SUBJECT: Workshop Summary

Enclosed find a review draft of the Summary of the January 25-26 Workshop. I apologize for the delay in sending this material.

The Enhancement Planning Team continues to press for the completed product. May I please have your comments by February 24? I plan to provide the Team with final copy on Monday, February 27.

JEL:cm
Enc.

- Late Trant
- Arotic Charr
- Acona
$-T_{1} U$.
* Bob Raleigh
mavim Hershkopt
- citations for

Nehring, 1982-83 copies??

- genetis lintr 89014 - mived fivnes -drfeatrol expcimes
-n maintan divere


 i:- Timinto finh cum $2-f \begin{array}{ll}\text { anmig core cumb }\end{array}$

1- diversity stock $2-3$ it arsith

- Tabusinta e R. New Brunswick - why?
- कprivate batchery.
-     - tate coop.'
- brown trair
- stocked sprimy | feortings |
| :---: |
| and | now zecomodete
* spzwning of survivim firs $(1987)$ Commitmment fr. Mass. 7ich-wild

Nehriy- Feetal Streembich.

## REVIEW DRAFT

Genetics Concerns in Salmon and Steelhead Conservation and Enhancement

Summary of the Genetics Workshop convened by the Genetics Work Group of the Enhancement Planning Team on January 25 and 26, 1984 in Seattle, Washington.

Compiled by Anne R.D. Kapuscinski
Edited by Anne R. D. Kapuscinski and James E. Lannan

## INTRODUCTION

This report summarizes the findings of a genetics workshop convened by the Genetics Work Group of the Enhancement Planning Team organized under the Salmon and Steelhead Conservation and Enhancement Act (PL 96-561). The purpose of the workshop was to assemble expert opinions about genetic concerns in fisheries enhancement activities. These expert opinions are to be synthesized into guidelines for evaluating salmon and steelhead enhancement projects.

In preparation for the workshop, the Genetics Work Group conducted a series of interviews ("prescoping interviews") with public agencies, private organizations, and individuals interested in enhancing Columbia River salmonid resources. A list of recurring concerns expressed by the parties interviewed was compiled, and the five most frequently expressed concerns were determined. The concerns are:

1. What is the impact of hatchery fish on wild stocks?
2. What is the impact of hatchery stock management?
3. What are the genetic impacts of harvest management?
4. What are the genetic impacts of habitat alteration?
5. Gene conservation.

At a "scoping session" on January 5, 1984, the Genetics Work Group developed a fictitious set of scenarios for each of the five concerns mentioned above. These scenarios were intended to summarize the statements of the various parties interviewed. The Group also developed a series of five questions to be used in evaluating the risks associated with each concern. It was the intent of the Group to have the expert panel at the workshop answer these questions for each of the five concerns. The questions are:
A. What basic genetic principles do you consider germane to evaluating this concern?
B. What evidence or examples would you cite as proof of your position?
C. Over what range of situations would your evaluation apply? Are there specific instances where it would not?
D. How would you assign priorities to alternative management strategies which might be invoked to alleviate this concern?
E. What types and levels of monitoring and evaluation practices would you suggest be applied to enhancement projects to insure that this concern is adequately addressed?

In discussing the several concerns, the panel limited its consideration to biological implication. Although it was recognized that the questions may also have sociological and/or economic implications, these were considered beyond the scope of the workshop by Genetics Work Group.

The Workshop was held January $25-26,1984$ at the Northwest and Alaska Fisheries Center in Seattle, Washington. The expert genetics panel was composed of:

Dr. Robert Behnke, Colorado State University
Dr. Ernie Brannon, University of Washington
Dr. Peter Dawson, Oregon State University
Dr. Joe Felsenstein, University of Washington
Dr. William Hershberger, University of Washington
Dr. John McIntyre, U.S. Fish and Wildilife Service
Dr. Fred Utter, National Marine Fisheries Service

Also attending the workshop were:
Mr. Mark Chilcote, Washington Department of Fisheries, (member, Genetics Work Group)
Mr. Don Fender, Consultant, (member, Genetics Work Group)
Mr. John Marsh, Columbia River Intertribal Fish Commission (Chairman, Genetics Work Group)
Dr. James Lannan and Ms. Anne Kapuscinski, Oregon State University (Rapporteurs)
Mr. Reg Reisenbichler, USFWS, (present at the request of Dr. McIntyre)

CONCERN 1. What is the impact of hatchery fish on wild stocks?

## A. Genetic Principles.

1. The fitness (adaptive value, capacity) of a stock may vary in different habitats. Also, different stocks in a common environment may have different fitnesses.

Fitness is defined as (1) the relative contribution of an individual in a breeding population to subsequent generations (individual fitness), and (2) the frequency distribution of individual fitnesses for a breeding_population (population fitness). Population fitness $(W)$ is described by its mean ( $\bar{W}$ ) and its variance $\left(V_{w}\right)$.

Fitness may be viewed as a quantitative trait. The phenotypic variance consists of components attributable to both genotype and environment. While the genotype limits the range that the values may assume, it is the sequence of environmental events encountered through the life history of an organism which determines the realized value.
2. The diversity of genetic information in a stock depends upon its history of inbreeding, random drift, selection, and gene exchange with other stocks.

The genetic history of a given hatchery stock and a given wild stock determines the genetic risk of gene flow between them, where genetic risk refers to detrimental alteration of one or the other stocks resulting from a change in quantity or kind of the genetic information in the stock. For example, previous gene flow between the wild stock and the hatchery's founder stock would reduce risk while the absence of previous gene flow would increase it.

