the repeated use of H_{supp} as broodstock should be minimized for efficient supplementation.

Baillie, S.M., C. Blackie, L. Gerardi, and P. Bentzen. 2015. Deciphering Hatchery Stock Influences on Wild Populations of Vermont Lake Trout. *Transactions of the American Fisheries Society* 144:124-139.

Abstract: To better understand the influence of hatchery practices on wild populations of Lake Trout *Salvelinus namaycush*, we used a landscape genetic approach to tease apart the population genetic patterns expected due to natural processes versus hatchery stocking, i.e., human-mediated gene flow. In several lakes across our study area in Vermont, the presence of exogenous mitochondrial DNA haplotypes supported our human-mediated gene flow hypothesis. Microsatellite DNA analyses showed introgression of hatchery genotypes into the wild populations. Nonetheless, clustering patterns within river drainages and signatures of isolation by distance were consistent with natural postglacial colonization. We conclude that though the genetic makeup of Vermont Lake Trout

populations has been influenced by stocking, a lack of genetic bottlenecks and concordance with landscape processes suggests that much of the indigenous genetic diversity remains intact. We were able to attribute departures from expectations based on natural genetic patterns to hatchery introgression in specific lakes. To preserve the adaptive potential of local populations that have persisted since the last ice age, we suggest areas for which hatchery supplementation could be minimized.

Berejikian, B. A., E.P. Tezak, T.A. Flagg, A.L. LaRae, E. Kummerow, and C.V.W. Mahnken. 2000. Social dominance, growth, and habitat use of age-0 steelhead (*Oncorhynchus mykiss*) grown in enriched and conventional hatchery rearing environments. *Canadian Journal of Fisheries and Aquatic Sciences*, 57:628-636.

Abstract: This study investigated whether culturing age-0 steelhead (*Oncorhynchus mykiss*) in habitat-enriched rearing tanks, containing a combination of in-water structure, underwater feeders, and overhead cover, affected competitive ability and habitat use compared with juveniles cultured in more conventional vessels. In laboratory tests, steelhead juveniles grown in the enriched tanks socially dominated size-matched competitors grown in conventional tanks. When both treatments were introduced into separate sections of a quasi-natural stream, no differences in growth were found between them. However, when intermixed, fish reared in the enriched tanks grew at a higher rate than conventionally reared competitors, suggesting greater competitive ability of juveniles grown in the enriched tanks. Visual isolation and defensible food resources in combination in the enriched tanks were considered as the primary factors causing the observed competitive asymmetries. Steelhead juveniles from the two rearing environments exhibited very similar use of woody structure in the quasi-natural stream, both in the presence and in the absence of mutual competition. Rearing steelhead in more naturalistic environments could result in hatchery fish that behave and integrate into the postrelease (natural) environment in a manner more similar to wild fish.

Berejikian, B. A., D. M. Van Doornik, J. A. Scheurer, R. Bush. 2009. Reproductive behavior and relative reproductive success of natural - and - hatchery - origin Hood Canal summer chum salmon (*Oncorhynchus keta*). *Canadian Journal of Fisheries and Aquatic Sciences*, 66:781-789.

Abstract: Estimates of the relative fitness of hatchery- and natural-origin salmon can help determine the value of hatchery stocks in contributing to recovery efforts. This study compared the adult to fry reproductive success of natural-origin summer chum salmon (*Oncorhynchus keta*) with that of first- to third-generation hatchery-origin salmon in an experiment that included four replicate breeding groups. Hatchery- and natural-origin chum salmon exhibited similar reproductive success. Hatchery- and natural-origin males obtained similar access to nesting females, and females of both types exhibited similar breeding behaviors and durations. Male body size was positively correlated with access to nesting females and reproductive success. The estimates of relative reproductive success (hatchery/natural = 0.83) in this study were similar to those in other studies of other anadromous salmonids in which the hatchery population was founded from the local natural population and much higher than those in studies that evaluated the lifetime relative reproductive success of nonlocal hatchery populations.

Brockmark, S., and J.I. Johnsson. 2010. Reduced hatchery rearing density increases social dominance, postrelease growth, and survival in brown trout (*Salmo trutta*). *Canadian Journal of*

Fisheries and Aquatic Sciences, 67(2):288-295.

Synopsis: Hatchery fish reared for conservation or supplementation often have difficulties adapting to natural conditions, resulting in poor performance in the wild. In a standard hatchery, fish are confined at high densities, which creates a social environment different from that experienced after release. Here we investigated how rearing density influences social dominance, postrelease growth, and survival in brown trout (*Salmo trutta*). Fish were reared at three density treatments: conventional hatchery density, half of conventional hatchery density, and natural density. Four months after hatching, dominance status was determined, and 36 fish from each treatment were released into an enclosed stream and recaptured after 36 days. Trout reared at natural density had higher dominance status and grew faster, both in the hatchery and in the natural stream, than trout from higher densities. Moreover, trout reared at natural density were twice as likely to survive in the stream as trout from higher densities. These novel results suggest that more natural rearing densities would facilitate the development of adaptive behaviour in hatchery salmonids and, thereby, their contribution to natural production.

Busack, C., and C.M. Knudsen. 2007. Using factorial mating designs to increase the effective number of breeders in fish hatcheries. *Aquaculture* 273:24-32.

Abstract: We used Monte Carlo simulations to evaluate the potential of full- and partial-factorial mating designs to increase the effective number of breeders in fish hatchery operations, using two probability distributions (normal and uniform) to generate individual fitness values, two methods (multiplicative and additive) of combining fitness values in individual matings, four full-factorial designs (10×10, 20×20, 40×40, 120×120), and three partial-factorial designs (2×2, 5×5, 10×10). Nb under full-factorial mating was nearly linearly related to, and quite predictable from Nb under single-pair mating. The higher the variance of family size under single-pair mating, the greater the Nb benefit of full-factorial mating; and the larger the population, the greater the full-factorial benefit. Under assumptions of additive combination of fitness values, full-factorial mating resulted in an average Nb increase of 33%. Partial-factorial designs as small as 2×2 achieved on average 45% of the Nb advantage attainable under full-factorial mating. The proportionate incremental Nb benefit from partial-factorial designs diminishes rapidly as the size of the design increases, but designs as small as 10×10 may attain such a large proportion of the full-factorial benefit as to render larger designs unnecessary.

Busack, C., C.M. Knudsen, G. Hart, and P. Huffman. 2007. Morphological Differences Between Adult Wild and First-Generation Hatchery Upper Yakima River Spring Chinook Salmon. *Transactions of the American Fisheries Society* 136:1076–1087.

Abstract: Four-year-old adult wild spring Chinook salmon *Oncorhynchus tshawytscha* at a supplementation hatchery were compared morphologically with their first-generation hatchery counterparts over three consecutive brood years (BYs) using thin-plate spline analysis on 12 digitized landmarks and an analysis of 27 truss characters based on the landmarks. Canonical discriminant analysis (CDA) of sex-specific partial warp scores correctly classified females to origin (hatchery or wild) with 75% accuracy (up to 84% accuracy for one BY) and males to origin with 65% accuracy (up to 89% accuracy for one BY). Classification to BY using sex- and BY-specific partial warps was 62% accurate for both females and males. The results of the truss analysis were very close to those

from the thin-plate spline analysis. Sex-specific CDAs correctly classified 75% of females and 68% of males to origin. Correct classification to BY was 61% for females and 58% for males. Consensus shapes based on partial warps suggested that hatchery fish of both sexes have longer and deeper heads and shallower midbodies than wild fish. They also appear to be somewhat shorter in the posterior body. Analysis of variance of individual truss characters led to the same general conclusion but also provided evidence that hatchery fish have wider anal fins. There was no evidence of sex-specific differences between hatchery and wild fish. Body proportion differences between hatchery and wild fish at the eight most diagnostic truss characters averaged 0.31 standard deviations in females and 0.35 standard deviations in males. In terms of actual measurement, these differences amounted to an average of 1.4% of the wild mean, providing little discriminatory power.

Chamberlin, J.W., T.E. Essington, J.W. Ferguson, and T.P. Quinn. 2011. The Influence of Hatchery Rearing Practices on Salmon Migratory Behavior: Is the Tendency of Chinook Salmon to Remain within Puget Sound Affected by Size and Date of Release? *Transactions of the American Fisheries Society* 140:1398–1408.

Abstract: The marine migrations of Pacific salmon *Oncorhynchus* spp., and especially Chinook salmon *O. tshawytscha*, vary greatly in duration and spatial extent. In Puget Sound, Washington, most Chinook salmon migrate from freshwater to the coastal waters of the Pacific Ocean before returning to spawn in their natal streams. However, some leave freshwater but remain in the semi-estuarine waters of Puget Sound until they mature and then return to freshwater to spawn. The objective of our study was to determine the effect of rearing conditions and hatchery location on the prevalence of this alternative pattern of marine distribution by hatchery-produced Chinook salmon in Puget Sound. We used coded wire tag recovery data to analyze the effect of release region, age, size, and date of release on the proportion of fish showing resident-type behavior, defined as recovery in Puget Sound fisheries outside the period when maturing salmon return from the coast. Based on 226 different release groups from 26 hatcheries throughout Puget Sound from 1972 to 1993, 24% of the fish recovered were classified as residents, though this is not an actual estimate of the percentage of fish displaying this distribution pattern. The best single predictor of residency was release region, suggesting that where fish enter the marine environment had the largest influence on whether they adopted resident behavior or migrated directly to the ocean. The overall best model included an interactive effect between release region and size at release, revealing that the propensity of large fish to remain resident varied significantly among regions. The actual mechanisms that create the diversity of distribution patterns are still unknown, but the effects of rearing conditions and release location provide useful information for the management of these salmon populations.

Clarke, L.R., M.W. Flesher, T.A. Whitesel, G.R. Vonderohe, and R.W. Carmichael. 2010. Postrelease Performance of Acclimated and Directly Released Hatchery Summer Steelhead into Oregon Tributaries of the Snake River. *North American Journal of Fisheries Management* 30: 1098-1109.

Abstract: In a study using 14 paired-release groups over 10 release years, we compared the performance of hatchery summer steelhead *Oncorhynchus mykiss* that were acclimated as smolts (AC) for 16–57 d before release into ponds supplied with ambient stream water with that of fish trucked from the hatchery and directly released (DR) into Spring, Deer, and Little Sheep creeks in northeastern Oregon. After releasing the fish into streams, we monitored out-migration travel times

and survival to Lower Granite Dam (LGD) on the Snake River using freeze brand marks or implanted passive integrated transponder tags in a subsample of each release group. Across all release groups, travel time was significantly slower for AC fish (34.7 d) than for DR fish (31.8 d), though there was no significant difference in survival probability to LGD. We used recoveries of coded wire tags to estimate smolt-to-adult survival (SAS) and a stray rate index (SRI) for the AC and DR strategies. Across all release groups, SAS was 33% higher and SRI 42% lower for AC steelhead. At each release site acclimation increased average SAS by at least 11% and decreased SRI by at least 16.5%. We found a significant, negative linear relationship between travel time to LGD and SAS; however, there was no significant relationship between survival to LGD and SAS, which implies that judgments about the success or failure of a novel rearing or release strategy should not be made based on out-migration survival. Acclimating juvenile steelhead produced significantly higher SAS and lower SRI in the hatchery program we evaluated.

Cuenco, M. L., T. W. H. Backman, and P. R. Mundy. 1993. The use of supplementation to aid in natural stock restoration. Pages 269-293 in J. G. Cloud and G. H. Thorgaard, editors. Genetic conservation of salmonid fishes. Plenum Press, New York.

Synopsis: Defines supplementation and the parameters of a successful supplementation program. Note that this document was published by tribal scientists long before hatchery reform became popular and widely advocated. Many of the recommendations in this publication are being used in studies contained in this bibliography.

Dahl, J., E. Pettersson, J. Dannewitz, T. Järvi, and A-C Löf. 2006. No difference in survival, growth and morphology between offspring of wild-born, hatchery and hybrid brown trout (*Salmo trutta*). Ecology of Freshwater Fish 15:388-397.

Abstract: We studied survival, growth and morphological characters in the offspring of native hatchery and wild-born anadromous brown trout (*Salmo trutta*) and their hybrids (wild-born female × hatchery male and wild-born male × hatchery female) in a 1-year field experiment. We also conducted laboratory studies where we examined social interactions between the offspring of the same hatchery and wild-born trout. All offspring were raised in a hatchery and nose tagged before being released into the stream. In total, 1125 individuals were released into the stream (1999) and a total of 614 individuals were recovered (2000). We found no differences in growth and survival between the offspring of hatchery, wild-born and hybrid trout. Morphology was also similar among groups, where only 38% females and 36% males were classified into the right category, which were only 12% better than random classification. In the laboratory experiment, we compared only the offspring of hatchery and wild-born trout with respect to growth, dominance, aggressiveness, feeding and activity. We found small differences between the offspring of hatchery and wild-born fish with respect to growth but this effect was not found in the field experiment. Our result suggests that the offspring of hatchery trout and hybrids between hatchery and wild-born trout performed equally well to the offspring of wild-born trout.

Dannewitz, J., E. Petersson, T. Prestegard, and T. Jarvi. 2003. Effects of sea-ranching and family background on fitness traits in brown trout *Salmo trutta* reared under near-natural conditions. Journal of Applied Ecology 40:241-250.

Summary (Author's words taken directly from publication):

1. Many threatened populations of salmonids depend on supplemental releases of hatchery-produced fish. Laboratory studies suggest that altered selection regimes in the hatchery may result in evolutionary changes of traits connected to fitness. Such changes can have profound effects on the performance of the hatchery fish following release in the natural environment, and may also affect the genetic characteristics of locally adapted wild populations. However, surprisingly few studies have looked at the ability of hatchery fish to compete with wild conspecifics under natural conditions.
2. We studied growth, survival and life-history adoption of a wild and a multigeneration sea-ranched strain of brown trout *Salmo trutta* in a semi-natural stream. The fish were planted in the stream as eyed eggs and their family and strain origins were later revealed by microsatellite markers.
3. In the first experiment, in which the experimental fish originated from a full-sib mating design, there were strong family effects on both growth and survival over the first growth season. In the second experiment, in which the experimental fish originated from a half-sib mating design, there were significant male and female effects on growth parameters but not on survival over the first growth season.
4. When family and male–female effects were accounted for, there were no differences between wild and sea-ranched trout in body size and condition factor after the first growth season, or in survival up to this stage. Nor was there any difference between the groups in the proportions that metamorphosed into the migratory smolt phase at 1 year of age.
5. Synthesis and applications. Our results suggest that wild-born trout of sea-ranched origin can successfully compete with trout of wild origin under semi-natural conditions. This indicates that the impact of hatchery selection on the performance of sea-ranched fish in the wild may not be as pronounced as previously thought. It is suggested that for salmonid populations that depend on supplemental stocking, more effort should be paid to minimizing negative environmental effects during hatchery rearing. The observed differences in fitness characters between families suggest that family effects should be taken into account in stocking programmes because the amount of genetic variation maintained within populations is related to the variance in family performance.

Dittman, A. H., D. May, D. A. Larsen, M. L. Moser, M. Johnston, and D. Fast. 2010. Homing and spawning site selection by supplemented hatchery- and natural-origin Yakima River spring Chinook salmon. *Transactions of the American Fisheries Society* 139:1014-1028.

Synopsis: This paper examined the homing patterns of supplemented Yakima River spring Chinook salmon releases from satellite acclimation facilities. The data indicated that supplementation increased the spatial range of spawning in the upper Yakima River. Natural- and hatchery-origin fish displayed similar spawning distributions within the upper Yakima Basin. Like their natural-origin counterparts, hatchery-origin fish demonstrated the ability to seek optimum spawning locations. This occurred especially in the absence of acceptable spawning conditions in their area of acclimation and release.

Eldridge, W.H. and K. Killebrew. 2008. Genetic diversity over multiple generations of supplementation: an example from Chinook salmon using microsatellite and demographic data. *Conservation Genetics* 9:13-28.

Abstract: 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 (N_e) 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 N_e 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 N_e 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.

Ford, M., Murdoch, A., Howard, S., 2012. Early male maturity explains a negative correlation in reproductive success between hatchery-spawned salmon and their naturally spawning progeny. *Conservation Letters* 5, 450–458.

Abstract: Adaptation of plants or animals to captivity is a risk associated with any captive breeding program that has the intent of returning organisms to the wild. The risk is particularly acute for species that are captively bred and released on a large scale, as is the case for many species of fish. Several studies, particularly in salmonids, have reported rapid adaptation of populations to captivity, but the mechanisms of such adaptations are not always clear. We evaluated a large three-generation pedigree of an artificially supplemented salmon population, and found that the fish with the highest reproductive success in captivity produce early maturing male offspring that have lower than average reproductive success in the wild. In contrast to an earlier study of steelhead trout, we found little evidence that parental origin of the captive spawners influenced the subsequent reproductive success of their naturally spawning progeny.

Fraser, D. J. 2008. How well can captive breeding programs conserve biodiversity? A review of salmonids. *Evolutionary Applications*, 1:535-586.

Synopsis: Review of existing literature relevant to genetic diversity and fitness issues in captive breeding and supplementation programs. Empirical and theoretical studies both suggest that most salmonid captive breeding programs can maintain genetic diversity over several captive generations. The apparent low N_e in some captive broodstocks might easily be avoided through the use of procedures that reduce genetic and other risks associated with captive breeding programs such as using local brood sources and minimizing generations in captivity. Many of the poorest performances of hatchery fish relative to wild fish involved nonlocal hatchery strains that had been in captivity for greater than five generations or that had undergone intentional artificial selection. There is little long-term evidence regarding whether captive-reared salmonids can or cannot be

reintroduced as self-sustaining populations. There are numerous examples of the ability of salmonids to evolve rapidly in the wild over several generations. Certainly, then, the possibility exists that a reintroduced population based on captive-reared fish could re-adapt to the wild environment under a similar timeframe. There is only very limited empirical research to suggest that maintaining several small isolated populations with periodic mixing may be more effective at reducing losses of genetic diversity and fitness than maintaining a single large population.

Fritts, A.L., J.L. Scott, and T.N. Pearsons. 2007. The effects of domestication on the relative vulnerability of hatchery and wild spring Chinook salmon to predation. *Canadian Journal of Fisheries and Aquatic Sciences* 64:813-818.

Abstract: We tested whether one generation of state-of-the-art hatchery culture influenced the vulnerability of Chinook salmon (*Oncorhynchus tshawytscha*) fry to predators. Size-matched hatchery and wild origin spring Chinook salmon fry were exposed to rainbow trout (*Oncorhynchus mykiss*) and torrent sculpin (*Cottus rhotheus*) predators in 10.8 m³ net pens. The hatchery origin fry were the offspring of first generation hatchery-reared broodstock, and the wild origin fry had no history of hatchery culture; both originated from the same stock. Wild origin fry were found to have a 2.2% ($p = 0.016$) survival advantage over hatchery origin fry during 2 years of predation challenges. The most important findings of this study are (i) domestication can affect the susceptibility to predators after only one generation of state-of-the-art hatchery culture practices, and (ii) the domestication effect was very small.

Gallinat, M.P. and W-Y. Chang. 2013. Phenotypic Comparisons among Natural-Origin, Hatchery-Origin, and Captive-Reared Female Spring Chinook Salmon from the Tucannon River, Washington, *North American Journal of Aquaculture*, 75:4, 572-581.

Abstract: We examined the effects of hatchery rearing on FL, weight, egg size, fecundity, relative fecundity, and reproductive mass of female spring Chinook Salmon *Oncorhynchus tshawytscha* from a population that had been in captivity for 0 (natural-origin), 18 (hatchery-origin), and 48 (captive-reared broodstock) months. Age-4 captive-reared broodstock females that were reared for their entire life in the hatchery environment had significantly lower mean FL, weight, fecundity, relative fecundity, and reproductive mass, but had significantly larger eggs than age-4 females from the other groups after correcting for body size. Hatchery-origin females had significantly lower fecundity than natural origin fish. Our findings illustrate a phenomenon of lower overall reproductive potential for hatchery-reared fish in the form of reduced fecundity that decreases as time spent in the hatchery environment increases. We also observed that progeny of captive-reared broodstock parents, released as smolts and recaptured as returning age-4 adults, have a size and fecundity distribution that is similar to the hatchery-origin adults, suggesting that the decrease in fecundity was not a genetically linked trait.

Habicht, C., T.M. Tobias, G. Fandrei, N. Webber, B. Lewis, and W.S. Grant. 2013. Homing of Sockeye Salmon within Hidden Lake, Alaska, Can Be Used to Achieve Hatchery Management Goals. *North American Journal of Fisheries Management* 33:777-782.

Abstract: The supplementation of natural populations of Pacific salmon *Oncorhynchus* spp. with hatchery fish poses unique management challenges. Two such challenges addressed in this study are

limiting the number of hatchery fish spawning with natural-origin fish and maximizing the number of natural-origin fish in the supplementation broodstock. In this study, we focus on stock enhancement of Sockeye Salmon *O. nerka* in Hidden Lake, Alaska, where the Trail Lakes Hatchery supplements the natural population with hatchery-raised fry. Production in Hidden Lake is limited by the availability of spawning habitat and not by juvenile rearing capacity. The hatchery collects broodstock from the lake and releases fry with thermally marked otoliths at one of two primary natural spawning sites in Hidden Lake each year. During this study, an average of 58% of the fish returning to the lake through a weir on the outlet stream were of hatchery origin. However, an average of 88% of the fish at the release site were hatchery-origin fish, indicating a nonrandom distribution of hatchery-origin spawners. **This pattern is consistent with homing to specific sites within the lake of either or both hatchery- and wild-origin fish.** However, this distribution results in a larger-than-desirable proportion of hatchery-origin fish spawning with natural-origin fish at the release site. The proportion of hatchery-origin fish used for brood is also larger than desirable because the site is also the broodstock collection site. We propose that releasing hatchery fish at a new location removed from the primary spawning areas and the hatchery broodstock collection site will reduce the proportion of hatchery-origin fish spawning with wild-origin fish and increase the proportion of wild-origin fish in the broodstock, if our results are due, at least in part, to homing of hatchery fish.

Haponski, A.E., H. Dean, B.E. Blake, and C.A. Stepien. 2014. Genetic History of Walleyes Spawning in Lake Erie's Cattaraugus Creek: a Comparison of Pre- and Poststocking. *Transactions of the American Fisheries Society* 143:1295-1307.

Abstract: Fish stocking (artificial supplementation) has been used to augment populations and angling opportunities. However, genetic composition and adaptations of native fish populations may be affected, raising management concerns. From 1995 to 2000, the New York State Department of Environmental Conservation stocked Walleye *Sander vitreus* fry and fingerlings from the Maumee River (western Lake Erie) into Cattaraugus Creek (eastern Lake Erie). We analyzed nuclear microsatellite (sat) DNA and mitochondrial DNA (mtDNA) variation in Cattaraugus Creek Walleyes for comparisons between prestocking and poststocking groups, among annual spawning runs (1998–2011), among age cohorts, and between sexes. Results for genetic differentiation (index F_{ST}) were not significant between prestocking and poststocking groups (sat: $F_{ST} = 0.003$; mtDNA: $F_{ST} < 0.001$), and the two groups did not resemble stocked Maumee River fingerlings (sat: $F_{ST} = 0.003$ – 0.012 ; mtDNA: $F_{ST} = 0.076$ – 0.090). Tests for differentiation were not significant among annual spawning runs (sat: $F_{ST} = <0.001$ – 0.007 ; mtDNA: $F_{ST} = <0.001$ – 0.049), among age cohorts (sat: $F_{ST} = <0.001$ – 0.006 ; mtDNA: $F_{ST} = <0.001$ – 0.097), or between sexes (sat: $F_{ST} < 0.001$; mtDNA: $F_{ST} < 0.001$). Genetic diversity levels were high and consistent (sat: observed heterozygosity [mean \pm SE] = 0.71 ± 0.04 ; mtDNA: haplotype diversity = 0.79 ± 0.01). Thus, despite stocking, the genetic signature of the native spawning run remained distinctive. However, the genetic composition of the local wild population and the stocking source should be assessed prior to any future supplementation plans.

Hayes, S.A., M.H. Bond, C.V. Hanson, and R.B. MacFarlane. 2004. Interactions between endangered wild and hatchery salmonids: can the pitfalls of artificial propagation be avoided in small coastal streams? *Journal of Fish Biology*, 65 (s1):101-121.

Abstract: Hatchery and wild juvenile populations of steelhead *Oncorhynchus mykiss* and coho salmon *Oncorhynchus kisutch*, in a small coastal watershed in central California, were sampled throughout the year in a stream and at a hatchery. Both species grew faster in captivity than in the wild. Hatchery fish of both species had elevated gill Na⁺, K⁺-ATPase activity, and thus were ready to enter sea water when planted during the wild fish migration. Downstream migrant trapping and stream surveys indicated that hatchery smolts went to sea soon after planting, consequently avoiding the effects of competition and predation that commonly occur when hatchery-bred juveniles are released. Adult steelhead were also sampled throughout the watershed. The return of hatchery steelhead was highly synchronized with that of wild steelhead, indicating that hatchery propagation had no adverse effects on the timing of the run. A disproportionate number of hatchery steelhead returned to the tributary where the hatchery was located, despite being planted throughout the watershed. Hatchery steelhead did not differ in mean age or size from wild steelhead. Observations of spawning indicated that hatchery and wild steelhead interbreed. Competition for mates or spawning substratum was rarely observed between hatchery and wild steelhead. Many of the problems commonly associated with artificial propagation can be avoided in small coastal watersheds when wild broodstock are used and fish are released as smolts.

Heard, W.R., 2011. Overview of salmon stock enhancement in southeast Alaska and compatibility with maintenance of hatchery and wild stocks. *Environmental Biology of Fishes* 94, 273–283.

Abstract: Modern salmon hatcheries in Southeast Alaska were established in the 1970s when wild runs were at record low levels. Enhancement programs were designed to help rehabilitate depressed fisheries and to protect wild salmon stocks through detailed planning and permitting processes that included focused policies on genetics, pathology, and management. Hatcheries were located away from significant wild stocks, local sources were used to develop hatchery broodstocks, and juveniles are marked so management can target fisheries on hatchery fish. Initially conceived as a state-run system, the Southeast Alaska (SEAK) program has evolved into a private, non-profit concept centered around regional aquaculture associations run by fishermen and other stakeholders that pay for hatchery operations through landing fees and sale of fish. Today there are 15 production hatcheries and 2 research hatcheries in SEAK that between 2005 and 2009 released from 474 to 580 million (average 517 million) juvenile salmon per year. During this same period commercial harvest of salmon in the region ranged from 28 to 71 million salmon per year (average 49 million). Contributions of hatchery-origin fish to this harvest respectively averaged 2%, 9%, 19%, 20%, and 78% for pink, sockeye, Chinook, coho, and chum salmon. Both hatchery and wild salmon stocks throughout much of Alaska have experienced high marine survivals since the 1980s and 1990s resulting in record harvests over the past two decades. Although some interactions between hatchery salmon and wild salmon are unavoidable including increasing concerns over straying of hatchery fish into wild salmon streams, obvious adverse impacts from hatcheries on production of wild salmon populations in this region are not readily evident.

Hedrick, P.W., D. Hedgecock, S. Hamelberg, and S.J. Croci. 2000a. The impact of supplementation in winter-run chinook salmon on effective population size. *Journal of Heredity*, 91(2): 112-116.

Abstract: Supplementation of young raised at a protected site, such as a hatchery, may influence the effective population size of an endangered species. A supplementation program for the endangered winter-run chinook salmon from the Sacramento River, California, has been releasing fish since

1991. A breeding protocol, instituted in 1992, seeks to maximize the effective population size from the captive spawners by equaling their contributions to the released progeny. As a result, the releases in 1994 and 1995 appear not to have decreased the overall effective population size and may have increased it somewhat. However, mistaken use of non-winter-run chinook spawners resulted in artificial crosses between runs with fish on Battle Creek, the site of the hatchery, resulted in limiting the contribution of the released fish to the target mainstem population. Rapid genetic analysis of captured spawners and a new rearing facility on the Sacramento River should alleviate these problems and their negative effect on the effective population size in future years.

Hedrick, P.W., V.K. Rashbrook, and D. Hedgecock. 2000b. Effective population size of winter-run chinook salmon based on microsatellite analysis of returning spawners. *Canadian Journal of Fisheries and Aquatic Sciences*, 57(12): 2368–2373.

Abstract: We previously estimated the predicted effective population size for the endangered winter-run chinook salmon, *Oncorhynchus tshawytscha*, based on a number of assumptions, including random survival and return of released fish. Here we present data from actual returning spawners, identified to family by microsatellite loci, and calculate the observed effective population size. In 1994 and 1995, the observed effective population sizes were 93.6 and 78.2% of predicted values, respectively, suggesting that the numbers of returning fish were very close to random expectations in 1994 and less close to random in 1995. The ratio of the effective population size to the adult number, N_e/N , was greater than unity for 1994 and approximately 0.5 in 1995. The high ratio in 1994 reflects the success of the breeding protocol to equalize individual contributions and near random returns, while the lower number in 1995 appears to be the result of both less successful equalization and less close to random returns in that year. These findings provide an optimistic outlook for the success of this supplementation program and suggest that the overall effective population size has not been greatly reduced, since returning spawners represent a broad sample of parents and not fish from only a few families.

Heggenes, J., M. Beere, P. Tamkee, and E. B. Taylor. 2006. Genetic diversity in steelhead before and after conservation hatchery operation in a coastal, boreal river. *Transactions of the American Fisheries Society* 135:251-267.

Abstract: The objectives of this study were to (1) investigate the genetic diversity of wild steelhead populations in the river before hatchery stocking and (2) assess the potential genetic impacts of interbreeding of returning hatchery adult fish with wild spawners over almost 20 years of large-scale hatchery operation. The level of population subdivision among Kitimat River samples was low (0.004) and not significantly different from 0. Tests of population subdivision between pre-hatchery and post-hatchery operation indicated no significant changes. Similar results were obtained using other measures of genetic differentiation (principal components analysis of microsatellite allele frequencies and Cavalli-Sforza genetic distance). Our data, however, did indicate a slight but significant reduction in allelic richness after hatchery stocking. Pairwise tests for genetic differentiation among samples from different yearclasses were nonsignificant. We conclude that for the current management regime there is little apparent impact of hatchery practices on either the genetic structure or variation within the lower main-stem Kitimat River steelhead, but there may be a reduction in rare alleles. The practice of using substantial numbers of wild fish and multiple year-classes in the hatchery may have minimized genetic changes via genetic drift.

Heggenes, J., M. Beere, P. Tamkee, and E. B. Taylor. 2011. Estimation of Genetic Diversity within and among Populations of *Oncorhynchus mykiss* in a Coastal River Experiencing Spatially Variable Hatchery Augmentation. *Transactions of the American Fisheries Society* 140:123-135.

