fisheries management
perspective

The Controversy about Salmon Hatcheries

ABSTRACT

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.

Introduction

Ernest L. Brannon
Donald F. Amend
Matthew A Cronin
James E. Lannan
Scott LaPatra
William J. McNeil
Richard E. Noble
Charlie E. Smith
André J.Talbot
Gary A. Wedemeyer
Harry Westers

Brannon is a professor at Center for Salmonid and Freshwater Species at Risk, University of Idaho, Moscow. He can be contated at aqua@uidaho.edu, 208/885-5830. Amend is a retired manager with the Southern Southeast Regional Aquaculture Association, Inc. in Ketchikan, AK. Cronin is senior scientist at Entrix in Anchorage, AK. Lannan is an emeritus professor at the Department of Fisheries and Wildlife, Oregon State University, Corvallis. LaPatra is senior scientist at Clear Springs Foods, Inc., Buhl, ID. McNeil is a retired professor from the Department of Fisheries and Wildlife, Oregon State University, Corvallis. Noble is retired chief of hatcheries, Washington Department of Fisheries, Olympia. Smith is retired director, U.S. Fish and Wildlife Service, Bozeman, MT. Talbot is senior scientist, Columbia River Inter-Tribal Fisheries Commission, Portland, OR. Wedemeyer is emeritus senior scientist, NFRC, Seattle, WA. Westers is a retired senior scientist, Michigan Department of Natural Resources, Lansing, MI.

Questions about the success of hatchery fish and their contribution to wild and native Pacific salmon and steelhead (*Oncorhynchus* ssp.) populations have garnered substantial controversy during the last century. Early in the history of hatchery production the issue was over-exploitation of wild fish mixed with hatchery fish that could sustain higher rates of harvest. The controversy shifted to objections about using hatcheries to mitigate for loss of habitat resulting from river development, such as hydropower production, and finally to concerns about the effect of hatchery fish on wild populations as reviewed by the National Research Council (1996). The general exclusion of hatchery fish from populations listed under the Endangered Species Act (ESA) (Waples 1991) intensified the debate, especially when hatchery programs, also sponsored under federal legislation, accounted for the majority of the salmon runs along the Pacific Coast. The present emphasis is now on supplementation programs designed to strengthen or to help recover native populations. However, two articles against hatchery fish coming from advisory committees (ISAB 2002; Myers et al. 2004) added notable uncertainty about the use of hatchery fish for supplementation of wild populations. The first was an article in *Fisheries* (vol. 27, no. 12), by the Independent Scientific Advisory Board (ISAB) to the National Marine Fisheries Service (NMFS now NOAA Fisheries). They recommended against allowing excess hatchery fish to spawn in the wild. The second was a recent article in *Science* (vol. 303:1980), by a committee that had previously advised NOAA Fisheries on matters related to ecology, and they favored excluding hatchery fish from listed salmon populations under the ESA. We disagree with those recommendations, and as a group of scientists with extensive experience in artificial propagation, we believe hatchery fish have an important role in fisheries management and salmon recovery. Therefore, to help give balance to the discussion on hatchery fish, we present a different perspective on artificial propagation and the literature pertaining to this component of fisheries science.

What are Hatchery Fish?

The term "hatchery fish" used in most reviews refers only to fish that have been reared and or incubated artificially in a building that houses incubation trays, troughs, and outside concrete or dirt raceways, and large surfaced or earthen ponds (Wedemeyer 2001). However, hatcheries are more than that and we are reminded they include stream-side gravel incubation boxes (Bams 1970), spawning channels (Cooper 1977), and engineered streams (Smith and Brannon 2002). In any of

these hatchery facilities, survival to the fry and advanced fingerling stages is greatly increased over that found under natural conditions.

The point is that artificial propagation varies in form and in the design of the facility, as well as in manner and intensity of culture programs, including the contribution of all stages to natural systems. A hatchery is another variation of the environment, albeit a variation often different from that found in natural streams and ponds frequented by juvenile salmon and steelhead, but our understanding of what constitutes a hatchery has to be broadened from that of the traditional incubation and rearing system in concrete facilities, especially as we contemplate hatchery reforms. Hatchery fish are products that come from all artificial incubation and rearing facilities that substitute for natural, unmanaged stream environments.

## The Genesis of the Hatchery Controversy

The decline of natural populations of salmon and steelhead has been associated with the effects of artificial propagation (Lichatowich 1999, Brannon et al. 1999). Hatchery fish now constitute a major part of Pacific salmon and steelhead populations. The Columbia River is an example. The Grand Coulee Maintenance Project, the Mitchell Act, and the Lower Snake River Compensation Plan were authorized under federal law to mitigate for the loss of the habitat and natural production resulting from the construction of Columbia and Snake River dams. As much as 90% of the Pacific salmon currently returning to Oregon, Idaho, and Washington are the result of hatchery production.

Other concerns also have been associated with hatchery fish, not the least of which is over-harvest of wild fish when mixed with hatchery populations that are able to sustain higher exploitation rates, and thus diminishing wild population strength even further than what was apparent from loss of habitat. The more pervasive concern, however, is the interbreeding of hatchery and wild fish. The fear is that introduction of non-local hatchery stocks will compromise the native gene pool, or that hatchery selection regimes in the local stock result in genetic changes unsuitable for the wild. The concerns deserve more attention to define the manner in which such problems might arise. The literature regarding hatchery fish has been renascent in differentiating the context of the problem, and documentation has often involved only the performance of non-local first-generation hatchery fish, where conditioning dominates the behavior of newly released fingerlings. Little or no assessment of long-term effects of hatchery fish on their parental population has been undertaken.

Apart from translocations of poorly adapted fish into new environments, many risks contemplated about hatchery fish are based on interpretations of laboratory studies, which are not necessarily directly applicable to natural systems. Similarly, extrapolating genetic changes observed in captive aquaculture populations or agency sport-fishing broodstock to conservation hatchery fish is hardly a legitimate analogy. However, there are justifiable concerns about hatchery fish management that need to be more critically examined. As indicated by the National Research Council (1996) supplementation itself has become confusing by the variability in its meaning. Rather than abandoning it, as suggested by NRC (1996), we believe supplementation should legitimately refer to artificial propagation for the sole purpose of complementing the productivity of the cognate population.

To clarify the culture option, it is important to provide a balanced assessment of artificial propagation, where both the risks and potential benefits are considered. With the major demographic changes occurring in the human population of Pacific Northwest, as noted by Lackey (2000), and the result-
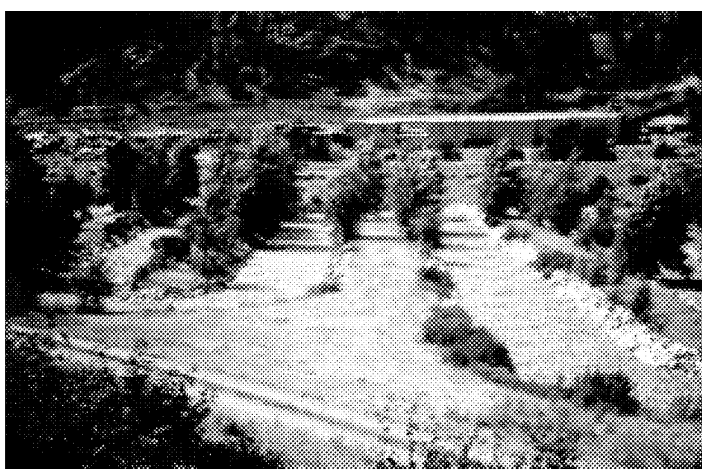
Pink salmon spawning channel on Seton Creek, British Columbia.

ing diminution of salmon and steelhead habitat from urbanization, agriculture, and logging, artificial propagation will continue to have a major role in sustaining sport and commercial fisheries. To be most effective in that role, we believe it is necessary that hatchery programs be consistent with the biological needs of the local populations and both wild and hatchery components should be considered part of the population complex. If hatchery production is not given rigorous and objective evaluation, and the results applied in the appropriate and beneficial manner for the management and conservation of Pacific salmon and steelhead, we fear that the health of the natural populations and survival of commercial and sport fisheries will be in jeopardy. Part of the resolution process is to be clear on what is being measured. Wild fish often include hatchery contributions from previous generations, and even the definition of wild fish used by NOAA Fisheries (Waples 1991) includes the progeny

of hatchery fish spawned in the wild. We believe a great part of the problem has been the confusion between process and management.

Confusing Artificial Propagation with Fisheries Management

In assessing the influence of hatchery fish on wild populations, or the success of hatchery fish in reproducing and establishing new populations, the confusion has been in not separating the influence of fisheries management from the actual process of artificial propagation (Brannon 1993). For example, in the past, managers often took advantage of available hatchery production to increase the number of fish in other streams for the sole purpose of providing greater harvest opportunity. The result was the introduction of a strain of fish poorly adapted to most receiving environments, with little or no prospect for sustained natural production. The primary factor responsible for poor natural reproductive success in these cases was management, unrelated to the culture process.

In other cases managers wanting to segregate hatchery fish from wild fish would select earlier hatchery spawners to create an early segment of the run that would eventually be separated from the wild population. The result was creation of an earlier returning hatchery stock, temporally displaced from the wild fish, but in most cases also unsuitable for the natural stream system because of asynchronous timing with the environmental template. The reduced effectiveness of the hatchery fish to reproduce naturally in those instances was not from the influence of artificial propagation, but rather management decisions that disengaged spawn timing from the environmental template of those systems.

Campton (1995) characterized the same problem in a comprehensive review on what was known about the genetic effects of hatchery fish on wild populations in the early 1990s. Reviewing the relevant hatchery studies, he concluded that what was generally perceived as problems with hatchery fish was actually the result of fisheries mismanagement. He stated that the absence of baseline data for most wild populations and pedigree data for hatchery populations precludes being able to unequivocally draw conclusions about hatchery effects on the genetics of wild fish. Ten years later we have little further insight on hatchery effects. Despite the lack of empirical evidence, hatchery fish are still the scapegoats for errors in fisheries management that overlook or disregard the importance of stock structure and biological requirements of anadromous salmonids. Effects of artificial propagation have to be separated from management effects.

However, Waples (1999) disagreed that such a differentiation should be made and suggests that because hatchery fish are a product of fisheries management, the effects of culture cannot be separated from the effects of management, and any problem related to the performance of those fish is thus a problem with the overall hatchery program. Such blurring of artificial propagation and management is not uncommon, and is the main reason why there is confusion and differences of opinion about hatchery fish and their ability to reproduce effectively in the natural environment. For example, Waples stated, "The effects on natural populations from an action such as selective breeding are the same whether one chooses to allocate this action to fish culture or fisheries management." The decisive point being missed, however, is that when one speaks of artificial propagation undertaken to achieve management objectives, such as selective breeding, one is in fact talking about fisheries management regardless of what processes are used to achieve those

objectives. The debate about hatchery fish that centers around inbreeding depression, outbreeding depression, and domestication selection has been confounded by the impact of management decisions on those respective factors. It is necessary to disengage the effects of management from the culture process if progress is to be made in understanding the influence of artificial propagation on performance in the wild. This is the essence of the question about hatchery fish. If involuntary selection occurs under culture conditions, unassociated with management and atypical of what occurs in nature, those changes are valid effects of artificial propagation and can be classified as domestication.

In defense of Waples' perspective, there are decisive issues regarding the effects of hatchery programs. The history of fisheries is rife with changes brought about by the use of hatcheries, and his example of selective breeding is a good illustration of measures intentionally taken to change the size and timing of hatchery fish. There is little doubt that such measures have moved those particular stocks away from the wild phenotype and most likely affected their performance in the wild. However, the consequences of management mitigated through the culture regime to achieve certain objectives need to be separated from how the culture process itself might alter fish performance in the wild, allegedly making them less fit. Management can be changed, and should be if it doesn't address the biological needs of the particular population. Unintentional effects of the culture process that might have negative effects on the fish performance or contribution in the wild are another matter. If artificial propagation causes substantive changes regardless of measures taken to eliminate or minimize such effects, that is the critical information needed to reassess or reform the application of artificial propagation.

The confusion between process and management was exemplified in the article by the ISAB (2002), in response to a question about letting excess hatchery fish spawn in the wild. The ISAB stated that the earlier return and spawn timing of hatchery adults, and their frequently younger ages at spawning, are evidence of domestication effects (natural selection in captivity) in anadromous populations. However, attributing those effects to the unintentional consequence of artificial propagation is mistaken. Spawn timing, which is largely genetically controlled, is subject to selection. Hatchery populations that return earlier do so because brood fish have been selected consistently from the earlier part of the returning run. Spawn timing can be altered simply by what segment of the returning population is selected for brood stock in the hatchery program. The recent Cowlitz coho salmon (*O. kisutch*) study on spawn timing of hatchery fish after 30 years of hatchery operation (Tipping and Busack in press) demonstrated both the susceptibility of that trait to selection, and the ability through hatchery breeding protocol to maintain historic timing patterns.

Younger age at return is also the result of hatchery program management, not an inherent property of artificial propagation. Decisions to use warmer temperatures during incubation accelerate development rates, resulting in earlier onset of feeding. Warmer temperatures and higher feeding rates promote more rapid growth, and large size at release hastens maturation, with fish returning a year sooner than what would be common in the parental native population (Feldman 1974). Artificial propagation of fish should not result in such changes, if natural timing and growth rate to migrant size of the wild fish are mimicked in the hatchery program. Managers have purposely induced such changes in hatchery populations to achieve certain objectives, but that is not domestication.