When the genetic variation (diversity of genetic information) is large in both stocks or when that of the hatchery stock is greater than the wild stock, the risk is less than when the genetic variation in the wild stock is greater or when it is very low in both stocks.
3. Dispersive processes (random genetic drift and inbreeding) cause (1) genetic differentiation between subpopulations, (2) reduction in genotypic variation within each subpopulation, and (3) an increase in the frequency of homozygotes (at the expense of heterozygotes) within each subpopulation. The tendency of systematic processes (migration, mutation, and selection) to bring gene frequencies to stable equilibria holds the dispersive processes in check.

Both dispersive processes and differences in the direction or intensity of natural selection may result in genetic differentiation between stocks. Migration may counteract genetic differentiation between stocks depending on the relative magnitudes of the dispersive and systematic processes acting on the stocks. The amount of genetic differentiation is a function of the absolute numbers of migrant individuals exchanged irrespective of stock size. In the absence of differences in natural selection acting on stocks, small numbers of immigrants can prevent substantial differentiation by random drift.
4. In the absence of gene flow between two stocks, genetic alteration of the stocks may occur if one stock exerts a selection pressure upon the other.

Competition for food or some other behavioral interaction in the natural habitat between fish from different stocks may reduce survival rate in the less capable stocks. This is equivalent to selection against certain genotypes leading to a change in the genetic makeup of the less capable stocks.

## B. Evidence

Rigorous scientific evidence upon which to base generalizations of genetic impacts of hatchery fish on wild stocks is lacking. However, observations from some studies and enhancement activities are consistent with the notion that hatchery and wild stocks may have different fitness values in some cases and a potential for genetic hazards cannot be excluded. The following evidence was cited:

Juvenile survival was greater for matings of wild fish spawning naturally than for hatchery fish spawning naturally in a Kalama River, Washington study (Chilcote, 1983). Progeny of the various crosses could be identified by unique isoenzyme markers. Unfortunately, the AGP allele used to identify the progeny of hatchery fish appeared to be subject to strong directional selection. Thus it was necessary to use a frequency dependent selection model to correct the estimates of fitness, which were based upon juvenile abundance because adult return data is not yet complete.

Survivals in sections of four natural streams and a hatchery pond was compared for Deschutes River steelhead trout juveniles from three matings: hatchery $x$ hatchery (HH), hatchery $x$ wild (HW) and wild $x$ wild (WW) (Reisenbichler and McIntyre, 1977). The numbers of juveniles from experimental matings differed significantly, with WW progeny most abundant, in five out of thirteen samples collected by electrofishing in the stream sections ( $P<0.05$ ); relative abundances of the three juvenile types showed no consistent trend in the other eight samples. The authors suggested that differences in the environmental conditions from stream to stream and sampling error resulting from using relatively small numbers of wild parents were possible causes for the lack of consistency observed in the relative abundances and lengths of fish. The relative abundance of adult returns from the experimental matings were not measured.

Genetic differences among wild and hatchery steelhead trout stocks within the Skagit River drainage were compared to those of wild British Columbia stocks using biochemical genetic profiles from 1979 brood year fish (Campton, unpublished manuscript). Average allele frequencies for the Skagit River and British Columbia wild stocks were virtually identical at all loci whereas the two hatchery stocks (south Tacoma winter-run and Skamania summer-run) differed significantly from the Skagit River and B.C. stocks at the LDH-4 locus. The author concluded that hatchery-reared fish had not contributed significantly to natural production in the Skagit River drainage.

A Trask River hatchery coho stock was introduced into Nehalem Bay, Oregon without prior knowledge of its susceptibility to the indigenous pathogen Ceratomyxa shasta. There is speculation that the subsequent decline of coho abundance in Nehalem Bay resulted from loss of C. shasta resistance in the wild stock due to interbreeding with the hatchery stock. Results from a natural challenge experiment, in which fish held in river water were monitored for $C$. shasta resistance, are consistent with this explanation. Resistance was highest in the wild Olson Creek stock, intermediate in the natural Fishhawk Creek stock of hatchery origin (two generations removed from Trask hatchery stock) and lowest in the Trask hatchery stock (J. Martin, ODFW, Personal Communication).

Some evidence was cited for little genetic risk associated with the presence of hatchery fish in natural habitats. Dr. Brannon alluded to the successful enhancement of Weaver Creek (Fraser River system) sockeye. The local wild stock was used to start the hatchery stock and the hatchery spawning channels provided a quasi-natural habitat. Dr. Behnke mentioned the persistence of wild Idaho redband trout in spite of repeated plantings of hatchery fish, implying that the native gene pool was unaffected by hatchery plants (Wishard et al., in press).

While there is no evidence of inbreeding depression in hatchery stocks of Pacific salmon and steelhead trout, the potential for genetic risk can not be ignored. Ryman (1970) reported lower survival, measured by recapture frequency, of inbred families of Atlantic salmon compared to noninbred families.

No direct evidence was given for the fourth genetic principle listed under concern one. Discussion relevant to application of this principle appears under guidelines for concern three.

## C. Range of Situations

The genetic principles cited above are applicable to all enhancement situations where artificial propagation is considered. In applying these principles, the objectives of the artificial propagation program and the types of fisheries to which the stocks will be exposed must be considered. Additional relevant discussion may be found under concerns two and three.
D. Guidelines and priorities (where applicable) for enhancement projects.

