# SALMONID GENETICS: STATUS AND ROLE IN AQUACULTURE

## A WORKSHOP REPORT

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# FOREWORD

This report summarizes proceedings of the fourth in a series of workshops on salmonid aquaculture sponsored by the Washington Sea Grant Marine Advisory Program and the College of Fisheries at the University of Washington. The first workshop, held September 21, 1973, encompassed all aspects of rearing salmon, including salt-water pen-rearing and ocean ranching, with related disease and economics questions. The second workshop was held April 17, 1974, and dealt with the subject of salmonid diseases. On December 19, 1974, a third workshop on ocean ranching in Washington was held. Copies of all four workshop reports are available from Sea Grant Communications, Division of Marine Resources, University of Washington, Seattle, WA 98105, for a handling charge of 50¢ each.

# ACKNOWLEDGMENTS

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Before we begin the major part of this workshop, I would like to comment briefly on genetics as it could be utilized in aquaculture. You may observe in the preceding statement the implication that the full potential of this science is not being used. This has been the case historically, and I think is still the case. It is an unfortunate set of circumstances because fish culture has much to gain from the practice of systematic genetic principles.

Why has this been the case, particularly since similar instances in plant and animal husbandry have shown such phenomenal gains in production in the past 100 years? Any number of reasons could be cited to answer this question, but there are several major areas that are most responsible. Two principal deterring factors were mentioned by *Dr. J.E. Wright* in a paper in The Pennsylvania Angler in 1951: (1) inadequately trained personnel at a large percentage of state and federal hatcheries, and (2) the lack of proper facilities. In addition to these I would add two more that play a part: (3) the ability adequately to rear and maintain fish, and (4) the existence of somewhat of a mystique and/or misunderstanding of the utilization of genetic principles. Let's take a more critical look at each of these and attempt to determine the extent to which they may decrease the interaction between fish culture and genetics.

The problem of inadequately trained personnel is still a very real one, but not insurmountable, nor does it necessarily mean that a genetically oriented program should not be considered. Actually good breeding experiments do not necessarily require intensive education and training in genetics on the part of those who conduct the experiments. *H.H. Smith* in a paper in 1924 credited the Japanese with developing gold-colored goldfish from the natural-colored, wild populations as early as 1500 A.D. This was well before the modern science of genetics was even thought about. In addition, a large part of the initial animal husbandry work was carried out by observant farmers who recognized the benefits of selective breeding. Both of these examples are relatively specifically goal-oriented and long-term, but show the results of the practice of one basic premise of genetic manipulation, the resemblance of relatives. We now have, perhaps, a more complex set of standards and a wider knowledge base in the science of genetics that needs some interpretation. In recognition of this, training in fish culture at a lot of schools now requires a basic genetics background for future fisheries biologists, which will in time rectify the lack of exposure to this field.

Probably the most difficult problem area to change in a reasonable time is the second one mentioned, that of the lack of proper facilities. Because of the demands of the public, the function of most hatcheries has been directed toward the production of increasingly larger numbers of fish at the least expense. As a consequence, a lot of emphasis has had to be placed on the production aspect of salmonid culture. Hatching and rearing facilities were thus designed for this purpose. This leaves

little opportunity to carry out a breeding program, which requires numerous small lots of fish under uniform conditions. Even with this problem there have been efforts to improve brood stocks where feasible, and some significant gains have been made. In addition, in recognition of the importance of genetics to fish culture, some rectification of this problem has been made with the development of stations directed specifically at genetics, such as the Sport Fisheries and Wildlife Laboratory in Beulah, Wyoming.

Closely allied to the facilities problem is the next area, that of our capability adequately to rear and maintain fish. It has just been within the past decade that we have had available adequate diets and disease-treatment methods. I recognize that these are not yet perfected, but we can now maintain brood fish and assure the survival necessary for genetic analysis. For this type of work healthy, live animals are needed to make crosses and allow the maximum expression of their genetic potential. On the other hand, while the freshwater rearing is at least ample, the addition of saltwater rearing opens up a whole new set of problems in nutrition and disease-treatment, particularly with development of brood stock. I think, however, that with our present knowledge and technology this will not be a long-term problem.

The final factor cited in deterring genetic work as part of fish culture is one of unfamiliarity with the science of genetics. Genetics is very basically the study of the inheritance and transmission of variable biological characteristics. Research has shown that these traits are determined by discrete units called genes and thus are predictable in their behavior. In addition, it is safe to say that the genes provide their carriers with the necessary information for every aspect of their structure, function, and other biological attributes. We then have a science that is predictable by basic probability and affects the entire biology of an organism. The methods of "sorting out" the details can be a problem, but the fundamentals are rather simple. The major way of eliminating the mystique and/or misunderstanding about genetics is by education and information dissemination. This is what we are here for today, and I think we should be successful with the interest demonstrated and the expertise of the moderators and the panel members present.

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## THE STOCK CONCEPT AND GENETIC CONSIDERATIONS
*William K. Hershberger**

The idea of different, naturally occurring stocks of fish is not a new
one, particularly with salmonids. In fact, the original work on races
was published by Heincke two years before the "rediscovery" of Mendel's
findings in 1900. Every biologist who has dealt with these species has
come face to face with this concept many times. If this is such an
accepted and pervasive idea, why open it up for discussion at this
workshop?

There are a number of reasons for raising the subject here. First of
all, as the title implies, there are some important genetic implications
inherent in this concept that have ramifications in management of the
fisheries resource and in developing strains for commercial production.
Additionally, in large part we are still dealing with natural or quasi-
natural fish populations rather than systematic breeding programs. As
a consequence, we must be aware and know what the stock concept implies
if these fish are to be successfully utilized for production. Finally,
there appears to be some question as to what a stock is, how it is de-
veloped, and the crucial genetic problems in manipulation of stocks
of fish.

What is a "stock" of fish, particularly with reference to salmonids? In
looking for a satisfactory answer to the question, the first thing we
notice is that it depends on who is defining this term. For instance,
based on a fishery, a stock can be defined as a group that recurs at the
same place each year. Since fisheries exploit spawning, feeding, or
migrating animals, they are found in regular positions in the migratory
circuit of the stock at the same season each year. Another definition,
used more commonly in reference to salmonids, is one species that in-
habits a particular stream (Larkin, 1972). This is more apropos to the
salmonid group since they have a marked tendency to return to the natal
stream and form a rather clear-cut breeding population. However, as is
also true of the first definition, this concept of stock contains
elements of convenience for management and may or may not represent bio-
logical reality. Within a stock in a given stream, there may be various
subgroups that are genetically discrete, depending on when and with
"whom" they spawn.

This last consideration is very important when looking at stocks on a
genetic basis. A geneticist's definition of stock would be based on the
reproductive aspects and can be stated as a "group of interbreeding or
potentially interbreeding individuals." The major difference between

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the geneticist's definition and the others is that it is based on the breeding and genetic interchange between members of a group, rather than the later life history characteristics of the fish. The two may coincide if a breeding population has a given migration circuit, but in most cases this is a rare occurrence.

Why is the geneticist's definition so narrow and why be concerned with this aspect? The science and the use of genetics are based on the transmission of inherited characteristics in animals, and unless it can be determined that the groups dealt with are breeding together to transmit their characteristics to the next generation, there is no way to say much about genetic differences. Second, it is safe to say that genetic factors influence to some degree every aspect of the biology of any organism, including fish. Additionally, any changes made in the genetic constitution of an animal are fairly permanent and are transmitted to subsequent generations perhaps to become a part of a given population.

Aside from these considerations, when we consider the strategies that can be developed for the successful maintenance of an animal species, what better way is there to take advantage of a wide array of habitats? If we break up a large population into small groups, each of which is optimally suited to a particular place in the total environment, there is a more efficient utilization of the available resources. This is what the salmonids as a group do. By a process called selection, which Graham Gall will discuss later, groups of fish over perhaps thousands of years have become adapted genetically to specific environments. As a consequence numerous stocks have been developed, each of which has an array of genotypes that allows maximum utilization of its habitat. A conservative estimate of the total number of such salmon stocks in existence on both sides of the Pacific was mentioned by Ricker (1972) as 10,000.

Before getting into the genetic implications of the stock concept in resource management and commercial salmon production, let me first mention a couple of genetic consequences that are characteristic of natural stock development. Because of the limitations on the extent of the environment to which a given set of genotypes are optimally adapted, the number of animals with these genotypes will be finite and perhaps rather small. Thus a stock is relatively small and some extent of inbreeding may result. Also, since the genotype of a stock is determined in response to pressure from different environments, extensive genetic differences will develop between groups. Ultimately, perhaps on an evolutionary time scale, this will lead to isolation such that two groups will not reproduce together. In fact, these two processes tend to work in concert to produce new species but can provide problems for both management and commercial culture. These problems will be examined as the two areas of fisheries manipulation are covered.

What genetic factors inherent in the stock concept should be considered in management of salmonids as a natural resource? Based on the genetic definition of a stock, there can exist within a given stream, a large number of stocks, substocks, etc., depending on the propensity of the

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fish to interbreed. Ideally each of these is a separate unit for management considerations and each generation of fish should be harvested in such a way that the conscious selection of harvesting maintains the next generation as much like the previous one as possible. To accomplish this with present fishing methods and management techniques is clearly an impossibility. Consequently the various stocks must be treated somewhat collectively; thus harvesting is based on the "home stream" concept. Such a practice is generally referred to as "natural management."

