

An Annotated Bibliography on the Impacts of Fish Hatchery Supplementation and Enhancement on Wild Populations



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Introduction

This bibliography and literature review was developed to summarize the impacts of fish stocking practices on top of self-sustaining (wild) populations. It has been prepared to summarize information pertaining to the current state of knowledge regarding fish stocking on top of existing wild populations which can readily be utilized by resources management staff and stocking proponents. Material cited in this bibliography was obtained by primarily researching papers published in scientific journals, mainly looking for papers dealing with salmonids, with most of the literature dealing with *Oncorhynchus* spp. The author acknowledges that other literature (technical or peer-reviewed) currently exists for this group of species as well as other species or families (e.g. Kerr et al. 1996), with the overall synopsis on the effects of supplementation for salmonids remaining relevant to these other species.

The stocking of propagated fishes has been a fisheries management tool for resource managers for more than a hundred years (Lichatowich 1999). During this time, the roles of propagated fish have been deemed to be important for addressing and enhancing opportunities to improve recreational, commercial, and aboriginal fisheries and restore depressed or lost fish populations. However, over the last 40 years, some of these efforts have been demonstrated to be environmentally risky, harmful to local populations, ineffective, or not cost effective and have been under careful scrutiny (Lichatowich 1999). Hatchery fish are generally considered to be fish that have been artificially spawned, reared and/or incubated artificially in a building that houses incubation trays, troughs, and outside concrete or dirt raceways and large surface or earthen ponds (Wedemeyer 2001). However, within this review, hatchery fish are more than that and fish propagated through stream-side gravel incubation boxes, spawning channels, and engineered streams are also considered hatchery fish.

Due to continued loss of habitat from urbanization, agriculture, pollution, and logging, as well as over-exploitation, artificial propagation will continue to have a major role in sustaining sport and commercial fisheries, especially put-delay-take fisheries and species at risk recovery. To be most effective in that role, it is believed that hatchery programs should be consistent with the biological needs of the local populations and when appropriate, both wild and hatchery components should be considered part of the population complex. If hatchery production programs are not given rigorous and objective evaluations, and the results of these evaluations applied in an inappropriate manner (e.g. driven by public opinion versus science-based evaluations), the health of wild populations and continued existence of these fisheries may be in danger. It has been documented that sometimes, under special circumstances, it may be beneficial to introduce additional genes into genetically-impoverished populations that exhibit reduced fitness, but that (a) the circumstances are very rare, and (b) there isn't very much applied data to support that this practice works. Under these circumstances, it is more probable that you might see a short-term increase in apparent productivity (e.g. Cena et al. 2006), but with longer-term negative consequences.

Hatchery programs can generally be classified into several broad categories – supplementation, enhancement, and mitigation. In supplemental programs, the primary

goal is to assist the local wild fish population, giving it a boost by supplementing the run size and resulting escapement. Enhancement programs are meant to supply more fish for harvest or recreation to create additional fishing opportunities. This latter program is often implemented through put-delay-take fisheries. It is not uncommon for these two programs to become hybridized. Mitigation hatchery programs often result as a trade-off for the loss of habitat (quality, function), or access to quality habitat (e.g. dams). Regardless of the type of program, the hatchery product will interact with both the wild fish and their environments in a variety of ways.

Stocking to increase a population of wild stocks can have detrimental effects by reducing the genetic diversity/viability of existing populations and encourage energy costly behavioural interactions. Pathogens are also capable of entering the ecosystem via the introduction of hatchery fish.

Genetic concerns about hatchery-reared fish fall into three categories: (1) direct genetic effects caused by introgression or hybridization; (2) indirect genetic effects caused by competition, predation, disease or any other factor that leads to reduced population size or altered selection regimes in the wild populations; and (3) genetic changes to hatchery stocks brought about by selection, drift, or stock transfers (Waples 1991).

This brief summary on the impacts of hatchery production is focused on how hatcheries affect the viability of wild/naturalized salmonids. The expanded bibliography includes abstracts of research conducted between wild salmonids and hatchery programs/fish, and their resulting impacts, concerns and warnings. The bibliography contains science based recommendations that are realistic, but require the public and management agencies to apply this science to their management, and educate stakeholders so progress can be made towards the management of wild/naturalized salmonid populations. Several important observations from the literature include:

- Naturally spawning hatchery fish from long-term hatchery cultivation produce 6-11% to the adult stage compared to wild fish (Leider et al. 1987; Araki et al 2007).
- In the first generation native broodstock hatchery fish (using wild salmonids for hatchery broodstock), the reproductive success of the hatchery fish spawning naturally in streams declines by 14% (males) and 2% (females) compared to wild fish spawning naturally in the river (Independent Science Review Panel 2011).
- In later generations (second and third) the reproductive success of native broodstock hatchery salmonid spawning naturally in streams is 50% (males) lower and 77% (females) lower than naturally spawning wild fish. (Independent Science Review Panel 2011).
- There is a genetic change in the hatchery salmonids that carries over to naturally produced progeny of hatchery-origin parents causing reduced reproductive fitness of wild-born descendants in the wild and the population fitness of subsequent generations (Araki et al. 2009; Independent Science Review Panel

2011).

- In just 6 generations native broodstock hatchery salmonid reproductive success is 29% to 54% that of wild steelhead (Berntson 2011).
- In order to maintain cost effective hatchery programs, access to healthy abundant wild salmonid populations is required (sensu Araki et al. 2008).
- The inability to incorporate genetic quality (additive and non-additive genetic effects), into supportive breeding programs can decrease offspring growth or survival by between 3% and 19% during the endogenous feeding stage alone, and projections to adulthood suggest that survivorship could be over four fold lower (Pitcher & Neff 2007).
- It is predicted that the recruitment performance for a salmonid population composed entirely of hatchery fish would be 13% of that for a population composed entirely of wild fish. There is no support that a population's reproductive performance is affected by the length of exposure to hatchery fish. In most cases, measures that minimize the interactions between wild and hatchery fish will be the best long-term conservation strategy for wild populations (Chilcote et al. 2011).
- In order to protect and rebuild wild salmonid populations harvest targeted on hatchery fish must be regulated to protect wild spawner abundance. Hatchery transfers among watersheds should be eliminated, and hatchery fish spawning in the wild should be excluded from wild fish spawning areas, unless part of reintroduction program (Lichatowich 1999; Independent Science Review Panel 2011).
- Impacts of hatchery fish on wild fish must be controlled so that competition for food and space for rearing juveniles in streams, estuary, or the lake/ocean support wild fish survival. Predation and predator attraction by hatchery fish should be controlled to protect survival of wild fish, and nutrient enrichment/food subsidies from natural spawning wild fish support and expand the productive capacity of the habitat. (Lichatowich 1999; Independent Science Review Panel 2011).
- Competition between wild and hatchery fish spawning naturally in a common habitat can reduce the production of wild juveniles by 50% (Kostow 2004).
- The cost to produce a hatchery salmonid that contributes to the catch (recreational or commercial) ranges from \$12 to over \$3,700 (Redman 2003). In the Great Lakes, cost per adult steelhead returning to the French River (Minnesota) was \$60.00 for fry-stocked fish, \$390.00 for hatchery reared steelhead, and \$90.00 for "kamloops" strain steelhead (Schreiner and Jones 1997). Most hatchery programs are funded with tax dollars and are not cost

effective relative to wild fisheries, making the hatchery program vulnerable to loss of funding as hatcheries compete for funding with other social needs for available dollars (Winton & Hilborn 1994).

References

Araki, H., B.A. Berejikian, M.J. Ford, and M.S. Blouin. 2008. Fitness of hatchery-reared salmonids in the wild. *Evolutionary Applications* 1(2): 342-355.

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*. 5: 621–624.

Araki, H., R.S. Waples, W.R. Arden, B. Cooper, M.S. Blouin. 2007. Effective population size of steelhead trout: influence of variance in reproductive success, hatchery programs, and genetic compensation between life-history forms. *Molecular Ecology* 16(5): 953-966.

Berntson, E.A., R.W. Carmichael, M.W. Flesher, E.J. Ward, and P. Moran. 2011. Diminished reproductive success of steelhead from a hatchery supplementation program (Little Sheep Creek, Imnaha Basin, Oregon). *Transactions of the American Fisheries Society* 140(3): 685 - 698.

Cena, C.J., Morgan, G.E., Malette, M.D., and D.D. Heath. 2006. Inbreeding, outbreeding and environmental effects on genetic diversity in 46 walleye (*Sander vitreus*) populations. *Molecular Ecology* 15: 303–320.

Chilcote, M.W., K.W. Goodson, and M.R. Falcy. 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.

Independent Science Review Panel 2011. Retrospective report: an expanded summary of the ISRP's review of results conducted for the research, monitoring and evaluation, and artificial production category review. Northwest Power & Conservation Council. Portland, OR.

Leider, S.A., J.J. Loch, and P.L. Hulett. 1987. Studies of hatchery and wild steelhead in the Lower Columbia Region. Progress Report for Fiscal Year 1987. Report No. 87-8. Washington Department of Wildlife.

Lichatowich, J. 1999. *Salmon without rivers: a history of the Pacific salmon crisis*. Washington DC. Island Press.

Kerr, S.J., B.W. Corbett, D.D. Flowers, D. Fluri, P.E. Ihssen, B.A. Potter, and D.E. Seip. 1996. Walleye stocking as a management tool. Percid community synthesis, Walleye Stocking Working Group, Ontario Ministry of Natural Resources, Peterborough. 80 p.

Kostow, K. 2004. Differences in juvenile phenotypes and survival between hatchery stocks and a natural population provide evidence for modified selection due to captive breeding. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 577–589.

Pitcher, T.E., and B.D. Neff. 2007. Genetic quality and offspring performance in Chinook salmon: implications for supportive breeding. *Conservation Genetics* 8: 607-616.

Redman, B. 2003. What role should hatchery fish have in ESA listings? *The Osprey*. 44: 3-5.

Schreiner, D.R., and T.S. Jones. 1997. Steelhead management in Minnesota: what path do we take? *Fish: To Stock or not to Stock*, Ontario Ministry of Natural Resources, Northwest Science & Technology. Thunder Bay, Ont. WP-003. 25 pp.

Waples, R.S. 1991. Genetic interactions between hatchery and wild salmonids: lessons from the Pacific Northwest. *Canadian Journal of Fisheries and Aquatic Sciences* 48 (SI): 124-156.

Winton, J., and R. Hilborn. 1994. Lessons from supplementation of Chinook salmon in British Columbia. *North American Journal of Fisheries Management* 14(1): 1-13.

Wedemeyer, G., ed. 2001. *Fish hatchery management*, second edition. American Fisheries Society, Bethesda, M.D.

Annotated Bibliography

Allendorf, F.W. 1991. Ecological and genetic effects of fish introductions. Canadian Journal of Fisheries and Aquatic Sciences 48(S1): 178-181.

The papers resulting from this symposium review the ecological and genetic effects of fish introductions throughout the world. Purposeful introductions rarely have achieved their objectives. Moreover, both intentional and unintentional introductions usually have been harmful to native fishes and other taxa through predation, competition, hybridization, and the introduction of diseases. We must learn from the past in order to avoid mistakes in the future. Introductions should not be used as a management tool without sufficient prior information and understanding to predict their effects. Introductions are often made or permitted because of the demands of certain interest groups (e.g. anglers or aquaculturists). Education of the public to the potential dangers and costs of such introductions is essential. Cooperation among management agencies is necessary to regulate and control both the purposeful and accidental introductions of fishes. Waples (1991) reviews the history of genetic interactions between hatchery and wild salmonids in the Pacific Northwest of the United States. He concludes that supplementation programs have not been successful and that such programs present a threat to the long term survival of Pacific salmon species. He suggests that the rule of (hatchery) supplementation programs should be first, do no harm. That is, such programs should not be undertaken unless there is adequate assurance that wild stocks will not be harmed. He also recommends that monitoring programs should be an integral part of any supplementation effort.

Allendorf, F.W., and S.R. Phelps. 1980. Loss of genetic variation in hatchery stock of Cutthroat Trout. Transactions of the American Fisheries Society 109: 537-543.

We have detected significant reduction in genetic variation at isozyme loci in a hatchery stock of west-slope cutthroat trout (*Salmo clarki*) in comparison to the wild stock from which it was derived 14 years earlier. This conclusion is supported by (1) a 57% reduction in the proportion of polymorphic loci, (2) a 29% reduction in the average number of alleles per locus, (3) a 21% reduction in the average heterozygosity per individual, and (4) significant changes in allelic frequencies between age-classes. This loss of variation is attributed to both a limited number of founders of the hatchery stock and the effects of genetic drift in the maintenance of the hatchery stock.

Araki, H. 2008. Hatchery stocking for restoring wild populations: A genetic evaluation of the reproductive success of hatchery fish vs. wild fish; 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 2008, pp. 153–167.

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.

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

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

Araki, H., B.A. Berejikian, M.J. Ford, and M.S. Blouin. 2008. Fitness of hatchery-reared salmonids in the wild. *Evolutionary Applications* 1(2): 342-355.

Accumulating data indicate that hatchery fish have lower fitness in natural environments than wild fish. This fitness decline can occur very quickly, sometimes following only one or two generations of captive rearing. In this review, we summarize existing data on the fitness of hatchery fish in the wild, and we investigate the conditions under which rapid fitness declines can occur. The summary of studies to date suggests: nonlocal hatchery stocks consistently reproduce very poorly in the wild; hatchery stocks that use wild, local fish for captive propagation generally perform better than nonlocal stocks, but often worse than wild fish. However, the data above are from a limited number of studies and species, and more studies are needed before one can generalize further. We used a simple quantitative genetic model to evaluate whether domestication selection is a sufficient explanation for some observed rapid fitness declines. We show that if selection acts on a single trait, such rapid effects can be explained only when selection is very strong, both in captivity and in the wild, and when the heritability of the trait under

selection is high. If selection acts on multiple traits throughout the life cycle, rapid fitness declines are plausible.

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* 5: 621–624.

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

Araki, H., R.S. Waples, W.R. Arden, B. Cooper, M.S. Blouin. 2007. Effective population size of steelhead trout: influence of variance in reproductive success, hatchery programs, and genetic compensation between life-history forms. *Molecular Ecology* 16(5): 953-966.

The effective population size is influenced by many biological factors in natural populations. To evaluate their relative importance, we estimated the effective number of breeders per year (N_b) and effective population size per generation (N_e) in anadromous steelhead trout (*Oncorhynchus mykiss*) in the Hood River, Oregon (USA). Using demographic data and genetic parentage analysis on an almost complete sample of all adults that returned to the river over 15 years (> 15 000 individuals), we estimated N_b for 13 run years and N_e for three entire generations. The results are as follows: (i) the ratio of N_e to the estimated census population size (N) was 0.17–0.40, with large variance in reproductive success among individuals being the primary cause of the reduction in N_e/N ; (ii) fish from a traditional hatchery program (H_{trad} : nonlocal, multiple generations in a hatchery) had negative effects on N_b , not only by reducing mean reproductive success but also by increasing variance in reproductive success among breeding parents, whereas no sign of such effects was found in fish from supplementation hatchery programs (H_{supp} : local, single generation in a hatchery); and (iii) N_b was relatively stable among run years, despite the widely fluctuating annual run sizes of anadromous adults. We found high levels of reproductive contribution of nonanadromous parents to anadromous offspring when anadromous run size is small,

suggesting a genetic compensation between life-history forms (anadromous and nonanadromous). This is the first study showing that reproductive interaction between different life-history forms can buffer the genetic impact of fluctuating census size on N_e .

Barton, M.L., and K.T. Scribner. 2004. Temporal comparisons of genetic diversity in Lake Michigan steelhead, *Oncorhynchus mykiss*, populations: Effects of hatchery supplementation. Environmental Biology of Fishes 69: 395-407.

Steelhead, *Oncorhynchus mykiss*, were first introduced into the Great Lakes in the late 1800s. Subsequently, natural recruitment across the Lake Michigan basin has been regularly supplemented by primarily one hatchery strain. Recently, multiple strains derived from locations across the species native range along the west coast of the United States have also been stocked by different management agencies. Prior to 1983, hatchery supplementation of Lake Michigan steelhead populations in Michigan was largely unsuccessful due to low smolting rates of small (<120 mm) hatchery yearlings (estimated survival 0.01%). Accordingly, contributions of hatchery fish to historical adult spawning runs in Michigan tributaries were low (0–30%) across six major drainages. Large yearlings of different hatchery strains (>150 mm) have been stocked exclusively since 1983, increasing estimates of survival to smolting (90%). Consequently, the proportion of hatchery adults in spawning runs increased to 13–79%. We examined the effects of changes in stocking practices on straying rates of hatchery steelhead and to temporal changes in levels of genetic diversity and relationships among populations. We used microsatellite loci to estimate allele frequencies for six populations sampled for two time periods (1983–1984 and 1998–1999). Measures of inter-population divergence (mean F_{ST}) were not significant for either time period. However, spatial genetic relationships among historical and contemporary populations were significantly correlated with geographic distance; a result not expected if gene flow (natural straying) among populations was mediated solely by hatchery supplementation. Increased numbers of alleles in spawning adults from populations can be attributed to alleles specific to recently introduced hatchery strains.