1. Prior to choosing a founder stock for a hatchery, the relative fitnesses and natural straying rates of the stocks under consideration should be determined. Also, determination of the harvest rate and types of fisheries to which the hatchery stock will be exposed is advised (see guidelines under concern three for more details).
2. Locally adapted stocks are the best candidates for starting a hatchery stock: stocks found closest to the hatchery site are of first priority; stocks from the local area are of second priority. A local area is a region within which there is sufficient gene flow to assume panmixia among all incfuded stocks. (Note that run timing differences may prevent gene flow between two stocks, thus perhaps excluding a stock from the local definition). In the absence of selection two stocks will have the properties of a single intermating population if only a few migrants are exchanged per generation (Soule and Wilcox 1980). It is impossible to specify the absolute number of migrants required for local panmixia because it will depend on the types and intensities of selection acting on each stock.
3. A small number of gametes taken from the largest possible number of wild males and females (ideally in equal proportions) should always be used in establishing a hatchery stock. This will reduce the possibility of genetic differentiation between the hatchery stock and local wild stocks. Additional guidelines for reducing such genetic differentiation are given under concern two. The only situation warranting exception to this guideline is when a separate terminal fishery on the hatchery stock is possible. See the guidelines under concern three for further discussion.

## E. Monitoring/evaluation of enhancement projects.

1. Frequent estimates of the reproductive fitness (i.e. adult return rates) of hatchery and local wild stocks is advised to determine a) the natural variation of fitness in time and b) any changes in fitness resulting from gene flow between hatchery and wild stocks.
2. Long term monitoring of migration rates between stocks is recommended to develop an understanding of changes in time and differences among large geographical areas.
3. The productivity of wild stocks should be evaluated using fitness measurements as outlined above. Their replacement with hatchery stocks may be appropriate if their productivity is very low, and if the intent in using the hatchery is to sustain fisheries rather than preservation of the wild stock.
4. Estimation of allelic frequencies with electrophoretic techniques are recommended for two purposes: a) stock identification and b) monitoring possible changes in the allelic frequencies of wild stocks resulting from breeding with a hatchery stock.

CONCERN 2. What is the impact of hatchery stock management?
A. Genetic Principles.

1. Inbreeding reduces the amount of genetic variation in a population.

The rate of inbreeding per generation is inversely proportional to the effective population size of the breeding individuals. The most general equation for this relationship is

$$
\Delta F=\frac{1}{2 \mathrm{Ne}}
$$

where $F$ is the inbreeding coefficient, $\Delta F$ is the change in $F$ from one generation to the next, and Ne is the effective population size.

Ne is usually smaller than $N$, the actual number of spawners in a stock. The calculation of Ne from $N$ depends on the departure of breeding structure of the stock from the breeding structure of an ideal population. In an ideal population
a. mating is at random
b. the sex ratio is $1: 1$
c. there is no immigration
d. the parents are of one age (i.e. there are no age classes)
e. the number of progeny per parent contributed to the next generation is constant.
2. Inbreeding depression, the reduction of the mean phenotypic value of quantitative traits, is a consequence of repeated inbreeding.
Inbreeding depression is thought to be caused by reduction in genetic variation, and it can accumulate over many generations in small populations. Inbreeding depression may be greatest for traits which which are components of fitness depending on the species (Soule and Wilcox, 1980). Because traits related to fitness are most susceptible to inbreeding depression, inbreeding is particularly undesirable for fish stocks existing in an unpredictable and dynamic natural habitat.

## 3. The direction of artificial selection may oppose that of natural selection.

A reduction of average fitness may result either a) by artificial selection against a trait of high adaptive value in the natural habitat or 2) by artificial selection against a trait genetically linked to another trait of high adaptive value in the natural habitat. The latter possibility occurs when there is a negative genetic correlation between a given trait and fitness; an increase in the mean phenotypic value of the trait decreases average fitness. Positive or no genetic correlations between fitness and quantitative traits are possible also.

The hatchery environment and specific hatchery practices (e.g. mating procedures) could select unintentionally against fitness in the natural habitat. Intentional artificial selection against a trait without prior knowledge of its correlation with fitness increases the risk of reducing the adaptability of a hatchery stock to the natural habitat. For example, if the number of age classes
in the spawning stock is positively correlated with fitness, then the culling of precocious males (jacks) from a hatchery broodstock could reduce the stock's fitness over the long term.
4. Adaptation, the acquisition or modification of traits which tends to improve population fitness in a given habitat, is a consequence of selection exerted by the habitat.

Although the phenotypic changes (especially changes over the long term) resulting from adaptation cannot be predicted before the fact, it is reasonable to expect a population to exhibit greatest average fitness in a habitat encountered by its recent ancestors.

A stock is best adapted to the natural habitat encountered by its parents barring the occurrence of a catastrophic event between generations (e.g. volcanic eruption).
5. The principles cited in concern one are also applicable to this concern.

## B. Evidence

There is no documented reduction in the average heterozygosity (measured over 30-40 loci detected by electrophoresis) of a salmon or steelhead trout hatchery stock when compared to the average calculated for the whole species. (Dr. Utter stressed the need to make within species comparisons because the average heterozygosity of each species is different.) The implication is that hatchery stocks have not experienced inadvertent inbreeding nor inbreeding depression. However, inbreeding depression has been shown in other artificially propagated fish. For example, there was a 6.9 to $21.2 \%$ reduction in the total percent recovery (reflecting the reduction in survival) of planted rainbow trout inbred at $F=0.25$ to 0.5 compared to outbred controls (Kincaid 1983). Thus inbreeding depression in hatchery stocks of salmon and steelhead trout is not impossible, particularly if the broodstock size is small for many consecutive breeding seasons.