However, on closer scrutiny even this is not compatible with biological reality. If we consider the fish in a given stream a reasonable approximation of a discrete population, there are other unnatural selective forces that can change the genetic makeup. For instance, techniques of fishing inflict selective mortality on salmon populations. It has been demonstrated that gillnets remove certain sizes of salmon. Generally early and late runs are harvested less than at seasonal peaks. The practice of harvesting mixed stocks inflicts mortality inconsistent with the dynamics of particular subunits. All of these will tend to change the genetic balance of a population, making it less adapted to its particular environment, and thus decreasing production. It may be that "natural management" is much more of an ideal than a realized fact.

Additionally, the information needed to even attempt to approach management on this basis is overwhelming, and perhaps we need to change our ideas. A few examples of the necessary information are:

1. The extent of genetic differences between subgroups

2. The seriousness of the loss of given subgroups

3. The extent and variability of harvest in the mixture of stocks

4. The population dynamics of each subgroup in order to determine permissible rates of harvest

We do not yet have methods to collect some of this information, and when we can, there is a sizeable investment to justify.

Perhaps, as Larkin (1972) has suggested, we need to change our emphasis to meet present requirements. Rather than emphasize the "uniqueness" of salmon "races," perhaps we should look at their variability and interchangeability. Characteristics that are detrimental to salmon in a fast-changing world could be selected against, rather than emphasizing the preservation of all genetic components. Salmon could be selected that are adapted to new environments, rather than placing emphasis on preventing changes in environments. All of these can be accomplished with the proper genetic techniques and their application, provided we are willing to assess the cost and make a change.

With the genetic characteristics of the stock concept that have been mentioned, what are the implications for commercial production of salmonids? As was mentioned previously, this type of subdivision can lead to relatively small units that are genetically quite diverse. These two characteristics can be both beneficial and detrimental to current aquaculture ventures.

On the negative side, the stocks we now have to work with are adapted totally, or at least to a large degree, to the natural environment. Consequently, there is a great degree of genetic diversity between and within stocks (there is a component of temporal variation to which populations must be adapted). On the other hand, in commercial production the fish are subjected to a single, relatively stable situation in captivity. Expression of the inherent genetic variability will thus give a very diverse response and result in a highly variable product. The result is a loss of efficiency and extra work to produce a crop.

A potential problem with using "available" stocks is one of genetic incompatibility. As a consequence of genetic divergence, stocks may become different enough that they will not satisfactorily reproduce together. A suggestion of such a problem was obtained in some breeding work we are doing with the Washington Department of Fisheries. The design of the crosses is shown in Figure 1. Eggs and sperm were collected from 30 females and 30 males in each population and the respective sex products pooled. The "pooled" gametes were then divided into three equal aliquots and crosses were made as shown.

| Males Females | Green River | Simpson | Skykomish |
|---|---|---|---|
| Green River | Green River x Green River | Simpson x Green River | Skykomish x Green River |
| Simpson | Green River x Simpson | Simpson x Simpson | Skykomish x Simpson |
| Skykomish | Green River x Skykomish | Simpson x Skykomish | Skykomish x Skykomish |

Figure 1. The experimental breeding design in three populations of coho salmon.

In Table 1 the data on mortality through "shocking" are shown for the crosses in 1974 and 1975. If these data are combined on the basis of the origin of the males and females (Table 2) in both years the crosses using Green River males show a higher mortality. It may be that the Green River

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coho salmon have genetically diverged enough to make them somewhat incompatible with the other populations used.

Table 1. Percent mortality (through "shocking") of eggs from the crosses of three populations of coho salmon reared at the Washington Department of Fisheries Green River hatchery.

| Population Crosses | 1974 | 1975 |
|---|---|---|
| Sim. x Sky. | 14.4 | 10.9 |
| Sim. x Sim. | 13.3 | 9.0 |
| Sim. x G.R. | 27.1 | 25.3 |
| | | |
| G.R. x G.R. | 12.2 | 7.3 |
| G.R. x Sim. | 7.6 | 3.2 |
| G.R. x Sky. | 9.7 | 8.7 |
| | | |
| Sky. x G.R. | 15.9 | 9.6 |
| Sky. x Sim. | 3.4 | 5.4 |
| Sky. x Sky. | 17.2 | 7.1 |

Table 2. Total percent mortality based on origin of parents of population crosses.

| Population Origin | 1974 ♀ | ♂ | 1975 ♀ | ♂ |
|---|---|---|---|---|
| Sim. | 18.4 | 8.1 | 15.3 | 5.8 |
| G.R. | 9.8 | 18.4 | 6.4 | 14.1 |
| Sky. | 12.0 | 13.8 | 7.4 | 8.9 |

The genetic variability found in natural stocks also has its beneficial aspects. Because of genetic divergence, there is a broad array of geno-types from which to select. This gives a good base on which to initiate a selection program. In addition, there is a potential for utilization of hybrid vigor. An example of this possiblitiy is shown in Table 3. These are results from the crosses mentioned previously and demonstrate that at least in early life stages some gains can be made by using hybrid fish, based on the stock from which they originated. In every case, the hybrid crosses show a better weight gain and conversion efficiency than the pure line crosses. This could be very meaningful when computing food costs.

For commercial production of salmon, the genetic implications of the stock concept can be very beneficial for the genetic source material and for utilizing hybrid vigor. However, some problems are inherent in this natural system, such as the high degree of variability and possibility of genetic incompatibility, that need to be recognized as disadvantages in a

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commercial operation. Because of these, it is mandatory that if arti-
ficial rearing of salmon is to be successful, separate and distinct
stocks compatible with these conditions must be developed.

It can be seen from this rather short consideration of the stock concept
that it has a major part to play in both resource management and commercial
salmon production. Knowledge concerning this idea and its genetic con-
sequences can give some insight into methods of more effectively utiliz-
ing salmon. Handling stocks on a genetic basis can thus perhaps yield
more successful results.

Table 3. Comparison of growth and food conversion efficiency of pure line
and hybrid crosses of coho salmon, based on three months of
rearing.

| Population Crosses | University of Washington hatchery | | Green River hatchery | |
|---|---|---|---|---|
| Population Crosses | Average weight (g) | Food efficiency (lb. food/ lb. fish) | Average weight (g) | Food efficency (lb. food/ lb. fish) |
| Sim. x G.R. | 3.53 | 1.35 | 2.24 | 1.47 |
| G.R. x G.R. | 3.07 | 1.31 | 2.08 | 1.30 |
| Average | 3.30 | 1.33 | 2.16 | 1.39 |
| Sim. x Sim. | 3.05 | 1.42 | 2.11 | 1.46 |
| G.R. x G.R. | 2.53 | 1.56 | 2.04 | 1.46 |
| Average | 2.79 | 1.49 | 2.08 | 1.46 |
| "Excess" | +.51 | -.16 | +.08 | -.07 |
| Sim. x Sky. | 3.59 | 1.28 | 2.41 | 1.28 |
| Sky. x Sim. | 3.53 | 1.21 | 2.44 | 1.10 |
| Average | 3.56 | 1.25 | 2.43 | 1.19 |
| Sim. x Sim. | 3.05 | 1.42 | 2.11 | 1.46 |
| Sky. x Sky. | 3.44 | 1.25 | 2.28 | 1.22 |
| Average | 3.25 | 1.34 | 2.20 | 1.34 |
| "Excess" | +.31 | -.09 | +.23 | -.15 |
| G.R. x Sky. | 3.20 | 1.26 | 2.12 | 1.34 |
| Sky x G.R. | 3.54 | 1.21 | 2.36 | 1.14 |
| Average | 3.37 | 1.24 | 2.24 | 1.24 |
| G.R. x G.R. | 2.53 | 1.56 | 2.04 | 1.46 |
| Sky. x Sky. | 3.44 | 1.25 | 2.28 | 1.22 |
| Average | 2.99 | 1.41 | 2.16 | 1.34 |
| "Excess" | +.38 | -.17 | +.08 | -.10 |

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# GENETIC DELINEATION OF SALMONID POPULATIONS BASED ON ELECTROPHORETIC DATA

*Fred M. Utter, Frederick W. Allendorf and Bernie May*[*]

The capability of managing a fishery on the basis of its component populations is an objective that has generally eluded salmonid biologists until recently because of the difficulties involved in defining these populations. Tagging and marking studies have provided useful information concerning origins and degrees of straying of fish but have been limited by the need for handling all treated individuals. Natural features such as scale characters and relative mineral composition have also proven actually or potentially useful for identification of areas of origin through reflections of natal environments. None of the above approaches are capable of genetically defining population structures, however, and such definitions are necessary if management is to be based on population structures.

A method has matured during the past decade through which definition of salmonid populations has been achieved in much greater detail and clarity than had previously been possible. This method is starch gel electrophoresis coupled with histochemical staining. The method is based on the separation of protein solutions in an electric field, and on the subsequent use of the specific activity of the protein (enzyme) in the staining process. Electrophoretic data are particularly useful for providing genetic information on populations because:

1. Properly selected variants reflect simply inherited traits that are constantly expressed throughout the life cycle of an individual, and are not directly affected by environmental variables.

2. This kind of variation permits actual counting of frequencies of different genes in collections taken from different areas; significantly different frequencies of genes from different areas are positive data that samples from these areas are genetically different. Data are also useful for estimating relationships among populations and amounts of inbreeding within them.

3. Frequencies of variants in a given population are stable attributes of that population and tend to persist at the same levels over many generations.