Abstract: The allelic variation at 10 microsatellite loci was assayed in potentially wild rainbow trout *Oncorhynchus mykiss* and steelhead (anadromous rainbow trout) collected from 11 tributaries and three upper main-stem river sites (n = 547) in the Kitimat River, central British Columbia, and compared with the variation in steelhead from areas within the lower river (n = 333), where a hatchery has operated since 1984. The objective was to see whether the genetic structure of *O. mykiss* in the upper river was influenced by hatchery-reared fish stocked in the lower river. Measures of genetic diversity indicated that tributary and upper-river diversity were similar to what has previously been documented for wild populations. The level of genetic subdivision (θ) was significant ($\theta = 0.031$), indicating that genetic structure exists, and was higher than that among sites located in the lower main-stem river where the hatchery operates ($\theta = 0.004$). Bayesian assignment clustering suggested the existence of a genetic structure (K = 3) in *O. mykiss* in the upper river. The overall spatial pattern, however, identified no clearly separate genetic populations; rather, the genetic structure appeared to be an overlapping mosaic of modestly genetically divergent localities. We conclude that indigenous wild *O. mykiss* populations exist in the tributaries and the upper main-stem river and its tributaries. These upper-river populations appear to have retained genetic diversity and differentiation despite extensive releases of hatchery fish in the lower river.

HSRG. 2005. Hatchery Scientific Review Group. Hatchery Reform in Washington State: Principles and Emerging Issues. *Fisheries*. Volume 30, Number 6. June 2005.

Synopsis: Makes recommendations for reforming hatchery operations to better meet goals of supporting sustainable fisheries and assisting with the conservation of natural populations. Many of the recommendations proposed by the HSRG were documented by Cuenco et al. in 1993 and are being used in studies contained in this bibliography.

Johnson, M.A. and T.A. Friesen. 2014. Genetic Diversity and Population Structure of Spring Chinook Salmon from the Upper Willamette River, Oregon. *North American Journal of Fisheries Management*. 34:853-862.

Abstract: Effective management of Pacific salmon requires an accurate understanding of both population genetic diversity and structure. Spring Chinook Salmon *Oncorhynchus tshawytscha* from the upper Willamette River (UWR), Oregon, are listed as threatened under the U.S. Endangered Species Act, and although this evolutionarily significant unit is recognized to be distinct from other Columbia River stocks, genetic relationships among its constituent hatchery and wild populations remain obscure. We used genotypic data from 13 microsatellite loci to test whether hatchery populations of UWR spring Chinook Salmon are most similar to wild populations within the same subbasin, or whether hatchery populations from different subbasins are more similar to each other than to local wild populations. We also tested for differences between the genetic diversities of hatchery and wild populations, as measured through heterozygosity and allelic richness. Our results suggest that populations are weakly structured among subbasins and, in all cases, hatchery

populations are genetically most similar to local wild populations. We also found heterozygosity to be higher ($P = 0.009$) in hatchery populations (median, 81.5%) than in wild populations (median, 75.2%), but observed no significant difference with respect to allelic richness ($P = 0.406$). We conclude that hatchery-origin UWR spring Chinook Salmon represent genetically appropriate founder populations for ongoing reintroduction programs and recommend that the conservation and recovery of this stock proceed through management actions developed specifically for each subbasin. We further recommend that current restrictions on hatchery stock transfers among UWR subbasins be continued to preserve extant population genetic structure.

Johnson, S.L., J.H. Power, D.R. Wilson, and J. Ray. 2010. A Comparison of the Survival and Migratory Behavior of Hatchery-Reared and Naturally Reared Steelhead Smolts in the Alsea River and Estuary, Oregon, using Acoustic Telemetry. *North American Journal of Fisheries Management* 30:55-71.

Abstract: We tracked three groups of steelhead *Oncorhynchus mykiss* smolts implanted with acoustic transmitters to determine whether the degree of hatchery domestication or the juvenile rearing environment (hatchery raceway versus natural stream) influenced migration timing and survival in the Alsea River and estuary, Oregon. Two groups consisted of age-1 smolts reared in concrete raceways. One hatchery-reared group (traditional brood group) was derived from the traditional Alsea River broodstock initially developed in the 1950s. The second hatchery-reared group (new brood group) was derived from naturally reared Alsea River adult steelhead that were captured and spawned at the hatchery beginning in the winter of 2000–2001. The third group (naturally reared group) consisted of age-2 naturally reared smolts captured in a downstream migrant trap located in a tributary stream near the hatchery. We placed transmitters in 74 traditional brood smolts, 76 new brood smolts, and 72 naturally reared smolts. Thirty-one acoustic receivers were located throughout the Alsea River and estuary and in the ocean offshore of the river mouth to monitor smolt movement. Neither the degree of hatchery domestication nor the juvenile rearing environment (hatchery raceway versus natural stream) appeared to influence the number of steelhead smolts that successfully migrated to the ocean. We found no significant difference between groups in their survival to the head of tide or to the mouth of the estuary. Most smolts from all three groups were detected at the head of tide (87% of fish from the traditional brood group, 78% from the new brood group, and 84% from the naturally reared group). However, survival was poor in the lower estuary for all three groups; we estimated that only 37% of the traditional brood group, 45% of the new brood group, and 47% of the naturally reared group survived to the ocean. The timing of migration through the river was highly variable in all three groups, and we found no significant differences in the rate of downstream movement from the release site to the head of tide. Mean residence time within the estuary was similar for all groups, although smolts from the naturally reared group showed less variability in estuary residence time than hatchery-reared smolts.

Kalinowski, S.T., D.M. Van Doornik, C.C. Kozfkay, and R. Waples. 2012. [Genetic diversity in the Snake River sockeye salmon captive broodstock program as estimated from broodstock records](#). *Conservation Genetics* 13:1183-1193.

Synopsis: Assessing the magnitude of any of the future challenges to sockeye salmon in the Snake River, is difficult; predicting the cumulative impact of factors affecting survival is a formidable challenge. However, the results of this present investigation provide reason for optimism.

Sockeye salmon in the Redfish Lake captive broodstock program appear to have retained approximately 95% of the genetic variation of the fish that founded the captive population, and we can hope that this is enough to avoid most of the harmful effects of inbreeding and to provide enough genetic variation for the population to adapt to future challenges.

Kassler, T.W. and C.A. Dean. 2010. Genetic Analysis of Natural-origin Spring Chinook and Comparison to Spring Chinook from an Integrated Supplementation Program and Captive Broodstock Program in the Tucannon River. Report to BPA, Project No. 2000-019-00, Contract Number 40744. WDFW, Olympia, WA.

Abstract: A collection of natural-origin spring Chinook from 1986 was compared to samples from two spawner groups (supplementation program and in-river spawners), and to collections of hatchery- and natural-origin from the Tucannon River. Samples from the captive brood program at the Tucannon River Hatchery were also compared. A microsatellite DNA analysis was conducted to determine if there have been any changes to the genetic diversity of spring Chinook in the Tucannon River. The measures of genetic diversity (heterozygosity and allelic richness) revealed similar levels within each spawner group and collection based on origin over time. Assessment of within population diversity indicates that the spawner groups and collections by origin have not undergone a loss of diversity and are not represented by family groups. We did detect that collections of the captive brood are not within Hardy-Weinberg proportions and have significant linkage disequilibrium as a possible result of using equal numbers of individuals from two brood years that are differentiated. The collection of captive brood progeny returns in 2008; however is within expected proportions and indicates there has not been a genetic change to the spawner group collection or collections by origin. The pairwise F_{ST} values identify the variation between any two groups is approximately 1.0% or less indicating the differences among the groups is small. Factorial correspondence analysis identifies similarity among collections that are separated by four years and represent the genetic differences among primary brood years and not genetic changes to the natural-origin collection from 1986. The combination of all the results demonstrates that the genetic diversity of spring Chinook in the Tucannon River has not significantly changed as a result of the supplementation or captive brood programs.

Knudsen, C.M., S.L. Schroder, C. Busack, M.V. Johnston, T.N. Pearsons, and C.R. Strom. 2008. Comparison of Female Reproductive Traits and Progeny of First-Generation Hatchery and Wild Upper Yakima River Spring Chinook Salmon. Transactions of the American Fisheries Society 137:1433-1445.

Abstract: Hatchery and wild female spring Chinook salmon *Oncorhynchus tshawytscha* from the upper Yakima River were compared to determine whether their reproductive traits had diverged after a single generation of artificial propagation. Fecundity, relative fecundity, individual egg mass, and total gamete mass were all significantly correlated with body length, while reproductive effort (gonadosomatic index) was not. Regressions of trait versus body length often differed significantly among brood years. Hatchery spring Chinook salmon were significantly smaller than wild females over the four brood years examined. After brood year and body length (when necessary) were accounted for, wild females had an average of 8.8% more total gamete mass, 0.8% more individual egg mass, 7.7% greater fecundity, and 0.8% greater reproductive effort than hatchery females. Relative fecundity (the number of eggs per centimeter of body length) was on average 1.3% greater

in hatchery females. We also compared body size at yolk absorption and egg-to-fry survival of the progeny from hatchery-by-hatchery and wild-by-wild matings. After differences in egg size were accounted for, hatchery fry were on average 1.0% heavier than wild fry. Egg-to-fry survival rates varied among years, with no consistent difference between hatchery and wild fry. The relationships between reproductive traits and body length were not significantly altered by a single generation of hatchery exposure. However, because hatchery females had smaller body sizes, the distributions of linked traits, such as total gamete mass and fecundity, differed by as much as 0.6 SD, probably resulting in some fitness loss. Our data support the idea that a single generation of state-of-the-art conservation hatchery propagation can produce fish with reproductive traits similar to those of wild fish, given comparable body size.

Lacroix, G.L. 2008. Influence of origin on migration and survival of Atlantic salmon (*Salmo salar*) in the Bay of Fundy, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 65:2063-2079.

Synopsis: Atlantic salmon smolts of wild and hatchery origin were tagged with ultrasonic transmitters and monitored at successive arrays of submerged receivers during migration from five watersheds in three regions of the Bay of Fundy, Canada. The early marine survival of migrating Atlantic salmon was estimated by monitoring their migration in estuarine and coastal habitats. Except in cases where hatchery fish were purposely forced to migrate later than their wild counterparts, the migration success did not differ significantly between groups of wild and hatchery smolts for rivers where both were simultaneously monitored. The responses of hatchery fish to delays in release indicated that synchronizing the readiness and release time of hatchery smolts to the timing of wild smolt runs may be crucial to successful management of the depleted or endangered salmon populations being sustained by hatchery programs in the Bay of Fundy.

Matala, A. P., W. Young, J. L. Vogel and S. Narum. 2012. Influences of Hatchery Supplementation, Spawner Distribution, and Habitat on Genetic Structure of Chinook Salmon in the South Fork Salmon River, Idaho. *North American Journal of Fisheries Management*. 32:346–359.

Synopsis: This study compared the genetic profile of Chinook salmon sampled below an exclusionary weir on the South Fork of the Salmon River, where supplementation has occurred for many years, with that of fish from above the weir, where only natural origin fish have access. They observed little genetic differentiation between the two groups, indicating that the supplementation program has not lead to a divergence with the wild population. They also compared these samples to samples from two neighboring populations, and observed significant differentiation inferring that despite substantial hatchery releases in the South Fork homogenization of fish across the basin has not occurred.

Monzyk, F.R., B.C. Jonasson, T.L. Hoffnagle, P.J. Keniry, R.W. Carmichael, and P.J. Cleary. 2009. Migration Characteristics of Hatchery and Natural Spring Chinook Salmon Smolts from the Grande Ronde River Basin, Oregon, to Lower Granite Dam on the Snake River. *Transactions of the American Fisheries Society* 138: 1093-1108.

Abstract: We investigated the patterns of travel time and survival of hatchery and natural smolts fitted with passive integrated transponder (PIT) tags through specific reaches of the migration

corridor during the 2000–2006 migration years for two populations originating in the Grande Ronde River basin (Lostine River and Catherine Creek). For both populations, median travel times for natural smolts were significantly longer in the upper reaches of the migration corridor but shorter in the lower reaches than for their hatchery counterparts. Also, among both hatchery and natural smolts, smaller individuals spent more time in the upper reaches, presumably feeding to attain a larger size before continuing their migration. Within populations, both hatchery and natural smolts showed similar patterns of survival through the reaches of the migration corridor above Lower Granite Dam. Size-selective mortality was evident for hatchery and natural smolts from both populations, especially in the upper reaches, larger individuals experiencing higher survival.

Moyer, G.R., M.S. Blouin, and M.A. Banks. 2007. The influence of family-correlated survival on N_b/N for progeny from integrated multi- and single-generation hatchery stocks of coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 64:1258-1265.

Abstract: There exist surprisingly few data on the final variance and mean of family sizes for hatchery-born fish at the adult stage. Thus, it is difficult to predict, for a conservation hatchery operation that minimizes the variance in progeny number, how much lower the true effective population size (N_e) of a cohort of hatchery-born adults will be than N_e predicted simply by the number of parents that produced them. We used parentage analysis to estimate the survival and N_e for two integrated stocks of hatchery coho salmon (*Oncorhynchus kisutch*). One hatchery is a multigeneration stock obtained by spawning 70% hatchery with 30% naturally reproducing fish, whereas the second is a single-generation stock derived from naturally reproducing coho. There was no significant difference in average overall survival between stocks, but observed N_e was significantly less than expected for each stock. Family-correlated survival contributed to roughly a 20% reduction in N_e over the freshwater and marine life stages. This reduction is similar to previous estimates and suggests a value that can be used when estimating the effective number of hatchery parents in applications of the Ryman-Laikre formula (at least for programs such as ours that attempt to equalize sex ratios and family sizes).

Moyer, G.R., J.D. Rousey, and M.A. Cantrell. 2009. Genetic Evaluation of a Conservation Hatchery Program for Reintroduction of Sicklefin Redhorse *Moxostoma* sp. in the Tuckasegee River, North Carolina. *North American Journal of Fisheries Management* 29: 1438-1443.

Abstract: Restoration and reintroduction efforts for the sicklefin redhorse *Moxostoma* sp. have been initiated by state, tribal, and federal agencies owing to the limited geographic distribution of this species and threats associated with the physical alteration of its habitat. A critical component of a successful reintroduction is that the source and recipient populations have similar genetic resources and life history patterns. We used 10 microsatellite loci to estimate and compare indices of genetic diversity between the Little Tennessee River population of wild adults and the hatchery broodstock being used for initial reintroduction efforts. We also compared relatedness values for the broodstock used for restoration efforts. There were no significant differences between hatchery broodstock and wild adults with respect to average gene diversity, but the average number of alleles for each brood year was significantly less than that for wild adults. While this trend persisted when the 2007 and 2008 brood years (combined) were compared with wild adults, the reduction was not significant. Finally, all hatchery crosses were among unrelated individuals. Our results highlight the importance of using genetic information to assist restoration and reintroduction efforts.

Pearsons, T. N. and G. M. Temple. 2007. Impacts of Early Stages of Salmon Supplementation and Reintroduction Programs on Three Trout Species. *North American Journal of Fisheries Management* 27:1-20.

Abstract: Salmon supplementation and reintroduction programs have the potential to negatively impact other valued fish taxa that are not the targets of enhancement (nontarget taxa [NTT]). Impacts of the supplementation of spring Chinook salmon *Oncorhynchus tshawytscha* and the reintroduction of coho salmon *O. kisutch* (hereafter supplementation) on populations of rainbow trout *O. mykiss*, steelhead (anadromous rainbow trout), cutthroat trout *O. clarkii*, and bull trout *Salvelinus confluentus* were evaluated after 5 years of stocking approximately 1 million yearling smolts in the upper Yakima River basin between 1999 and 2003. Field methods included backpack electrofishing and snorkeling in tributaries and drift-boat electrofishing in the main stem. We used three sequential steps in our evaluation: (1) we determined whether spatial overlap occurred between supplemented fish and NTT; (2) if overlap occurred, we determined whether a change in abundance, size, or biomass occurred during supplementation; and (3) if a change occurred, we determined whether the change could be reasonably attributed to supplementation. Salmon rarely overlapped cutthroat trout or bull trout in tributaries, but some overlap with cutthroat trout occurred in relatively high elevations of the main stem and considerable overlap with rainbow trout occurred in tributaries and the main stem. Except in steelhead, the lower 90% confidence limit (CL) of abundance, size, and biomass was above the containment objective for NTT that overlapped significantly with salmon. We used rainbow trout as an analog for steelhead. The lower 90% CL of rainbow trout abundance and size in tributaries and the main stem and biomass in the main stem was below the containment objective for steelhead. However, comparisons of rainbow trout abundance, size, and biomass between tributaries and main-stem sections with relatively high and low salmon abundances revealed that the change was probably not the result of supplementation (before–after control–impact paired site analysis: $P > 0.05$). Our data indicate that early stages of salmon supplementation have not impacted trout species in the upper Yakima River basin beyond predetermined containment objectives.

Pearsons, T.N., A.L. Fritts, and J.L. Scott. 2007. The effects of hatchery domestication on competitive dominance of juvenile spring Chinook salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 64:803-812.

Abstract: We tested the null hypotheses that competitive dominance among juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in contest and scramble experiments would not be affected by domestication selection after one generation of state-of-the-art hatchery culture. Dyadic challenges of size-matched juvenile fish were conducted after a 6-day acclimation in 113.4 L aquaria. Differences in dominance and frequency of different types of agonistic interactions used were not significantly different in contest ($n = 505$) or scramble ($n = 363$) competition experiments ($P > 0.05$). However, wild origin fish were more aggressive than hatchery origin fish in both types of experiments ($P \leq 0.05$). Furthermore, wild origin fish gained more weight than hatchery origin fish during contest experiments, and hatchery origin fish lost less weight than wild origin fish in scramble experiments ($P \leq 0.05$). Dominant fish, regardless of origin, grew more than subordinate fish in both contest and scramble experiments ($P \leq 0.05$). Our results indicate that aggression, and growth mediated by competition, can be affected by domestication after only one generation of state-of-the-art hatchery culture; however, impacts to competitive dominance appear to be small.

Rosenberger, S.J., W.P. Connor, C.A. Peery, D.J. Milks, M.L. Schuck, J.A. Hesse, and S.G. Smith. 2013. Acclimation enhances postrelease performance of hatchery fall Chinook salmon subyearlings while reducing the potential for interaction with natural fish. *North American Journal of Fisheries Management* 33:519-528.

Abstract: One form of prerelease acclimation of hatchery anadromous salmonid *Oncorhynchus* spp. juveniles is to truck the fish to remote points for extended holding at low densities in rearing vessels (e.g., tanks, raceways, or in-ground ponds) supplied with river water. We conducted a 3-year study to determine whether such acclimation enhanced the postrelease performance of hatchery fall Chinook Salmon *O. tshawytscha* subyearlings and reduced the potential for interaction with natural fall Chinook Salmon subyearlings. In comparison with hatchery subyearlings that were released directly into the lower Snake River just downstream of the acclimation facility, acclimated hatchery subyearlings (1) passed downstream to Lower Monumental Dam (the third dam encountered during seaward migration) faster, (2) passed the dam earlier, and (3) survived from release to the dam tailrace at higher rates. The differences in downstream passage rate and dam passage timing were also much greater between acclimated hatchery subyearlings and natural subyearlings than between directly released hatchery subyearlings and natural subyearlings. Thus, acclimation provided a survival advantage to the hatchery fish while reducing the potential for (1) aggressive and nonaggressive social interactions with natural fish while in transit through the reservoirs associated with Lower Granite, Little Goose, and Lower Monumental dams; and (2) confinement with natural fish at those three dams, where fish collection and raceway holding were followed by transport in tanker trucks. Our findings support acclimation as a method for enhancing postrelease performance of hatchery fall Chinook Salmon subyearlings and reducing their potential interactions with natural conspecifics.

Schroder, S. L., C. M. Knudsen, T. N. Pearsons, T. W. Kassler, S. F. Young, C. A. Busack, and D. E. Fast. 2008. Breeding Success of Wild and First-Generation Hatchery Female Spring Chinook Salmon Spawning in an Artificial Stream. *Transactions of the American Fisheries Society*, 137:1475-1489.

Abstract: First generation hatchery and wild spring Chinook salmon from the upper Yakima River, Washington State were placed into an artificial stream and allowed to spawn. Seven independent test groups were placed into the stream from 2001 through 2005. No differences were detected in the egg deposition rates of wild and hatchery females. Pedigree assignments based on microsatellite DNA, however, showed that the eggs deposited by wild females survived to the fry stage at a 5.6% higher rate than those spawned by hatchery females. Subtle differences between hatchery and wild females in redd abandonment, egg burial, and redd location choice may have been responsible for the difference observed. Body size did not affect the ability of females to spawn or the survival of their deposited eggs. How long a female lived was positively related to her breeding success but female origin did not affect longevity. The density of females spawning in portions of the stream affected both egg deposition and egg-to-fry survival. No difference, however, was found in the overall distribution patterns of the two types of females. Other studies that have examined the effects of a single generation of hatchery culture on upper Yakima River Chinook have disclosed similar low-

level effects on adult and juvenile traits. The cumulative impact of such differences will need to be considered when hatcheries are used to restore depressed populations of salmon.

Schroder, S. L., C. M. Knudsen, T. N. Pearsons, T. W. Kassler, S. F. Young, E.P. Beall, and D. E. Fast. 2010. Behavior and Breeding Success of Wild and First-Generation Hatchery Male Spring Chinook Salmon Spawning in an Artificial Stream. *Transactions of the American Fisheries Society*, 139:989-1003.

Abstract: Spring Chinook salmon *Oncorhynchus tshawytscha* native to the upper Yakima River, Washington, were placed into an artificial stream to evaluate the effect of a single generation of hatchery culture on their spawning behavior and ability to produce offspring. From 2001 to 2005, seven independent test groups containing wild and hatchery fish were placed into the stream. The effects of body weight, spawning ground longevity, attack frequency, social dominance, courting frequency, and mate number on breeding success in hatchery and wild males were evaluated. Differences in male agonism due to male origin were found. Wild males exhibited higher attack rates and greater social dominance than did hatchery males. However, the observed inequalities in agonism and dominance appeared to be largely caused by differences in body weight between the two types of males: wild males were, on average, 9% heavier than hatchery males. Wild and hatchery males did not differ in the frequency of courting behaviors or in the number of mates. Pedigree analyses based on DNA showed that hatchery and wild males had comparable breeding success values. Consequently, a single generation of hatchery exposure appeared to have a low effect on spring Chinook salmon male breeding success in our experimental setting.

Sharma, R, G. Morishima, S. Wang, A. Talbot, and L. Gilbertson. 2006. An evaluation of the Clearwater River supplementation program in western Washington. *Canadian Journal of Fisheries and Aquatic Sciences*, 63(2): 423-437.

Synopsis: After three generations of study, an integrated coho supplementation program in a Washington coastal stream documented no empirical evidence that the program negatively affected the fitness of the target population. This study demonstrates that a supplementation (hatchery) program, in this case following new and innovative operational protocols, can produce smolts that have nearly the same survival rate to adults as that of wild smolts and can result in more adult coho returning to the Clearwater basin. This benefit appears possible without short-term adverse impacts to either intrinsic productivity or the number of naturally produced smolts.

Sharpe, C.S., P.L. Hulett, C.W. Wagemann, M.P. Small and A.R. Marshall. 2010. Natural Reproductive Success of First-generation Hatchery Steelhead Spawning in the Kalama River: A Progress Report. Washington Department of Fish and Wildlife, Fish Program, Fish Science Division. (<http://wdfw.wa.gov/publications/00969/wdfw00969.pdf>)

Synopsis: The goal of the Kalama research program is to identify and empirically quantify risks imposed by hatchery programs on natural production of anadromous salmonids, and identify strategies to manage those risks. Studies of steelhead genetics, ecology, and life history have been ongoing in the Kalama River since the mid-1970's. A primary objective of Kalama research work has been to assess the relative reproductive performance and contribution of hatchery and wild steelhead spawning in the wild. We did not detect a difference in reproductive success of the wild broodstock

hatchery spawners: the proportions of offspring from Hatchery \times Hatchery (HH), Hatchery \times Wild (HW), and Wild \times Wild (WW) spawners closely approximated the proportions expected under the null hypothesis with reproductive success of hatchery spawners equal to that of wild spawners. Reproductive success of first-generation wild broodstock hatchery fish appeared to be similar to that of wild fish in the first replicate of our experiment. The outcome is in agreement with initial results from a similar reproductive success study on the Hood River, Oregon (Araki et al. 2006), where first generation wild-broodstock winter-run steelhead appeared to be as reproductively competent as the wild fish from which they were derived (but see Araki et al. 2007 and Araki et al. 2008). Because we present results from only the first of three replicates the results should be considered preliminary.

Small, M.P., K. Currens, T.H. Johnson, A.E. Frye, and J.F. Von Bargen. 2009. Impacts of supplementation: genetic diversity in supplemented and unsupplemented populations of summer chum salmon (*Oncorhynchus keta*) in Puget Sound (Washington, USA). *Canadian Journal of Fisheries and Aquatic Sciences*, 66:1216-1229.

Abstract: In supplementation programs, hatcheries employ wild-origin fish as brood stock and their offspring are allowed into wild spawning areas. Resource managers use supplementation to support imperiled salmonid populations, seeking to increase census size and possibly effective population size (N_e), while minimizing risks of genetic diversity loss and domestication from hatchery intervention. Here we document impacts of 5–10 years of supplementation on threatened summer-run chum salmon (*Oncorhynchus keta*) in Hood Canal (HC) and Strait of Juan de Fuca (SJF) in Washington State and compare them genetically with unsupplemented summer- and fall-run chum salmon from HC and South Puget Sound. Microsatellite allele frequencies identified four run-timing and geographic groups. HC and SJF summer chum salmon genetic relationships followed a metapopulation pattern of isolation by distance, similar to patterns prior to supplementation, suggesting that supplementation minimally impacted population structure. In most supplemented subpopulations, we detected no effects on diversity and N_e , but high variance in individual pairwise relatedness values indicated over-representation of family groups. In two subpopulations, hatchery impacts (decreased diversity and lower N_e) were confounded with extreme bottlenecks. Rebounds in census sizes in all subpopulations suggest that general survivorship has improved and that possible hatchery effects on genetic diversity will be overcome.

Smith, C.T., R. French, J. Lovtang, and D. Hand. 2014. Genetic Composition of the Warm Springs River Chinook Salmon Population Maintained following Eight Generations of Hatchery Production. *Transactions of the American Fisheries Society*, 143:1280-1294.

Abstract: Balancing the disparate objectives of fishery augmentation and conservation of an endemic fish population presents a substantial challenge. In the case of Warm Springs National Fish Hatchery (Warm Springs Hatchery), strategies for achieving both objectives included incorporation of natural fish into the hatchery broodstock and restricting proportions of hatchery fish on the spawning grounds. The hatchery has been more successful in implementing the latter than the former. We analyzed 76 single nucleotide polymorphism markers in Spring Chinook Salmon *Oncorhynchus tshawytscha* collected from the Warm Springs River in 1976–1977 (prior to hatchery production) and 2001–2011 (posthatchery) to examine whether the genetic characteristics of the endemic population had changed during that time. Pre- and posthatchery collections clustered together when compared with those from Round Butte Hatchery, which has a nearby segregated program, and other Columbia

River populations. The difference between pre- and posthatchery collections was nonsignificant, but posthatchery samples exhibited significantly lower expected heterozygosity. We observed some evidence of reduced effective size and increased genetic drift in fish produced at Warm Springs Hatchery (relative to natural-origin fish) and even stronger evidence of this in fish produced at Round Butte Hatchery. We conclude that natural-origin Chinook Salmon returning to the Warm Springs River form a distinct group within the interior Columbia Basin spring-run lineage and have changed very little over the past eight generations. We further speculate that differences between hatchery- and natural-origin fish at Warm Springs Hatchery are expected to increase if hatchery operations remain static (i.e., little integration of natural-origin fish and incorporation of Round Butte Hatchery fish in the broodstock).

Stephenson, S.M., M.D. Neufeld, S.C. Ireland, S. Young, R.S. Hardy, and P. Rust. 2013. Survival and Dispersal of Sonic-Tagged, Hatchery-Reared Burbot Released into the Kootenay River. *Transactions of the American Fisheries Society*, 142:1671-1679.

Abstract: As part of recovery efforts for the Kootenay population of Burbot *Lota lota*, we monitored 109 sonic-tagged, hatchery-reared Burbot released at 1–3 years of age throughout Kootenay Lake and the Kootenay River over a 3-year period. Our objectives were to evaluate broodstock choice, assess differences in survival and dispersal by release site and age, and evaluate spawning movements. Overall, release survival was high (66%) and there was dispersal throughout the system (up to 235 km), involving both lacustrine and riverine habitat. Spawning movements were extensive (up to 59 km/d upstream) and suggest the use of known spawning locations. However, most age-1 releases had lower survival and remained in the release tributaries for 1 year postrelease, which was longer than expected and which warrants further investigation. Overall, this telemetry study provides a positive outlook on the current aquaculture rehabilitation efforts for Kootenay Burbot and provides direction for further work.

Sturdevant, M.V., Fergusson, E., Hillgruber, N., Reese, C., Orsi, J., Focht, R., Wertheimer, A., Smoker, B., 2011. Lack of trophic competition among wild and hatchery juvenile chum salmon during early marine residence in Taku Inlet, Southeast Alaska. *Environmental Biology of Fishes* 94, 101–116.

Abstract: Early marine trophic interactions of wild and hatchery chum salmon (*Oncorhynchus keta*) were examined as a potential cause for the decline in harvests of adult wild chum salmon in Taku Inlet, Southeast Alaska. In 2004 and 2005, outmigrating juvenile chum salmon were sampled in nearshore habitats of the inlet (spring) and in epipelagic habitat at Icy Strait (summer) as they approached the Gulf of Alaska. Fish were frozen for energy density determination or preserved for diet analyses, and hatchery stocks were identified from the presence of thermal marks on otoliths. We compared feeding intensity, diets, energy density, and size relationships of wild and hatchery stocks (n=3123) across locations and weeks. Only hatchery fish feeding intensity was negatively correlated with fish abundance. In both years, hatchery chum salmon were initially larger and had greater energy density than wild fish, but lost condition in early weeks after release as they adapted to feeding on wild prey assemblages. Diets differed between the stocks at all inlet locations, but did not differ for hatchery salmon between littoral and neritic habitats in the outer inlet, where the stocks overlapped most. Both diets and energy density converged by late June. Therefore, if density-dependent interactions affect wild chum salmon, these effects must be very rapid because survivors

in Icy Strait showed few differences. Our study also demonstrates that hatchery release strategies used near Taku Inlet successfully promote early spatial segregation and prey partitioning, which reduce the probability of competition between wild and hatchery chum salmon stocks.

Suk, H.Y., B.D. Neff, K. Quach, and Y.E. Morbey. 2011. Evolution of introduced Chinook salmon (*Oncorhynchus tshawytscha*) in Lake Huron: emergence of population genetic structure in less than 10 generations. *Ecology of Freshwater Fish*, 21:235-244, corrigendum 21:494.

Abstract: Population genetic structure was detected in Chinook salmon *Oncorhynchus tshawytscha* in their non-native range of Lake Huron using microsatellite DNA. All Chinook salmon in this system descend from Green River, Washington cohorts, originally transplanted to Michigan hatcheries in the late 1960s. We tested for population genetic differentiation of age 0 fish collected from 13 rivers and two hatcheries in 2007. The amount of genetic differentiation among collection sites was low but statistically significant, with F_{ST} values ranging from 0.036 to 0.133 and R_{ST} values ranging from 0.008 to 0.157 for specific loci. Based on pairwise F_{ST} and R_{ST} values and Bayesian cluster analysis, the Maitland River population in the Main Basin of Lake Huron was genetically distinct from the remaining collection sites. Based on analysis of bycatch data from commercial gill net fisheries, Chinook salmon likely colonised the Main Basin by 1975 (10 generations ago) and the North Channel and southern Georgian Bay regions by 1980 (eight generations ago). Thus, population genetic structure has emerged in Lake Huron Chinook salmon in <10 generations.

