International Selective Breeding Programs: Constraints and Future Prospects

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Abstract

Internationally, only a few efficient breeding programs for fish are in operation. In Norway, a national breeding program has been running since 1975 for Atlantic salmon and rainbow trout. Iceland has just started a breeding program for farming and sea ranching Atlantic salmon. Breeding programs in Canada and Sweden for farming Atlantic salmon and rainbow trout, respectively, and Israel runs a cross-breeding program for carp. Some private companies also claim to run breeding programs. The knowledge necessary to develop efficient breeding programs is available for just a few species. This includes salmonids, channel catfish, tilapia and carp. For most of the species it is not possible to carry out controlled mating and reproduction because their reproduction biology is not yet satisfactorily understood. Prospects for genetic gain in fishes are very good and are even better than in other farm animals. A genetic gain of 10 to 20% per generation has been shown to be obtainable. Because breeding programs in fish can be centralized, it is expected that the cost will be relatively low compared to most farm animals. The profitability for fish breeding programs is also likely to be very high. The most serious constraint to running a breeding program is the risk of spreading diseases from breeding centers to the farming industry, and the potential infection of wild populations. Domesticated stock may escape and spawn with wild populations, thus reducing the genetic variation and fitness within the wild strains. An interesting challenge is how to start a breeding program. All present breeding programs in Norway were initiated and implemented by research institutions. In the farm animal industry, however, private companies and farmers' cooperatives dominate. To stimulate interest and initiate breeding programs it is necessary to demonstrate potential for genetic gain in each species, and then show the benefits and economic potentials to researchers, farmers, farmers' organizations and officials.

Introduction

The purpose of a breeding program is to change the average performance of a population in a defined direction to the benefit of industry and the consumer market. A breeding program is more complex than a breeding research project, which usually studies just a part of a breeding program and examines how to make the program more efficient and more applicable.

The main elements of a breeding program include:

> Definition of the breeding goals,

> Description of the breeding and selection methods to be used,

> Detailed information of how the animals should be tested in order to estimate breeding values,

> Detailed description of how and when each trait is measured or judged,

> Economic value of each trait,

> Selection indexes to be used,

> Guidelines for selection of broodstock,

> Expected genetic change per generation.

The theoretical basis for breeding and selection was primarily conceived during the first three decades of this century. Scientists central to the development of animal breeding theory were Sewall Wright and Jay L. Lush. The first efficient breeding and selection programs in plants and farm animals were started in the mid-1930s. Since then, breeding and selection programs have been developed for plants and farm animals in most countries. The increase in productivity and product quality has been tremendous. Today one can not really think of using animals and plants not developed through breeding and selection for food production.

Conditions for a Breeding Program

It is essential that the entire reproduction cycle for the species in question be controlled in captivity to control fertilization, hatching and first feeding.

An inexpensive marking or tagging system is a great advantage and is a necessity for a breeding program that tests families.

It must be possible to measure and record traits of interest on many animals at a reasonable cost and within a certain time interval.

The industry must have interest in buying broodstock/milt/eggs/fry or fingerlings.

The economic traits included in the breeding goal must show additive and/or non-additive genetic variation.

Breeding Methods

Since inbreeding should be avoided in any breeding program there are two methods available for practical use:

> Cross-breeding - crossing strains or inbred lines and

> Pure-breeding - mating animals less related than the average in the population.

Choice of a breeding method depends primarily on the type of genetic variation present in the traits of interest.

Cross-breeding may be used if non-additive genetic variation is considerable, while selection and pure-breeding should be used to exploit additive genetic variation. Additive genetic variation is due to the additive genetic effects (intermediate) while non-additive genetic variation is due to dominance and epistacy effects. It is not always easy to decide which breeding method to use, however, Gjedrem (1985) concluded that if there is additive genetic variation, one should always apply pure-breeding combined with selection. And if the component of non-additive genetic variance is considerable, pure-breeding should be combined with cross-breeding. As a rule, cross-breeding should be part of a breeding program when the heterosis effect is larger than the expected genetic gain per generation in a pure-breeding program.

Methods of Selection

Individual selection is the most widely used method of fish selection. It is easy to practice, the cost for testing and recording to estimate breeding values is low compared to other methods of selection and it does not extend the interval between generations. However, individual selection has limitations. The efficiency is low for traits with low heritability, can hardly be used for all or none traits such as dead or alive and age at maturation, and it cannot be used for carcass quality traits. In fish breeding this usually limits individual selection to growth rate.

