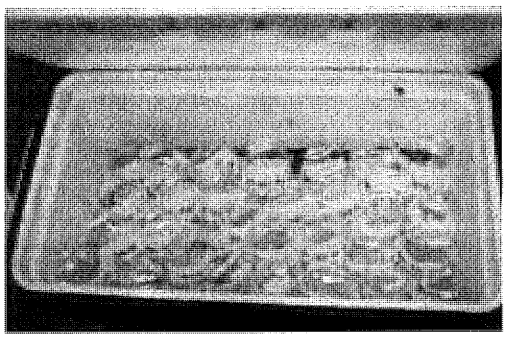
Hatchery Surpluses in the Pacific Northwest

ABSTRACT

Chinook salmon (*Oncorhynchus tshawytscha*), hatchery-reared as juveniles, returned to the upper Columbia River Basin in numbers exceeding broodstock and fishery needs during the spring of 2000. Plans to euthanize these adults were opposed by some regional stakeholders, who preferred letting them spawn naturally in streams also used by endangered spring-run chinook salmon. The National Marine Fisheries Service requested that the Independent Scientific Advisory Board review the scientific literature and conclude whether it was biologically sound to permit hatchery-origin adult salmon to spawn in the wild in large numbers. Substantial experimental evidence demonstrates that domestication selection can genetically alter hatchery populations in a few generations and that hatchery-origin adults returning from the ocean and spawning in the wild produce fewer progeny than adults of wild origin spawning in the wild. More limited evidence suggests that interbreeding between hatchery-origin adults and wild fish can reduce the fitness of the wild population. We conclude that decisions whether or not to permit hatchery-origin adults to spawn in the wild should be based on the needs of wild populations and the ability of the habitat to support additional reproduction, not based simply on the availability of hatchery-origin adults returning from the ocean.

PHOTOS BY RICK WILLIAMS



Lookingglass cryo sperm samples

The Issue

In 2000, more than 1,000 adult spring-run chinook salmon (*Oncorhynchus tshawytscha*) returned to the upper Columbia River in the United States. Many of these adults were "Carson" stock, reared to the smolt stage at the Leavenworth, Winthrop, and Entiat National Fish Hatcheries and released into the Columbia River Basin. The Carson stock was developed 50 years ago by collecting spring-run chinook as they passed Bonneville Dam. Those fish were assumed to have originated from multiple locations within the Columbia River Basin and are reared at several locations. This hatchery stock is not included in the upper Columbia River spring-run chinook evolutionarily significant unit (ESU) listed under the Endangered Species Act (ESA) (Federal Register 1999). The federal agencies' plans for 2000 proposed to exclude these fish from reproducing in areas where listed upper Columbia River spring-run chinook spawn, such as the Methow River Basin. That is, agencies planned to collect and euthanize the excess hatchery-origin adults, rather than permit them to spawn in rivers used by listed salmon. This plan was protested by basin tribes and others who believed that allowing these hatchery-origin fish to spawn would help recover listed populations. Some salmon were killed at the Winthrop Hatchery, but others were eventually released to spawn naturally in local rivers. During the spring and summer of 2001 the number of

The Independent Scientific Advisory Board

The Independent Scientific Advisory Board (ISAB) members include
Peter A. Bisson, research fish biologist and team leader, USDA Forest Service Pacific Northwest Research Station, Olympia, Washington;
Charles C. Coutant, senior research ecologist, Oak Ridge National Laboratory, Oak Ridge, Tennessee;
Daniel Goodman, professor and director, Environmental Statistics Group, Department of Ecology, Montana State University, Bozeman;
Robert Gramling, professor of sociology and director, Center for Socioeconomic Research, University of Louisiana at Lafayette;
Dennis Lettenmaier, professor of civil and environmental engineering, University of Washington, Seattle;
James Lichatowich, private consultant, Alder Fork Consulting, Columbia City, Oregon;
William Liss, professor of fisheries, Department of Fisheries and Wildlife, Oregon State University, Corvallis;
Eric Loudenslager, fish hatchery manager and adjunct professor, Department of Fisheries Biology, Humboldt State University, Arcata, California;
Lyman McDonald, consulting statistician, Western Ecosystems Tech. Inc., Cheyenne, Wyoming;
David Philipp, senior professional scientist, Center for Aquatic Ecology, Illinois Natural History Survey, and professor, University of Illinois, Champaign;
Brian Riddell, research scientist, Department of Fisheries and Oceans Canada, Nanaimo, British Columbia, Canada.
Eric Loudenslager can be contacted at ejl1@humboldt.edu.

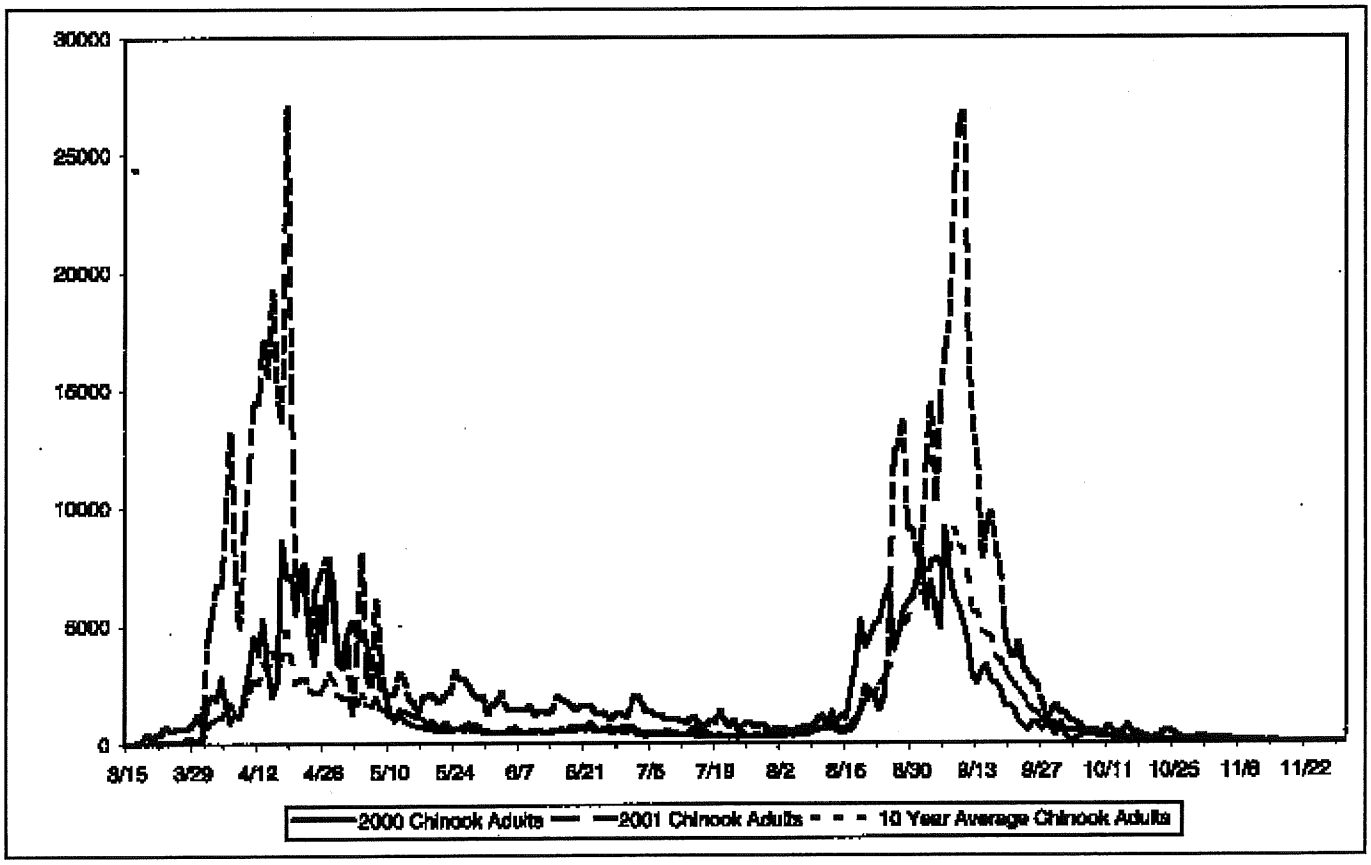
adult wild and hatchery-origin salmon returning to the Columbia River Basin eclipsed the previous year (Figure 1). If we are entering, as some believe, a regime shift in ocean conditions favoring improved marine survival for Columbia River Basin salmon, years with surplus hatchery adults could recur frequently over the next decade. It appears possible, therefore, that the region will continue to face the issue of what to do with surplus hatchery-origin adult salmon.