4. The methodology allows collection of relatively large amounts of data in a given period of time.

Our group has been actively engaged in the electrophoretic study of salmonid populations over the past 10 years. This summary reviews some applications of electrophoretic data in the study of fish populations from the perspective of these studies.

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The power of electrophoretic data for genetically defining populations has been demonstrated in studies of salmonid populations of the Pacific Northwest. Previously unrecognized major population units have been identified that are rather surprising in some instances. Although geography plays a major role in the structuring of these units, it is not necessarily true that geographically proximal populations are genetically the most similar. Genetic structuring of some populations is also less closely tied to time of return and anadromy than had previously been thought. Below are some examples of major population units defined through electrophoretic studies carried out by our group and other laboratories of the Pacific Northwest.

A major genetic division of rainbow trout populations occurs east and west of the Cascade Crest. Both anadromous and landlocked populations east of the Crest in both the Fraser and Columbia River drainages are more similar to one another than to any populations of west slope drainages of the Cascades. Similarly, west slope populations are genetically more similar to one another than to those of the east, regardless of whether they return in the summer or the winter. This separation presumably dates back to the last period of glaciation, which receded about 10,000 years ago. The inland populations are probably descendents of rainbow trout that populated large inland lakes formed by Columbia and Fraser River drainages impounded behind the glaciers. The coastal populations appear to have descended from another source.

Major population units of coho salmon are distinctly defined over the entire drainages of the Columbia and Fraser Rivers where a single type of the serum protein - transferrin (Tfn AA) is found in well over 90% of the fish. All other drainages between and on either side of these large river systems (including those directly adjacent to, but not joining the Columbia River) have frequencies of AA types of less than 10%. This abrupt discontinuity may reflect selective factors favoring the AA transferrin type in the large river systems.

Fall chinook salmon populations from streams of both Washington and Oregon entering the Pacific Ocean are genetically distinct from populations of Puget Sound or Columbia River tributaries. Both of these population units, in turn, are genetically different from spring run chinook salmon of the Columbia River.

Estimation of component populations of mixed fisheries for two populations and a single variant genetic system is a simple matter of direct proportionality. Analysis becomes more complex as the numbers of populations and variant systems increase. Computer analysis involving maximum likelihood methods is a feasible approach to this problem that is being developed and applied by personnel of our group.

## Hatchery Populations

Determining the effects of plantings of hatchery fish on native salmonids of the same species is a major concern to management biologists. Native fish are a valuable reservoir of genetic variation and provide a useful supplement to the fishery even in stocks that are largely maintained through hatcheries. Although native fish may be more adapted to a particular area than hatchery fish, they are potentially endangered through hatchery plantings by factors including (1) competition for spawning and rearing ground resulting from large hatchery releases, (2) possible earlier hatching of progeny of hatchery fish resulting in a competitive advantage, and (3) hybridization of native and hatchery fish resulting in disruption of adaptive gene pools.

Biochemical genetic markers are very useful for studying the effects of hatchery plantings on native fish provided there are differences in gene frequencies between the two groups. Genetically marked hatchery fish require no special handling prior to release, and long-term effects of plantings can be measured because genetic markers are passed on to subsequent generations.

The population of summer run steelhead from the Skamania hatchery of the Washington State Department of Game has a variant form of the enzyme alpha glycerophosphate dehydrogenase (AGPD) which occurs with a frequency of about 0.15. This variant is absent from native steelhead of the Kalama River (Washington) and from winter run steelhead of the Game Department's South Tacoma hatchery that have been planted in the Kalama River; the variant is therefore useful for following the effects of plantings of Skamania hatchery fish on other steelhead stocks of the Kalama River. The data indicate that Skamania hatchery fish planted in the main stream tend to enter tributaries prior to their seaward migration. Adult fish from hatchery plantings return near the point of release and many of them spawn successfully. Descendents of these fish apparently hatch earlier than those other stocks based on their larger size in a given sampling area. Almost all of the residualized steelhead of the Kalama River appear to be from the Skamania hatchery.

## Genetic Marking

The potential value of a genetic marker for the identification of populations increases as the differences in its frequency increase between populations. The sample size needed to demonstrate differences between two populations decreases to the point where individual fish can be identified if different alleles for a particular protein are fixed in the two populations. Such a situation rarely occurs naturally within a species--particularly among populations where gene flow is possible--but can be straightforwardly created through artificial propagation.

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We are presently working with the Washington State Department of Game to create genetically marked stocks for maximizing genetic differences between these stocks and native fish in areas where the stocks are to be planted. One such stock is being bred from Skamania hatchery fish for introduction into previously unplanted tributaries of the Kalama River. Selection is based on the AGPD variant. In the first generation, males carrying two doses of the variant gene (i.e. homozygous--about 2% of those screened) are mated with randomly selected females. In the next generation there are sufficient individuals of both sexes that are homozygous for the variant for the derivative population to be brought to fixation at this time.

Two potential pitfalls that must be kept in mind during the development of projects of this kind are inbreeding and differential selection (i.e., nonrandom survival of different genetic types) against alternate forms of a given protein. Effects of inbreeding can be minimized through the selection of an adequate number of breeders during early phases of the program. The possibility of differential selection emphasizes the need to continually seek evidence of differential environmental effects on parent and selected progeny stocks.

We foresee artificial genetic marking of hatchery stocks becoming a very useful management tool. The fate of hatchery and wild fish presently is of more than biological interest in salmonid fisheries of the Pacific Northwest. Recent Washington State court decisions have indicated that native Americans may be entitled by treaty to 50% of the natural spawning salmonids returning to rivers of ancestral fisheries but to a lesser share of hatchery fish. Sea ranching is a concept being developed currently in which privately reared salmon are released to grow naturally in the marine environment, and are then harvested by the releasing organization upon their return. Genetically marked stocks have obvious management implications in both of these instances.

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GENETICS AND MANAGEMENT WITHIN THE
WASHINGTON DEPARTMENT OF FISHERIES
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The Washington State Department of Fisheries does not have an ongoing
salmon genetics program as such. We have considerable interest in, and
have contributed support to, both the hatchery coho studies described at
this program by Dr. Hershberger and the genetic delineation studies by
Dr. Utter relating to chinook. Primarily we are aware that certain know-
ledge about genetics could be of great significance to salmon management,
and we would like to promote such information. But our lack of specific
expertise means that we will need some guidance.

The Washington Department of Fisheries (WDF) operates 30 major artificial
production stations for salmon, and consequently in various selection and
stocking actions the Department makes many decisions that affect the
genetic makeup of Washington's salmon populations. Thus it is clear that
lack of an organized program for genetic consideration does not mean that
genetic decisions are not being made; they are made constantly. The
obvious question is, how can they be made better?

The history of stock utilization at WDF facilities should provide some
insight into both the magnitude and the nature of problems that can occur.
One highly controversial aspect was the policy in force for decades but
now largely abandoned whereby eggs were freely transferred from hatchery
to hatchery throughout the state and sometimes further. Because hatcheries
have most often been located on major salmon-producing streams, this intro-
duction of foreign stocks with typically rather different characteristics
from existing native stocks suggests the possibility of dilution or even
eradication of native types. No doubt this has occurred extensively. I
believe this approach to stock selection arose from acting merely out of
convenience and from failure to consider the effects that hatcheries could
have either on wild stocks or on fishery utilization. In my view the
effect has largely been bad.

Several years ago a program was generated to improve WDF hatchery stocks
by obtaining eggs from fish thought to have special value in the fisheries.
These included early-running chinook and coho, strains of especially
bright or large fish, and in a number of cases--e.g., Skagit and Soleduck--
elimination of imported stocks in favor of native fish that appear to have
desirable characteristics. In addition, this program employed a large
amount of crossing--for example, spring chinook bred with fall chinook,
hoping to obtain summer-running chinook--where certain characteristics
were not directly and easily obtainable. There were also pure imports
such as cherry salmon (*O. masou*) from Japan. Finally, there was an attempt
to use complex experiments to learn the genetic component of chinook and

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coho that remained resident in Puget Sound and consequently were important to a major sport fishery.

Without listing details, there have been some outstanding successes in the straight stock transfers; the crosses largely have not amounted to much, at least so far; but major breakthroughs have occurred in hatchery production of Puget Sound resident stocks--although the product was ultimately achieved by environmental rather than genetic manipulation. The cherry salmon have done well in some lakes, but have not shown important new values thus far in marine releases.

Now Washington State is proposing enhancement by artificial production to double or perhaps triple salmon production in the state. Whatever follies or perhaps sensible genetic decisions have occurred in the past have an opportunity to be multiplied manifold. As I previously indicated, such programs tend to be driven by convenience, which in my view has opposed maximum use of genetic possibilities in the past and could easily happen again. Certainly the "mix-em-up, anything-goes" approach of recent years-- of which I was a part, incidentally--was not conducted under review by management-oriented geneticists. Undoubtedly we should all consider how best this can be done in the future to avoid wasted opportunities or even genocide and to achieve the economic advantages that genetic knowledge can surely provide if given a chance.

# GENETICS IN WASHINGTON DEPARTMENT
## OF GAME FISHERY MANAGEMENT
*Rodney M. Woodin**

The use of genetics in fishery management programs of the Washington
Department of Game is centered in two areas. These are the selective
breeding of hatchery stocks for enhancement programs and the use of genetic
marks for research purposes, which also involves selective breeding.