14

The confusion between process and management has also been abetted by some of the sportsmen's literature. An article recently published in the *Osprey*, the newsletter of the Federation of Fly Fishers, is an example. A study on the comparative performance of hatchery and wild steelhead *(O. mykiss)*, spawned, incubated, and reared under natural conditions was conducted on Forks Creek in the Willapa basin of southwestern Washington (McLean 2003). The wild fish outperformed the hatchery fish, and it was reported that the difference was caused by artificial propagation. Unfortunately, that wasn't the whole story. The hatchery fish did not originate from Forks Creek. The experimental hatchery steelhead were the Bogachiel River/Chambers Creek stock hybrid, and thus were unrelated to the endemic wild Forks Creek steelhead to which they were compared. Among other differences, there was a major temporal separation in spawn timing between the stocks. Bogachiel River/Chambers Creek fish are asynchronous with the incubation and emergence timing pattern of the native fish in the system, and that is an overwhelming factor contributing to their poor performance. Introduction of fish asynchronous with the environmental template can be so crippling to progeny success that no fisheries manager would expect out-of-basin wild fish to perform as well as the native fish in local conditions. Thus, it is ironic that when hatchery fish are asynchronous, it is hatchery effects that are given the blame rather than timing.

Another management problem incorrectly attributed to artificial propagation is the effect of excessive numbers of hatchery fish released into a given stream. Habitat carrying capacity in Pacific Northwest streams is generally less than 0.1 juvenile/m^2 of surface area (Nickelson et al. 1986; Bjornn and Reiser 1991; Mullan et al. 1992; Chapman et al. 1995). However, stocking rates in hatchery programs involve tens of thousands of fish released at one time at a single site, and the impact of that number of fish on the native population, or even on their own success, has not been given much attention. Furthermore, limiting releases to smolts does not guarantee that some degree of residence will not occur, and such changes in population density of the receiving streams with given carrying capacities can be disrupting irregardless of whether introductions are hatchery fish or not.

The effect of management decisions involving hatchery releases on the productivity of wild fish was demonstrated in the study on Oregon coastal coho by Nickelson (2003). Twelve streams and two lakes were included in the study on the influence of hatchery fish on wild coho productivity, measured as the density-independent rate of reproduction. Productivity was not related to the proportion of hatchery fish in the population, which followed the same conclusion that Lannan (2002) found for Oregon coastal coho, and suggests equivalent reproductive success among wild and hatchery contributions. These results are consistent with other studies that have shown similar spawning success of hatchery and wild female salmon, but contrary to the allegation that hatchery fish are less productive under natural spawning conditions. Similar to decreases in wild Chinook salmon *(O. tshawytscha)* productivity with increased interactive competition from hatchery releases (Levin et al. 2001),

Nickelson (2003) showed productivity of wild coho decreased with increased numbers of hatchery smolts. In support of conclusions of Flagg et al. (1995) and Einum and Fleming (2001), Nickelson suggested that management practices could be a major problem in wild salmon productivity, and should be changed to more effectively address the needs of wild populations.

There is general agreement that the indiscriminant use of hatchery fish has contributed to the decline of native fish in the Pacific Northwest, but there is no evidence that such decreases were the result of artificial propagation. For that reason it is important to differentiate between the effect of management decisions involving the use of cultured fish, and the effect of artificially propagated fish on the corresponding natural population. The performance of hatchery fish has often been biased both by management's use of hatchery fish and by the experimental design used in assessment studies. These problems have been common in research on artificial propagation, and have aggravated our ability to understand the potential of artificial propagation.

Review of Hatchery Fish Performance

Different reviews of hatchery fish performance have been made in recent times. In some cases the reviews have been of selected information for purposes of making recommendations (ISAB 2002) or supporting program developments of the agencies involved (IHOT 1994; Brannon et al. 1999), and less frequently based simply on assessment of hatchery technology. The ISAB (2002) article in *Fisheries*, for example, was in response to a request by NOAA Fisheries for a recommendation on whether or not excess hatchery fish should be permitted to spawn in the wild. The ISAB concluded that substantial experimental evidence demonstrated 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. They also said more limited evidence suggested that interbreeding between hatchery-origin adults and wild fish can reduce the fitness of the wild population. It was stated that genetic and ecological hazards become substantial with high proportions of hatchery fish in a population, and ISAB recommended against letting excess hatchery fish spawn in the wild.

While the ISAB recommendations undoubtedly were meant to put caution above uncertainty, their interpretation of the literature used to justify their point of view was reminiscent of the same problems confounding assessment mentioned above. Therefore, it is helpful to re-examine some of the often quoted references on hatchery fish as well as some more recent papers on artificial propagation to challenge their interpretation and provide a broader perspective on domestication, comparative reproductive success, fitness, and the genetic and ecological hazards associated with artificial propagation. For this purpose, we have segregated the present review with regard to laboratory studies, field investigations, and inferential observations under natural conditions.

> **...it is ironic that when hatchery fish are asynchronous, it is hatchery effects that are given the blame rather than timing.**

Laboratory Evidence on the Effect of Hatchery Propagation

Several scientists have studied performance variations and inter-actions of wild and hatchery conspecifics under laboratory conditions. Vincent (1960) compared wild and domesticated brook trout (*Salvelinus fontinalis*) and concluded that domesticated fish showed increased juvenile growth rates, were less wary of people, and demonstrated a stronger feeding response. We included Vincent in our citations because it is often quoted as evidence that hatchery fish are less fit or that the study was additional ancillary evidence of acclimatization to the culture experience. We agree that this behavior is evidence of acclimation or adaptation to a captive environment, but caution must be taken in how the study applies to conservation hatcheries. Food-oriented aggressive behavior in domesticated commercial rainbow trout (*O. mykiss*) is understandable, given that artificial selection occurs under such operations for rapid growth. The point is, however, that 90 years of captive isolation occurred with Vincent's domestic stock, and there is little relevance of this condition to conservation hatchery fish, or relationship to conservation hatchery practices, except for intentionally higher growth rates.

Agonistic Responses and Predator Avoidance

Johnsson and Abrahams (1991) tested the willingness of progeny of a domesticated strain of rainbow trout crossed with wild steelhead to risk entering territory of a predator compared to progeny of the pure steelhead strain. In two of the four trials in the study rainbow trout progeny showed significantly greater risk. The paper was quoted by ISAB as empirical evidence of selection associated with artificial propagation, and has been similarly quoted by other researchers on hatchery effects. Although the study did show potentially selective differences between strains tested, one cannot legitimately suggest that behavior differences observed in commercially-selected aquaculture strains of rainbow trout can be related to the behavior of open strains of hatchery-propagated steelhead. In the Johnsson and Abrahams study, the trout were a captive strain that most likely originally had different behavior patterns and had undergone 20 years of selective breeding for the qualities desirable in commercial aquaculture. However, it is noteworthy that in light of suggestions that hatchery fish are at greater risk to predation, the behavior of the captive strain did not translate into greater fingerling mortality in performance evaluation. Both strains showed identical survival percentages upon exposure to the predator.

Swain and Riddell (1990) and Riddell and Swain (1991) showed greater agonistic behavior among newly emerged hatchery coho salmon compared to wild coho grown in a common environment. The difference in behavior, with hatchery fish showing higher agonistic levels over wild fish, was attributed to additive genetic variance, although strongly influenced by a single male. It was implied that such behavior would be a disadvantage in the wild, most likely resulting in greater vulnerability to predators. In contrast, however, in similar studies by Berejikian et al. (1996) it was demonstrated that steelhead from a hatchery population showed less aggressive behavior in the first month compared to wild steelhead. It is noteworthy that in this case less aggressive behavior appeared to result in greater vulnerability to predation by sculpins (Berejikian 1995), but aggressiveness increased among the hatchery steelhead over time. It is also noteworthy that with some experience their per-formance at avoiding sculpins improved markedly over their naïve performance. In another study by Berejikian et al. (1999a) with hatchery and wild coho half-sib progeny in growth and survival experiments, results suggested that the hatchery experience endowed the fish with a competitive advantage over the wild fish. Implications of such laboratory results on behavior and survival of hatchery fish in the wild are difficult to project because of the unknowns. However, experience in natural-like habitat appear to improve performance of hatchery fish in the wild. Berejikian et al. (1999b) demonstrated in competitive performance trials that steelhead juveniles raised in habitat-enriched rearing tanks outperformed their counterparts raised in standard rearing containers.

Dominance and predator avoidance in domesticated and wild masu salmon (*O. masu*) was examined by Yamamoto and Reinhardt (2003) and the domesticated strains were neither dominant nor more aggressive than the wild strains. However, they did appear to leave cover more readily than wild fish in the presence of chemically simulated predator risk, which suggested they were more vulnerable to predation. However, juvenile hatchery masu salmon in a study by Reinhardt et al. (2001), in both laboratory trials and releases in a stream environment, outperformed their wild counterpart in survival and growth, even in the presence of predators, which was counter to their potentially higher risk vulnerability. Interpretation of these results must take into consideration that the wild masu juveniles were from a natural stream, and exposure to laboratory conditions for testing would not necessarily represent the responses they might show in their natural environment.

A study by Dellefors and Johnsson (1995) was conducted on wild and hatchery reared age 1+ sea trout (*Salmo trutta*) tested as combined groups in the presence of a large constrained rainbow trout. Although the wild fish reduced their risk exposure during non-feeding periods compared to the hatchery fish, wild and hatchery fish showed the same overall risk performance in the presence of the predator. Hatchery fish grew better than wild fish, which may have been a result of wild fish confinement, but the wild fish had experienced nearly a year of stream residence before capture and one would expect that such experience would have resulted in stronger predator avoidance. That was not apparent, except during non-feeding periods. However, in the study by Johnsson et al. (2001) on wild and farmed Atlantic salmon (*S. salar*), responsiveness to predators was shown to be more pronounced among the wild fish.

In a study on contest and scramble competition of juvenile brown trout (*Salmo trutta*) in laboratory studies, the farmed fish from the same source as the wild fish both reared in the hatchery grew faster than the wild fish, but showed no differences from wild fish in the behavior trials (Petersson and Jarvi 2000). Growth differences were related to possible selection for faster growth under farm conditions. Hedenskog et al. (2002) also examined wild and domesticated brown trout from a common stock and found that while growth rate was higher among the farmed strain, there were no differences in activity except that wild fish demonstrated greater agonistic behavior.

Under prolonged artificial propagation, behavior can be altered as the result of different selection pressures. However, these particular examples of farmed fish vs. wild fish performance show that the influence of artificial propagation on changing patterns of behavior is not necessarily definitive. Farmed fish have generally undergone intentional selection regimes with specific objectives, whether for market value or other qualities, and are the most extreme deviations from the natural forms. Consequently, while using them as surrogates

16

for conservation hatchery fish is unwarranted, they do demonstrate the extent of divergence that can occur from artificial selection and or genetic drift, and what traits can be altered.

Morphological Differences

Laboratory work also has demonstrated differences in the morphology of fish under culture conditions. Swain et al. (1991) detected small morphological divergences in hatchery coho from that of wild coho in controlled studies. They attributed the difference largely to the rearing environment. Fleming and Gross (1989) also found morphological differences between wild and hatchery produced coho after returning successfully from natural marine rearing. Much of the distinction was geographical, suggesting regional based affects, but some differences were related to long-term hatchery propagation and closed brood cycles. Implications of these changes on survival under natural conditions are uncertain, but Fleming and Gross (1994) demonstrated morphological divergence was exaggerated in multigenerational sea-ranched coho, and Fleming et al. (1997a) demonstrated that morphological differences can negatively affect breeding success in cultured fish. Fleming et al. (1994) found some differences between farmed and wild coho disappeared when reared naturally in marine waters.

Differences also exist in morphologies of natural populations of salmon, and have been equated with phenotypic plasticity inherent in salmonid species (Taylor and McPhail 1985). Such differences may be an expression of pre-adaptation to the conditions represented in different environments. Morphological differences observed in juvenile coho reared in a lake environment and the tributary stream environment by Swain and Holtby (1989), presumably in wild fish closely related but under different environmental influences, may be an example of such plasticity. Fish in a hatchery environment respond to the differences found in those conditions, but the morphological differences that result do not necessarily imply those differences are deleterious (Taylor 1986).

Morphological differences in hatchery fish are probably influenced by crowding, flow patterns, and spatial effects of that environment, and thus should be subject to amelioration with changes in hatchery pond design and loading densities, if such differences are disadvantageous to survival. Experience in working with hatchery and wild fish has shown that one factor often overlooked in hatchery/wild fish comparisons is the effect that age of returning adults has on morphology. Many of the secondary sexual characteristics in salmon are exaggerated among older fish, even when their size is not significantly larger than the younger fish.

Laboratory Study Synopsis

As demonstrated by the above citations, there are some contrasting results in laboratory studies on hatchery and wild fish performance. There appears to be good evidence that genetic changes from the wild parental genotype can occur through multiple generations of artificial propagation of salmon and trout under captive conditions where selection for aquaculture benefits may have occurred. There is also evidence that behavioral differences and perhaps morphological changes can occur in fish involved with standard hatchery programs. The long-term implications of these changes on performance in the wild, or the effects from wild and hatchery fish interbreeding are difficult to ascertain. Different responses by different groups of fish occur, as well as differences in interpretation of those responses on survivability. What these studies do show, however, is that artificial environments can alter

behavior and morphology under controlled conditions, which should not be dismissed, especially if a genetic basis for such differences is isolated.