Among agency biologists and public stakeholders, there are both proponents and opponents of permitting excess hatchery-origin adults to spawn in the wild. Some are concerned that large numbers of hatchery-origin salmon spawning in the wild would have negative genetic and/or demographic impacts on extant wild populations. Others believe that spawning in the wild by hatchery-origin salmon would make a positive contribution to the status of depleted wild populations. As a consequence of this controversy, the National Marine Fisheries Service (NOAA Fisheries) requested that the Independent Scientific Advisory Board (ISAB, an 11 member board of independent scientists serving NOAA Fisheries and the Northwest Power Planning Council's Fish and Wildlife Program for the Columbia River Basin) review this issue by answering six multi-part questions. Two of the questions received most of the attention in our reply to NOAA Fisheries. Our answers to those questions were reorganized into this perspective article, because we believe they have fisheries management implications throughout the Pacific Northwest. The two questions were:

- For either supplementation or mitigation programs, is it possible to have more adult hatchery fish available to spawn than can be used in a biologically sound manner, for spawning either in the hatchery or in the wild?
- If it is possible to have more hatchery fish than can be spawned in a biologically sound manner, what factors should be considered in evaluating at what level of spawning the adverse effects on natural populations outweigh potential benefits? Can the ISAB suggest any general guidelines about how to determine this level? How will this level vary with factors such as stock history, broodstock and rearing protocols, duration of the program, etc.?

In answering the first question, the ISAB focused on the scientific credibility of the purported evidence of potentially deleterious effects on wild salmon from hatchery-origin adults spawning with them. We concluded that the evidence is credible and substantial. Consequently, we concluded that it is indeed possible for more adult hatchery-reared salmon to return to spawn naturally than is biologically sound for the sustainability of wild populations. Several lines of evi-

Figure 1. Abundance of adult chinook salmon returning to the Columbia River Basin, and elsewhere in the Pacific Northwest, during the years 2000 and 2001 exceeded the 10 year average. High run-off during smolt outmigration and improved ocean conditions is believed to be responsible. Many believe a regime shift in ocean conditions could result in healthy runs of salmon over the next decade.



dence, both theoretical and empirical, suggest that there can be deleterious demographic effects when excessive numbers of hatchery-origin salmon interact with wild salmon. Evidence also indicates that there could be deleterious genetic interactions when hatchery-reared and wild salmon interbreed. Our consideration of the ecological and genetic mechanisms that would be the source of the deleterious effects are outlined without distinction among different kinds of hatchery programs. "Hatchery-origin adults" refers to individuals derived from eggs spawned and incubated, and then emergent fry reared, usually to the smolt stage, in a hatchery, regardless of the previous hatchery history of the parents. "Wild salmon" in this article, refers to those individuals derived from eggs spawned and incubated in the natural environment, regardless of the possible hatchery history of the parents. We note that our usage of "wild" probably is not identical with the NOAA Fisheries usage of "natural populations" in their letter, since NOAA Fisheries is almost certainly concerned with effects on listed ESUs. In developing the answer to the second question, consideration is given to incorporating information on the history of hatchery influences on the wild population and the purpose of the hatchery program.

The fisheries management problems created by an apparent surplus of hatchery-origin adult salmon are not limited to the Columbia River Basin, but occur throughout the Pacific Northwest (Table 1). For example, in coastal Oregon, the Oregon Department of Fish and Wildlife began phasing out a poorly performing stock of coho salmon (*Oncorhynchus kisutch*) from the Fall Creek Hatchery on the Alsea River in 1998. Because hatchery-origin adults returning to the river after 1998 were not needed for producing another generation of hatchery fish, they were collected and euthanized by clubbing. A video of this activity made by citizens led to a lawsuit intended to halt the destruction of this stock the following year. That request for an injunction was denied. In addition, in the Klamath River Basin in California, several thousand fall-run chinook returned to the Iron Gate and Trinity River hatcheries in 1995, overwhelming the ability of the state agency to spawn or even hold all the fish. In reaction, the gates to the fish ladders were closed, and as a result hatchery-origin fish strayed and spawned throughout the basin. Klamath River Basin tribes and watershed groups that had ongoing restoration projects for wild salmon were angered and insisted that in the future the California Department of Fish and Game develop plans to handle surplus hatchery-origin adult salmon. In the fall of 2000, nearly 70,000 fall-run chinook salmon returned to the Iron Gate Hatchery where they were electroanesthetized and processed for food programs throughout northern California.

Demographic Concerns

The interest in providing hatchery-origin adults the opportunity to spawn in the wild lies in the hope of producing increased numbers of wild-origin offspring. Conventional hatchery programs do not intend for their salmon to spawn naturally. In some conventional hatchery programs, some returning adults do stray into adjacent tributaries or avoid capture at weirs. There is documentation that these fish sometimes spawn in the wild and produce progeny and at other times do not (Marshall et al. 2000). We are not aware of studies that demonstrate that reproduction by stray adult salmon from conventional hatchery programs makes meaningful contributions to the abundance of naturally spawning salmon populations. This viewpoint is widely shared in the Pacific Northwest (Cuenco et al. 1993). In the Columbia River Basin, and elsewhere along the West Coast, there are artificial production programs collectively referred to as supplementation, intended to aid conservation of depleted natural populations. We are not aware of peer-reviewed studies demonstrating sustainably increased natural-origin juvenile or adult abundance from the reproduction of hatchery-origin adults in any of these supplementation programs.

Substantial sustainable harvest or lasting recovery of persistently depressed populations from an increased egg deposition during years of extraordinarily high abundance of returning adults is both unlikely, on theoretical grounds, and inconsistent with field observations. Salmon and steelhead populations are characterized by significant inter-annual variation in spawner/recruit relationships (Peterman 1987; Cramer 2000; Ham and Pearsons 2000). Most of the variation appears to be a consequence of density-independent environmental variation, largely

Table 1. Use of chinook and coho salmon returning to Pacific Northwest hatcheries in 1999[1].

Region	Species	Total Return	Spawned		Released		Mortality		Killed	
			N	%	N	%	N	%	N	%
Coast	Coho	170,674	27,800	16.3	27,800	16.3	11,470	16.7	86,158	50.5
	Chinook	117,036	13,827	11.8	13,827	11.8	8,366	7.1	53,264	45.5
Columbia	Coho	154,802	51,710	33.4	51,710	33.4	2,891	1.9	71,966	46.5
	Chinook	139,382	12,875	9.2	12,875	9.2	6,508	4.7	68,702	49.3
Total	Coho	325,476	79,510	24.4	79,510	24.4	14,362	4.4	158,124	48.6
	Chinook	256,418	26,702	10.4	26,702	10.4	14,874	5.8	121,966	47.6

Whiteaker et al. (2000)[1]

manifested in variation in survival in the first year after entry into marine waters. Within a stock there are typically many years with relatively low adult abundance interspersed with occasional years of enormous abundance. For example, in Oregon, Cramer (2000) observed more than a 50–fold difference among annual recruits per spawner for coho salmon naturally produced in coastal streams. In addition, survival to age 2 of smolts released from the Cowlitz Salmon Hatchery annually varied 10–fold for spring-run chinook, 20–fold for fall-run chinook, and 30-fold for coho salmon (Cramer 2000). Deviations in the spawner/recruit relationships were asynchronous not only among species within a river system, but also among river systems for a single species. Both the Ricker (1954) and Beverton-Holt (1957) deterministic stock-recruitment relationships account for little of this variation (Peterman 1987; Cramer 2000). This variation suggests that the number of spawning adults may be of secondary importance in determining the variation in recruitment (though logically it must influence the mean).