There is a little more evidence for artificial selection against natural adaptation. Earlier run timing (which may alter the optimum timing for spawning and fry emergence in the wild) has been observed in many salmon stocks as a consequence of using only the early returning adults for hatchery broodstock. Contemporary hatchery practice attempts to avoid this nonadaptive selection by randomizing matings during hatchery operations.

Dr. Utter mentioned the lack of data to support the widely accepted belief that hatchery fish are inherently less disease resistant than wild fish. He conjectured that the higher rearing densities experienced by hatchery fish compared to wild fish may actually select for disease resistance. Of course, these comments do not preclude the susceptibility of an imported hatchery stock to a pathogen which was not present in its original habitat. Dr. Dawson argued that the potential for genetic disasters in plant monoculture (where plots of a crop are highly inbred) is not analagous to the potential in salmonid stocks owing to the lack of evidence for inbreeding or greatly reduced genetic variation in hatchery stocks.

Ricker (1972) documented indirect evidence which indicates there is a high degree of local adaptation in salmon stocks. Dr. Brannon added that detailed examinations have shown very specific local adaptations (e.g. fry migration patterns) in Fraser River sockeye stocks (Brannon 1967, Raleigh 1967).

Numerous stock transplantation studies were cited to support the concept of specific local adaptation. In a review of the literature, Withler (1982) stated that transplants within the Pacific salmon's range have been unsuccessful in producing new anadromous stocks, except where natural colonization has been prevented by an obvious physical barrier. When a chinook stock from the Elwha River (which empties into the Straits of Juan de Fuca) was transferred 150 km east to the University of Washington hatchery, it showed the lowest percent return to the hatchery, followed by the hybrid (Elwah x University) stock (Brannon and Hershberger, in press). All possible reciprocal matings were made among a local (Big Creek hatchery, Or.) coho stock and two transplanted coho stocks from the Soleduck River, Wa. and the Smith River, Or. (ODFW 1983). The percent returns of adults from pure transplanted and hybrid stocks were much lower than that of the pure Big Creek stock. The same trend was obtained for the relative resistance of progeny from each cross to $C$. shasta challenges under laboratory conditions (Hemmingsen and Holt, 1984).

Bams (1976) reported a tenfold increase in the percent return of a hybrid (local males $\times$ transplanted females) pink salmon stock compared to the pure transplanted stock. Because there was no control (pure local stock), it is impossible to distinguish between two very different explanations for the results: (a) heterosis for homing ability or (b) better homing ability due to the presence of local paternal genes. If the former explanation was correct, the percent return of the pure local stock would have been lower than that of the hybrid.

Hybrid vigor for return rate was observed in a $3 \times 3$ factorial comparison of coho salmon hatchery stocks planted in the Green River, Washington. According to Dr. Hershberger, the contribution to the fishery of one hybrid (Green River $x$ Skykomish) stock was greater than that of the pure Green River stock. The percent return rate was comparable to that of the pure Green River stock. The success of this and some other Pacific salmon transplants suggests that a high degree of local adaptation does not always prevent a stock from adapting to a new habitat. The successful establishments of new and persistent stocks outside the native range of Pacific salmon include (1) chinook salmon transplanted from California to New Zealand, (2) pink salmon moved from Sakhalin to the Kola Peninsula and (3) coho, chinook and pink salmon transplanted to the Great Lakes (Withler 1982).

## C. Range of Situations

Two questions must be addressed in applying genetic principles to the alleviation of Concern two;
a. What is the purpose of the hatchery production?
b. Will the hatchery stock be harvested separately or in a mixed stock fishery?

When the goal of a hatchery is fishery enhancement or wild stock conservation, inbreeding should be avoided and every effort should be made to maintain high fitness of the hatchery stock in the natural habitat. On the other hand, intentional inbreeding may be an appropriate research tool for a hatchery stock designated for experimentation. The use of inbred lines in selective breeding and crossbreeding experiments could provide some of the data needed to improve our ability to alleviate both Concern 1 and 2 by finding a happy medium between adaptation to the hatchery and natural habitat. Some examples of information obtainable from experimental designs routinely used in livestock and plant breeding studies (Falconer 1981, Becker 1975) are 1) the relative importance of genetic and environmental control
of stock fitness by partitioning the phenotypic variance into genetic and environmental components; 2) genetic correlations between fitness (or components of fitness) and other quantitative traits; 3) the prevalence of hybrid vigor for fitness and other traits in different stocks and species; 4) the relative susceptibility (measured by comparing rates of inbreeding) of different stocks and species to inbreeding depression.

The issues raised in discussion of concern two (and all other concerns) do not apply to the farming (as opposed to ranching) of salmonids. When fish are not released into the natural habitat, intensive selective breeding and the modification of natural fitness may be appropriate.
D. Guidelines and priorities (where applicable) for enhancement projects

1. All the guidelines listed under concern one also apply to concern two.
2. In the case of limited availability of local stock for starting a hatchery stock, the first priority is to allow more breeding seasons for reaching the incubation capacity of the hatchery, making sure that no less than 50 spawners of each sex are mated every season. The second priority is to supplement the local broodstock with a stock transplanted from the closest possible geographical area and to cross a transplanted spawner with a local spawner whenever possible.
3. Several breeding guidelines should be practiced together in an established enhancement hatchery. Some crosses between wild and hatchery fish should be included in hatchery matings every season unless the fisheries on the wild and hatchery stocks are separate (see guidelines for concern three). Random mating and representative use of fish from all parts of a run will reduce the chances of inadvertent domestication selection. Intentional selection on a given trait should be avoided. If avoidance is impossible, selection must be conducted in accordance with standard statistical designs (Becker 1975) and careful records must be kept for all breeding activities to permit the thorough evaluation. Other appropriate practices are outlined by Hynes et al. (1981) and by Hershberger and Iwamoto (1983).