Berejikian, B.A., S.B. Mathews, and T.P. Quinn. 1996. Effects of hatchery and wild ancestry and rearing environments on the development of agonistic behavior in steelhead trout (*Oncorhynchus mykiss*) fry. Canadian Journal of Fisheries and Aquatic Sciences 53: 2004-2014.

At emergence, fry from a wild steelhead trout (*Oncorhynchus mykiss*) population displayed higher levels of one type of mirror-elicited agonistic behavior (swimming against a mirror) than did fry from a locally derived hatchery (domesticated) population. Newly emerged wild fry also dominated hatchery fry in size-matched dyadic dominance challenges. However, given an approximately 3.0-4.5% size advantage, hatchery fry dominated smaller wild competitors in 68% of encounters, indicating that small size differences at emergence can strongly influence dominance. Hatchery fry reared in a natural stream channel for 105 days were more aggressive than those reared in hatchery tanks and than wild fry reared in either environment. In otherwise identical hatchery tanks, low density and low food rations were associated with elevated agonistic behavior by hatchery fry, but not by wild fry. This study suggests that four to

seven generations of domestication has resulted in behavioral divergence of the hatchery population from its wild donor population. The extent to which such differences determine the outcomes of interactions between of spring of wild and hatchery steelhead spawning in streams will depend on the size differences and emergence dates of the populations as well as genetic bases of aggression.

Berejikian, B.A., E.P. Tezak, and S.L. Schroder. 2000. Reproductive behavior and breeding success of captively reared Chinook Salmon. North American Journal of Fisheries Management 21(1): 255–260.

Release of captively reared adults is one of several strategies currently being used to maintain imperiled populations of chinook salmon *Oncorhynchus tshawytscha* in the Pacific Northwest. This study evaluated the breeding behavior and success of captively reared chinook salmon released at maturity into a controlled-flow stream channel. Female egg deposition was 49.5%, which is much lower than that reported for wild populations, but egg-to-fry survival was 62.5%. Females abandoned 40% of the nests they constructed, and males were often absent during the female's nest construction. The underlying causes of these presumed behavioral deficiencies might have limited the breeding success of the population. The efficacy of adult release strategies should be assessed within the context of other potential release options, keeping in mind the objectives of the individual program. Under current culture practices, the reproductive success of captively reared chinook salmon that are released as adults may be less than that of wild salmon.

Berejikian, B.A., E.P. Tezak, L. Park, E. LaHood, S.L. Schroder, and E. Beall. 2001. Male competition and breeding success in captively reared and wild coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 58(4): 804-810.

In the Pacific Northwest, releasing captively reared adult salmon (*Oncorhynchus* spp.) for natural spawning is an evolving strategy for the recovery of imperiled populations. However, the ability of captively reared fish to spawn naturally may be compromised by their artificial rearing environments. In this study, wild coho salmon (*O. kisutch*) males out-competed captively reared males and controlled access to spawning females in 11 of 14 paired trials in laboratory stream channels. In two cases where satellite males were observed participating in spawning, DNA genotyping results determined that they did not sire any of the progeny. When spawning occurred at night and was not observed, DNA results confirmed behavior-based determinations of dominance made before dark. Dominance was established soon after the males were introduced into a common arena containing a sexually active female. We hypothesize that decisions by subordinate males to avoid direct competition may have minimized conflict. The competitive inferiority of captively reared coho salmon in this and a previous study probably reflects deficiencies in rearing environments, which fail to produce appropriate body coloration and body shape and perhaps alter natural behavioral development.

Berntson, E.A., R.W. Carmichael, M.W. Flesher, E.J. Ward, and P. Moran. 2011. Diminished reproductive success of steelhead from a hatchery supplementation program (Little Sheep Creek, Imnaha Basin, Oregon). Transactions of the American Fisheries Society 140(3): 685-698.

Hatchery supplementation programs are designed to enhance natural production and maintain the fitness of the target population; however, it can be difficult to evaluate the success of these programs. Key to the success of such programs is a relatively high reproductive success of hatchery fish. This study investigated the relative reproductive success (RRS) of steelhead *Oncorhynchus mykiss* (anadromous rainbow trout) by creating pedigrees for hatchery and natural spawning steelhead. We genotyped adult steelhead that returned to a weir and were released upstream to spawn in Little Sheep Creek, a tributary to the Imnaha River in eastern Oregon. The broodstock for this supplementation program were originally chosen from natural-origin steelhead returning to the weir and in subsequent years consisted of both natural- and hatchery-origin individuals. Microsatellite analyses showed the broodstock to be genetically similar to the natural population across years. We also genotyped adult resident rainbow trout from multiple locations upstream of the weir and determined the parentage of progeny collected at various life history stages, including returning adults in subsequent years. Analysis of progeny sampled at both the juvenile and adult life stages suggested that the RRS of hatchery-origin fish was 30–60% that of their natural-origin counterparts. Using generalized linear models to address the importance of various factors associated with reduced reproductive success, we found that the greatest effects on RRS were origin (natural versus hatchery), length, return date, and the number of same-sex competitors. Natural parents were less negatively affected by same-sex competitors. Differential survival of juveniles and the behavior of offspring and/or spawning adults may all contribute to diminished fitness in hatchery-reared salmon, although it could not be determined to what extent these effects were of a persistent, heritable nature as distinct from an environmental effect associated with hatchery rearing and release strategies.

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): 12-31.

The use of hatcheries has been a subject of lengthy debate in the management of salmon and trout resources in the Pacific Northwest. The problem has resulted in part from the wide distribution of hatchery fish in circumstances where natural populations were disadvantaged by management policy involving hatchery fish and the confusion of the effects of management with the effects of artificial propagation. Recently, the controversy has been epitomized by the recommendations to fisheries management agencies that excess hatchery fish should not be allowed to spawn in the wild, and hatchery fish should be excluded from salmon populations listed under the Endangered Species Act. The authors of the present article disagree with those recommendations and conclude that hatchery fish have an important role in recovery and supplementation of wild stocks. The present article is an attempt to help give balance to the discussion

by providing a different perspective on hatchery fish and the literature pertaining to artificial propagation.

Buhle, E.R., K.K. Holsman, M.D. Scheuerell, and A. Albaugh. 2009. Using an unplanned experiment to evaluate the effects of hatcheries and environmental variation on threatened populations of wild salmon. *Biological Conservation* 142: 2449-2455.

Efforts to conserve depleted populations of Pacific salmon (*Oncorhynchus* spp.) often rely on hatchery programs to offset losses of fish from natural and anthropogenic causes, but their use has been contentious. We examined the impact of a large-scale reduction in hatchery stocking on 15 populations of wild coho salmon along the coast of Oregon (USA). Our analyses highlight four critical factors influencing the productivity of these populations: (1) negative density-dependent effects of hatchery-origin spawners were 5 times greater than those of wild spawners; (2) the productivity of wild salmon decreased as releases of hatchery juveniles increased; (3) salmon production was positively related to an index of freshwater habitat quality; and (4) ocean conditions strongly affect productivity at large spatial scales, potentially masking more localized drivers. These results suggest that hatchery programs' unintended negative effects on wild salmon populations, and their role in salmon recovery, should be considered in the context of other ecological drivers.

Byrne, A., T.C. Bjornn, and J.D. McIntyre. 1992. Response of native steelhead to hatchery supplementation programs in an Idaho river. *North American Journal of Fisheries Management* 12: 62-78.

A life history model was used to predict the response of native steelhead in the Lochsa River, Idaho to long-term supplementation with hatchery fry and smolts. The four key factors affecting the response of the native fish to a stocking program were (1) the number of native spawners, (2) the number of stocked fish, (3) the number and fitness of progeny from stocked fish, and (4) the amount of mating between hatchery and native fish. Long-term stocking of fry or smolts led to the extinction of native fish in some scenarios. The model can be used to help assess the risks and benefits of proposed stocking programs.

In most scenarios, supplementation of native stocks with hatchery stocks caused replacement, not enhancement, of native stocks. The present day approach to deficits of steelhead abundance - build more hatcheries - should cause alarm to biologists concerned with the preservation of native stocks until it is demonstrated that supplementation can be done in a way that does not reduce the fitness of the native stock.

Caroffino, D.C., L.M. Miller, A.R. Kapuscinski, 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.

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.

Chebanov, N.A., and B.E. Riddell. 1998. Spawning success of wild and hatchery Chinook. Journal of Ichthyology 38(7): 517-526.

According to the results of field experiments with Chinook salmon spawners of various origins, i.e., those resulting from natural spawning (wild) and those resulting from artificial reproduction (hatchery), under conditions of joint spawning, a description of their spawning behavior and relative success in spawning is given. It is established that, at extremely high temperatures and low water levels in the region of investigation, as well as during the earlier introduction of hatchery fish to the spawning grounds, the hatchery females and the wild males had certain advantages in competing for spawning places and spawning mates. It is inferred from these observations, that, under optimum hydrological conditions and with the simultaneous introduction of fish of different origins to the spawning grounds, the wild spawners are more successful in spawning.

Chilcote, M. W. 2003. Relationship between natural productivity and the frequency of wild fish in mixed spawning populations of wild and hatchery steelhead (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Sciences 60: 1057-1067.

The proportion of wild fish in 12 mixed populations of hatchery and wild steelhead (*Oncorhynchus mykiss*) was evaluated for its relationship to mean and intrinsic measures of population productivity. The population mean of $\ln(\text{recruits}/\text{spawner})$ was used to represent mean productivity. Intrinsic productivity was represented by values for the Ricker a parameter as estimated from fits of spawner and recruit data. Significant regressions ($p < 0.001$) were found between both measures of productivity and the proportion of wild fish in the spawning population (P_w). The slopes of the two

regressions were not significantly different ($p = 0.55$) and defined a relationship suggesting that a spawning population comprised of equal numbers of hatchery and wild fish would produce 63% fewer recruits per spawner than one comprised entirely of wild fish. Study findings were not sensitive to likely levels of data error or confounded by extraneous habitat correlation with P_w as a critical variable. For natural populations, removal rather than addition of hatchery fish may be the most effective strategy to improve productivity and resilience.

Chilcote, M.W., K.W. Goodson, and M.R. Falcu. 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.

We found a negative relationship between the reproductive performance in natural, anadromous populations of steelhead trout (*Oncorhynchus mykiss*), coho salmon (*O. kisutch*), and Chinook salmon (*O. tshawytscha*), and the proportion of hatchery fish in the spawning population. We used intrinsic productivity as estimated from fitting a variety of recruitment models to abundance data for each population as our indicator of reproductive performance. The magnitude of this negative relationship is such that we predict the recruitment performance for a population composed entirely of hatchery fish would be 0.128 of that for a population composed entirely of wild fish. The effect of hatchery fish on reproductive performance was the same among all three species. Further, the impact of hatchery fish from “wild type” hatchery broodstocks was no less adverse than hatchery fish from traditional, domesticated broodstocks. We also found no support for the hypothesis that a population’s reproductive performance was affected by the length of exposure to hatchery fish. In most cases, measures that minimize the interactions between wild and hatchery fish will be the best long-term conservation strategy for wild populations.

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

We compared the relative reproductive success of naturally spawning, summer-run hatchery and wild steelhead trout *Salmo gairdneri* by electrophoretic examination of juveniles for a specific genetic marker. The success of hatchery fish in producing smolt offspring was only 28% of that for wild fish. We also found that 62% of the naturally produced summer-run smolts were offspring of hatchery spawners. Their dominance occurred because hatchery spawners, within the watershed we examined, effectively outnumbered wild spawners by at least 4.5 to 1. We suggest that, under such conditions, the genetic integrity of wild populations may be threatened. We also suggest that hatchery fish may be an important component of the spawner-to-smolt recruitment relationship for summer-run steelhead.

Christie, M.R., M.L. Marine, R.A. French, and M.S. Blouin. 2012. Genetic adaptation to captivity can occur in a single generation. Proceedings of the National Academy of Sciences (In press).

Captive breeding programs are widely used for the conservation and restoration of threatened and endangered species. Nevertheless, captive-born individuals frequently have reduced fitness when reintroduced into the wild. The mechanism for these fitness declines has remained elusive, but hypotheses include environmental effects of captive rearing, inbreeding among close relatives, relaxed natural selection, and unintentional domestication selection (adaptation to captivity). We used a multigenerational pedigree analysis to demonstrate that domestication selection can explain the precipitous decline in fitness observed in hatchery steelhead released into the Hood River in Oregon. After returning from the ocean, wild-born and first-generation hatchery fish were used as broodstock in the hatchery, and their offspring were released into the wild as smolts. First-generation hatchery fish had nearly double the lifetime reproductive success (measured as the number of returning adult offspring) when spawned in captivity compared with wild fish spawned under identical conditions, which is a clear demonstration of adaptation to captivity. We also documented a tradeoff among the wild-born broodstock: Those with the greatest fitness in a captive environment produced offspring that performed the worst in the wild. Specifically, captive-born individuals with five (the median) or more returning siblings (i.e., offspring of successful broodstock) averaged 0.62 returning offspring in the wild, whereas captive-born individuals with less than five siblings averaged 2.05 returning offspring in the wild. These results demonstrate that a single generation in captivity can result in a substantial response to selection on traits that are beneficial in captivity but severely maladaptive in the wild.

Christie, M.R., M.L. Marine, R.A. French, R.S. Waples, and M.S. Blouin. 2012. Effective size of a wild salmonid population is greatly reduced by hatchery supplementation. Heredity (In press).

Many declining and commercially important populations are supplemented with captive-born individuals that are intentionally released into the wild. These supplementation programs often create large numbers of offspring from relatively few breeding adults, which can have substantial population-level effects. We examined the genetic effects of supplementation on a wild population of steelhead (*Oncorhynchus mykiss*) from the Hood River, Oregon, by matching 12 run-years of hatchery steelhead back to their broodstock parents. We show that the effective number of breeders producing the hatchery fish (broodstock parents; N_b) was quite small (harmonic mean $N_b=25$ fish per brood-year vs 373 for wild fish), and was exacerbated by a high variance in broodstock reproductive success among individuals within years. The low N_b caused hatchery fish to have decreased allelic richness, increased average relatedness, more loci in linkage disequilibrium and substantial levels of genetic drift in comparison with their wild-born counterparts. We also documented a substantial Ryman–Laikre effect whereby the additional hatchery fish doubled the total number of adult fish on the spawning grounds each year, but cut the effective population size of the total population (wild and hatchery fish combined) by nearly two-thirds. We further demonstrate that the Ryman–Laikre

effect is most severe in this population when (1) >10% of fish allowed onto spawning grounds are from hatcheries and (2) the hatchery fish have high reproductive success in the wild. These results emphasize the trade-offs that arise when supplementation programs attempt to balance disparate goals (increasing production while maintaining genetic diversity and fitness).

Close, T.L. 1999. Spawning interactions of hatchery and naturalized anadromous form Rainbow Trout *Oncorhynchus mykiss* in a Lake Superior tributary. Minnesota Department of Natural Resources, Investigational Report 473.

Two strains of rainbow trout *Oncorhynchus mykiss* are managed in the Minnesota waters of Lake Superior. Abundance of the naturalized and self-sustaining steelhead strain has declined since a hatchery strain called “kamloops” was introduced in the 1970s. There are several possible causes for the decline, but hybridization of the two strains is suspected of contributing to the steelhead decline. Forty-six steelhead and Kamloops spawners with strain specific homozygous alleles at the LDH-2 locus were radio tagged and stocked into a 1,200 m study reach to observe movements to spawning areas, observe spawning interactions, and to measure juvenile production and survival. Spawners of both strains distributed in the reach and most spawners remained in the study reach long enough to spawn. Young-of-the-year (YOY) densities were low in the fall when 44 hybrid and 13 pure strain steelhead YOY were captured. Seven hybrids and six steelhead were captured one year later. It was not possible to determine how many spawning pairs produced the captured hybrids, thus the apparent difference in overwinter survival may have been a parental effect and not a strain effect. We now know that viable hybrids can be produced in the wild and that they can survive North Shore stream winters. If appropriate non-lethal genetic markers can be identified, additional work is needed to measure juvenile Kamloops and hybrid survival in the wild, the extent of past hybridization, and the practicality of genetically rehabilitating the steelhead stock.

Daugherty, D.J., T. M. Sutton, and R. W. Greil. 2003. Life-history characteristics, population structure, and contribution of hatchery and wild steelhead in a Lake Huron tributary. Journal of Great Lakes Research 29(3): 511-520.