The selective breeding programs of the production hatcheries are best
illustrated in the steelhead program. The two races of steelhead, winter-
run and summer-run, are both propagated artificially and have undergone
intensive selective breeding.

The winter-run stock is maintained at two stations: South Tacoma and
Cowlitz River. The selection on the South Tacoma stock has been primarily
to get an early egg take, which expedites the production of smolts
in one year of rearing. The specific data on the timing of the egg take
at South Tacoma have not been compiled, but the general result is that the
peak of spawning for this stock has been changed from mid-March to mid-
January. The Cowlitz River stock has been supplemented with South Tacoma
stock and the majority of the program aimed also at the January spawning
peak. However, some March and April spawners are utilized to maintain
greater diversity in this stock. This diversity is desired principally
to have fish available to the fishery in March and April. Also, at the
Cowlitz River, selection for steelhead with a life history of one season
in the hatchery and three seasons of saltwater rearing before maturity
was initiated in 1970. There are no good, hard data available on the
results of this selection process because of sampling problems, but a
definite increase in three-year saltwater adults is apparent. The entire
breeding program for the 1976 brood utilized three-year saltwater adults
as determined by size selection for both males and females, greater than
32 inches (Jack Ayerst, personal communication, 1976). The intent of
this selection is to increase the frequency of large steelhead in the
fishery.

The summer-run steelhead stock is maintained at the Skamania Hatchery on
the Washougal River. Selection at this station has been for both early
egg take and one-year fresh water, three-year saltwater rearing prior to
maturity. Sampling of the adult return to the Skamania Hatchery is
facilitated by the low water conditions in the summer season and represent-
ative data are available for this stock. The shift in time of egg take
from the third week of March to the first of February is illustrated in
Figure 1. The general increase in size of the returning adults at the
Skamania Hatchery, as well as the specific size difference and relative

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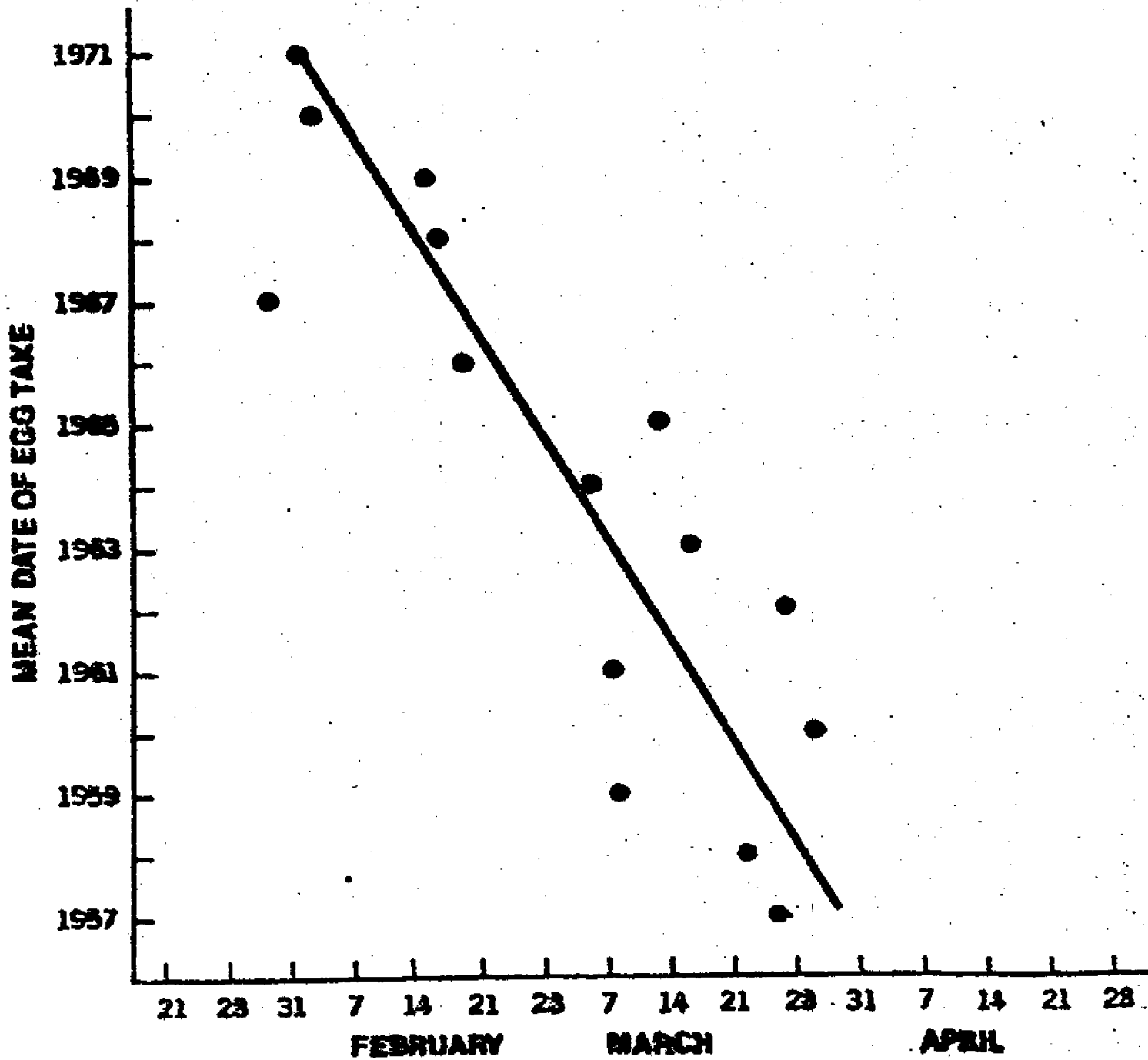
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FIGURE 1.    Mean date of steelhead egg take at Skamania Hatchery
             (Marvin Hull and Brian J. Allee.  Unpublished Manuscript, 1972)

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abundance of two-year saltwater versus three-year saltwater adults is shown in Figure 2. Again, the selection of three-year saltwater adults is designed to increase the frequency of large steelhead in the fishery.

The use of genetic marks is new in the field of fisheries. The technique is described by Allendorf and Utter, 1975. These genetic marks are being utilized to aid in the assessment of the impact of hatchery smolt plants of steelhead on native populations of steelhead.

Genetic marks are being utilized in two situations where new rearing facilities have been constructed and are resulting in hatchery plants into areas not previously subject to direct plants of hatchery smolts.

The first area of study involves summer-run steelhead from the Skamania stock being reared in Gobar Pond and released into Gobar Creek, a tributary to the Kalama River. A variant form of AGPDH was utilized as the mark. The selective breeding for this mark has been conducted twice, and the first release of genetically marked smolts will be made in May, 1976.

When collecting data for a background genetic profile in Gobar Creek during 1974, we discovered that about 50% of the juvenile steelhead population was descendant from the Skamania stock. This is despite the fact that no smolt plants had ever been made into this tributary. However, the main Kalama River has had a long history of plantings from this stock. During the 1975 field season, sampling conducted in all of the major tributaries of the Kalama River revealed a contribution of Skamania stock from 0.0 to 100% with an average of 29%.

Analysis of the distribution pattern for the Skamania stock in the wild rearing populations was limited by the sample numbers and locations, but a systematic sampling scheme will be initiated during the 1976 field season. The primary significance of this data is the positive proof that hatchery stocks are contributing to the wild rearing populations of juvenile steelhead. The next step in this analysis is to determine whether the Skamania stock spawning in the natural environment complete the total life history and produce adult steelhead. This question will be examined during the 1976 field season by sampling adults at the Washington Department of Fisheries Kalama Falls fishway.

The second area of study involves winter-run steelhead from the South Tacoma Hatchery being reared at the Mayr Brothers Pond for release into the Wishkah River. A combination of variation in three enzyme systems-- TO, LDH, AND MDH--is being used for the mark. Selective breeding for this mark has also been conducted twice, and the first genetically marked smolts will be released in April, 1976.

The Wishkah River received only one plant of hatchery steelhead smolts in the twenty years prior to the establishment of the new rearing facilities. This plant of 7,000 smolts was made in 1963. Collection of samples for background genetic profiles indicated no South Tacoma stock presently in the population.