## E. Monitoring and evaluation of enhancement projects

1. Transplanted stocks should be marked to monitor their fitness and to exercise control over whether or not returning adults are crossed with adults from the local stock.
2. Careful and continual record keeping is advised for all hatcheries, including data on breeding schemes, means and variances of production traits (especially of fitness related traits), and average heterozygosities.
3. Contractors should be required to explain how the guidelines for concern one and two will be met before undertaking an enhancement project.

CONCERN 3. What are the genetic impacts of harvest management?

## A. Genetic Principles

1. For any quantitative trait, selection can change the distribution of phenotypes in the population by removing certain genotypes from the reproductive population.

Because the phenotypic variances of all life history traits have a genetic component, selection exerted by a fishery can modify the life history of a stock. However, it is difficult to predict the responses to selection (i.e. the phenotypic changes) in an exploited stock due to the following complications: a) harvest methods may impose different types of selection (e.g. mass selection, disruptive selection, stabilizing selection) on different traits and at different times; b) natural selection may oppose or reinforce fishery selection but its form, intensity and changes in time are also unpredictable; c) genetic correlations between traits and the proportional contributions of environmental and genotypic components to phenotypic variation can change in time and will influence the expression of the entire phenotype.

## 2. The direction of artificial selection may oppose that of natural selection.

Selection imposed by fishing gear (e.g. removal of the larger fish) and by the timing of harvest could select unintentionally against fitness in the natural habitat.
3. A substantial decrease in population size heightens the dispersive processes (random genetic drift and inbreeding) which cause (1) genetic differentiation between subpopulations, (2) reduction in genotypic variation within each subpopulation, and (3) an increase in the frequency of homozygotes (at the expense of heterozygotes) within each subpopulation.

Many livestock and laboratory breeding studies (Falconer 1981) have demonstrated the reduction of average value in traits related to fitness when the genetic diversity of a population is greatly reduced. Thus, a stock's persistence over the long term may be jeopardized (via a significant decline in the variance and mean of its frequency distribution for fitness) if the size of the reproductive stock is depressed for many consecutive generations. Stated another way, the maintenance of genetic variation within a stock permits the maintenance of variation in fitness which, in turn, increases the probability of a stock's long term adaptation to a dynamic and unpredictable environment.
4. Different stocks in a common environment may have different fitnesses.

When the less productive (i.e. less fit) stocks in a mixed stock fishery experience a high exploitation rate, their abundance may be severly depressed due to overfishing of the reproductive individuals. According to genetic principle (3) discussed above, the concomitant loss of genetic variation and variance of fitness probably will accelerate this decline in abundance and may drive the stock to extinction.
5. Genetic differentiation exists between stocks due to their different histories of inbreeding, drift, migration, and selection.

The extinction of a stock is tantamount to a loss of genetic diversity within the species. The perpetuation of a species is contingent upon the maintenance of sufficient genetic diversity to allow adaptation to environmental changes over the long term.

## B. Evidence

There is no direct proof of life history trait modification on stock fitness reduction due to fishing selectivity owing to a lack of the necessary data (e.g. partitioning of phenotypic variances, genetic correlations). The complications listed under the first genetic principle for this concern could confound attempts to obtain this kind of evidence. Ricker (1981) invoked the response to fishing selectivity as part of the explanation for observed long term changes in the average size and average age of Pacific salmon. For example, a decrease in mean size could reflect a slow change in the genetic makeup of a stock because of the tendencies to take more of the older fish and more of the larger fish of any age in the catch.

The historical record for the Columbia River fishery on spring, summer and fall chinook provides indirect evidence for the third and fourth genetic principles relevant to this concern. While the catch in early years consisted almost entirely of spring and summer chinook, the catch of summer chinook declined drastically leading to a bimodal distribution (spring and fall peaks) of the run in later years. Van Hyning (1968) concluded that overfishing was largely responsible for the disappearance of the summer stock. Reproductive overfishing probably explains the decline of the less productive stocks in a mixed stock fishery in the case of: (1) Columbia Basin upriver bright chinook stocks which are harvested with the more productive lower river Tule stock; (2) unenhanced wild sockeye stocks which are caught with the highly productive, channel-raised stock of Babine Lake (Jackson, 1984); and (3) less productive pink salmon stocks of S.E. Alaska which have been exploited at very high rates (e.g. $72 \%$ in 1982) (Alexandersdottir and Mathisen, 1982).