Since within-family selection and progeny testing have shown less efficiency, an alternative selection method family selection, can be used. (Falconer 1961; Gall and Huang 1988 a, b; Gjedrem 1985). Family selection is relatively efficient compared to individual selection for traits with low heritability, it can be applied for all or none traits, meat quality traits and it does not the interval between generations.

Family selection is of particular interest in fish because of high fecundity; large numbers of half- and full-sib groups can be produced. Since it is impossible to mark newly hatched larvae or fry, each family must be reared in separate tanks for the first months of their lives. This type of rearing will, however, introduce some environmental effects common to families.

Generally, a combination of individual and family selection will be more efficient than using just one method (Falconer 1961).

Breeding and selection in fish

- **Rainbow trout**

In their natural habitat rainbow trout are spring spawners. In 1936, Lewis (1944) started to select for fall spawning at Hot Creek Hatchery, California. Early spawning and faster growth rate was obtained by using individual selection. Selection for early spawning has been applied since then, and Siitonen and Gall (1989) observed a median spawn date of 15 August for the 1980 and 1981 year-classes. They estimated a response to selection for early spawning of seven days per generation during each of six generations.

Donaldson and Olson (1955) and Donaldson (1970) presented results from a selection experiment based on individual selection that started in 1932 at the College of Fisheries, University of Washington, Seattle. Growth rate and number of eggs per spawn increased markedly and the age at first maturation was reduced. Since there was no control group, the results were phenotypic values such as genetic response and environmental change. The selection was not continued when Donaldson retired but the Donaldson strain of rainbow trout has been distributed to many countries for fish farm use. In Sweden, Sylven and Elvingson (1992) compared Donaldson's strain with three other strains of rainbow trout and found that it ranked lowest and was 54% below their best strain, which had been selected for five generations for growth rate.

Kato (1978) selected rainbow trout for spawning twice a year in and obtained a response. After one generation of selection 40% of its progenies spawned twice a year. During three generations of individual selection for body weight at 147 days in a fall spawning stock of rainbow trout, Kincaid et al. (1977) obtained a 67% increase in body weight and a correlated response in increased hatching percentage and fry survival.

At the Rainbow Trout Symposium held at the University of Stirling, Scotland in 1990, Gjedrem (1992) discussed breeding plans for rainbow trout and described the national breeding program for rainbow trout in Norway. This program was started in 1972 and has now completed six generations of selection. In each generation about 120 full-sib families within about 30 half-sib families were tested. The selection has been on high body weight at harvest after 1.5 years in seacages (at 2.5 years of age) and low frequency of early maturity during their first winter at sea. A weak selection for survival in the freshwater period was practiced. Family selection was applied for all traits and combined individual selection and family selection was used for growth rate. Gjerde (1986) reported a genetic gain of 13% per generation for body weight in the first two generations of selection.

In Sweden, breeding programs have been developed for rainbow trout and arctic char with a similar design of that used for rainbow trout in Norway (Elvingson personal communication).

Cross-breeding of rainbow trout has given varying results. Ayles and Baker (1983) found significant heterosis for both growth and survival of some but not all crosses. Gjerde (1988) studied the heterosis effect in a diallele cross among six inbred groups. Total heterosis was significant for all traits studied. Total heterosis for weight at slaughter ranged from 17% below to 18% above the non-inbred control groups. Hørstgen-Schwark et al. (1986) found that the mean growth performance of all the crossbred fish were not significantly different from that of the purebreds.

- **Salmon**

In 1949 an individual selection program for chinook salmon under sea ranching conditions was started at University of Washington, Seattle by Lauren R. Donaldson (Donaldson and Menasveta 1961). According to Donaldson (1968), the selection response was significant for growth rate and fecundity from 1960 to 1967.

A Nordic research project in Atlantic salmon ranching was started at the Institute of Freshwater Fisheries, Iceland in 1987 (Jonasson 1993). The purpose was to study the genetic variation in return frequency and growth rate. For three year-classes a significant genetic variation in return frequencies have been obtained (Jonasson, personal communication). This project has now been transformed into a family selection breeding program in order to increase return frequencies and growth rate. Each year 100 full-sib families within about 30 half-sib groups are tested by releasing them into the sea. A corresponding number of families are used in a breeding program for fish farming. So far, records of response to selection have not been available (Jonasson, personal communication).