Life-history characteristics, size structure, and relative composition of hatchery-reared and wild-produced steelhead *Oncorhynchus mykiss* in the Carp River, Michigan, were examined to determine if population attributes were similar between origins. Quantitative scale analyses were used to determine the origin and life-history attributes of adult fish captured during their spring spawning migration from 1995–1998. Hatchery males and females comprised 40% and 23%, respectively, of the spawning migration, while wild males and females comprised 19% and 18%, respectively. Male and female hatchery steelhead had shorter stream-residence durations (1 year) than wild fish (2 years). Both genders of hatchery individuals also reached reproductive maturity at younger ages (males, 3 years; females, 4 years) than wild fish (5 years). The number of years between repeat-spawning events was the same (1 year), irrespective of gender or origin. However, the number of fish captured during repeat-spawning events differed between origins (hatchery males: 42%; wild males: 9%; hatchery females: 23%; and

wild females: 26%). The median number of years in lake residence prior to maiden spawning did not differ between hatchery and wild fish (males, 2 years; females, 3 years). Median length-at-age estimates differed between hatchery and wild male steelhead at age 4 (66 cm and 58 cm, respectively), while the median length-at-age for all other age classes did not differ, irrespective of gender and origin. Our results suggest that differences in life-history characteristics exist between hatchery-reared and wild-produced Carp River steelhead, and that system-specific management objectives should be considered prior to the initiation of stocking efforts.

Dickson, T.A., and H.R. MacCrimmon. 1982. Influence of hatchery experience on growth and behavior of juvenile Atlantic salmon (*Salmo salar*) within allopatric and sympatric stream populations. Canadian Journal of Fisheries and Aquatic Sciences 39: 1453-1458

Hatchery-reared Atlantic salmon (*Salmo salar*), wild Atlantic salmon and brook trout (*Salvelinus fontinalis*) (O+ year-class fish) were observed in allopatric or paired sympatric populations using stream tanks at the Matamek Research Station, Quebec. Hatchery-reared salmon maintained a position just off the substrate, a position intermediate to that occupied by wild salmon (bottom) and trout (midwater). Growth rates of hatchery-reared and wild salmon were not statistically different. Neither type had an interactive advantage. It is concluded that the behavioral pattern of hatchery-reared salmon was intermediate to that of wild salmon and trout. This behavioral shift may account for poor survival of planted Atlantic salmon juveniles, a phenomenon suggesting the need for a reexamination of present live release programs using juvenile hatchery-reared salmon.

Einum, S., and I.A. Fleming. 2001. Ecological interactions between wild and hatchery salmonids. Nordic Journal of Freshwater Research 75: 56-70.

The common management practice of introducing artificially produced fish into wild populations has raised concerns among fishery biologists. In part, these concerns arise from the observation that hatchery-produced fish commonly differ from wild fish in ways that may influence ecological interactions between them. In this review, we use a meta-analytical approach to provide quantitative tests for such differences and show that the hatchery rearing of salmonids results in increased pre-adult aggression, decreased response to predators, and decreased survival. Changes in growth rates are common, but less consistent. Changes in other fitness related traits such as migration, feeding, habitat use and morphology also occur. Based on the presented evidence we conclude that differences between hatchery-reared and wild fish may have negative implications for the success of stocking programs. A number of studies reporting population responses to stocking support this, suggesting that the performance of hatchery fish and their interactions with wild fish is of such a character that many of the current stocking practices may be detrimental to the recipient populations.

Fenderson, O.C., W.H. Everhart, and K.M. Muth. 1968. Comparative agonistic and feeding behavior of hatchery-reared and wild salmon in aquaria. Journal of the Fisheries Research Board of Canada 25: 1-14.

When hatchery-reared and wild landlocked Atlantic salmon (*Salmo salar*) parr of the same age and size were permitted to compete for social dominance and for food in aquaria, twice as many hatchery salmon attained dominance as wild salmon. Dominant hatchery salmon also showed a higher intensity of aggressiveness than dominant wild salmon, displaying a higher and more variable mean nipping rate. Socially dominant salmon ate more food per fish than subordinates, but there were no statistically significant differences in feeding rate between dominant hatchery and dominant wild salmon, or between subordinate hatchery and subordinate wild salmon. Hatchery salmon displayed lower feeding rates than wild salmon when they were held in separate compartments of an aquarium and compared at three temperatures. This difference in feeding rate probably was not a reflection of differences in adaptation to temperature or food preference, but, rather, was the result of interference with feeding caused by the more intense social interaction among hatchery fish. It is suggested that high levels of aggressiveness may contribute to mortalities of hatchery-reared salmon planted in streams because of loss of feeding time, excessive use of energy, and increased exposure to predators.

Fleming, I.A. and E. Petersson. 2001. The ability of released hatchery salmonids to contribute to the natural productivity of wild populations. Nordic Journal of Freshwater Research 75: 71-98.

The success and implications of hatchery release programs are intimately tied to the reproductive capabilities of the hatchery fish in the wild. Moreover, reproductive interactions are important in understanding the ecological and genetic threats that hatchery fish may pose to wild populations. Reproductive success is a key to self-sustainability, shaping natural and sexual selection, and influencing the genetic diversity of populations and the implications of parental traits and decisions for offspring survival and success. We then address how rearing and release programs affect the reproductive traits and performance of fish. A review of such programs reveals that in the few cases where adequate assessments have been made released fish frequently fail to attain self-sustainability and/or contribute significantly to populations. Clearly, new approaches based on sound scientific research are needed and these need to be tailored specifically to the management objectives.

Fleming, I.A., B. Jonsson, and M.R. Gross. 1994. Phenotypic divergence of sea-ranched, farmed, and wild salmon. Canadian Journal of Fisheries and Aquatic Sciences 51: 2808-2824.

We quantified divergence in phenotype of sea-ranched, farmed, and wild Atlantic salmon (*Salmo salar*) of a common genetic stock (River Imsa, Norway). These first-generation fish were also contrasted with a fifth-generation farmed population (Norwegian commercial strain) and with wild and multigeneration sea-ranched

populations of coho salmon (*Oncorhynchus kisutch*). In comparisons using mature Atlantic salmon male parr, cultured juveniles had smaller heads and fins and narrower caudal peduncles and could be distinguished from wild juveniles with 100% accuracy. When juveniles were reared to adulthood in the natural marine environment, some environmentally induced differences due to juvenile hatchery rearing persisted but many disappeared. This was particularly true for head and trunk morphology. Greater adult divergence from the wild state was observed in multigeneration sea-ranched coho salmon, suggesting that evolutionary changes may accumulate with time. Continued farming of salmon juveniles through adulthood increased environmentally induced phenotypic divergence considerably. Both rayed-fin sizes and body streamlining decreased. Fifth-generation Norwegian farmed salmon showed the greatest morphological differences. Both the proportion of a fish's life history and number of generations spent in culture are thus probably important determinants of phenotypic divergence of cultured fish from their wild state.

Fleming, I.A., B. Jonsson, M.R. Gross, and A. Lamberg. 1996. An experimental study of the reproductive behavior and success of farmed and wild Atlantic salmon. *Journal of Applied Ecology* 33: 893-905.

1. Escape of cultured organisms into natural ecosystems may threaten wild populations both ecologically and genetically. In the aquaculture industry, farmed Atlantic salmon often escape and enter the spawning grounds of wild salmon. We report experiments to assess the competitive and reproductive abilities of fifth generation farmed salmon and their potential impacts upon wild salmon.

2. The farmed and wild females had similar levels of competitive behavior, however, they differed in reproductive behavior and success. Farmed females displayed less breeding behavior, constructed fewer nests, retained a greater weight of eggs unspawned, were less efficient at nest covering, incurred more nest destruction, and suffered greater egg mortality than wild females. As a result, farmed females had less than one-third of the reproductive success of wild females.

3. The farmed males were even less successful than the farmed females in competition with the wild fish. They were less aggressive, courted less, partook in fewer spawnings, and achieved only an estimated one to three percentage of the reproductive success of the wild males.

4. The farmed males exhibited inappropriate mating behavior, that led to poor fertilization success, even in the absence of competition with wild males.

5. Adult farmed fish are thus likely to be relatively unsuccessful in natural environments due to a competitive and reproductive inferiority apparently resulting from domestication.

Fleming, I.A., and M.R. Gross. 1993. Breeding success of hatchery and wild coho salmon in competition. *Ecological Applications* 3(2): 230-245.

The divergence of hatchery fish in traits important for reproductive success has raised concerns about their ability to rehabilitate wild populations, and the threat that their inevitable straying poses to biological diversity through introgression. We therefore undertook a study of the breeding competition and success of sea-ranched hatchery fish placed in direct competition with wild fish. Experiments using wild and hatchery coho salmon were conducted within a controlled stream channel, allowing selective manipulation of breeding competition and density.

Hatchery fish particularly males, were competitively inferior to wild fish, being less aggressive and more submissive. As a consequence, hatchery males were denied access to ovipositing females; they partook in fewer spawnings, held more distal positions in spawning hierarchies, and attained only an estimated 62% of the breeding success of wild males. By contrast, competition did not appear to inhibit hatchery females as overtly as males. Hatchery and wild females exhibited similar levels of aggressive behavior, however hatchery females did suffer greater delays in the onset of breeding, failed to spawn larger proportions of their eggs, and lost more eggs to nest destruction by other females. They averaged an estimated 82% of the breeding success of wild females. There was thus a sex bias in the breeding disadvantage of hatchery fish, with males suffering more than females. Furthermore, the breeding disadvantage was density dependent with the relative success of hatchery to wild fish declining with increasing density. These results imply that hatchery fish have restricted abilities to rehabilitate wild populations, and may pose ecological and genetic threats to the conservation of wild populations.

Flick, W.A., and D.A. Webster. 1964. Comparative first year survival and production in wild and domestic strains of brook trout, *Salvelinus fontinalis*. *Transactions of the American Fisheries Society* 93: 58-69.

Brook trout (*Salvelinus fontinalis*) from three wild populations were compared with domesticated hatchery strains with respect to growth, survival, and production in semi-natural environments (drainable ponds). Eggs from all strains were hatched and reared in the hatchery and planted as spring or fall fingerlings. Over-summer survival consistently favored wild strains (65 to 76 percent compared with 43 to 58 percent survival for domestic strains). Over-winter survivals were not different, although the effect may have been masked by other overriding factors in the test waters. Domestic strains maintained the initial size advantages held at the planting. Larger size at planting was due to faster growth rate during hatchery existence. Net production, based on recovery weight less stocking weight, was similar for wild and domestic groups during the over-summer period (higher survivals in wild strains balanced by size advantage of domestic), but domestic groups generally showed lower production or net losses in the over-winter period.

Foerester, R.E. 1931. A comparison of the natural and artificial propagation of salmon. Transactions of the American Fisheries Society 61(1): 121-130.

To introduce for consideration the question of the value of and benefits derived from artificial propagation of salmon as compared with natural propagation may appear to many as the unearthing of a well-gnawed bone of controversy, but it must be remembered that there is still lacking that definite, concrete, scientific information on which an argument should be properly based. Consequently in reporting further results of a fundamental research into the problem a discussion of the subject becomes necessary. The attitude of fish culturists, in the main, is well known. They are convinced that artificial propagation is vastly superior to the natural process. Many scientists, however, who are interested in the conservation of our fisheries but who are quite impartial toward the various propagational methods, are still skeptical of the romantic picture painted by the practical fish-culturist and are not yet convinced that the picture is actually a true portrayal of the facts. For this, incidentally, they have been roundly accused of partisanship toward natural propagation and of being impervious to argument favoring artificial methods. It is freely admitted that there are undoubtedly certain situations where artificial propagation of salmon has been successful and certain circumstances or conditions that make, in certain areas, the practice of this method desirable but broadly speaking such instances are but isolated cases. The fundamental principles governing the practices of both natural and artificial propagation have, until recently, been overlooked and before warranted decision is justified a definite survey and study of these fundamental factors is required. An outline of the investigation into the natural and artificial propagation of sockeye salmon at Cultus lake, British Columbia, was presented before this Society in 1928. Further illuminating records are now reported.

Ford, M.J. 2002. Selection in captivity during supportive breeding may reduce fitness in the wild. Conservation Biology 16(3): 815-825.

I used a quantitative genetic model to explore the effects of selection on the fitness of a wild population subject to supportive breeding. Supportive breeding is the boosting of a wild population's size by breeding part of the population in captivity and releasing the captive progeny back into the wild. The model assumes that a single trait is under selection with different optimum trait values in the captive and wild environments. The model shows that when the captive population is closed to gene flow from the wild population, even low levels of gene flow from the captive population to the wild population will shift the wild population's mean phenotype so that it approaches the optimal phenotype in captivity. If the captive population receives gene flow from the wild, the shift in the wild population's mean phenotype becomes less pronounced but can still be substantial. The approach to the new mean phenotype can occur in less than 50 generations. The fitness consequences of the phenotypic shift depend on the details of the model, but a >30% decline in fitness can occur over a broad range of parameter values. The rate of gene flow between the two environments, and hence the outcome of the model, is sensitive to the wild environment's carrying capacity and the population growth rate it can support. The results have two important implications for

conservation efforts. First, they show that selection in captivity may significantly reduce a wild population's fitness during supportive breeding and that even continually introducing wild individuals into the captive population will not eliminate this effect entirely. Second, the sensitivity of the model's outcome to the wild environment's quality suggests that conserving or restoring a population's habitat is important for preventing fitness loss during supportive breeding.

Ford, M.J., J.J. Hard, B. Boelts, E. LaHood, and J. Miller. 2008. Estimates of natural selection in a salmon population in captive and natural environments. *Conservation Biology* 22(3): 783–794.

Captive breeding is a commonly used strategy for species conservation. One risk of captive breeding is domestication selection—selection for traits that are advantageous in captivity but deleterious in the wild. Domestication selection is of particular concern for species that are bred in captivity for many generations and that have a high potential to interbreed with wild populations. Domestication is understood conceptually at a broad level, but relatively little is known about how natural selection differs empirically between wild and captive environments. We used genetic parentage analysis to measure natural selection on time of migration, weight, and morphology for a coho salmon (*Oncorhynchus kisutch*) population that was subdivided into captive and natural components. Our goal was to determine whether natural selection acting on the traits we measured differed significantly between the captive and natural environments. For males, larger individuals were favored in both the captive and natural environments in all years of the study, indicating that selection on these traits in captivity was similar to that in the wild. For females, selection on weight was significantly stronger in the natural environment than in the captive environment in 1 year and similar in the 2 environments in 2 other years. In both environments, there was evidence of selection for later time of return for both males and females. Selection on measured traits other than weight and run timing was relatively weak. Our results are a concrete example of how estimates of natural selection during captivity can be used to evaluate this common risk of captive breeding programs.

Fraser, D.J. 2008. How well can captive breeding programs conserve biodiversity? A review of salmonids. *Evolutionary Applications* 1(4): 535-586.

Captive breeding programs are increasingly being initiated to prevent the imminent extinction of endangered species and/or populations. But how well can they conserve genetic diversity and fitness, or re-establish self-sustaining populations in the wild? A review of these complex questions and related issues in salmonid fishes reveals several insights and uncertainties. Most programs can maintain genetic diversity within populations over several generations, but available research suggests the loss of fitness in captivity can be rapid, its magnitude probably increasing with the duration in captivity. Over the long-term, there is likely tremendous variation between (i) programs in their capacity to maintain genetic diversity and fitness, and (ii) species or even intraspecific lifehistory types in both the severity and manner of fitness-costs accrued. Encouragingly, many new theoretical and methodological approaches now exist for

current and future programs to potentially reduce these effects. Nevertheless, an unavoidable trade-off exists between conserving genetic diversity and fitness in certain instances, such as when captive-bred individuals are temporarily released into the wild. Owing to several confounding factors, there is also currently little evidence that captive-bred lines of salmonids can or cannot be reintroduced as self-sustaining populations. Most notably, the root causes of salmonid declines have not been mitigated where captive breeding programs exist. Little research has also addressed under what conditions an increase in population abundance due to captive-rearing might offset fitness reductions induced in captivity. Finally, more empirical investigation is needed to evaluate the genetic/fitness benefits and risks associated with (i) maintaining captive broodstocks as either single or multiple populations within one or more facilities, (ii) utilizing cryopreservation or surrogate broodstock technologies, and (iii) adopting other alternatives to captive-rearing such as translocations to new habitats. Management recommendations surrounding these issues are proposed, with the aim of facilitating meta-analyses and more general principles or guidelines for captive-breeding. These include the need for the following: (i) captive monitoring to involve, a priori, greater application of hypothesis testing through the use of well-designed experiments and (ii) improved documentation of procedures adopted by specific programs for reducing the loss of genetic diversity and fitness.

Fraser, D.J., A.M. Cook, J.D. Eddington, P. Bentzen, and J.A. Hutchings. 2008. Mixed evidence for reduced local adaptation in wild salmon resulting from interbreeding with escaped farmed salmon: complexities in hybrid fitness. *Evolutionary Applications* 1(3): 501-512.