Although there is no direct documentation for reproductive overfishing leading to the extinction of lesser productive stocks in a mixture of stocks, Ricker (1973) demonstrated the potential for this process by simulation. Furthermore, numerous studies have shown the occurrence of mixtures of stocks of unequal productivity in a fishery. Hemmingsen et al. (1979) compared the 1975 broodyear recoveries (in the fishery and hatchery) of Big Creek and two hybrid hatchery coho stocks (reciprocal crosses of Big Creek $\times$ Umpqua and Big Creek $\times$ Soleduck). The percent recoveries of three year and two year fish was greater for the Big Creek stock ( $1.70 \%$ ) than for the hybrid stocks $(0.55 \%-1.02 \%$ ). The trend was similar in the expanded statistics (accounting for fishery sampling biases) on percent recoveries of three year fish: $5.39 \%$ for the Big Creek stock and $1.57 \%-2.94 \%$ for the hybrid stocks. Using a less specific separation of Oregon Coast coho into wild and hatchery stocks (based on scale characteristics), Scarnecchia and Wagner (1980) concluded that hatchery fish contributed to $75 \%$ of the catch in the Oregon ocean sport fishery.

## C. Range of situations

Application of the relevant genetic principles to the third concern will vary depending on the feasibility of breaking up a mixed stock fishery into separate harvests. It is generally assumed that the optimum exploitation rate for wild stocks is lower than that for hatchery stocks, owing to the proportionally larger
releases from hatcheries. Thus, wild stocks are highly susceptible to overexploitation in mixed stock fishery. This problem provides the rationale for avoiding mixed stock harvests.
D. Guidelines and priorities (where applicable) for enhancement projects

1. Whenever it is possible, separate fishing of stocks is recommended via establishment of subterminal or terminal fisheries. Then, genetic separation of wild and hatchery stocks may be appropriate. For example, run timing differences between wild and hatchery stocks can be maintained in the absence of gene flow. Consideration should be given to the potential for causing genetic alteration of $t^{2}$ wild stocks through competition selection with hatchery stocks (refer to the fourth genetic principle under concern one) before implementing this guideline.
2. When a mixed stock fishery is inevitable, the first priority is to reduce the exploitation rates to accommodate the less productive (i.e. wild) stocks. The second priority is to reduce the risk of overexploiting wild stocks by implementing a terminal fishery. Maintenance of genetic similarity between hatchery and wild stocks (to make their productivities as similar as possible) is advised for either priority. Specific guidelines for keeping genetic similarity are given under concerns one and two.
E. Monitoring and evaluation of enhancement projects
3. Better documentation of the genetic effects of harvest methods via carefully designed experiments is advised. Changes in age class structure, size at a given age, fecundity, reproductive success, and genetic diversity should be continuously monitored. Estimation of heritabilities and partitioning of phenotypic variances for traits related to yield (e.g. growth rate) and fitness (e.g. reproductive success) are recommended also. However, possible temporal changes in these data should not be ignored.
4. Recommendations for mixed stock fisheries include:
a. monitoring outmigrations and escapements of different stocks;
b. monitoring the oceanic distributions and run timings of different stocks
c. establishment of programs for long term monitoring of these factors.
5. The Regional Council must include consideration of genetic problems when allocating fish resources, especially in the case of mixed stock harvests.
6. Further study (or at least monitoring of research results) on the behavior of sterile fish in the natural habitat is warranted. Releases of sterile hatchery fish could provide a means of separating harvests on wild and hatchery stocks.

CONCERN 4. What are the genetic impacts of habitat alteration?

## A. Genetic principles

1. The perpetuation of a population is contingent upon the maintenance of sufficient genetic diversity to allow adaptation to environmental changes over the long term.

The risk of extinction for a stock subjected to fishing and natural mortality in a variable environment is reduced when a broad level of genetic variation is maintained over consecutive generations. A broad level of variation is most important in the face of rapid changes in the habitat. Substantial reduction of genetic variation can result when the size of the reproductive stock is depressed for many consecutive generations (refer to the third principle given under concern three).
2. The adaptive capacity of a species has boundaries; the range of phenotypic expression is limited by the genetic composition of the species.

No species can adapt to an infinite variety of changes in its natural habitat. This concept also applies to any subset of a species (e.g. stock, group of stocks).
3. The direction of artificial selection may oppose that of natural selection.

In the context of this Concern, artificial selection constitutes any alteration of the natural habitat caused by human activities (e.g. dam construction, logging). A stock's average fitness could decline as explained in principle three under concern two.
4. Genetic differentiation exists between stocks due to their different histories of inbreeding, random drift, migration and selection.

The extinction of a stock is tantamount to a loss of genetic diversity within the species. The perpetuation of the species is contingent upon the maintenance of sufficient genetic diversity to allow adaptation to environmental changes over the long term.

## B. Evidence

There is no documentation of a decline of genetic variation within a fish stock (or species) due to habitat alteration because the appropriate data has not been collected. Baseline estimates of genetic variation present before habitat alteration are necessary to detect a significant decline.

A few examinations of the ability of Pacific salmon to adapt to habitat alterations were mentioned by Dr. Brannon. Laboratory experiments showed large changes in emergence timing of coho fry in response to $1^{\circ} \mathrm{C}$ incremental changes of water temperature (Dong 1981). Chinook salmon showed a similar response to increased water temperatures in the natural habitat resulting from the installation of the Ross and Baker dams on the Skagit River (Graybill et al. 1979). Although adults did not change their spawning time, fry emergence was advanced by one month. More data on the subsequent generations would be required to ascertain the response of stock fitness to the selection pressure imposed by this temperature change.

The record of successful transplantations of Pacific salmon outside their native range (see discussion of evidence for concern two) demonstrates the adaptability of salmon to habitat alterations falling within their physiological boundaries. Chinook salmon transplanted from Little White Salmon River (a tributary of the Columbia) to the Deschutes River in Southern Puget Sound showed adaptation to their new habitat in only two generations; the ratio of local stock to Little White Salmon stock returns was $11: 1$ in the first generation and $4: 1$ in the second generation (Ricker 1972).