FIGURE 2  SIZE COMPARISON OF THE 1965 and 1975 ADULT STEELHEAD
TRAPPED AT SKAMANIA HATCHERY

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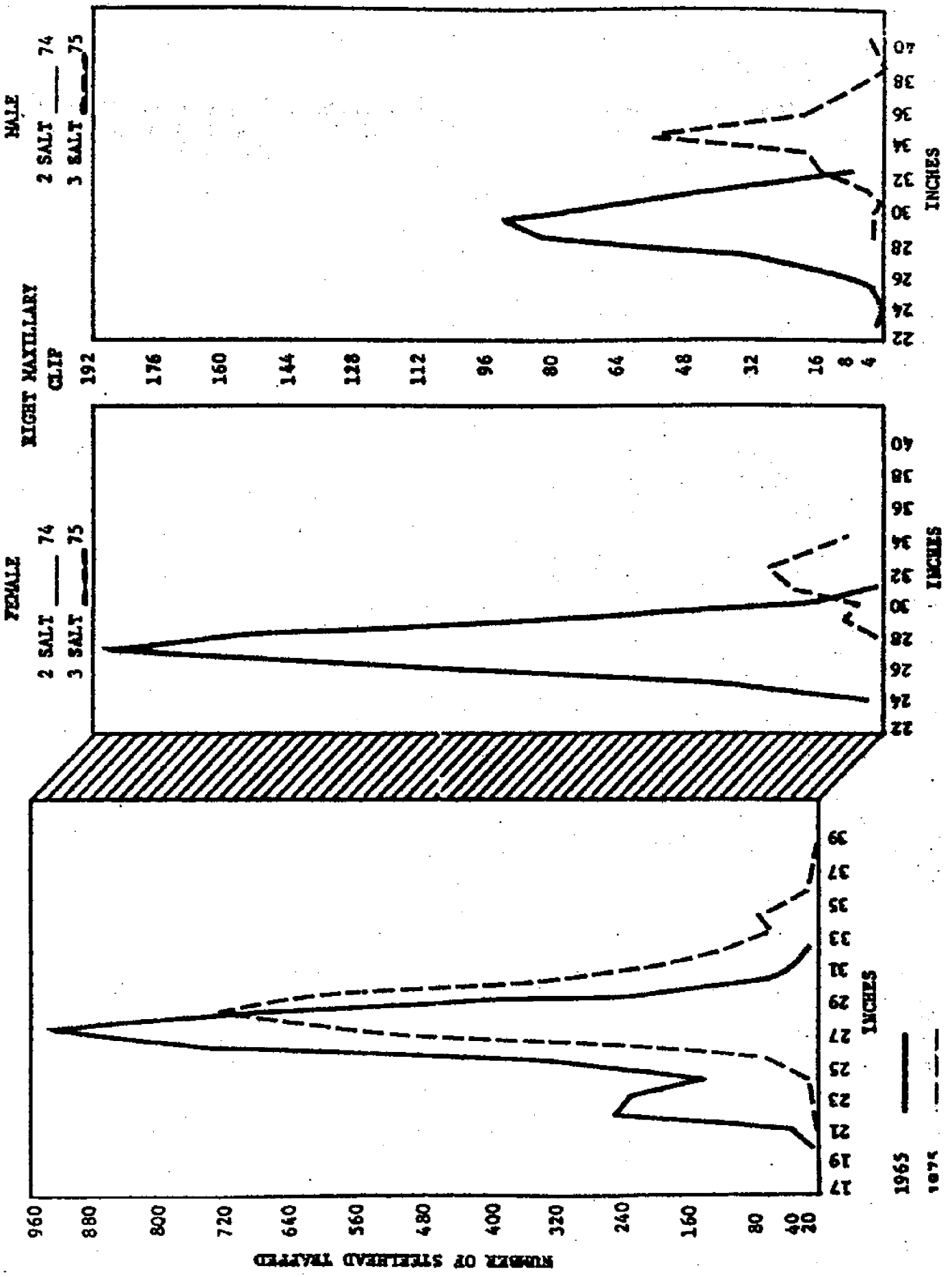
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One of the major areas of emphasis of the salmonid aquaculture program at
the College of Fisheries is genetics and breeding. In order to provide
some idea of the scope of the program, I would like to review briefly a
number of different investigations currently underway. At the College of
Fisheries we are now working primarily with three species: the chinook
salmon (*Oncorhynchus tshawytscha*), the coho salmon (*O. kisutch*), and the
rainbow trout (*Salmo gairdneri*). The research work on each of these is of
a distinct nature, but commonly aimed at finding methods through genetic
manipulation to develop stocks for particular objectives of the fishery.

For the past four years the genetics program with chinook salmon has been
directed at investigating the use of different year-classes for breeding.
There has been some work done by others indicating that use of younger
maturing salmon, for instance "jack" salmon, yields a larger proportion
of this age adult in a returning population. The potential thus exists
for this to be a strongly genetically determined trait that is easily rec-
ognizable and easily utilized. In addition, there is the possiblility that
the growth and/or migration characteristics could cause the same effect.
Both of these two possibilities could be of potential value for commercial
aquaculture or state agencies in managing fish production.

In 1971 crosses were made with two age-classes of adult chinook salmon.
One group consisted of progeny from crossing three-year-old females with
two-year-old males ("jacks"), and the other group was from crosses of
three-year-old females with three-year-old males. Although the results
from these fish returning as adults are yet incomplete, several things can
be stated to date. The group with the "jacks" as male parents had more
(3.5X) two-year-old males returning than the other group and more (1.5X)
three-year-old adults returning in the next year (1974), and the average
size of the individual fish was smaller. Since equal numbers of the prog-
eny from the original crosses were released, there is, based on the number
of returning adults, a better survival in the group with two-year-old
male parents. In addition, although the returning fish are smaller in
this cross, there is a greater return in total biomass, or weight. This
may be advantageous in an ocean-ranching situation where the harvest is
on returning adult fish.

In subsequent years (1972 and 1973), the same crosses were made again and
additional crosses were added to include three-and four-year-old males and
females. Although the majority of the progeny from these crosses have
not yet returned as adults, the same general trend is emerging from the
initial results. More males return as "jacks" in those crosses with a

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two-year-old male parent; but when a four-year-old female is crossed with a "jack," fewer males return as two-year-olds. Overall it appears that the lesser the "total age" of the parents, the faster the maturation rate and the better the survival in the progeny.

Additional data are being collected on the ocean phase of the life history of these fish to obtain information on their distribution and growth in salt water. From the results obtained so far, few conclusions can be stated, but there seems to be a differential contribution to the Puget Sound sport fishery based on the available data from the specific crosses made. No results from the commercial fishery have yet been obtained.

To summarize the chinook breeding, it appears that using age at maturity as a selection trait can provide a tool to manipulate the characteristics of the returning adult population. The amount of genetic influence has yet to be determined, but from initial results it seems to play a large role. Thus the possibility exists to breed a chinook salmon population for the return age desired.

The coho salmon breeding work is designed around the concept of "accelerated rearing." This practice is one in which coho salmon smolts are produced in six months instead of the normal eighteen months; rapid growth is achieved by use of "warm" water and maximum feeding. With this treatment mature adults are produced in two years, rather than the normal three. In addition to this method allowing for more rapid genetic selection with the shortened life cycle, there is also a very dramatic change in the selective pressures on the accelerated coho salmon. These fish are subjected to an entirely new environmental regimen.

In order for a coho stock to perform maximally under these new conditions, selection for the correct genetic composition will have to occur. This is very basically the design of our current program for coho salmon. Returning adults from crosses involved in the accelerated rearing program are assessed on the basis of such phenotypic characteristics as weight, length, return percentage, egg production, and fry production. Those crosses that show the best total performance are then utilized for the next generation. Results of this program to date indicate, on the basis of increased survival to return, that successful adaptation to the different rearing conditions is being achieved. In addition, genetic variation as determined by electrophoretic separation of proteins is being monitored to assess changes that may be caused by the selection program.

Two other genetics programs using salmon are currently underway at other sites in cooperation with the Washington Department of Fisheries and NMFS. As I mentioned earlier today the program with WDF is an assessment of three stocks and their hybrids to determine if a coho salmon strain can be developed for a variety of management schemes. Briefly, the results to date have shown a differential viability between crosses, particularly with the males of one stock, a significant degree of hybrid vigor in growth and conversion efficiency in interstock crosses, a genetically mediated difference in susceptibility to "cold-water" disease, and a large increase

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in genetic variability between crosses, as measured by electrophoresis.
While it has been shown that genetic manipulation can produce gains in
the hatchery phase of rearing, data from the fishery are not yet available
to complete the analysis.

The program in cooperation with the NMFS laboratory at Manchester, Wash-
ington, is directed toward development of a salmon brood stock for use in
saltwater pen culture. Samples of chinook salmon interyear class crosses
made at the University of Washington in 1973 and 1974 were vaccinated
against *Vibrio* and placed in saltwater pens in June of 1974 and 1975. These
fish were marked to indicate the cross from which they originated. Indi-
vidual weights and lengths were taken monthly throughout the first year
of saltwater residence. Analysis of the growth data did not indicate any
significant differences among the various crosses during this time period.
However, the fish with four-year-old female parents grew slightly faster
and were apparently more resistant to handling stress and disease problems
as evidenced by their higher survival. It was also noted in the fall of
1975 that a large proportion of the fish from crosses made in 1974 with
two- and three-year-old parents matured as "jacks." Crosses will be made
with the saltwater-reared chinook salmon in 1976 to further assess these
fish as the start of a brood stock.

The program with rainbow trout has a solid base of more than 40 years of
work done by Dr. Lauren Donaldson and is aimed at further progress in
brood stock development and genetic characterization of this rather unique
strain. Two areas of genetic improvement are currently receiving emphasis;
the first of these is attempting through breeding techniques to enhance
the viability of the eggs and fry produced by females that mature in
their second year of life. While egg production is good at this stage,
there is a relatively high mortality and the resulting fry are less hardy.
Other factors such as diet play a role in this also, but genetic changes
can have a large influence on sex cell production and can be permanently
introduced. In addition, a shortened life cycle with better fry
production will allow more intense selection over time.

A second area presently being investigated is the alleviation of inbreed-
ing problems. Probably because of inbreeding caused by a small breeding
population, some undesirable characteristics were noticed in the rainbow
stock. To alleviate these problems, the University of Washington strain
was outcrossed with the Washington Department of Game's Spokane strain.
These fish are now being analyzed, and initial results show some definite
improvements in reproductive traits. In addition, the genetic variation
introduced from the Spokane strain is being monitored by electrophoresis
to follow any changes concurrently with selection. The original Univer-
sity strain had little variation as measured by this method, but the
protein polymorphism shown by electrophoresis was rather unique. Thus
it is of interest to determine if these unique traits will again be
developed in response to the prevalent environmental conditions.