Tatara, C.P., S.C. Riley, and B.A. Berejikian. 2011. Effects of Hatchery Fish Density on Emigration, Growth, Survival, and Predation Risk of Natural Steelhead Parr in an Experimental Stream Channel. *North American Journal of Fisheries Management* 31:224-235.

Abstract: Hatchery supplementation of steelhead *Oncorhynchus mykiss* raises concerns about the impacts on natural populations, including reduced growth and survival, displacement, and increased predation. The potential risks may be density dependent. We examined how hatchery stocking density and the opportunity to emigrate affect the responses of natural steelhead parr in an experimental stream channel and after 15 d found no density-dependent effects on growth, emigration, or survival at densities ranging from 1-6 hatchery parr/m². The opportunity for steelhead parr to emigrate reduced predation by coastal cutthroat trout *O. clarkii clarkii* on both hatchery and natural steelhead parr. The cutthroat trout exhibited a type-I functional response (constant predation rate with increased prey density) for the hatchery and composite populations. In contrast, the predation rate on natural parr decreased as hatchery stocking density increased. Supplementation with hatchery parr at any experimental stocking density reduced the final natural parr density. This decline was explained by increased emigration from the supplemented groups. Natural parr had higher mean instantaneous growth rates than hatchery parr. The proportion of parr emigrating decreased as parr size increased over successive experimental trials. Smaller parr had lower survival and suffered higher predation. The final density of the composite population, a measure of supplementation effectiveness, increased with the hatchery steelhead stocking rate. Our results indicate that stocking larger hatchery parr (over 50 d postemergence) at densities within the carrying capacity would have low short-term impact on the growth, survival, and emigration of natural parr while increasing the density of the composite population; in addition, a stocking density greater than 3 fish/m² might be a good starting point for the evaluation of parr stocking in natural streams.

Temple, G.M. and T.N. Pearsons. 2012. Risk management of non-target fish taxa in the Yakima River Watershed associated with hatchery salmon supplementation. *Environmental Biology of Fishes* 94:67–86.

Abstract: Hatchery cultured salmon have the potential to interact strongly with other valued fish taxa (nontarget taxa; NTT) in the natural environment. Monitoring and managing adverse interactions between hatchery supplemented salmon and NTT is one unique characteristic of a hatchery salmon supplementation program in the Yakima River, Washington. In this study, we evaluate impacts of spring Chinook salmon *Oncorhynchus tshawytscha* and coho salmon *O. kisutch* reintroduction to 15 NTT after 11 years of stocking approximately one million yearling smolts annually in the upper Yakima Basin between 1999 and 2009. Our risk management monitoring indicated changes in important response variables for NTT were within acceptable limits. Rigorous pre-implementation planning likely prevented many undesirable ecological impacts from the hatchery supplementation program. We illustrate a number of important features associated with risk management of hatchery and wild fish interactions. First, pre-project planning can eliminate many risks of concern and substantially reduce the need for risk containment during project implementation. Second, the sieve approach for monitoring impacts provided an acceptable balance between monitoring effort and risk containment ability, although in some cases, we would not detect impacts of interest. Third, rare and dispersed species that cannot be monitored effectively benefit from risk averse hatchery release strategies. Fourth, risk containment monitoring programs can be used to refute unsubstantiated claims of undesirable impacts. In short, our experience suggests that risk management of ecological interactions can occur by using a combination of pre-project adjustments through risk assessment and risk reduction, and by cost-effective risk containment monitoring and management.

Van Doornik, D.M., R.S. Waples, M.C. Baird, P. Moran, and E.A. Berntson. 2011. Genetic Monitoring Reveals Genetic Stability within and among Threatened Chinook Salmon Populations in the Salmon River, Idaho. *North American Journal of Fisheries Management* 31:96-105.

Abstract: Identifying and understanding temporal genetic changes within fish populations is important for the management of these populations, especially those of conservation concern. Such changes are often the result of genetic drift, which can be exacerbated when the size of a population decreases. Using molecular-genetics techniques, we monitored nine populations of Chinook salmon *Oncorhynchus tshawytscha* in the Salmon River, Idaho, to determine how the genetic characteristics within and among these populations have changed over time. We found no evidence of change in the level of heterozygosity or allelic richness over three to four generations in eight of the populations. This is probably due to the fact that the populations all maintained a sufficiently large effective size, even though a few of the populations did show a decline in effective size. Also, the genetic structure among the populations did not change appreciably over time. Populations that had been supplemented with hatchery-reared fish showed genetic similarity to the within-basin hatchery source population, presumably because of the extensive use of native fish for hatchery brood stocks and minimal out-of-basin stock transfers. The lack of a detectable decline in these populations' levels of genetic diversity is encouraging, given the species' threatened status under the U.S. Endangered Species Act.

Van Doornik, D.M., D.L. Eddy, R.S. Waples, S.J. Boe, T.L. Hoffnagle, E.A. Berntson, and P.

Moran. 2013. Genetic Monitoring of Threatened Chinook Salmon Populations: Estimating Introgression of Nonnative Hatchery Stocks and Temporal Genetic Changes. *North American Journal of Fisheries Management* 33:693-706.

Abstract: Conservation efforts aimed at Pacific salmon (*Oncorhynchus* spp.) populations have frequently utilized artificial propagation in an attempt to increase fish abundance. However, this approach carries the risk of unwanted changes in the genetic characteristics of the target population and perhaps others that might incidentally be affected. We used genetic monitoring techniques to estimate the amount of introgression that has occurred from nonnative hatchery stocks into native populations and to determine the extent of genetic changes that have occurred in association with supplementation efforts over the past 20–50 years in Snake River Chinook Salmon *O. tshawytscha* populations from northeastern Oregon. A total of 4,178 fish from 13 populations were genotyped for 12 microsatellite DNA loci. Expected heterozygosity values for each sample ranged from 0.707 to 0.868. Estimates of the effective number of breeders per year in the naturally spawning populations ranged from 20.6 to 459.1, whereas in the hatchery populations they ranged from 33.8 to 1,118.8. We found that introgression from the Rapid River Hatchery stock was particularly noticeable in the early 1990s but that it appears to have had a substantial effect on only two of the native populations (Lookingglass Creek and the upper Grande Ronde River) despite the ample opportunities for introgression to occur. All seven of the native populations sampled have maintained their levels of within-population genetic diversity throughout the sampling period. Overall, this region's supplementation efforts appear to have had a minimal effect on the genetic diversity of its Chinook Salmon populations.

Van Doornik, D.M., M.A. Hess, M.A. Johnson, D.J. Teel, T.A. Friesen, and J.M. Myers. 2015. Genetic Population Structure of Willamette River Steelhead and the Influence of Introduced Stocks. *Transactions of the American Fisheries Society* 144:150-162.

Abstract: Conservation genetics studies are frequently conducted on Pacific salmon *Oncorhynchus* spp. to delineate their population structure and to quantify their genetic diversity, especially for populations that have experienced declines in abundance and are subject to anthropogenic activities. One such group of salmonids is steelhead *O. mykiss* (anadromous Rainbow Trout) from the Willamette River, a tributary of the Columbia River. Within the Willamette River there are multiple steelhead life history and run-timing types, some of which originated from nonnative populations. Late winter-run steelhead and Rainbow Trout are native to the Willamette River, whereas early winter-run and summer-run steelhead have been introduced into the system via releases from artificial propagation efforts. We conducted genetic analyses of Willamette River steelhead to determine the effect that nonnative steelhead released into the Willamette River basin have had on the genetic population structure of native steelhead. We found genetic differentiation among the samples that separated steelhead into four population groups that corresponded to run type. Possibly due to local adaptation, the native run type has retained its genetic distinctiveness from the introduced types, despite there being opportunities for gene flow among all types. Introduced early winter-run steelhead appear to be the origin of steelhead inhabiting certain Willamette River tributaries where native steelhead did not historically spawn.

If there are negative hatchery effects, are they reversible?

Bosch, W. J., T. H. Newsome, J. L. Dunnigan, J. D. Hubble, D. Neeley, D. T. Lind, D. E. Fast, L. L. Lamebull, and J. W. Blodgett. 2007. Evaluating the Feasibility of Reestablishing a Coho Salmon Population in the Yakima River, Washington. *North American Journal of Fisheries Management* 27:198-214.

Abstract: Historical returns of coho salmon to the Yakima River Basin were estimated to range from 45,000 to 100,000 fish annually but declined to zero by the 1980s after decades of overexploitation of fishery, water, and habitat resources. In 1996 the Yakama Nation and cooperators initiated a project to determine the feasibility of reestablishing a naturally spawning coho population in the Yakima River. The Yakima coho project explored whether successful recolonization was feasible when multi-generational, hatchery-reared coho were reintroduced to native habitats. After 10-20 years of outplanting, we compared data for adult returns of known natural- and hatchery-origin coho. We found that natural-origin coho returned at a significantly larger size than hatchery-origin coho. Mean egg mass and mean egg size of natural-origin females were greater than those of hatchery-origin females, though the differences were statistically significant for only one of three sample years. Natural-origin adults returned (2 to 9 days) and spawned (5 days) later than their hatchery-origin counterparts. Preliminary indices of smolt-to-adult survival for natural-origin coho were 3.5 to 17.0 times survival indices of hatchery-origin coho. The number of coho returning to historical native spawning habitats in upriver areas generally increased. Spawning surveys demonstrated the existence of robust and sustainable spawning aggregates in various locations in the basin. Hatchery releases from local brood source parents had significantly higher smolt-to-smolt survival than releases from out-of-basin hatchery broodstock, but some of these observed differences in survival could have been due in part to differences in smolt size. We conclude that hatchery-origin coho, with a legacy of as many as 10 to 30 generations of hatchery-influence, demonstrated their ability to reestablish a naturalized population after as few as 3 to 5 generations of outplanting in the wild. Note that natural-origin coho adult returns to spawning areas above Willamette Falls confirm these results. After decades of outplanting hatchery-origin coho from multiple hatcheries including Oregon coastal hatcheries, releases above Willamette Falls were terminated in 1998. Now, 3-4 coho generations after hatchery-origin releases were terminated, adult coho returns to Willamette Falls numbered 25,300 in 2009 and will likely exceed 30,000 in 2010.

Carmona-Catot, G, P.B. Moyle, and R.E. Simmons. 2012. Long-term captive breeding does not necessarily prevent reestablishment: lessons learned from Eagle Lake rainbow trout. *Reviews in Fish Biology and Fisheries*, 2012, Volume 22, Number 1, Pages 325-342.

Abstract: Captive breeding of animals is often cited as an important tool in conservation, especially for fishes, but there are few reports of long-term (<50 years) success of captive breeding programs, even in salmonid fishes. Here we describe the captive breeding program for Eagle Lake rainbow trout, *Oncorhynchus mykiss aquilarum*, which is endemic to the Eagle Lake watershed of northeastern California. The population in Eagle Lake has been dependent on captive breeding for more than 60 years and supports a trophy fishery in the lake. Nevertheless, the basic life history, ecological, and genetic traits of the subspecies still seem to be mostly intact. Although management has apparently minimized negative effects of hatchery rearing, reestablishing a wild population

would ensure maintenance of its distinctive life history and its value for future use as a hatchery fish. An important factor that makes reestablishment possible is that the habitat in Eagle Lake is still intact and that Pine Creek, its major spawning stream, is recovering as habitat. With the exception of an abundant alien brook trout (*Salvelinus fontinalis*) population in Pine Creek, the habitat factors that led to the presumed near-extinction of Eagle Lake rainbow trout in the early twentieth century have been ameliorated, although the final stages of reestablishment (eradication of brook trout, unequivocal demonstration of successful spawning migration) have still not been completed. The Eagle Lake rainbow trout story shows that long-term captive breeding of migratory salmonid fishes does not necessarily prevent reestablishment of wild populations, provided effort is made to counter the effects of hatchery selection and that natural habitats are restored for reintroduction. Long-term success, however, ultimately depends upon eliminating hatchery influences on wild-spawning populations. Extinction of Eagle Lake rainbow trout as a wild species becomes increasingly likely if we fail to act boldly to protect it and the Eagle Lake watershed.

Conover, D. O., S. B. Munch, and S. A. Arnott. 2009. Reversal of evolutionary downsizing caused by selective harvest of large fish. *Proceedings of the Royal Society B*. doi:10.1098/rspb.2009.0003.

Synopsis: Evolutionary responses to the long-term exploitation of individuals from a population may include reduced growth rate, age at maturation, body size and productivity. Theoretical models suggest that these genetic changes may be slow or impossible to reverse but rigorous empirical evidence is lacking. Here, we provide the first empirical demonstration of a genetically based reversal of fishing-induced evolution. We subjected six populations of silverside fish (*Menidia menidia*) to three forms of size-selective fishing for five generations, thereby generating twofold differences among populations in mean weight and yield (biomass) at harvest. This was followed by an additional five generations during which size-selective harvest was halted. We found that evolutionary changes were reversible. Populations evolving smaller body size when subjected to size-selective fishing displayed a slow but significant increase in size when fishing ceased. Neither phenotypic variance in size nor juvenile survival was reduced by the initial period of selective fishing, suggesting that sufficient genetic variation remained to allow recovery. These results show that populations have an intrinsic capacity to recover genetically from harmful evolutionary changes caused by fishing, even without extrinsic factors that reverse the selection gradient.

Doyle, R.M., R. Perez-Enriquez, M. Takagi, and N. Taniguchi. 2001. Selective recovery of founder genetic diversity in aquacultural broodstocks and captive, endangered fish populations. *Genetica* 111:291-304.

Abstract: Hatchery broodstocks used for genetic conservation or aquaculture may represent their ancestral gene pools rather poorly. This is especially likely when the fish that found a broodstock are close relatives of each other. We re-analysed microsatellite data from a breeding experiment on red sea bream to demonstrate how lost genetic variation might be recovered when gene frequencies have been distorted by consanguineous founders in a hatchery. A minimal-kinship criterion based on a relatedness estimator was used to select subsets of breeders which represented the maximum number of founder lineages (i.e., carried the fewest identical copies of ancestral genes). UPGMA clustering of Nei's genetic distances grouped these selected subsets with the parental gene pool, rather than with the entire, highly drifted offspring generation. The selected subsets also captured much of the

expected heterozygosity and allelic diversity of the parental gene pool. Independent pedigree data on the same fish showed that the selected subsets had more contributing parents and more founder equivalents than random subsets of the same size. The estimated mean coancestry was lower in the selected subsets, meaning that inbreeding in subsequent generations would be lower if they were used as breeders. The procedure appears suitable for reducing the genetic distortion due to consanguineous and over-represented founders of a hatchery gene pool.

Fraser, D. J. 2008. How well can captive breeding programs conserve biodiversity? A review of salmonids. *Evolutionary Applications*, 1:535-586.

Galbreath, P.F., M.A. Bisbee Jr., D.W. Dompier, C.M. Kamphaus, and T.H. Newsome. 2014. Extirpation and Tribal Reintroduction of Coho Salmon to the Interior Columbia River Basin. [Fisheries](#), 39:77-87.

Abstract: 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.

Tymchuk, W. E., C. Biagi, R. Withler, and R. H. Devlin. 2006. Growth and behavioral consequences of introgression of a domesticated aquaculture genotype into a native strain of coho salmon. *Transactions of the American Fisheries Society* 135:442-455.

Abstract: Selective breeding for enhanced growth in Pacific salmon *Oncorhynchus* spp. and other fish typically involves use of the largest mature individuals to breed for future generations of aquaculture broodstock. Owing to an altered selection regime, faster-growing fish may not be as adapted to the natural environment as wild fish. To increase understanding of the genetic changes underlying selection for enhanced growth that results in phenotypic differentiation of farmed from wild Pacific salmon, multiple generations of pure and hybrid families were generated for coho salmon *O. kisutch*, including pure farm (D), pure native (Ch; a natural strain propagated by wild and hatchery production), F₁ and F₂ hybrids, and F₁ × wild backcross (B_{Ch}) genotypes. The family groups were reared in the laboratory under controlled conditions as (1) individual genotypic groups, (2) mixed groups under culture conditions, and (3) mixed groups under enriched (seminatural) conditions. The growth of the fish was tracked until smoltification. There was a significant genotype effect on growth performance (mass and length), with rankings as follows: D > F₂ > F₁ > B_{Ch} > Ch. This ranking remained the same in all three rearing environments. Behavioral differences were

observed among the families, the fast-growing domesticated families showing a reduced antipredator response relative to the slow-growing wild families. Expression of the phenotypic differences in the hybrids and backcrosses, together with the results from a joint-scale analysis on line means, suggests that additive genetic effects contribute significantly to the divergence between the fast- and slow-growing strains. As phenotypic differences between strains are largely a consequence of additive gene action, the phenotypic effects of domestication are largely diluted within two generations of backcrossing to wild salmon. Knowledge of the genetic changes responsible for altered growth rates is crucial to our ability to predict the consequences of introgression of domestic strains into wild populations of salmon.

Kitada, S., H. Kishino, and K. Hamasaki. 2011. Bias and significance of relative reproductive success estimates based on steelhead trout (*Oncorhynchus mykiss*) data: a Bayesian meta-analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 68:1827-1835.

Abstract: The evaluation of the reproductive success (RS) of hatchery fish in the wild is one of the most important issues in hatchery supplementation, aquaculture, and conservation. Estimates of the relative reproductive success (RRS) have been used to evaluate RS. Because RRS may vary greatly depending on cross, years of release, and environmental conditions, we introduced a log-normal distribution to quantify the variation. The classical estimator of RRS based on multiple measurements is contrasted with the mean of this distribution. We derived the mean, variance, and relative bias and applied our Bayesian hierarchical model to 42 empirical RRS estimates of steelhead trout (*Oncorhynchus mykiss*) in the Hood River, Oregon, USA. The RRS estimate generally had an upward bias. Although the average level of RRS implied the reproductive decline of hatchery fish and wild-born hatchery descendants, we could not reject the null hypothesis that hatchery fish and their descendants have the same chance of having smaller RS than wild fish as they do of having larger RS than wild fish.

Neville, H.M. and L. Bernatchez. 2013. Coding Gene Single Nucleotide Polymorphism Population Genetics of Nonnative Brook Trout: The Ghost of Introductions Past. *Transactions of the American Fisheries Society*, 142: 1215-1231.

Abstract: Fish have been translocated throughout the world, and introductions often have been executed repeatedly and have used mixtures of different strains from the native range. This history might have contributed to their invasive potential by allowing introduced and invading populations to circumvent expected reductions in genetic diversity from founder effects in a scenario termed the “genetic paradox” of invasions. We characterize patterns of genetic diversity in nonnative Brook Trout *Salvelinus fontinalis*, which have been introduced across the western United States for over a century but have also invaded broadly and pose a primary threat to native trout. We analyzed 155 coding gene single nucleotide polymorphisms (SNPs) in 34 nonnative Brook Trout populations sampled across eight large river systems as well as samples from the only four hatchery strains with documented use in Idaho. We uncovered similar within-population genetic diversity and large effective population sizes in naturalized populations compared with hatchery samples. Naturalized populations also showed substantial genetic structuring (maximum pairwise $F_{ST} = 0.23$) across and even within watersheds and indicated suggestions of admixture in certain regions. Assignment probabilities confirmed two main hatcheries as the origin of most fish collected in the field; however, the four hatcheries were excluded as being the origin for 8% of individuals, mirroring results from

clustering analyses and suggesting the influence of an additional unsampled hatchery source or sources. Simulated admixtures of hatchery samples produced genetic patterns similar to those observed in field samples, further supporting an influence of multiple historic hatchery stocks on the contemporary genetic structure of Brook Trout in Idaho. Our study highlights the potential contribution of historic hatchery and introduction practices in creating genetically variable and structured naturalized Brook Trout populations across Idaho, which may have allowed these fish to defy the “genetic paradox” early on in their nonnative history and set the stage for successful establishment and subsequent invasion.

Are hatchery effects genetically based? Could deleterious effects attributed to hatchery programs be due to environmental or other factors?

Baudron, A.R., C.L. Needle, A.D. Rijnsdorp, C.T. Marshall. 2014. Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. *Global Change Biology*. [doi: 10.1111/gcb.12514](https://doi.org/10.1111/gcb.12514).

Abstract: Decreasing body size has been proposed as a universal response to increasing temperatures. The physiology behind the response is well established for ectotherms inhabiting aquatic environments: as higher temperatures decrease the aerobic capacity, individuals with smaller body sizes have a reduced risk of oxygen deprivation. However, empirical evidence of this response at the scale of communities and ecosystems is lacking for marine fish species. Here, we show that over a 40-year period six of eight commercial fish species in the North Sea examined underwent concomitant reductions in asymptotic body size with the synchronous component of the total variability coinciding with a 1–2 °C increase in water temperature. Smaller body sizes decreased the yield-per-recruit of these stocks by an average of 23%. Although it is not possible to ascribe these phenotypic changes unequivocally to temperature, four aspects support this interpretation: (i) the synchronous trend was detected across species varying in their life history and life style; (ii) the decrease coincided with the period of increasing temperature; (iii) the direction of the phenotypic change is consistent with physiological knowledge; and (iv) no cross-species synchrony was detected in other species-specific factors potentially impacting growth. Our findings support a recent model-derived prediction that fish size will shrink in response to climate-induced changes in temperature and oxygen. The smaller body sizes being projected for the future are already detectable in the North Sea.

Beacham, T. D. 2010. Revisiting Trends in the Evolution of Egg Size in Hatchery-Enhanced Populations of Chinook Salmon from British Columbia. *Transactions of the American Fisheries Society*, 139: 579-585.

Synopsis: Hatchery enhancement has been reported to result in an increase in egg size in coho salmon *Oncorhynchus kisutch* and a decline in egg size in Chinook salmon *O. tshawytscha*. Egg size may be directly influenced by selection, a larger egg size evolving as a consequence of hatchery incubation. Alternatively, a smaller egg size could evolve as a correlated response to fecundity selection, and a unidirectional change in egg size over time may reflect selection and an underlying

genetic change in the population. To address this question, temporal trends in egg size were investigated for two hatchery-enhanced populations of Chinook salmon from Vancouver Island, British Columbia. After the effect of female length variation was removed by standardizing egg sizes to a female of common length (the overall mean for each population), there was no temporal trend in egg size from the 1970s to 2008 for any of the hatchery-enhanced populations evaluated. These results do not support a previous report of genetically based declines in egg size in hatchery-enhanced Chinook salmon populations from this region.

Bellinger, K. B., G. H. Thorgaard, and P. A. Carter. 2014. Domestication is associated with reduced burst swimming performance and increased body size in clonal rainbow trout lines. *Aquaculture* 420–421 (2014) 154–159.

Abstract: Domestication selection combined with inadvertent selection for high growth rate and large body size are common in hatchery salmonids. However, evolutionary trade-offs of various fitness components with body size and domestication are likely. This study explores potential trade-offs between growth and sprint swim performance among five clonal lines of rainbow trout (*Oncorhynchus mykiss*), varying in the number of generations under domestication. We hypothesized that clonal lines of trout derived from highly domesticated populations would have higher growth rates but slower sprint swimming performance relative to clonal lines derived from less domesticated populations. Individuals from each of the five lines were repeatedly measured for body size and sprint swimming performance over 10–15 weeks. Our findings indicate significant differences in body size and sprint swimming performances between the less-domesticated and the more-domesticated lines, with more domesticated lines being larger but poorer swimmers. Implications for the survival and reproduction of hatchery salmonids released into the wild are explored.

Breckenridge, J.K., S.M. Bollens, G. Rollwagen-Bollens, and G.C. Roegner. 2014. Plankton Assemblage Variability in a River-Dominated Temperate Estuary During Late Spring (High-flow) and Late Summer (Low-flow) Periods. *Estuaries and Coasts*, May 2014, doi:DOI 10.1007/s12237-014-9820-7.

Abstract: Seasonally variable freshwater flows are known to influence estuarine plankton assemblages. There has been little recent study of the plankton dynamics of the Columbia River Estuary (CRE), a large, river-dominated estuary that has experienced great modification to its hydrological cycle. Zooplankton (>75 µm) were collected during four late spring (high-flow) cruises and three late summer (low-flow) cruises in 2005 and 2006. Surface-water microplankton (5–200 µm) were collected during cruises in 2005. Zooplankton and phytoplankton assemblage composition varied along an axial salinity gradient and between flow periods. Estuarine zooplankton were strongly seasonal and dominated by the calanoid copepod *Eurytemora affinis* in the late spring, high-flow period and by the invasive calanoid *Pseudodiaptomus forbesi* in the late summer, low-flow period. The phytoplankton assemblage was dominated by freshwater diatoms, primarily *Aulacoseira* spp. The ciliate *Mesodinium rubrum* (= *Myrionecta rubra*) reached high densities during the low-flow period, but otherwise, distinct high-flow and low-flow phytoplankton assemblages were not detected. Comparison to prior studies in the CRE suggests that the plankton assemblage composition during

the low-flow period has undergone considerable change, which may in turn have important trophic implications.

Buckland-Nicks, J.A., M. Gillis, and T.E. Reimchen. 2011. Neural network detected in a presumed vestigial trait: ultrastructure of the salmonid adipose fin. *Proceedings of the Royal Society, Series B Biology* : [rspb.2011.1009v1-rspb20111009](https://doi.org/10.1098/rspb.2011.1009).

Synopsis: If the adipose fin is in fact functioning as a precaudal flow sensor, allowing optimal maneuverability in turbulent water, ... then it is logical that swimming in non-turbulent waters would be largely unaffected by removal of the adipose fin. This hypothesis could explain why previous studies found that clipping of the adipose fin had no effect on stamina, susceptibility to predation or growth, as these studies were conducted in non-turbulent water. Other research, however, did find that growth was significantly affected by adipose fin clipping when fish were swimming in turbulent water. There are also suggestions that the adipose fin has a potential role during courtship as males have a larger fin than females and the latter appear to prefer males with a relatively larger adipose fin. Past research has proposed that both these factors may reflect a selective landscape in streams where males are subject to greater swimming demands than that of females. The occurrence of a larger adipose fin in males may relate to hydrodynamic functionality owing to the greater complexity and density of the nerve net in a larger fin.

Chittenden, C.M., C.A. Biagi, J.G. Davidsen, H. Kondo, A. McKnight, O.P. Pedersen, P.A. Raven, A.H. Rikardsen, J.M. Shrimpton, B. Zuehlke, R.S. McKinley, and R.H. Devlin. 2010. Genetic versus rearing-environment effects on phenotype: hatchery and natural rearing effects on hatchery- and wild-born coho salmon. *PLoS One*. 2010 Aug 19;5(8):e12261.

Abstract: With the current trends in climate and fisheries, well-designed mitigative strategies for conserving fish stocks may become increasingly necessary. The poor post-release survival of hatchery-reared Pacific salmon indicates that salmon enhancement programs require assessment. The objective of this study was to determine the relative roles that genotype and rearing environment play in the phenotypic expression of young salmon, including their survival, growth, physiology, swimming endurance, predator avoidance and migratory behaviour. Wild- and hatchery-born coho salmon adults (*Oncorhynchus kisutch*) returning to the Chehalis River in British Columbia, Canada, were crossed to create pure hatchery, pure wild, and hybrid offspring. A proportion of the progeny from each cross was reared in a traditional hatchery environment, whereas the remaining fry were reared naturally in a contained side channel. The resulting phenotypic differences between replicates, between rearing environments, and between cross types were compared. While there were few phenotypic differences noted between genetic groups reared in the same habitat, rearing environment played a significant role in smolt size, survival, swimming endurance, predator avoidance and migratory behaviour. The lack of any observed genetic differences between wild- and hatchery-born salmon may be due to the long-term mixing of these genotypes from hatchery introgression into wild populations, or conversely, due to strong selection in nature--capable of maintaining highly fit genotypes whether or not fish have experienced part of their life history under cultured conditions.

Copeland, T., D.A. Venditti, and B.R. Barnett. 2014. The Importance of Juvenile Migration Tactics to Adult Recruitment in Stream-Type Chinook Salmon Populations. *Transactions of the American Fisheries Society* 143:1460-1475.

Abstract: The existence of multiple migration tactics within a population has been observed for several fish species, and they may contribute differentially to adult recruitment. Relative contribution by juveniles using the same habitats on different schedules is variable; therefore, understanding and conserving this diversity should be important to fisheries managers. We investigated adult recruitment by two distinct juvenile migration tactics in several spawning populations of stream-type Chinook Salmon *Oncorhynchus tshawytscha* in Idaho: those leaving the spawning grounds as subyearlings during June through November (downstream rearing, or DSR, type) and those emigrating from natal areas 1 year after emergence (natal reach rearing, or NRR, type). The DSR type had greater juvenile abundance in all populations, although the NRR type exhibited better survival from the natal reach to the migratory corridor. The DSR type had greater survival from smoltification to adult return to freshwater compared with the NRR type. More DSR emigrants than NRR emigrants returned to freshwater as adults, although the difference was influenced by cohort and population. Adult recruits to stream-type Chinook Salmon populations in Idaho are comprised mostly of DSR emigrants, i.e., fish that dispersed from their natal habitats and reared in reaches downstream. This finding is ubiquitous, although the size of the effect depends on cohort and population. We demonstrated that juvenile Chinook Salmon in Idaho do indeed use downstream rearing habitats effectively, thereby increasing recruitment of adults back to the spawning gravels in these populations. This study illustrates how dispersive life histories are essential to achieve the full productive potential of migratory stream fish populations.

Gow, J.L., P. Tamkee, J. Heggenes, G.A. Wilson, and E.B. Taylor. 2011. Little impact of hatchery supplementation that uses native broodstock on the genetic structure and diversity of steelhead trout revealed by a large-scale spatio-temporal microsatellite survey. *Evolutionary Applications*, Volume 4, Issue 6, pages 763-782.

Abstract: Artificial breeding programs initiated to enhance the size of animal populations are often motivated by the desire to increase harvest opportunities. The introduction of non-native genotypes, however, can have negative evolutionary impacts. These may be direct, such as introgressive hybridization, or indirect via competition. Less is known about the effects of stocking with native genotypes. We assayed variation at nine microsatellite loci in 902 steelhead trout (*Oncorhynchus mykiss*) from five rivers in British Columbia, Canada. These samples were collected over 58 years, a time period that spanned the initiation of native steelhead trout broodstock hatchery supplementation in these rivers. We detected no changes in estimates of effective population size, genetic variation or temporal genetic structure within any population, nor of altered genetic structure among them. Genetic interactions with nonmigratory *O. mykiss*, the use of substantial numbers of primarily native broodstock with an approximate 1:1 male-to-female ratio, and/or poor survival and reproductive success of hatchery fish may have minimized potential genetic changes. Although no genetic changes were detected, ecological effects of hatchery programs still may influence wild population productivity and abundance. Their effects await the design and implementation of a more comprehensive evaluation program.

Harnish, R.A., R. Sharma, G.A. McMichael, R.B. Langshaw, and T.N. Pearsons. 2014. Effect of hydroelectric dam operations on the freshwater productivity of a Columbia River fall Chinook salmon population. *Canadian Journal of Fisheries and Aquatic Sciences*, 71:602-615.