Hershberger et al. (1990), using combined individual and family selection for increased body weight in coho salmon during four generations, obtained an average of 10.1% gain per generation in weight over an eight month period. Realized heritabilities were estimated to be 1.22 ± 0.32 for the odd-year line and 0.81 ± 0.30 for the even-year line, while the heritability determined by ANOVA remained at a level of 0.20. The experiment was terminated after a period of

10 years when an improvement of 60% had been reached.

In Norway, AKVAFORSK started a selection program in the fall of 1971. Since the generation interval is four years in Norwegian Atlantic salmon, four year-classes were formed by sampling broodstock from 41 river strains. Selection began in the fall of 1975. Data from the first generation were used to estimate phenotypic and genetic parameters and to develop a breeding program (Gunnes and Gjedrem 1978). At present, four generations of selection have been completed in all four year-classes; selection for increased growth rate in the first two generations and for increased growth rate and low frequencies of early sexual maturation in the following generations. Since 1990, the families have been tested for resistance against furunculosis in challenge tests with one-year-old fingerlings (Gjedrem et al. 1991). Each year 120 full-sib families are tested. Selection is based on family selection for low frequency of early maturation, disease resistance and combined selection for growth rate (Refstie 1990).

Response to selection for growth rate was estimated to be 14.6% in the first generation for growth rate (Gjerde 1986). In later generations, the genetic gain has most likely been about 10% for growth rate and 8% for age at early maturation. In the third generation of the four year-classes, the selection differential for body weight was estimated to vary between 10.6 and 14.2% per generation (Gjerde, personal communication).

In 1982 AKVAFORSK approached the Fish Farmers Association to develop a national breeding program based on the AKVAFORSK stock for Atlantic salmon and rainbow trout in Norway. The national breeding program was realized in 1986 and new breeding station and multiplier stations were established. Today about 75% of all Atlantic salmon farmed in Norway comes from the national breeding program.

The Atlantic Salmon Federation, St. Andrews, Canada, has started a breeding program for the Canadian salmon farming industry. Family selection is applied for the traits; length at harvest, percentage non-grilse (salmon that do not mature their first year at sea), and percentage S^1 smolt (Friars, personal communication).

There are few reports on cross-breeding in salmon. Gjerde and Refstie (1984) crossed five strains of Atlantic salmon and estimated generally low non-additive genetic variance, particularly for traits recorded in the later stages of life.

Gjedrem et al. (1991) reviewed the literature concerning genetic variation in survival in Atlantic salmon and found it to be rather low. However, applying challenge tests Gjedrem et al. (1991) found a high heritability for resistance against furunculosis while Gjedrem and Gjøen (1993) found a moderate heritability for resistance against furunculosis, BKD and cold-water vibriosis.

Rye and Refstie (1993) estimated genetic parameters for carcass quality traits in Atlantic salmon. They found that heritability estimates were medium to high for the different traits studied. Similar results were obtained by Gjerde and Schaeffer (1989) in rainbow trout. It can, therefore, be concluded that the carcass quality traits show considerable genetic variation.

• **Carp**

A long term selection program was conducted in Israel and it was concluded that individual selection alone was not an effective method for improving growth rate in domesticated common carp (Moav and Wohlfarth 1976). However, heterosis for growth rate and disease resistance have been shown (Moav et al. 1975). Comparisons between different crosses led to the identification of two parental strains. These are practically the only brood stocks in commercial use today (Wolhfarth et al. 1987).

Suzuki and Yamaguchi (1980) studied the heterosis effect by crossing Chinese, Japanese and European races of common carp. Significant heterosis was found in seven of 12 F_1 hybrids. Of the F_1 hybrids the cross between yamato and mirror carp had the highest growth rate.

In 1963 in Russia, V.S. Kirpichnikov started selecting for resistance to dropsy disease in common carp by applying challenge tests. Individual selection within breeds produced varying results. Five generations of selection in mirror carp and Ukrainian Ropsha hybrid carp gave higher gain than seven generations in Ropsha carp. Maximum gain was found among Ukrainian Ropsha hybrid carp. After the fifth generation of selection, the selected line had a mortality of 10.7% compared to 51.0% in the control group (Ilyassov 1987).

• **Channel catfish**

Dunham (1987) reported that the domesticated strain grew faster than wild strains. One generation of individual selection for growth rate in channel catfish gave genetic change of 12 to 18% in all populations evaluated. Bondary (1983) used a combination of family and individual selection for high and low growth rate at 40 weeks of age. Body weight changes, measured as deviations from control line, were about 20% in both directions. Realized heritability for body weight was estimated to 0.10.