## C. Range of situations

The time unit for measuring the rate of adaptation to habitat alterations must be number of generations. Thus the adaptive response of a species with a long generation time (e.g. chinook salmon) will be slower (in terms of calendar time) than that of a species with a shorter generation time (e.g. pink salmon).

A priori, it is impossible to measure the direction and intensity of selection exerted on a stock by a habitat alteration or to predict quantitatively the adaptive response of the stock. Therefore, little can be said about the genetic implications of habitat alteration before the fact.
D. Guidelines and priorities (where applicable) for enhancement project

1. Contractors should demonstrate the presence of adequate genetic diversity for adaptation in all impacted stocks prior to undertaking a project involving habitat alterations.
2. Also, contractors must show that the altered habitat will accommodate the range of possible life histories of the impacted salmonid species. It must be emphasized that Pacific salmon cannot adapt rapidly to a broad variety of conditions.
3. Guidelines for stock selection given under concerns one and two should be followed when using transplants to replace stocks lost due to previous detrimental habitat alterations. Of course, any possible habitat restoration is advised prior to restocking expenditures.
E. Monitoring and evaluation of enhancement projects
4. Data on salmonid life history patterns and variation should be collected before and after the natural habitat is changed.
5. Recomendations given for monitoring hatchery stocks under concerns one and two also apply to the monitoring of restocking programs.

## CONCERN 5. Gene Conservation

## A. Genetic Principles

1. The perpetuation of a population is contingent upon the maintenance of sufficient genetic diversity to allow adaptation to environmental changes over the long term.
2. Genetic differentiation exists between stocks due to their different histories of inbreeding, drift, migration and selection.

The extinction of a stock is tantamount to a loss of genetic diversity within the species. Selection of each hatchery stock from a different gene pool is one way of maintaining genetic variation in the species. Hatchery or natural stocks can be designated as gene preserves, i.e. sources of genetic diversity for future enhancement projects.
B. Evidence

The panelists did not present any information on Pacific salmon and steelhead trout applicable to this concern because there are no gene banks for these species at present. Also, historical records on the genetic composition of natural stocks are unavailable, making it difficult to document any recent loss of genes or genetic variability. Thus, the relative success of using hatchery or natural stocks to preserve genetic variability is not known.

However, Dr. Utter supplied evidence for genetic changes and loss of genetic variability at isozyme loci in hatchery stocks of trout compared to their wild derivatives (Allendorf and Phelps 1980, Ryman and Stahl 1981). Authors of both studies suggested that their findings could be explained by the use of a small number of founders and the effects of genetic drift in the hatchery stock. No decline in production characters associated with isozyme changes in the hatchery stocks was reported, although this has been observed when genetic variability is reduced via inbreeding experiments (see evidence for concern two). These findings suggest that hatchery stocks may be inappropriate gene banks unless the guidelines under concerns one and two are followed for maintaining genetic similarity between wild and hatchery stocks.

## C. Range of situations

Dr. Utter commented (after the Jan. 25-26 meeting) on the need to decide between preserving individual genes or naturally occurring gene complexes. However, this question was not discussed directly by the panelists.

One opinion is that a gene bank should maintain alleles, not specific allele frequencies, because the latter can be quickly changed by selection or dispersive processes (Allendorf and Phelps 1980). This can be achieved by implementation of one plan proposed by Krueger et al. (1981): make separate collections of fish from each of several genetically different stocks; perform all possible crosses among the stocks in a hatchery; then stock the progeny in the natural habitat.

Another opinion is that natural patterns of genetic variation should be maintained whenever gene flow may occur between hatchery and wild stocks. In this case, appropriate gene banks would be stocks existing in natural refuges; enhancement would be done with stocks from waters environmentally similar to those being rehabitated (Krueger et al. 1981).
D. Guidelines and priorities (where applicable) for enhancement projects

1. The following guidelines apply to the selection of stocks for gene conservation:
a. all large stocks should be conserved with first priority given to those coming from all major geographical areas inhabited by the species and second priority given to those coming from less important geographical areas;
b. all small stocks should be conserved with first priority given to endangered and to enhanced stocks.

## E. Monitoring and evaluation of enhancement projects

The genetic structure of all stocks designated as gene preserves should be monitored continuously. Similar monitoring is advised for wild stocks when there is a potential for gene flow between them and a gene bank. Isozyme variability, reproductive structure (e.g. number of spawners per generation, straying rates), and other biological and life history data (see Utter 1981) can provide insight into the genetic composition of a given stock. Maintenance of genetic variation within a stock is the most important criterion for evaluating the success of any gene conservation project.

## ADDITIONAL CONCERNS

The panelists briefly mentioned concerns (listed below) about the incorporation of genetic matters into the more comprehensive process of salmon and steelhead conservation and enhancement.

1. Genetic guidelines will be overlooked at other levels of decision making.
2. Enhancement projects will be implemented before adequate genetic information is available to evaluate and monitor them; on the other hand, excessive delay in making decisions due to a need for more research could harm enhancement and conservation opportunities in the future.
3. Geneticists without a background in fisheries science may not be able to address adequately the alleviation of genetic problems in enhancement and conservation projects.
4. The association between economic and genetic issues cannot be ignored in the decision making process.
5. To avoid misunderstanding and inappropriate application guidelines, the final draft of guidelines should be as clear and simple as possible.