Abstract: Altering the timing and magnitude of discharge fluctuations can minimize the adverse effects of operating hydroelectric dams on the productivity of downstream salmon populations. Hydroelectric operations at Priest Rapids Dam during the mid-1970s resulted in dewatering of fall Chinook salmon (*Oncorhynchus tshawytscha*) redds, causing mortality of intragravel life stages. Since then, a series of operational constraints have been implemented at Priest Rapids Dam to reduce the effects of discharge fluctuations on the population of fall Chinook salmon that spawns and rears downstream from the dam. Initial protections that focused on preventing redd dewatering were subsequently increased to include postemergence life stages. We used stock–recruit analyses to identify changes to the population’s freshwater productivity that occurred over a 30-year period and coincided with changes to dam operations. We observed a 217% increase in productivity that corresponded with constraints enacted to prevent redd dewatering and an additional 130% increase that coincided with enactment of constraints to limit stranding and entrapment of juveniles. The information gained from this study may be used to guide efforts elsewhere to mitigate the effects of hydroelectric dam operations on downstream fish populations.

Haskell, C.A., K.F. Tiffan, and D.W. Rondorf. 2013. The Effects of Juvenile American Shad Planktivory on Zooplankton Production in Columbia River Food Webs. *Transactions of the American Fisheries Society*, 142: 606-620.

Abstract: Columbia River reservoirs support a large population of nonnative American Shad *Alosa sapidissima* that consume the zooplankton that native fishes also rely on. We hypothesized that the unprecedented biomass of juvenile American Shad in John Day Reservoir is capable of altering the zooplankton community if these fish consume a large portion of the zooplankton production. We derived taxon-specific estimates of zooplankton production using field data and a production model from the literature. Empirical daily ration was estimated for American Shad and expanded to population-level consumption using abundance and biomass data from hydroacoustic surveys. *Daphnia* spp. production was high in early summer but declined to near zero by September as shad abundance increased. American Shad sequentially consumed *Daphnia* spp., copepods, and *Bosmina* spp., which tracked the production trends of these taxa. American Shad evacuation rates ranged from 0.09 to 0.24/h, and daily rations ranged from 0.008 to 0.045 g·g⁻¹·d⁻¹ (dry weight) over all years. We observed peak American Shad biomass (45.2 kg/ha) in 1994, and daily consumption (1.6 kg/ha) approached 30% (5.3 kg/ha) of zooplankton production. On average, American Shad consumed 23.6% of the available zooplankton production (range, <1–83%). The changes in the zooplankton community are consistent with a top-down effect of planktivory by American Shad associated with their unprecedented biomass and consumption, but the effects are likely constrained by temperature, nutrient flux, and the seasonal production patterns of zooplankton in John Day Reservoir. American Shad add to the planktivory exerted by other species like *Neomysis mercedis* to reduce the capacity of the reservoir to support other planktivorous fishes. The introduction of American Shad and other nonnative species will continue to alter the food web in John Day Reservoir, potentially affecting native fishes, including Pacific salmon *Oncorhynchus* spp.

Hinrichsen, R.A., D.J. Hasselman, C.C. Ebbesmeyer, and B.A. Shields. 2013. The Role of Impoundments, Temperature, and Discharge on Colonization of the Columbia River Basin, USA, by Nonindigenous American Shad. *Transactions of the American Fisheries Society*, 142: 887-900.

Abstract: Ecologists have become increasingly aware of the combined effects of habitat disturbance and climate change on the establishment and proliferation of invasive species. Long-term data on the population of the invasive American Shad *Alosa sapidissima* in the U.S. portion of the Columbia River basin provide an opportunity to examine how habitat disturbances affect the abundance and spatial distribution of an invasive species in a heavily modified environment. After the establishment of American Shad in the Columbia River in the late 1800s, the drainage was transformed from its natural lotic state to a series of reservoirs, with concomitant changes to discharge and temperature regimes, which are confounded by climate change. As the Columbia River was dammed, American Shad extended its range and increased in abundance. A large and rapid increase in spawning population abundance (recruits per spawner = 63) followed completion of The Dalles Dam in 1957, which inundated Celilo Falls, a natural barrier to upriver American Shad migration. Regressions revealed that the annual percentage of American Shad migrating upstream from McNary Dam varied with water temperature and discharge ($R^2 = 0.72$), but not population density. When Atlantic coast rivers were dammed, however, American Shad lost spawning habitat and declined in abundance. Understanding the rapid colonization of the Columbia River by American Shad may reveal ways to help American Shad recolonize rivers where they are native. Understanding the roles of water temperature and discharge may allow us to project effects of climate change on the future distribution and abundance of American Shad in the Columbia River basin. Our results suggest that dam construction and alterations to the temperature and discharge regimes of the Columbia River have contributed to the increase in abundance and spatial distribution of American Shad. These changes might have improved the reproductive success of American Shad by providing access to additional spawning grounds and creating suitable juvenile rearing conditions.

Hoffnagle, T.L., R.W. Carmichael, K.A. Frenyea, and P.J. Keniry. 2008. Run timing, spawn timing, and spawning distribution of hatchery- and natural-origin spring Chinook salmon in the Imnaha River, Oregon. *North American Journal of Fisheries Management* 28:148-164.

Abstract: We evaluated 16 years (1990–2005) of weir collection and spawning ground survey data to examine differences in run timing, spawn timing, and spawning distribution between naturally and hatchery-reared Chinook salmon *Oncorhynchus tshawytscha* in the Imnaha River, Oregon, and to look for changes in these variables over time. We compared run timing based on arrival time at the weir and found that naturally reared Chinook salmon arrived earlier than hatchery-reared fish in all 16 years. Carcasses of naturally reared fish of either or both sexes were recovered on the spawning grounds earlier than carcasses of hatchery-reared fish for all years combined and during 5 of 16 years, indicating earlier spawning by naturally reared fish. We compared spawning distribution using the percent of female carcasses recovered in each spawning ground survey reach. The percent recovery of the carcasses of naturally reared females was greater in reaches above the weir than below the weir and these carcasses were farther upstream than those of hatchery-reared females. For females of hatchery origin, carcasses were more commonly found in reaches closer to and below the weir (the smolt release location). Alternate management strategies designed to improve the maintenance of genetic integrity and life history characteristics of the Imnaha River Chinook salmon

population should be considered, implemented, and evaluated. Collection strategies should be modified to ensure that the hatchery broodstock is representative of the entire natural run, and release strategies should be developed to promote a spawning distribution of hatchery adults that mimics the distribution of natural Imnaha River Chinook salmon.

Hughes, R.M., S. Dunham, K.G. Maas-Hebner, J.A. Yeakley, C. Schreck, M. Harte, N. Molina, C.C. Schock, V.W. Kaczynski, and J. Schaeffer. 2014. A review of urban water body challenges and approaches: (1) rehabilitation and remediation. *Fisheries*, 39:18-29.

Abstract: We review how urbanization alters aquatic ecosystems, as well as actions that managers can take to remediate urban waters. Urbanization affects streams by fundamentally altering longitudinal and lateral processes that in turn alter hydrology, habitat, and water chemistry; these effects create physical and chemical stressors that in turn affect the biota. Urban streams often suffer from multiple stressor effects that have collectively been termed an “urban stream syndrome,” in which no single factor dominates degraded conditions. Resource managers have multiple ways of combating the urban stream syndrome. These approaches range from whole-watershed protection to reach-scale habitat rehabilitation, but the prescription must be matched to the scale of the factors that are causing the problem, and results will likely not be immediate because of lengthy recovery times. Although pristine or reference conditions are far from attainable, urban stream rehabilitation is a worthy goal because appropriate actions can provide ecosystem improvements as well as increased ecosystem service benefits for human society.

Johnson, L., B. Anulacion, M. Arkoosh, O.P. Olson, C. Sloan, S.Y. Sol, J. Spromberg, D.J. Teel, G. Yanagida, and G. Ylitalo. 2013. Persistent Organic Pollutants in Juvenile Chinook Salmon in the Columbia River Basin: Implications for Stock Recovery. *Transactions of the American Fisheries Society*, 142: 21-40.

Abstract: Among the populations of Pacific salmon and steelhead *Oncorhynchus mykiss* (anadromous Rainbow Trout) that inhabit the Columbia River basin there are currently 13 Evolutionarily Significant Units listed as threatened or endangered under the U.S. Endangered Species Act. While habitat loss, dams, overharvest, and climate change have been implicated in declining abundance of Chinook Salmon *O. tshawytscha* in the Columbia River, chemical contaminants represent an additional, yet poorly understood, conservation threat. In this study we measured concentrations of persistent organic pollutants in juvenile Chinook Salmon from various Columbia River stocks and life history types to evaluate the potential for adverse effects in these threatened and endangered fish. Polychlorinated biphenyls (PCBs) and dichlorodiphenyltrichloroethane (DDTs), recognized contaminants of concern in the Columbia basin, are the primary focus of this paper; other contaminants found in these fish, such as polybrominated diphenyl ethers and polycyclic aromatic hydrocarbons, are described in other publications. We frequently detected PCBs and DDTs in juvenile salmon and salmon diet samples from the lower Columbia River and estuary. In some cases, concentrations in salmon were above estimated thresholds for effects on growth and survival. The tidal freshwater portion of the estuary, between Portland, Oregon, and Longview, Washington, appeared to be an important source of contaminants for juvenile salmon and a region in which salmon were exposed to toxicants associated with urban development and industrial activity. Highest concentrations of PCBs were found in fall Chinook Salmon stocks with subyearling life histories, including populations from the upper Columbia and Snake rivers, which feed and rear in the tidal freshwater and estuarine portions of the river for

extended periods. Spring Chinook Salmon stocks with yearling life histories that migrate more rapidly through the estuary generally had low PCB concentrations, but high concentrations of DDTs. Lipid content was low (<1%) in many of the fish examined, contributing to high lipid-adjusted contaminants concentrations in some samples.

Lister, D.B. 2014. Natural Productivity in Steelhead Populations of Natural and Hatchery Origin: Assessing Hatchery Spawner Influence. Transactions of the American Fisheries Society, 143: 1-16.

Abstract: Natural productivity, the number of natural-origin adult recruits per parent, is an important parameter for assessing population status of steelhead *Oncorhynchus mykiss* (anadromous Rainbow Trout) and Pacific salmon *Oncorhynchus* spp. listed under the U.S. Endangered Species Act. Hatchery-origin adults comprise a majority of many salmon and steelhead spawning populations. In such cases, the utility of natural productivity estimates is affected by uncertain reproductive fitness of hatchery spawners and by possible ecological or genetic interactions among hatchery and natural fish. This study examined options for analyzing population census data to assess hatchery spawner effects on natural productivity of mixed steelhead populations including spawners of hatchery and natural origin. It compared productivity in three mixed and reference (natural) population pairs, and estimated productivity as natural recruits per total spawners of natural and hatchery origin ($Rnat/Stot$) or as natural recruits per natural spawner ($Rnat/Snat$). Natural productivity estimated as $Rnat/Stot$ reflected hatchery program scale, not productive capacity of natal streams. This analytical approach masked natural production dynamics in populations with a major hatchery spawner proportion, and was therefore of limited use for determining hatchery spawner influence. Productivity estimated as $Rnat/Snat$ indicated similar productivity of reference and mixed populations, and an absence of hatchery spawner effect, in the case of (1) a large hatchery stray component, and (2) a hatchery supplementation program. In the third pairing, $Rnat/Snat$ productivity of the mixed population significantly exceeded that of the reference population, suggesting natural spawner abundance is below carrying capacity. Hatchery spawners contributed to natural productivity in that case, but in the presence of reduced natural spawner density. These findings suggest that hatchery spawners are unlikely to affect natural production of a mixed steelhead population unless natural spawner abundance is below carrying capacity.

Mackey, G., J.E. McLean, and T.P.Quinn. 2001. Comparisons of Run Timing, Spatial Distribution, and Length of Wild and Newly Established Hatchery Populations of Steelhead in Forks Creek, Washington. North American Journal of Fisheries Management 21: 717-724.

Synopsis: In Washington State, the approach to management of wild and hatchery steelhead trout *Oncorhynchus mykiss* has been to separate the timing of return and spawning by the two groups through selective breeding for early timing in hatchery fish. However, overlap in timing and spatial distribution could permit genetic and ecological interactions. To evaluate this management approach, we compared the timing, spatial distribution, and size of adult steelhead in the wild and newly established hatchery populations of Forks Creek, Washington. Hatchery fish tended to return and spawn about 3 months before wild fish but there was some temporal overlap. Radio-tracking indicated that the spatial distributions of the populations overlapped considerably, permitting interbreeding and ecological interactions. However, the hatchery fish tended to stay closer to the hatchery, consistent with olfactory imprinting on the hatchery's water supply. Wild females were

larger than hatchery females (median fork lengths were 670 and 644 mm, respectively), and wild males and females varied more in length than did hatchery fish of the same sex. In the first year in which naturally spawned offspring of hatchery fish might have returned, we observed a marked increase in early-returning unmarked (i.e., naturally spawned) adults, suggesting that some hatchery fish spawned successfully in the creek.

Meador, J.P. 2014. Do chemically contaminated river estuaries in Puget Sound (Washington, USA) affect the survival rate of hatchery-reared Chinook salmon? *Canadian Journal of Fisheries and Aquatic Sciences*, 71:162-180.

Abstract: This study examined the rate of survival for hatchery-reared, ocean-type juvenile Chinook salmon (*Oncorhynchus tshawytscha*) to the adult life stage in relation to contamination status for estuaries where they temporarily reside. The hypothesis tested here is that juvenile Chinook from Puget Sound (Washington, USA) area hatcheries exhibit differential survival as categorized by the state of contamination in their respective natal estuaries. Data were examined from 20 hatcheries that released fish to 14 local estuaries in the Greater Puget Sound area over 37 years (1972–2008). A parallel analysis was also conducted for coho salmon (*Oncorhynchus kisutch*) outmigrating from many of the same hatcheries. For all years combined, juvenile Chinook transiting contaminated estuaries exhibited an overall rate of survival that was 45% lower than that for Chinook moving through uncontaminated estuaries, which was confirmed when tested year by year. The results for coho originating from the same hatcheries and sharing a similar marine distribution indicated no substantial differences among estuaries. These observations have important implications for wild juvenile Chinook that spend more time in the estuary compared with hatchery-reared fish.

Meredith, C., B. Roper, and E. Archer. 2014. Reductions in Instream Wood in Streams near Roads in the Interior Columbia River Basin. *North American Journal of Fisheries Management*, 34:493-506.

Abstract: Despite the success of recent management efforts to reduce streamside logging, instream wood recovery may be limited by the presence of near-stream roads. We investigated the relationships between the presence of near-stream roads and the frequency and volume of different size-classes of wood in streams in the interior Columbia River basin. We developed models to evaluate the average reduction in instream wood for streams near roads (<30 m or 30–60 m). We compared this with the changes in wood frequency and volume related to changes in environmental conditions such as precipitation, bank-full width, gradient, and forest cover as well as to changes in grazing-related management. In order to extrapolate our findings to the entire study area, we used a GIS approach to determine the distance to roads for randomly selected sites throughout the study area. Sites <30 m from a road had 65 (26%) fewer pieces of total wood, 33 (34%) fewer pieces of coarse wood, 31 (37%) fewer pieces of pool-forming wood, and 37 m³ (42%) less wood volume per kilometer than sites >60 m from a road. We also observed significant reductions at sites 30–60 m from a road, but these were about half those documented for sites <30 m. Changes in environmental conditions and grazing intensity had effects similar to those of being near a road. Based on our GIS analysis, approximately 29% of the sites in the study area are within 60 m of a road, and this percentage is even greater if unroaded catchments are excluded. Our results provide strong evidence that the presence of roads has significantly reduced habitat conditions for salmonids in the interior

Columbia River basin and illustrate the need for road removal or relocation projects to increase wood in streams.

Milbrink, G., T. Vrede, L.J. Tranvik, and E. Rydin. 2011. Large-scale and long-term decrease in fish growth following the construction of hydroelectric reservoirs. *Canadian Journal of Fisheries and Aquatic Sciences*, 68:2167-2173.

Abstract: Hydroelectric reservoirs retain large volumes of water and have a global impact on sea level, elemental cycles, and biodiversity. Using data from a total of 90 historical and recent surveys in nine regulated and eight unregulated alpine and subalpine lakes, we show an additional large effect of reservoirs, i.e., that impoundment causes drastically decreased fish growth and thereby great negative consequences for inland fisheries in Scandinavia. Following a long period (40–65 years) after impoundment, the length and mass of Arctic charr (*Salvelinus alpinus*) of the single age class 4+ years was, on average, 35% and 72% lower, respectively, in impounded versus natural lakes in northern Scandinavia. The effect was stronger at higher altitudes and can be mitigated by addition of inorganic nutrients. We suggest that the decreased fish growth is a consequence of lowered ecosystem productivity, oligotrophication, caused by impoundment, resulting in erosion and loss of the littoral ecosystem as well as delayed flooding and leakage of nutrients from the riparian zone until after the growing season.

Nakamura, T. 2013. Effects of Flow Reduction on a Whitespotted Char Population in a Japanese Mountain Stream. *North American Journal of Fisheries Management* 33: 1142-1148.

Abstract: I evaluated the effects of long-term (about 270 d/year) and large-volume (83.3% at mean flow) reductions in stream flow on a population of Whitespotted Char *Salvelinus leucomaenis*. I compared a range of biological parameters (density, biomass, condition factor, and age composition) between populations of char in the free-flowing (above dam) and regulated (below dam) sections of a Japanese mountain stream over a 4-year period. The density and biomass of age-1 and older fish was significantly lower in the regulated section than in the free-flowing section: 32.8% reduction in density and 42.5% in biomass. The mean condition factor of age-1 and older fish was significantly lower in the regulated section. In addition, the percentage of age-2 and older fish in the total catch was significantly lower in the regulated section. Except for flow, the physical environment was similar in both the free-flowing and regulated sections. Thus, the changes I observed in the regulated section were likely caused by flow reduction. I hypothesize that a decrease in food availability associated with the reduction in flow caused the decrease in density and condition factor in the regulated section. I also speculate that an increase in density in the pools due to flow reduction resulted in increased aggression among conspecifics. In turn, this results in an increase in the emigration of individuals, particularly older and larger fish, in the regulated section. The decreases in the density, condition factor, and the number of older and larger fish following the reduction in flow probably explain the decrease in biomass in the regulated section.

Nielsen, J.L., S.M. Turner, and C.E. Zimmerman. 2011. Electronic tags and genetics explore variation in migrating steelhead kelts (*Oncorhynchus mykiss*), Ninilchik River, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, 68:1-16.

Synopsis: Fine-scale tag data on kelt movements, life history analyses, and genetics from this study suggest that steelhead have multiple migratory and reproductive phenotypes that contribute to reproductive success and population structure over time. Conservation and management of one or two reproductive phenotypes may not be sufficient in this complex species.

Nielsen, E.B. and J.L. Morace. 2014. Foodweb transfer, sediment transport, and biological impacts of emerging and legacy organic contaminants in the lower Columbia River, Oregon and Washington, USA: Contaminants and Habitat (ConHab) Project. *Science of the Total Environment*, 484:319-321.

Synopsis: The investigation began with scientific researchers measuring for contaminants, including pesticides, flame retardant compounds, and ingredients from common household products, in the water and osprey eggs at 10 different locations along the Columbia River. The study states that several chemicals have been found at levels that exceed screening level values in Oregon Department of Environmental Quality guidance. Along with human health concerns, these contaminants may also have an adverse effect on the river system's food web in general. Results show that fish become more stressed and contaminated further downstream in the Columbia River, as more urban runoff enters the river.

Perkin, J.S., Z.R. Shattuck, J.E. Gerken and T.H. Bonner. 2013. Fragmentation and Drought Legacy Correlate with Distribution of Burrhead Chub in Subtropical Streams of North America. *Transactions of the American Fisheries Society*, 142: 1287-1298.

Abstract: Burrhead Chub *Macrhybopsis marconis* is a species of special concern endemic to subtropical streams in south Texas. We documented life history attributes and historical patterns in abundance and distribution to aid in understanding range-wide declines of the species among the Colorado and Guadalupe-San Antonio River systems. Life history results suggest Burrhead Chub lives for 2 years, reaches sexual maturity at age-1, and spawns multiple clutches during March–September. Review of museum vouchers revealed Burrhead Chub is now missing from 26% of its historical range, including most impounded stream segments. There was a significant difference in the size of stream fragments for which Burrhead Chub is missing or still persists. Timing of many extirpations occurred after fragmentation and coincided with a record drought (1949–1959) when range-wide stream flows were exceedingly low during the Burrhead Chub reproductive season. Furthermore, extensive historical collections taken during 1950–1961 in the Guadalupe River revealed a decline in relative abundance in upstream reaches as the drought continued. Based on these data, we hypothesize that Burrhead Chub experienced range-wide declines associated with historical drought conditions in desiccated stream fragments. Following the drought, stream flows recovered but recolonization by Burrhead Chub was blocked by impoundments in many fragments. These findings support previous linkages between stream connectivity, flow magnitude, and the persistence of fish populations while providing insight into the mechanisms driving freshwater fish declines in the plains of North America.

Seamons, T.R., L. Hauser, K.A. Naish, and T.P. Quinn. 2012. Can interbreeding of wild and artificially propagated animals be prevented by using broodstock selected for a divergent life history? [Evolutionary Applications](#), 5:705-719.

Abstract: Two strategies have been proposed to avoid negative genetic effects of artificially propagated individuals on wild populations: (i) integration of wild and captive populations to minimize domestication selection and (ii) segregation of released individuals from the wild population to minimize interbreeding. We tested the efficacy of the strategy of segregation by divergent life history in a steelhead trout, *Oncorhynchus mykiss*, system, where hatchery fish were selected to spawn months earlier than the indigenous wild population. The proportion of wild ancestry smolts and adults declined by 10–20% over the three generations since the hatchery program began. Up to 80% of the naturally produced steelhead in any given year were hatchery/wild hybrids. Regression model selection analysis showed that the proportion of hatchery ancestry smolts was lower in years when stream discharge was high, suggesting a negative effect of flow on reproductive success of early-spawning hatchery fish. Furthermore, proportions of hybrid smolts and adults were higher in years when the number of naturally spawning hatchery-produced adults was higher. Divergent life history failed to prevent interbreeding when physical isolation was ineffective, an inadequacy that is likely to prevail in many other situations.

Snow, C.G., A.R. Murdoch, and T.H. Kahler. 2013. Ecological and Demographic Costs of Releasing Nonmigratory Juvenile Hatchery Steelhead in the Methow River, Washington. *North American Journal of Fisheries Management* 33: 1100-1112.

Abstract: We classified juvenile hatchery summer steelhead *Oncorhynchus mykiss* released from Wells Hatchery, Washington, from three brood years (2002–2004) as those that migrated volitionally (VM) from rearing ponds or as those that were forced out of rearing ponds after volitional migration concluded (NM). Fish were implanted with PIT tags prior to release and we used recreational angling equipment to recapture tagged fish to estimate the relative contribution rates of VM and NM release groups to the stream-resident population of juvenile hatchery summer steelhead in the Twisp River. We also evaluated the survival for each group from release to McNary Dam, and from release to adult return (SAR) at Bonneville and Wells dams on the Columbia River. Overall, we estimated that 82% of stream-resident hatchery juvenile summer steelhead originated from releases of NM fish. The probability of survival from release to McNary Dam was significantly greater for VM groups (mean, 0.4817; SE, 0.023) than for NM groups (mean, 0.2182; SE, 0.021) within each year. The mean SAR to Bonneville and Wells dams was 1.54% and 1.26%, respectively, for VM fish and 0.37% and 0.32%, respectively, for NM fish; the differences were significant between groups within each year. As an index of release strategy performance, VM releases resulted in one stream-resident fish recaptured for every 7.8 adults returned, while NM releases produced one stream-resident fish recaptured for every 0.48 adults returned. These results suggest that managers employ a volitional release strategy to significantly reduce the abundance of stream-resident juvenile hatchery steelhead by not releasing NM fish into waters inhabited by anadromous fishes, thereby reducing negative ecological interactions between hatchery residual steelhead and wild salmonids at little cost to adult returns.

Thériault, V., G.R. Moyer, and M.A. Banks. 2010. Survival and life history characteristics among wild and hatchery coho salmon (*Oncorhynchus kisutch*) returns: how do unfed fry differ from smolt releases? *Canadian Journal of Fisheries and Aquatic Sciences*, 67:486-497.

and

Thériault, V., G.R. Moyer, L.S. Jackson, M.S. Blouin, and M.A. Banks. 2011. Reduced reproductive success of hatchery coho salmon in the wild: insights into most likely mechanisms. *Molecular Ecology* 20:1860-1869.

Synopsis: Molecular parentage analysis was used to evaluate the lifetime reproductive success of hatchery- and natural-origin coho salmon allowed to reproduce in the wild in the Umpqua River Basin, Oregon. Relative reproductive success for hatchery-origin fish released as smolts and returning as age-3 adults was significantly less than that of natural-origin coho in 2 of 3 study brood years for females and in all 3 study broods for males. However, returning hatchery-origin adult coho (released as smolts) were significantly smaller than natural-origin returns. The smaller size of adult returns could explain the observed differences in reproductive success (e.g., smaller females could have fewer eggs and smaller males may not compete as successfully for mates). The study found no significant difference in reproductive success between hatchery-origin fish with two hatchery-origin parents and those with two natural-origin parents. This indicates that any differences in reproductive success in the wild were not passed on to progeny (i.e., observed differences were likely due to environmental and not genetic effects).

Tiffan, K.F. and W.P. Connor. 2011. Distinguishing between Natural and Hatchery Snake River Fall Chinook Salmon Subyearlings in the Field Using Body Morphology. *Transactions of the American Fisheries Society*, 140: 21-30.

Abstract: We used body morphology to distinguish between natural- and hatchery-origin subyearling fall Chinook salmon *Oncorhynchus tshawytscha* in rearing areas of the Snake River and at a downstream dam during seaward migration. Using subjective eye and body shape characteristics, field personnel correctly classified 88.9-100% of natural subyearlings (N = 626) and 90.0-100% of hatchery subyearlings (N = 867) in rearing areas from 2001 to 2008. The morphological characteristics used by these personnel proved to have a quantitative basis, as was shown by digital photography and principal components analysis. Natural subyearlings had smaller eyes and pupils, smaller heads, deeper bodies, and shorter caudal peduncles than their hatchery counterparts during rearing and at the dam. A discriminant function fitted from this set of morphological characteristics classified the origin of fish during rearing and at the dam with over 97% accuracy. We hypothesize that these morphological differences were primarily due to environmental influences during incubation and rearing because it is highly probable that a large portion of the natural juveniles we studied were the offspring of hatchery x hatchery mating in the wild. The findings in this paper might provide guidance for others seeking to differentiate between natural and hatchery fish.

Tiffan, K.F., J.M. Erhardt, and S.J. St. John. 2014. Prey Availability, Consumption, and Quality Contribute to Variation in Growth of Subyearling Chinook Salmon Rearing in Riverine and Reservoir Habitats. *Transactions of the American Fisheries Society*, 143: 219-229.

Abstract: We examined prey availability, prey consumed, and diet energy content as sources of variation in growth of natural fall Chinook Salmon *Oncorhynchus tshawytscha* subyearlings rearing in riverine and reservoir habitats in the Snake River. Subyearlings in riverine habitat primarily consumed aquatic insects (e.g., Diptera, Ephemeroptera, Trichoptera), of which a high proportion was represented by adult, terrestrial forms. In the reservoir, subyearlings also consumed aquatic insects but also preyed heavily at times on nonnative lentic amphipods *Corophium* spp. and the

mysid *Neomysis mercedis*, which were absent in riverine habitats. The availability of prey was typically much higher in the reservoir due to *N. mercedis* often composing over 90% of the biomass, but when this taxon was removed from consideration, biomass estimates were more often higher in the riverine habitat. Subyearling diets during 2009–2011 were generally 17–40% higher in energy in the riverine habitat than in the reservoir. Observed growth in both length and weight were significantly higher in the riverine habitat than in the reservoir. Little is known about how temporal and spatial changes in the food web in large river landscapes influence populations of native anadromous fishes. Our results provide a glimpse of how the spread and establishment of nonnative prey species can reduce juvenile salmon growth in a large river impoundment, which in turn can affect migration timing and survival.

Torterotot, J-B, C. Perrier, N.E. Bergeron, and L. Bernatchez. 2014. Influence of Forest Road Culverts and Waterfalls on the Fine-Scale Distribution of Brook Trout Genetic Diversity in a Boreal Watershed. *Transactions of the American Fisheries Society*, 143: 1577-1591.

Abstract: Habitat fragmentation has become an increasing concern in conservation biology and is of prime importance with the expansion of forest road networks toward boreal and arctic regions. The aim of this study was to evaluate the effects of artificial and natural barriers to fish movement on the fine-scale distribution of genetic diversity in Brook Trout *Salvelinus fontinalis*. We genotyped 995 individuals sampled from 25 locations in a boreal watershed fragmented by culverts and natural waterfalls. Using a landscape genetics approach, we tested whether the presence of both types of barrier resulted in decreased genetic diversity and increased divergence within isolated locations. Results showed that genetic divergence was enhanced between sites separated by barriers and that genetic diversity was reduced within sites located upstream of barriers. Moreover, the observed changes in levels of divergence and diversity were correlated with the number of barriers. Overall, our results suggested that the effects of culverts and natural waterfalls were similar. To our knowledge, this is the first study illustrating the effects of forest road culverts and natural waterfalls on the distribution of genetic diversity in Brook Trout within a boreal watershed. We discuss our results in the context of boreal forest road network expansion and in light of the need to better understand the potential impacts of road infrastructure on the long-term persistence of fish populations.

Ward, E.J., J.H. Anderson, T.J. Beechie, G.R. Pess, and M.J. Ford. 2015. Increasing hydrologic variability threatens depleted anadromous fish populations. *Global Change Biology*, doi: 10.1111/gcb.12847.

Abstract: Predicting effects of climate change on species and ecosystems depend on understanding responses to shifts in means (such as trends in global temperatures), but also shifts in climate variability. To evaluate potential responses of anadromous fish populations to an increasingly variable environment, we performed a hierarchical analysis of 21 Chinook salmon populations from the Pacific Northwest, examining support for changes in river flows and flow variability on population growth. More than half of the rivers analyzed have already experienced significant increases in flow variability over the last 60 years, and this study shows that this increase in variability in freshwater flows has a more negative effect than any other climate signal included in our model. Climate change models predict that this region will experience warmer winters and more variable flows, which may limit the ability of these populations to recover.

Background / Additional Reading

Bosch, W. J. 2004. The promise of hatchery-reared fish and hatchery methodologies as tools for rebuilding Columbia Basin salmon runs: Yakima Basin overview. American Fisheries Society Symposium 44:151-160.

Synopsis: Overview of Yakima Basin Projects and why supplementation is necessary.

Brannon, E. L., D. F. Amend, M. A. Cronin, J. E. Lannon, S. LaPatra, W. J. McNeil, R. E. Noble, C. E. Smith, A. J. Talbot, G. A. Wedemeyer, and H. Westers. 2004. The controversy about salmon hatcheries. Fisheries 29(9): 12-30.

Synopsis: Reviews literature that has been often cited to show the negative effects of hatcheries and explains how poor experimental designs or the use of inappropriate (e.g., non-local origin, multiple generations in hatcheries) hatchery stocks contributed to the negative results reported in these papers. Documents many examples where fish from traditional hatcheries have spawned successfully and done well under natural conditions.