Interbreeding between artificially-selected and wild organisms can have negative fitness consequences for the latter. In the Northwest Atlantic, farmed Atlantic salmon recurrently escape into the wild and enter rivers where small, declining populations of wild salmon breed. Most farmed salmon in the region derive from an ancestral source population that occupies a nonacidified river (pH 6.0–6.5). Yet many wild populations with which escaped farmed salmon might interbreed inhabit acidified rivers (pH 4.6–5.2). Using common garden experimentation, and examining two early-life history stages across two generations of interbreeding, we showed that wild salmon populations inhabiting acidified rivers had higher survival at acidified pH than farmed salmon or F_1 farmed-wild hybrids. In contrast, however, there was limited evidence for reduced performance in backcrosses, and F_2 farmed-wild hybrids performed better or equally well to wild salmon. Wild salmon also survived or grew better at nonacidified than acidified pH, and wild and farmed salmon survived equally well at nonacidified pH. Thus, for acid tolerance and the stages examined, we found some evidence both for and against the theory that repeated farmed-wild interbreeding may reduce adaptive genetic variation in the wild and thereby negatively affect the persistence of depleted wild populations.

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

Efforts to conserve depleted populations of Pacific salmon (*Oncorhynchus* spp.) often rely on hatchery programs to offset losses of fish from natural and anthropogenic causes, but their use has been contentious. We examined the impact of a large-scale reduction in hatchery stocking on 15 populations of wild coho salmon along the coast of Oregon (USA). Our analyses highlight four critical factors influencing the productivity of these populations: (1) negative density-dependent effects of hatchery-origin spawners were 5 times greater than those of wild spawners; (2) the productivity of wild salmon decreased as releases of hatchery juveniles increased; (3) salmon production was positively related to an index of freshwater habitat quality; and (4) ocean conditions strongly affect productivity at large spatial scales, potentially masking more localized drivers. These results suggest that hatchery programs' unintended negative effects on wild salmon populations, and their role in salmon recovery, should be considered in the context of other ecological drivers.

Gharrett, A.J., and W.W. Smoker. 1991. Two Generations of hybrids between even-and odd-year Pink Salmon (*Oncorhynchus gorbuscha*): A test for outbreeding depression. Canadian Journal of Fisheries and Aquatic Sciences 48(9): 1744-1749.

Hybrids of genetically isolated odd- and even-year pink salmon (*Oncorhynchus gorbuscha*) from the same stream were made by fertilizing eggs with cryopreserved milt. Anadromous first-generation (F_1) hybrids and controls returned to the hatchery at equal rates (153 of 5483 and 160 of 5492, respectively), on the same average date, and with the same size. However, variances of F_1 size (female length and weight and male length) exceeded variances of control sizes, suggesting increased genetic variation in F_1 's. Only 11 of 5165 F_2 's returned. F_2 's were similar meristically and in size to fish of their parents' generation, but were bilaterally more asymmetric in number of gill rakers and in combined numbers of gill rakers and of branchiostegals. Increased F_1 variation followed by low F_2 returns and increased bilateral asymmetry is a pattern to be expected when coadapted allele complexes are disrupted by outbreeding depression.

Gharrett, A. J., W. W. Smoker, R. R. Reisenbichler, and S. G. Taylor. 1999. Outbreeding depression in hybrid pink salmon. Aquaculture 173: 117-129.

Fewer F_2 hybrids between even-and odd-bloodline pink salmon (*Oncorhynchus gorbuscha*), which are lines that are genetically isolated by their strict two-year life cycle, survived than did F_2 controls, indicating outbreeding depression. Cryopreserved sperm of 40 broodyear 1990 males and of 40 broodyear 1991 males fertilized equal subsamples of eggs from 40 broodyear 1992 females. Return rates of F_1 hybrids (1.73%) and controls (1.63%) in 1994 did not differ significantly ($P=0.30$). F_2 hybrid and control were made from 40 males and 40 females selected at random from each

return group. Offspring were differentially marked and released. In 1996, returns differed significantly ($P=0.011$) between hybrids ($n=34$, 0.34%) and controls ($n=44$, 0.42%). The low rate of return of the control fish was similar to the measured return of a much larger group of tagged Auke Creek pink salmon, and probably not an artifact of the experiment. Although no increase in fluctuating asymmetry of paired meristic counts of hybrids exceed measurements of controls, suggesting heterosis for those traits. The observations of decreased survival in F2 hybrids confirm previous work [Gharrett, A.J., Smoker, W.W., 1991. Two generations of hybrids between even and odd-year pink salmon. *Canadian Journal of Fisheries and Aquatic Science* 48(9): 1744-1749]. Although divergence between pink salmon broodlines is large and outbreeding depression might be expected in such unlikely hybrids, the results document the occurrence of outbreeding depression in salmon and signal caution in making management and aquacultural decisions that may create the possibility of outbreeding depression in self-sustaining or cultured populations.

Goodman, D. 2005. Selection equilibrium for hatchery and wild spawning fitness in integrated breeding programs. *Canadian Journal of Fisheries and Aquatic Sciences* 62(2): 374-389.

Some salmon hatchery programs intentionally integrate the wild and hatchery population by taking naturally spawned fish as some fraction of the broodstock and allowing hatchery progeny to constitute some fraction of the adults spawning in the wild. This circumvents some ecological concerns about the effects of hatchery fish on the "wild" population while still reaping some of the benefits of increased potential for harvest, but it increases some genetic concerns. Here, we model phenotypic evolution in the integrated population to investigate the effects on natural spawning fitness at the joint selection and demographic equilibrium. We find a potential, but not a certainty, depending on quantitative aspects of the management interacting with biological characteristics of the stock, for substantial erosion of natural spawning fitness, compared with the original wild population, including the possibility of runaway selection driving natural spawning fitness effectively to zero. The vulnerability to such evolutionary deterioration increases with the magnitude of the contribution of hatchery breeding to the total production and increases with harvest. The response of the selection equilibrium to increasing contribution of hatchery progeny to the broodstock can exhibit a catastrophic discontinuity.

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* 4(6): 763-782.

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.

Grant, W.S. 2011. Understanding the adaptive consequences of hatchery-wild interactions in Alaska salmon. Environmental Biology of Fishes (In press).

About 31% of salmon harvested in Alaska comes from the hatchery production of hundreds of millions of pink and chum salmon and smaller numbers of sockeye, Chinook, and coho salmon. The numbers of hatchery-reared juveniles released in some areas are greater than the numbers of juveniles from wild populations. However, virtually nothing is known about the effects of hatchery fish on wild populations in Alaska. Possible effects of these interactions can be inferred from studies of salmonids in other areas, from studies of other animals, and from theory. Numerous studies show a complex relationship between the genetic architecture of a population and its environment. Adaptive responses to nature and anthropogenic selection can be influenced by variation at a single gene, or more often, by the additive effects of several genes. Studies of salmonids in other areas show that hatchery practices can lead to the loss of genetic diversity, to shifts in adult run timing and earlier maturity, to increases in parasite load, to increases in straying, to altered levels of boldness and dominance, to shifts in juvenile out-migration timing, and to changes in growth. Controlled experiments across generations show, and theory predicts, that the loss of adaptive fitness in hatchery salmon, relative to fitness in wild salmon, can occur on a remarkably short time scale. All of these changes can influence survival and impose selective regimes that influence genetically based adaptive traits. The preservation of adaptive potential in wild populations is an important buffer against diseases and climate variability and, hence, should be considered in planning hatchery production levels and release locations. The protection of wild populations is the foundation for achieving sustained harvests of salmon in Alaska.

Gross, M. 1998. One species with two biologies: Atlantic salmon (*Salmo salar*) in the wild and in aquaculture. Canadian Journal of Fisheries and Aquatic Sciences 55(S1): 131-144.

Today, over 94% of all adult Atlantic salmon (*Salmo salar*) are in the aquaculture niche and wild numbers continue to decline while aquaculture numbers increase. The developmental and evolutionary forces in the aquaculture or "domestic" niche are so unlike those in the wild niche that two distinct biologies are being created from the

original Atlantic salmon species. We may now need to recognize a new biological entity - *Salmo domesticus* - and treat it as an "exotic" when it escapes into the wild. Escapement therefore raises important concerns about ecological and genetic impacts, both within and outside the native range of *Salmo salar*. This paper explains why escaped domestic Atlantic salmon have had an impact on wild Atlantic salmon populations and now threaten Pacific salmonids as well. A polarization of views between aquaculturists and environmentalists will not resolve the problems. The three interest groups in fisheries - aquaculture, biodiversity, and capture - must begin to work together if we are to take up the challenge of preserving biodiversity and if aquaculturists, who hold the future of Atlantic salmon in their hands, can be expected to willingly prevent further impacts from their industry.

Gross, M., B. Neff, and I. Fleming. 1999. American Society of Ichthyologists and Herpetologists Annual Meeting 1999. Organized by Andrew Hendry and Drew Hoysak. <http://www.zoology.ubc.ca/~ahendry/Rssymp.html>

Although salmon supplementation and conservation programs often use hatchery fish, there is a lack of empirical knowledge about their behavior, ecology and reproductive success in the wild. We now present the results of several experiments in which we studied their behavior and ecology and quantified their reproductive success. Both wild and hatchery coho salmon were allowed to freely breed within a spawning channel in the wild. The behaviors and interactions of the fish were recorded and after all spawning had been completed we collected the alevins from the nests. Using microsatellite genetic markers, we determined the parentage, including maternity and paternity, of the fish. Several important relationships emerged, including that between male position in the mating hierarchy and paternity, between male size and reproductive success, between stock type (hatchery or wild) and paternity, and between mating partner and success. Overall, hatchery males attended fewer mating hierarchies, obtained lower paternity within a position, and made up only about a third of the male contribution to the next generation. Hatchery females were also significantly less successful than wild females. Hatchery fish were therefore relatively maladapted and decreased the wild population's effective population size. Finally, our measures of reproductive success within hierarchies may be widely applicable to studies of salmon in the field. This research is supported by NSERC and DFO of Canada, and NINA of Norway.

Hegenes, 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.

Allelic variation at 10 DNA microsatellite loci was assayed in scale samples of steelhead *Oncorhynchus mykiss* ($n = 333$) collected between 1976 and 2003 from the lower main stem of the Kitimat River, British Columbia. Our objectives were to (1) investigate the genetic diversity of wild steelhead populations in the river before hatchery stocking began in 1984 (baseline samples: 1976–1977, 1983–1984; $n = 145$) 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 (1987–2003; $n = 188$). The annual target number of wild broodstock adults used for hatchery production was

40 (20 of each sex) but varied from 9 to 39 among years. The level of population subdivision (θ) among Kitimat River samples was low (0.004) and not significantly different from 0. Tests of θ 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 year-classes 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.

Hilborn, R. 1992. Hatcheries and the future of salmon in the northwest. *Fisheries* 17(1): 5-8.

Artificial propagation is often seen as a way to maintain and increase or augment fish stocks that have suffered from habitat loss and overexploitation. Large-scale hatchery programs for salmonids in the Pacific Northwest have largely failed to provide the anticipated benefits; rather than benefiting the salmon populations, these programs may pose the greatest single threat to the long-term maintenance of salmonids. Fisheries scientists, by promoting hatchery technology and giving hatchery tours, have misled the public into thinking that hatcheries are necessary and can truly compensate for habitat loss. I argue that hatchery programs that attempt to add additional fish to existing healthy wild stocks are ill advised and highly dangerous.

Hilborn, R., and J. Winton. 1993. Learning to enhance salmon production: lessons from the Salmonid Enhancement Program. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 2043-2056.

We evaluate the Salmonid Enhancement Program (SEP) to determine its effectiveness at producing adult fish in the catch and its ability to learn from experience. The original goal of SEP was to produce up to 86 metric tons of salmon per year, and it has relied primarily on three major technologies: hatcheries, spawning channels, and lake enrichment to achieve this goal. We estimate that SEP's annual production is about 12,400 tons of salmon per year. Thus, the program has fallen short of its objective. We show that SEP has devoted considerable effort in evaluating individual facilities and sites, however, SEP has been unable or unwilling to evaluate overall program success and direction. Due to natural variation in survival rates, it is difficult to determine, even after 15 years, which technologies are likely to be successful. Furthermore, there is a paucity of information on wild stocks and the extent to which these enhancement activities have an effect on their numbers. We conclude that no technology has been proven, that 15 years is insufficient to determine which technologies to explore, and that programs like SEP must rely on outside evaluation of overall program success and outside direction for program guidance.

Hindar, K., N. Ryman, and F. Utter. 1991. Genetic effects of cultured fish on natural fish populations. Canadian Journal of Fisheries and Aquatic Sciences 48: 945-957.

This paper addresses the genetic consequences of aquaculture on natural fish populations. The study is motivated by rapidly increasing numbers of intentionally and accidentally released fish and is based on empirical observations reported in the literature. A wide variety of outcomes, ranging from no detectable effect to complete introgression or displacement, has been observed following releases of cultured fish into natural settings. Where genetic effects on performance traits have been documented, they always appear to be negative in comparison with the unaffected native populations. These findings are consistent with theoretical considerations of the implications of elevated levels of gene flow between cultured and locally adapted natural populations; they raise concerns over the genetic future of many natural populations in the light of increasing numbers of released fish. Strategies for the genetic protection of native populations from the effects of aquaculture are outlined including more secure containment, the use of sterilized fish, and modifying the points of rearing and release. We recommend strong restriction on gene flow from cultured to wild populations and effective monitoring of such gene flow.

Hulett, P. L., C. S. Sharpe, AND C. W. Wagemann. 2004. Critical need for rigorous evaluation of salmonid propagation programs using local wild broodstock. Pages 253-262 in M. Nickum, P. Mazik, J. Nickum, and D Mackinlay, editors. Propagated fish in resource management. American Fisheries Society Symposium 44, Bethesda, Maryland.

The use of local wild broodstocks for hatchery production, whether intended to boost natural production (supplementation) or to provide fishing opportunity (harvest augmentation), has increasingly been prescribed as a means to aid in the recovery of depressed salmonid stocks in the Pacific Northwest. Controversy over the efficacy and risks of such propagation programs continues despite years of recommendations from numerous science review panels that resolution of this issue is a critical need for development of recovery strategies. Moreover, a recent review of supplementation programs found them generally to be lacking key elements of evaluation. A particularly notable finding of that review was the absence of data on the performance of the hatchery fish in the wild or the survival of their naturally produced offspring. We propose here some key elements to be evaluated in supplementation type programs. We also report on observations from a steelhead *Oncorhynchus mykiss* wild broodstock program in the Kalama River (southwest Washington) that further emphasize the need for rigorous evaluation of such programs. For example, achieving basic program objectives (e.g., collecting representative broodstock, meeting rearing and release targets, and minimizing adverse ecological or genetic impacts of the propagation program on the wild population) involved unexpected logistical challenges that could hinder program success, yet could go unnoticed absent rigorous evaluation protocols. We also describe the magnitude of genetic swamping (Ryman-Laikre effect) that could result from the spawning of wild broodstock-origin adults that returned in 2002: up to 75% of the

potential spawners were hatchery fish whose parents comprised only 18% of the wild population the previous generation. These observations support the contention that understanding the roles of propagated fish in the management, conservation, and recovery of salmonid fishes will not be obtained without substantial increases in the scope and rigor of evaluation of such programs.

Jonsson, B., and I.A. Fleming. 1993. Enhancement of wild salmon populations. In G. Sundnes (ed.) 1993. Human impact on self-recruiting populations. An International Symposium, Kongsvoll, Norway, 7-11 June.

Habitat destruction, overexploitation and species introductions are causing declines in salmon populations and resulting in a growing need for enhancement. Enhancement may occur through supplementation of wild populations with hatchery-reared fish, as well as by improvements in spawning and rearing habitats. Management regulations also may be used to protect habitats and populations against destruction and over exploitation. Although the fitness of hatchery salmon in nature is lower than that of wild salmon, supplementation has been used to enhance populations successfully, at least in the short term. However, supplementation is not without problems and conflicts. It can result in the spread of contagious diseases, in ecological interference with wild populations, and in the disruption of the genetic structure of wild populations through introgression, genetic drift, and unintentional changes in selection regimes. Thus, the use of supplementation to enhance populations should be carefully considered, even when only a single generation boost to a population seems warranted. Protection and restoration of habitat, combined with adequate management regulation, are likely to provide the only true long-term means to enhancing populations.

Jonsson, B., and N. Jonsson. 2006. Cultured Atlantic salmon in nature: a review of their ecology and interaction with wild fish. ICES Journal of Marine Science 63: 1162-1181.