Although uncertain as to their direct application in the field, laboratory studies have an important role in attempting to isolate reasons for differences in observed behavior. If hatchery fish performance in the wild is different from their wild counterparts, laboratory studies can provide definition under controlled conditions that may help provide better understanding of the factors influencing performance. Making the transition from laboratory observations to conclusions about hatchery fish performance in the field, however, may be another matter. Based on studies conducted on brown trout, Dannewitz et al. (2003) suggested that caution must be used in applying laboratory results to fish in the natural stream. They showed that the impact of hatchery selection on performance of fish in the wild may not be as pronounced as previously thought. Because behavior and performance of fish under natural conditions is the result of many factors, the predictability of hatchery fish survival success based simply on laboratory analysis requires that a level of prudence be exercised in making direct applications.

Field and Study Stream Evidence on the Effect of Hatchery Propagation

Studies of hatchery and wild fish in simulated stream settings are the most realistic comparisons of relative performance, apart from long-term field studies in the natural environment. In this section we review hatchery and juvenile behavior, adult spawning performance, and comparisons of hatchery and wild fish in natural streams.

Juvenile Behavior

Reisenbichler and McIntyre (1977) preformed one of the basic studies often cited as evidence on poorer performance of hatchery fish. The research compared Deschutes River wild steelhead with hatchery steelhead and hatchery x wild crosses of the same stock from the egg stage to the migrant stage in four different study streams. Sections in those streams were isolated and the eggs planted for natural incubation, emergence and rearing, and then evaluated by trapping migrants leaving the stream sections during the subsequent months. Some of the migrants may have been missed because the migrant traps were dysfunctional after November of the second year, but wild fish out-performed hatchery fish in two cases with significantly higher survival as a notable difference. It is important to put the biological implications of the remainder of the study in perspective, especially when survival among the three groups was not significantly different in the other two streams. When 9,000 eggs each from hatchery and wild fish were planted in each of the two streams with the most functional traps, and only 243 hatchery vs. 250 wild, and 347 hatchery vs. 369 wild fingerlings respectively were recovered, the differences do not show a decided disadvantage to hatchery fish.

Also noteworthy were the biological implications of the performance of the hatchery/wild crosses. One of the concerns about hatchery fish often voiced is the loss of fitness of wild fish interbreeding with hatchery fish. However, in this study the hatchery/wild crosses equaled or exceeded the performance of the wild fish in two of the four streams. Although such little evidence can hardly be interpreted in anyway as conclusive, the fact that the crosses showed no loss of fitness in those instances suggests at least some optimism that wild/hatchery interbreeding may not be a very serious problem when genetically similar fish are involved, and that

inter-stock hybrids may enjoy additive genetic variance and epistatic effects (Wade and Goodnight 1998) that can facilitate functional benefits.

Rhodes and Quinn (1999) studied performance of young coho of the same genetic source in two southwestern Washington streams. One test group was denied river experience for the first two months post-emergence and then released into the natural stream. Their subsequent stream survival over the remainder of their stream residence phase was compared with the wild-type group that experienced only the natural stream and no hatchery exposure. The study had some interesting implications. There were no differences in survival to the early fall between the fingerlings that had experienced early hatchery rearing and fingerlings that experienced only stream life. This was contrary to what we have seen in hatchery pre-smolt conditioning. An important aspect of the study was also the wild-type group. These fish were initially released in the stream and recaptured after two months of natural rearing to be marked and then released for the comparative performance phase over the rest of the rearing period. However, these wild-type fry represented the survivors of the natural culling mortality experienced during the first two months in the wild. The hatchery fish had no comparative pre-conditioning mortality in the hatchery prior to the test, and still they performed as well as the wild-type coho during subsequent stream rearing. This was contrary to the speculation that cultured fish carry a genetic load in the absence of selective mortality in the hatchery environment that results in higher mortality after release. However, the cultured fish were about 10% larger than the wild-type to begin with, which may have compensated for any potential negative effects they could have accrued from hatchery conditioning.

Similarly, Bohlin et al. (2002) comparing one-year old hatchery and wild brown trout in a stream study demonstrated no differences in survival between the two groups, suggesting that competitive performance was similar between hatchery and wild fish. The hatchery fish in the Bohlin et al. study also had a size advantage at the beginning of the study. However, in the study by Dannewitz et al. (2003), comparing performance of wild progeny from wild and second-generation hatchery brown trout in an experimental stream, there was no size difference, and they showed the same survival as wild-type fish from the egg stage through the freshwater phase of their life history. The hatchery trout had undergone seven generations of artificial propagation and differed in several fitness-related traits, and still performed the same as the wild trout.

In a hatchery performance and stream release study of Atlantic salmon by Einum and Fleming (1997), the results were similar again. Native, farmed, and hybrid (farmed x native) were compared in juvenile performance and post-release survival. The authors reported farmed salmon (sixth generation originating from a mixture of stocks) were genetically different than the wild stock, and farmed fish were more aggressive and dominated wild fish in pair-wise contests, which putatively represented a risk to wild fish if farmed fish were to escape to natural streams. However, there were no differences in survival in responses to simulated predation, or in feeding on natural food organisms in the nursery streams after the hatchery stock had been fed only pellets for six generations in captivity. Post-release survival in the stream sections was the same after approximately two months of natural rearing, and the farmed fish and the hybrids grew better than the wild fish during the stream rearing phase, which were opposite of results reported by Fleming and Einum (1997). Interstock hydrids did not demonstrate any loss of adaptive homeostasis, but showed patterns intermediate or similar to

the farmed variety, which also adds further confidence that wild/hatchery interbreeding of compatible genotypes are not at significant risk.

Putting the juvenile studies in perspective, the results of Rhodes and Quinn (1999), Bohlin et al. (2002), Dannewitz et al. (2003), and Einum and Fleming (1997), are quieting to some of the concerns that have been raised about the fitness of hatchery fish and the risks associated with their use as reported by Reisenbichler and McIntyre (1977), Fleming and Gross (1994), and the ISAB (2002). Lower survival in streams, greater vulnerability to predation, and domestication effects of artificial propagation were not major factors when hatchery and wild fish of similar quality were tested under similar densities. These studies suggest that artificially propagated fish can perform comparable to their wild conspecifics and suggest that they can also contribute to the wild population.

Adult Spawning Performance

There is evidence that the environment associated with the artificial propagation may have an influence on the subsequent reproductive behavior of returning adults. Reduced spawning success among artificially propagated fish has been shown in a series of unrelated studies. Fleming and Gross (1993) demonstrated that first-generation hatchery coho originating from similar coastal streams, but not of the same genetic origin, were less aggressive and less successful in spawning than were wild forms. Hatchery males spawned less frequently when in highly dense spawning situations, and reduction in successful pairing was affected by the dominance of wild males. Size advantage was important in male dominance. First-generation hatchery female success was more similar to that of wild females.

Fleming et al. (2000) compared the natural reproductive success of commercially-farmed Atlantic salmon from the Norway's national breeding program with that of wild salmon, regarding the influence that escapees from farms may have on wild fish. Spawning success was inferior to wild fish, again primarily among males. However, the survival of the progeny fingerlings in freshwater and in the marine phase was not significantly different between farmed and wild fish, which was surprising given the differences in the selective environments, and the fact that farmed fish have undergone artificial selection for traits different from wild fish. This was another result inconsistent with allegations of reduced fitness of hatchery progeny in the natural environment. The less than expected survival rate of wild fish in freshwater in the presence of farmed fish was attributed to the farmed fish creating a negative competitive interaction with the wild fish, in this case.

The study by Chebanov and Riddell (1998) on hatchery and wild Chinook salmon spawning success showed similar results to the above coho and Atlantic salmon studies, where hatchery males tended to be less successful in spawning than wild males. In this study hatchery males were less aggressive than wild males, they showed lower use of milt reserves in three out of five trials, but if they had prior first choice of the female, which the authors called "the first host," they tended to be more successful than wild males with delayed entry in the same trials. The hatchery females actually were more successful than the wild females, which was interpreted by the authors to mean that wild and hatchery females showed equivalent reproductive performance.

The above three studies demonstrate in a variety of salmon species that spawning success of artificially propagated fish, primarily males, can be less successful than wild fish. Berejikian et al. (1997,

2001a, b) also have shown similar results with Chinook and coho salmon, which adds further evidence that reduced reproductive success can occur with cultured fish in competition with wild fish, and can be traced to experiences under artificial propagation. However, in the Fleming et al. (1997a; 2000) and Berejikian et al. (1997, 2001a, b) studies, the cultured fish tested were from captive broodstock, and that is very different than using returning hatchery adults. As shown with the Bonneville Power Administration funded Captive Broodstock Technologies program (Venditti et al. 2000), even adults reared from wild parr under hatchery conditions perform poorly when released to spawn naturally. They are often asynchronous in timing and may not be very competitive if they spawn at all. What the captive brood spawning studies show, however, is that long-term experience of the hatchery environment can interfere with spawning behavior and timing among fish released into natural systems, and this appears related to being reared in the absence of appropriate environmental cues.

There is uncertainty about the mechanisms involved in reducing assertive tendencies in reproductive behavior of hatchery males, especially when hatchery fish show higher aggressiveness at other stages, but it may be related to the high densities of fish in hatchery scenarios. As suggested by Berejikian et al (2001b), one factor may be wild-type coloration, but there is also the uncertainty about intraspecific attraction or rejection of potential mates affecting assessment in such comparisons. The unexpected outcome from the Chebanov and Riddell (1998) study that researchers need to consider, was the tendency of the different groups of fish to prefer mates of their own origin. The implications of this observation are that in mixed populations inherent preferences may add a major bias in assessment of dominance. Another factor that may influence results in such studies is the difference in the onset of maturation. If one group enters breeding readiness slightly later than the other, it would influence assessment of male courtship success, assertiveness, solo male spawnings, and spawning performance.

The experimental evidence, therefore, shows that hatchery conditioning can have effects that last through adult maturation, resulting in reduced reproductive success under controlled simulated natural conditions, in the presence of more aggressive wild fish. Depriving Atlantic salmon juveniles of the river experience (Fleming et al. 1997b), on average, lowered spawning success, primarily among males, similar to other studies. In the study by Fleming et al. (1997a) on Atlantic salmon, and in the Berejikian et al. studies with captive brood, the altered spawning behavior that resulted was considered environmentally induced, and thus limited to the exposed generation. As shown by Fleming et al. (2000), freshwater and marine rearing performances are not necessarily affected. The Rhodes and Quinn (1999) study on young coho performance was a corollary on stream residence, where hatchery exposed and wild-type fry showed no difference in subsequent stream survival over the remainder of their stream residence phase.

So how should the evidence on reduced spawning success among hatchery fish be rationalized? While captive brood behavior can't be applied to the conservation hatchery situation, the exaggerated exposure to that environment does show the magnitude of change that the artificial rearing experience can have. When fish from the more typical hatchery environment were tested, it suggested that even shorter-term exposure to the artificial environment can influence reproductive assertiveness, at least among males.

Although controlled arenas with prescribed mate options and sex ratios are atypical of natural spawning conditions, and thus caution

should be used when attaching biological significance, if the effective reproductive performance is reduced in the wild, it is a factor that must be considered.

This same question was addressed by Fleming and Petersson (2001), and they also considered that studies showing reduced reproductive performance of hatchery fish would raise a concern in supplementation programs. Among their five studies reviewed on male spawning success, only two involved native, non-captive brood hatchery fish, and one participated in fewer spawnings while the other was the same as the wild. In the other traits the native, non-captive brood hatchery males showed no differences in aggression, and in courting they were divided compared to wild males. The difficulty in these reviews is that few studies are available that compare native fish. Most of the studies on non-native fish involve over 15 years of culture, and the original culture programs were not intended to match wild fish characteristics. In 39 populations examined by Fleming and Petersson (2001) for contribution to natural productivity, only 3 were native, which raises the question of whether or not true supplementation could ever have occurred in the majority of examples.

In enhancement or supplementation programs there are very different competitive scenarios for sites and mates than what would occur among spawning fish under natural stream conditions. As observed by Berejikian et al. (1997), hatchery fish manifest all of the appropriate courtship and spawning behavior, and successfully reproduce with viable offspring. Under natural conditions, without the temporal and spatial constraints of the study parameters present on the spawning grounds, the potential effects of the culture experience may not be expressed.