Columbia River Inter-Tribal Fish Commission. 1995. WY-KAN-USH-MI WA-KISH-WIT Spirit of the Salmon. The Columbia River Anadromous Fish Restoration Plan, Vol. I and II. Portland, Oregon.

Columbia River Inter-Tribal Fish Commission. 2000. WY-KAN-USH-MI WA-KISH-WIT Spirit of the Salmon. The Columbia River Anadromous Fish Restoration Plan Update, Vol. I and II. Portland, Oregon.

Dompier, D. W. 2005. The Fight of the Salmon People: Blending Tribal Tradition with Modern Science to Save Sacred Fish. Xlibris Corporation, www.Xlibris.com.

Gallinat, M. P., and L. A. Ross. 2008. Tucannon River Spring Chinook Salmon Hatchery Evaluation Program, [2007 Annual Report](#). WDFW, Olympia, WA.

Narum, S.R., T.L. Schultz, D.M. Van Doornik, and D. Teel. 2008. Localized genetic structure persists in wild populations of Chinook salmon in the John Day River despite gene flow from outside sources. Transactions of the American Fisheries Society 137:1650-1656.

Abstract: Samples of Chinook salmon *Oncorhynchus tshawytscha* collected from four spawning areas in the John Day River, Oregon (n = 330), were genotyped with 13 microsatellite loci to test for bottlenecks and temporal stability within sites as well as genetic differentiation among sites, and to estimate gene flow from outside populations. Since the John Day River has never been stocked with hatchery-reared fish, this study provided the opportunity to evaluate the genetic integrity and structure of Chinook salmon in a wilderness area amid many hatchery-supported populations in the Columbia River. No tests for bottlenecks (Wilcoxon tests for heterozygosity excess) were significant, and the temporal variation was slight and not significant within any spawning reach except for the

collections from the Middle Fork John Day River. Overall, the genetic distance estimates suggest that there are three distinct subpopulations in the John Day River, namely, those in (1) the North Fork John Day River (including Granite Creek), (2) the Middle Fork John Day River, and (3) the upper main-stem John Day River. These genetic relationships were supported by results from a neighbor-joining dendrogram. Assignment tests indicate that out-of-basin straying occurs throughout the John Day River, the largest percentage of strays going to the North Fork John Day River. Immigration may have acted to avert genetic bottlenecks and maintain genetic diversity in populations with fluctuating census size. Yet the genetic substructure of the Chinook salmon in the John Day River indicates natural reproduction from philopatric individuals, possibly with higher reproductive success than immigrants. The evidence presented here elucidates the balance of philopatry and dispersal acting to maintain genetic diversity and localized structure among the Chinook salmon of the John Day River.

Perrier, C., G. Evanno, J. Belliard, R. Guyomard, and J-L. Baglinière. 2010. Natural recolonization of the Seine River by Atlantic salmon (*Salmo salar*) of multiple origins. *Canadian Journal of Fisheries and Aquatic Sciences*, 67(1): 1-4.

Abstract: The restoration of previously extinct salmon populations is usually achieved with stocking programmes, but natural recolonization can also occur through the straying of individuals from nearby populations. Here we investigated the origin of Atlantic salmon (*Salmo salar*) that recently recolonized the Seine River (France). The degradation of this river had led to the extinction of the population, but since the 1990s, the water quality has greatly improved. Although no stocking was performed, 162 individual salmon were recently observed by video-counting. Seven fish were sampled for morphological and genetic analyses. These individuals were genotyped at 17 microsatellites markers and their probable source populations were identified using baseline samples from regional and distant populations. Four of the sampled individuals were grilse and three were multi-sea-winter fish. Genetic analyses revealed that the fish partly originated from a nearby stock but also from distant populations, suggesting long-distance straying. This natural recolonization of a large river by strayers from several origins is discussed in terms of population sustainability and management.

References

- RASP (Regional Assessment of Supplementation Planning). 1992. Supplementation in the Columbia River Basin, Parts 1-5. Report DOE/[BP 01830-11](#), Bonneville Power Administration.
- RIST (Recovery Implementation Science Team). 2009. Hatchery Reform Science. A review of some applications of science to hatchery reform issues. More information on the RIST, as well as an electronic copy of this report, can be found at <http://www.nwfsc.noaa.gov/trt/index.cfm>.

CRITFC Comments on Mitchell Act DEIS, Review of Fitness Studies

Review of Studies Providing Measures of Relative Fitness and Relative Reproductive Success

Analyses and the proposed alternatives presented in draft environmental impact statement (DEIS) for the Mitchell Act (MA) rely heavily on use of the proportionate natural influence (PNI) and the proportion of hatchery-origin spawners (pHOS) standards proposed by the Hatchery Scientific Review Group (HSRG 2009). Strict application of these standards can put severe restrictions on the scale of hatchery programs, and on the numbers of hatchery-origin fish that are permitted to augment abundance of a natural spawning population. Hence, all of the proposed alternatives in the MA DEIS, other than Status Quo, require moderate to substantial reductions in current and proposed hatchery programs in the basin.

Justification for the PNI and pHOS standards are based on the presumption that hatchery rearing will affect a substantial negative effect on fitness of a natural population that is receiving hatchery-origin adults, and that this effect is genetically-based. This presumption is derived from assessment of results of studies that provide quantified measures of relative fitness (RF) or relative reproductive success (RRS) of the hatchery-origin (HO) versus natural-origin (NO) fish. In particular, two recent studies of Hood River steelhead (Araki et al. 2007b and 2009) are widely cited as “proof” that hatchery programs have dramatically large deleterious effects on natural population productivity, and that even over a small number of generations, these effects will rapidly accumulate so as to render natural fitness of the affected population significantly reduced.

We feel that this conclusion is exaggerated and misrepresents the scientific data that exists across the breadth of studies that have examined the issue. Further, focus on this single aspect to drive hatchery management policy in the Columbia basin ignores benefits that hatcheries may have on other viable salmonid population (VSP) parameters – abundance, spatial structure and diversity (McElhany et al. 2000), and completely disregards the associated legal, social and political issues related to fisheries and mitigation responsibilities for operation of the hydrosystem. It is for these reasons, as summarized in the cover letter to our comments, that the tribes recommend that NOAA not proceed on developing a preferred alternative and a final environmental impact statement based on the proposed document.

In this document, however, we concentrate solely on the rationale behind our conclusion that the presumption that use of hatcheries to supplement natural salmonid populations will significantly depress population fitness is exaggerated and misrepresents the available data. We provide synopses of all (to our knowledge) currently available information from studies of anadromous salmonids that have derived quantified measures of RF and RRS, then have summarized these data in a table and series of figures. The data were compiled from published manuscripts, technical reports and oral presentations made at scientific meetings. Results for several of these reports were previously presented within Table 1 of Araki et al. (2008) and/or in Figure 4 of the report Hatchery Reform Science by the Recovery Implementation Science Team (RIST 2009),

copied below. Information from additional studies, many of them recently described for ongoing programs, are also presented.

Of note, substantial caution is required in interpreting these results, especially when illustrated together within a graph such as RIST (2009) Figure 4, whose format was followed in the summary graphs. The data are not necessarily directly comparable. The methodologies used to obtain the RF and RRS measures differ greatly among studies, and the management schemes followed by the hatchery programs vary dramatically in terms species, source of the broodstock, broodstock management, and hatchery rearing and juvenile release practices. These issues and how they affect the resulting RF/RRS data are described in more detail below, followed by the synopses, and table and graphs. a) Some of the measures are of RF, representing differential survival between various life stages of HO and NO fish, while other studies are of RRS, involving differential natural spawning success plus survival to various life stages. b) Results for six different species are represented among these studies. However, the substantial differences in life histories among species will undoubtedly have varying impact on how hatchery rearing may affect reproductive fitness and survival. For example, except for one study each of Atlantic and Chinook salmon, the studies (limited to those using local broodstock sources) that provided the lowest measures of RF/RRS were of steelhead (Figures 2a and 2b). c) Some of the studies compare performance of hatchery stocks from non-local sources – often following several generations of deliberate selection for altered run/spawn timing, growth and/or behaviors relative to the natural population to which they were compared. When the objective is to assess effects of Supplementation hatchery programs (e.g., as described by Cuenco et al. 1993) for the purposes of rebuilding depressed populations, results from these studies using non-local hatchery stocks must necessarily be excluded (as was done in Figures 3 and 4). d) Some of the studies involve hatchery programs which followed segregated broodstock management (only HO adults were incorporated into the broodstock), while others integrated NO fish into the broodstock (from small proportions to 100%, depending on the program) each generation. The two approaches will have obvious impacts on the extent to which genetically-based impacts on fitness may accumulate over generations. e) The majority of the studies are indicated as “Confounded” within the “Effect on RF/RRS” column in the summary table. That is, results of the comparison between performance of HO and NO fish does not solely represent a genetically-based effect on fitness, but instead represents possible genetic effects plus confounding non-heritable environmental effects associated with the different spawning and juvenile life histories experienced by the fish being compared. If it possible to parse out the environmental effects from the overall RF/RRS measure, the resulting estimate for heritable RF/RRS would be closer to 1.0, and the data points for measures <1.0 would shift upwards. To illustrate this, the RF and RRS data from studies indicated as Confounded and < 1.0 were recalculated on the presumption that 50% of this difference was due to non-genetic effects. Graphing of the modified data (Figures 4a and 4b) provides a much more moderated impression of the magnitude might be of a deleterious effect of hatchery rearing that could accumulate (due to its heritable/genetic nature) over generations. Of note, even in those studies whose “Effect on RF/RRS” in the summary table is indicated

as “Genetic” (studies whose “common garden” designs permitted comparison of RF or RRS of fish with similar immediate rearing histories, but with differential natural versus hatchery genetic backgrounds), there are invariably additional confounding environmental effects that may have influenced results of the studies, typically to the detriment of the HO fish.

f) In Figures 3 and 4, results from the Araki et al. (2007a and b, 2009) for Hood River (HR) steelhead are differentiated from those of other studies using local source broodstock. These results from Araki et al 2007b and 2009 (although not those from 2007a, as they indicate non-significant effects on natural fitness following a generation of hatchery rearing), as indicated above, have been widely referenced to support the view that hatchery effects on natural population fitness are substantially negative and threaten their viability, and that hatchery programs must therefore be reduced in scope and duration. However, examining the compiled results for all of the studies presented here, it is evident that the RRS measures for HR steelhead are at the extreme low end of the range for reported data. In light of the “outlier” nature of these HR steelhead data, normal scientific caution requires that they be noted as cause for concern, but that to the extent that one is permitted to make generalized statements, it would be that the magnitude of heritable effects of a properly managed hatchery supplementation program will likely of a much reduced magnitude relative to that indicated by the HR steelhead studies.

g) Again, a reminder is appropriate that recommendations on how salmonid hatchery programs are scaled and managed – in particular for supplementation of depressed natural stocks - must not be based solely on possible deleterious fitness effects, but must also consider counteracting positive effects on the other VSP parameters - population abundance, diversity and spatial structure. Additionally, decisions of how best to manage hatchery programs within the Columbia basin must not be made in isolation from the social, political and legal issues associated with fisheries mitigation and alternative actions (restoration of freshwater habitat, changes in hydrosystem management to reduce mortality, and harvest management) that might be effective in rebuilding the basin’s salmon stocks.

In view of the substantial variation among study designs and the great dispersion of the resulting RF/RRS data, one cannot justifiably draw a general conclusion as to the magnitude of the effect that hatchery rearing may have on productivity of a natural population. The data do imply, however, that appropriate management of a hatchery program can diminish negative effects on reproductive fitness, both of an environmental and a genetic basis. Instead of imposing a single set of management standards (PNI and pHOS), hatchery programs need to be designed on a species and river-specific basis. The management plans must also be adaptive in nature so as to respond to environmental variation and to changes in population VSP parameters.

Abbreviations: H - hatchery
W - wild HO - hatchery-
origin NO - natural-origin

References

Hatchery Scientific Review Group (HSRG). 2009. Columbia River hatchery reform system-wide report. (http://www.hatcheryreform.us/hrp/reports/system/welcome_show.action)

McElhany, P., M. H. Ruckelshaus, M. J. Ford, T. C. Wainwright, and E. P. Bjorkstedt. 2000. Viable salmonid populations and the recovery of evolutionarily significant units. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-42,156 p.

(<http://www.nwfsc.noaa.gov/publications/techmemos/tm42/tm42.pdf>)

Recovery Implementation Science Team (RIST). 2009 RIST (Recovery Implementation Science Team). 2009. Hatchery Reform Science. National Marine Fisheries Service (NMFS) Northwest Regional Office, Salmon Recovery Division, Portland OR.

(<http://www.nwfsc.noaa.gov/trt/index.cfm>)

Table 1 - Araki et al. 2008 Evolutionary Applications 1(2): 342-355

Table 1. Conditions, methodologies and estimated relative fitness (RF) in studies that compared the relative fitness hatchery and wild salmonids. Genetic effects are presumed where hatchery and natural adults were artificially spawned and the fitness of the resulting offspring was compared (assumes environmentally-mediated maternal effects of rearing from egg to smolt have no effect on offspring fitness). All paternal effects are also assumed to be genetic (assuming no grandparental maternal effects). Genetic and environmental effects are considered confounded where hatchery-born and wild-born fish are directly compared because they experienced very different juvenile environments. The duration of the hatchery fish in captivity is expressed in the number of generations in captivity (NGC), which was approximated as years of hatchery operation divided by modal age at sexual maturity. In integrated programs, where either wild fish are spawned in the hatchery or hatchery-origin fish spawn in the natural environment, the ancestry of hatchery and wild fish may differ by only a single generation, even if the duration of the hatchery program is much longer.

I. Completed Study	Species	Life History segment	Method	Effect on RF	NGC	RF*
Broodstock of nonlocal origin						
Chilcote et al. (1986)	Steelhead (<i>Oncorhynchus mykiss</i>)	Lifetime	Group genetic mark	Confounded	6	0.13
Leider et al. (1990)						
Fleming and Gross (1993)	Coho (<i>O. kisutch</i>)	Adult-to-fry	Individual behavior	Confounded	5	(m) 0.62 (f) 0.82
McLean et al. (2003)	Steelhead	Lifetime	Mixed stock analysis	Confounded	10+	0.02–0.11
McLean et al. (2004)	Steelhead	Adult-to-smolt	Mixed stock analysis	Confounded	10+	0.04–0.07
Araki et al. (2007a)	Steelhead (winter-run)	Lifetime	Pedigree	Confounded	10+	(m) 0.06 (f) 0.11
Araki et al. (2007a)	Steelhead (summer run)	Lifetime	Pedigree	Confounded	10+	(m) 0.35 (f) 0.37
Scenario 2: Local origin						
Reisenbichler and McIntyre (1977)	Steelhead	Egg-to-parr	Group genetic mark	Genetic	2	0.8
Reisenbichler and Rubin (1999)	Steelhead	Fry to age-1	Group genetic mark	Genetic	6	0.8
Fleming et al. (1997)	Atlantic salmon (<i>Salmo salar</i>)	Adult to fry	Individual behavior	Environment	1	(m) 0.48 (f) ~1.0
Dannewitz et al. (2004)	Brown trout (<i>S. trutta</i>)	Egg-to-parr	Pedigree	Genetic	7	1.27
McGinnity et al. (2004)	Atlantic salmon	Egg-to-adult	Pedigree	Genetic	5	~1.0
Dahl et al. (2006)	Brown trout	Parr to parr (1 year in stream channel)	Nose tag	Genetic	7	~1.0
Ford et al. (2006)	Coho	Adult-to-smolt	Pedigree	Confounded	25	(m) 1.01 (f) 0.74
Araki et al. (2007a,b)	Steelhead (winter-run, integrated)	Lifetime	Pedigree	Confounded	1	(m) 0.70 (f) 0.88
					2	(m) 0.32 (f) 0.30
				Genetic	1 vs 2†	(m) 0.55 (f) 0.55

*m, male, f, female, when the relative fitness (RF) was estimated separately for each sex of parent.

†Hatchery fish having one wild parent and one first-generation hatchery parent (NGC-2) compared to hatchery fish having two wild parents (NGC-1).

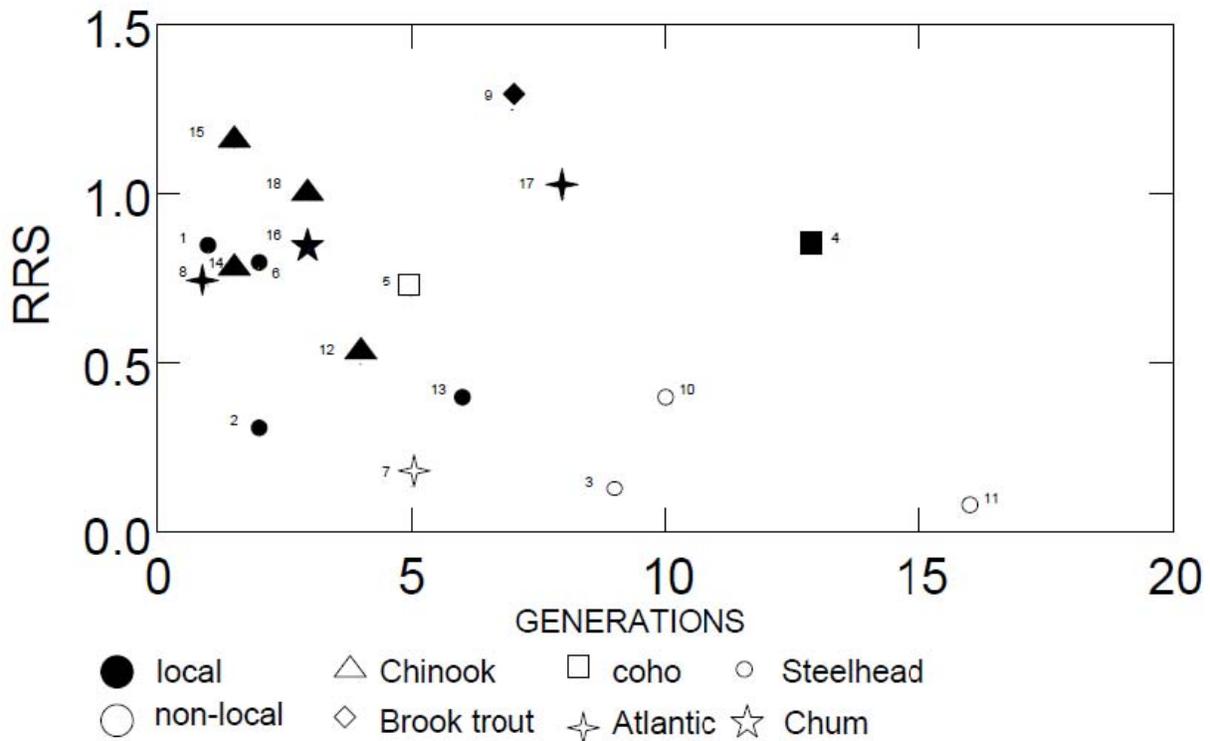
RIST Figure 4

Figure 4 – Summary of relative fitness estimates by species, broodstock origin, and generations in the hatchery (compiled by Berejikian, NWFSC). 1 - Araki et al. (2007b)), 2 - Araki et al. (2007b), 3 - Leider et al. (1990), 4 - Ford et al. (2006), 5 - Fleming and Gross (1993), 6 - Reisenbichler and McIntyre (1977), 7 - Fleming et al. (2000), 8 - Fleming et al. (1997), 9 - Dannewitz et al. (2003), 10 - Araki et al. (2007a), 11 - Araki et al. (2007a), 12 - Murdoch et al. (2008), 13 - Moran and Waples (2007), 14 - P. Moran (NWFSC, personal communication), 15 - P. Moran (NWFSC, personal communication), 16 – Berejikian et al. (2008), 17 - McGinnity et al. (1997.), 18 – Leth (2005).

Hatchery broodstock of Non-Local origin

Leider, S. A., P. L. Hulett, J. J. Loch, and M. W. Chilcote. 1990. Electrophoretic comparison of the reproductive success of naturally spawning transplanted and wild steelhead trout through the returning adult stage. *Aquaculture* 88:239-252.

(preceded by: Chilcote, M.W., S.A. Leider, and J.L. Loch. 1986. Differential reproductive success of hatchery and wild summer-run steelhead under natural conditions. *Transactions of the American Fisheries Society* 115:726-735.)

- Electrophoretically identifiable Skamania (out-of-basin, segregated) stock Steelhead smolts stocked into the Kalama River in 4 successive broodyears
- Returning adults, beginning 2 years later, identified, and smolt production (Chilcote et al 1986) then adult production (Leider et al 1990) estimated for naturally spawning Skamania stock versus wild Kalama stock
- Relative productivity of Skamania stock was 75-79% for adult-to-smolt production (originally reported as 28% by Chilcote?), and 11-13% for adult-to-adult production
- Note: Poorer performance of Skamania stock was to have been expected – this hatchery stock differed from the Kalama River steelhead in life history, including altered timing for adult return, spawning timing, timing of seaward migration, and number of years spent at sea. These changes were the result of generations of intentional artificial selection and stock mixing. Additionally, there is the confounding environmental factor of comparing natural spawning performance of two groups of fish with different juvenile life history experience – hatchery rearing versus natural rearing – which should bias results against HO fish.

Fleming, I. A., and M. R. Gross. 1993. Breeding success of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in competition. *Ecological Applications* 3:230-245.

- Adult Quinsam Hatchery coho (segregated for 4-5 generations) stocked into an artificial stream with 2 groups of wild returning adults from nearby rivers in 1988 and in 1989
- Time of capture and pre-stocking handling similar between stocks within years; fish were size-matched between stocks
- Compared spawning behaviors and estimated egg production per individual as a measure of breeding success
- Breeding success of hatchery females = 82%, and of hatchery males = 62% relative to wild
- Hatchery-reared females did experience greater delays in the onset of breeding, suffered more injuries, and nest site locations were significantly different from wild-reared females, but had a longer life span in the multiple density experiments. The delays in the onset of breeding and the longer life span may be due to their inability to directly compete with wild females for optimal territory, or could be a tactic to reduce the likelihood of nest superimposition
- Hatchery males in the multiple density experiments were more submissive, less aggressive, and incurred more injuries than did wild fish
- Note: RRS was evaluated in competition, therefore cannot determine if difference was attributable to competition and/or to inherent differences in productivity between stocks; is unclear if traits in hatchery stock had undergone directed selection during segregated

breeding. Additionally, there is the confounding environmental factor of comparing natural spawning performance of two groups of fish with different juvenile life history experience – hatchery rearing versus natural rearing – which should bias results against HO fish

McGinnity, P., Stone, C., Taggart, J.B., Cooke, D., Cotter, D., Hynes, R., McCamley, C., Cross, T. and A. Ferguson. 1997. Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: use of DNA profiling to assess freshwater performance of wild, farmed and hybrid progeny in a natural river environment. *J. Marine Sci.* 54: 998-1008.

- Study designed to control for confounding environmental factors, to compare eyed-egg to parr/smolt survival of progeny from wild versus farmed stock adults in a natural river
- Wild = native Burrishoole stock (Ireland), and Farmed = Norwegian Mowi strain (6 to 8 generations intense segregated selective breeding for net-pen culture)
- In 2 years (1993 and 1994), between 6 to 15 adults per stock (wild versus farmed) and per sex were factorially mated, and the eggs reared to the eyed-stage
- Known numbers of viable eye-eggs per cross were pooled, then placed in egg boxes and planted into a stream devoid of other salmon
- Parr sampled by electroshocking and smolts collected in traps
- Relative total number of juveniles collected: $W \times W > W \times H > H \times W > H \times H$; however, even the maximum difference ($H \times H = 83\%$ and 81% of $W \times W$) was not statistically different
- Note: By making the crosses artificially and out-planting viable eyed-eggs, the study design avoids confounding environmental effects of differential homing and spawning success and differential survival to the eyed-stage. The Farmed stock was of out-of-basin source and had been in segregated intensive selective breeding for 6 to 8 generations for net-pen rearing.

Fleming, I. A., K. Hindar, I. B. Mjølnerod, B. Jonsson, T. Balstad, and A. Lamberg. 2000. Lifetime success and interactions of farm salmon invading a native population. *Proceedings of the Royal Society, Series B Biology* 267:1517-1523.

- 22 out-of-basin Norway National Breeding Program farm stock adult Atlantic salmon and 17 native wild salmon placed upstream of weir in small (1 km) river for natural spawning in Nov 1993; fish were homozygous for alternative MEP-2 alleles;
- 0+ parr sampled by electrofishing fall 1994, and out-migrating smolts captured in trap in 1995 and 1996; and juveniles genotyped for MEP-2
- The proportions of WW, WH and HH were similar for parr versus smolt (therefore no observation of progressive decrease in productivity beyond parr); essentially all hybrid fish had W mothers
- Relative fitness: $WW = 68\%$, $WH = 26\%$, $HH = 6\%$, approximately; therefore $RRS \approx 18\%$ [= $(6 \times 2 + 26)/22 / (68 \times 2 + 26)/17 = 38/22 / 162/17$], although the manuscript indicates lifetime RRS was 16%
- Observations of spawning behavior indicated that farm males had 24% the “spawning success” relative to wild males - courted fewer females and participated in fewer spawnings

- Farm females constructed fewer nests and had significantly smaller eggs, and showed only 32% “spawning success” relative to wild females
- Note: Oddly, the # of males and females within each group of adults was not provided, so RRS could not be estimated within sexes. The total number of adult progeny for the 39 broodfish on which this assessment was based only 26 fish. However, RRS ≈ 0.16 was similar when measured at the age 0 stage (122 fish) and at out-migration (352 fish), giving greater credence to the determination for the adult RRS measure in spite of it being based on such a small sample size. While results of this study might be applicable to assessing productivity of farmed fish following escape from net-pens, it is not appropriate for inferring effects of hatchery supplementation. The farmed stock being tested had undergone intense selective breeding over 5 generations, for improved growth in net-pen rearing and fecundity (likely related to the smaller egg size of farm females?), making it predictable that there might be a reduction in natural reproductive performance. Reduced egg size is associated with selection for high fecundity, which typically occurs in a selective breeding program for farmed stock, and small egg size (and smaller size of fry) is known to correlate positively with small fry size, and small fry size with reduced fry survival in nature. The design is severely confounded in that natural reproductive performance of NO fish was being compared to adult fish coming straight out of farm net-pens – held 1 month in round tanks, then “dumped” into the river.

McLean, J. E., P. Bentzen and T. P. Quinn. 2004. Differential reproductive success of sympatric, naturally spawning hatchery and wild steelhead, *Oncorhynchus mykiss*. Environmental Biology of Fishes 69: 359–369.

- Forks Creek hatchery stock created with Bogacheil Hatchery stock derived from Bogacheil R + Chambers Creek hatchery stock) – 10 generations of segregated hatchery rearing
- Smolts released and adults allowed to spawn naturally in Forks Creek for two years (1996 and 1997); thereafter, HO fish culled at the weir
- Hatchery stock is genetically distinct, and has been deliberately selected for early return and spawn timing
- Age 1+ juveniles sampled and mixed stock analysis used to assign them to hatchery or wild parents; presumed little or no hybrid crosses due to large (2+ month) differences in average return timing (and presumably spawn timing) between hatchery and wild
- 1996 smolts per female: W=18.8, H = 1.07, H/W = 0.57
- 1997 smolts per female: W=24.5, H = 1.33, H/W = 0.54
- But, W females generally larger/more fecund than H females; after adjusting for size/fecundity, 1996 H/W = 0.043 (... how was this lower than before adjustment???) , and 1997 H/W = 0.071
- Note: Poor performance of the hatchery fish is entirely to be expected, given the manner in which they were deliberately selected for return/spawn timing that is altered from that of wild stock. Additionally, there is the confounding environmental factor of comparing natural spawning performance of two groups of fish with different juvenile life history experience – hatchery rearing versus natural rearing – which should bias results against HO fish.

McLean, J. E., P. Bentzen and T. P. Quinn. 2003. Differential reproductive success of sympatric, naturally spawning hatchery and wild steelhead trout (*Oncorhynchus mykiss*) through the adult stage. Canadian Journal of Fisheries and Aquatic Sciences 60: 433-440.

- Examination of adult returns from the 1996 and 1997 broodyears described above in McLean et al. (2004)
- Broodyear of adult progeny assigned according to scale age
- Hatchery stock is genetically distinct, and has been deliberately selected for early return and spawn timing (see above)
- Adult progeny assigned to hatchery or wild parents using mixed stock analysis; presumed no hybrid crosses due to large (2+ month) differences in average return timing (and presumably spawn timing) between hatchery and wild
- 1996 average adult progeny per female: W=3.73, H = 0.41, H/W = 0.110
- 1997 average adult progeny per female: W=6.70, H = 0.16, H/W = 0.024
- Note: As stated above (McLean et al 2004), poor performance of the hatchery fish is entirely to be expected, given the manner in which they were deliberately selected for return/spawn timing that is altered from that of wild stock. Additionally, there is the confounding environmental factor of comparing natural spawning performance of two groups of fish with different juvenile life history experience – hatchery rearing versus natural rearing – which should bias results against HO fish.

Araki, H., W. R. Ardren, E. Olsen, B. Cooper, and M. S. Blouin. 2007a. Reproductive success of captive-bred steelhead trout in the wild: evaluation of three hatchery programs in the Hood River. Conservation Biology 21 (1), 181-190.

- See below: Hatchery broodstock on Local origin – Integrated broodstock management

Hatchery broodstock of Local origin – Segregated broodstock management

Reisenbichler, R. R., and J. D. McIntyre. 1977. Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout, *Salmo gairdneri*. Journal of the Fisheries Research Board of Canada 34:123-128.

- Deschutes River HO and NO adult steelhead were captured and artificially spawned such that their progeny were electrophoretically identifiable
- Equal numbers of HH, HW and WW eyed-eggs or unfed fry were then stocked into sections of 4 natural streams or a hatchery pond
- periodic samples of surviving fry collected by electrofishing or in traps
- in 5 of 12 samples collected in the four natural streams: (2 of 4, 1 of 3, 0 of 3, and 2 of 2), WW fry survived significantly better than HH, and HW was intermediate; in the other 7 of 12 samples there was no statistical difference
- in the hatchery pond, in contrast, HH fish survived significantly better than WW, with HW intermediate
- Note: The HO population had gone through 2 generations of apparently non-random segregated hatchery breeding (there was already noted a difference in spawn timing

between HO and NO steelhead – although spawning for this study was conducted on the same day) which potentially biases results against the HO fish. Additionally, the study was conducted in competition, without comparisons of performance under separate rearing. The conclusion that the HH fish were “genetically different” overstates the weight of the data, but if the HH fish are genetically different, isn’t it likely due to broodstock management and not to an unavoidable effect of hatchery rearing?

Reisenbichler, R. R., and S. P. Rubin. 1999. Genetic changes from artificial propagation of Pacific salmon affect the productivity and viability of supplemented populations. *IC ES Journal of Marine Science* 56:459-466.