Cross-breeding among strains of channel catfish selected for improved body weight has also been studied. Fifty-five percent of the crosses resulted in positive heterosis for growth rate (Dunham and Smitherman 1983). They conclude that heterosis declined over time. Dunham (1987) showed that cross-breeding can also improve disease resistance.

• **Tilapia**

Jarimopas (1988) reported a response to individual selection for body weight in red tilapia of 15.7% after the second generation. However, Hulata et al. (1989); Teichert-Coddington and Smitherman (1988) and Huang and Liao (1990) found no response to individual selection for body weight in Nile tilapia.

In the Philippines, a breeding experiment with Nile tilapia called Genetic Improvement of Farmed Tilapia (the GIFT project) has been carried out since 1988 (Pullin et al. 1991). The first generation was a comparison of seven tilapia strains. In the second generation a full diallele cross between eight tilapia strains was completed and a weak selection for growth rate was practiced among the pure and cross-bred groups produced in the third generation. In the fourth and fifth generations selection for body weight took place based on combined family and individual selection. The response to selection was 23% in body weight in the fourth generation and the fish in the fourth generation grew 70% faster than the most commonly produced strain in the Philippines (Eknath, personal communication).

The selected fish from the GIFT project will be used to start a national breeding program in the Philippines this year. International Center For Living Aquatic Resources Management (ICLARM) is building up an international network of ten countries in Asia and Africa with the purpose of starting national breeding programs and disseminating fish from the GIFT project (Eknath, personal communication).

Genotype - Environment Interaction

When planning a breeding program it is important to know if genotype-environment interactions are present. If there is no interaction, the breeding plan can concentrate on the best strain or combine the best strains into a synthetic population. On the other hand, if a significant genotype-environment interaction exists, the response to selection will be reduced and consequently, it may be desirable to develop strains for different environments.

In rainbow trout, Atlantic salmon, tilapia and selected lines of channel catfish negligible genotype-environmental interactions have been found (Gunnes and Gjedrem 1981; 1978; Eknath, personal communication; Dunham 1987). In common carp and cross-bred channel catfish genotype-environment interaction has been shown (Moav 1976; Dunham 1987). The magnitude of the interaction must be determined before deciding how many strains will be used in a district or a country.

Prospects for Genetic Gain

The conclusion from the review of different species is that there exists considerable additive genetic variation in most of the economic important traits studied. This means that selection programs will give response. Results from cross-breeding experiments vary from one experiment to another and consequently it is not possible to conclude whether cross-breeding should be used in a breeding program.

In the large scale selection programs that use a combination of family and individual selection carried out in Atlantic salmon (Gjerde 1986), coho salmon (Hershberger et al. 1990), rainbow trout (Gjerde 1986) and tilapia (Eknath, personal communication) the genetic gain in body weight per generation varied between 10.1% and 23.0%. Considerable genetic gain has also been obtained for age at maturation (Gjerde 1986) and disease resistance (Ilyassov 1987; Gjedrem et al. 1991).

The genetic gain obtained in fish is higher than in farm animals. The main reason might be that it is possible to have a higher selection intensity in fish because of high fecundity. The genetic variation of growth rate is very high and is usually much higher than in farm animals.

The profitability for a breeding program in fish is therefore likely to be very high. Gjerde and Olsen (1990) estimated the economic value of a genetic gain of 10% in body weight and 8% in reduced frequency of early maturation equal to US$0.20 per kg produced per generation in Atlantic salmon. For a production of 100,000 tons, the economic gain will be in the order of US$20 million per year while the yearly cost to run the breeding program will be around US$2.5 million.

Constraints for a Breeding Program

A breeding goal is likely to remain constant for traits like growth rate and disease resistance. However, for traits like meat quality, consumers may change their opinion and prefer a quality that differs from the one selected. This type of risk is difficult to avoid. However, it is very important for a breeding organization to carefully study market preferences particularly concerning product quality.

When a breeding program is centralized, as discussed above, there is a risk that infectious diseases can be transferred from breeding centers to the industry and cause problems. To avoid this it is extremely important that breeding centers and multiplier stations work within strict hygienic standards, carefully control the importation of new fish and do everything possible to produce healthy fish.

Genotype-environment interaction must be investigated at the start of a breeding program. In the GIFT project the strain-environment interaction was negligible for body weight and survival when the eight strains were tested in several very different environments (Eknath et al. 1993). In Norway, genotype-environment interaction represented between 1.2% and 5.5% of the variation in body weight in Atlantic salmon and rainbow trout studied under a variety of environmental conditions (Gunnes and Gjedrem 1978; 1981). As a result, selection can be carried out in a single population for each year-class.