Comparisons in Natural Streams

Studies undertaken in natural streams provide insight about the cause of performance differences as well as the importance of experimental design in the interpretation of results. The Nickelson et al. (1986) study, routinely quoted as evidence against hatchery fish, was also cited by ISAB as one of the most thorough studies of the actual contribution of natural spawning hatchery origin salmon. However, if one looks at how the Nickelson et al. study was designed, it is apparent that it wasn't a test of the effects of artificial propagation, but rather the performance of an out-of-basin hatchery population in comparison to native fish in the receiving system. Hatchery presmolt coho originating from a different river system were planted in 15 streams and their performance compared to wild fish performance in 15 reference streams. It was concluded that hatchery fish were less productive because the resulting adults produced proportionally fewer juveniles, and thus it would be assumed that fewer adults would return in the subsequent generations. However, regarding its application to effects of artificial propagation, the study was confounded by variables other than fish culture. The hatchery stock was not from the streams studied, the spawn timing was much earlier than the wild fish, the hatchery fish were released at a much larger size than the wild fish, and stocking densities of hatchery fish were much higher than wild fish density in the non-stocked reference streams. For instance, hatchery stocking levels were 3.9 fish/m^2 of expected summer surface area, or nearly 10 times the observed natural seeding level found in non-stocked streams, and the fish were planted on top of the indigenous residents. In ascertaining the effects of artificial propagation, the study masked the effects of the hatchery experience by differences in spawn timing and home-stream syn-

chrony, and the carrying capacities of the hatchery fish streams were compromised.

Other often-quoted studies demonstrating poor performance of hatchery fish are Chilcote et al. (1986) and Leider et al. (1990). These studies deserve attention because while they contribute to our knowledge about management scenarios, and their undertaking no doubt required extensive time and support, they are examples that show how careful one must be in interpreting the results. Skamania hatchery steelhead from the Washougal River have experienced strong selection for larger size and earlier timing since the 1950s, which moved their spawning earlier by as much as three months, and thus they were asynchronous even with their native Washougal steelhead, as well as with most other steelhead populations. These fish were transferred and released in the Kalama River for comparison with the Kalama steelhead under natural conditions, and they performed poorly. Among other shortcomings, most noteworthy were the severe spawn timing differences between the stocks, and the negative influence of the genetic marker (AGP-1 described as allele A') on fitness of the hatchery fish. The marker used to identify Skamania hatchery fish was alleged to result in a survival disadvantage (but see Campton et al. 1991). While these studies may be relevant infor-

Engineered streams duplicate natural stream habitat, but increase production through managed flow, fish density control, and nutrient enhancements.

mation on risks to natural production by introducing asynchronously timed strains of steelhead, and potential problems with genetic markers, they should not be used for assessment of artificial propagation effects. Stock source, timing differences, and the negative influence of the genetic marker (or misidentification of wild cutthroat, *O. clarki*)) were overwhelming influences that biased hatchery fish performance.

Hulett et al. (1996) have also been quoted regularly as evidence that hatchery fish do not perform as well as wild fish. Hulett et al. used three year-classes of winter steelhead in the Elochoman River and compared them with an admixed hatchery population made up of fish from the Elochoman and Cowlitz rivers and Chambers Creek. The hatchery stock spawned earlier than the wild stock. Again, similar to McLean (2003), Nickelson et al. (1986), and Chilcote et al. (1986), and several other studies, the experimental design used cannot be applied to assess the influence of artificial propagation. The fish demonstrated different spawning times and represented different stock sources. There is little doubt about the outcome when hatchery fish are asynchronously timed with the stream environment (Brannon et al. 2004).

Unwin (1997), reporting on hatchery and naturally produced Chinook of common origin at the Glenariffe research station in New Zealand, found that hatchery fingerling survival was four times higher than naturally produced fry, but relative to their larger size the hatchery fingerlings performed poorly. The primary factors responsible were assumed to be associated with culture practices and limited success during their first year of marine residence. Nonetheless, in other studies at the same research station it was found that fish of hatchery origin were increasing in the adult spawning population, suggesting that hatchery fish were spawning successfully and integrating with and perhaps even displacing wild fish. Of course since Chinook were originally introduced in New Zealand, success of hatchery fish establishing themselves as wild fish is not surprising, and the differences between wild and hatchery Chinook in this case may be negligible. A major point of interest was the suggestion that ocean-type life history appeared more successful than stream-type life history forms, which might be anticipated when considering the temperature regimes and the fact that New Zealand stream beds tend to be unstable because of pumice like substrate. Such conditions, especially slightly warmer rearing temperatures, would be expected to encourage ocean-type life history behavior and dissuade extended freshwater residence (Brannon et al. 2004).

The recent studies on the Hood River in Oregon are most noteworthy with regard to the overall performance of local stocks in artificial propagation (Blouin 2003). When releasing out-of-basin hatchery steelhead in the Hood River, there was little or no evidence of reproductive success. However, if the hatchery fish originated from the local Hood River stock, their reproductive success in the subsequent generation was no different than the performance of the wild fish. It appears that the temporal asynchrony of the exotic strain was one of the factors responsible for the poor performance of out-of-basin steelhead, reminiscent of the McLean (2003), Nickelson et al. (1986), and Chilcote et al. (1986) studies. The hatchery fish originating from the local population possess the temporal synchrony and other characteristics acquired by the fish that have adapted to the Hood River environment, and their overall performance was as effective as the wild fish. If there was reduced reproductive performance of the hatchery fish, it was not apparent in the return success.

Disease Transmission

Another concern often quoted regarding the risk associated with hatchery fish is disease transmission (Busack and Currens 1995; ISAB 2002). Of course diseases are not created in hatcheries, but while cultured populations can be considered a potential reservoir of infectious agents because of intensive culture practices, there is little evidence to suggest that disease transmission to wild stocks is routine (Flagg et al. 2000). The biological significance of aquatic animal pathogens in hatchery effluent is unknown. Knowledge regarding pathogen survival, the environmental fate of pathogens and host susceptibility in aquatic ecosystems is very limited. Additionally, there are no reliable, standardized, or validated methods for testing effluents for aquatic animal pathogens. There are internationally accepted analytical methods available to qualify and/or quantify aquatic animal pathogens in tissues. These methods are used in the regulatory control programs that have been successful at limiting the introduction of important fish pathogens into new regions (LaPatra 2003).

However, the allegation associated with artificial propagation is the introduction of diseases with the transfer of fish. The best known example is the Currens et al. (1997) study, which showed that transfer of rainbow trout from the coast of Oregon into the Deschutes River Basin resulted in the high susceptibility of the interbred wild/hatchery fish to a myxosporean parasite endemic to the Deschutes system, a parasite absent from coastal watersheds and for which coastal rainbow had no immunity. The transferred rainbow trout in this study were a hatchery domesticated strain, and when they interbred with resistant Deschutes wild trout, the resistance of resulting progeny was reduced. The ISAB used this as an example of the potentially deleterious effects of interbreeding hatchery-cultured fish and wild fish based on disease susceptibility. However, it was a spurious example because it had nothing to do with artificial propagation, nor did it reveal a weakness in hatchery fish. The deleterious effect it represents is the flaw in management decisions that superimpose hatchery fish on a template foreign to their adaptive legacy, and disrupts local stock specificity refined by decades of natural selection.

The same problem was reported by Bartholomew et al. (1989) where Siletz River steelhead were susceptible to the *Ceratomyxa shasta* parasite compared to the resistant strain of North Santiam steelhead. In this case it was the introduction of fish carrying an exotic parasite for which local fish had no immunity. The transfer created the same problem as observed in the transfer of naïve coastal fish into the Deschutes. Local stocks that co-evolve with parasites tend to be less susceptible to their infection than introduced fish, whether hatchery or wild in origin. Mortality of naïve fish from lower resistance to diseases that are exotic to their experience has nothing to do with artificial propagation.

Field Studies Synopsis

We recognize there are studies that show differences in the behavior patterns of hatchery juveniles compared to their wild conspecifics. Also, as demonstrated above, there are studies that show hatchery and wild juvenile fish performance in stream environments can be compatible with no apparent disadvantage to either. There is also evidence that shows spawning ability in competitive controlled contests can be superior among wild fish to that of first-generation hatchery fish, and principally among males. The impact of such influences under test conditions may not be directly applicable to the natural environment for several reasons, but

nonetheless there remains a potential for some reduction in reproductive performance of hatchery fish in certain conditions. There is uncertainty if these differences observed in constrained studies translate to the natural environment, or if the degree of difference is biologically significant under field conditions. We reason, therefore, it is possible that artificial propagation can be employed to successfully meet management objectives to supplement wild populations when care is given to stock source and rearing operations. Risks associated with local-origin hatchery fish must be weighed against the benefits they offer. In our judgement the results of stream studies provide little evidence that the risk of biological impairment is too high to allow excess hatchery fish of local origin to spawn in the wild.

Inferential Observations Under Natural Conditions

The number of unsuccessful hatchery introductions is unknown because such information is seldom published, but there is no doubt that the history of hatchery propagation shows a predominance of failed attempts. In many of those instances even the basic biological requirements of the species were overlooked in translocations, such as transplants of sockeye fry to systems lacking a lacustrine environment in early British Columbia hatchery programs on the Fraser River (Thompson 1945), and the disregard of population structure in the early years of hatchery development on the Columbia River (Brannon 2000). Supplementation also has an equivocal history of success (Steward and Bjornn 1990), again often without attention to specific biological requirements of the population. There is much that can be inferred about the potential of artificial propagation with hatchery reform based on what has been observed in results from standard hatchery operations.

Success of Some Standard Hatcheries

Wild salmon and steelhead demonstrate a substantial capacity to respond to the dynamic nature of their freshwater environments. That adaptability is manifest in the diversity of life history forms, as well as the flexibility of genotypes to accommodate environmental variation (Brannon et al. 2004). Hatchery fish carry the same potential and versatility.

Most noteworthy among recent hatchery programs is the pink salmon *(O. gorbushca)* non-profit hatchery program success in Prince William Sound (PWS), Alaska. Hatchery production has been overwhelming (Hilborn and Eggers 2000; Wertheimer et al. 2001). Four hatcheries were built in PWS during the 1970s to enhance the pink salmon harvest fishery. Although supplementation of the wild fish has occurred, that was never the intention of the hatchery program. Mean annual adult pink salmon returns to PWS, based on Alaska Department of Fish and Game enumeration surveys prior to hatchery production, were around 5.2 million fish. Since the hatchery returns started, the mean annual adult production has been in excess of 26 million, and the largest run in the history of PWS occurred in 2003, with 57 million fish. Analysis of otolith marks of hatchery fish in streams relatively close (20 km) to the hatcheries have shown the majority of spawners have been hatchery strays, accounting for over 70% of the fish in some sample collections (Joyce and Evans 1999; Collins 2002), but overlapping with the same temporal distribution of the native fish and of similar genetic origin. Redd surveys taken from the late segment of the runs suggest that hatchery strays are reproducing successfully with native fish (Collins et al, 2000), and based on the last 12 years of

return data, wild fish in streams with high levels of hatchery strays are as productive as streams with low levels of stray fish (Brannon unpublished data). Because pink salmon use freshwater only for spawning and incubation, the temporal synchrony in spawning with the stream temperature profile for optimum emergence timing and marine entry is the primary environmental requirement for good performance, and in the case of the Prince William Sound pink salmon hatcheries, the production is synchronized with the adjacent wild populations.

Puget Sound has had hatchery/harvest fishery programs for 100 years, accounting for the majority of fish produced in the sound. Supplementation research has been ongoing for several years. Fuss (1998, 2002) demonstrated that coho and Chinook salmon raised in hatcheries can spawn successfully and do well under natural conditions. Similarly, Berejikian et al. (2004) have shown captive brood steelhead spawning naturally in the Hamma Hamma River on Hood Canal have spawning success, egg viability and egg to fry survival rates comparable to what is expected with wild steelhead. In these preliminary studies hatchery fish performance was within the range expected for wild fish, and impairment of hatchery steelhead male reproductive success has not been apparent.

Three established supplementation hatchery programs are noteworthy. One is on the Sooes River entering the Pacific Ocean just south of Cape Flattery on the northwestern tip of Washington (Brannon et al. 1999). Fewer than 100 fall Chinook were reaching the spawning grounds in some years, and the Makah National Fish Hatchery was built in the lower river to help recover the population. A breeding plan was followed to maintain the diversity present. The hatchery took the major portion of the small run, and allowed the rest to spawn naturally. The hatchery fish and the naturally spawning fish were commingled as a single population, but a limited number of adults were permitted to spawn above the hatchery. With increased returns, more adults were passed upstream of the hatchery, exceeding 800 fish, with a corresponding increase in spawning density. Age-3 returns from hatchery propagation started in 1984, and by 2002 well over 8,000 fish were returning from both the hatchery and the natural production. The success of the program is attributed to working with the native stock adapted to the short-run coastal system, and avoiding non-native introductions.

The second supplementation program mentioned here is on the White River with spring Chinook salmon (PSCFMP 2003). Numbers dropped to less that 10 adults in the mid-1980s. The hatchery program has been successful in returning over 400 adults annually to the hatchery through the 1990s and over 2,000 untagged adults returned to their historical spawning grounds in the fall of 2001. Supplementation started out with a captive brood program and in recent years has involved only artificial propagation from returning fish. Adults returning from the ocean to the Puget Power Diversion Dam in the basin are transported upstream to spawn naturally. The Puget Sound recreational fisheries have been the main source of harvest, responsible for over 90% of the take. The ability of the habitat to sustain the run is not considered adequate at this time, and in both the White and Sooes rivers it is anticipated that hatchery production will continue into the foreseeable future because of their contributions to the associated fisheries.