- This manuscript reviews several published reports on relative fitness of HO and NO, but also provides data on an study, indicated as “in progress”, that the authors are conducting on Clearwater River (Idaho) summer steelhead (although no subsequent publication was found in the literature ...?)
- For the latter, very few details of the study design were provided
- In two broodyears, adults of hatchery-origin (North Fork Clearwater origin, 6 generations in segregated rearing) and wild-origin (Middle Fork Clearwater) were apparently artificially spawned, and their eggs reared to the eyed-stage prior to “release” (in a natural stream environment ...?)
- Age 1+ parr apparently captured and identified as H vs. W by some means (?)
- Survival of the eyed-eggs to age 1+ parr for hatchery compared to wild – RF was approx. 0.8 (average for the 2 broodyears? - indicated simply as a data point in Figure 1)
 - Note: The lack of details and data on study design, and the inability to find a subsequent published report/manuscript cast doubt on the reliability of these data. The hatchery stock, while derived from a nearby wild population, had apparently been in segregated rearing for 6 generations.

McGinnity, P., P. Prodohl, N. O. Maoileidigh, R. Hynes, D. Cooper, N. Baker, B. O’Hea and A. Ferguson.. 2004. Differential lifetime success and performance of native and non-native Atlantic salmon examined under communal natural conditions. *Journal of Fish Biology* 65(Suppl. A):173–187.

- compare relative survival: A) eyed-egg to smolt survival, and B) eyed-egg to adult - of wild (W) versus native ranched stock (R) versus wild non-native (nN) Owenmore River stock released in a natural river
- Wild = native Burrishoole stock (Ireland), and sea-ranched = native Burrishoole stock after 18 generations of segregated rearing, non-native = wild Owenmore River stock (80 km north)
 - A) eyed-egg to smolt: known number of eyed eggs for each cross type planted in artificial redds, and progeny sampled as parr and smolts by electrofishing and in out-migrant trap
 - A) Relative survival eyed-egg to smolt: R = 98% and nN = 81%; the R stock did, however, show greater early out-migration as 1+ pre-smolts and a higher proportion that were mature

- B) smolt to adult: smolts for each cross type were reared in the hatchery, microtagged, and released; survival to adult stage measured by sampling in fishery and in in-migrant trap
- B) Relative survival smolt to adult (after accounting for estimated capture rate in coastal fishery): R = 104% (11.8% / 11.3%) and nN = 27% (3.1% / 11.3%); also, R showed a sex-ratio of returning adults significantly skewed in favor of females while W was 1:1, and time of freshwater entry for R was significantly delayed relative to W
- The low nN survival to adult did not appear to be due to straying
- Note: Common garden rearing eliminates primary confounding environmental effects. Despite 18 generations of segregated hatchery spawning/juvenile rearing, the sea-ranched stock (derived from wild Burrishoole stock) showed no differences in survival. In contrast, the wild non-native stock showed significant reduction in survival, despite the fact that its native coastal stream was only 80 km distant

Dannewitz, J., E. Petersson, T. Prestegard, and T. Järvi. 2003. Effects of sea-ranching and family background on fitness traits in brown trout *Salmo trutta* reared under near-natural conditions. *Journal of Applied Ecology* 40:241-250.

- Comparisons of eyed-egg to parr survival of eyed-eggs planted in egg boxes within an artificial stream (110 m, 345m²)
- factorial matings (in 1997 and 1999) of wild stock (W), versus sea-ranched stock (S) (local origin, 7 generations segregated), versus reciprocal hybrids (WxS and SxW); 10 females and 10 males each per stock
- Stream drained and 0+ parr collected and assigned parentage via microsatellite analyses
- In both years, survival to parr was numerically greater for SxS versus WxW, and in one year survival of hybrids was lower than for intra-stock crosses, and was greater for hybrids with S female parent
- After accounting for family effects (wide variation in survival between families) no significant difference in survival between crosses
- Note: HO fish were from a segregated hatchery stock; NO and HO fish both created by artificial spawning and planting of eggs in egg boxes – therefore eliminating confounding environmental effect of comparing fish with differing juvenile life histories

Dannewitz, J., E. Petersson, J. Dahl, T. Prestegard, A. Lofs and T. Järvi. 2004. Reproductive success of hatchery-produced and wild-born brown trout in an experimental stream. *Journal of Applied Ecology* 41: 355-364.

- In 2000, 6 females and 6 males each from a wild stock (W) and a sea-ranched stock (S) (local origin, 7 generations segregated) stocked into an artificial stream (110 m, 345m²) for natural spawning
- Stream drained and 0+ parr collected and assigned parentage
- Parr production was greater for the hatchery stocks, although difference was not significant; of note, there was great disparity in individual parentage, with a single WxS mating producing the majority of parr
- No assortative mating observed

- Reproductive success was not significantly different between stocks; RRS reported as 1.27 in Table 1 (Araki et al. 2008), although am unsure how this was calculated ...?
 - Note: The sea-ranched stock was segregated for 7 generations, and there is the confounding environmental factor of comparing natural spawning performance of two groups of fish with different juvenile life history experience – hatchery rearing versus natural rearing – both conditions should bias results against sea-ranched stock
 - (Experiment was repeated in 2001 with S (7th generation) and new first generation -created from wild parents - hatchery stock; first generation hatchery males fathered more progeny than seventh generation males, although no difference observed between females)

Dahl, J., E. Petersson, J. Dannewitz, T. Jarvi, and A. C. Lof. 2006. No difference in survival, growth and morphology between offspring of wild-born, hatchery and hybrid brown trout (*Salmo trutta*). Ecology of Freshwater Fish 15:388–397.

- Comparison of juvenile FW survival (age1 to age 2 parr)
- 10 matings each made in fall 1998 of wild stock (W), sea-ranched stock (S) (local origin, 7 generations segregated), and reciprocal hybrids (WxS and SxW); 10 females and 10 males each per stock
- After 1 year rearing under hatchery conditions (size was similar among cross types) the parr were nose tagged and stocked into an artificial stream (110 m, 345m³) for an additional 1 year FW rearing under natural conditions
- At harvest, no differences among cross types – neither for survival (approx. 40%) nor for growth
- Note: As for the 2 Dannewitz studies of this same stock, segregated rearing of this sea-ranched (hatchery) stock affected no difference in survival

Hatchery broodstock of Local origin – Integrated broodstock management

Araki, H., W. R. Ardren, E. Olsen, B. Cooper, and M. S. Blouin. 2007a. Reproductive success of captive-bred steelhead trout in the wild: evaluation of three hatchery programs in the Hood River. Conservation Biology 21 (1), 181-190.

- A study comparing RRS of traditional (out-of-basin segregated) summer run (Skamania – 1995 & 1996) and winter run (Big Creek - 1991) hatchery stocks used to supplement the depressed wild Hood River steelhead.
- Also, compared RRS of new integrated winter run hatchery fish (1995 to 1997) to wild Hood River steelhead
- Microsatellite and parentage analysis performed on DNA extracted from archived scales collected since 1991 on all natural origin fish arriving at Powerdale Dam (and passed upstream for natural spawning), and all hatchery origin fish that were passed upstream
- RRS Big Creek (1991) females = 0.11, males = 0.06
- RRS Skamania (1995 & 1996 – average of values with and without consideration of estimated angling upstream of Powerdale Dam) females = 0.37 and males = 0.35
- RRS of first generation hatchery reared fish produced from wild origin broodfish (1995 to 1997 – average of values with and without consideration of estimated angling upstream of Powerdale Dam) females = 1.08 and males = 0.98

- Quote from Abstract: “These are the first data to show that a supplementation program with native broodstock can provide a single-generation to the boost to the size of a natural steelhead population without obvious short-term fitness costs.”
- However, they also caution: “On the other hand, crosses between hatchery fish of either type (traditional or supplementation) were less fit than expected, suggesting a possible interaction effect.”
- Note: see below

Araki, H., B. Cooper, and M. S. Blouin. 2007b. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. *Science* 318:100-103.

- As described above, a supplementation hatchery (captive, C) program for winter-run steelhead in the Hood River began in 1991, using only wild (W) fish as parents. Substantial numbers of returning adult progeny (C) began in 1995.
- Beginning in 1995, the supplementation hatchery program used some of these HO returning adults as broodstock (in each case crossing them to wild fish to produce second generation of HO fish - C(CxW), as well as additional crosses with only wild x wild broodstock - C(WxW); and wild crosses - W(WxW) - also occurred each BY
- In 1998, 1999 and 2000, these second and first generation HO fish, and the wild fish, were allowed to spawn naturally. Their adult progeny were detected in run years beginning in 2001, and RRS calculated relative to wild fish, and relative to each other - C(CxW) vs. C(WxW).
- RRS of C(WxW) vs. wild (involves a difference associated with 1 generation of hatchery rearing): females = 0.77 and males = 0.49 (average for the 3 BYs). This comparison is confounded by environmental effect of the two groups of fish having experienced different spawning and juvenile rearing experiences.
- RRS of C(CxW) vs. wild (involves a difference associated with 1.5 generations of hatchery rearing): females = 0.30 and males = 0.32 (average for the 3 BYs). This comparison is confounded by environmental effect of the two groups of fish having experienced different spawning and juvenile rearing experiences.
- RRS of C(CxW) vs. C(WxW) (involves a difference associated with 0.5 generations of hatchery rearing): females = 0.55, and for males = 0.55 (average for the 3 BYs). This design is not confounded by environmental effects, as both groups were spawned and reared in the common hatchery environment. Therefore, the observed reduction in fitness is apparently due entirely to a genetic influence derived from a single generation of hatchery rearing in one of the grandparents.
- Note: see below

Araki, H., B. Cooper, and M. S. Blouin. 2009. Carry-over effect of captive breeding reduces reproductive fitness of wild-born descendants in the wild. *Biology Letters* doi: 10.1098/rsbl.2009.0315 (<http://rsbl.royalsocietypublishing.org/content/5/5/621.full.pdf+html>)

- the Hood River began in 1991, using only wild fish as parents for the winter run steelhead supplementation program. Substantial numbers of returning adult progeny (C) began in 1995.

- Beginning in 1995, some of these returning HO adults spawned naturally with each other - W(CxC) or with a wild fish - W(CxW), as well as additional wild x wild crosses - (WxW) - occurred
- In 1998, 1999 and 2000, these fish were allowed to spawn naturally, and their adult progeny were detected in run years beginning in 2001, and RRS calculated relative to wild fish, and relative to each other - W(CxC) vs. W(CxW) vs. W(WxW)
- RRS for W(CxW) vs. W(WxW), involving 0.5 generation difference in hatchery rearing, was: females = 0.84, and males = 0.92
- RRS for W(CxC) vs. W(WxW), involving 1 generation difference in hatchery rearing, was: females = 0.42, and males = 0.31
- This design, because the fish were all spawned and reared in the common natural environment, effectively limits observed differences in productivity to genetic causes
- Note: see below

Notes regarding Araki et al studies of Hood River steelhead:

- The authors report a series of RRS estimations following analysis of data from different subsets of BYs, involving a) comparisons of hatchery origin fish to wild fish which are confounded by environmental effects due to the fish having experienced differing spawning and juvenile rearing backgrounds, or b) comparisons of fish with NO vs. HO differences in grand-parentage, but similar parentage (common parental spawning and rearing environments), such that observed productivity differences can be attributed solely to genetic effects.
- The differences attributable to genetic effects in the latter studies are dramatic, and generally increase in magnitude with increase in the number of generations of hatchery rearing in the background of the fish. And, it is these results in particular which have been highly publicized and are cited by the HSRG and in the Mitchell Act draft EIS, as providing the rationale for (greatly) reducing the scale of current hatchery supplementation programs, and for impeding initiation of new programs.
- On the other hand, RRS measures reported in these studies for the comparisons that are confounded by environmental effects tend to be of a (much) lower magnitude. There is an apparent contradiction between these results, which the authors have not adequately addressed.
- Concerning these RRS comparisons which are confounded by environmental effects, in Araki et al. (2007a) the authors state: “Wild and hatchery fish experience very different freshwater environments. Thus, any fitness differences we observed could have a genetic or environmental origin, and a lack of difference (*RRS in their 2007a study was not significantly different from 1.0*) could conceivably include environmental deviations that are the opposite of genetic effects.” The authors anticipate that genetic effects associated with hatchery rearing will be negative, therefore the environmental effects must be positive??? By what mechanism(s) do the authors suspect that spawning and juvenile rearing in a hatchery improves natural spawning success and productivity of these hatchery-origin fish when they reach the adult stage? Common sense, and data from other studies, would indicate that these environmental effects will also likely be negative, and would be additive to negative genetic effects. Therefore, if one observes a measure of RRS that is not significantly different from 1.0 in a study where the genetic and

environmental influences on productivity are confounded, one must conclude that the portion attributable solely to genetic effects was even smaller, and certainly insignificant. Likewise, for a measure of RRS that is lower than 1.0, if the proportion of the reduction attributable to environmental effects could be subtracted from the overall reduction, the RRS value would increase, and the RRS measure is graphed such as in RIST Figure 4, the data point would shift upwards towards 1.0, such as illustrated in Figures 3a and 3b.

- And, not only are the RRS measures from the genetic-effect only designs of a larger magnitude than expected relative to their RRS measures for their confounded designs, they are also at the extreme low end for the array of RF and RRS measures observed in other studies (not including those studies which made comparisons involving non-local stocks, which would be invalid if the intent is to assess impacts of a hatchery supplementation program, *sensu* Cuenco et al 1993).
- While there is no denying the “elegance” of the designs in Araki et al. 2007b and Araki et al. 2009 that restrict observed productivity differences to genetic effects, taken in context with results across the breadth of published studies, scientific caution dictates that one be much more reticent presuming the generalized predictions of dramatic and rapid fitness loss associated with supplementation that have resulted from the manner by which the authors’ results have been publically presented and vaunted.
- One additional potentially confounding factor to these Araki et al. studies relates to the manner by which broodstock for the winter run steelhead program were chosen. These fish were sampled from among the winter run adults upon their return to the fish trap at Powerdale Dam. However, the Hood River also has a run of summer run steelhead, and there is overlap in return timing between stocks, and managers are certain that some level of misidentification has occurred in the past. The summer and winter runs have differing spawning and juvenile rearing life histories, such that hybridization between stocks will likely result in fish maladapted for one life history or the other. This situation was discussed by Matala et al (2009), and a relatively reliable molecular genetics test to distinguish between ecotype was described. To assure the readers that the differences that they are not, at least in part, attributable to the artifact of use of misidentified or hybridized individuals among the winter-run broodstock, Araki et al need to test and report that such was or was not the case.

Matala, A. P., R. French, E. Olsen and W. R. Ardren. 2009. Ecotype distinctions among steelhead in Hood River, Oregon, allow real-time genetic assignment of conservation broodstocks. *Transactions of the American Fisheries Society* 138: 1490-1509.

Fleming, I. A., A. Lamberg, and B. Jonsson. 1997. Effects of early experience on the reproductive performance of Atlantic salmon. *Behavioral Ecology* 8:470-480.

- Study to assess the environmental effects of juvenile rearing on spawning success - differences between wild reared adults and adults that were hatchery reared
- Salmon from a “common genetic background” (achieved by mixing wild-origin and sea-ranch hatchery-origin fish both in the river for natural spawning and in the hatchery broodstock ... am unclear as to how equivalent the genetic background would be ...?) were produced by natural spawning and rearing, and by artificial spawning and hatchery rearing

- Upon smolting, the sea-ranched smolts were released into the river with the wild smolts
- Adults were captured after 1 year (90%) or 2 years (10%) in the ocean, then stocked into experimental spawning arenas at varying densities and sex-ratios
- Observations made on spawning behaviors, and on number of eyed-eggs produced
- Sea ranched and wild males differed in competitive and reproductive performance, with wild males having significantly higher reproductive success
- There were few differences in competitive and reproductive performance between sea ranched and wild females
- Body size was shown to play a key role in competition in both sexes, with larger individuals being more aggressive
- A few of the large males in each arena dominated spawning, and attained considerably higher reproductive success than all other males
- For females, larger body size principally provided higher fecundity, but also influenced competitive behavior and early egg survival, likely through the effects on nest quality. In males, body size was highly correlated with aggressive behavior
- RRS for males averaged approx. 0.48; RRS for females was approx. 1.0
- Therefore, because the fish were from a common genetic background, “our results suggest that the differences in reproductive performance may be ascribed to early juvenile experience and related to the development of specialized skills important for not only early life, but also later river life”. This study indicates that environmental conditions may account for some (a large?) portion of the observed differences in reproductive success of HO versus NO – at least among males, rather than hatchery-dependent genetic changes.

Leth, B. D. 2005. Reproductive success of hatchery and natural origin Chinook salmon (*Oncorhynchus tshawytscha*) in a stream with a history of supplementation management. Master’s thesis. University of Idaho, Moscow, Idaho.

- RRS comparison of juvenile recruits per spawner for BY 2002 Pahsimeroi River spring/summer Chinook for BY 2002 NO and HO (first generation - produced from wild parents) adults
 - Chi square analysis, within sexes, of observed and expected numbers of progeny
 - For both males and females, no significant differences –
- | RRS | 95% assignment | 80% assignment | average | Females | 0.89 | 1.11 | 1.00 |
|-----|----------------|----------------|---------|---------|------|------|------|
| | | | | Males | 1.21 | 1.23 | 1.22 |
- Acclimation site downstream, but not dramatically, of the primary spawning area
 - Spawning area surveys showed similar distribution and spawn-timing of HO and NO adults
 - There was no evidence of assortative mating
 - Note: HO fish from an only partially integrated stock – they were 3rd generation, with 1st generation being 50% segregated HO fish, crossed to NO fish in the 2nd generation; additionally, there is the confounding environmental factor of comparing natural spawning performance of two groups of fish with different juvenile life history experience – hatchery rearing versus natural rearing – which should bias results against HO fish

Ford, M., H. Fuss, B. Boelts, E. LaHood, J. Hard, and J. Miller. 2006. Changes in run timing and natural smolt production in a naturally spawning coho salmon (*Oncorhynchus kisutch*) population after 60 years of intensive hatchery supplementation. *Canadian Journal of Fisheries and Aquatic Sciences* 63:2343-2355.

- Minter Creek coho salmon have undergone approx. 25 generations of supplementation following a segregated (?) hatchery program that used a broodstock of local origin, but with no restrictions (culling) of HO spawners (so the wild population was integrated)
- In 2000 and 2001, similar numbers of NO and HO adults were passed upstream of hatchery weir for natural spawning
- Size and run-timing similar between HO and NO, but run-timing much earlier than historic timing
- RRS not significantly different from 1.0 for both sexes: males = 1.01, females = 0.74
- Note: The wild population was integrated and so the NO fish tested had an unknown proportion of hatchery ancestry (as inferred by the altered run timing). The authors speculate that the lack of difference in RRS is most likely due to fitness of the NO stock having already been substantially reduced due to effects of their hatchery ancestry, such that the additional generation of hatchery rearing in the HO resulted in a reduction in fitness that was too small to be detected within the power of the study design and analysis. There is also the additional confounding environmental factor in the design of comparing natural spawning performance of two groups of fish with different juvenile life history experience – hatchery rearing versus natural rearing – which should bias results against HO fish.

Berejikian, B. A., D. M. Van Doornik, J. A. Scheurer, R. Bush. 2009. Reproductive behavior and relative reproductive success of natural - and - hatchery - origin Hood Canal summer chum salmon (*Oncorhynchus keta*). *Canadian Journal of Fisheries and Aquatic Sciences*, 66:781-789.

- In both 2004 and 2005, NO and HO (3 generations, integrated) Quilcene River (Puget Sound WA) adult chum salmon were collected and stocked into an artificial stream – 12 fish per sex for both stocks
- Spawning behavior observed, and fry collected and genotyped for parentage assignment
- Similar spawning behaviors between stocks
- RRS not significantly different from 1.0 (males = 1.03; females = 0.72)
- Note: there is the confounding environmental factor of comparing natural spawning performance of two groups of fish with different juvenile life history experience – hatchery rearing versus natural rearing – which should bias results against HO fish

Schroder, S. L., C. M. Knudsen, T. N. Pearsons, T. W. Kassler, S. F. Young, C. A. Busack, and D. E. Fast. 2008. Breeding Success of Wild and First-Generation Hatchery Female Spring Chinook Salmon Spawning in an Artificial Stream. *Transactions of the American Fisheries Society*, 137:1475-1489.

- Report of 7 trials in which ripe wild-origin and first generation hatchery-origin females

and males were stocked into an artificial stream for spawning

- Observations were made on spawning behaviors and redd characteristics, and fry were collected to assess relative adult-to-fry reproductive success via microsatellite DNA parentage analysis
- No differences detected in the egg deposition rate; subtle differences between hatchery and wild females in redd abandonment, egg burial, and redd location choice
- Average RRS for females = 0.94
- Geomean RRS calculated as the straightforward ratio of progeny identified with a H or W female parent divided by the total number of H or W female parents =0.86 (from Table 8 in Schroder et al. 2010)
- Note: Artificial stream design eliminates confounding influences attributable to differential homing and spawning distribution of HO and NO fish. In 6 of the 7 trials the W females were larger than the H females, although “body weight had no effect on egg deposition, egg-to-fry survival, or on the capacity to convert absolute fecundity to fry”.

Schroder, S. L., C. M. Knudsen, T. N. Pearsons, T. W. Kassler, S. F. Young, E.P. Beall, and D. E. Fast. 2010. Behavior and Breeding Success of Wild and First-Generation Hatchery Male Spring Chinook Salmon Spawning in an Artificial Stream. Transactions of the American Fisheries Society, 139:989-1003.

- Report of 7 trials in which ripe wild-origin and first generation hatchery-origin females and males were stocked into an artificial stream for spawning
- Observations were made on spawning behaviors, and fry were collected to assess relative adult-to-fry reproductive success via microsatellite DNA parentage analysis
- Male breeding success increased with weight, and wild males were on average slightly larger than hatchery origin males
- RRS calculated as the straightforward ratio of progeny identified with a H or W male parent divided by the total number of H or W males parents (adult + jack + precocious parr); geomean for RRS was 0.95
- Note: Artificial stream design eliminates confounding influences for differential homing and spawning distribution. RRS was not significantly different from 1.0, even without removing confounding effects

Williamson, K. S. A. R. Murdoch, T. N. Pearsons, E. J. Ward, and M. J. Ford. 2010. Factors influencing the relative fitness of hatchery and wild spring Chinook salmon (*Oncorhynchus tshawytscha*) in the Wenatchee River, Washington, USA. Canadian Journal of Fisheries and Aquatic Sciences 67: 1840-1851.

(Replaces: Murdoch, A., T. Pearsons, T. Maitland, M., and K. Williamson. 2008. Monitoring the reproductive success of naturally spawning hatchery and natural spring Chinook salmon in the Wenatchee River. BPA Project No. 2003-039-00. Bonneville Power Administration, Portland, Oregon. <http://pisces.bpa.gov/release/documents/documentviewer.aspx?doc=P106770>. Department of Energy, Bonneville Power Administration.)

- Report of RRS results for two BYs (2004 and 2005) of wild and hatchery origin Wenatchee/Chiwawa River spring Chinook, based on juvenile (out-migrating age 1 smolts) per spawner

- Integrated hatchery supplementation program in 4th generation (began 1989)
- Average RRS for females = 0.52, and for males = 0.32
- However, analyses showed significant confounding environmental effects:
 - o females – very large effect for spawning location (concentration in lower river due to homing to acclimation site – higher spawner density and poorer habitat) and lesser effects for age/size (in part attributable to accelerated growth in hatchery) and for run-timing
 - o males – very large effects for spawning location (concentration in lower river due to homing to acclimation site – higher spawner density and poorer habitat) and for age/size (tendency to return higher % of jacks, attributable to accelerated growth in hatchery), and lesser for run-timing
- Note: because these confounding effects are in large part environmental (non-heritable effects associate with hatchery rearing practices), RRS attributable to genetic effects is much closer to 1.0 (when using spawning location as a predictor in two alternative statistical models, the effect of origin diminished in both, becoming non-significant in one of them) Additional non-genetic confounding factors associated with the different juvenile life history experience – hatchery rearing versus natural rearing –could bias results against HO fish

Sharpe, C. S, P. L. Hulett, C. W. Wagemann, M. P. Small and A. R. Marshall 2010. Natural Reproductive Success of First-generation Hatchery Steelhead Spawning in the Kalama River: A Progress Report. Washington Department of Fish and Wildlife, Fish Program, Fish Science Division FPA 09-07.

- Progress report with nearly complete RRS data for 2003 broodyear of Kalama River summer run steelhead
- Hatchery stock initiated with wild adults from 1998 to 2000 run years; age 1 smolts (a portion acclimated) and released
- Adult returns (progeny) sampled in 2007, and assigned parentage to via microsatellite analyses
- RRS for progeny assigned with 2 BY 2003 parents = 1.0
- RRS for progeny assigned with only 1 BY 2003 parent = 0.55
- Note: This study is ongoing, and these data should be updated annually. Recruits per spawner were low of 873 HO and 897 NO parents, only 70 (two parents) + 66 (one parent) progeny were identified among the 2007 returns.

Baird, M. E. Berntson E., T. Hoffnagle, S. Boe, J. Harbeck, R. Carmichael and P. Moran. 2008. Relative Reproductive Success in Spring Chinook Lostine River, Grande Ronde Basin. Oral presentation at the Lower Snake River Compensation 2008 Annual Meeting. (<http://www.fws.gov/lsnakecomplan/Happings/2008AnnualMeeting.html>)

- Catherine Creek spring Chinook hatchery program
- RRS reported for 4 BYs (2002 to 2005) based on juvenile (parr) recruits per spawner
- Slide 9: Females – geomean (1.88, 1.16, 1.55, 0.94) = 1.34
- Slide 9: Males – geomean (1.11, 0.58, 0.81, 1.33) = 0.91

- Note: The study design has the confounding environmental factor of comparing natural spawning performance of two groups of fish with different juvenile life history experience – hatchery rearing versus natural rearing – which should bias results against HO fish. The PPT presentation also provides RRS information on Lostine River spring Chinook and Little Sheep Creek steelhead – however, more recent information for these two programs is provided in the presentations described below.

Bernston, E. 2009. Relative Reproductive Success in Spring Chinook Lostine River, Grande Ronde Basin. Oral presentation at the Nez Perce Tribe, Department of Fisheries Resources Management, 2009 Symposium on Salmon Supplementation.

(<http://www.nezperce.org/~dfrm/Research/2009%20Symposium.html>)

- Lostine River spring Chinook hatchery program initiated as a captive broodstock program with captured wild parr in 1996, followed by integrated supplementation program with returning adults in 1997 – 1.5 generations
- RRS reported for BY 2001, 2002 and 2005, based on juvenile (parr) recruits per spawner
- Slide 8: Females - geomean (1.13, 2.12, 0.84) = 1.26
- Slide 8: Males - geomean (0.76, 0.90, 1.91) = 1.09
- Note: The study design has the confounding environmental factor of comparing natural spawning performance of two groups of fish with different juvenile life history experience – hatchery rearing versus natural rearing – which should bias results against HO fish.

Bernston et al. Coastwide Salmon Genetics Meeting 2010 presentation (submitted: Bernston, E.A., R.W. Carmichael, M.W. Flesher, E.J. Ward and P. Moran *In Review*. Swimming against the current: diminished reproductive success of hatchery fish complicates the use of supplementation in Snake River steelhead recovery. Submitted to Transactions of the American Fisheries Society) (replaces: Moran, P., and R. S. Waples. 2007. Monitor and evaluate the genetic characteristics of supplemented salmon and steelhead. Project number 1989-096-00. Research Progress Report Oct 5, 2007. Report to Bonneville Power Administration.

<http://pisces.bpa.gov/release/documents/documentviewer.aspx?doc=P107430>)

- Reports RRS results for Little Sheep Creek steelhead – integrated supplementation program initiated in 1982 – 5 generations
- All adults passed above the weir were tissue sampled, and juveniles were collected annually
- Geomean RRS for adult-to-juvenile (2000 to 2005) = 0.39 for females, and 0.51 for males
- Geomean RRS for adult-to-adult (2000 to 2003) = 0.32 for hatchery females, and 0.50 for males
- RRS adult-to-juvenile and adult-to-adult very similar
- Note: Hatchery juveniles undergo accelerated rearing for release at age 1+, whereas naturally spawned and reared juveniles do not out-migrate until age 2+ or 3+, which no doubt affects differences in age and size of the adults. Data for location of juvenile

capture indicated that hatchery fish spawned primarily in the lower reaches (likely a homing response to acclimation location), while wild fish spawned more evenly throughout the river, including upper reaches where spawner densities were lower and habitat quality was higher. Is some (substantial?) proportion of lowered productivity of hatchery fish attributable to these effects? The study design has additional confounding environmental factors associated with comparing natural spawning performance of two groups of fish with different juvenile life history experience – hatchery rearing versus natural rearing – which should bias results against HO fish.

Supportive breeding boosts natural population abundance with minimal negative impacts on fitness of a wild population of Chinook salmon

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Abstract

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 F_1 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 $W \times W$ matings. Mean RRS of $H \times W$ and $H \times H$ 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.

Keywords: parentage analysis, reproductive success, salmonids, supplementation

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Introduction

Artificial breeding programmes are widely used for the conservation of threatened or endangered species and for the restoration of declining populations (IUCN 1998; Frankham *et al.* 2002; Fraser 2008). Conditions associ-

ated with artificial rearing, such as the absence of predators, food availability and disease treatments, result in selective pressures that are widely different from natural environments. Artificially reared organisms are thus subject to adaptation to captivity (i.e. domestication selection; Frankham *et al.* 2002; Ford *et al.* 2008). Large-scale, human-mediated releases of plants and animals occur worldwide, and when artificially reared individuals are released to the wild, there can be negative genetic effects on native or wild populations (reviewed in Laikre *et al.* 2010). Specifically, considerable concern exists over domestication selection because

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reproductive fitness of wild populations can be reduced when artificially reared individuals mate with wild counterparts (Araki *et al.* 2009). Additionally, gene flow from these individuals into native or wild populations can homogenize genetic structure of wild populations (Eldridge *et al.* 2009) and disrupt the capacity of natural populations to adapt to changing environmental conditions (McGinnity *et al.* 2009).

Hatchery-reared Pacific salmon and steelhead (*Oncorhynchus spp.*) are commonly released into the wild environment to boost abundance of declining populations, mitigate for environmental and habitat disturbances and to enhance harvest fisheries. Salmonid hatcheries are broadly classified by having conservation or harvest objectives (reviewed in Naish *et al.* 2007). Traditional salmonid hatchery programmes with harvest objectives are designed to increase the population census size using hatchery-origin fish that are reared for multiple generations in an artificial environment, and often with out-of-basin (i.e. nonlocal) brood stock that may not be locally adapted to environmental conditions. Due to the nature of traditional hatchery programmes, fish are subject to negative genetic impacts such as inbreeding (reviewed in Wang *et al.* 2002), domestication selection (Heath *et al.* 2003; Reisenbichler *et al.* 2004; Christie *et al.* 2011) and reduced fitness due to repeated generations in captivity (Araki *et al.* 2007a). In contrast, supplementation programmes are designed to mitigate for ongoing limiting factors to survival (i.e. dams, removal of individuals in harvest fisheries, habitat degradation, etc.) with the goal of increasing natural population size for conservation and population recovery purposes, while striving to minimize the genetic impact to natural populations (Cuenco *et al.* 1993; Waples *et al.* 2007). Integrating wild-origin individuals into supplementation brood stock is one method that can be used to help offset potential negative effects on fitness (Wang & Ryman 2001; Duchesne & Bernatchez 2002; Ford 2002). Artificially produced offspring from brood stock (either hatchery or wild-origin) are subsequently released into the wild to spawn. This approach has caused some concern because the artificial environment can select for individuals that may be poorly adapted to the natural environment (Johnsson *et al.* 1996; Pearsons *et al.* 2007; Frankham 2008; Christie *et al.* 2011), and hatchery-reared fish may impose negative impacts to the fitness of wild fish (Araki *et al.* 2009).