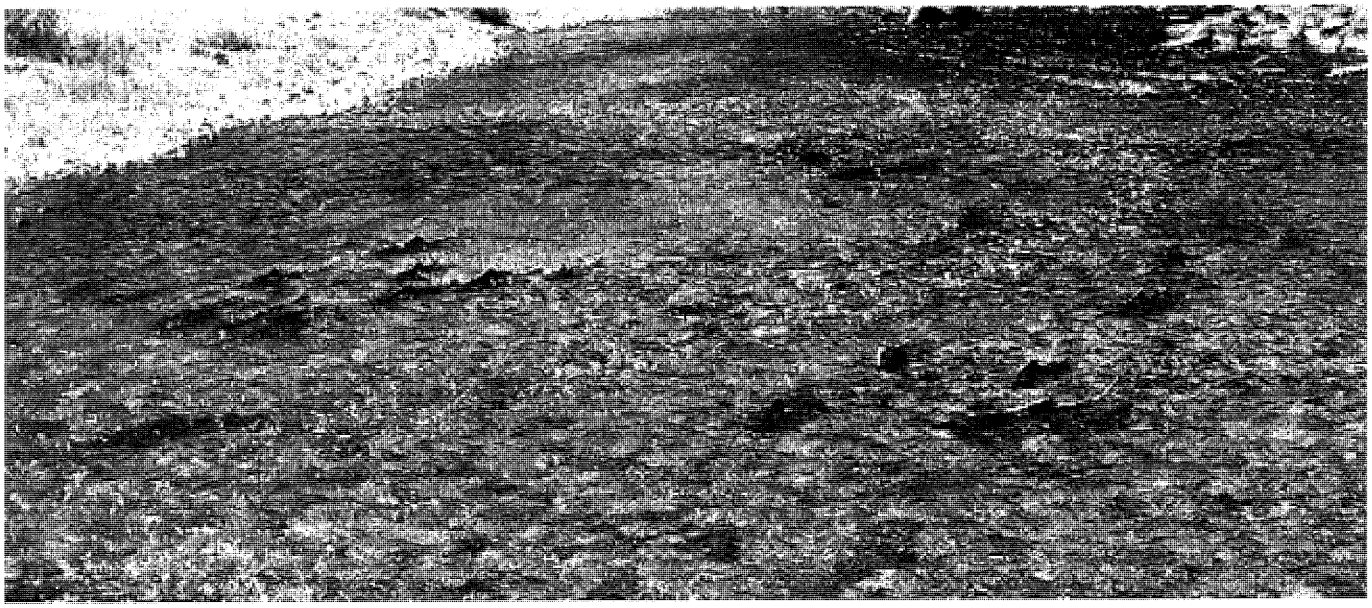
One of the more thorough studies of the actual contribution of natural spawning by hatchery-origin salmon raises further doubts about this strategy of allowing hatchery-origin adults to spawn with wild salmon. Nickelson et al. (1986) found that increasing fry abundance in coastal Oregon streams by introducing juvenile hatchery-origin coho salmon did not increase the number of fish that subsequently returned as adult salmon. This lack of adult response to juvenile stocking was likely due to fry densities in the streams overshooting their carrying capacity. More importantly, however, compared to control locations, fewer fry were produced in the streams in which hatchery-origin adults returned and spawned. This reduced juvenile production was attributed to the early run timing and spawning by this particular hatchery stock (Nickelson et al. 1986). In this instance, the failure of hatchery-origin adults to produce progeny abundance equivalent to control streams is believed to be due to use of a hatchery stock poorly matched to the natural environment (Cuenco et al. 1993).

Genetic Concerns

The genetic structure of populations reflects the interaction of a number of evolutionary processes. Genes change in form and function through mutation. Transmission of genes from parents to offspring, systems of mating, and migration of individuals among populations combine to create novel genotypes and even new organizational patterns for genes within individuals. It is these novel genotypes and gene organizational patterns that, together with natural selection under different environmental conditions, produce the life history variation we observe in salmon. Some novel genotypes produce fish that have increased abilities to survive and reproduce. Through natural selection those genotypes are perpetuated differentially over others. Other novel genotypes produce fish incompatible with their environment and these lineages perish.

One widespread viewpoint based on that evolutionary paradigm is that interbreeding between hatchery-reared and wild salmon could produce offspring with incompatible genotypes, thereby making it more difficult to recover wild salmon, even eliminating the wild populations that are the objects of our recovery efforts. In wild salmon, a decrease in fitness caused by interbreeding with hatchery-reared salmon could result from two possible mechanisms. First, because wild salmon are adapted to non-hatchery environments and are likely to have genotypes different from those in hatchery salmon, gene flow from hatchery salmon to wild salmon could result in outbreeding depression (i.e., a decrease in fitness caused by the mating of too distantly related parents; see below). Genetic divergence between hatchery and

Abundance of naturally spawning salmon varies substantially from year to year and is influenced by density-independent survival as well as parent stock size.



wild populations of salmon can result either from a difference in stock origins or as a consequence of adaptation to the hatchery environment (e.g., domestication selection). Their subsequent interbreeding could alter the fitness of naturally reproducing fish. Second, inbreeding depression could occur as a consequence of reduced effective population size within the group of augmented adult spawners (see below).

Outbreeding Depression

When genetically divergent populations interbreed, the resulting progeny may be less fit than their parents through the loss of local adaptations (Templeton 1986). When hatchery-origin salmon are allowed to spawn with wild fish, a loss of local adaptation may occur as a result of two processes. First, there can be a reduction in the frequency of favorable alleles among spawners when less favorable alleles are added in high frequency from a hatchery population. Because hatchery survival rates are much greater than in salmon rearing in the wild, deleterious mutations, which are typically eliminated by natural selection, can be maintained in a hatchery. When there is systematic migration of adults of hatchery-origin to natural spawning grounds, locally adaptive alleles will be swamped by hatchery alleles when the migration rate exceeds the selective difference between the genotypes (Felsenstein 1997). For example, if there is a 10% difference in the fitness of the two alleles in a wild population, then immigration rates for hatchery salmon of more than 10% will overwhelm natural selection, assuming all hatchery fish spawn. Second, different ancestral lineages (e.g., stocks, ESUs, demes) that exhibit similar life history patterns are likely to do so using different combinations of genes (i.e., coadapted gene complexes; Dobzhansky 1937, 1948). These different coadapted gene complexes are generated when specific alleles become combined into advantageous multilocus genotypes through random genetic drift, but are maintained by natural selection. Disrupting these combinations through interbreeding can change the life history phenotype of the progeny, reducing the fitness of the resulting population.

Powerdale Fish Facility

Through either of the above mechanisms, the loss of fitness incurred by the affected individuals is termed outbreeding depression. Outbreeding depression in offspring can occur whenever sufficiently divergent populations interbreed, as could happen when hatchery salmon of non-local source spawn with local wild salmon. The time required for the fitness of the interbred population to increase back to original levels (provided there were no further interbreeding) would vary, perhaps being as short as tens of generations or as long as hundreds. Templeton (1986) cautions, however, that severe outbreeding depression during the first few generations following an interbreeding event could increase near-term extinction probability for the local population. Hatchery-origin salmon only one or two generations removed from the wild, however, might or might not cause substantial outbreeding depression when interbreeding with the wild salmon population from which they were derived (Lynch 1997). Outbreeding depression is more likely to occur when interbreeding is between genetically differentiated populations, such as when a hatchery broodstock is from non-local sources.