The third example is the Sacramento River winter-run Chinook project, which is also a successful supplementation effort. The winter-run Chinook are unique to the Sacramento and represent the evolution of a very late spawning strategy and 0-age emigrants to marine waters. Historically, they utilized warm incubation groundwater in the McCloud River in the upper Sacramento basin, and then emigrated as fry. Shasta Dam blocked the adult spawning migration and, because of declining numbers, a hatchery supplementation program was initiated to sustain the population. The program to recover these unique salmon has been successful in stabilizing and perhaps even increasing the effective population size of the Sacramento winter-run Chinook population (Hedrick et al. 2000).

Supplementation in the Columbia River Basin has also been active. Genetic analysis of rainbow trout in the Yakima River by Campton and Johnston (1985) suggest that hatchery introductions from outside the system have successfully integrated with the endemic rainbow, and in the absence of competition from anadromous forms, have increased in abundance sufficiently to sustain a respectable fishery. Even the Carson Chinook salmon introduced into the Methow River of the mid-Columbia and propagated in the federal hatchery at Winthrop for many years, are shown to have integrated with the wild Chinook spawning naturally in the river (Narum et al. 2002). The wild fish were from introductions in the early 1940s by the Grand Coulee Fish Maintenance Project redistributing spring Chinook blocked by Grand Coulee Dam (Mullan et al. 1992). Native Methow River spring Chinook had been eliminated by a dam constructed near the mouth of the river in 1915, and after its removal, the Winthrop hatchery, built to help mitigate for Grand Coulee, re-established the run with spring Chinook from the mid and upper Columbia, including Carson spring Chinook intercepted in the lower river.

Another interesting example is the cultured Chinook salmon out-planted in Lookingglass Creek in the Salmon River system (Lofy and McLean 1995; Lofy et al. 1998; McLean and Lofy 2000). In this case an out-of-basin stock was introduced from the Rapid River hatchery, tributary to the Little Salmon River, and hatchery fish spawner-to-spawner return rate has been similar to wild fish. The base of reference used in the evaluation is important because it overcomes the unintended bias that exists in most hatchery evaluations. Hatchery fish survival compared to wild fish is generally based on smolt-to-adult returns. However, it is hardly legitimate to compare hatchery fish naïve to the natural environment and protected from high incubation and rearing mortality, with wild fish that have already endured very high pre-smolt mortality and consequently are better conditioned as the remaining survivors to confront the challenges they experience as emigrants on the way to marine waters. Wild fish egg, fry, and fingerling mortality should not be ignored, and when adult to adult or egg to adult survival is used as the criterion, hatchery fish can show equal or even superior returns in many cases. The problem is that fish conditioned to the hatchery environment experience their highest mortality immediately after release when they are most vulnerable to predation. They are usually in high densities, disoriented from transport, and must become conditioned to their new environment, which leaves them very susceptible to the hazards during natural emigration. The Rapid River Chinook performance is also notable because this stock was considered unsuitable for release on account of the expected negative effects of domestication on performance.

Mullan et al. (1992) found no difference between wild and hatchery steelhead smolt success in the mid-Columbia. However, the large size of hatchery steelhead is the factor contributing to their success, rather than to their competitive ability with same-size wild fish. It is also noteworthy that Lannan (2002), using several years of

comparative data on Oregon coastal coho, found no difference in productivity between river basins with and without hatchery programs.

Phillips et al. (2000) demonstrated the success of the Umatilla salmon and steelhead supplementation programs working in concert with habitat restoration. Irrigation withdrawals, among other things, extirpated Chinook and coho salmon in the Umatilla prior to 1920 and severely depressed steelhead. Restoration of spring and fall Chinook and coho, and supplementation of steelhead, began prior to 1985. Carson spring Chinook, coastal coho, and native steelhead were used as brood stock. Chinook and coho have become established in the system and steelhead have been sustained at the same spawn timing as the original population. Given that both hatchery and wild fish have been spawning naturally in the Umatilla system with increased return success, hatchery contributions are considered to be quite successful for all three species. However, age and sex ratio among hatchery returns have changed from that of the wild fish. This is probably attributable to the larger size at the time of release, but age at return is expected to revert to the natural pattern in subsequent wild generations.

The research conducted by Chilcote (2003) is an interesting contrast. Twelve populations of steelhead, from four coastal and eight Columbia River Basin streams in which hatchery fish contributed at various levels, were studied over a 15-year period. The analysis showed that productivity in terms of recruits per spawner was negatively correlated with increases in the proportion of hatchery fish. However, Chilcote recognized that there were several uncertainties in his assumptions. The uncertainties included total and wild spawner abundance estimates, the sample size to determine percent hatchery fish, the ability to account for strays, the recruitment model, density dependence, and the assumption that levels of supplementation were independent of wild productivity. Because of those uncertainties and the absence of the relevant data to review, it is impossible to evaluate the validity of the conclusions that hatchery contributions resulted in decreased productivity of natural spawners (see Cramer et al. 2003). The only factor affecting productivity was the influence of hatchery contributions, regardless of the source and the spawn timing of the hatchery fish, and also regardless of habitat quality. Those conclusions were most curious. The habitat variables, for instance, were road density and proportion of consolidated basin geology, and did not include the significant habitat parameters of spatial diversity and nutrient productivity. Highest steelhead survival was in those populations that negotiated the greatest number of dams, but that relationship could not be isolated from adjacent stray hatchery contributions.
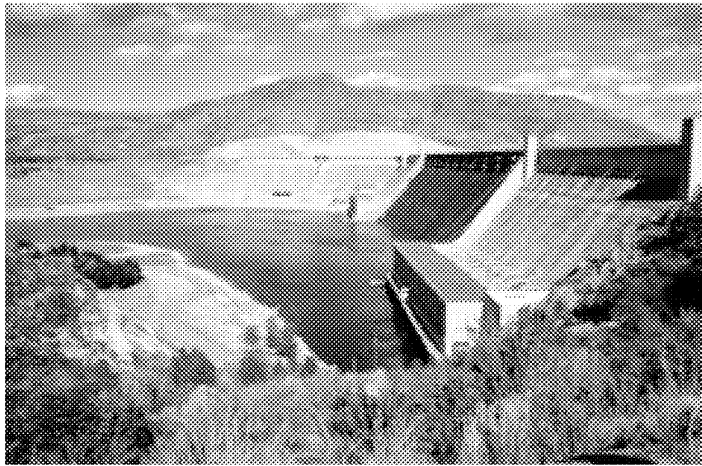
Steelhead productivity was good in those streams with hatchery fish of local origin, all of which adds to the uncertainty about the validity of the study assumptions.

As shown in the above references, hatchery fish performance is not entirely unfavorable. Some hatchery fish do well under natural conditions, but in many cases the factors that permit their success, such as larger size at release, substitute for weaknesses in traits that are responsible for wild fish success, and may tend to misrepresent their comparative performance. The point that should not be missed in the above citations, however, is that these were fish from conventional hatchery programs, including translocation of stocks in some cases. Hatchery raised fish are naïve to circumstances in the natural environment because of their acquired experience during culture, and thus increased performance of the subsequent generations of progeny with stream experience in the wild would be expected. Hatchery reform to address the biological needs of the fish should improve long-term performance. We believe that if Columbia Basin hatcheries are to have success in enhancing natural production and restore self-sustaining populations, the conceptual foundation has to be more specific in addressing the needs of the wild salmon and steelhead populations. Integrating the hatchery complex within the Columbia Basin ecosystem and still meeting the commercial, tribal, and public fishery objectives requires a model rigorously defined around the biology of the component species.

Ancillary Evidence on Hatchery Fish Performance

There is also considerable ancillary evidence on hatchery fish performance from reports on introductions that should not be overlooked. The success of self-sustaining Chinook salmon populations originating from Sacramento River hatchery transplants to New Zealand streams provides strong evidence for the potential of hatchery fish to do well and adapt to new circumstances. Transferred at the beginning of the last century (and only short-term hatchery experience), the translocated Chinook salmon not only established natural spawning populations with diverse life histories (Quinn et al. 2000, Unwin et al. 2000), they also had to overcome significantly greater challenges to become self-sustaining in the southern hemisphere than hatchery fish in the Pacific Northwest.

The success of transplanted Pacific salmon spreading in the Great Lakes provides further testimony of hatchery fish successfully establishing natural spawning populations. Great Lakes Chinook, coho, and pink salmon, without benefits of a marine environment, had to overcome significantly greater environmental challenges to reproduce naturally than they do in the Pacific Northwest, including the ability to accommodate poor water quality and different

Grand Coulee Dam blocked 73,000 square miles of upper Columbia River Basin.

23

temperature regimes. The uncertainty in evaluation is that hatchery production continues to occur in the Great Lakes, which makes it difficult to identify the sources responsible for success of the introduced salmon. However, both the New Zealand and Great Lakes experiences demonstrate the flexibility of Pacific salmon to accommodate change.

Several other naturally reproducing hatchery fish also provide long-term evidence of successful hatchery introductions, such as spring Chinook in the Methow basin and fall Chinook in the Yakima River, Chinook in Lake Coeur d' Alene, and coho in the Yakima River. It is interesting that the coho re-introduction program in the mid-Columbia, including the Yakima, is demonstrating improved survival among second- and third-generation progeny compared to first-generation hatchery fish (Witty 2003). These results tend to support the expectation that survival success of hatchery introductions should increase among subsequent broods spawning in the wild. It has also been shown that the Umatilla hatchery coho exhibited similar productivity to that of predominantly wild coho populations (Phillips et al. 2000), adding further evidence against the allegations that hatchery fish don't perform well in the wild. Hidden Falls hatchery on Baronoff Island, Alaska, has shown interesting results with coho propagation over the last 15 years (www.nsraa.org). Out-of-basin coho reared under natural conditions in Deer Lake experienced the exceptional smolt-to-adult survival rates of 5 to 24%. Coho of the same stock and propagated under standard techniques at the Hidden Falls hatchery, have shown smolt-to-adult survival rates ranging from 6 to 29%, and thus a performance as good as the fish raised in the wild. Although neither the hatchery nor the wild smolts had to experience any emigration risks or exposure to predation during the transition from freshwater to marine residence, the hatchery environment didn't result in any apparent disadvantage in survival to the adult stage thereafter.

It is noteworthy that the various examples of ancillary observations are not experimental results, but long-term circumstantial evidence of populations that have become established using hatchery fish. We interpret these successes as positive evidence that artificial propagation can contribute to naturally spawning, self-sustaining salmonid populations over the long-term with honing of the traits important to those populations through natural selection. We also reiterate that many attempts with hatchery fish introduction have failed, and such failures can no doubt be attributed at least in part to fish poorly adapted for the environmental challenge that confronted them. In most cases we believe the primary negative influence has been management decisions that were contrary to the biological needs of the fish.

The Genetic Issue: Risks and Benefits

Assessment of the hatchery fish performance is not simply their success in the natural environment compared to wild fish, but also, and perhaps more importantly, the genetic implications associated with hatchery fish integration. Alterations in the genetics of salmon and steelhead from artificial propagation can have effects on native populations of these species, and certainly, as we have reviewed above, when spawn timing patterns are altered there will be definite negative fitness implications, apart from other potential risks. Identifying the changes and assessing their effects, however, is not a simple matter, and interpretations can be easily influenced by the social context of the issue. For example, hatcheries are considered

undesirable by some critics because they are alleged to introduce anomalies in the natural reproduction process, such as lowering genetic diversity, unequal representation of breeders, single male use on multiple females, and effect of pooled milt. Similar phenomena in natural populations, however, are apparently not recognized, such as specificity at the cost of diversity, inbreeding in isolated populations, the effect of dominance in offspring representation, assortative mating, infidelity of single males, and pooled milt among a, b, and g males with given females. We suggest that artificial propagation should be viewed as a powerful tool in the conservation of wild fish by the ability it gives management to maintain population structure in the presence of stochastic environmental perturbations, population crashes, and selective fisheries.

Genetic Risks of Artificial Propagation

The citations discussed below on genetic risks associated with hatchery fish do not generally talk about the level of risk involved, and we want to briefly comment on that subject. Genetic diversity in salmon and steelhead populations is extensive, and usually within-population diversity exceeds diversity between populations. When we talk about diversity we are usually referring to quantitative allele frequencies rather than fixed unique alleles. Allele frequency differences are often used as surrogates implying effects in functional life history traits. However, because these putatively neutral alleles are not subject to natural selection, frequency differences may have little or no relationship to survival and reproductive prowess. Therefore, caution must be exercised in how the metrics used in genetics are interpreted in risk associated with artificial propagation.

Temporal variability in the allele frequencies occur regularly within populations and should not be confused with long-term multi-generation responses to selection regimes that result in different means and or variances in phenotypic characters (IDFG 1991, 1993; Powell and Faler 2000).

Fitness traits are polygenic and fitness variation is a continuous variable. Theory tells us that relatively low levels of gene flow (1 to 10 individuals/generation) between populations will prevent their differentiation. Hatchery and wild fish gene exchange is much higher even when wild fish are not intentionally included in the hatchery breeding population. Consequently in stable hatchery environments where mortality is relatively low, if non-intentional genetic selection occurs, the level of differentiation between wild and hatchery fish originating from the same gene pool will be limited. We suggest that with attempts made in artificial propagation to minimize genetic alterations in the hatchery segment of the population, natural selection in the spawners and progeny of the natural spawning segment will continue to be a major influence on the population structure.

