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Gjerde B., Rye M.

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Design of breeding programmes in aquaculture species: Possibilities and constraints

B. Gjerde and M. Rye
Akvaforsk, Institute of Aquaculture Research Ltd
N-1432 ås, Norway

SUMMARY - Most aquaculture species are genetically much closer to their wild counterparts than are important terrestrial animals and plant species used in agriculture. The prospect for improvement of aquaculture stocks by utilizing additive genetic variance, documented in several aquatic species during the last 15-20 years, should be exploited through long term selective breeding programmes to develop high performing breeds. Crossbreeding to capitalize on non-additive genetic effects, polyploidy or sex manipulation, may be applied for further improvement. The high fecundity of aquatic species allows large genetic gains to be obtained through high selection intensities. However, a small number of breeding individuals may account for a large proportion of the genetic makeup of successive generations. Hence the rate of inbreeding may be high resulting in fitness depression, loss of additive genetic variance and high response variability. Consequently, great attention must be paid both when designing and implementing selective breeding programmes in aquatic species. The high fecundity facilitates concentration of resources in one or few breeding centres. Genetic gain obtained in the nucleus may be disseminated throughout the industry with a minimum delay through multipliers. The high fecundity makes it possible to have a broad long term breeding objective in the nucleus, while at the same time applying selection for a single or a few traits when producing grow-out animals. High benefit/cost ratios are therefore to be expected in breeding programmes for aquatic species. The two greatest obstacles of efficient family selection programmes are the present tagging system for which family groups have to be reared separately until individuals are large enough to be tagged and the lack of methodology to record traits on live breeding candidates. Microsatellite DNA profiling for family identification represents a major advance in selective breeding of aquatic species allowing different family groups to be kept in a common tank from fertilization onwards.

Key words: Breeding programmes, design, aquatic species, improvement strategies, selection methods.

RESUME *- "Conception de programmes d'amélioration génétique chez les espèces aquacoles : Possibilités et contraintes". La plupart des espèces aquacoles sont génétiquement beaucoup plus proches de leurs congénères sauvages que ne le sont entre eux les grands animaux terrestres et espèces végétales utilisés en agriculture. Les perspectives de l'amélioration des populations aquacoles moyennant l'utilisation de la variance genétique additive, décrites pour plusieurs espèces aquatiques pendant ces 15-20 dernières années, devraient être exploitées au travers de programmes de sélection à long terme afin de mettre au point des races hautement performantes. Les croisements, pour valoriser la polyploïdie à effets génétiques non additifs, ou la manipulation des sexes, peut être appliquée pour avancer encore dans l'amélioration. La grande fécondité des espèces aquatiques permet d'obtenir de forts gains génétiques par de fortes intensités de sélection. Cependant, un petit nombre d'individus en reproduction peuvent être responsables d'une grande partie de la constitution génétique des générations ultérieures. De là que le taux de consanguinité puisse être élevé et résulter en dépression de la vigueur, perte de variance génétique additive et grande variabilité de la réponse. Par conséquent, il faut faire attention lors de la conception et de l'application de programmes de sélection chez les espèces aquatiques. La grande fécondité facilite la concentration des ressources dans un seul ou quelques centres d'amélioration génétique. Le gain génétique obtenu dans ce noyau doit être diffusé dans l'industrie dans un délai minimum au travers des multiplicateurs. La haute fécondité fait qu'il soit possible d'avoir un vaste objectif d'amélioration à long terme dans le noyau, tout en appliquant la sélection pour une ou plusieurs caractéristiques lors de la production d'animaux adultes. Des rapports élevés bénéfices/coûts sont donc à espérer pour les programmes d'amélioration génétique des espèces aquatiques. Les deux plus grands obstacles pour des programmes efficaces de sélection familiale sont le*

système actuel d'identification et par conséquent les groupes familiaux doivent être élevés séparément jusqu'au moment où les individus ont suffisamment grandi pour les identifier par étiquette, ainsi que le manque d'une méthodologie pour enregistrer les caractéristiques sur les candidats vivants à l'amélioration. Les profils à l'aide d'ADN microsatellite pour l'identification familiale représentent un grand progrès pour la sélection chez les espèces aquatiques, car ceci permet d'élever plusieurs groupes familiaux dans un réservoir commun à partir du moment de la fertilisation.