This sampling of projects will give you some idea of our goals and emphasis
in the genetic studies of salmonids. The information obtained from these

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programs can be directly applied to a number of aquaculture schemes to achieve desired goals. With a continuing emphasis on areas important to aquaculture, we can define heritable characteristics that can be utilized in managing salmonid populations. In this way definitive guidelines and directions can be formulated with predictable success.

INTRODUCTORY REMARKS
*Lauren R. Donaldson*[*]

At the turn of the century, the great educator-naturalist Dr. David Starr Jordan published a short paper, "The Trout and Salmon of the Pacific Coast" (Jordan, 1906). In this paper, Dr. Jordan describes the natural history of the salmonid fishes, speciation, distribution, and adaptations. He makes repeated reference to the extremely varied conditions of habitat under which the fish live and the role of isolation in the evaluation of the species and local races.

Some sixty years later, Dr. William F. Thompson, (1965) who had been a graduate student of Dr. Jordan's, in a paper published just after his death, wrote of the Darwinian principle of adaptation of species by natural selection.

> This principle applies to the salmon along our coasts. Each stream or lake has its own extremely complex characteristics, and if salmon live in one of them we find that these salmon are adapted in an equally complex way to that environment. We are far from under-standing these two complexes, the fish and the environment, but we do know that in order to return to the place for which it has been fitted the salmon returns from the sea to its home stream, there to meet and breed with its own kind. Thus it develops and perpetuates the genetic characters which fit it for survival in that stream. So we have a multitude of groups of salmon, each self-perpetuating, which we loosely term races, and which the scientist calls gene pools, each fitted to survive in a particular home. If it leaves this home the race either dies off or readapts.

It is obvious that the salmonid gene pool is very complex; to take maximum advantage of the potential requires many generations of continuous effort. A paper (Donaldson, 1963) I presented at the Second Governors' Conference on Pacific Salmon in 1963 stated in part:

> To be successful, a program of breeding should be continued for many generations by the best qualified personnel available. The old adage, "Real progress comes slowly--but slipping back is fast," really applies to efforts to build a better brood stock of salmon or trout.

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Previous discussions this morning explored the concept of a stock. The stock concept provides a conceptual framework within which one can discuss management-related genetic problems with exploited populations. In practice, however, the stock concept has found limited application in fisheries management because exploitation typically occurs during periods when several stocks are present in a common fishing ground. It is not possible to manage the exploitation of discrete stocks under these circumstances.

Le us define salmon ranching as the artificial propagation of salmon in hatcheries, the release of these animals to harvest energy and nutrients from natural production, and the subsequent harvest at or near the site of release. By this definition, salmon ranching is a management option that provides the opportunity to apply the stock concept to the management of Pacific salmon fisheries.

The genetic objectives of stock management are to maintain the inherent genetic variation of the stock on the one hand, and exploit this variation for economic gains and management purposes on the other. These objectives present a dilemma for the fisheries manager, for the nature of genetic variation in populations remains the subject of considerable scientific and philosophical controversy. In the face of this controversy, the fisheries biologist must nonetheless make management decisions having profound genetic implications.

Whereas the maintenance of variability comprises the topics of other speakers here today, I will direct my discussion largely towards the problem of stock improvement.

To place the problem in perspective, let us consider the nature of the characters that might be improved as a consequence of selective breeding programs in salmon ranching. These are of three types. One type relates to maximizing the proportion of fish released that return to be harvested. Another includes characters that influence the value of the fish harvested, such as size and condition at the time of harvest. A third class of characters relates to production efficiency. Time of return and age at return are examples of this class.

Each of these characters manifests variation in stocks of salmon. In cases where some of this variation is attributable to heritable considerations, it may be possible to exploit the genetic variability to realize economic gains. The point here is that it is the variability which makes the gains

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possible. However, we have already recognized that our understanding of the nature of the variability is incomplete. The question that arises is: How then can we exploit this variation if we don't understand it?

Statistical methods exist that permit us to make statistical inferences about variation without really understanding its true nature. Applying these methods to the present problem, we can answer two questions that are essential to developing a breeding program. First, we can test the hypothesis that the observed variation results to some degree from heritable considerations. Further, if heritable considerations are implicated, we can observe statistical patterns that are useful in directing a breeding program.

The rationale underlying the partitioning of variation into genetic and nongenetic components is based upon the resemblence of relatives. For characters for which a significant proportion of variation is genetic in nature, one expects the variance among relatives to differ from the population at large. Thus one can accomplish a regression analysis of off-spring on parents as one approach to partitioning variance into genetic and nongenetic components. Alternately, one can accomplish an analysis of the variance between and within groups of individuals of known relationships.

Regardless of which approach is employed to partition variance, the statistical concept is equivalent. The data are compared to a linear additive model which predicts that the genetic contributions of individuals will combine with others in an additive manner. We can thus define additive genetic variance, that is the proportion of the genetic variance which fits the model, and nonadditive genetic variance, or that which is inconsistent with predictions of the model.

We have already noted that a character can respond to selection only if the character displays a significant proportion of genetic variation. Whether or not this genetic variance is additive or nonadditive is an important consideration in directing a selective breeding program, for it dictates which breeding method must be employed.

The breeding methods employed by plant and animal breeders are variations of two basic concepts. In one of these, termed individual or mass selection, selection is based upon the appearance of parents. For example, if body size is the character being selected, parents are chosen from the largest individuals in the population. This method is effective with characters that manifest significant amounts of additive genetic variance.

When dealing with characters in which the genetic variance is nonadditive, it is not possible to select a potential parent on the basis of his or her appearance. It is necessary to judge breeding performance by observing the progeny. This is because the progeny phenotype is dependent upon specific combinations of parents rather than on parental phenotypes.

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The importance of additivity (or nonadditivity) to breeding methods is now apparent. The application of mass selection to characters lacking additive genetic variance may be conterproductive, while progeny testing is wasteful when dealing with characters having significant additive genetic variance.

Let us return our attention now to the problem of selective breeding in salmon ranching. It is obvious at this point that we would certainly benefit from having estimates of additive and nonadditive genetic variance for characters of interest. Unfortunately, the experiments from which these estimates result are technically complicated and of relatively long duration. Thus we cannot reasonably expect this information to become available for some time. The sooner we get started, the sooner we can undertake rational breeding programs.

In the meantime, although we cannot be certain as to how to best pursue selective breeding, there are theoretical considerations that direct us towards what not to do.

The first of these relates to inbreeding and will be the topic of another speaker.

The second tells us to avoid mass selection. This follows from the relationship between some of the characters to the concept of reproductive fitness. For purposes of discussion, reproductive fitness is a statistical concept that expresses the average contribution of a member of a population to subsequent generations. Quantitative genetic theory predicts that if one partitioned the variance of fitness, any genetic variance present would be found to be nonadditive. Thus, for any character closely related to reproductive fitness, we would expect to observe that any genetic variance would be largely nonadditive.

Recall that one type of character of cardinal interest to salmon ranchers relates to the proportion of fish released that return to the hatchery. This is an example of a character that has an obviously close relationship to fitness. Theory predicts that the genetic variance of this character would be largely nonadditive.

In ocean ranching, all characters are, in one sense, related to fitness, since the success of ocean ranching depends on fish returning. Indiscriminate mass selection could actually decrease returns, and therefore should be avoided.

# SELECTION FOR IMPROVED PERFORMANCE

*Graham A.E. Gall**

Selection and breeding are basic components of fish production just as they are for all animal production systems and should be given at least as much attention and thought as feeding and management. We do not have to ask the question, "Should we practice selection in our operation?" because selection will always be occurring either naturally or artificially. Each time an individual does not survive to reproduce or each time we, as managers, decide not to use an individual in reproduction, these individuals have been culled and selection has been practiced. The question we must ask is, "How should we define our selection program?"

We can be optimistic that selection can produce results if the system we wish to use is properly designed and is carried out in an orderly and consistent fashion. At the same time we must be realistic in our expectations. Genetic improvement through selection will take time, the length of time being dependent on how long it takes the stock to reach sexual maturity. Consequently, it is necessary to make a definite commitment to a specific program and stay with it long enough to realize results. The alternative is to allow chance to determine the genetic fate of the stock, an alternative with the odds of economic success much below those expected at the usual gambling table.

The most rapid response can probably be expected for stocks recently collected from a natural population. This process of domestication should be carefully controlled so that the greatest possible proportion of the stocks' good qualitites can be retained for future improvement. We can assume that at least five generations will be required for a selection program to show marked changes in performance. If a stock reaches sexual maturity at two years of age and we obtain all our future breeding stock from two-year-old fish, we must acknowledge that ten years will be a reasonable time in which to expect substantial changes.

The characters (traits) of importance in production, such as the number of eggs spawned and growth rate, are controlled, genetically, by a large number of genes. Therefore, there will be a very few, if any, individuals that carry truly superior forms of all these genes. The objective of a selection program is to identify those individuals with the greatest number of superior genes. We refer to the genetic make-up of an individual as its geno-type, and the quality of the genotype as the individual's breeding value.

The identification of individuals with superior genotypes (breeding value) is further complicated by the fact that the environment each individual fish receives varies from day to day and from month to month. The characteristic as we see it, referred to as the phenotype, will be influenced

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by the environment such that individuals with apparently superior phenotypes will not all have superior breeding values. For example, the fish that is able to obtain the most feed for whatever reason, will probably grow fastest. This does not necessarily mean that progeny from that fish will also show the most rapid growth. We can then think of the phenotype of a fish, that is, the quantity we measure, as being made up of the effects of the genetic ability of the fish, its genotype, plus the influence of the environment on that fish.