Domestication Selection

For interbreeding to alter population fitness through the loss of adaptation (outbreeding depression), there needs to be genetic divergence between the interbred populations. For most salmon species genetic differentiation among populations from different geographic regions (ESUs) is well documented. Consequently, even if both parents were of wild origin, interbreeding between individuals from different ESUs could have negative fitness consequences. In addition to this genetic divergence among wild populations, domestication selection within hatcheries can lead to genetic divergence of wild and hatchery salmon from the same ESU. This divergence would result from selective pressures in the hatchery being different from those in the wild, i.e., differences in survival and growth resulting from unique hatchery rearing environments. This domestication selection of the hatchery stock represents "natural" selection to the hatchery environment (Campton 1995). Domestication selection is typically inferred from improved survival of progeny under culture and changes in behavioral characteristics and reproductive performance (Doyle et al. 1995). Although domestication selection is unavoidable, there are strategies to minimize the deleterious effects of hatchery rearing on survival in the wild, such as the "NATURES" rearing program (Flagg and Nash 1999). Because there has been considerable variation among salmon husbandry practices in the past, current hatchery stocks likely vary widely in their degree of domestication.

Reduced Effective Population Size—Inbreeding

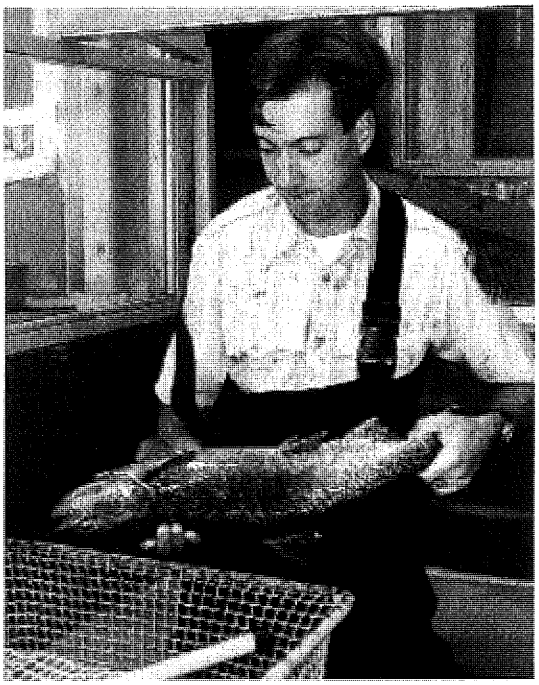
Population size has important consequences for maintaining similar genetic characteristics in parental and progeny populations. Inbreeding occurs in randomly mating small populations, and random genetic drift increases the variance in allele frequencies. The rate of inbreeding and genetic drift is a function of the genetically effective population size (N_e). Family structure of a salmon population, i.e., the sex ratio, the distribution of progeny per family, and the relative proportions of progeny from wild and captively bred individuals, is very important for determining N_e (Lande and Barrowclough 1987; Ryman and Laikre 1991; Ryman et al. 1995). When progeny from a limited number of parents

make up a substantial proportion of a wild spawning population, N_e is substantially less than the census number of adults, N. This circumstance is most likely to arise when a hatchery (which provides a large survival advantage to only a portion of a population, thereby causing over-representation of only a few family groups) contributes a significant portion of the spawning population. The result is an increased rate of inbreeding that could result in inbreeding depression, i.e., the reduction in the fitness of the progeny of too closely related parents, because these progeny are more often homozygous for deleterious recessive alleles than the progeny of more distantly related parents. Deleterious recessive alleles arise by mutation and are present in most populations, although the frequency of these deleterious alleles is typically low because of selection against them.

Alternative Viewpoints

The overview and theoretical background presented above represents a widely held viewpoint among evolutionary biologists and conservation geneticists. We concur with this viewpoint. Nevertheless, we are aware of dissenting viewpoints that challenge these arguments. For example, Kapuscinski and Lannan (1984, 1986) suggest that the goal for genetic management of exploited fish populations should be to maintain the "variance in fitness" (Kapuscinski and Lannan 1984) or to "maintain the probability distribution of fitness" (Kapuscinski and Lannan 1986). This model incorporates substantial genetic exchange among populations, as would be likely when hatchery-origin adults are spawning naturally with wild salmon. Ryman (1991), however, reported that one of the formulae used in this model produces erroneous results and demonstrated that employing it to manage salmon could actually lead to populations with reduced fitness.

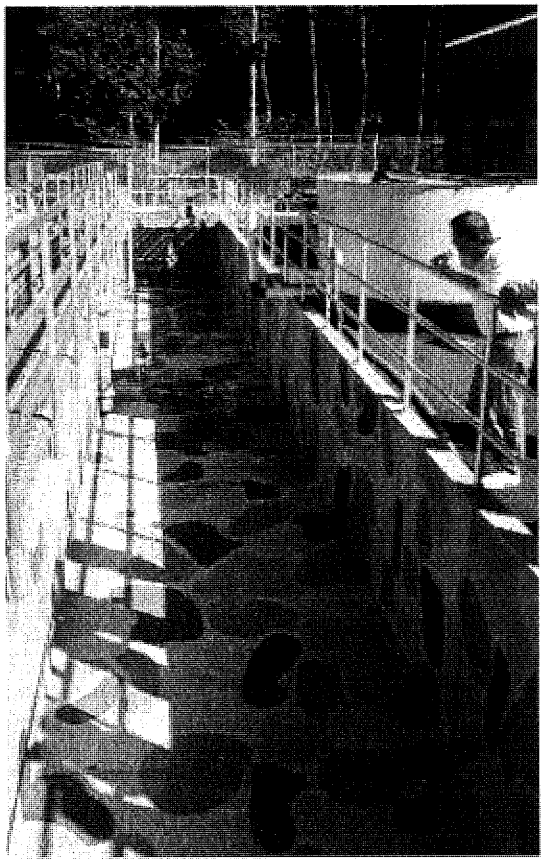
Moav et al. (1978) suggested that it is possible to improve yields in wild populations by hybridizing them with domestic populations selected for production traits, and Wolhfarth (1993) encouraged a similar proposal. Nelson and Soule (1987) took exception to Moav et al. (1978), concluding that they did not incorporate the inability to contain the genetic consequences of their activities when performed in unconfined rivers and oceans, and that they presumed that introgression (the incorporation of genes from the domestic stock into the wild population) would have no consequences for wild populations. In addition, Reisenbichler (1997) pointed out that the data from anadromous salmon that Wolhfarth (1993) interpreted as demonstrating hybrid vigor were misinterpreted. We have found no successful examples of programs in which crossbreeding wild anadromous salmon with hatchery stocks has improved the survival of the wild stocks.



Domestication selection from spawning and rearing salmon in hatcheries, as in Oregon's Lookingglass Hatchery on the Grande Ronde River, results from adaptation to the captive environment.

We acknowledge that claims of local populations being optimally adapted is something that might be profitably reviewed in some depth. Gould and Lewontin (1979) criticized biologists for casually generating adaptation scenarios to explain the various traits of an organism. New approaches to studying adaptation using comparative phylogenetic and experimental methods offer opportunities to explore this question (Rose and Lauder 1996; Orzack and Sober 2001). Within any given environment a population's relative fitness will, of course, be constrained by its genes, which are a product of the population's evolutionary history and breeding structure. As the environment changes, and as the population's genetic attributes change, so would we expect its relative fitness to the environment to change. Some of the existing genotypes within a population will be more fit than others in that new environment, and natural selection will favor individuals with those genotypes. Across the numerous semi-isolated subpopulations that make up a salmon metapopulation, we expect some will be very well adapted to their current environment and others less so (Scudder 1989). We believe the real issue is not whether a given population is now "optimally fit" for some specific environment, but rather how management actions (e.g., allowing hatchery fish to interbreed in the wild) would affect the relative fitness of that population in the future.