***Mots-clés** : Programmes d'amélioration génétique, conception, espèces aquatiques, stratégies d'amélioration, méthodes de sélection.*

Introduction

The science of applied selective breeding and genetics has contributed greatly to the steadily increasing productivity in animal husbandry and plants. Today the high yields from agriculture are based almost entirely on genetically improved domesticated breeds. This has not been true for aquaculture where the supply of fish is mainly based on harvesting wild populations. Aquatic species are therefore, in the genetic sense, still much closer to the wild state than are the major terrestrial animals and food crops (Eknath *et al.*, 1991). Recent estimates show that less than 1% of the world's total aquaculture production is based on genetically improved stocks (Gjedrem, 1997). There is therefore a great disparity between the need for increased aquaculture production and the genetic quality of the stocks available to meet that need.

Breeding programmes in aquaculture are scarce. However, during the recent years the prospects for substantial genetic improvement have been well documented in several species (e.g., Gjedrem, 1983, 1985; Eknath and Doyle, 1990). This potential should be exploited through long term genetic breeding programmes to develop better performing breeds for aquaculture purposes.

In aquaculture research the main focus so far has been on increasing the productivity through the improvement of management procedures related to the rearing environment, feed and feeding practices, control of diseases, etc. However, full benefits of investments in management improvements can only be obtained through genetically improved animals that are able to take full advantage of these improvements.

Fecundity, inbreeding and effective population size

The possibility in many fish species to strip and collect eggs and milt separately makes it possible to obtain a wide variety of family groups designs. A high number of large full-sib as well as maternal and/or paternal half-sib groups may be produced from a set of simultaneously stripped spawners, and spawning may often be synchronised or induced. In traditional farmed animals these options are not available or at least very difficult to obtain.

The high fecundity of most fish allows higher genetic gains to be obtained compared to farm animals through high selection intensities. This means that a very small number of individuals can make a large contribution to the genetic make-up of

successive generations. Hence the rate of inbreeding can be high, resulting in depression in fitness and other important traits (Gjerde *et al.*, 1983) and loss of additive genetic variance counteracting further genetic improvement. As a result, the farmers may observe poor survival and growth of the seed and wild broodstock is therefore often used to 'refresh' culture stocks (Eknath and Doyle, 1990).

The detrimental effects of inbreeding can be important even with selection procedures which do not make use of family information (Gjerde *et al.*, 1996). Also, the use of a small number of parents can lead to highly variable responses, a measure of the risk of breeding programmes (Nicholas, 1989; Meuwissen and Woolliams, 1994; Gjerde *et al.*, 1996). Consequently, restrictions on the rate of inbreeding to limit its negative effect are important when implementing selective breeding programmes in fish. Greater care therefore has to be taken both when designing and running selective breeding programmes in aquatic species as compared to programmes for farm animals.

The high fecundity in fish make it possible to have a broad long term breeding objective in the nucleus, while at the same time applying selection for a single or a few traits when producing grow-out animals and thus reducing the conflict between short term and long term breeding objectives as seen in breeding programmes for livestock species.

Base population

The importance of considering the genetic base when starting selective breeding for additive genetic performance in fish has been demonstrated in selection experiments failing to show response (Moav and Wohlfart, 1976; Hulata *et al.*, 1986; Teichert-Coddington and Smitherman, 1988). The authors suggests that genetic bottlenecks and high level of inbreeding may have limited the genetic variation significantly by the start of the experiments. The genetic variability in the base population may be secured by forming a synthetic population that is composed of several genetically diverse populations or stocks (Skjervold, 1982); this strategy has been followed in breeding programmes for Atlantic salmon and rainbow trout in Norway (Gjedrem *et al.*, 1987), for Nile tilapia in the Philippines (Eknath *et al.*, 1993) and for rohu carp in India (Reddy *et al.*, 1996).

Even if cultured stocks are available, wild populations may be valuable contributors to a synthetic population because of the moderate genetic difference between wild and cultured stocks. This has been clearly demonstrated when establishing the base population of Nile tilapia in the Philippines (Eknath *et al.*, 1993) and of rohu carp in India (Reddy *et al.*, 1996).