While the risks attributed to artificial propagation are legitimate concerns, they are also largely theoretical, with limited evidence of any risk from artificial propagation in actual supplemented populations. Diversity in allele frequencies may provide insight to the ability of the population to respond to environmental change, but high diversity is not necessarily an attribute of highly fit populations. Spawn timing is a trait that probably has the most significant influence in salmonid fitness (Brannon et al. 2004), as demonstrated in numerous studies, and is easily monitored. Variance in that trait is rather narrow in a given population compared to the species range. High variability in spawn timing would be advantageous for a population colonizing new habitats,

but a disadvantage to the survivability of a given population. Spawn timing is a fitness trait where changes would be readily detectable if artificial propagation induced temporal asynchrony with the temperature regime, and one that could be re-aligned if necessary (Tipping and Busack 2004).

Phenotypic flexibility is also a critical fitness trait of salmonids, and is probably most evident in their response to temperature. As poikilotherms, incubation rates of salmonid embryos are highly variable depending on the temperature regime (Alderdice and Velson, 1978; Tang et al. 1987; Brannon 1987), but very predictable at any given temperature. Such flexibility in response to temperature adjusts rate of development per unit of temperature to compensate for the effect of temperature variation on emergence timing (Brannon et al. 2004). Phenotypic flexibility is also very evident in the morphological characteristics of young salmonids exposed to different temperatures, such as fin-ray counts, and other morphologies of fish of common parentage exposed to different environments (Taylor 1985).

In some instances risks associated with outbreeding depression, inbreeding depression, and domestication have been confounded by the impact of management decisions on those respective factors. We agree that outbreeding depression or introduction of different alleles and the break up of co-adapted gene complexes from interbreeding wild fish with out-of-basin fish threatens stock structure and can reduce fitness. However, outbreeding depression in salmonids has been primarily a problem created by the distribution and mixing of stocks in fisheries management (Ayerst 1977; Fessler 1977; Leider et al. 1986; Brannon et al. 2004). In the Columbia Basin, translocation of hatchery fish outside their natal systems has been routine over the years (Busack et al. 1979; Peven 1992; Flagg et al. 1995) and is still part of management practice. Productivity can suffer from outbreeding, but the level of impact is influenced by frequency of translocation, numbers of fish involved, and degree of dissimilarity with the native fish. Even where genetic mixing has occurred, little is known about its long-term effects (Utter et al. 1995). We suggest straying, which can amount to substantial numbers even in natural populations (Sharp et al. 1993), has definite evolutionary implications important to population fitness and longevity.

Inbreeding, or reduction in diversity from interbreeding of like individuals, is related to the effective size of the population, (N_e), which represents the genetic diversity present, rather than simply the number of fish in the population. This was considered a problem in many hatchery programs of the past, where single males were used on many females, and only small numbers of breeders were used to sustain the hatchery population. Reduction in diversity could result in limitations in the ability of the population to respond to environmental challenges or opportunities to colonize new habitat. Of course many anadromous salmonids are associated with smaller streams, and inbreeding could also be common in such populations if they were isolated. Colonization can also be assumed to start with relatively few founding members in many cases, which means they may start as inbred populations. We believe increasing the number of brood fish in the hatchery population, including wild fish, and following the breeding protocol that maintains the

diversity within the local gene pool, will help overcome many of the risks associated with inbreeding. The supplementation program to recover the Sacramento winter-run Chinook is an example of stabilizing or increasing the effective population size through artificial propagation (Hedrick et al. 2000).

Domestication, defined as the consequence of unintentional selection in hatcheries and referred to by Campton (1995) as natural selection in the hatchery environment, represents the most likely genotypic change that could occur in hatchery fish. Some of the behavioral characteristics in hatchery fish demonstrated through to maturity were associated with artificial propagation. Domestication is in proportion to selective mortality in the hatchery, and that is relatively low in the majority of cases, which suggests that the culture environment does not generate major genetic alterations. However, post-release mortality is relatively high, and this is the selective force suspected by Reseinbichler and Rubin (1999) that might cause genotypic divergence of hatchery fish. There has been little research to determine whether post-release mortality is any more or less selective than what has occurred among wild fish. One should not assume, for example, that dominance or interactive relationships among post-release fish would not have occurred in the wild among the same individuals, or that selection in hatchery environments will in any way change the primary factors for which population specificity has evolved. Hatchery environments are relatively stable, compared to the major seasonal, annual, and stochastic variations that occur in the natural environment that can influence resulting genotypes. Mortality in the field is not always beneficial to the population, and a significant proportion of the mortality experienced is also random. Nevertheless, the Reseinbichler and Rubin post-release model warrants further consideration as a source of difference between hatchery and wild fish, and thus potentially the source of inherent risk associated with artificial propagation. We also can be mistaken by assuming the source of genetic change is from hatchery selection. As Cross and King (1983) pointed out, a large component of change in allele frequencies is related to founder effects and genetic drift rather than selection, and hence emphasizes the importance of using sufficient brood stock.

Risks attributed to genetic changes also need to be scrutinized more carefully regarding the effects of artificial propagation. For

Natural spawning habitat for spring Chinook in the upper Salmon River.

example Reisenbichler and Rubin (1999) listed eight studies where genetic differences were alleged between hatchery and wild populations of andromous Pacific salmon that should reduce the fitness of hatchery fish. However, three of these were not Pacific salmon, and at least four were either equivocal in genetic implications or incorrectly attributed to cultural effects as shown in the present review. For instance the statement that thermal units required to the emergence stage of chum salmon (O. keta) increased from 1800 TUs to 2350 TUs by genetic alterations in the Netarts Bay, OR, chum salmon hatchery was incorrect. An increase in incubation of 550 TU over such a short period of time (less than two brood cycles) would have been impossible from genetic alterations. It is suggested the increase observed in the number of TUs was simply the result of using warmer water during incubation. The number of temperature units required from fertilization to emergence are not constant, but increase with mean temperature, as shown by (Dong 1981; Brannon 1987). At a mean temperature of 45°F, about 1800 TUs (100 days) are required to yolk absorption, while at 57°F the requirement increases to 2350 TUs (94 days).

Greater detail on the risks associated with hatchery production is provided by NFHRP (1994), Busack and Currens (1995), Campton (1995), Flagg et al. (1995), NRC (1996), and Einum and Fleming (2001), and the reader should consult those references for more information, but also be aware that without experience in species life history and artificial propagation there is the interpretative tendency to conform to the prevailing social context of the issues. Performance inferences are often based on first generation hatchery fish in the wild, progeny of captive brood, or populations that have undergone intentional selection for commercial traits, and that will influence results. There is also paucity of similar efforts and papers on hatchery fish from scientists that actually have long-term experience associated with hatchery production and the benefits or risks of hatchery fish. This is rather curious when the hatchery controversy is such a major issue in the Pacific Northwest and such a major item in agency budgets.

Benefits of Artificial Propagation

Artificial propagation is not without benefits beyond the contribution to sport and commercial fishing opportunities. In contrast to the risks, benefits have not been given much attention in wild/hatchery fish evaluations. As mentioned above, artificial propagation is a tool to maintain population structure in the presence of potential negative environmental stochastic influences and the fishery. Understanding the impact of such influences can allow managers to compensate for potentially negative population effects in hatchery programs by targeting the well being of wild fish, if the fisheries biologists understand gene flow rates and ecological differences, as cautioned by Storfer (1998).

The biological soundness of increasing population size through artificial propagation, and thus avoiding the pitfalls of small inbreeding populations, as well as maintaining genetic diversity, is also a benefit that should not be marginalized. Historically, high spawning ground densities were characteristic of natural populations and the condition under which stock specificity evolved through intense natural selection pressures. Higher spawning ground densities help hone stock characteristics, and maintaining sufficient numbers of fish through hatchery production assures that population sizes can remain above the threshold where inbreeding and genetic drift are of greatest concern.

In that regard, salmon and steelhead populations targeted for supplementation or assistance are generally declining and their failure to sustain themselves may not be entirely related to the fishery or habitat degradation, but rather to eroding fitness. Because genetic drift in small natural populations can have greater effects on gene frequencies than natural selection in small populations (Whitlock 2000; Orr 2000), there is an implication that in some cases small populations may not be at optimum fitness. Since hatchery fish represent the adaptive legacy of their originating population, increasing population size with reduction in random mortality among hatchery populations provides a benefit in maintaining the genetic variance on which natural selection can hone fitness in the extant population.

Contrary to popular rhetoric, we suggest that loss of genetic diversity is not a problem in conservation hatcheries. In the Columbia River, hatchery fish are no less diverse than wild fish, and in some hatcheries examined there is greater diversity than in the wild (Brannon et al. 2004). The fundamental issue of preserving genetic variation as a benefit of artificial propagation has been largely ignored in the hatchery controversy. Genetic variance is considered an important benefit in wild populations, and therefore sustaining such a benefit by artificial propagation is a positive contribution that hatcheries can have. Rather than being faulted for incomplete representation of the wild brood, artificial propagation can assist in maintaining genetic variance by using large numbers of broodstock.

Artificial propagation can also reveal and preserve new genetic variation. Rare alleles are always at risk of being lost by random mortality events during the high losses that accompany natural incubation and rearing. Because of the low mortality of fish in hatcheries, rare alleles have a chance of remaining through their freshwater rearing phase, and if they are beneficial, have a chance to express that advantage in subsequent generations of the population.

Another benefit is that hatcheries serve as repositories of genetic material for conservation of populations at risk of extinction. This is a feature that is inherent in hatchery programs because hatchery fish represent the evolutionary legacy and genetic structure of the ancestral native stock, which are the features that recovery programs must take advantage of under the ESA.

Finally, anadromous salmonids are a primary source of nutrient recruitment in freshwater streams (Stockner 2003). With management objectives allowing only enough escapement for replacement needs, productivity of freshwater systems has suffered by reduction in nutrification from reduction of carcasses. Excess hatchery fish spawning in the wild help restore nutrients in the areas accessible to anadromous salmonids. Nutrient addition to streams, using sterilized carcasses of hatchery fish and processing wastes in nutrient logs, is also an option that can be applied to help recover stream productivity.

Hatchery Management Reform

We are among those scientists that advocate hatchery reform. Hatchery management in the greater part of the twentieth century neglected stock structure and the need for synchrony between life history forms and their specific stream environments. Atlantic salmon (Hansen and Jonsson 1991), Chinook salmon and steelhead (Brannon et al. 2004), pink salmon (Gharrett and Smoker 1993), sockeye salmon (Brannon 1987), and rainbow trout (Siitonen and Gall 1989) all show strong genetic predisposition in migratory and or spawn timing.

Translocation of incompatible genotypes has been demonstrated to provide little or no benefit to supplementation (Nickelson et al. 1986; Chilcote et al. 1986; Steward and Bjornn 1990; McLean 2003), but that is to be expected. When hatchery populations are introduced in new environments that represent differences in weeks or months from their historic mean spawning times, their ability to survive in that environment will be affected proportionally to the temporal displacement. So it is predictable that Chambers Creek steelhead from central Puget Sound will not do well in Forks Creek, and that Skamania steelhead would not do well in the Kalama River. Chambers Creek and Skamania steelhead were out of temporal synchrony with their acquired streams. To alleviate the encumbrance of such large disadvantages, hatchery reform must assure that critical genetic components of the population are not disabled by the culture environment or the management regime of the hatchery.

Attending to the biological needs requires knowledge about the carrying capacity of the system in which hatchery fish are employed, the size and age structure of the population supplemented, and timing of the various life history phases. The benefit of large releases of hatchery fish is questionable, and may displace the native fish (Nickelson 2003). To maximize survival, hatchery fish are often released at sizes larger than wild fish, which can competitively overwhelm wild fish and cause higher mortality of the smaller conspecifics. Managers wanting to target certain fisheries, an earlier release date, or segregation between hatchery and wild fish, purposefully move hatchery return or spawn timing. The result may address the objective of the management program, but in most cases the fish are much less suitable for that stream system, and represent a risk to overlapping segments of the wild fish.

Research is needed to resolve the uncertainties involved with domestication. We believe some of what is referred to as domestication is not associated with changes in genotype, but rather are acquired phenotypic changes that may disappear when in the natural environment or in subsequent generations of natural production. We feel that negative effects of domestication can be significantly decreased by improved breeding programs and elimination of intentional selection regimes contrary to the natural template. Other forms of artificial propagation developed to simulate wild-type habitat have significant advantages. Clearly, sockeye spawning channels on the Fraser River are facilities where spawning densities, flow, and silt loads are controlled with 10-fold increases in production (Ewert et al. 2002), and the adult returns appear to show no reduced productivity that might be associated with inbreeding or domestication after 40 years of operation. New hatchery concepts such as engineered streams have many characteristics of the natural environment, including some levels of predation, but provide much higher survival rates compared to the natural stream system (Smith and Brannon 2002). And the NATURES studies are also assessing how present hatchery facilities can be altered to discourage artificial conditioning (Flagg and Nash 1999). The landscape perspective (Williams et al. 2003), suggests another model for hatchery reform that is directed at the health of the ecosystem, with emphasis on monitoring and analysis to understand population responses.

We do not concur with the ISAB (2002) recommendations to prevent hatchery fish from spawning in the wild, or sanction the extermination of hatchery populations of salmon and steelhead. To exterminate hatchery fish is to consciously extirpate linkages of historical significance and a portion of the genetic diversity that is important to the sustaining ability and adaptive evolution of the species. We believe there is sufficient evidence that hatchery fish can produce progeny comparable to wild fish, and that the genetic and ecological hazards can be minimized if the wild fish gene pool is represented.