Under certain circumstances, some infusion of new genetic material might be beneficial to some populations. For example population geneticists propose that small populations of endangered species could accumulate a substantial number of mildly deleterious alleles through genetic drift, putting them at risk of "mutational meltdown," which could lead to extirpation (Gabriel and Burger 1994). We certainly believe this is one of the conceptual and strategic problems facing the technical recovery teams and stakeholders within the framework of recovery plans for all ESA listed populations, not just salmon. One option that has been proposed to reduce this hazard would be to introduce small numbers of individuals from other populations (Frankham 1999). Because of the high risk associated with the decrease in fitness due to outbreeding depression, we believe that deliberate introductions to increase genetic variation in an effort to counteract perceived inbreeding difficulties must be considered very carefully before implementation. Indeed, it would be inappropriate to assume that any given wild population would be improved genetically through interbreeding with hatchery-origin salmon (NRC 1995: 137–140). One reason for this high level of caution is that the technical and analytical tools currently available are insufficient to identify which populations are at risk of mutational meltdown and to determine both how to select donor individuals for injecting this new genetic material and how to perform the introductions. Recent reviews of inbreeding problems in endangered species (Hedrick and Kalinowski 1999; Frankham 1999) identify only four examples where introductions were used as an intervention to restore fitness lost through inbreeding in wild populations. In these examples wild caught, not artificially propagated, individuals were used in all interventions. Furthermore, in contrast to the numbers of adult hatchery-reared salmon potentially available to interbreed with wild salmon in the Columbia River Basin, the scale of the introduction in each of these examples was quite limited.



Parkdale Camo Raceway

Empirical Evidence

Although theoretical considerations show that it is "possible" for hatchery-origin salmon spawning in the wild to be biologically undesirable, we must rely on experimental studies that compare hatchery-origin and wild salmon to provide the evidence about the likelihood of biological impairment. Unfortunately, interpreting these studies in the context of whether or not there can be excess hatchery-reared salmon spawning with wild salmon is not always straightforward. Nonetheless, to focus on the consequences of hatchery-reared adults spawning in the wild, we considered empirical evidence documenting the domestication of hatchery fish, the successes of hatchery fish spawning in the wild, and the consequences of interbreeding between hatchery-reared and wild salmon.

There are a number of life-history and behavioral characteristics in hatchery salmon that are attributed to domestication selection. For example, in comparison to wild salmon, hatchery-reared adults generally return from the ocean and spawn earlier in the year and frequently at younger ages. Although this is the most commonly cited and accepted evidence of domestication in anadromous populations, there is additional evidence of selection associated with artificial propagation. Crossbred steelhead X domestic rainbow trout (*Oncorhynchus mykiss*) juveniles risked exposure to predators more often than wild steelhead (Johnsson and Abrahams 1991). Steelhead from a hatchery population exhibited more aggressive behavior and were vulnerable to more frequent predation by sculpins than wild steelhead (Berejikian 1995; Berejikian et al. 1996). Similarly, hatchery-reared coho salmon exhibited increased agonistic behavior that was attributed to additive genetic variation (Swain and Riddell 1990; Riddell and Swain 1991). Morphology of hatchery-reared coho salmon is altered from their natural counterparts, although the genetic basis for that observation is less certain (Fleming and Gross 1989; Swain et al. 1991). Increased juvenile growth rates, together with a feeding response rather than a fright response to the presence of people, is additional ancillary evidence of acclimatization to culture (Vincent 1960).

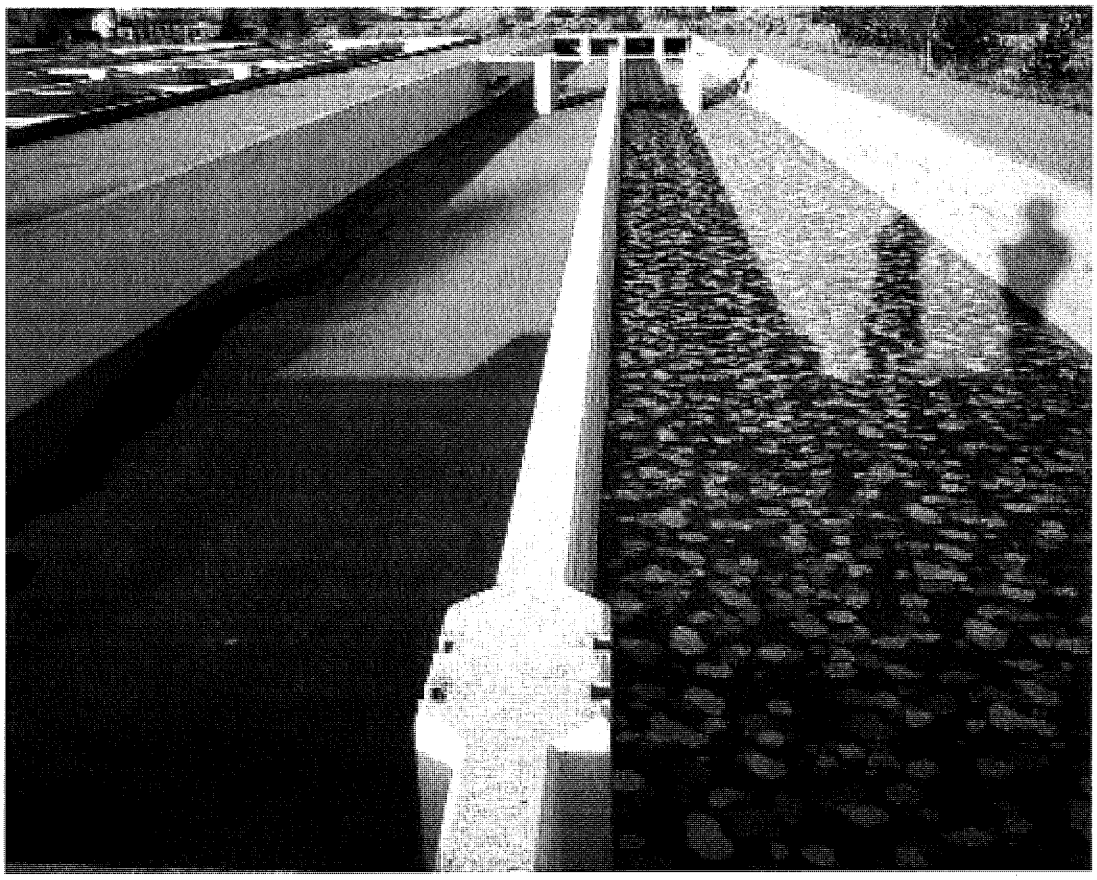
When hatchery-origin adults migrate onto natural spawning grounds, there are at least three questions of interest: do the hatchery-origin salmon spawn, do the hatchery-origin salmon produce offspring equally as well as wild salmon, and does interbreeding between hatchery-origin and wild salmon affect the fitness of the wild population? Although hatchery-reared chinook, coho, and Atlantic salmon (*Salmo salar*) have reduced mating success compared to their wild conspecifics, particularly the hatchery-origin males, evidence demonstrates that some hatchery-origin adults will

spawn in the wild (Fleming and Gross 1993; Chebanov and Riddell 1998; Fleming et al. 2000).