The concern over hatchery fish spawning in the wild is supported by theoretical work that shows that even if local, wild-born fish are used for brood stock each year, domestication selection in the hatchery could lead to fitness consequences for the wild population (Lynch & O'Hely 2001; Ford 2002; Goodman 2005; Chilcote *et al.* 2011). However, additional studies demonstrate that

increasing the proportion of wild-born individuals into the captive population can slow the rate of genetic adaptation to captivity (Frankham & Loebel 1992) and reduce inbreeding in supplementation programmes (Duchesne & Bernatchez 2002). Empirical studies have shown that hatchery-reared salmonids have lower reproductive success in the wild compared with wild-origin fish in the first generation (Araki *et al.* 2007b; Williamson *et al.* 2010; Berntson *et al.* 2011; Theriault *et al.* 2011; Anderson *et al.* 2012), but few studies have investigated fitness effects over multiple generations. Two recent studies that examined fitness over two generations focused on a single population of steelhead trout (*Oncorhynchus mykiss*) and demonstrated that an increased number of generations in captivity can have negative fitness consequences on the population, but results were highly variable across years (Araki *et al.* 2007a, 2009). Fitness declines of hatchery-reared fish in the wild have been attributed to a number of causes. Hypotheses include the absence of sexual selection in the hatchery environment (stronger effect on hatchery males than females—Theriault *et al.* 2011; Anderson *et al.* 2012), the use of nonlocal origin brood stock over multiple generations (Chilcote *et al.* 1986; McLean *et al.* 2003; Araki *et al.* 2007b), differences in spawning location and age (Williamson *et al.* 2010), as well as body size, return date and the number of same-sex competitors (Berntson *et al.* 2011). Despite evidence that hatchery-reared fish can have lower reproductive success in the wild compared with their wild-origin counterparts, the potential for benefits from supplementation programmes using local-origin fish for brood stock warrants more extensive study. Specifically, when hatchery-reared fish are allowed to spawn naturally, can supportive breeding boost abundance while minimizing negative fitness impacts on wild fish?

Despite the need for this type of evaluation of supplementation programmes, all published studies evaluating reproductive success of hatchery-reared salmonids in the natural environment focus on programmes that use both wild and hatchery-reared fish as brood stock, and supplementation was initiated prior to the study of the target programme. In addition, studies have largely been focused on steelhead, which are typically reared in the hatchery to smolt within 1 year before being released as juveniles, rather than rearing to age 2 or older as typically found in nature (Araki *et al.* 2007a,b, 2009; Berntson *et al.* 2011). Recent studies are available for a few other salmonids (Berejikian *et al.* 2009, chum salmon; Williamson *et al.* 2010 and Anderson *et al.* 2012, Chinook salmon; Theriault *et al.* 2011, coho salmon), but none have estimated lifetime relative reproductive success (RRS) over multiple generations in the wild. Thus, there is a need for greater species coverage as

well as multi-generation studies that examine supportive breeding programmes from the initiation of supplementation. Further, additional studies of Chinook salmon (*Oncorhynchus tshawytscha*) in natural environments may be critical because of the extensive use of hatchery supplementation for this species and the potential for relatively high fitness of hatchery-reared fish of this species (Schroder *et al.* 2008, 2010). The available RRS studies on Chinook salmon in the wild evaluate adult to juvenile production (Williamson *et al.* 2010) and colonization of newly accessible habitat (Anderson *et al.* 2012), and no published RRS studies have evaluated the lifetime fitness (adult to adult) of this species over multiple generations.

Here, we assess the lifetime fitness of Chinook salmon in Johnson Creek, a tributary to the South Fork Salmon River (SFSR) in central Idaho, USA, by following an ongoing supplementation programme for two generations (1998–2010), beginning with the first year (1998) that wild-origin returns were taken into the hatchery and used for brood stock. We use genetic parentage assignments to test the following: (i) Does the hatchery programme provide a demographic boost to the wild population over

two generations? (ii) Are there differences in reproductive success between wild and hatchery-reared fish spawning in nature? (iii) Are there short-term (approximately two generations) genetic consequences of supplementation—that is, do hatchery-reared fish spawning in nature reduce the fitness of the wild population?

Methods

Study site and sample collection

The Salmon River basin is one of the largest subbasins of the Columbia River and covers approximately 36 000 thousand square kilometres within the Northern Rocky Mountains of central Idaho. The Interior Columbia Technical Recovery Team (ICTRT) identified three unique populations of spring/summer Chinook salmon that occur within the SFSR: the SFSR mainstem, the Secesh and the East Fork SFSR. Johnson Creek is the primary spawning aggregate of Chinook salmon within the East Fork SFSR (Fig. 1) and represents one of 32 spring/summer Chinook salmon populations listed under the Endangered Species Act in the Snake River

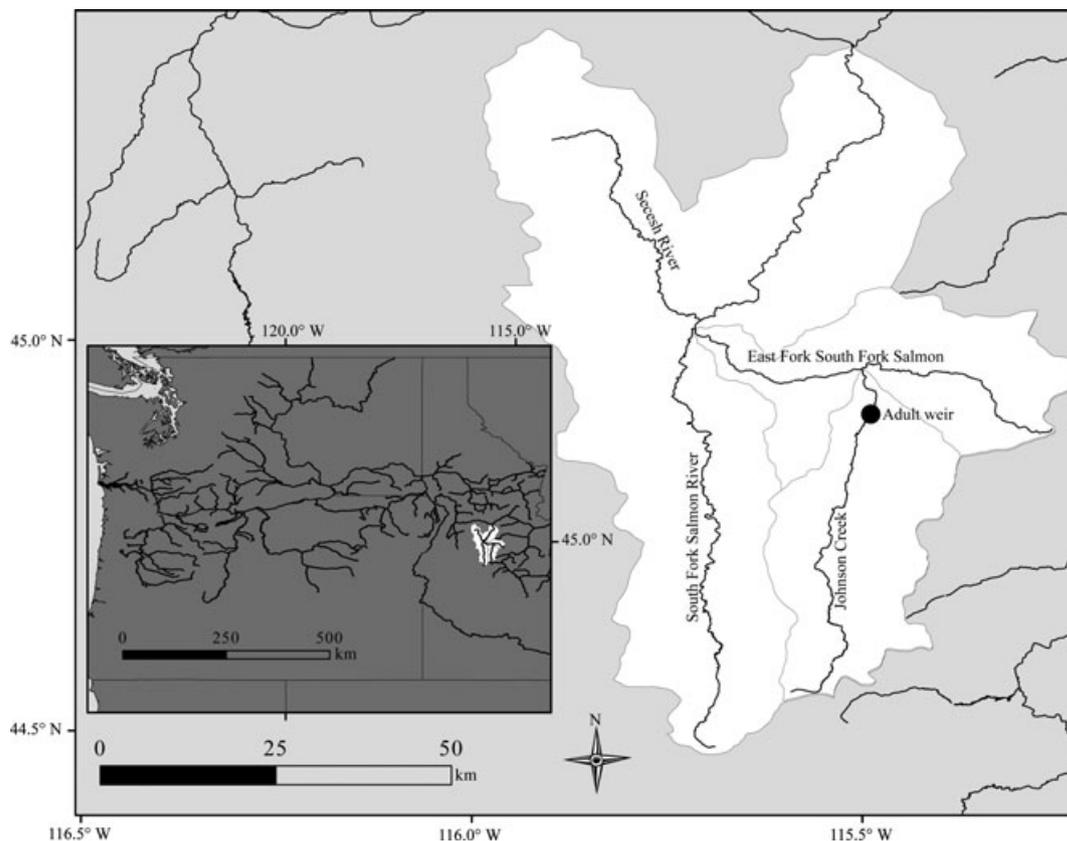


Fig. 1 Map of the study area, showing location of the weir. Inset map shows the location of the South Fork Salmon River basin highlighted in white.

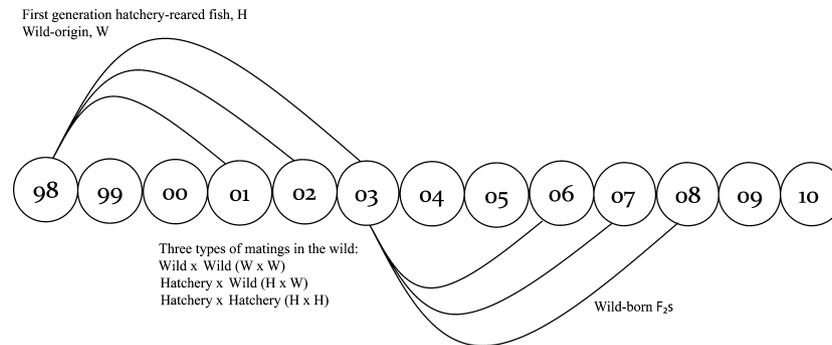


Fig. 2 Sampling design for the study. Illustrated is the sampling design for the first year of supplementation in 1998, but the same design applies to annual brood stock collections for 2000 to 2005 (5-year-olds from brood year, BY 2005 return in 2010, the last sampling year of this study). Circles represent the BY, corresponding to the year that adults return to Johnson Creek to spawn. This example shows first-generation hatchery fish (F_1) from BY 1998, which return to spawn alongside their wild-origin counterparts in 2001 (age 3, 'jacks'), 2002 (age 4) and 2003 (age 5). Mating among hatchery-reared and wild-origin fish occurred in every year beginning in 2001 to create wild-born F_2 s, which return 3–5 years later. The example follows age 5 fish (born in 1998) that returned as adults in year 2003 and produced wild-born fish (F_2 s) that returned in years 2006 through 2008.

Evolutionarily Significant Unit (ICTRT 2005). The putative wild Chinook salmon population aggregations in these three areas of the SFSR remain intact despite substantial releases of hatchery stock for supplementation and harvest augmentation in the SFSR mainstem (Matala *et al.* 2012). A supplementation programme was initiated in 1998 by the Nez Perce Tribe in an effort to prevent extirpation by increasing natural production of Chinook salmon in Johnson Creek.

Tissue samples and associated biological data were collected from 7726 returning adults encountered at the Johnson Creek picket-style weir, and during annual multiple-pass spawning ground surveys conducted upstream and downstream of the weir from 1998 to 2010. The weir occurs downstream of approximately 94% of the spawning habitat (Rabe & Nelson 2010). In the field, gender was determined by physical morphology, fork length was measured to the nearest centimetre, and origin was identified through the presence/absence of marks, tags or clips (hatchery fish have a coded wire tag and/or a visual implant elastomer tag; hatchery strays from other locations have adipose fins removed). If a fish had no visible mark, it was inferred to be produced in the wild. A tissue sample from the caudal fin was taken for genetic analysis, and these individuals were marked with an individually numbered operculum disk tag. Nontagged fish were sampled on multiple-pass spawning ground surveys upstream and downstream of the weir to achieve a high sampling rate over the course of the study (78–100%; annual mean = 95%). Only wild-origin (W , defined as fish born and reared in the natural environment, regardless of parentage), returning adults were selected for brood stock each year; all wild adults

not collected for brood stock and all hatchery-origin adults were released upstream of the weir to spawn naturally. The actual genetic composition of fish used for brood stock was 98% wild origin because a total of seven hatchery-reared fish over the period of 2001 through 2005 were unintentionally used as brood stock (5 fish from brood year, BY, 1998 and 2 fish from BY 2000). Hatchery smolts were released directly into Johnson Creek after rearing in a hatchery environment for 18 months. No fish were collected as brood stock in 1999 because only 22 fish returned, and all were allowed to spawn naturally.

The proportion of returns by age class to Johnson Creek varied between hatchery-reared and wild-origin fish. The majority of wild-origin fish returned at age 4 (mean, 62%), followed by age 5 (mean, 28%), and a smaller proportion returned at age 3 that were exclusively males (termed 'jacks'; mean, 10%). Most hatchery-reared fish returned to Johnson Creek at age 3 (mean, 43%, all males) and 4 (mean, 49%); with a smaller proportion that returned at age 5 (mean, 8%). Adult offspring from the first year of supplementation (BY 1998) returned to Johnson Creek at ages 3, 4 and 5 in 2001, 2002 and 2003, respectively. All returning F_1 hatchery-reared fish (H) were released upstream of the weir for natural spawning with their wild F_1 counterparts (Fig. 2). Offspring that resulted from naturally spawning F_1 s from BY 1998 (first year of supplementation) were termed F_2 and returned to the Johnson Creek weir as adults in 2004 to 2008 (Fig. 2). The same type of sampling scheme was achieved in each return year through 2005, as the last of the offspring (5-year-olds) from BY 2005 returned in 2010. Genetic parentage analysis was used to assign wild-origin F_2 returns back to their F_1 parents.

Parentage analysis

Genomic DNA was extracted from fin tissue following manufacturer's protocols for QIAGEN DNeasy extraction kits, and individuals were genotyped using 15 microsatellite loci: *Ots100* (Nelson & Beacham 1999), *Ots3M* (Greig & Banks 1999), *Ssa408* (Cairney *et al.* 2000), *OMM1080* (Rexroad *et al.* 2001), *Ots211*, *Ots212*, *Ots213*, *Ots201b*, *Ots208b* (Greig *et al.* 2003), *OtsG474*, *Ots311* (Williamson *et al.* 2002), *Ogo2*, *Ogo4* (Olsen *et al.* 1998), *Ots9* (Banks *et al.* 1999) and *Oki100* (K. Miller, unpublished data). Markers were amplified and genotyped as described by Narum *et al.* (2010). Briefly, fluorescently labelled PCR products were separated with fragment analysis chemistry on an Applied Biosystems 3730 Genetic Analyzer and genotyped with GeneMapper software. MSeXcel Microsatellite toolkit was used to identify duplicate genotypes. Duplicates resulted from fish sampled first at the weir, and again on a redd or spawning ground survey. Use of operculum tags to mark fish at the weir minimized the occurrence of duplication to 58 individuals, and in each of these cases, only the first capture sample at the weir was included in the analysis.

To assign returning adult offspring to parent(s), we used an exclusion approach with the program CERVUS 3.0 (Marshall *et al.* 1998; Kalinowski *et al.* 2007). Individuals genotyped for at least 12 of the 15 loci were included in parentage analyses. For single-parent-offspring comparisons, only those exhibiting no mismatches at a minimum of 14 common loci were considered true parent-offspring groupings. Only one mismatching locus was allowed for trios (offspring matching two parents), with at least 12 loci in common among all three individuals. These thresholds were highly conservative to avoid false assignments, and genotyping error was estimated to be very low at <1% based on concordance of quality control tests with repeated genotyping using approximately 5% of the samples; however, this approach may not account for all potential errors in the study. Returning F_1 offspring (*W* and *H*) were assigned to parents for each BY from 1998 to 2005 (with the exception of BY 1999 hatchery-reared parents, described above). For example, F_1 offspring (*W* and *H*) from BY 1998 returned in years 2001 through 2003 (Fig. 2). Specifically, salmon returning in 2001 through 2003 were tested against biologically plausible candidate parents (i.e. BY 1998). Following our second and third objectives, respectively, F_2 offspring were assigned to F_1 parents in two ways: (i) Second-generation (F_2) offspring returning in years 2004–2010 were assigned to F_1 parents from BY 1998 and 2000 (i.e. F_2 are the grand-offspring of F_0 fish that spawned in 1998 and 2000). This allowed us to specifically follow

two initial brood years of supplementation through the second generation. (ii) Second-generation (F_2) offspring returning in 2006–2010 were assigned to F_1 parents that spawned naturally in 2003–2005. This also allowed us to follow the second-generation returns, however, targeting combined age groups in each of these F_1 brood years increased our sample size and allowed direct comparison to published literature (Araki *et al.* 2009) and allowed for evaluation of genetic impacts to wild fish when hatchery fish mate with them. These brood years were chosen because all parents and offspring were sampled during the years of our study.

We empirically evaluated parentage assignment error rate by attempting to assign offspring returning in 2001 to 2005 to parents used for brood stock in 1998 and 2000. Parentage assignment errors fall into two categories: type A and B errors (different from Type I and II statistical errors; Araki & Blouin 2005). The failure to assign a true parent when that parent is in the sample, type A error, was determined by first attempting to assign hatchery-reared offspring to parents that were used for brood stock (all hatchery-reared fish should assign to a parent). Specifically, we evaluated offspring that assigned to parent pairs (or 2 of 2 brood stock parents) because we have no way of validating the single-parent assignments from hatchery mating records. We then calculated concordance between the parentage assignment results and the mated parents indicated by hatchery records; an error was recorded if a hatchery-reared fish did not assign to a parent or if it assigned to parents that did not match hatchery mating records. Type B error, assignment to an untrue parent (occurs when the true parent is absent or when the true parent is present but failed to be assigned), was calculated by attempting to assign wild-origin fish to parents that were used for brood stock (no wild-origin fish would have brood stock parents) and attempting to assign hatchery-reared fish to parents not used for brood stock. The stringency of the parentage assignment criteria used influences type A and type B errors as described in Araki & Blouin (2005). Specifically, Araki & Blouin (2005) found that type B error in their data set for steelhead was 1.4% when no mismatches were allowed, but jumped up to 30.5% when two mismatches were allowed. Because type B error is used to calculate unbiased RRS, minimizing this error ensures the minimum bias on RRS.

Relative reproductive success

Using parentage analysis, we estimated lifetime reproductive success, that is, the number of returning adult offspring produced per adult individual. Lifetime reproductive success was estimated for F_0 fish that

produced F_1 s in the hatchery and in the wild and estimated for returning adult F_1 fish that produced adult F_2 offspring in the natural environment. Using our empirically derived type B error rate, we obtained unbiased estimates of RRS following equation 14 from Araki & Blouin (2005). RRS estimates were not corrected for effects of harvest because there is no differential harvest between hatchery and wild fish (Johnson Creek hatchery fish are not adipose marked; therefore, there is no influence of a mark selected fishery).

To address our first objective and determine whether the supplementation programme provided a demographic boost to the natural population, we compared the numbers of offspring produced by fish that were removed from the wild and taken into the hatchery intended for use as brood stock versus individuals that were allowed to spawn in the natural environment (BY 1998–2005, with exception of BY 1999; Table 1). The numbers of adult offspring produced each year (1998–2005) and the numbers of adult grand-offspring produced from BY 1998 and BY 2000 were calculated based on parentage exclusion results for both artificially and naturally spawning individuals. Not all fish taken for brood stock had the opportunity to contribute offspring to the next generation due to prespawn mortality, unsuccessful spawning or culling of eggs to prevent disease. In addition, not all individuals had complete genetic data; therefore, some parent–offspring

Table 1 Comparison of the number of returning adult offspring (including jacks) produced by fish removed at the weir for hatchery brood stock and the number of returning adult offspring produced by fish allowed to spawn in the natural environment

Brood year	<i>n</i> , Brood stock	<i>n</i> , Natural spawners	Hatchery produced adult offspring relative to wild
1998	55	104	2.77
1999	0	22	n/a
2000	72	87	1.22
2001	147	1334	5.35
2002	96	1103	5.48
2003	79	715	8.01
2004	57	271	5.29
2005	75	123	4.70
Mean			4.69

n is the sample size for the number of wild fish removed at the weir intended for use as brood stock (even if they did not have the opportunity to contribute offspring to the next generation), and the number of wild and hatchery fish allowed to spawn in the natural environment. Both *n* categories represent all individuals that were sampled, regardless of the occurrence of incomplete genetic data.

relationships were not possible to detect in our analyses. To take the most conservative approach, we counted all potential parents that were removed at the weir for brood stock, even if they did not have the opportunity to contribute offspring. We also counted all potential parents that were sampled regardless of the completeness of genetic data.

Our second objective was to determine whether there were differences in reproductive success between hatchery-reared and wild-origin fish spawning naturally (reproductive success of F_1 fish produced from BY 1998 and 2000). Mean reproductive success was estimated separately for males and females by age class. First-generation (F_1) offspring from BYs 1998 and 2000 returned as jacks (age 3 males) in 2001 and 2003, and F_1 males and females (ages 4 and 5) returned in 2002 through 2005 (Fig. 2). To compare reproductive success separately for jacks, males and females in each year, we calculated RRS by dividing the average reproductive success of hatchery-reared fish by the average reproductive success of wild fish of the same gender and age. RRS estimates were calculated in two ways to include (i) all F_1 potential parents and (ii) only successful F_1 parents that contributed to the next generation by producing one or more returning adult offspring. To compare reproductive success of hatchery-reared males and females, we calculated RRS by dividing the average reproductive success of hatchery-reared males by the average reproductive success of hatchery-reared females of the same age.

Finally, to assess the effect of hatchery-reared fish on the fitness of wild-origin fish, we compared the reproductive success among mating types in the wild for BY 2003 to 2005 ($H \times H$, $H \times W$, $H \times -$ vs. $W \times W$ and $W \times -$; where ‘-’ equals one unknown/unassigned parent). Age classes were combined in each return year (i.e. RS of all returns in a given year was evaluated), but comparisons were made separately for males and females in addition to an analysis of sexes combined (Table 3). If hatchery rearing reduces the fitness of wild-origin fish, we would expect the $H \times W$ mating type to produce significantly fewer returning adult offspring than the $W \times W$ mating type.

We tested statistical significance of all RRS estimates with a two-tailed permutation procedure using the comparison of means algorithm applied in PERM 1.0 (Duchesne *et al.* 2006) set at 10 000 permutations. To evaluate the power of our analysis, we used the distribution of reproductive success differences from the permutation tests to calculate the minimum difference in reproductive success that we could detect with 80% and 95% probability. Overall RRS values were estimated by weighted geometric means (by number of offspring), and corresponding *P*-values were calculated on the basis of Fisher’s combined probability.

Results

Parentage analysis

Combined nonexclusion probability for assignment of the first parent, second parent and parent pair was $2.30E-07$, $2.91E-10$ and $2.25E-17$, respectively (Table S1, Supporting information). Approximately 97.6% of samples (7481 of 7668; Table S2, Supporting information) were successfully genotyped at 12 or more loci and were included in parentage analysis. Of the adult offspring returning in 2001–2010 (representing BY 1998–2005), 87% on average were assigned a single parent or parental pair, with assignment success ranging from 69% in return year 2003 to 95% in 2005. Lower weir efficiencies (i.e. sampling rate of returning potential parents) in the initial years of the study (mean weir efficiency for 1998 and 2000 was 63%) likely influenced the assignment success rate. Improvements made to weir operation were accompanied by parentage assignment success rates consistently >90% beginning for fish returning in 2005 through 2010. Distribution of the number of offspring produced by fish that returned to spawn in the wild in 1998 through 2005 was highly skewed. The majority of natural spawners (both hatchery-reared and wild) produced no adult offspring, and approximately 32% of all females produced one or more returning adult offspring (Fig. S1, Supporting information). Only 16% of hatchery males produced adult

offspring compared with 25% of wild males (mean for 1998 through 2005). The number of hatchery-reared and wild-origin F_1 counterparts (born in 1998 and 2000) that returned and successfully reproduced in years 2001 through 2005 is shown in Table 2, and the number of F_2 fish that hatched in the wild in BYs 2003 to 2005 is shown in Table 3.

No offspring were compatible with more than one set of parents. There were 36 (0.9% of parentage assignments) offspring that assigned to a single parent in 1 year (with zero mismatches) and assigned to a parental pair in a different year. In these few cases, the assignment to two parents was accepted given the lower value of the combined nonexclusion probability of parent pairs compared with single-parent assignments. Approximately 5% of the parentage assignments were not logically possible, the majority of which occurred in the first supplementation year, 1998. In the cases where 'wild' offspring assigned to parent pairs that were mated in the hatchery, these offspring ($n = 97$, 80% were from BY 1998) were treated as hatchery-reared in subsequent RRS analyses because their hatchery mark was likely not observed during field sampling. A total of 125 offspring were not counted in RRS estimates. Specifically, 56 'wild' offspring assigned to a brood stock parent and a naturally spawning parent, 63 'wild' offspring assigned to a single brood stock parent, and 6 'hatchery' offspring assigned to parents

Table 2 Relative reproductive success (RRS) of successful (produced at least one returning adult offspring) female, male and jack F_1 fish from brood year (BY) 1998 and 2000

Return year	n F1 (H/W)	RS Hatchery	Variance hatchery	RS Wild	Variance wild	RRS*	P -value	80%/95% Power [†]	Age of returns
Females (4- & 5-year-old)									
2002	29/13	1.21	0.31	1.23	0.19	0.98	1.00	0.84/0.75	4 year from BY 1998
2003	20/43	1.25	0.20	1.30	0.41	0.96	0.83	0.85/0.76	5 year from BY 1998
2004	32/32	3.19	3.64	2.63	4.50	1.22	0.30	1.24/1.36	4 year from BY 2000
2005	8/3	4.25	1.07	5.00	9.00	0.85	0.55	0.85/0.58	5 year from BY 2000
Overall female [‡]						1.11	0.84		
Males (4- & 5-year-old)									
2002	24/32	1.21	0.26	1.25	0.39	0.97	0.83	0.85/0.74	4 year from BY 1998
2003	6/28	1.67	0.67	1.36	0.61	1.23	0.39	1.37/1.53	5 year from BY 1998
2004	26/36	2.54	4.34	3.17	4.43	0.80	0.27	0.78/0.66	4 year from BY 2000
2005	0/0	—	—	—	—	—	—	—	5 year from BY 2000
Overall male						0.89	0.56		
Jacks (3-year-old)									
2001	10/0	1.10	0.10	—	—	—	—	—	3 year from BY 1998
2003	15/8	1.20	0.31	1.75	1.07	0.68	0.16	0.88/0.66	3 year from BY 2000
Overall jack						—	—		

n is the sample size for number of naturally spawning successful (produced one or more returning adult offspring) hatchery-reared and wild F_1 fish from BY 1998 and BY 2000.

*RRS is calculated as the RS of hatchery-reared fish over the RS of wild-origin fish, and associated P -values are based on two-tailed permutation tests. Overall RRS was estimated using weighted geometric means, and the according P -values were calculated.

[†]Statistical power is the RRS value that would be significant with 80% and 95% probability.

[‡]Overall RRS estimate for females does not include return year 2005 due to low sample size.

Table 3 Relative reproductive success (RRS) of naturally spawning F₁ parents by mating type

Return year	<i>n</i> F ₂ offspring assigned	RRS*	<i>P</i> -value	80%/95% Power†
<i>H</i> × <i>H</i> vs. <i>W</i> × <i>W</i>				
Females				
2003	4/62	0.87	0.83	0.87/0.43
2004	40/79	0.76	0.17	0.76/0.67
2005	30/22	1.14	0.67	1.36/1.55
Overall female		0.87	0.58	
Males				
2003	4/62	1.03	1.00	1.31/1.58
2004	40/79	0.94	0.76	0.77/0.67
2005	30/22	1.02	1.00	1.50/1.74
Overall male		0.98	1.00	
Overall both sexes		0.94	0.95	
<i>H</i> × <i>W</i> vs. <i>W</i> × <i>W</i>				
Females				
2003	41/62	1.05	0.68	1.13/1.18
2004	108/79	1.12	0.48	1.21/1.32
2005	68/22	1.30	0.33	1.35/1.49
Overall female		1.14	0.62	
Males				
2003	41/62	0.96	0.85	0.88/0.80
2004	108/79	1.08	0.67	1.21/1.31
2005	68/22	0.93	0.83	0.69/0.51
Overall male		1.00	0.96	
Overall both sexes		1.07	0.92	
<i>H</i> × – vs. <i>W</i> × –				
Females				
2003	4/10	0.90	1.00	0.78/0.78
2004	5/15	0.72	0.77	0.63/0.41
2005	6/7	0.85	1.00	0.86/0.57
Overall female		0.82	1.00	
Males				
2003	1/4	—	—	—
2004	5/9	1.31	0.65	1.44/1.67
2005	2/8	0.75	1.00	0.75/0.75
Overall male		1.06	0.93	
Overall both sexes		0.91	1.00	

n is the sample size for the number of wild-born F₂ offspring that assigned to each parental mating type.

*RRS is calculated as the RS of hatchery-reared fish over the RS of wild-origin fish, and associated *P*-values are based on two-tailed permutation tests. Overall RRS was estimated using weighted geometric means, and the according *P*-values were calculated on the basis of Fisher's combined probability.

†Statistical power is the RRS value that would be significant with 80% and 95% probability.

that were not used for brood stock. A small opportunity exists for spawning downstream of the weir, and these particular types of matings (brood stock × natural spawner) may have occurred in low numbers before one parent was taken into the hatchery. For example,

there were 20 'wild' offspring from BY 1998 that assigned to two parents, where one parent was removed at the weir for brood stock, and the other parent was a natural spawner. These 20 offspring had one male parent in common that mated with multiple females (not used for brood stock). The male parent in this case successfully mated downstream of the weir before being captured for brood stock. These instances were not included in error estimates, and likewise these particular offspring were not included in RRS estimates.

For the empirical evaluation of parentage assignment errors, we found that all hatchery-reared offspring (identified via coded wire tags and/or visual implant elastomer tags) were assigned to parents that were used as brood stock, but 3.5% did not assign to the known mated parent pairs indicated by hatchery records (type A error). Inaccurate hatchery records cannot be distinguished from parentage errors and were therefore included in error estimates. Assignment of offspring to an untrue parent(s) resulted in overall 2.0% type B error (78 of 3933 offspring assigned to untrue parents). Specifically, 3.0% of hatchery-reared offspring assigned to one parent not used for brood stock, and 1.6% of wild-origin offspring assigned to one parent used for brood stock. Type B errors were confined to single-parent assignments only, as there were no trios.

Relative reproductive success

Demographic boost from hatchery-reared fish?

The numbers of returning adult offspring produced by fish removed for brood stock compared with their naturally spawning counterparts were variable each year. A range of 1.22 (BY 2000) to 8.01 (BY 2003) times as many returning adult offspring were produced in the hatchery compared with in the wild (Table 1). Averaged across all seven brood years, fish removed for brood stock produced 4.69 times more returning adult offspring (average for BY 1998 and BY 2000: 2.00) and 1.32 times as many returning adult grand-offspring on average for two brood years (BY 1998: 1.37; and 2000: 1.28) compared with their naturally spawning counterparts. Even though survival advantages of the hatchery environment were no longer present in the second generation (as these fish produced offspring in the wild environment), the demographic boost provided by the hatchery from BY 1998 and BY 2000 continued in the second generation.

Differences in hatchery-reared versus wild-origin reproductive success?

Estimates of RRS for hatchery-reared and wild-origin naturally spawning F₁ offspring (from BYs 1998 and 2000) are shown separately for jacks, males and females

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by age class in Table S3 (Supporting information, for all potential parents) and Table 2 (for successful spawners only). For hatchery-reared F_1 females, mean RRS = 1.00 ($P = 0.19$), and none of the comparisons were significantly different from 1.0 (Table S3, Supporting information). For hatchery-reared adult males, mean RRS = 0.64 ($P < 0.01$) and was significantly lower in 2002 and for the 3 years combined (Table S3, Supporting information). Only one jack year was compared because wild-origin jacks that returned in 2001 did not produce any adult offspring. Unbiased RRS for hatchery-reared jacks in 2003 was 0.32 and was significantly lower ($P < 0.01$) than wild-origin counterparts (Table S3, Supporting information). The age 5 offspring from BY 2000 were not included in overall RRS estimates due to small sample size (0 males and only 12 females returned in 2005). Hatchery-reared male to hatchery-reared female RRS was 0.54 ($P = 0.03$, age 4 from BY 1998) in 2002, 1.21 ($P = 0.77$, age 5 from BY 1998) and 0.60 ($P = 0.03$, age 4 from BY 2000) in 2004.