### Selection Response

It is obvious that not all the differences we observe among fish will be due to differences in their genotypes. The importance of this concept to our appreciation of expected response to a selection program can most easily be described by considering an example. Let us assume we are interested in improving weight at one year of age. We can define the steps in selection in the following way:

P= the average weight at 1 year of all the fish produced in a season. The heaviest individuals are to be selected from this group.

B= the average weight at 1 year of the fish selected to be breeders (parents) of the next generation.

SD=B-P, the difference between the average weights of the breeders and the total group represents the superiority of the fish retained as breeders. This quantity, SD, is referred to as the Selection Differential. How large a value it will have will be determined primarily by the proportion of fish that must be used as breeders.

O= the average weight at 1 year of age of all the progeny of the selected breeders. If the average environment has remained relatively constant and selection was effective, we would expect the value of O to be larger than that of P.

R= O-P, the difference in the average weight of the fish produced in consecutive generations. This represents the improvement realized from one generation of selection. The quantity, R, is referred to as the Response to selection.

The ration of Response realized (R) to Selection Differential applied (SD) measures the genetic superiority of breeders, that is, the extent to which these breeders would be expected to produce superior offspring. It represents that proportion of the observed superiority of the breeders that was due to the breeders having superior genotypes. This ration, R : SD, is referred to as the heritability of the trait. An example, for yearling weight in rainbow trout (measured in grams), may look like this: average weight of all fish, P = 200 g; average weight of selected breeders, B = 250g (if 10% of the fish are kept as breeders); and, the average weight of the offspring, ) = 220 g. Then the Selection Differential (SD) equals 250 - 200 = 50 g, and the Response (R) equals 220 - 200 = 20 g. The heritability of yearling weight (R : SD) is 20 : 50 - 0.40. As has been observed in experiments, the heritability indicates that 40% of the apparent superiority

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of the breeders was due to their having superior genotypes. The remaining 60% was the result of the selected breeders' having received, by chance, a better than average environment.

Our discussion of the steps involved in carrying out a selection program points out a number of factors that must be considered in any breeding program. Because the environment plays an important role in determining the accuracy with which we can select superior breeders, it is desirable that all of the fish in the group being used for selection be treated as equally as possible so as not to give an environmental advantage to some fish. It is also necessary to identify in some way the fish that have been selected as breeders, since selection will not always be carried out at the same time as spawning.

From the point of view of inbreeding, it is obvious that the size of the breeding population is determined by the number of fish selected and used as breeders since they are the only individuals leaving progeny to continue the stock. That is, the next cycle of selection will be practiced only on their offspring with all other fish being marketed as production. The identification of fish according to family can also be a worthwhile under- taking. Since it is possible with most species of fish to obtain large numbers of offspring from individual breeders, the selected broodstock can consist of a relatively large number of fish from only a few parents. If the fish are marked by families, it is then possible to avoid matings between brothers and sisters at spawning time and thus avoid inbreeding depression in the production stock.

## Choosing the Traits

In considering characteristics of fish that might influence the efficiency of production, we could prepare a very lengthy and comprehensive list of possibly 10 or 15 traits. Obviously, it would be impossible to include all of these in a selection program simply because of the effort and expense required to gather all the information for all the fish. Great care must be taken in defining the minimum number of traits necessary for an effective program. The procedures we use to measure a trait and the stage in the life cycle at which the measurements are taken are also integral parts of the definition of the trait. We can use three criteria as guides to the genetic importance of traits we may consider in a selection program. First, the trait should define a biological entity, that is, it is a reflection of the fish's genotype. For example, selection for low egg mortality in a situation where it is known that egg mortality is determined primarily by the care with which the eggs are handled would result in selection for egg handling, not for superior breeding values of the fertility of males.

Second, the trait must be defined to represent the genotype we are interested in improving. If our primary interest is in increased growth rate of fingerlings, the measurement of growth in the first few weeks after hatch- ing is much more likely to measure the quality of eggs rather than the innate ability of the fry to grow. Use of this trait in selection would result in selection for females with superior breeding values for egg

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quality. If the measurement of growth is delayed until the fingerlings
have outgrown the maternal influence of the egg, then the trait will meas-
ure the breeding value of the fish's ability to grow. It has been
estimated that growth of rainbow trout cannot be accurately measured during
the first 150 days of life.

The third guide to the importance of a trait is the extent to which the
definition represents an economic entity. The objectives of any selection
program should be to increase economic value of the stock from the view of
net production. If a trait with little or no economic value is included
in the program, improving performance of that trait will have little or no
effect on net improvement in economic value. For example, selection for
increased egg number in a stock with high fecundity would have little net
effect because the cost of producing an egg is already minimal compared to
other production costs.

There is another very important reason for minimizing the number of traits
in a selection program. The larger the number of traits we try to improve,
the smaller the improvement we can expect in any one of the traits. This
is because we cannot critically cull individuals inferior in performance
for one trait since this same individual may be superior for some other
trait. Consequently, we are forced to compromise in culling with the result
that we tend to select a higher proportion of average individuals.

For example, if we were to select only for large numbers of eggs per female
in a rainbow trout stock that spawns at two years of age, we could expect
to achieve about a 30% improvement in ten years of selection. If, on the
other hand, we selected for both number of eggs and for large size at one
year of age, we would expect only about a 22% improvement in number of eggs
per female, a substantial loss from considering just one additional trait.
To carry the example further, if there were five more traits included in
the program, that is, a total of seven traits were selected for simulta-
neously, then we would expect only a 10% improvement in number of eggs
after ten years of selection.

However, when more than one trait is included in the program, we expect to
achieve improvement in performance for all the traits. In fact, in a
program designed to select for number of eggs and yearling weight, we
could expect a 70% improvement in yearling size as well as the 22% im-
provement in number of eggs. If yearling weight was one of the seven
traits considered in the large selection scheme, we would expect about a
40% improvement in yearling weight after 10 years.

These few examples demonstrate very clearly that the greatest total improve-
ment will be achieved if selection is practiced for all the traits important
in production performance. But it is also clear that improvement in eco-
nomic performance will be achieved only if the traits are of economic
importance. To take an extreme case, if neither number of eggs nor year-
ling weight were economically important, the selection program would pro-
duce large fish that spawned a large number of eggs but with no reduction
in the cost of production. A more realistic situation, at least under

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most conditions, would be the case in which improving number of eggs had little or no economic value but increasing yearling size was highly advantageous because the fish required less feed and reached market size at an earlier age. Then, the inclusion of number of eggs along with yearling weight in a selection program would result in only the 70% improvement in yearling weight rather than approximately a 100% improvement that might be expected if selection had been practiced for only yearling weight for the ten-year period. In other words, the net improvement in production efficiency was reduced because a trait was included that would not yield an economic improvement. Obviously, the inclusion of seven traits, as shown above, would have a drastic effect on economic improvement if they could not be shown to have significant economic impact on the production system.

The effect of inbreeding in broodstock populations received very little attention in the past even though it has been recognized as a problem, especially in hatchery stocks. Available literature reports that inbreeding causes a general decrease in growth and survival and an increase in the frequency of deformed and stunted fish.

Any discussion of inbreeding requires that we begin with a few basic difinitions of terms:

Inbreeding--the mating of individuals that are related to each other by ancestry.

Outbreeding--the mating of individuals that are unrelated.

Coefficient of inbreeding (F)--the probability that two genes at any position on the chromosomes in an individual are identical because they are derived from a common ancestor.

Inbreeding depression--reduction of the mean observed value of characters associated with reproductive capacity or physiological efficiency.

A program was begun at the Fish Genetics Laboratory in 1970 to measure the effect of known inbreeding levels on several traits directly affecting fish production. The method used to measure inbreeding depression was the differences between inbred and outbred half-sib families that were reared concurrently to one year of age in a standardized rearing environment.

The actual depression estimates tended to fluctuate from year to year and from strain to strain, but all showed patterns similar to that found in the 1974 tests (Tables 1 and 2). Significant increases in the frequency of crippled fry and feed conversion and decreases in fish survival and growth rate were found at both the $F = 0.25$ inbreeding level (one generation of brother-sister mating) and the $F = 0.375$ inbreeding level (two generations of brother-sister mating). Depression estimates at the $F = 0.375$ level were, however, markedly higher in most of the traits. Work with other inbreeding levels (not shown) clearly demonstrates that inbreeding depression increases with each increase in inbreeding. A second trend demonstrated in these studies was the increasingly pronounced effect of inbreeding on growth rate with increasing age (Tables 1 and 2). The deleterious effect of inbreeding at these two levels on number of fish produced and weight was:

| Inbreeding loss in: | F = 0.25 | F = 0.375 |
|---|---|---|
| Number of fish | 17.4% | 47.9% |
| Weight of fish (fingerling plants) | 22.3% | 54.9% |
| Weight of fish (catchable plants) | 36.6% | 65.4% |

*United States Fish and Wildlife Service Fish Genetics Laboratory, Beulah, Wyoming*

Table 1. Inbreeding depression observed in fall strain (F = 0.25) 1974.

| Characteristic | Common Female Parent[a] | | Common Male Parent[b] | | Average |
| | Outbred Mean | Depression % | Outbred Mean | Depression % | Depression % |
| --- | --- | --- | --- | --- | --- |
| Crippled fry (%) | 3.6 | 111.9 | 12.0 | -36.7 | 37.6* |
| Mean weight (g) at: | | | | | |
| 126 days | 2.4 | 1.0 | 2.7 | 8.8* | 4.9 |
| 147 days | 4.4 | 2.8 | 4.6 | 9.3* | 6.1* |
| 189 days | 14.2 | 13.1* | 15.0 | 16.8* | 15.0* |
| 364 days | 202.8 | 25.7* | 191.3 | 20.8* | 23.2* |
| Fry survival (%): | | | | | |
| To 84 days | 73.9 | 5.0 | 93.7 | 18.6* | 11.8* |
| To 147 days | 71.0 | 9.0* | 89.7 | 20.2* | 14.6* |
| Feed conversion | 1.3 | 10.4* | 1.5 | 0.8 | 5.6* |

a/ Common female parent was the same fish in both the inbred and the outbred family.
b/ Common male parent was the same fish in both the inbred and the outbred family.
* Significance at (P < 0.05).