When cultured Atlantic salmon are released into nature, they compete with wild fish for food, space, and breeding partners. As a result of morphological, physiological, ecological, and behavioural changes that occur in hatcheries, their competitive ability often differs from that of wild fish. These changes are partly phenotypic and partly genetic. Cultured juveniles' faster growth rate influences age and size at smolting and maturity, reproductive output, and longevity. Fast-growing parr tend to smolt younger, produce more but smaller eggs, attain maturity earlier, and die younger. Juvenile learning influences a number of behavioural traits, and differences in early experience appear to affect feeding and spawning success, migratory behaviour, and homing ability. Genetic change in hatcheries is chiefly the result of natural selection, with differential mortality among genotypes and broodstock selection based on production traits such as high adult body mass and fast growth rate. Experimental evidence has revealed that cultured parr's greater aggression often allows them to dominate wild parr, although smaller cultured parr can be subordinated if they co-occur in fast-flowing water and if wild smolts have established prior residence. During spawning, the fitness of wild salmon is superior to that of cultured conspecifics. Cultured males are inferior to wild

males in intra-sexual competition, courting, and spawning; cultured females have greater egg retention, construct fewer nests, and are less efficient at covering their eggs in the substratum than their wild counterparts. In rivers, the early survival of cultured offspring is lower than that of their wild counterparts. The lifetime reproductive success of farmed fish has been estimated at 17% that of similar-sized wild salmon. As a result of ecological interaction and through density-dependent mechanisms, cultured fish may displace wild conspecifics to some extent, increase their mortality, and decrease their growth rate, adult size, reproductive output, biomass, and production.

Johnsson, J.I., and M.V. Abrahams. 1991. Interbreeding with domestic strain increases foraging under threat of predation in juvenile steelhead trout (*Oncorhynchus mykiss*): an experimental study. Canadian Journal of Fisheries and Aquatic Sciences 48(2): 243-247.

The foraging behaviour of laboratory-reared juvenile steelhead trout (*Oncorhynchus mykiss*) and steelhead/domesticated rainbow trout hybrids were compared. In 10 replicate experiments, 10 fish from each strain were allowed to choose between foraging in a safe area or an area containing a predator. The hybrid trout were significantly more willing to risk exposure to the predator than were the steelhead. It was possible that differences in the relative willingness to risk exposure may have reflected differences in their susceptibility to predation. A second experiment measured the susceptibility of these two strains to the predator by simulating standardized encounters between predator and prey. Both strains suffered identical mortality rates and therefore were considered to be equally susceptible to the predator. This experiment confirmed that the hybrid trout were significantly more willing to take risks than the wild steelhead. These results indicate that interbreeding between escaped hatchery and wild fish may have a potentially damaging effect on the wild population.

Johnson, R.C., P.K. Weber, J.D. Wikert, M.L. Workman, R.B. MacFarlane, M.J. Grove, and A.K. Schmitt. 2012. Managed metapopulations: do salmon hatchery 'sources' lead to in-river 'sinks' in conservation? PloS One 7(2): (In press).

Maintaining viable populations of salmon in the wild is a primary goal for many conservation and recovery programs. The frequency and extent of connectivity among natal sources defines the demographic and genetic boundaries of a population. Yet, the role that immigration of hatchery-produced adults may play in altering population dynamics and fitness of natural populations remains largely unquantified. Quantifying, whether natural populations are self-sustaining, functions as sources (population growth rate in the absence of dispersal, $\lambda > 1$), or as sinks ($\lambda < 1$) can be obscured by an inability to identify immigrants. In this study we use a new isotopic approach to demonstrate that a natural spawning population of Chinook salmon, (*Oncorhynchus tshawytscha*) considered relatively healthy, represents a sink population when the contribution of hatchery immigrants is taken into consideration. We retrieved sulfur isotopes ($^{34}\text{S}/^{32}\text{S}$, referred to as $\delta^{34}\text{S}$) in adult Chinook salmon otoliths (ear bones) that were deposited during their early life history as juveniles to determine whether individuals were produced in hatcheries or naturally in rivers. Our results show that only 10.3% (CI = 5.5

to 18.1%) of adults spawning in the river had otolith $\lambda^{34}\text{S}$ values less than 8.5‰, which is characteristic of naturally produced salmon. When considering the total return to the watershed (total fish in river and hatchery), we estimate that 90.7 to 99.3% (CI) of returning adults were produced in a hatchery (best estimate = 95.9%). When population growth rate of the natural population was modeled to account for the contribution of previously unidentified hatchery immigrants, we found that hatchery-produced fish caused the false appearance of positive population growth. These findings highlight the potential dangers in ignoring source-sink dynamics in recovering natural populations, and question the extent to which declines in natural salmon populations are undetected by monitoring programs.

Kenaston, K.R., R.B. Lindsay, and R.K. Schroeder. 2001. Effect of acclimation on the homing and survival of hatchery winter steelhead. North American Journal of Fisheries Management 21(4): 756-773.

We evaluated prerelease acclimation of hatchery winter steelhead *Oncorhynchus mykiss* in Whittaker Creek, a tributary of the Siuslaw River, Oregon, as a management strategy to attract returning adults to a release site where they could be removed. The objective was to reduce the number of hatchery fish in wild steelhead spawning areas while providing hatchery steelhead for recreational fisheries. We found no significant difference in homing rate or survival between hatchery steelhead acclimated for 30 d and those trucked from the hatchery and directly released. For the 1991-1993 broods, a mean of 92% of directly released fish and 97% of acclimated fish were accounted for in Whittaker Creek. In contrast, 15% of adults from hatchery smolts released at four traditional sites in the main-stem Siuslaw River were accounted for in Whittaker Creek. The spatial distribution of the catch in recreational fisheries was similar for the direct and acclimated groups; that catch, however, was nearer Whittaker Creek than the catch from traditional releases. The study shows that acclimation of juveniles is not necessary to achieve a high rate of homing of adult hatchery steelhead to a release site. Direct tributary releases combined with an adult collection facility can be used as a management strategy to minimize effects of hatchery fish on wild stocks, yet still provide recreational harvest.

Knudsen, C. M., S. L. Schroder, C. A. Busak, M. V. Johnston, T. N. Pearson, W. J. Bosch, and D. E. Fast. 2006. Comparison of life history traits between first-generation hatchery and wild upper Yakima River spring Chinook salmon. Transactions of the American Fisheries Society 135: 1130-1144.

Life history traits in hatchery and wild spring Chinook salmon *Oncorhynchus tshawytscha* from the upper Yakima River were compared to determine whether locally adapted traits had diverged after one generation of state-of-the-art artificial propagation. Sex composition in wild- and hatchery-origin fish differed in three of four brood years ($P \leq 0.01$). The proportion of hatchery males, primarily age 3, increased from 38% to 49% over time. Conversely, the sex composition of wild fish did not exhibit a similar linear trend. Most hatchery- and wild-origin fish reached maturity at age 4 ($\geq 76\%$), followed in magnitude by ages 3 and 5. Wild mean age at maturation demonstrated no

significant trend over time, while hatchery mean age at maturation declined ($P = 0.05$). Mean lengths of 3–5-year-old hatchery fish were shorter than those of wild fish of the same age (differences of 2.7 cm for age 3, 1.7 cm for age 4, and 1.9 cm for age 5). Likewise, body weights of hatchery fish were lower than those of wild fish (differences of 0.3 kg for age 3, 0.3 kg for age 4, and 0.6 kg for age 5), representing a change in body size of between 0.5 and 1.0 standard deviation (SD). Median arrival timing of hatchery and wild fish at a broodstock collection site just downstream of ancestral spawning grounds showed no consistent difference. However, the median arrival date of age-3 fish was 19–20 d later than that for fish of ages 4 and 5 ($P < 0.01$). Mean spawn timing of hatchery fish was significantly earlier (5.1 d) than that of wild fish in a “common-garden” experiment ($P < 0.05$). We estimate that fitness could be reduced by as much as 1–5% for traits diverging from their optima by 0.5–1.0 SD. The degree of genetic determination of the divergence is unknown, but future monitoring will help clarify this. Perhaps the most important conclusion of our study is that even a hatchery program designed to minimize differences between hatchery and wild fish did not produce fish that were identical to wild fish.

Kostow, K. 2011. Strategies for reducing the ecological risks of hatchery programs: Case studies from the Pacific Northwest. Environmental Biology of Fishes (In press)

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

Kostow, K. 2004. Differences in juvenile phenotypes and survival between hatchery stocks and a natural population provide evidence for modified selection due to captive breeding. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 577–589.

Juvenile phenotypes and fitness as indicated by survival were compared for naturally produced steelhead (*Oncorhynchus mykiss*), a new local hatchery stock, and an old nonlocal hatchery stock on the Hood River, Oregon, U.S.A. Although the new hatchery stock and the naturally produced fish came from the same parent gene pool, they differed significantly at every phenotype measured except saltwater age. The characteristics of the new hatchery stock were similar to those of the old hatchery stock. Most of the phenotypic differences were probably environmentally caused. Although such character changes would not be inherited, they may influence the relative fitness of the hatchery and natural fish when they are in the same environment, as selection responds to phenotypic distributions. A difference in fitness between the new hatchery stock and naturally produced fish was indicated by significant survival differences. Acclimation of the new hatchery stock in a “seminatural” pond before release was associated with a further decrease in relative smolt-to-adult survival with little increase in phenotypic similarity between the natural and hatchery fish. These results suggest that modified selection begins immediately in the first generation of a new hatchery stock and may provide a mechanism for genetic change.

Kostow, K.E., A. R. Marshall, and S. R. Phelps. 2003. Naturally spawning hatchery steelhead contribute to smolt production but experience low reproductive success. *Transactions of the American Fisheries Society* 132: 780–790.

We used genetic mixture analyses to show that hatchery summer-run steelhead *Oncorhynchus mykiss*, an introduced life history in the Clackamas basin of Oregon, where only winter-run steelhead are native, contributed to the naturally produced smolts out-migrating from the basin. Hatchery-produced summer steelhead smolts were released starting in 1971, and returning adults were passed above a dam into the upper Clackamas River until 1999. In the 2 years of our study, summer steelhead adults, mostly hatchery fish, made up 60% to 82% of the natural spawners in the river. Genetic results provided evidence that interbreeding between hatchery summer and wild winter steelhead was likely minor. Hatchery summer steelhead reproductive success was relatively poor. We estimated that they produced only about one-third the number of smolts per parent that wild winter steelhead produced. However, the proportions of summer natural smolts were large (36–53% of the total naturally produced smolts in the basin) because hatchery adults predominated on the spawning grounds during our study. Very few natural-origin summer adults were observed, suggesting high mortality of the naturally produced smolts following emigration. Counts at the dam demonstrated that hatchery summer steelhead predominated on natural spawning grounds throughout the 24-year hatchery program. Our data support a conclusion that hatchery summer steelhead adults and their offspring contribute to wild winter steelhead population declines through competition for spawning and rearing habitats.

Kostow, K.E., S. Zhou. 2006. The effect of an introduced summer steelhead hatchery stock on the productivity of a wild winter steelhead population. Transactions of the American Fisheries Society 135: 825–841.

We investigated the effect of a hatchery program for summer steelhead *Oncorhynchus mykiss* on the productivity of a wild winter steelhead population in the Clackamas River, Oregon. We used a suite of Ricker and Beverton–Holt stock–recruitment models that incorporated species interaction variables to demonstrate that when high numbers of hatchery summer steelhead adults were present the production of wild winter steelhead smolts and adults was significantly decreased. We found that large releases of hatchery smolts also contributed to the decrease in wild adult productivity. Averaged over the results of our models, a 50% decline in the productivity parameter (the number of recruits per spawner at low densities) and a 22% decline in the maximum number of recruits produced in the basin were observed when high numbers of hatchery fish were present. We concluded that over the duration of the hatchery program, the number of hatchery steelhead in the upper Clackamas River basin regularly caused the total number of steelhead to exceed carrying capacity, triggering density-dependent mechanisms that impacted the wild population. The number of smolts and adults in the wild winter steelhead population declined until critically low levels were reached in the 1990s. Hatchery fish were removed from the system in 2000, and early results indicate that the declining trends have reversed.

Krueger, C.C., and B. May. 1991. Ecological and genetic effects of salmonid introductions in North America. Canadian Journal of Fisheries and Aquatic Sciences 48(S1): 66-77.

Stocking of non-native salmoninae into North American waters began around 1870. Brown trout from Europe established populations across North America and is the only successful inter-continental introduction. Introductions of native salmonids within North America but outside their native ranges have been common. Ecological effects of salmonid introductions, include competition, predation on native salmonids and other fishes, environmental modification through digging of redds in stream bottom substrates during spawning, and introduction of parasites and disease to native fish. Direct genetic effects may result through selective forces and/or a reduction of effective population size, genetic drift, and inbreeding. Management actions used to remove non-native salmonid populations include chemical reclamation and construction of barriers to movement. Salmonid stocking as a management practices is appropriate for species or population rehabilitation. Continued stocking of non-native salmonids should cease where viable native salmonids populations exist. New introductions of Eurasian species should not be made because effects are unpredictable. Aquaculture and the creation of transgenic fish pose special threats to North American salmonids. The era of widespread, intentional introductions of salmonids by man justifiably is drawing to a close.

Krueger, C.C., and B. W. Menzel. 1979. Effects of stocking on genetics of wild brook trout populations. Transactions of the American Fisheries Society 108: 277-287.

The study was undertaken to evaluate the long-term genetic impact of maintenance stocking upon wild brook trout (*Salvelinus fontinalis*) populations in Wisconsin. Trout were collected from streams of the Wolf and Fox River drainages and from the Osceola State Trout Hatchery. The stocking histories of the streams ranged from unstocked to heavily stocked for many years. The planted fish consisted primarily of fingerling and catchable brook and brown trout (*Salmo trutta*). Blood plasma and whole-eye homogenate samples were analyzed electrophoretically for transferrin (Tf) and lactate dehydrogenase (Ldh-B sub 2) systems. Esterase was monomorphic in all samples, but Tf and LDH displayed genetic polymorphism. The occurrence of several Tf A/A phenotypes among wild fish is notable because previous genetic studies considered the combination to be lethal. The hatchery stock was genetically distinct from most wild populations at both loci. Variation of Tf allelic frequencies among wild populations suggested an undisturbed natural geographic pattern. There were significant correlations between Ldh-B sub 2 allelic frequencies and stream stocking histories, however, with the wild type allele decreasing in importance as stocking intensity increased. This relationship does not seem to reflect interbreeding between wild and hatchery trout. Rather, it may indicate alteration of selective pressures induced by ecological interactions between the two stocks.

Largiader, C.R., and A. Scholl. 1996. Genetic introgression between native and introduced brown trout (*Salmo trutta* L.) populations in the Rhone River basin. Molecular Ecology 5(3): 417-426.

In the Doubs River (Rhone drainage) two distinct brown trout (*S. trutta*) phenotypes are observed. One phenotype is locally called Doubs trout and is characterized by four black stripes on the sides, similar to perch (*Perca fluviatilis* L.) and the other is the common phenotype of the fluvatile ecotype of brown trout, *Salmo trutta* f. *fario*. Protein data for three samples from the Doubs show that the Doubs trout belongs to the Mediterranean population group of brown trout, whereas the *fario* phenotype originates from stocking with hatchery strains of Atlantic basin origin. The two forms, however, do not hybridize freely. This is indicated by considerable gametic phase disequilibrium between alleles of hatchery and Doubs trout at one sampling site, and by lack of intermediate genotypes and phenotypes at another sampling site. The introgression patterns observed at the two sites suggest that differences in local habitat conditions can affect the degree of hybridization and introgression.

Leary, R.F., F.W. Allendorf, and K.L. Knudsen. 1985. Developmental instability as an indicator of reduced genetic variation in hatchery trout. Transactions of the American Fisheries Society 114: 230-235.

We present evidence for reduced developmental stability in a hatchery stock of westslope cutthroat trout *Salmo clarki lewisi*. These fish have a high frequency of two

obvious morphological deformities and an unusually high amount of asymmetry at five bilateral meristic traits. We have previously reported that this stock has a reduced amount of genetic variation at 35 isozyme loci compared to the wild population from which it was derived. The loss of genetic variation in this stock apparently has reduced the ability of these fish to develop precisely along genetically determined developmental pathways. We also present the biological rationale and the methods for using fluctuating asymmetry as a diagnostic tool for detecting the effects of the loss of genetic variation in cultured stocks of fish.

Levin, P.S., and J.G. Williams. 2002. Interspecific effects of artificially propagated fish: an additional conservation risk for salmon. *Conservation Biology* 16(6): 1581-1587.

For more than 120 years, hatcheries have released enormous numbers of Pacific salmon to compensate for numerous human insults to their populations, yet the ecological effects of this massive effort are poorly understood. We tested the hypothesis that hatchery-reared steelhead salmon (*Oncorhynchus mykiss*) released into the Snake River Basin negatively affect the survival of wild Snake River steelhead and chinook (*O. tshawytscha*) salmon. Because climatic conditions can influence salmon survival, we included an index of the El Niño–Southern Oscillation (ENSO) as a covariate in our analyses. Based on time series of hatchery releases and rates of smolt-to-adult survival, we demonstrate that the survival of wild chinook salmon is negatively associated with hatchery releases of steelhead. The state of the (ENSO) did not affect the strength of this relationship. We observed no relationship between survival of wild steelhead and steelhead hatchery releases. Our results suggest that industrial-scale production of hatchery fish may hinder the recovery of some threatened salmonids and that the potential interspecific impact of hatcheries must be considered as agencies begin the process of hatchery reform.

Levin, P.S., R.W. Zabel, and J.G. Williams. 2001. The road to extinction is paved with good intentions: negative association of fish hatcheries with threatened salmon. *The Royal Society of London* 268: 1153-1158.