In F_1 return years 2002–2004 (from BY 1998 and BY 2000), 40% of wild males and 31% of hatchery-reared males produced at least one adult offspring; 45% of wild females and 41% of hatchery-reared females produced at least one adult offspring (Table S4, Supporting information). Of the wild and hatchery fish that successfully reproduced (i.e. one or more adult offspring), RRS estimates were very similar and not statistically significant between any comparisons (Table 2; Fig. 3). For hatchery-reared F_1 females, unbiased RRS ranged from 0.96 ($P = 0.83$) to 1.22 ($P = 0.30$), and mean RRS = 1.11 ($P = 0.84$). For hatchery-reared F_1 males, unbiased RRS ranged from 0.80 ($P = 0.27$) to 1.23 ($P = 0.39$), and mean RRS = 0.89 ($P = 0.56$). Unbiased RRS for hatchery-reared jacks in 2003 was 0.68, but was not significantly lower ($P = 0.16$) than wild-origin counterparts (Table 2; Fig. 3).

Hatchery impacts to fitness of wild fish?

Comparisons of reproductive success for naturally spawning F_1 fish by mating type ($H \times H$, $H \times W$, $H \times -$ vs. $W \times W$ and $W \times -$) are shown separately for males and females in Table 3 (reproductive success and variance estimates are shown in Table S5, Supporting information). Compared with the fitness of mating by two wild-origin parents ($W \times W$), the mating by two hatchery-reared parents ($H \times H$) and one hatchery-reared and one wild-origin ($H \times W$) parent averaged 94.3% and 107.0%, respectively, for both sexes combined and was not significantly different from 1.0 in any comparison (Table 3; Fig. 4). Although RRS point estimates varied among years for both males and females, they were not significantly different from 1.0 in any comparison (Table 3). Four offspring assigned to $H \times H$ matings in

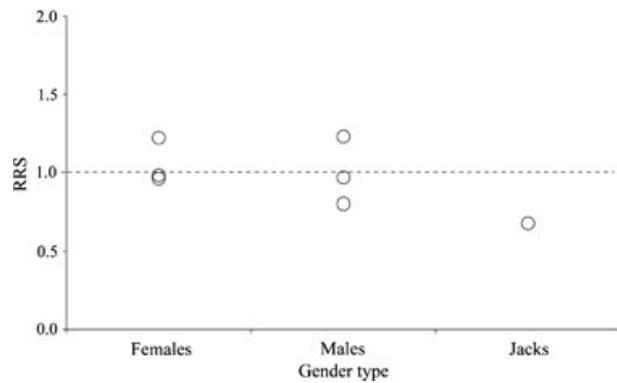


Fig. 3 Relative reproductive success (RRS) of successful F_1 spawners that produced one or more adult offspring (from BY 1998 and 2000), hatchery-reared relative to wild-origin fish for each gender type. Each point represents the estimate of RRS for each year compared and used to quantify overall RRS estimates; 2002–2004 (see associated Table 2). The dotted line (RRS = 1.0) represents where reproductive success of hatchery-reared fish is equal to that of wild-origin fish. Jacks are 3-year-old males.

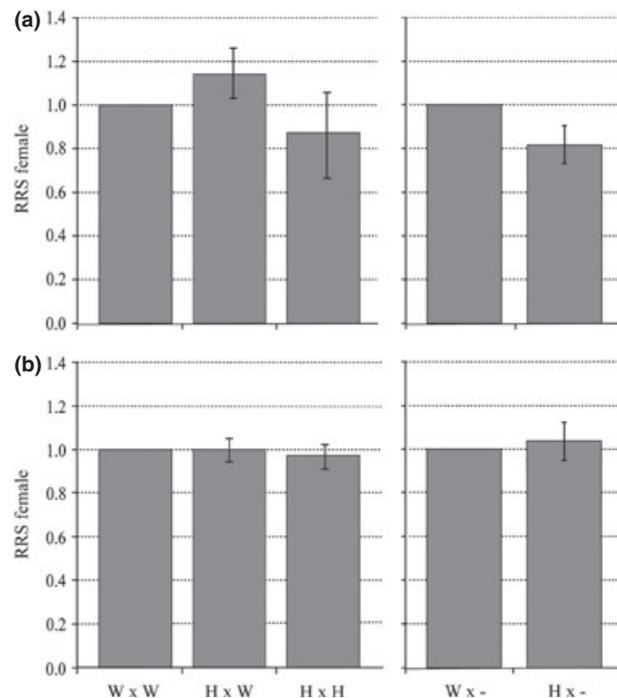


Fig. 4 Relative reproductive success (RRS) of each F_1 mating type in the wild, relative to $W \times W$ or $W \times -$ (RRS = 1.0, by definition). ‘-’ equals unknown/unassigned parent. (a) Female F_1 s, (b) male F_1 s. Weighted geometric mean RRS among return years 2003–2005 is plotted for $H \times W$ and $H \times H$ relative to $W \times W$ on the left panels, and for $H \times -$ relative to $W \times -$ on the right panels. Error bar represents 1 SD.

2003, and RRS of $H \times H$ females relative to $W \times W$ females was 0.87. The small sample size for $H \times H$ matings in 2003 was due to few F_1 hatchery females return-

ing that year relative to wild, because most of the hatchery females produced in 1998 largely returned as 4-year-olds (65%) in 2002. Table S3 (Supporting information) shows the breakdown of sample sizes by age and sex for fish returning from the two initial supplementation years. Specifically, in return year 2003, there were almost twice as many wild 5-year-old females returning from BY 1998 compared with 5-year-old hatchery females (which largely returned as 4-year-olds in 2002). Removing year 2003 (due to small sample size) in overall estimates of RRS for $H \times H$ vs. $W \times W$ comparisons for males and females revealed similar results to those reported in Table 3 (females: RRS = 0.86, $P = 0.36$, males: RRS = 0.96, $P = 0.97$). Despite small sample sizes for single-parent assignments, comparisons over all years for both sexes ($H \times -$ vs. $W \times -$) yielded similar results where $H \times -$ produced offspring at 90.5% of $W \times -$, which was also not significantly different from 1.0 (Table 3; Fig. 4).

Discussion

The primary goals of the supplementation programme appear to have been met by providing a demographic boost to the wild population without significantly reducing fitness during the initial two generations of supportive breeding. Hatchery rearing of wild fish resulted in more wild-born adults in the next two generations than if fish had been left to spawn in nature, presumably due to survival advantages conferred by hatchery rearing. We generally fail to reject the null hypothesis that reproductive success of hatchery-reared fish is equal to that of wild-origin fish. The exception of significantly low values of RRS in BYs 2002 and 2003 was driven by hatchery males that did not reproduce, and thus had no effect on fitness of the wild population. Our results show that the reproductive success of successful hatchery-reared parents was not significantly different from wild and that mating types involving hatchery-reared parent(s) ($H \times H$, $H \times W$; or $H \times -$) were not significantly different from mating by wild-origin parent(s) ($W \times W$; or $W \times -$). Thus, evidence does not support that Chinook salmon reared for a single generation in the hatchery had negative fitness effects on wild-origin fish in Johnson Creek.

Further investigation into significantly low reproductive success of hatchery-reared males compared with wild males in 2 years revealed that this result was largely driven by individuals that produced no offspring: (i) 3-year-old males (jacks) from BY 2000 and (ii) 4-year-old males from the first supplementation year, BY 1998. Low reproductive success of hatchery-reared jacks compared with their wild-origin jack counterparts may be due to differences in rearing conditions, such as

increased growth opportunities in the hatchery environment. The incidence of early maturation in hatchery Chinook salmon is higher than in the wild (Larsen *et al.* 2004), as is the case in Johnson Creek. Hatchery-reared jacks from BY 2000 comprised 41% of the F_1 hatchery returns, whereas wild-origin jacks comprised only 13% of F_1 wild returns from BY 2000. In general, jacks are at a disadvantage for breeding success compared with large males that have better access to mating with females (Foote *et al.* 1997; Berejikian *et al.* 2010), and the higher incidence of jacks produced in the hatchery may further impact reproductive success compared with their wild-origin jack counterparts. Despite the higher incidence of jacks among hatchery returns, there is no evidence of a shift in age at return for the natural population over time (data not shown). The consequences, if any, of the hatchery jacks on the long-term viability of the natural population will be evaluated in the future.

The lowest values of RRS were observed for age 4 hatchery returns in 2002 (from BY 1998) for both males and females. This result was only statistically significant for males, but RRS estimates were below one for females returning from the first year of supplementation, and power to detect significant differences in these comparisons was low. This result is consistent with Araki *et al.* (2007b), who found that hatchery-reared fish did slightly worse in the first major return year of supplementation. However, the comparisons for females returning in 2004 and 2005 (representing the second year of supplementation, BY 2000) showed RRS estimates >1 . High annual variation in RRS of hatchery-origin fish is common in these types of studies (Araki *et al.* 2009), and additional annual comparisons will be needed to better understand the effect of hatchery rearing on the fitness of hatchery females in Johnson Creek.

Many hatchery-reared fish that returned to spawn in 2002 (from BY 1998, age 4) did not produce offspring, and this may be due to density-dependent effects and sexual selection. Return year 2002 had >1000 returning adults, making it the third highest return of Chinook salmon to Johnson Creek, behind only 2001 and 2010. Fleming & Gross (1993) observed hatchery-reared fish to be at a reproductive disadvantage compared with wild fish under high densities, with this effect especially pronounced in males. Density may also have had an effect in 2001 and 2010, but we could only compare the age 3 component (jacks) in 2001 because the eight natural jacks did not produce returning offspring, and in 2010 will not be evaluated until offspring return in 2013 through 2015. Density effects on fitness may result from hatchery-reared males showing less aggression compared with wild males when competing for access to spawning females (Fleming *et al.* 1996; Pearsons *et al.* 2007), possibly an outcome of relaxed selection in the

hatchery environment (Theriault *et al.* 2011). Indeed, two studies on the reproductive success of Chinook salmon also showed a stronger effect of hatchery rearing on males than on females (Williamson *et al.* 2010; Anderson *et al.* 2012).

Our study may provide additional support of relaxed selection in the hatchery as a mechanism for reduced reproductive success. Similar to Theriault *et al.* (2011), we found that F_1 hatchery-reared males had significantly reduced fitness compared with hatchery-reared females, suggesting a role for sexual selection. The reduction in fitness for males may be attributable to the artificial mating of competitively less fit males (e.g. less aggressive) that may not have otherwise successfully reproduced in the wild. In addition, the reduced reproductive success of hatchery males in 2 years may also be influenced by environmental effects in the hatchery.

Reproduction in the natural environment allows an opportunity for selection to act, providing a fitness advantage to individuals that are best suited to the local environment. Although genetic adaptation to captivity can occur rapidly (e.g. Christie *et al.* 2011), it is important to recognize that selection also acts in the natural environment when hatchery-reared fish return to spawn, where only a portion successfully contributes offspring to the next generation. These are the individuals that have the potential to directly impact fitness of the wild population, but we found no evidence of a negative fitness effect on wild fish when hatchery fish mated with them, and this was consistent for both males and females. Reproductive success of $H \times H$ pairings compared with $W \times W$ pairings for 2 of the 3 compared years resulted in RRS <1.0 for females and lower RRS for $H \times -$ females relative to $W \times -$ females in all three comparisons. Possible concern is warranted with regard to the RS of $H \times H$ pairings, as they may not produce as many returning adult offspring as $W \times W$ or $W \times H$ pairings.

We found no significant reduction in fitness of the hatchery fish that were successful during reproduction and more importantly, and we found no reduction in the fitness of wild fish when they mated with hatchery fish—a result that is novel compared with other published RRS studies. Araki *et al.* (2007b) found that first-generation hatchery fish (from a traditional hatchery) were reproductively less fit than wild fish and that second-generation wild-born fish produced from two hatchery parents had even lower reproductive fitness, suggesting a carry-over effect of artificial rearing that inflicted negative fitness impacts to wild fish (Araki *et al.* 2009). The lack of prior history of hatchery influence in our system, as evidenced by a lack of hatchery influence detected in Johnson Creek and the Secesh River (un-supplemented) compared with the heavily supplemented upper mainstem of the SFSR (Matala *et al.* 2012), may be an impor-

tant difference between the hatchery programme evaluated in our study and the systems that have been evaluated in other studies. Domestication impacts from nearby hatchery releases are possible despite the effort to exclude hatchery strays from Johnson Creek; however, those impacts are greatly reduced compared with other systems that are the topic of published RRS studies. Minimal prior hatchery influence in Johnson Creek further increases the potential to detect significant differences in RS between hatchery and wild fish, yet evidence for differences was limited to males that did not produce any offspring. In addition, domestication impacts are further reduced due to the nature of the Johnson Creek supplementation programme as the genetic composition of brood stock represents wild-origin fish that experience their entire life cycle in the natural environment. Minimal domestication impacts in Johnson Creek may help to explain why we did not find that hatchery fish reduced the fitness of wild fish. For example, steelhead in the Hood River system (Araki *et al.* 2007b, 2009) had a history of out-of-basin hatchery influence prior to initiation of their RRS study, and hatchery fish were incorporated into brood stock each year. Similarly, programmes that were the subject of the RRS studies by Williamson *et al.* (2010), Berntson *et al.* (2011) and Theriault *et al.* (2011) also involve hatchery programmes that use brood stock comprised in large part (up to 70–80%) by hatchery-reared fish each year. Indeed, even a few generations of domestication can have negative effects on natural reproduction in the wild (Araki *et al.* 2007a; Christie *et al.* 2011). These empirical studies indicate that use of primarily hatchery-origin fish in brood stock may result in poor performance in the wild (more generations of domestication selection) and may translate to reductions in fitness of wild fish when hatchery-reared fish mate with them.

Our study does not directly estimate genetic versus environmental components of differences between hatchery-reared and wild-origin fish (F_1 s experienced different rearing environments), which would allow us to determine whether there is a carry-over effect of artificial rearing (as found in analysis of F_2 RRS by Araki *et al.* 2009). However, based on our results thus far, it would be unexpected to see a fitness decline between the F_1 and F_2 generations because the F_2 generation is an additional generation removed from potential domestication effects, and we did not observe fitness declines of wild fish in the F_1 generation when they mated with hatchery-reared fish. We recognize that even though only wild-origin fish are used as brood stock each year, the effects of hatchery rearing may inflict small changes in fitness that may not result in significant differences in one generation, but the possibility exists for changes to accumulate over time. The effect of supplementation on the natural popula-

tion over greater than two generations will be evaluated in future years.

Our power to detect significant differences in reproductive success between hatchery-reared and wild-origin fish varied annually and is comparable to published studies where, in some years, a 50% or greater reduction in hatchery-reared reproductive success would be needed to detect a significant difference from wild-origin reproductive success (Araki *et al.* 2007a,b; Theriault *et al.* 2011). Despite some single years with reduced power, combining probabilities across multiple data sets (years) for both single-sex and mating type comparisons did not yield significant results (with the exception of males described above). Further, removal of years with low sample size had no appreciable effect on RRS comparisons. Overall, our study represents one of the most thorough data sets from a wild population to evaluate relative fitness of a supportive breeding programme. This is evident from the number of years (13) included to represent a multiple generation pedigree of spawning adults, number of fish genotyped (7481), number of microsatellite loci (15) and proportion of offspring that were able to be assigned to parents (87%). These numbers compare favourably to other studies of RRS (Araki *et al.* 2007a,b, 2009; Williamson *et al.* 2010; Berntson *et al.* 2011; Theriault *et al.* 2011; Anderson *et al.* 2012).

A variety of management protocols and strategies exist among Pacific salmonid hatchery programmes (Naish *et al.* 2007; Paquet *et al.* 2011), and each species represents multiple genetic lineages and life history traits (Waples *et al.* 2001). Given such diversity, from relatively few and isolated RRS studies conducted so far, it would be premature to generalize that all hatchery-reared fish are significant drivers of fitness declines in wild populations. Specifically, perhaps steelhead, which have been the focus of many RRS studies, are simply more prone to reduced fitness due to hatchery rearing practices. In hatcheries, prior to release in the wild, steelhead juveniles are reared for 1 year until smoltification, a physiological process that prepares fish for transition from freshwater to saltwater. The accelerated smoltification process in the hatchery deviates from the typical 2-year time frame to smolt in nature. Alternatively, Chinook salmon are reared in hatcheries for a time frame more similar to their natal juvenile rearing time of 1 year. Populations experiencing a captive environment that is most similar to what is experienced in the natural environment may show the least divergence from the original wild population (Shuster *et al.* 2005), and risks of genetic adaptation to artificial environments are reduced with fewer numbers of generations in captivity (reviewed in Williams & Hoffman 2009). Nevertheless, our results place into question the

generalization that all hatchery fish are significant drivers for fitness declines by demonstrating that supplementation programmes, under certain management practices (e.g. using local wild-origin brood stock, minimal time spent in captivity), can successfully boost population size with minimal negative impacts to the fitness of Chinook salmon in the wild.

In the face of environmental perturbations, fishery harvest and habitat alterations, the ability for anadromous salmonids at risk of extinction to recover to sustainable levels is uncertain. Supportive breeding is simply one of the many tools needed to re-build depressed populations and maintain abundance. In addition to salmonids, many species are incapable of sustaining themselves predominately due to human impacts, and the need to take individuals into a captive environment for long-term survival is a reality for many threatened and endangered species. A goal for captive programmes is to limit deleterious genetic changes during captivity, so that the long-term viability of a population in the wild environment is maximized. One way to minimize the effects of adaptation to captivity, and perhaps subsequent negative impacts on wild populations, is to incorporate some portion of wild genes into the captive population each year. Our study highlights the value in using wild individuals adapted to local environmental conditions for supportive breeding.

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References

- Anderson JH, Faulds PL, Atlas WI, Quinn TP (2012) Reproductive success of captive bred and naturally spawned Chinook salmon colonizing newly accessible habitat. *Evolutionary Applications*, **1752–4571**, 1–15.
- Araki H, Blouin MS (2005) Unbiased estimation of relative reproductive success of different groups: evaluation and correction of bias caused by parentage assignment errors. *Molecular Ecology*, **14**, 4097–4109.
- Araki H, Cooper B, Blouin MS (2007a) Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. *Science*, **318**, 100–103.

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- Araki H, Ardren WR, Olsen E, Cooper B, Blouin MS (2007b) Reproductive success of captive-bred steelhead trout in the wild: evaluation of three hatchery programs in the Hood River. *Conservation Biology*, **21**, 181–190.
- Araki H, Cooper B, Blouin MS (2009) Carry-over effect of captive breeding reduces reproductive fitness of wild-born descendants in the wild. *Biology Letters*, **5**, 621–624.
- Banks MA, Blouin MS, Baldwin BA *et al.* (1999) Isolation and inheritance of novel microsatellites in Chinook salmon (*Oncorhynchus tshawytscha*). *Journal of Heredity*, **90**, 281–288.
- Berejikian BA, Van Doornik DM, Scheurer JA, Bush R (2009) Reproductive behavior and relative reproductive success of natural- and hatchery-origin Hood Canal summer chum salmon (*Oncorhynchus keta*). *Canadian Journal of Fisheries and Aquatic Sciences*, **66**, 781–789.
- Berejikian BA, Van Doornik DM, Endicott RC *et al.* (2010) Mating success of alternative male phenotypes and evidence for frequency-dependent selection in Chinook salmon, *Oncorhynchus tshawytscha*. *Canadian Journal of Fisheries and Aquatic Sciences*, **67**, 1933–1941.
- Berntson EA, Carmichael RW, Flesher MW, Ward EJ, Moran P (2011) Diminished reproductive success of Steelhead from a hatchery supplementation program (Little Sheep Creek, Imnaha Basin, Oregon). *Transactions of the American Fisheries Society*, **140**, 685–698.
- Cairney M, Taggart JB, Hoyheim B (2000) Atlantic salmon (*Salmo salar* L) and cross-species amplification in other salmonids. *Molecular Ecology*, **9**, 2175–2178.
- Chilcote MW, Leider SA, Loch JJ (1986) Differential reproductive success of hatchery and wild summer-run steelhead under natural conditions. *Transactions of the American Fisheries Society*, **115**, 726–735.
- Chilcote MW, Goodson KW, Falcy MR (2011) Reduced recruitment performance in natural populations of anadromous salmonids associated with hatchery-reared fish. *Canadian Journal of Fisheries and Aquatic Sciences*, **68**, 511–522.
- Christie MR, Marine ML, French RA, Blouin MS (2011) Genetic adaptation to captivity can occur in a single generation. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 238–242.
- Cuenco ML, Backman TWH, Mundy PR (1993) The use of supplementation to aid in natural stock restoration. In: *Genetic Conservation of Salmonid Fisheries* (eds Cloud JG, Thorgaard GH), pp. 269–293. Plenum Press, New York.
- Duchesne P, Bernatchez L (2002) An analytical investigation of the dynamics of inbreeding in multi-generation supportive breeding. *Conservation Genetics*, **3**, 47–60.
- Duchesne P, Etienne C, Bernatchez L (2006) PERM: A computer program to detect structuring factors in meaningful social units. *Molecular Ecology Notes*, **6**, 965–976.
- Eldridge WH, Myers JM, Naish KA (2009) Long-term changes in the fine-scale population structure of coho salmon populations (*Oncorhynchus kisutch*). *Heredity*, **103**, 299–309.
- Fleming IA, Gross MR (1993) Breeding success of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in competition. *Ecological Applications*, **3**, 230–245.
- Fleming IA, Jonsson B, Gross MR, Lamberg A (1996) An experimental study of the reproductive behaviour and success of farmed and wild Atlantic Salmon (*Salmo salar*). *Journal of Applied Ecology*, **33**, 905.
- Footo CJ, Brown GS, Wood CC (1997) Spawning success of males using alternative mating tactics in sockeye salmon, *Oncorhynchus nerka*. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 1785–1795.
- Ford MJ (2002) Selection in captivity during supportive breeding may reduce fitness in the wild. *Conservation Biology*, **16**, 815–825.
- Ford MJ, Hard JJ, Boelts B, LaHood E, Miller J (2008) Estimates of natural selection in a salmon population in captive and natural environments. *Conservation Biology*, **22**, 783–794.
- Frankham R (2008) Genetic adaptation to captivity in species conservation programs. *Molecular Ecology*, **17**, 325–333.
- Frankham R, Loebel DA (1992) Modeling problems in conservation genetics using captive *Drosophila* populations: rapid genetic adaptation to captivity. *Zoo Biology*, **11**, 333–342.
- Frankham R, Ballou JD, Briscoe DA (2002) *Introduction to Conservation Genetics*, pp. 419–447. Cambridge University Press, Cambridge, UK.
- Fraser DJ (2008) How well can captive breeding programs conserve biodiversity? A review of salmonids. *Evolutionary Applications*, **1**, 535–586.
- Goodman D (2005) Selection equilibrium for hatchery and wild spawning fitness in integrated breeding programs. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 374–389.
- Greig C, Banks MA (1999) Five multiplexed microsatellite loci for rapid response run identification of California's endangered winter Chinook salmon. *Animal Genetics*, **30**, 316–317.
- Greig C, Jacobson DP, Banks MA (2003) New tetranucleotide microsatellites for fine-scale discrimination among endangered Chinook salmon (*Oncorhynchus tshawytscha*). *Molecular Ecology Notes*, **3**, 376–379.
- Heath DD, Heath JW, Bryden CA, Johnson RM, Fox CW (2003) Rapid evolution of egg size in captive salmon. *Science*, **299**, 1738–1740.
- Interior Columbia Technical Recovery Team (ICTRT) (2005) Interior Columbia Basin TRT: Viability Criteria for Application to Interior Columbia Basin Salmonid ESUs. Attachment E: Population/Major Population Grouping Summaries (by ESU). Available at: http://www.nwfsc.noaa.gov/trt/trt_documents/viability2005_july_draft.pdf (accessed 12 March 2012).
- IUCN (1998) Guidelines for Reintroductions. Available at: <http://www.iucn.org/knowledge/tools/tools/conservation/> (Accessed 12 March 2012).
- Johnsson JL, Petersson E, Jonsson E, Björnsson BT, Jarvi T (1996) Domestication and growth hormone alter antipredator behaviour and growth patterns in juvenile brown trout, *Salmo trutta*. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 1546–1554.
- Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology*, **16**, 1099–1106.
- Laike L, Schwartz MK, Waples RS, Ryman N, The GeM Working Group (2010) Compromising genetic diversity in the wild: unmonitored large-scale release of plants and animals. *Trends in Ecology and Evolution*, **25**, 520–529.
- Larsen DA, Beckman BR, Cooper KA *et al.* (2004) Assessment of high rates of precocious male maturation in a

- spring Chinook salmon supplementation hatchery program. *Transactions of the American Fisheries Society*, **133**, 98–120.
- Lynch M, O'Hely M (2001) Captive breeding and the genetic fitness of natural populations. *Conservation Genetics*, **2**, 363–378.
- Marshall TC, Slate J, Kruuk LEB, Pemberton JM (1998) Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology*, **7**, 639–655.
- Matala AP, Young W, Vogel JL, Narum SR (2012) Influences of hatchery supplementation, spawner distribution and habitat on genetic structure of Chinook salmon (*Oncorhynchus tshawytscha*) in the South Fork Salmon River, ID. *North American Journal of Fisheries Management*, **32**, 346–359.
- McGinnity P, Jennings E, deEyto E *et al.* (2009) Impact of naturally spawning captive-bred Atlantic salmon on wild populations: depressed recruitment and increased risk of climate-mediated extinction. *Proceedings of the Royal Society of London, Series B*, **276**, 3601–3610.
- McLean JE, Bentzen P, Quinn TP (2003) Differential reproductive success of sympatric, naturally spawning hatchery and wild steelhead trout (*Oncorhynchus mykiss*) through the adult stage. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 433–440.
- Naish KA, Taylor JE, Levin PS *et al.* (2007) An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. *Advances in Marine Biology*, **53**, 61–194.
- Narum SR, Hess JE, Matala AP (2010) Examining genetic lineages of Chinook salmon in the Columbia River Basin. *Transactions of the American Fisheries Society*, **139**, 1465–1477.
- Nelson RJ, Beacham TD (1999) Isolation and cross species amplification of microsatellite loci useful for study of Pacific salmon. *Animal Genetics*, **30**, 228–229.
- Olsen JB, Bentzen P, Seeb JE (1998) Characterization of seven microsatellite loci derived from pink salmon. *Molecular Ecology*, **7**, 1087–1089.
- Paquet PJ, Flagg T, Appleby A *et al.* (2011) Hatcheries, conservation, and sustainable fisheries—achieving multiple goals: results of the Hatchery Scientific Review Group's Columbia River basin review. *Fisheries*, **36**, 547–561.
- Pearsons TN, Fritts AL, Scott JL (2007) The effects of hatchery domestication on competitive dominance of juvenile spring Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences*, **64**, 803–812.
- Rabe CD, Nelson DD (2010) Status and Monitoring of Natural and Supplemented Chinook Salmon in Johnson Creek, Idaho. Report of Nez Perce Tribe to Bonneville Power Administration, Portland, Oregon. Available at: <https://piscis.bpa.gov/release/documents/documentviewer.aspx?doc=P124099>.
- Reisenbichler RR, Rubin S, Wetzel L, Phelps S (2004) Natural selection after release from a hatchery leads to domestication in steelhead, *Oncorhynchus mykiss*. In: Stock Enhancement and Sea Ranching (eds Leber M, Kitada S, Blankenship HL, Svasand T), pp. 371–384. Blackwell Publishing Ltd, Oxford.
- Rexroad CE, Coleman RL, Martin AM, Hershberger WK, Killefer J (2001) Thirty-five polymorphic microsatellite markers for rainbow trout (*Oncorhynchus mykiss*). *Animal Genetics*, **32**, 317–319.
- Schroder SL, Knudsen CM, Pearsons TN *et al.* (2008) Breeding success of wild and first generation hatchery female spring Chinook salmon spawning in an artificial stream. *Transactions of the American Fisheries Society*, **137**, 1475–1489.
- Schroder SL, Knudsen CM, Pearsons TN *et al.* (2010) Behavior and breeding success of wild and first generation hatchery male spring Chinook Salmon spawning in an artificial stream. *Transactions of the American Fisheries Society*, **139**, 989–1003.
- Shuster SM, Miller MP, Lang BK, Zorich N, Huynh L, Keim P (2005) The effects of controlled propagation on an endangered species: genetic differentiation and divergence in body size among native and captive populations of the Socorro Isopod (Crustacea: Flabellifera). *Conservation Genetics*, **6**, 355–368.
- Therault V, Moyer GR, Jackson LS, Blouin MS, Banks MA (2011) Reduced reproductive success of hatchery Coho salmon in the wild: insights into most likely mechanisms. *Molecular Ecology*, **20**, 1860–1869.
- Wang J, Ryman N (2001) Genetic effects of multiple generations of supportive breeding. *Conservation Biology*, **15**, 1619–1631.
- Wang S, Hard JJ, Utter FM (2002) Salmonid inbreeding: a review. *Reviews in Fish Biology and Fisheries*, **11**, 301–319.
- Waples RS, Gustafson RG, Weitkamp LA *et al.* (2001) Characterizing diversity in salmon from the Pacific Northwest. *Journal of Fish Biology*, **59**, 1–41.
- Waples RS, Ford MJ, Schmitt D (2007) Empirical results of salmon supplementation in the Northeast Pacific: a preliminary assessment. In: Ecological and Genetic Implications of Aquaculture Activities (ed. Bert TM), pp. 383–403. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Williams SE, Hoffman EA (2009) Minimizing genetic adaptation in captive breeding programs: A review. *Biological Conservation*, **142**, 2388–2400.
- Williamson KS, Cordes JF, May B (2002) Characterization of microsatellite loci in Chinook salmon (*Oncorhynchus tshawytscha*) and cross-species amplification in other salmonids. *Molecular Ecology Notes*, **2**, 17–19.
- Williamson KS, Murdoch AR, Pearsons TN, Ward EJ, Ford MJ (2010) Factors influencing the relative fitness of hatchery and wild spring Chinook salmon (*Oncorhynchus tshawytscha*) in the Wenatchee River, Washington, USA. *Canadian Journal of Fisheries and Aquatic Sciences*, **67**, 1840–1851.

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Data accessibility

Sample locations and microsatellite data: DRYAD entry doi: 10.5061/dryad.19p14.

Supporting information

Additional Supporting Information may be found in the online version of this article.

Table S1 Summary statistics for each microsatellite locus.

Table S2 Number of individuals by origin for each return year that were genotyped for this study, and were included in parentage analysis.

Table S3 Relative reproductive success (RRS) of female, male and jack F_1 fish (including potential parents producing zero adult offspring) from BY 1998 and 2000.

Table S4 Supplementary information for Table 2, showing the proportion of F_1 fish (from BY 1998 and 2000) that produced one or more returning adult offspring in 2002–2004.

Table S5 Supplementary information for Table 3, showing average reproductive success (RS) and variance estimates.

Fig. S1 Histogram of estimated fitness (i.e. number of offspring produced) for hatchery- and wild-origin female natural spawners from 1998 through 2005.

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