Table 2. Inbreeding depression observed in fall strain (F = 0.375) 1974.

| Characteristic | Common Female Parent[a] | | Common Male Parent[b] | | Average |
| | Outbred Mean | Depression % | Outbred Mean | Depression % | Depression % |
| --- | --- | --- | --- | --- | --- |
| Crippled fry (%) | 11.8 | 163.8* | 10.2 | 219.1* | 191.5* |
| Mean weight (g) at: | | | | | |
| 126 days | 2.4 | -0.6 | 3.1 | 24.5* | 12.0* |
| 147 days | 4.3 | 2.2 | 5.3 | 24.6* | 13.4* |
| 189 days | 14.0 | 15.7* | 15.7 | 24.5* | 20.1* |
| 364 days | 196.3 | 35.6* | 172.5 | 31.5* | 33.5* |
| Fry survival (%): | | | | | |
| To 84 days | 49.7 | 29.3* | 65.4 | 39.3* | 34.3* |
| To 147 days | 59.1 | 19.3* | 62.3 | 40.1* | 34.7* |
| Feed conversion | 1.4 | 12.8* | 1.3 | 17.0* | 14.9* |

a/ Common female parent was the same fish in both the inbred and the outbred family.
b/ Common male parent was the same fish in both the inbred and the outbred family.
* Significance at (P < 0.05).

The actual loss to the producer will be increased somewhat above these figures because of the higher feed conversion found in inbred fish.

## What can be done about inbreeding?

Inbreeding is a natural phenomenon that occurs in all closed populations to some degree. The rate at which inbreeding occurs in a population is largely dependent upon the number of individuals that contribute progeny to the succeeding generation. As long as the population remains closed to introductions, inbreeding levels will continue to accummulate in spite of everything that the broodstock manager might do. There are, however, some basic procedures that can be implemented to reduce the rate of further inbreeding buildup.

Approaches to minimizing the amount of inbreeding accumulation fall into two categories: (1) the use of large random mating populations, and (2) the use of a rotational line mating scheme. The use of the random mating approach is the simpler approach. Here, each fish is used (excluding only seriously abnormal individuals) and matings are made as one male to one female until a sufficiently large number have contributed to the next generation Some examples of the expected inbreeding increase per generation with specific numbers of brood fish are shown below:

| Number of females | Number of males | Expected inbreeding per generation |
|---|---|---|
| 100 | 100 | 0.2% |
| 50 | 50 | 0.5% |
| 50 | 25 | 0.7% |
| 25 | 25 | 1.0% |
| 10 | 10 | 2.0% |
| 10 | 5 | 3.0% |
| 5 | 5 | 5.0% |

It is apparent, therefore, that a minimum of 25 pairs should be used as parents to hold down inbreeding and 50 to 100 pairs would be preferred. It should also be noted that it is the sex used in the smallest numbers that contributes most to inbreeding. For this reason, an equal number of males and females should be utilized. In order to obtain the number of fish needed at one spawning date, future broodstock eggs should be taken during peak spawning activity.

The second approach, rotation line crossing, is more effective in minimizing inbreeding and also allows the manager to practice intensive selection for desired traits, but requires more labor and is a more complicated system to implement. In this approach, the total population is randomly divided into three groups or lines that are maintained separately (Figure 1). During the spawning season, males of line A (dash line) are mated to females of line E (solid line), males of B to females of C, and males of C to females of A. Resulting progeny for each line are then maintained separately until maturity, when the process is repeated. Eggs for use in production programs would be fertilized in the same way as eggs for future

Figure 1. Three line rotational mating system.
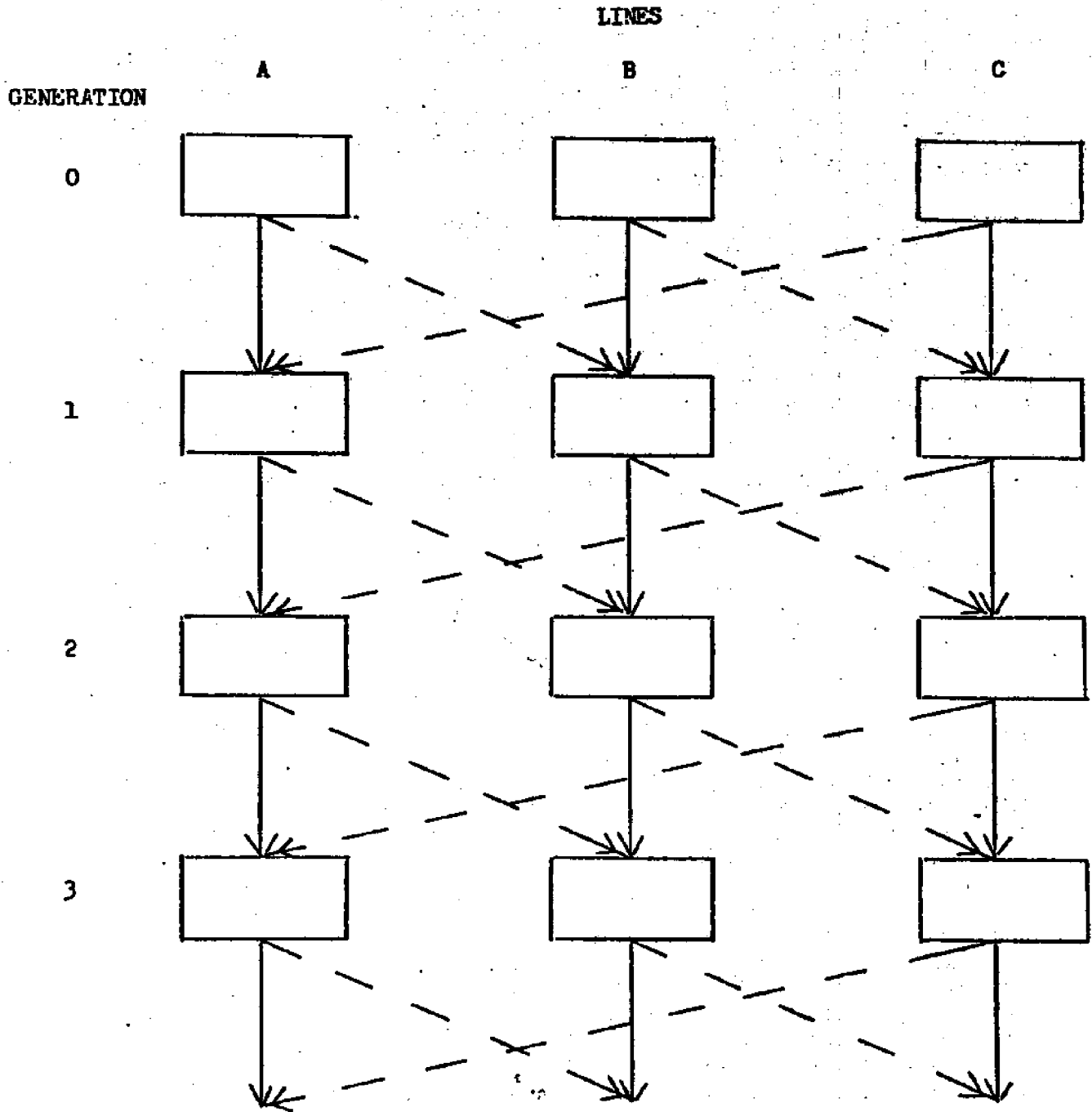
broodstock. The rate of inbreeding increases under this system will be approximately one-half that of the random mating system if the same numbers of fish are used, with one-third coming from each line.

Once inbreeding has progressed to a point where performance is unsatisfactory, the above systems will no longer help and steps will need to be taken to lower the level of inbreeding. This can be done only by introducing a new stock to cross into the existing population to produce a strain hybrid. Special care must be exercised in choosing the particular strain to be introduced. Factors to be considered are: (1) Does the new strain carry traits that are undesirable? (2) Does the new strain carry traits that will complement the present strain? (3) Are the old and new strains sufficiently different (genetically) to produce hybrid vigor? If these criteria are met, then the cross has a good chance of improving the broodstock; however, this can be assured only after the cross is made and tested in the production situation.

The three basic approaches described here for controlling inbreeding can be modified in numerous ways to meet the needs of each situation. The broodstock manager will need to decide what steps are necessary in each situation on the basis of the severity of the inbreeding problem and the planned production requirements of that broodstock.

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