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

Lichatowich, J.A. and J.D. McIntyre. 1987. Use of hatcheries in the management of Pacific anadromous salmonids. American Fisheries Society Symposium 1: 131-136.

Confidence in the use of hatcheries for managing Pacific anadromous salmonids has waxed and waned several times in the past 100 years. Now that many of the technological problems have been solved, other problems associated with integration of hatchery fish into natural ecosystems are being identified. The Oregon coho salmon fishery is used as an example to point out the kinds of problems confronting managers - problems that include (1) the overharvest of wild stocks by fisheries geared up to harvest the more productive hatchery stocks, (2) density-dependent survival in both freshwater and marine environments that may be associated with large releases of smolts from hatcheries, and (3) outplanting of hatchery fish to supplement natural spawning that can, if not carefully implemented, reduce survival of the natural and hatchery juveniles. Managers will have to give thoughtful consideration to these problems so that hatcheries are effective tools of management.

Lynch, M., and M. O'Hely. 2001. Captive breeding and the genetic fitness of natural populations. Conservation Genetics 2: 363-378.

Many populations of endangered species are subject to recurrent introductions of individuals from an alternative setting where selection is either relaxed or in a direction opposite to that in the natural habitat. In many cases, fish hatcheries, for example, such population structures can lead to a scenario in which alleles that are deleterious (and ordinarily kept at low levels) in the wild can rise to high frequencies and, in some cases, go to fixation. We outline how these genetic responses to supplementation programs can develop to a large enough extent to impose a substantial risk of extinction for natural populations on time scales of relevance to conservation biology. The genetic supplementation load can be especially severe when a captive population that is largely closed to import makes a large contribution to the breeding pool of individuals in the wild, as these conditions insure that the productivity of the two-population system is dominated by captive breeders. However, a substantial supplementation load can even develop when the captive breeders are always derived from the wild, and in general, a severe restriction of gene flow into the natural population is required to reduce this load to an insignificant level. Domestication selection (adaptation to the captive environment) poses a particularly serious problem because it promotes fixations of alleles that are deleterious in nature, thereby resulting in a permanent load that cannot be purged once the supplementation program is terminated. Our results suggest that the apparent short-term demographic advantages of a supplementation program can be quite deceiving. Unless the selective pressures of the captive environment are closely managed to resemble those in the wild, long-term supplementation programs are expected to result in genetic transformation that can eventually lead to natural population no longer capable of sustaining themselves.

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 America Journal of Fisheries Management 21(4): 717-724.

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.

Marchetti, M.P., and G.A. Nevitt. 2003. Effects of hatchery rearing on brain structures of rainbow trout, *Oncorhynchus mykiss*. Environmental Biology of Fishes 66: 9-14.

In this study, we contrast brain morphology from hatchery and wild reared stocks to examine the hypothesis that in salmonid fishes, captive rearing produces changes in brain development. Using rainbow trout, *Oncorhynchus mykiss*, as a model, we measured eight regions of the salmonid brain to examine differences between wild and hatchery reared fish. We find using multiple analysis of covariance (MANCOVA), analysis of covariance (ANCOVA) and discriminant function analysis (DFA) that the brains of hatchery reared fish are relatively smaller in several critical measures than their wild counterparts. Our work may suggest a mechanistic basis for the observed vulnerability of hatchery fish to predation and their general low survival upon release into the wild. Our results are the first to highlight the effects of hatchery rearing on changes in brain development in fishes.

Mason, J. W., O. M. Brynildson, and P. E. Degurse. 1967. Comparative survival of wild and domestic strains of brook trout in streams. Transactions of the American Fisheries Society 96: 313-319.

Survival and growth of progeny of domestic, domestic x wild, and wild strains of brook trout (*Salvelinus fontinalis*) were compared after these trout were released during the fall as fingerlings 9 to 10 months old in selected sections of streams. One group of the

wild strain was hatched and reared in the wild. Other groups were hatched and reared in the hatchery. The domestic strain had the highest over-winter survival in three of five streams. In only one stream did the wild strain have the highest over-winter survival. In the four streams investigated during the fall, the wild strain had the highest summer-survival. Survival of the domestic and domestic x wild strains through the summer fishing season was generally too low to evaluate survival of these strains through the second winter. The domestic strain grew most rapidly in the hatchery followed by the domestic x wild strain. This growth advantage was not maintained after release into streams. Brook trout of the domestic strain were harvested early in the fishing season and did not contribute to the late-season catch, whereas the domestic x wild and wild strains were harvested throughout the fishing season.

McDonald, D.G., C.L. Milligan, W.J. McFarlane, S. Croke, S. Currie, B. Hooke, R.B. Angus, B.L. Tufts, and K. Davidson. 1998. Condition and performance of juvenile Atlantic salmon (*Salmo salar*): effects of rearing practices on hatchery fish and comparison with wild fish. Canadian Journal of Fisheries and Aquatic Science 55(5): 1208-1219.

This study examined the effects of various modifications of rearing practices on hatchery-reared Atlantic salmon (*Salmo salar*) fingerlings and compared condition and performance of hatchery fingerlings (age 0⁺) and yearlings (age 1⁺) with those of wild-reared Atlantic salmon. Reduced fish density (and increased ration) in rearing tanks promoted increased growth and condition factor and significant changes in muscle composition, including increased muscle lipid content and glycolytic enzyme activity, specifically phosphofructokinase and lactate dehydrogenase. However, these changes had no effect on anaerobic capacity. Moreover, swimming performance was poorer in fingerlings reared at low compared with normal density. Raising the water velocity from 0 to 4 cm ·s⁻¹ (~0.7 body length ·s⁻¹) had overall beneficial effects, most notably increased endurance in fixed velocity sprint tests and a reduction of ion loss in an epinephrine challenge test. Increasing velocity to 9 cm ·s⁻¹ had no further effects. Wild fingerlings were larger with better fin quality and superior anaerobic capacity and swim performance. Even larger differences were seen between hatchery-reared and wild yearlings. It is concluded that significant changes in morphology, physiology, and muscle biochemistry of juvenile Atlantic salmon can be brought about by changing hatchery rearing conditions, but these changes are of limited effectiveness in reducing the difference between hatchery-reared and wild fish.

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.

Hatchery propagation of salmonids has been practiced in western North America for over a century. However, recent declines in wild salmon abundance and efforts to mitigate these declines through hatcheries have greatly increased the relative abundance of fish produced in hatcheries. The over-harvest of wild salmon by fishing mixed hatchery and wild stocks has been of concern for many years but genetic interactions between populations, such as hybridization, introgression and outbreeding

depression, may also compromise the sustainability of wild populations. Our goal was to examine whether a newly established hatchery population of steelhead trout successfully reproduced in the wild and to compare their rate of reproductive success to that of sympatrically spawning native steelhead. We used eight microsatellite loci to create allele frequency profiles for baseline hatchery and wild populations and assigned the smolt (age 2) offspring of this parental generation to a population of origin. Adults originating from a generalized hatchery stock artificially selected for early return and spawning date were successful at reproducing in Forks Creek, Washington. Although hatchery females ($N = 90$ and 73 in the two consecutive years of the study) produced offspring that survived to emigrate as smolts, they produced only 4.4–7.0% the number produced per wild female ($N = 11$ and 10). This deficit in reproductive success implies that the proportion of hatchery genes in the mixed population may diminish since deliberate releases into the river have ceased. This hypothesis is being tested in a long-term study at Forks Creek.

McLean, J.E., T.R. Seamons, M.B. Dauer, P. Bentzen, and T.P. Quinn. 2008. Variation in reproductive success and effective number of breeders in a hatchery population of steelhead trout (*Oncorhynchus mykiss*): examination by microsatellite-based parentage analysis. Conservation Genetics 9: 295-304.

Conservation programs that release captive-bred individuals into the wild to mix with naturally produced individuals are an increasingly common method of supporting or enhancing weak or reduced populations that otherwise may not be self-sustaining. Captive and supportive breeding can be important conservation tools for species with small or declining populations; however, in the case of hatcheries producing salmonid fishes, detailed evaluation of spawning programs is rare. We examined variation in reproductive success, measured by adult offspring production, from three parental generations of hatchery-bred steelhead trout (*Oncorhynchus mykiss*) using an exclusion-based method of genetic parentage assignment. Reproductive success varied greatly among individuals (especially males) and was correlated with fecundity and maternal spawning date. Estimates of egg to smolt survival for the population as a whole among years ranged from 64% to 95%, marine survival ranged from 0.32% to 2.30%, and the number of adults produced per female ranged from 0 to 18 and the number of adults produced per male ranged from 0 to 32. The effective number of breeders ranged from 11% to 31% of the census population size for that brood year. These ratios fell within estimates from estimates of N_e/N in chinook (*O. tshawytscha*) and rainbow trout (*O. mykiss*) hatchery populations.

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(4): 433-440.

We used multilocus microsatellite analysis to compare the reproductive success of naturally spawning wild steelhead trout (*Oncorhynchus mykiss*) with a newly established sympatric hatchery population in Forks Creek, Washington, U.S.A. Hatchery steelhead

spawning in the wild had markedly lower reproductive success than native wild steelhead. Wild females that spawned in 1996 produced 9 times as many adult offspring per capita as did hatchery females that spawned in the wild. Wild females that spawned in 1997 produced 42 times as many adult offspring as hatchery females. The wild steelhead population more than met replacement requirements (approximately 3.7–6.7 adult offspring were produced per female), but the hatchery steelhead were far below replacement requirements (<0.5 adults per female). The survival differential was greatest in the freshwater environment (i.e., production of seaward-migrating juveniles), but survival at sea favored the hatchery population in 1 year and the wild population in the next. The poor performance of the hatchery population may be a consequence of spawning too early in the winter, generations of inadvertent domestication selection, or a combination of these two.

McMichael, G.A., T.N. Pearsons, and S.A. Leider. 1999. Behavioral interactions among hatchery-reared steelhead smolts and wild *Oncorhynchus mykiss* in natural streams. North American Journal of Fisheries Management 19(4): 948-956.

The potential for hatchery fish to negatively impact wild fish has been identified as a concern for dwindling stocks of naturally produced anadromous salmonids in the Pacific Northwest. Using a control treatment approach, we performed a multiscale examination of potential behavioral impacts of releases of hatchery-produced steelhead *Oncorhynchus mykiss* (anadromous rainbow trout) on preexisting wild populations of *O. mykiss* (anadromous and potamodromous) over a 4-year period. We released approximately 33,000 conventionally reared hatchery steelhead smolts (treatment) into an upper Yakima River tributary in 1991, 1992, 1993, and 1994 and investigated behavioral interactions and small-scale displacement (0.2–5.0 m). Snorkelers conducted behavioral observations and observed small-scale displacements in treatment and control streams for approximately 1 month following releases. Hatchery steelhead were generally larger than wild *O. mykiss* and dominated most (68%) contests. The types of behavioral interactions observed differed between control and treatment streams ($P < 0.01$). Behavioral interactions involving physical contact (e.g., nips) were observed more frequently in treatment streams than in control streams, whereas those involving nonphysical contact displays (e.g., threats and chases) were more frequent in control streams. Contrary to our expectations, total behavioral interaction rates were generally higher in control streams than in treatment streams, though the difference was not statistically significant ($P = 0.07$). Hatchery steelhead displaced wild *O. mykiss* in 79% of the contests observed between these groups. Our results indicate that the behavior of hatchery steelhead can pose risks to preexisting wild *O. mykiss* where the two interact. Strategies to minimize undesirable risks associated with behavior of released hatchery steelhead should be addressed if protection and restoration of wild *O. mykiss* stocks is the management goal.

Miller, R.B. 1953. Comparative survival of wild and hatchery-reared cutthroat trout in a stream. Transactions of the American Fisheries Society 83: 120-130.

Gorge Creek, a typical small mountain trout stream on the eastern slope of the Rocky Mountains, was used in a test to measure survival and weight changes in hatchery-reared cutthroat trout (*Salmo clarki*). A resident population of this species exists in the stream. The experimental procedure was to introduce groups of trout into enclosures 1/2 to 3/4 mile long; each trout in a group was given a numbered Petersen tag and weighed before planting. Recapture by angling and reweighing were carried out throughout the season of planting and also in later summers. In this way six lots of pond-reared, one lot of stream-reared, and one lot of transplanted wild cutthroat were studied. Pond-reared fish exhibited very low survivals over the first (0 to 4.9 percent) and second (0 to 3.1 percent) winter. Survival was largely independent of age. Transplanted wild trout showed survivals of 46.0 percent to 29.0 percent to the second and third summers, respectively. Stream-reared hatchery fish gave an intermediate value (17.2 percent to the second summer). All lots of trout lost weight for some 30 or 40 days when superimposed on a resident population. This loss was more severe and was regained more slowly in pond-reared trout than in transplanted wild trout. It is held that the low survivability of hatchery fish is due to the absence of natural selection at early stages in the life history.

Miller, L.M., T. Close, and A.R. Kapuscinski. 2004. Lower fitness of hatchery and hybrid rainbow trout compared to naturalized populations in Lake Superior tributaries. Molecular Ecology 13: 3379-3388.

We have documented an early life survival advantage by naturalized populations of anadromous rainbow trout *Oncorhynchus mykiss* over a more recently introduced hatchery population and outbreeding depression resulting from interbreeding between the two strains. We tested the hypothesis that offspring of naturalized and hatchery trout, and reciprocal hybrid crosses, survive equally from fry to age 1+ in isolated reaches of Lake Superior tributary streams in Minnesota. Over the first summer, offspring of naturalized females had significantly greater survival than offspring of hatchery females in three of four comparisons (two streams and 2 years of stocking). Having an entire naturalized genome, not just a naturalized mother, was important for survival over the first winter. Naturalized offspring outperformed all others in survival to age 1+ and hybrids had reduced, but intermediate, survival relative to the two pure crosses. Averaging over years and streams, survival relative to naturalized offspring was 0.59 for hybrids with naturalized females, 0.37 for the reciprocal hybrids, and 0.21 for hatchery offspring. Our results indicate that naturalized rainbow trout are better adapted to the conditions of Minnesota's tributaries to Lake Superior so that they outperform the hatchery-propagated strain in the same manner that many native populations of salmonids outperform hatchery or transplanted fish. Continued stocking of the hatchery fish may conflict with a management goal of sustaining the naturalized populations.

Moyer, G.R., M.S. Blouin, and M.A. Banks. 2007. The influence of family-correlated survival on N_e/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.

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).

Naish, K.A., J. E. Taylor III, P. S. Levin, T.P. Quinn, J. R. Winton, D. Huppert, and R. Hilborn. 2008. An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. Advances in Marine Biology 53: 61-194.

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

accurate marking and production of hatchery fish with high survival rates, and it is not yet clear whether selective fishing will prevent overharvest of wild populations. Finally, research demonstrating disease transmission from hatchery fish to wild populations was observed to be equivocal; evidence in this area has been constrained by the lack of effective approaches to studying the fate of pathogens in the wild. We then reviewed several approaches to studying the economic consequences of hatchery activities intended to inform the social decisions surrounding programmes, but recognized that placing monetary value on conservation efforts or on hatcheries that mitigate cultural groups' loss of historical harvest opportunities may complicate these analyses. We noted that economic issues have rarely been included in decision making on hatchery programmes. We end by identifying existing major knowledge gaps, which, if filled, could contribute towards a fuller understanding of the role that hatchery programmes could play in meeting divergent goals. However, we also recognized that many management recommendations arising from such research may involve trade-offs between different risks, and that decisions about these trade-offs must occur within a social context. Hatcheries have played an important role in sustaining some highly endangered populations, and it is possible that reform of practices will lead to an increase in the number of successful programmes. However, a serious appraisal of the role of hatcheries in meeting broader needs is urgently warranted and should take place at the scientific, but more effectively, at the societal level.

Narum, S.R., M.S. Powell, R. Evenson, B. Sharp, and A.J. Talbot. 2006. Microsatellites reveal population substructure of Klickitat River native steelhead and genetic divergence from an introduced stock. North American Journal of Fisheries Management 26: 147-155.

Determining fine-scale genetic diversity and structure is critical for the conservation and management of populations, especially those under heavy anthropogenic influence. We analyzed 446 individuals at nine microsatellite loci to determine the local population structure of naturally produced steelhead *Oncorhynchus mykiss* and genetic differentiation from introduced hatchery strain steelhead in the Klickitat River of the Pacific Northwest. We detected significant genetic structure among steelhead in various tributaries to the Klickitat River; the most divergent population was located above a waterfall that acts as a partial upstream migration barrier (average pairwise $F_{ST} \approx 0.13$; $P < 0.0001$). Analysis of mixtures indicated an estimate of six to seven genetically distinct populations of naturally reproducing steelhead in this river system. The hatchery strain appears to remain genetically distinguishable from native stocks (average pairwise F_{ST} of 0.078 with $P < 0.0001$), as only 4.0% of naturally produced steelhead had their most likely assignment to the hatchery strain. These results indicate that the genetic integrity and variation of native Klickitat River steelhead have been maintained despite repeated hatchery introductions and that the potential is high for restoring this threatened population. Further, this study suggests that hierarchical analyses of mixtures to identify distinct populations in a watershed are a valuable method for directing management of reproductively isolated populations.