Similarly, we do not agree with Myers et al. (2004) that hatchery-bred salmon should be excluded from distinct population segments when considering protection under the ESA. Progeny of hatchery fish from the local stock performing in the wild and subjected to natural selection are not inherently inferior to their native counterparts. Admittedly, the Myers et al. article was only an opinion and thus provided no data, but reflected the view partisan to the conviction that natural is best. We can agree that natural is best if natural is sufficient. Unfortunately natural is not sufficient with existing habitat under any scenario of what the future will bring if we have a core commitment to harvest fisheries. Differences in opinion in large part are influenced by the social context of our perspectives. In that regard we appreciate Einun and Fleming's (2001) statement that many of the reports reviewed in their work may be biased toward negative effects of stocking, but negative effects must be acknowledged. We agree that negative effects can not be ignored, and neither should positive effects. We have attempted to balance the negative by pointing out the positive side, and if the positive can be built on to improve management of hatchery programs and the fish they produce, it will build a better future for both the resource and the users. With the human population growth continuing in the Pacific Northwest and the necessity to look at multiple uses of water to meet the economic needs that accompany growth, we have to manage smarter. Smarter means first maintaining what habitat is remaining and creating new habitat opportunities. It means hatcheries working to match the genetic diversity and behavior of fish in the local population to meet the biological needs of the resource. It means using progeny of the local stock of salmon when enhancing the local salmon population, and it means working within the carrying capacity of the habitat.

It is mistaken to generalize that all hatchery fish are separate or different from wild fish when they are derived from the target population. Hatchery fish represent the legacy of their originating stock structure and we need to assure that they can reinforce the ability of their wild counterparts to sustain themselves. Our emphasis, therefore, must be on improving resource management rather than the impossible task of depending only on natural production in stochastic systems that seriously challenge the ability of anadromous salmonids to sustain themselves in the face of harvest fisheries and greater demands on the environment.

Conclusions

Hatchery produced salmon and steelhead successfully established to provide harvest fisheries often have had negative impacts on wild conspecifics because management decisions and hatchery operations were unrelated to the biological needs of either the introduced or the recipient populations. Reforms, therefore, are necessary in the management of fisheries that will address the biological needs of anadromous salmonid populations, and reforms are necessary in hatchery programs that will assure hatchery fish are compatible genetically and behaviorally with the recipient population.

Artificially propagated salmon and steelhead populations represent the evolutionary legacy and genetic constitution of the native fish from which they originated. Hatchery fish, therefore, can maintain population sizes sufficiently large to avoid inbreeding and genetic drift, maintain and increase genetic diversity, and provide security against risk of extinction by supplementing, enhancing, and otherwise sustaining the parent population. Excess hatchery fish from the local population should not be prevented from spawning in the wild and contributing to the wild segment of the population.

Changes that can occur through artificial selection demonstrate the inherent ability of salmon and steelhead to accommodate change through instruments of phenotypic flexibility and adaptability. Local stock sources, temporal synchrony in emigration and spawning, juvenile size and time of introduction, appropriate supplementation densities, and preservation of local genetic diversity are requirements that must be emphasized in artificial propagation. If hatchery representatives of the local population are exposed to the environmental variables of their native streams, natural selection will hone their traits to maintain the functional wild fish template. Artificial propagation can stabilize populations and maintain fitness of hatchery fish with equivalent quality and reproductive performance as wild fish; preserving their legacy and reducing the genetic and ecological hazards that wild fish will otherwise face. Hatchery fish from the local population should not be excluded from the distinct population segment considered for listing under the ESA.

First generation hatchery fish will continue to be the dominant influence in supplementation, which underscores the importance of hatchery programs to prioritize facilities and protocol that condition hatchery fish for the natural environment. Hatchery programs must monitor hatchery fish behavior, stream distribution, community interactions, stream capacity, freshwater growth, and marine migratory destinations to assess and make appropriate alterations in the management of hatchery contributions.
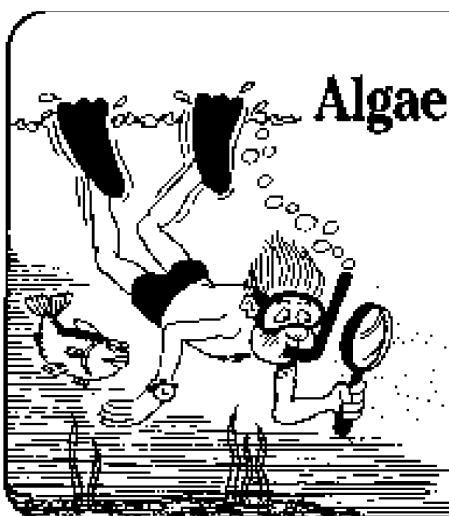
References

Alderdice, D. F., and R. P. J. Velson. 1978. Relationship between temperatures and incubation time for eggs of Chinook salmon (*Oncorhynchus tshawytscha*). Journal of the Fisheries Research Board of Canada 35:69-75

Ayerst, J. D. 1977. The role of hatcheries in rebuilding steelhead runs of the Columbia River system. Pages 84-88 *in* B. Schwiebert, ed. Columbia River salmon and steelhead. American Fisheries Society, Special Publication 10, Bethesda, Maryland.

Bams, R. A. 1970. Evaluation of a revised hatchery method tested on pink and chum salmon fry. Journal of Fishery Research Board Canada 27:1429–1452.

Bartholomew, J. L., C. E. Smith, J.S. Rohovec, and J. L. Fryer. 1989. Characterization of a host response to the myxosporean parasite, *Ceratomyxa shasta*, by histology, scanning electron microscopy, and immunological techniques. Journal of Fish Diseases 12:509-522.

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

Berejikian, B. A., E. P. Tezak, S. L. Schroder, C. M. Knudsen, and J. J. Hard. 1997. Reproductive behavioral interactions between spawning wild and captivity reared coho salmon (*Oncorhynchus kisutch*). ICES Journal of Marine Science 54:1040-1049.

Berejikian, B. A., E. P. Tezak, S. L. Schroder, T. A. Flagg, and C. M. Knudsen. 1999a. Competitive differences between newly emerged offspring of captive-reared and wild coho salmon. Transactions of the American Fisheries Society 128:832-839.

Berejikian, B. A., E. P. Tezak, T. A. Flagg, A. L. LaRae, E. Kumerow, and C. V. W. Mahnken. 1999b. Social dominance, growth, and habitat use of age-0 steelhead (*Oncorhynchus mykiss*) grown in enriched and conventional hatchery rearing environments. Canadian Journal of Fisheries and Aquatic Sciences 57:628-636.

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

Berejikian, B. A., E. P. Tezak, and S. L. Schroder. 2001b. Reproductive behavior and breeding success of captive reared Chinook salmon. North American Journal of Fisheries Management 21:255-260.

Berejikian, B., and ten others. 2004. Hamma Hamma River steelhead supplementation. Hatchery Scientific Review Group research review. Puget Sound and Coastal Washington Hatchery Reform Projects. February 2004, Olympia, Washington.

Bjornn, T. C., and D. W. Reiser. 1991. Habitat requirements of salmonids in streams. Pages 83-138 *in* W. R. Meehan, ed. Influences of forest and rangeland management on salmonid fishes in their habitats. American Fisheries Society Special Publication 19, Bethesda, MD.

Blouin, M. 2003. Relative reproductive success of hatchery and wild steelhead in the Hood River. Final Report. BPA Contract 9245, Project # 1988-053-12. Corvallis, OR.

Bohlin, T., L. F. Sundström, J. I. Johnsson, J. Höjesjö, and J. Pettersson. 2002. Density-dependent growth in brown trout: effects of introducing wild and hatchery fish. Journal of Animal Ecology 71:683-692.

Brannon, E. L. 1987. Mechanisms stabilizing salmonid fry emergence timing. Pages 120-124 *in* H. D. Smith, L. Margolis, and C. C. Wood, eds. Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Canadian Special Publication of Fisheries and Aquatic Sciences 96.

_____. 1993. The perpetual oversight of hatchery programs. Fisheries Research 18:19-27.

_____. 2000. The salmon crisis: a lesson in semantics. Pages 55-75 *in* P. Koss and M. Katz, eds. What we don't know about Pacific Northwest fish runs: an inquiry into decision-making under uncertainty. Proceedings of the Portland State University Salmon Symposium, Portland, OR.

Brannon, E. L., K. P. Currens, D. Goodman, J.A. Lichatowich, B.E. Riddell, and R.N. Williams; W. E. McConnaha, chair. 1999. Review of artificial anadromous and resident fish in the Columbia River basin. Part I: A scientific basis for Columbia River production programs. Council Document 99-4. Scientific Review Team, Independent Scientific Advisory Board, Northwest Power Planning Council, Portland, Oregon.

Brannon, E., M. Powell, T. Quinn, and A. Talbot. 2004. Population structure of Columbia River Basin Chinook salmon and steelhead trout. Reviews in Fisheries Science 11(1):1-120.

Busack, C. A., R. Halliburton, and G. A. E. Gall. 1979. Electrophoretic variation and differentiation in four strains of domesticated

rainbow trout *Salmo gairdneri*. Canadian Journal of Genetic Cytology 21:81-94.

Busack, C. A., and K. P. Currens. 1995. Genetic risks and hazards in hatchery operations: fundamental concepts and issues. American Fisheries Society Symposium 15:71-80.

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.

Campton, D. E., F. W. Allendorf, R. J. Behnke, and F. M. Utter. 1991. Reproductive success of hatchery and wild steelhead comment regarding Chilcote et al. 1985. Transactions of the American Fisheries Society 120:816-827.

Campton, D. E., and J. M. Johnston. 1985. Electrophoretic evidence for a genetic admixture of native and nonnative rainbow trout in the Yakima River, Washington. Transactions of the American Fisheries Society 114:782-793.

Chapman, D., C. Peven, A. Giorgi, T. Hillman, and F. Utter. 1995. Status of spring Chinook salmon in the mid-Columbia region. Don Chapman Consultants, Inc., Boise, Idaho.

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

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

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.

Collins, K. 2002. Percentage of hatchery fish strays in Prince William Sound streams using otolith marks. Research Report 02-1, University of Idaho, Moscow.

Collins, K. C., Brannon, E. L., Moulton, L. L., Cronin, M. A., and Parker, K. R. 2000. Hydraulic sampling protocol to estimate natural embryo mortality of pink salmon. Transactions of the American Fisheries Society 129: 827-834.

Cooper, A. C. 1977. Evaluation of the production of sockeye and pink salmon at spawning and incubation channels in the Fraser River system. Progress Report 36. International Pacific Salmon Fisheries Commission, New Westminster, B.C., Canada.

Cramer, S. P., D. B. Lister, P. A. Monk, and K. I. Witty. 2003. A review of abundance trends, hatchery and wild fish interactions for the middle Columbia steelhead ESU. Cramer and Associates, Inc., Sandy, OR.

Cross, T. F, and J. King. 1983. Genetic effects of hatchery rearing in Atlantic salmon. Aquaculture 33:33-40.

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.

Dannewitz, J., E. Petersson, T. Prestegaard, and T. Järvi. 2003. Effects of sea-ranching and family background on fitness traits in brown trout *Salmo trutta* reared under near-natural conditions. Journal of Applied Ecology 40(2):241-250.

Dellefors, C., and J. I. Johnsson. 1995. Foraging under risk of predation in wild and hatchery-reared juvenile sea trout (*Salmo trutta* L.). Nordic Journal of Freshwater Research 30:31-37.

Dong, J. N. 1981. Thermal tolerance and rate of development of coho salmon embryos. M.S. thesis, University of Washington, Seattle.

Einum, S., and I. A. Fleming. 1997. Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. Journal of Fish Biology 50:634-651.

_____. 2001. Implications of stocking: ecological interactions between wild and released salmonids. Nordic Journal of Freshwater Resources 75:56–70.

Ewert, V., D. Lofthouse, and E. Brannon. 2002. Artificial spawning channels: another hatchery concept. Pages 121-128 *in* E. L. Brannon and D. MacKinlay, eds. Hatchery reform: the science and the practice. International Congress on the Biology of Fish, Congress 2000, Vancouver, Canada.

Feldman, C. L. 1974. The effect of accelerated growth and early release on the timing, size, and returns of coho salmon (*Oncorhynchus kisutch*). M.S. thesis, University of Washington, Seattle.

Fessler, J. 1977. A case study in fish management—the Deschutes River: what we know and don't know. Pages 121-126 *in* E. Schwiebert, ed. Columbia River salmon and steelhead. American Fisheries Society Special Publication 10, Bethesda, Maryland.

Flagg, T. A., and C. F. Nash, eds. 1999. A conceptual framework for conservation hatchery strategies for Pacific salmonids. U.S. Department of Commerce, National Oceanic and Atmospheric Administration Technical Memorandum NOAA Fisheries—NWFSC-38.

Flagg, T. A., B. A. Berejikian, J. E. Colt, W. W. Dickhoff, L. W. Harrell, D .J. Maynard, C. E. Nash, M. S. Strom, R. N. Iwamoto, and C. V. W Mahnken. 2000. Ecological and behavioral impacts of artificial production strategies on the abundance of wild salmon populations. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-41.