## LITERATURE CITED

Alexandersdottir, M. and O. A. Mathisen. 1982. Change in S.E. Alaska pink salmon (Oncorhynchus gorbuscha) populations, 1914-1960. FRI-UW-8212 55 pp.
Allendorf, F. W. and S. R. Phelps. 1980. Loss of genetic variation in a hatchery stock of cutthroat trout. Trans. Am. Fish. Soc. 109:537-543.

Bams, R. A. 1976. Survival and propensity for homing as affected by presence or absence of locally adapted paternal genes in two transplanted populations of pink salmon (Oncorhynchus gorbuscha). J. Fish. Res. Board Can. 33:27162725.

Becker, W. A. 1975. Manual of Quantitative Genetics. Third Edition. Washington State University Press, Pullman.

Brannon, E. L. 1967. Genetic control of migrating behavior of newly emerged salmon fry. Int. Pac. Salmon Fish. Comm. Can., Prog. Rep. No. 16. 31 pp.
Campton, D. F. Genetic structure of steelhead trout populations in the Skagit river drainage: electrophoretic comparisons between hatchery and wild populations. Wa. State Dept. of Game, unpublished manuscript.

Chilcote, M. 1983. Page $80-87$ in: The reproductive fitness of hatchery and wild steelhead. Washington Environmental Foundation. Seattle, Wn.

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

Falconer, Ne 1981. Introduction to Quantitative Genetics. Longman Group,
Ltd. New York.
Graybill, J. P., R. L. Burgner, J. C. Gislason, P. E. Huffman, R. H. Wyman, R. G. Gibbons, K. W. Kurko, J. J. Stoker, T. W. Foman, A. P. Stayman and B. M. Eggers. 1979. Assessment of the reservoir - related effects of the Skagit project on downstream fishery resources of the Skagit River, Washington. Final report for City of Seattle. Department of Lighting, Seattle, Washington. FRI-UN7905.

Hemmingsen, A. R., J. W. Westgate and J. F. Conrad. 1979. Development of techniques for salmon and steelhead trout hatcheries. Oregon Department of Fish and Wildife Annual Progress Report. Fish Research Project AFC-77-3.
Hemmingsen, A. R. and R. H. Holt. 1984. Susceptibility of three stocks of coho salmon and their hybrids to Ceratomyxa shasta. Unpublished manuscript. 13 pp .
Hershberger, W. K. and R. N. Iwamoto. 1983. Genetics manual and guidelines for the Pacific salmon hatcheries of Washington. University of Washington. 83 pp .

Hynes, J. D., E. H. Brown, Jr., J. H. Helle, N. Ryman and D. A. Webster. 1981. Guidelines for the culture of fish stocks for resource management. Can. J.
Fish. Aquat. Sci. $38: 1867-1876$.

Jackson, K. 1984. Toward a fish habitat decision on the Kemano completion project. A discussion paper. D.F.O. Habitat Management Division.

Kincaid, H. L. 1983. Inbreeding in fish populatons used for aquaculture. Aquaculture 33:215-227.

Krueger, C. C., A. J. Gharett, T. R. Dehring, and F. W. Allendorf. 1981. Genetic aspects of fisheries rehabilitation programs. Can. J. Fish. Aquat. Sci. 38:1877-1881.

Oregon Department of Fish and Wildlife. 1983. Hatchery practices. Annual Progress Report. Fish Research Project.

Raleigh, R. F. 1967. Genetic control in lakeward migrations of sockeye salmon (Oncorhynchus nerka) fry. J. Fish. Res. Board Can. 24:2613-2622.

Reisenbichler, R. R. and J. D. McIntyre. 1977. Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout, Salmo gairdneri. J. Fish. Res. Board Can. 34:123-128.

Ricker, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations. In The Stock Concept in Pacific Salmon. R. C. Simon and P. A. Larkin, eds. H. R. Macmillan Lectures in Fisheries. Vancouver: University of British Columbia.

Ricker, W. E. 1973. Two mechanisms that make it impossible to maintain peak period yields from stocks of Pacific salmon and other fishes. J. Fish. Res. Bd. Can. 30:1275-1286.

Ricker, W. E. 1981. Changes in the average size and average age of Pacific salmon. Can. J. Fish. Aquat. Sci. 38:1636-1656.

Ryman, N. 1970. A genetic analysis of recapture frequencies of released young of salmon (Salmo salar). Hereditas 65:159-160.

Scarnecchia, D. L. and H. H. Wagner. 1980. Contribution of wild and hatcheryreared coho salmon Oncorhynchus kisutch, to the Oregon ocean sport fishery. Fish. Bull. 77:617-623.

Soule, M. E. and B. A. Wilcox. 1980. Conservation Biology: An EvolutionaryEcological Perspective. Sinauer Associates Inc. Sunderland, Mass. 395 pp.

Utter, F. M. 1981. Biological criteria for definition of species and distinct intraspecific populations of anadromous salmonids under the U.S. Endangered Species Act. of 1973. Can. J. Fish. Aquat. Sci. 38:1626-1635.

Van Hyning, J. M. 1968. Factors affecting the abundance of fall chinook salmon in the Columbia River. Ph.D. thesis. Department of Fisheries and Wildilife. Oregon State University. 424 pp.

Wishard, L. N., J. E. Seeb, F. M. Utter and D. Stefan. In press. A genetic investigation of suspected redband trout populations. Copeia.

Withler, F. C. 1982. Transplanting Pacific salmon. Can. Tech. Rep. Fish. Aquat. Sci. No. 1079. 27 pp.