Neff, B.D., S.R. Garner, and T.E. Pitcher. 2011. Conservation and enhancement of wild fish populations: preserving genetic quality versus genetic diversity. Canadian Journal of Fisheries and Aquatic Sciences 68: 1139-1154.

Nearly 40% of commercial fisheries have now collapsed or are in serious decline. In response, governments have invested millions of dollars into artificial breeding programs, but many programs have failed to rehabilitate dwindling wild stocks. This failure may in part lie in the lack of knowledge about the genetic architecture of fitness: the genes and genotypes that are associated with individual performance. In this paper we discuss (i) artificial breeding programs, (ii) the genetic architecture of fitness, (iii) additive and nonadditive genetic effects on fitness, (iv) genetic diversity and evolvability, and (v) natural breeding and adaptation. We argue that most breeding programs do not maintain genetic adaptations and may consequently be ineffective at rehabilitating or enhancing wild populations. Moreover, there is no evidence that preserving genetic diversity as measured from neutral genetic markers increases fish performance or population viability outside of populations that experience strong inbreeding depression, and limited data that genetic diversity increases the potential for populations to adapt to changing environments. We suggest that artificial breeding programs should be used only as a last resort when populations face imminent extirpation and that such programs must shift the focus from solely preserving genetic diversity to preserving genetic adaptations.

Negus, M.T. 1999. Survival traits of naturalized, hatchery, and hybrid strains of anadromous rainbow trout during egg and fry stages. North American Journal of Fisheries Management 19(4): 930-941.

Two strains of anadromous rainbow trout *Oncorhynchus mykiss*, naturalized steelhead and kamloops (not the pure Kamloops strain from British Columbia, hence not capitalized) currently inhabit the Minnesota waters of Lake Superior and may have the potential to hybridize. This could compromise the genetic integrity of the naturalized steelhead population. Both strains are supplemented by annual stocking, despite the fact that the steelhead population reproduces naturally. Egg viability and fry behavior experiments were undertaken to evaluate the potential for hybridization and to provide information for future management of the two strains. The kamloops eggs were slightly smaller, but sizes overlapped substantially with steelhead egg sizes. Mortality of kamloops eggs from spawning to hatching was greater than steelhead eggs. Steelhead fry exhibited a greater fright response (wariness) than kamloops fry when startled by movement over their tanks. Hybrid egg survival and wariness traits were intermediate to those of the pure strains, but more closely resembled those of the maternal strain. These traits appeared to be heritable. Reevaluation of steelhead and kamloops management will be necessary in the future, taking into account the popularity of the kamloops fishery and the potential for degradation or elimination of the naturalized steelhead strain.

Nelson, T.C., M.L. Rosenau, and N.T. Johnston. 2005. Behavior and survival of wild and hatchery-origin winter steelhead spawners caught and released in a recreational fishery. *North American Journal of Fisheries Management* 25: 931-943.

Mandatory catch and release of wild fish and supplementation with hatchery-reared fish are commonly used to sustain sport fisheries on low-abundance populations of wild steelhead. However, their effectiveness in limiting angling mortality on wild fish is uncertain. We radiotagged 226 (125 wild, 101 hatchery) angled adult steelhead *Oncorhynchus mykiss* near the mouth of the Vedder-Chilliwack River, British Columbia, in 1999 and 2000 and monitored their subsequent movements to determine survival to spawning and overlap in the distributions of inferred holding sites, spawning sites, and spawning times. The distributions of prespawning holding sites did not differ between wild and hatchery fish in either year, but spawning locations differed. Holding and spawning sites used by hatchery fish were restricted to the lower two-thirds of the river, downstream of the hatchery where they were reared but well upstream of their smolt release site. Wild fish spawned throughout the watershed. Spawning times did not differ between wild and hatchery fish, but varied with run timing. The maximum mortality from the initial catch and release and radio-tagging was 1.4% in 1999 and 5.8% in 2000; true mortality rates were lower because tag regurgitation was indistinguishable from death. The fishery subsequently killed 2.5% of tagged wild fish and harvested 20% (1999) and 43% (2000) of the hatchery fish. Seventy-two tagged fish were recaptured and released in the sport fishery up to three times without any mortality before spawning. Hatchery fish were recaptured at twice the rate of wild fish. At least 92% of unharvested fish spawned, and 75% of successful spawners survived to emigrate from the watershed. The incidence of postspawning death did not vary with the frequency of capture and release. Catch-and-release angling imposed small costs in terms of survival; however, behavioral differences existed between adult wild fish and the adult F1 progeny of wild fish reared to smolt stage in a hatchery.

Nickelson, T. 2003. The influence of hatchery coho salmon (*Oncorhynchus kisutch*) on the productivity of wild coho salmon populations in Oregon coastal basins. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 1050-1056.

To aid in the recovery of depressed wild salmon populations, the operation of hatcheries must be changed to reduce interactions of juvenile hatchery fish with wild fish. Evidence suggests that productivity of wild populations can be reduced by the presence of large numbers of hatchery smolts in lower rivers and estuaries that attract predators. An index of productivity based on the density-independent rate of reproduction of wild coho salmon (*Oncorhynchus kisutch*) in 12 Oregon coastal river basins and two lake basins was negatively correlated with the average number of hatchery coho salmon smolts released in each basin. The index of productivity was not significantly correlated with the average proportion of hatchery coho salmon in each naturally spawning population or with habitat quality. Alterations to hatchery programs that could encourage recovery of wild populations include (i) avoiding release of large numbers of smolts in areas with high concentrations of wild fish, (ii) decreasing the number of smolts released, and (iii)

using a volitional release strategy or a strategy that employs smaller release groups spread temporally.

Nickelson, T.E., M.F. Solazzi, and S.L. Johnson. 1986. Use of hatchery coho salmon presmolts to rebuild wild populations in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 43: 2443-2449.

We evaluated the effectiveness of using hatchery coho salmon presmolts to rebuild wild populations in Oregon coastal streams. Juvenile and adult populations were monitored in 15 stocked and 15 unstocked streams from summer 1980 until summer 1985. During the summers following the planting of presmolts, the number of juveniles per square meter of pool surface area was higher in the stocked streams than in the unstocked streams. However, wild juveniles were significantly less abundant in the stocked streams during the 2 years when density of wild juveniles was estimated separately from hatchery juveniles. Adult returns to the stocked streams were not significantly different from adult returns to the unstocked streams, but returns tended to be earlier in the stocked streams than in the unstocked streams. Despite similar numbers of adults per kilometer in the stocked streams and unstocked streams in the years the presmolts returned to spawn, the resulting densities of juveniles in the stocked streams were significantly lower than the densities of juveniles in the unstocked streams. We concluded that early time of spawning of the hatchery coho salmon was largely responsible for their failure to rebuild the populations in the streams stocked with presmolts.

Page, K.S., M.T. Negus, M.C. Ward, and T.L. Close. 2011. Simulated effects of nonintrogressive hybridization with a stocked hatchery strain of rainbow trout on the sustainability and recovery of naturalized steelhead populations in Minnesota waters of Lake Superior. North American Journal of Fisheries Management 31(6): 1065-1076.

A model was developed to explore the impacts of nonintrogressive hybridization with a stocked hatchery strain of rainbow trout *Oncorhynchus mykiss* (Kamloops strain [KAM]) on the sustainability and recovery of naturalized steelhead (anadromous rainbow trout) populations in Minnesota tributaries of Lake Superior. The model was used to assess the extinction risk of Lake Superior steelhead over a 50-year period based on multiple KAM stocking scenarios, initial population sizes, and levels of assortative mating. No extinctions occurred in simulated steelhead populations regardless of initial size after a one-time introduction of KAM; however, the risk of extinction due to nonintrogressive hybridization increased dramatically for scenarios involving annual stocking of KAM. The level of assortative mating among KAM and steelhead greatly influenced the risk of steelhead population decline or extinction for all scenarios. Results of the model support the contention that nonintrogressive hybridization could be an impediment to the sustainability and recovery of the steelhead population in Lake Superior.

Pearson, T.N., A. L. Fritts, and J. L. Scott. 2007. The effects of hatchery domestication on competitive dominance of juvenile spring Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 64: 803-813.

Efforts to conserve depleted populations of Pacific salmon (*Oncorhynchus* spp.) often rely on hatchery programs to offset losses of fish from natural and anthropogenic causes, but their use has been contentious. We examined the impact of a large-scale reduction in hatchery stocking on 15 populations of wild coho salmon along the coast of Oregon (USA). Our analyses highlight four critical factors influencing the productivity of these populations: (1) negative density-dependent effects of hatchery-origin spawners were 5 times greater than those of wild spawners; (2) the productivity of wild salmon decreased as releases of hatchery juveniles increased; (3) salmon production was positively related to an index of freshwater habitat quality; and (4) ocean conditions strongly affect productivity at large spatial scales, potentially masking more localized drivers. These results suggest that hatchery programs' unintended negative effects on wild salmon populations, and their role in salmon recovery, should be considered in the context of other ecological drivers.

Pitcher, T.E., and B.D. Neff. 2007. Genetic quality and offspring performance in Chinook salmon: implications for supportive breeding. Conservation Genetics 8: 607-616.

Each year salmon and other fishes are caught and used for supportive breeding programs that attempt to augment natural populations that are threatened with extinction. These programs typically mate individuals randomly and as such they overlook the importance of genetic quality to offspring fitness and ultimately to ensuring population health. Here, we use Chinook salmon (*Oncorhynchus tshawytscha*) and a fully crossed quantitative genetic breeding design to partition genetic variance in offspring performance (growth and survival) to additive and non-additive genetic effects as well as maternal effects. We show that these three effects contribute about equally to the variation in survival, but only non-additive genetic and maternal effects contribute to variation in growth. Some of the genetic effects could be assigned to variation at the class IIB locus of the major histocompatibility complex, but the maternal effects were not associated with egg size and we found no relationship between dam phenotypic measures and offspring survival or growth. We also found no relationship between sire sexually selected characters and offspring survival or growth, which is inconsistent with a "good genes" hypothesis. Finally, we show that incorporation of genetic quality into supportive breeding programs can increase offspring growth or survival by between 3% and 19% during the endogenous feeding stage alone, and projections to adulthood suggest that survivorship could be over four fold higher.

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.

Relative growth and survival of offspring from matings of hatchery and wild Deschutes River (Oregon) summer steelhead trout, *Salmo gairdneri*, were measured to determine if hatchery fish differ genetically from wild fish in traits that can affect the stock–recruitment relationship of wild populations. Sections of four natural streams and a hatchery pond were each stocked with genetically marked (lactate dehydrogenase genotypes) eyed eggs or unfed swim-up fry from each of three matings: hatchery × hatchery (HH), hatchery × wild (HW), and wild × wild (WW). In streams, WW fish had the highest survival and HW fish the highest growth rates when significant differences were found; in the hatchery pond, HH fish had the highest survival and growth rates. The hatchery fish were genetically different from wild fish and when they interbreed with wild fish may reduce the number of smolts produced. Hatchery procedures can be modified to reduce the genetic differences between hatchery and wild fish.

Reisenbichler, R.R., and S.P. Rubin. 1999. Genetic changes from hatchery propagation affect productivity and viability of wild populations. ICES Journal of Marine Science 56: 459-466.

A number of published studies have shown genetic differences between hatchery and wild anadromous Pacific salmon (*Oncorhynchus spp.*) Nevertheless, none of these studies has provided compelling evidence that artificial propagation poses a genetic threat to conservation of naturally spawning populations. Hence constructive debate and consensus on how to limit deleterious genetic effects from artificial propagation have been limited or ineffectual, often because participants don't agree that a problem exists. When the published studies and three studies in progress are considered collectively, however, they provide strong evidence for a problem - evidence that the fitness for natural spawning and rearing can be rapidly and substantially reduced by artificial propagation. This issue takes on great importance in the Pacific Northwest where supplementation of wild salmon populations with hatchery fish has been identified as an important tool for restoring these populations. Recognition of negative aspects may lead to restricted use of supplementation, and better conservation, better evaluation, and greater benefits when supplementation is used.

Rhodes, J. S., and T. P. Quinn. 1999. Comparative performance of genetically similar hatchery and naturally reared juvenile coho salmon in streams. North American Journal of Fisheries Management 19: 670-677.

Hatchery-reared salmon have been reported to be inferior to wild fish in some studies and competitively superior in others. We examined the influence of early rearing environment (hatchery versus natural) on the summer survival, movement, and growth of genetically similar juvenile coho salmon *Oncorhynchus kisutch* in streams. In each of 2 years, 5,000–10,000 fry from a hatchery cohort were placed above barrier falls in each of two streams to rear naturally at low density. The rest were reared at high

density in hatchery raceways. After 3 months (late spring), we electrofished the streams, marked the naturally reared salmon caught, and then added equal numbers of marked hatchery-reared salmon to the streams. The streams were electrofished again in the summer to monitor survival, movement, and growth. Hatchery-reared and naturally reared juveniles survived equally well (about 90% survived each summer), and few fish of either rearing type emigrated from the study streams. Hatchery fish were about 10% larger than naturally reared fish at the time of introduction, but there was no evidence for size-related survival in the streams. When adjusted for size, hatchery fish grew at faster rates than naturally reared fish. Our results suggest that hatchery-reared coho salmon perform similarly to naturally reared salmon when introduced into streams in low numbers and with a relatively small size advantage.

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 divergent life history. *Evolutionary Applications* (In press).

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.

Schroeder, R.K., R.B. Lindsay, and K.R. Kenaston. 2001. Origin and straying of hatchery winter steelhead in Oregon coastal rivers. *Transactions of the American Fisheries Society* 130(3): 431-441.

We evaluated the origin and straying of hatchery steelhead *Oncorhynchus mykiss* among 16 rivers on the Oregon coast to examine rearing or release practices that might contribute to straying. Data were collected on the returning adults of three brood years that had been differentially marked and released as smolts in 1990–1992. The percentage of strays averaged 11% (range, 4–26%) of the samples of hatchery and wild fish in 11 streams where hatchery steelhead were released. Stray hatchery fish composed a mean of 22% (range, 9–43%) in 5 streams without hatchery releases. The two predominant factors that contributed to straying were releases of stocks transplanted from their natal basins and releases into adjacent basins. Releases of

transplanted stocks into adjacent basins accounted for 41% of the strays, while releases of transplanted stocks into nonadjacent basins accounted for 29% of the strays. Local stocks of steelhead released into adjacent basins accounted for 16% of the strays. The incidence of straying by hatchery fish and its widespread occurrence in Oregon coastal rivers present genetic and ecological risks to wild populations of winter steelhead. Strategies to reduce straying may include using local brood stocks, rearing and releasing fish within their natal basins, reducing the numbers of hatchery fish released, and eliminating some hatchery releases altogether.

Skaala, O., K.E. Jorstad, and R. Borgstrom. 1996. Genetic impact on two wild brown trout (*Salmo trutta*) populations after release of non-indigenous hatchery spawners. Canadian Journal of Fisheries and Aquatic Sciences 53: 2027-2035.

A genetically marked hatchery strain of brown trout (*Salmo trutta*) was employed to study the genetic impact from non-indigenous hatchery fish on wild stocks. The hatchery spawners were released in autumn 1989 into the spawning localities of two wild trout stocks in River Oyreselv, Norway. The F₁ generation was sampled and genotyped at the 0+, 1+, and 2+ stages. Juveniles carrying the genetic markers were found in both localities, proving that the introduced spawners had spawned among themselves and with the wild stocks. Estimates of survival rates of 0+ trout revealed that survival was nearly three times higher in wild trout than in hybrids of wild and introduced trout, possibly because of a difference between introduced and wild stocks in size of eggs and alevins. The frequency of the marker alleles in the F₁ generation declined during the 2-year observation period.

Sosiak, A.J., R.G. Randall, and J.A. McKenzie. 1979. Feeding by hatchery-reared and wild Atlantic salmon (*Salmo salar*) parr in streams. Journal of the Fisheries Research Board of Canada 36: 1408-1412.

Hatchery-reared Atlantic salmon (*Salmo salar*) parr were captured 1-3 mo after release in streams, along with wild parr from the same streams. Identification of their stomach contents showed total number of organisms and number of taxa per stomach were greater and there was a higher index of stomach fullness in wild than in hatchery parr resident — 2 mo in a stream. Wild parr consumed more Brachycentridae, Hydroptilidae, Diptera, and Plecoptera than did hatchery parr, but sometimes less Odontoceridae and Heptageniidae. These differences may have arisen from size-dependent food selection, the effects of feeding experience, or possible microhabitat differences between wild and hatchery parr.

Sterne, J.K. Jr. 1995. Supplementation of wild stocks: a cure for the hatchery problem or more problem hatcheries? Coastal Management 23: 123-152.