There are several studies with steelhead and one with chinook salmon that compare the survival, in natural settings, of progeny from hatchery-reared adults with that of their wild counterparts. Reisenbichler and McIntyre (1977) produced wild, hatchery, and wild X hatchery steelhead families and compared their performance both in the hatchery environment and in small tributary streams in the Deschutes River, Oregon. Compared at the time of emergence through age-1, families with wild ancestry had better survival than hatchery or hatchery X wild families in streams, whereas in a hatchery the hatchery families survived best. Chilcote et al. (1986) and Leider et al. (1990) produced genetically marked Washougal River-strain hatchery summer steelhead smolts that they released in the Kalama River, Washington where there is also a population of naturally spawning steelhead. After migrating to the ocean these marked steelhead returned to the river as adults to spawn. The hatchery and wild components of the adult spawning population, as well as the contribution of both components to the resulting progeny, were estimated using the genetic mark. The proportion of underyearling progeny contributed by hatchery-reared adults was less than expected based on the proportion of those adults in the spawning population. Furthermore, the relative survival of the progeny of hatchery-origin adults continued to decline through the smolt and returning adult life stages.

Hulett et al. (1996; cited from Reisenbichler and Rubin 1999) produced three year classes of genetically marked hatchery winter steelhead smolts from the Elochoman River, Washington and released them in the Kalama River. After migrating to the ocean, these fish returned as adults to spawn in the river. The proportions of hatchery and wild components of the adult spawning population and their progeny were estimated using the genetic mark. The relative survival of the progeny of hatchery-reared adults was evaluated as smolts and as returning adults. In two of the three year classes, the progeny of wild steelhead survived better to the smolt stage, but in one year class the progeny of the hatchery steelhead survived better. Relative production of returning adults from wild steelhead exceeded the production from hatchery-reared steelhead in all three year classes.

Reisenbichler and Rubin (1999) produced two year classes of hatchery-origin and wild summer steelhead, releasing some into the Clearwater River as fry and maintaining some in a hatchery environment. Comparisons at age-1 demonstrated reduced survival of hatchery steelhead in the wild and reduced survival and growth of the wild steelhead in the hatchery. Finally, Reisenbichler and Rubin (1999) evaluated the performance of Warm Springs River, Oregon, spring-run chinook salmon of hatchery and wild origin in the Little White Salmon River. Relative survival of hatchery chinook test groups



Hatchery reform in the Columbia River Basin includes experiments to rear juveniles against more natural backgrounds. Raceways at Sawtooth Hatchery in Idaho are painted to simulate the color patterns of cobble in a stream.

released as button-up fry in January and evaluated in August was less than that of wild test groups.

Although evidence to evaluate the fitness effects of interbreeding between hatchery-origin and wild Pacific salmon is largely unavailable, except for the Reisenbichler and McIntyre (1977) experiment with steelhead, one study (Currens et al. 1997) demonstrated the potentially deleterious effects of interbreeding between hatchery-reared domestic and resident wild rainbow trout based on disease susceptibility. *Ceratomyxa shasta*, a myxosporean parasite of salmonid fishes that is common within the Deschutes River Basin, can cause lethal infections. Susceptibility to infection varies among species and populations of trout and salmon, depending in part on their history of exposure. Populations inhabiting regions where the parasite occurs exhibit resistance, whereas populations from regions where the parasite is absent are often quite susceptible. In the Metolius River, Oregon coastal strains of hatchery-reared rainbow trout have been stocked to provide recreational angling. Genetic and morphological analyses indicate that these hatchery trout have interbred with native resident rainbow trout. Experimental tests in which fish were challenged by exposure to *C. shasta* demonstrated that the coastal-strain hatchery-reared rainbows (where the parasite is largely absent) were most susceptible, native Deschutes River steelhead least susceptible, and native Metolius rainbows interbred with coastal-strain hatchery-reared rainbows demonstrated intermediate susceptibility.

We believe that these experimental results, considered in light of widely recognized evolutionary and population genetics theory, provide convincing evidence that:

- Domestication selection can genetically alter hatchery populations in a relatively few generations.
- Hatchery-reared adults returning from the ocean and spawning in the wild generally produce progeny that do not survive as well as progeny from adults of wild origin.

and persuasive indication that:

- Interbreeding between hatchery-reared adults and wild fish can reduce the fitness of wild populations.

All of these studies have some limitations because of inherent difficulties in design and execution when working with natural populations. For example, the steelhead studies in the Kalama River contrasted the performance of a domesticated stock of steelhead from the Washougal River with native wild steelhead in the Kalama River. The poor performance of the Washougal steelhead could have been due to their being from another basin rather than being due to some general effect of hatchery domestication. We do not ignore such shortcomings, but believe these studies still lend credence to the conclusion that interbreeding of wild populations with hatchery-reared adults could be detrimental.

Risk and the Burden of Proof

We believe the available empirical evidence demonstrates a potential for deleterious interactions, both demographic and genetic, from allowing hatchery-origin salmon to spawn in the wild. We further believe that the potential for benefits is not great, and certainly not worth the hazards accompanying interbreeding between populations, whether they are of wild or hatchery-origin. Furthermore, we believe that the risks are too substantial to be ignored when the outcome of these management actions is irreversible and involves ESA listed species. As a result, we recommend that management agencies be very cautious when considering allowing hatchery-origin adult salmon to spawn in the wild.

Neither theoretical nor empirical evidence establishes threshold levels below which hazards to wild populations can be ignored. Quantitative treatment of the risks and benefits reveals a management conundrum; the relationship between benefits and risk, and the tradeoff between different types of risk are both quite complex. Typically, both benefits and risks increase together. For example, when there is a very low proportion of hatchery-reared adults spawning with wild salmon, genetic risks would not be particularly great, but at the same time, the potential demographic boost for the wild population also would be quite small, certainly insufficient to meet most management objectives. On the other hand, when there is a high proportion of hatchery-origin adults spawning with wild populations, demographic boosts are conceptually possible, but the risks of genetic and ecological hazards become substantial. If these hazards materialize, they would offset the biological benefits of any population increase, and the program could also fail to meet management objectives. Similarly, program design elements aimed at reducing one hazard, e.g., inbreeding hazards, often can increase other hazards, such as domestication hazards. Consequently, there are no simple formulae or guidelines to determine the levels at which interbreeding becomes risk-free.

The scientific evidence does not support indiscriminately permitting hatchery-reared salmon to spawn naturally throughout the Columbia River Basin. Decisions to permit hatchery-origin adults to spawn in the wild should be based on the conservation requirements of wild populations and the ability of the habitat to support additional reproduction, not based simply on the availability of hatchery-origin adults returning from the ocean. The Northwest Power Planning Council's 2000 Fish and Wildlife Plan presents a general framework for considering under what circumstances different approaches to artificial production are appropriate. The decision to

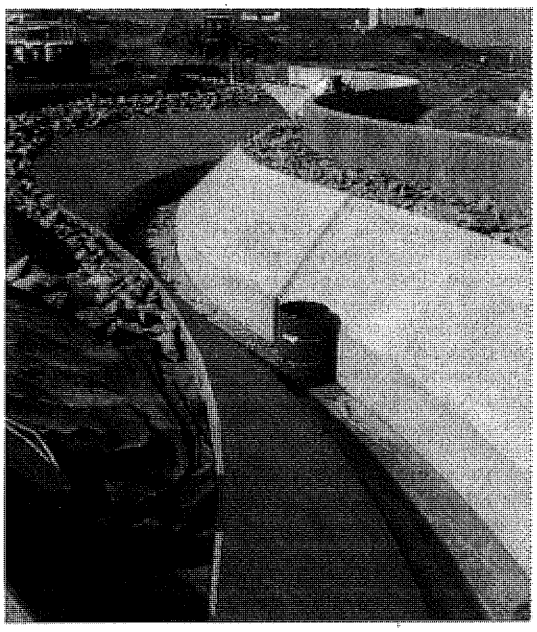
permit hatchery-origin salmon to spawn in the wild properly should be made in the larger context of sub-basin assessments and provincial recovery planning. The Washington Department of Fish and Wildlife has developed a benefit-risk assessment procedure derived from earlier efforts of M. Ford (NOAA Fisheries) and K. Currens (Northwest Indian Fisheries Commission) that discusses relevant factors such as stock history, broodstock and rearing protocols, and duration of the program. This type of assessment is needed for each wild population and each hatchery program.