When reproducing species with high fecundity, inbreeding can occur rapidly. Since inbreeding reduces fitness and growth, it must be kept at a minimum. In a breeding program based on tagged families it is quite easy to avoid mating close relatives. When individual selection is used without fish identification, it may be difficult to avoid inbreeding. However, it should be possible to reduce the inbreeding problem by dividing the breeding population into at least two subpopulations. Broodstock should be selected and produced within each subpopulation and fish for farming should be produced by crossing subpopulations.

Fish selected for farming often become domesticated. These fish are considered a potential problem as some of them may escape and mix with wild stocks of the same species. In particular, there are two potential problems:

> The escapees may be disease carriers. If these fish mix with wild fish they may spread the infection,

> The domesticated fish may interspawn and reproduce or cross with the wild population. It is argued that this type of hybridization will reduce the genetic variation between the wild strains and reduce their fitness.

The transfer of diseases between farmed and wild fish may be a problem and should be taken seriously. Reduction of escapees and preventing disease is the best way to reduce this problem. Concerning the genetic influence from domesticated fish, fish farmers should do their utmost to reduce escapement. This is also in their own economical interest. So far it has been shown that escaped domesticated Atlantic salmon will spawn and the eggs will hatch in rivers. However, little is known about how the fry of domesticated parents may compete with wild fry in the river. Since domesticated fish have been selected for a life in captivity, it is not likely that they can compete in the wild. If they are not well adapted, natural selection will reduce their frequency in the next generation. It should be taken into account that all selected traits in a breeding program are quantitative traits, which are regulated by a large number of genes and that each generation of selection will lead to minor change in gene frequencies.

Another constraint mentioned in connection with selection programs is a possible reduction of genetic variation. According to Falconer (1961) inbreeding will reduce genetic variance. The effect of selection on the genetic variation has been discussed by several authors. Fimland (1979) showed that a small reduction in the genetic variation is expected during the first generations of selection until stabilization is reached. The level of this stabilized state depends on selection intensity of parents and the accuracy of selection. If the accuracy of selection does not exceed 0.6 the stabilized level will not be lower than 80%. The true variation will be reestablished to the initial variation if selection is terminated. Enfield (1974), selecting for pupa weight in tribolium in 120 generations, found no reduction in genetic or phenotypic variation during the selection period. Long term breeding programs of large populations of farm animals, normally do not result in reduction of genetic variation.

Recommendations

Family information should be used in a breeding program for fish because:

> Combined selection is more efficient than individual selection,

> For economic traits like disease resistance, age at maturation and meat quality, individual selection is inefficient and partly impossible,

> In order to identify the fish and keep pedigree records to avoid inbreeding, families must be reared separately until tagging. Family information will then be available,

> A combination of family and individual selection is more efficient than each of them alone.

It is possible to produce large numbers of eggs and sperm from a few selected fish. Consequently, the breeding work can be centralized and only a few breeding centers are needed. A breeding center should be able to test a large number of half- and full-sib families each year. The breeding center must be able to control the entire life-cycle of the fish and testing should be done under environmental conditions similar to those found in the farming industry.

When testing, estimations of breeding values and selections are centralized. The breeding work, therefore, can be conducted in a more sophisticated way by applying available theoretical and practical knowledge. The fish farmer should receive egg/fry/fingerling or broodstock. The farmer needs no new technology and no new equipment to grow improved fish. Introduction of breeding programs in aquaculture is of interest particularly in developing countries because of needs for increased protein production.

Families breeding values should be based on test results from several private farms under commercial conditions. If family testing is conducted in an experimental environment, there is the risk of developing a population unsuitable in some commercial environments, although the genotype-environmental interaction is low.

If the genotype-environment interaction is considerably more, then one population should be developed. The number of populations needed will depend on the magnitude of the interaction. Thus, to avoid an environment where the improved fish do not adapt well, it is important to carefully study the genotype-environment interaction in a breeding program.

The improved fish will grow faster and the farmer can chose to grow the same size fish using a shorter production time, or grow bigger fish using the same production time and improved fish. The increased survival of the improved fish will result in a larger biomass production and the reduced use of antibiotics. If meat quality is included in the breeding goal, the farmer will be able to market a better quality fish at a higher price. The end result for the farmer should be higher production of better quality fish and a reduction in production costs.

By applying selection, the fish farmer creates an advantage over fisheries. Farmers can produce a quality product when the consumer wants it any time of the year.

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