Supplementation is a hatchery technology that attempts to correct for many of the problems associated with traditional hatcheries. Indian tribes along the Columbia River plan to use this technology to restore many of the badly damaged runs in the basin. The technology is not without risk to wild fish populations, however, and a rift has

developed between tribes and conservation groups, which generally oppose the construction of any new hatcheries intended to augment production. The Endangered Species Act, the National Environmental Policy Act, the Northwest Power Act, and tribal treaty rights all play a role in the current conflict. The author examines the scientific, legal, and policy positions on the two sides of the debate and offers possible solutions.

Swain, D.P., and B.E. Riddell. 1990. Variation in agonistic behavior between newly emerged juveniles from hatchery and wild populations of coho salmon, *Oncorhynchus kisutch*. Canadian Journal of Fisheries and Aquatic Sciences 47: 565-571.

We compared agonistic behavior of newly emerged coho salmon (*Oncorhynchus kisutch*) between hatchery and wild populations using mirror image stimulation tests. We used hatchery populations from two different regions of Vancouver Island, B.C., each matched with a wild population from its region. In both comparisons, hatchery juveniles were more aggressive than wild juveniles. Rates of aggressive display increased with time since emergence for both hatchery and wild fish, as did the differences in behavior between the two types. By the sixth day of observation (13 d postemergence), the overall effect of fish type was highly significant for all aggressive behaviors. Since the individuals compared were reared from eggs under identical conditions, these differences are presumably genetic. Comparisons involved relatively few families from each population. However, because heritability was moderate to low within populations, and variance between population types exceeded variance among families within populations, these results indicate real differences at the population level. These results may have important implications for programs to rebuild wild populations using hatchery transplants and for selective breeding programs to develop domestic stocks of coho.

Tatara, C. P., and B.A. Berejikian. 2011. Mechanisms influencing competition between hatchery and wild juvenile anadromous Pacific salmonids in fresh water and their relative competitive abilities. Environmental Biology of Fishes (In press).

Avoiding negative effects of competition from released hatchery salmonids on wild fish is a primary concern for recovery efforts and fisheries management. Several factors affect competition among juvenile salmonids including: (1) whether competition is intra- or interspecific, (2) duration of freshwater cohabitation of hatchery and wild fish, (3) relative body size, (4) prior residence, (5) environmentally induced developmental differences, and (6) fish density. Intraspecific competition is expected to be greater than interspecific because of greater niche overlap between conspecific hatchery and wild fish. Competition is expected to increase with prolonged freshwater cohabitation. Hatchery smolts are often larger than wild, and larger fish are usually superior competitors. However, wild fish have the advantage of prior residence when defending territories and resources in natural streams. Hatchery-induced developmental differences are variable and can favor both hatchery and wild fish. Although all these factors influence competitive interactions, fish density of the composite population (wild

+ hatchery fish) in relation to habitat carrying capacity likely exerts the greatest influence. The extent of competition and relative competitive ability of wild and hatchery fish can be determined by additive and substitutive experimental designs, respectively, and the limited body of substitutive experiments suggests that the relative competitive ability of hatchery and wild fish is approximately equal when measured as growth. Conducting substitutive experiments becomes difficult as the spatial and temporal scales increase. Large-scale experiments comparing supplemented and control reaches or streams hold some promise for quantifying the effects of released hatchery fish on wild fish behavior, growth and survival.

Taylor, E.B. 1986. Differences in morphology between wild and hatchery populations of juvenile coho salmon. *The Progressive Fish-Culturist* 48: 171-176.

To assess the degree of morphological divergence between wild and hatchery-reared juvenile coho salmon (*Oncorhynchus kisutch*), juveniles from five hatcheries and five wild populations in south-coastal British Columbia were studied. The morphology of hatchery coho salmon was significantly less variable than the morphology of wild-reared juveniles with respect to individual characteristics and overall body form. Populations that were close geographically tended to be similar morphologically in wild-wild and hatchery-hatchery comparisons, but not when wild and hatchery populations were compared together. A principal components analysis suggested a distinct grouping of juvenile coho salmon into hatchery and wild morphological types. Discriminant function analysis and jackknifed classification procedure indicated that juvenile coho salmon could be classified as either hatchery or wild in origin with over 90% accuracy. The morphological differences and the reduced variation of hatchery juveniles observed in this study probably result, in large part, from environmental differences and the greater homogeneity of hatchery environments compared to natural rivers and streams.

Theriault, 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(9): 1860-1869.

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

hatchery fish in the wild: (i) hatchery fish released as unfed fry that survived to adulthood still had low RS relative to wild fish, (ii) age-3 male hatchery fish consistently showed a lower relative RS than female hatchery fish (suggesting a role for sexual selection), and (iii) age-2 jacks, which use a sneaker mating strategy, did not show the same declines as 3-year olds, which compete differently for females (again, implicating sexual selection).

Unwin, M.J. 1997. Fry-to-adult survival of natural and hatchery-produced chinook salmon (*Oncorhynchus tshawytscha*) from a common origin. Canadian Journal of Fisheries and Aquatic Sciences 54(6): 1246-1254.

Fry-to-adult survival rates for chinook salmon (*Oncorhynchus tshawytscha*) from Glenariffe Stream, a tributary of the Rakaia River, New Zealand, were estimated for fish of both natural and hatchery origin. Survival of naturally produced fry, most of which leave Glenariffe Stream within 24 h of emergence, averaged 0.079% (range 0.013-1.17%). For hatchery fish released at 8-12 months, standardised to a mean weight of 38 g, survival covaried with weight at release consistently across all brood years and averaged 0.34% (range 0.008-3.28%). Survival rates for hatchery fish were four times higher than for naturally produced fry, but were extremely poor relative to their size at release. Survival rates for fish of natural and hatchery origin were positively correlated, suggesting that recruitment of both stocks is primarily controlled by common influences within the marine environment, probably during the first winter at sea. Stock-recruitment analysis for the natural population showed little tendency for recruitment to increase with stock size, suggesting that marine survival rates may be density dependent. Although the reasons for the relatively poor survival of hatchery fish are unclear, the results provide a case study in which hatchery fish appear to have a poorer "fitness to survive" than their natural counterparts.

Verspoor, E. 1988. Reduced genetic variability in first-generation hatchery populations of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 45: 1686-1690.

Levels of genetic variation were measured in first-generation Atlantic salmon (*Salmo salar*) cultured for stock enhancement programs in eastern Canada and compared with variation in wild stocks. One regulatory and 19 structural protein loci were screened of which 10 were polymorphic. Mean heterozygosity and number of alleles per locus were positively correlated with the effective number of adults (N) used to establish the hatchery groups and averaged 26 and 12% lower, respectively, than wild stocks. The observations are consistent with a loss of genetic variability in the hatchery salmon from random drift caused by using small numbers of salmon for broodstock.

Vincent, R.E. 1960. Some influences of domestication upon three stocks of Brook Trout (*Salvelinus fontinalis* Mitchill). Transactions of the American Fisheries Society 89(1): 35-52.

Three stocks of brook trout – domestic, wild, and first generation removed from wild

stock were tested and observed for effects of domestication. The domestic stock had been selectively bred for 90 years, whereas the wild stock came from an isolated lake in the Adirondack Mountains. To reduce differential environmental influence to a minimum, the three lots were reared from eggs in adjacent rearing troughs at the same water temperature. After 1 year under these hatchery conditions the domestic fish were 5.2 inches in length and the wild, 3.6 inches. Throughout the rearing domestic stock were tamer and exhibited less fright than wild-stock fish. Laboratory tests showed that wild stock could stand a greater concentration of accumulated metabolites, that they could endure higher water temperature, and that domestic stock had a surface response whereby they moved to the surface of a rearing trough or a tall aquarium. Domestic fish also lacked the desire to conceal themselves. Stamina tests conducted by swimming 1,522 fish individually until exhausted in a small trough showed that the wild stock had greater stamina throughout the size range tested. Survival trials in a small stream and a pond indicated that wild fish experienced less mortality and had growth rate similar to or better than domestic fish in both habitats. After 73 days in the small stream 20 percent of the domestic and 33 percent of the wild stock survived. Domestic fish grew 0.34 inches and wild fish, 0.48 inches. Survival was 43 percent for the domestic and 65 percent for the wild after 108 days in a pond, while length increase was 2.6 inches for the domestic and 2.5 inches for the wild stock. The domestic increased more in weight. After being in a pond for nearly 4 months, the domestic stock had acquired little wariness.

Vincent, R.E. 1987. Effects of stocking catchable-size hatchery Rainbow Trout on two wild trout species in the Madison River and O'Dell Creek, Montana. North American Journal of Fisheries Management 7(1): 91-105.

The fall population of 2-year-old and older wild brown trout (*Salmo trutta*) more than doubled (160% increase), in both total numbers and biomass, 4 years after the last catchable-size hatchery rainbow trout were stocked in the Varney section of the Madison River, Montana; wild rainbow trout (*Salmo gairdneri*) numbers increased eight times (868%) and their biomass increased 10 times (1,016%) during the same period. Brown trout biomass peaked within 2 years after stocking ceased, whereas wild rainbow trout biomass continued to increase for 4 years. Numbers of wild brown and rainbow trout 10.0-17.9 in long showed the greatest increases after stocking ceased. Flow variations had little effect on the total biomass of 2-year-old and older wild trout during stocking years ($t = 1.24$), but stocking had a significant negative correlation ($r = -0.953$) with total biomass. When catchable-size hatchery rainbow trout were stocked for three consecutive years into a previously unstocked section of O'Dell Creek, Montana, the 2-year-old and older wild brown trout population was reduced 49% in total number and biomass. Wild brown trout 10.0-17.9 in long showed significant declines in numbers after stocking was initiated, whereas those smaller than 10.0 in showed no significant change in numbers. A temporary decline in growth rates of yearling through 4-year-old brown trout was observed in O'Dell Creek during the first 2 years of stocking. Measurable movement of marked wild trout in the lower (stocked) section of O'Dell Creek accelerated during years of stocking. Stocking of catchable-size hatchery

rainbow trout had no detectable adverse effect on wild brown trout through their first 18 months of life in either lower O'Dell Creek or the Varney section of the Madison

Waples, R.S. 1991. Genetic interactions between hatchery and wild salmonids: lessons from the Pacific Northwest. Canadian Journal of Fisheries and Aquatic Sciences 48(S1): 124-133.

The potential for genetic interactions between hatchery and wild populations of salmonids in northwestern North America has increased considerably in recent decades. Efforts to mitigate severe losses to many wild stocks caused by overfishing, destruction of habitat, and blockage of migratory routes have focused on boosting artificial production in public hatcheries. Opportunities for genetic interactions between hatchery and wild fish will increase if efforts to supplement wild production with hatchery-reared fish continue. Concerns center on three issues: (1) direct genetic effects (caused by hybridization and introgression); (2) indirect genetic effects (principally due to altered selection regimes or reductions in population size caused by competition, predation, disease, or other factors); and (3) genetic changes to hatchery stocks (through selection, drift, or stock transfers), which magnify the consequences of hybridization with wild fish. Strategies for minimizing these genetic risks and monitoring the consequences of various management options are discussed, and some important areas for future research are identified.

Waples, R.S. 1999. Dispelling some myths about hatcheries. Fisheries 24(2): 12-21.

Contributing to the controversies that have surrounded fish hatcheries in recent years are a number of misconceptions or myths about hatcheries and their effects on natural populations. These myths impede productive dialogue among those with differing views about hatcheries. Most of the myths include a measure of truth, which makes it difficult to recognize the elements that are not true. Consideration of these myths leads to the following conclusions: (1) Hatcheries are intrinsically neither good nor bad their value can be determined only in the context of clearly defined goals; (2) genetic changes in cultured populations can be reduced but not eliminated entirely; (3) empirical evidence exists of many adverse effects of hatcheries, but some risks have been overstated; and (4) monitoring and evaluation programs are important but should not be used as a substitute for developing risk-averse hatchery programs in the first place. A key step in resolving some of the controversies will be moving toward agreement on a common version (rather than two or more separate versions) of the realities about hatcheries. More efforts are needed in four major areas: identifying goals, conducting overall cost:benefit analyses to guide policy decisions, improving the information base, and dealing with uncertainty.

Weber, E.D., and K.D. Fausch. 2003. Interactions between hatchery and wild salmonids in streams: differences in biology and evidence for competition. Canadian Journal of Fisheries and Aquatic Sciences 60(8): 1018-1036.

Competition between hatchery-reared and wild salmonids in streams has frequently been described as an important negative ecological interaction, but differences in behavior, physiology, and morphology that potentially affect competitive ability have been studied more than direct tests of competition. We review the differences reported, designs appropriate for testing different hypotheses about competition, and tests of competition reported in the literature. Many studies have provided circumstantial evidence for competition, but the effects of competition were confounded with other variables. Most direct experiments of competition used additive designs that compared treatments in which hatchery fish were introduced into habitats containing wild fish with controls without hatchery fish. These studies are appropriate for quantifying the effects of hatchery fish at specific combinations of fish densities and stream carrying capacity. However, they do not measure the relative competitive ability of hatchery versus wild fish because the competitive ability of hatchery fish is confounded with the increased density that they cause. We are aware of only two published studies that used substitutive experimental designs in which density was held equal among treatments, thereby testing for differences in competitive ability. Additional substitutive experiments will help managers to better understand the ecological risk of stocking hatchery fish.

Winton, J., and R. Hilborn. 1994. Lessons from supplementation of Chinook salmon in British Columbia. North American Journal of Fisheries Management 14(1): 1-13.

Supplementation, as used here, is planting of all life stages of hatchery-reared fish to increase natural production of anadromous salmon and steelhead trout. Through the Salmonid Enhancement Program (SEP), Canada has been experimenting with supplementation techniques at a number of British Columbia hatcheries for the past fifteen years. The original objective of this report was to ascertain the success of supplementation efforts at four British Columbia hatcheries as measured by the program goals of increased harvest; and enhancement, preservation, and rehabilitation of natural stocks in a cost-effective manner. This objective was not attainable because, while these four hatcheries have been experimenting with various spawning, rearing, and release strategies, they have never monitored natural stock survival or escapement - a situation common to other Canadian supplementation hatcheries as well. Thus while the hatcheries direct operating costs to produce a hatchery-reared chinook surviving to catch and escapement have been estimated (\$380 at Quesnel Hatchery, \$47 at Snoolti Creek, \$85 at Spius Creek, and \$45 at Kitimat) the effects of supplementation on the natural stocks, and hence the full costs or benefits of these hatcheries and of the program as a whole, are unknown. From the Canadian experience to date, therefore, one is not able to determine whether supplementation is an effective way to enhance natural stocks.

Youngson, A.F., and E. Verspoor. 1998. Interactions between wild and introduced Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 55(S1): 153-160.

Wide latitude exists for genetic, behavioural, and ecological interactions between introduced and wild Atlantic salmon (*Salmo salar* L.). These can occur at all stages of the life cycle and across the range of natural environments the species exploits. Because of the large number of variables and scales involved, each interaction scenario and its outcome is expected to be unique. However, as a general rule, interactions are likely to be negative in their effect on the viability of wild populations. In theory, it ought to be possible to develop approaches for managing interactions, but in the particular case of genetic effects this is especially difficult. It is possible to put forward two guiding genetic principals for intentional introductions. Firstly, when introductions are used to maximize local abundance, genotypic diversity must be maintained so that mean individual fitness remains undiminished after interaction has occurred. Secondly, when introductions are used to alter local frequencies of phenotypes, the population's capacity to remain viable in the longterm must not be impaired. Both principals are pragmatic and aim to conserve or restore the genetic capacity of populations to evolve rather than seeking the preservation of their current condition.

Zaporozhets, O.M., and G.V. Zaporozhets. 2011. Some consequences of Pacific salmon hatchery production in Kamchatka: changes in age structure and contributions to natural spawning populations. Environmental Biology of Fishes (In press).

Aggregate hatchery production of Pacific salmon in the Kamchatka region of the Russian Federation is very low (< 0.5% of total harvest, with five hatcheries releasing approximately 41M juvenile salmon annually), but contributions in certain rivers can be substantial. Enhancement programs in these rivers may strongly influence fitness and production of wild salmon. In this paper we document significant divergence in demographic traits in hatchery salmon populations in the Bolshaya River and we estimate the proportion of hatchery chum salmon in the total run in the Paratunka River to demonstrate the magnitude of enhancement in this system. We observed a reduction in the expression of life history types in hatchery populations (ranging from 1 to 9 types) compared to wild populations (17 types) of sockeye salmon in the Bolshaya River. We found similar trends in Chinook salmon in the same river system. This reduced life history diversity may make these fish less resilient to changes in habitat and climate. We estimate hatchery chum salmon currently contribute 17-45% to the natural spawning population in the Paratunka River. As hatchery fish increase in numbers at natural spawning sites, this hatchery production may affect wild salmon production. It is important to investigate the risk of introgression between hatchery and wild salmon that can lead to reduction in salmon fitness in Kamchatka rivers, as well as the potential of ecological interactions that can have consequences on status of wild salmon and overall salmon production in this region.