Our most serious concern centers on the demographic and genetic interactions between hatchery stocks with a long history of cultivation and wild stocks, particularly those wild stocks that are ESA listed. The issues are different in streams where wild salmon have been extirpated and there is little likelihood of natural recolonization. In this case, it might be reasonable to develop a program designed to establish a run from scratch using hatchery-origin adults from a stock chosen for that purpose. From a genetic standpoint the key to success in that situation would lie in choosing the best source of the broodstock—one that is most compatible with the environment of the river system, and knowing when to stop outplanting, so that natural selection to evolve adaptations to the receiving environment could proceed without interference from continuing hatchery domestication selection. From an ecological standpoint, success in reestablishing a new population would also depend on correcting the problems that contributed to the extirpation in the first place.

There have been millions of hatchery juveniles released into Pacific northwest streams in the past 50 years. Many of the adults produced by these introductions were permitted to spawn naturally. It is reasonable to take the effects of these past activities into account when making management decisions in each specific circumstance. In locations where a wild population is confirmed to be a feral hatchery population, the consequences of the outcome of natural spawning by hatchery-origin adults might not be of ESA concern. Genetic evidence however, confirms that these past activities have not homogenized the native stocks (Utter et al. 1996; Marshall et al. 2000). The outcome of past stock transfers and hatchery practices has left a mixed legacy on the extant populations. For example, even though Carson stock spring-run chinook were propagated in Willamette River hatcheries, genetic markers characteristic of Carson stock are absent from recent Willamette River samples (Myers et al. 1998). Apparently, these stock transfers did not establish a lasting legacy. Similarly, hatchery-origin adult Columbia River fall-run chinook stray into the Snake River and are found on the spawning grounds. However, samples of out migrating juvenile fall-run chinook do not have the changes in allele frequencies expected if natural production from stray Columbia River fall-run chinook hatchery-origin adults was appreciable (Marshall et al. 2000).

Admittedly, there is uncertainty about the severity and scale of the detrimental effects that may actually be realized from genetic and ecological hazards associated with allowing hatchery-origin salmon to spawn with wild salmon. We are unable to say, for example, if interbreeding will result in a 10 % or any other reference level of reduction in the fitness of the wild population, or whether any unintended consequence will be realized within the wild populations. Historically, in salmon management as well as in the management of other natural resources, scientific uncertainty surrounding the magnitude and range of detriment has been used to excuse proceeding with possibly hazardous activities (Ludwig et al. 1993; Dayton 1998). Examples in salmon management include setting minimally restrictive fishery harvest and developing quite liberal land and water management policies, including those dealing with hydroelectric development. In some cases the consequences of these policy decisions have been very costly to the resource base and disruptive for the human communities that depend on those resources, including the consequences of lost fishing opportunities for the Native American community in the Pacific Northwest. Implementing actions to attempt to reverse harm can be similarly disruptive.

For situations in which there is scientific uncertainty, a precautionary approach has been recommended as a desirable fishery management option (Dayton 1998; Musick 1999). This precautionary approach requires those proposing potentially harmful activities to demonstrate they will not produce adverse impacts or to establish precautionary measures to detect problems and intervene if those problems are realized (Hilborn 1997). A precautionary approach also suggests that management actions be reversible if found to yield unintended results. Because it is virtually impossible to "undo" the genetic changes caused by allowing hatchery and wild salmon to interbreed, the ISAB advocates great care in permitting hatchery-origin adult salmon to spawn in the wild.



Clearwater Nez Perce Tribal Hatchery "Natures" Stream

Needed Future Actions

The recent NOAA Fisheries Federal Columbia River Power System Biological Opinion (21 December, 2000, www.nwr.noaa.gov/1hydrop/hydroweb/docs/Final/2000Biop.html) and the

Federal Caucus Basinwide Recovery Strategy (www.salmonrecovery.gov/strategy.shtml) both conclude that they are unable to assess the impacts of hatchery releases on wild populations because of insufficient monitoring and evaluation of past activities. The inability of regional managers to assess the impacts of hatcheries on wild stocks should alarm all of the Columbia River Basin's constituencies. The absence of adequate evaluation makes the task of reforming artificial production more challenging. Realistically, years of data are needed to assess these impacts. Because the region does not have the luxury of years of accumulated data, important decisions on improving programs will need to be made using the data that are available.

Scientists and managers need to establish the level of impact that is acceptable to individual populations and ESUs from allowing hatchery-origin salmon to spawn in the wild. For such a decision to be made, it will then be necessary to determine how that impact can be estimated with limited data. Once decided, it will be necessary to assess the potential for altering hatchery programs. Hatchery Genetic Management Plans are currently being prepared for Columbia River Basin hatcheries. The Northwest Power Planning Council formed an Artificial Production Advisory Committee to advise the council on artificial production reform and realignment in the Columbia River Basin. Perhaps these groups can begin the process of developing these endpoints and criteria.

Beyond these immediate decisions, a well-designed, large-scale experiment designed specifically to assess the effects of hatchery-derived spawning on wild populations is needed. We strongly urge all basin stakeholders to join together in support of such a basinwide experiment designed to assess the success of the supplementation strategy in general. This experiment would require the production of a large number of individuals tagged with neutral genetic marks, as well as an alteration of the annual stocking regimes at different sites throughout the basin for a number of years. Similar experiments have been suggested by the NOAA Fisheries Recovery Science Review Panel (http://research.nwfsc.noaa.gov/cbd/trt/rsrp_mar01.pdf). The long-term benefits from this experiment would be substantial and would go well beyond providing the guidance for hatchery reform. It is time to implement such an experiment.

References

Berejikian, B. A. 1995. The effects of hatchery and wild ancestry and experience on the relative ability of steelhead trout fry (*Oncorhynchus mykiss*) to avoid a benthic predator. Canadian Journal of Fisheries and Aquatic Sciences 52:2476-2482.

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 behaviour in steelhead trout (*Oncorhynchus mykiss*) fry. Canadian Journal of Fisheries and Aquatic Sciences 53:2004-2014.

Beverton, R. J. H., and **S. J. Holt.** 1957. On the dynamics of exploited fish populations. Fishery Investment Series 2. Volume 19. United Kingdom Ministry of Agriculture and Fisheries, London.

Campton, D. 1995. Genetic effects of hatchery fish on wild populations of Pacific salmon and steelhead: What do we really know? American Fisheries Society Symposium 15:337-353.

Chebanov, N. A., and **B. E. Riddell.** 1998. The spawning behavior, selection of mates, and reproductive success of chinook salmon (*Oncorhynchus tschawytscha*) spawners of natural and hatchery origins under conditions of joint spawning. Journal of Icthyology 38:517-526.

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.

Cramer, S. P. 2000. The effect of environmentally driven recruitment variation on sustainable yield from salmon populations. Pages 485-503 *in* E. E. Knudsen, C. R. Steward, D. D. MacDonald, J. E. Williams, and D. W. Reiser, eds. Sustainable fisheries management: Pacific salmon. Lewis Publishers, Boca Raton, Florida.

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

Currens, K. P., A. R. Hemmingsen, R. A. French, D. V. Buchanan, C. B. Schreck, and **W. L. Hiram.** 1997. Introgression and susceptibility to disease in a wild population of rainbow trout. North American Journal of Fisheries Management 17:1065-1078.

Dayton, P. K. 1998. Reversal of the burden of proof in fisheries management. Science 279:821-822.

Dobzhansky, T. 1937. Genetics and the origin of species. Harvard University Press, Cambridge, Massachusetts.

_____. 1948. Genetics of natural populations. XVIII. Experiments on chromosomes of *Drosophila pseudoobscura*. Genetics 35: 288-302.