Flagg, T. A., F. W. Waknitz, D. J Maynard, G. B. Milner, and C. V. W. Mahnken. 1995. Impact of hatcheries on native coho salmon populations in the lower Columbia River. American Fisheries Society Symposium 15:366-375.

Fleming, I. A., and S. Einum. 1997. Experimental tests of genetic divergence of farmed and wild Atlantic salmon due to domestication. ICES Journal of Marine Science 54:1051-1063.

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.

_____. 1994. Breeding competition in a Pacific salmon (Coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. Evolution 48:637-657.

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 B 267:1517-1523.

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.

Fleming, I. A., B. Jonsson, M. R. Gross, and A. Lamberg. 1997a. An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (vol. 33, pg. 893, 1996). Journal of Applied Ecology 34:835-835.

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

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

Fuss, H. J. 1998. Hatcheries are a tool: they are as good or as bad as the management goals that guide them. Pages 19-28 *in* E. L. Brannon and W. C. Kinsel, eds. Proceedings of the Columbia River anadromous salmonid rehabilitation and passage symposium. Aquaculture Research Institute, University of Idaho.

_____. 2002. What needs to be reformed, the objectives, technology or the fish? Pages 1-16 *in* E. L. Brannon and D. MacKinlay, eds. Hatchery reform: the science and the practice. International Congress on the Biology of Fish, Congress 2002, Vancouver, Canada.

Gharrett, A. J., and W. W. Smoker. 1993. Genetic components in life-history traits contribute to population structure. Pages 197-201 *in* J. G. Cloud and G. H. Thorgaard, eds. Genetic conservation of salmonid fishes. Plenum Press, London.

Hansen, L. P., and B. Jonsson. 1991. Evidence of a genetic component in the seasonal return pattern of Atlantic salmon, *Salmo salar* L. Journal of Fish Biology 38:251-258.

Hedenskog, M., E. Petersson, and T. Järvi. 2002. Agonistic behavior and growth in newly emerged brown trout (*Salmo trutta* L) of sea-ranched and wild origin. Aggressive Behavior 28:145-153.

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

Hilborn, R., and D. Eggers. 2000. A review of the hatchery programs for pink salmon in Prince William Sound and Kodiak Island, Alaska. Transactions of American Fisheries Society 129:333-350.

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. RAD96-01. Washington Department of Fish and Wildlife, Olympia.

IDFG (Idaho Department of Fish and Game). 1991, 1993. Idaho Department of Fish and Game annual reports and data. Boise.

ISAB (Independent Scientific Advisory Board). 2002. Hatchery surpluses in the Pacific Northwest. Fisheries 27(12):16-27

IHOT (Integrated Hatchery Operations Team). 1994. Policies and procedures for Columbia Basin anadromous salmonid hatcheries. Bonneville Power Administration. DOE/BP-2432. Portland Oregon.

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 53:1546-1554.

Johnsson, J. I., J. Hjesjo, and I. A. Flemming. 2001. Behavioural and heart rate responses to predation risk in wild and domesticated Atlantic salmon. Canadian Journal of Fisheries and Aquatic Sciences. 58:788-794.

Joyce, T. L. and D. G. Evans. 1999. Otolith marking of pink salmon in Prince William Sound hatcheries, 1995-1998. Exxon Valdez oil spill restoration project final report (Restoration Project 99188), Alaska Department of Fish and Game, Cordova.

Lackey, R. T. 2000. Restoring wild salmon to the Pacific Northwest: chasing an illusion. Pages 91-143 in P. Koss and M. Katz. What we don't know about Pacific Northwest fish runs: An inquiry into decision-making under uncertainty. Proceedings of the Portland State University Salmon Symposium, Portland, OR.

Lannan, J. E. 2002. Abundance and productivity of naturally spawning Oregon coastal coho salmon (Oncorhynchus kisutch) in rivers with and without hatchery stocks. Pages 107-116 in E. L. Brannon and D. MacKinlay, eds. Hatchery reform: the science and the practice. International Congress on the Biology of Fish, Congress 2002, Vancouver, Canada.

LaPatra, S. E. 2003. The lack of scientific evidence to support the development of effluent limitations guidelines for aquatic animal pathogens. Aquaculture 226:191-199.

Leider, S. A., M. W. Chilcote, and J. J. Loch. 1986. Comparative life history of hatchery and wild steelhead trout Salmo gairdneri of summer winter races in the Kalama River, Washington. Canadian Journal of Fisheries and Aquatic Sciences 43:1398-1409.

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.

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. Proceedings of the Royal Society of London B 268:1153-1159.

Lichatowich, J. A. 1999. Salmon without rivers: a history of the Pacific salmon. Island Press, Washington, D.C.

Lofy, P. T., M. L. McLean, and R. W. Carmichael. 1998. Evaluation of reestablishing natural production of spring chinnok in Lookingglass Creek, Oregon, using a non-endemic hatchery stock. Lower Snake River Report. Confederated Tribes of the Umatilla Indian Reservation Project # 63, Contract number 14-48-01-98-J020. Bonneville Power Administration. Portland, OR.

Lofy, P. T. and M. L. McLean. 1995. Lower Snake River compensation plan. CTUIR evaluation studies for 1994. CTUIR Project No. 63. BPA Contract no. 14-48-0001-J036. LaGrande, OR.

McLean, J. 2003. When hatchery steelhead spawn in the wild: a case study from Forks Creek, Washington. The Osprey 46.

McLean, M. L. and P. T. Lofy. 2000. Lower Snake River Compensation Plan. CTUIR evaluation studies for 1998. CTUIR Project No. 63. BPA Contract no. 14-48-0001-J036. LaGrande, OR.

Mullan, J. W., K. R. Williams, G. Rhodus, T. W. Hillman, and J. D. McIntyre. 1992. Production and habitat of salmonids in mid Columbia River tributary streams. U.S. Fisheries and Wildlife Service Monograph I:1-489.

Myers, R. A, S. A. Levin, R, Lande, F. C. James, W. W. Murdoch and R. T. Paine. 2004. Hatcheries and endangered salmon. Policy Forum. Science 303:1980.

NFHRP (National Fish Hatchery Review Panel). 1994. Report of the National Fish Hatchery Review Panel. The Conservation Fund, Arlington, Virginia.

National Research Council. 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington, DC.

Narum, S., C. Beasley, J. Whiteaker, A. Talbot, and M. Powell. 2002. Admixture of ESA-listed and unlisted stocks of spring Chinook salmon (Oncorhynshus tshawytscha; Walbaum) within the Methow River, Washington. International Congress on the Biology of Fish, Congress 2000, Vancouver, Canada.

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.

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

Orr, H. A. 2000. Adaptation and the cost of complexity. Evolution 54(1): 13-20.

Petersson, E., and T. Jarvi. 2000. Both contest and scramble competition affect the growth performance of brown trout, Salmo trutta, parr of wild and sea-ranched masu salmon juveniles. Environmental Biology of Fish 59:211-218.

Peven, C. M. 1992. Spring and summer Chinook spawning ground surveys on the Wenatchee River Basin, 1994. Chelan Public Utility District, Wenatchee, Washington.

Phillips, J. L., J. Ory, and A. J. Talbot. 2000. Anadromous salmonid recovery in the Umatilla River Basin, Oregon: a case study. Pages 1287-1308 in Watershed management for endangered species. Journal of the American Water Resources Association 36(6):1287-1308.

Powell, M. and J. Faler. 2000. Genetic analysis of threatened Chinook salmon (Oncorhynchus tshawytscha) populations from the Snake River. Pages 37-45 in R. D. Armstrong and P. A. Kucera, eds. Salmonid genetics in the Snake River Basin. Environment Fish and Wildlife, Bonneville Power Administration, Portland and Lower Snake River Compensation Plan, U.S. Fish and Wildlife Service, Boise. DOE/BP-30423-4.

PSCFMP (Puget Sound Chinook Fisheries Management Plan). 2003. Northwest Indian Fisheries Commission, East Olympia, Washington.

Quinn, T. P., M. J. Unwin, and M. T. Kinnison. 2000. Evolution of temporal isolation in the wild: genetic divergence in timing of migration and breeding by introduced Chinook salmon populations. Evolution 54:1372-1385.

Reinhardt, U. G., T. Yamamoto, and S. Nakano. 2001. Effects of body size and predators on intracohort competition in wild and domesticated juvenile salmon in a stream. Ecological Research 16: 327-334.

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 Fishery 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.

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.

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.

Sharp, D., Sharr, S., and Peckham, C. 1993. Homing and straying patterns of coded wire tagged pink salmon in Prince William Sound. Pages 335-337 in Exxon Valdez Oil Spill Symposium Abstract Book. Exxon Valdez Oil Spill Trustee Council, Anchorage, Alaska.

Siitonen, L., and Gall, G. A. E. 1989. Response to selection for early spawn date rainbow trout, Salmo gairdneri. Aquaculture 78:153-161.

Smith, D. L., and E. L. Brannon. 2002. An alternative hatchery concept for wild-like coho salmon. Pages 141-146 in E.L. Brannon

and D. MacKinlay, eds. Hatchery reform: the science and the practice. American Fisheries Society Physiology Section International Congress of the Biology of Fish, Congress 2002, Vancouver, Canada.

Steward, C. R., and T. C. Bjornn. 1990. Supplementation of salmon and steelhead stocks with hatchery fish: A synthesis of published literature. Technical Report 90-1, Part 2. U.S. Department of Energy, Bonneville Power Administration, Portland, Oregon.

Stockner, J. G. 2003. Nutrients in salmonid ecosystems; sustaining productivity and biological diversity. American Fisheries Society Symposium 34, Bethesda, Maryland.

Storfer, A. 1998. Gene flow and endangered species translocations: a topic revisited. Biological Conservation 87:173-180.

Swain, D. P., and L. B. Holtby. 1989. Differences in morphology and behaviour between juvenile coho salmon (Oncorhynchus kisutch) rearing in a lake and in its tributary stream. Canadian Journal of Fisheries and Aquatic Sciences 46:1406–1414.

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 47:566-577.

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.

Tang, J., M. D. Bryant, and E. L. Brannon. 1987. Effect of temperature extremes on the mortality and development rates of coho salmon embryos and alevins. Progressive Fish Culturist 49:167-174.

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

Taylor, E. B., and J. D. McPhail. 1985. Variation in body morphology among British Columbia populations of coho salmon, Oncorhynchus kisutch. Canadian Journal of Aquatic Sciences 42:2020-2028.

Tipping, J. M. and C. A. Busack. In press. Selection for compressed run-timing in Cowlitz hatchery coho salmon. North American Journal of Aquaculture: 66: in press.

Thompson, W. F. 1945. Effect of the obstruction at Hell's Gate on the sockeye salmon of the Fraser River, International Pacific Salmon Fisheries Commission, Bulletin 1. New Westminster, British Columbia, Canada.

Unwin, F. M. 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 54:1246-1254.

Unwin, M. J., T. P. Quinn, M. T. Kinnison, and N. C. Boustead. 2000. Divergence in juvenile growth and life history in two recently colonized and partially isolated Chinook salmon populations. Journal of Fish Biology 57:943-960.

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, Bethesda Maryland.

Venditti, D., C. Willard, C. Looney, P. Kline and P. Hassemaer. 2000. Captive rearing program for Salmon River Chinook salmon. Annual report, project number no. 199700100, (BPA report DOE/BP-00004002-2).

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.

Wade, M. J. and C. J. Goodnight. 1998. Perspective: The theories of Fisher and Wright in context of metapopulations: when nature does small experiments. Evolution 52:1537-1553.

Waples, R. S. 1991. Definition of "species" under the Endangered Species Act: application to Pacific salmon. NOAA Technical Memorandum NMFS F/NWC-194, Northwest Fisheries Science Center, Seattle.

_____. 1999. Dispelling some myths about hatcheries. Fisheries 24(2):12-21.

Wedemeyer, G., ed. 2001. Fish hatchery management, second edition. American Fisheries Society, Bethesda, MD.

Wertheimer, A. C., W. W. Smoker, T.L. Joyce, and W.R. Heard. 2001. Hatchery pink salmon in Prince William Sound: enhancement or displacement? Proceedings of the 20th Northeast Pacific pink and chum salmon workshop. National Marine Fisheries Service (NMFS), NOAA Fisheries. Seattle, Washington.

Whitlock, M. C. 2000. Fixation of new alleles and the extinction of small populations: drift load, beneficial alleles, and sexual selection. Evolution 54(6): 1855-1861.

Williams, R. N., J. A. Lichatowich, P. R. Mundy, and M. Powell. 2003. Integrating artificial production with salmonid life history, genetic, and ecosystem diversity: a landscape perspective. Issue paper for Trout Unlimited, West Coast Conservation Office, Portland.

Witty, K. I. 2003. An assessment of juvenile coho outmigration survival (2001) and adult coho salmon migration survival (2002), Yakima Basin. Cramer and Associates, Inc. Sandy, OR, prepared for the Yakima Basin Defense Coalition, Yakima, WA.

Yamamoto, T., and U. G. Reinhardt. 2003. Dominance and predator avoidance in domesticated and wild masu salmon, Oncorhynchus masu. Fisheries Science 69:88-94.

\\svbcvanfp01\Cohen-Comm\DFO\20100719\Personal_Drives\Archive Folders\Inbox\

CAN174751_0020