Doyle, R. W., C. Herbinger, C. T. Taggart, and **S. Lochmann.** 1995. Use of microsatellite polymorphism to analyze genetic correlations between hatchery and natural fitness. American Fisheries Society Symposium 15:205-211.

Federal Register. 1999. Endangered and threatened species; threatened status for three chinook salmon evolutionarily significant units (ESUs) in Washington and Oregon, and endangered status for one chinook salmon ESU in Washington. Federal Register 64(56):14308-14328.

Felsenstein, J. 1997. Population differentiation and evolutionary processes. Pages 31-43 *in* W. S. Grant, ed. Genetic effects of straying of non-native hatchery fish into natural populations. U.S. Department of Commerce, NOAA Technical Memorandum NOAA Fisheries—NWFSC-30.

Flagg, T. A., and **C. F. Nash** (editors). 1999. A conceptual framework for conservation hatchery strategies for Pacific salmonids. U. S. Department of Commerce, NOAA Technical Memorandum NOAA Fisheries—NWFSC-38.

Fleming, I. A., and **M. R. Gross.** 1989. Evolution of adult female life history and morphology in a Pacific salmon (coho: *Oncorhynchus kisutch*). Evolution 43:141-157.

_____. 1993. Breeding success of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in competition. Ecological Applications 3:230-245.

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

Frankham, R. 1999. Quantitative genetics in conservation biology. Genetical Research 74:237-244.

Gabriel, W., and **R. Burger.** 1994. Extinction risk by mutational meltdown: synergistic effects between population regulation and genetic drift. Pages 69-86 *in* V. Loeschcke, J. Tomiuk, and S. K. Jain, eds. Conservation genetics. Birkhauser Verlag, Basil, Switzerland.

Gould, S. J., and **R. C. Lewtonin.** 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptionist programme. Proceedings of the Royal Society of London B205:581-598.

Ham, K. D., and **T. N. Pearsons.** 2000. Can reduced salmonid population abundance be detected in time to limit management impacts? Canadian Journal of Fisheries and Aquatic Sciences 57:17-24.

Hedrick, P., and **S. T. Kalinowski.** 1999. Inbreeding depression in conservation biology. Annual Review of Ecology and Systematics 31:139-162.

Hilborn, R. 1997. Uncertainty, risk, and the precautionary principle. Pages 100-106 *in* E. L. Pikitch, D. D. Huppert, and M. P. Sissenwine, eds. Global trends: fisheries management. American Fisheries Society Symposium 20.

Hulett, P. L., **C. W. Wagemann**, and **S. A. Leider.** 1996. Studies of hatchery and wild steelhead in the lower Columbia region, progress report for fiscal year 1995. Report No. RAD 96-01. Washington Department of Fish and Wildlife, Olympia.

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: 243-247.

Kapuscinski, A. R. D., and **J. E. Lannan.** 1984. Application of a conceptual fitness model for managing Pacific salmon fisheries. Aquaculture 43:135-146.

_____. 1986. A conceptual fitness model for fisheries management Canadian Journal of Fisheries and Aquatic Sciences 43:1606-1616.

Lande, R., and **G. F. Barrowclough.** 1987. Effective population size, genetic variation, and their use in population management. Pages 89-123 *in* M. E. Soule, ed. Viable populations for conservation. Cambridge University Press, N.Y.

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

Ludwig, D., **R. Hilborn**, and **C. Walters.** 1993. Uncertainty, resource exploitation, and conservation: lessons from history. Science 260:17,36.

Lynch, M. 1997. Inbreeding depression and outbreeding depression. Pages 59-67 *in* W. S. Grant, ed. Genetic effects of straying of non-native hatchery fish into natural populations. U. S. Department of Commerce, NOAA Technical Memorandum NOAA Fisheries—NWFSC-30.

Marshall, A. R., **H. L. Blankenship**, and **W. P. Connor.** 2000. Genetic characterization of naturally spawned Snake River fall-run chinook salmon. Transactions of the American Fisheries Society 129:680-698.

Moav, R., **T. Brody**, and **G. Hulata.** 1978. Genetic improvement of wild fish populations. Science 201:1090-1094.

Musick, J. A. 1999. Criteria to define extinction risk in marine fishes. Fisheries 24 (12): 6-14.

Myers, J. M., **R. G. Kope**, **G. J. Bryant**, **D. Teel**, **L. J. Lierheimer**, **T. C. Wainwright**, **W. S. Grant**, **F. W. Waknitz**, **K. Neely**, **S. T. Lindley**, and **R. S. Waples.** 1998. Status review of chinook salmon from Washington, Idaho, Oregon and California. U.S. Department of Commerce, NOAA Technical Memorandum NOAA Fisheries—NWFSC-35.

National Research Council (NRC). 1995. Science and the Endangered Species Act. National Academy Press, Washington, D.C.

Nelson, K., and **M. Soule.** 1987. Genetical conservation of exploited fishes. Pages 345-364 *in* N. Ryman and F. M. Utter, eds. Population genetics and fishery management. Washington Sea Grant Program, University of Washington Press, Seattle.

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

Orzack, S., and **E. Sober.** 2001. Adaptationism and optimality. Cambridge University Press, New York.

Peterman, R. M. 1987. Review of the components of recruitment of Pacific salmon. American Fisheries Society Symposium 1: 417-429.

Reisenbichler, R. R. 1997. Genetic factors contributing to declines of anadromous salmonids in the Pacific northwest. Pages 223-244 *in* D J. Stouder, P. A. Bisson, and R. J. Naiman, eds. Pacific salmon and their ecosystems: status and future options. Chapman and Hall, New York.

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.

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

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada 11:559-623.

Riddell, B. E., and **D. P. Swain.** 1991. Competition between hatchery and wild coho salmon (*Oncorhynchus kisutch*): genetic variation for agonistic behavior in newly-emerged wild fry. Aquaculture 98:161-172.

Rose, M. R., and **G. V. Lauder.** 1996. Adaptation. Academic Press, San Diego.

Ryman, N. 1991. Conservation genetics considerations in fishery management. Journal of Fish Biology 39(A): 211-224.

Ryman, N., and **L. Laikre.** 1991. Effects of supportive breeding on the genetically effective population size. Conservation Biology 5:325-329.

Ryman, N., **P. E. Jorge**, and **L. Laikre.** 1995. Supportive breeding and variance effective population size. Conservation Biology 9:1619-1628.

Scudder, G. G. E. 1989. The adaptive significance of marginal populations: a general perspective. Pages 180-185 *in* C. D. Levings, L. B. Holtby, and M. A. Henderson, eds. Proceedings of the national workshop on effects of habitat alteration on salmonid stocks. Canadian Special Publication of Fisheries and Aquatic Sciences 105.

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 47:566-571.

Swain, D. P., **B. E. Riddell**, and **C. B. Murray.** 1991. Morphological differences between hatchery and wild populations of coho salmon (*Oncorhynchus kisutch*): environmental versus genetic origin. Canadian Journal of Fisheries and Aquatic Sciences 48:1783-1791.

Templeton, A. R., 1986. Coadaptation and outbreeding depression. Pages 105-116 *in* M. E. Soule, ed. Conservation biology: the science of scarcity and diversity. Sinauer Associates Inc., Sunderland, MA.

Utter, F. M., **D. Chapman**, and **A. R. Marshall.** 1995. Genetic population structure and history of chinook salmon of the upper Columbia River. Pages 149-165 *in* J. L. Nielsen, ed. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society Symposium 17.

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

Whiteaker, J., **A. J. Talbot**, **D. Hatch**, **C. Beasley**, and **R. Hooff.** 2000. Hatchery reform begins with a review of current hatchery practices. CRITFC report. Columbia River Inter-Tribal Fish Commission, Portland, OR.

Wolhfarth, G. W. 1993. Genetic management of natural fish populations. Pages 227-230 *in* J. G. Cloud and G. H. Thorgaard, eds. Genetic conservation of salmonid fishes. Plenum Press, New York.