Improvement strategies

Several genetic improvement strategies are available. From traditional farm animals it is known that additive genetic improvement is the best strategy for long term progress. The basic requirement of this strategy is that the traits we want to improve show additive genetic variation. Continuous response to selection depends

on the maintenance of genetic variation which will be maintained through properly designed and run breeding programmes. Experiences from breeding programmes in farm animals and new findings in fish (Gjerde *et al.*, 1996) may be used to obtain an acceptable rate of inbreeding accumulation and to avoid genetic bottle-necks. Selection may then be carried out over many generations without serious loss of genetic variation.

The breeding strategies that may be applied to produce commercial fry are less restricted than those for breeding within the nucleus. Crossbreeding, ploidy manipulations, sex manipulation, etc. may be applied to increase further the productivity of the commercial fry.

For body weight, generally low non-additive effects (<10%) are reported when crossing different stocks of rainbow trout (Ayles and Baker, 1983), Atlantic salmon (Gjerde and Refstie, 1984), Nile tilapia (Bentsen *et al.*, 1997) and Indian rohu carp (Gjerde *et al.*, 1997). Although higher heterotic effects (up to 30%) are reported in common carp (Bakos, 1979; Wohlfarth, 1993; Suzuki and Yamaguchi, 1980), some of the pure stocks appear to perform as well as the best strain cross.

Results from the above studies on Atlantic salmon, Nile tilapia and rohu carp suggest that the specific non-additive effect of crossing two specific stocks may be more important than the general non-additive effects of crossing several stocks. The specific effect may not be predicted from the general non-additive effects of each stock. The study on Nile tilapia also suggest that additive genetic performance may be more robust towards environmental variation, a finding that should be tested in other species as well.

A recent study on Atlantic salmon (Rye and Mao, 1997) indicate that non-additive genetic effect constitute a significant proportion of the total variance for growth. The possible utilisation of this component in an applied breeding program need further study.

The successful exploitation of heterosis by maize breeders using the inbred-hybrid technique during the second quarter of this century stimulated animal breeders to investigate this as a possible scheme for controlled hybridisation of poultry and swine (Bell, 1982). This approach, however, failed in animal breeding due to poor viability of inbred individuals and the time and cost required to produce inbred lines (Bowman, 1959). In domestic animals and poultry, deliberate inbreeding is now utilised for experimental purposes only (Abplanalp, 1974). Further, according to Falconer (1989), the largest improvement in hybrid maize comes from additive variance in the base population. These experiences should not be ignored by fish breeders.

Developments in the techniques of gynogeneses and sex reversal (Thorgaard, 1986) could facilitate fast production of inbred lines in fish. However, unless the inbred lines are derived from different base populations, inbreeding and crossing without selection for additive gene effects will not produce any genetic improvement. In addition the lines must be crossed to evaluate their crossbred performance. Therefore, the cost and time involved in developing and test-crossing inbred lines

would only be justified by large heterotic effects compared to the expected selection response over the same period of time.

Selection methods

Several selection methods are available to exploit the additive genetic variation. The methods differ with respect to which type of relatives provide information used for the selection decisions. Which method to choose depends on several factors. Among the most important are the heritability of the trait(s), the nature of the trait (e.g., normally distributed or binary; whether records can be obtained on live individuals etc.) and the reproductive capacity of the species. The objective of all methods is to maximise the probability of correctly ranking the animals with respect to their *breeding values*, an estimate of each individual's ability for producing high/low performing offspring.

The breeding value of an individual cannot be measured directly. It can only be estimated on the basis of the phenotypic values of the trait(s). Due to the high fecundity in aquaculture species the selection methods usually applied are *individual selection* (mass selection), *family selection* or a combination of the two (*combined selection*). For none of these selection methods can the breeding values be estimated with 100% accuracy. The true breeding values will therefore remain unknown and to a certain extent will be masked by environmental effects and possibly by gene interaction effects (non-additive genetic effects).

Individual selection

When breeding candidates are selected according to their own phenotypic performance only, this is called individual or mass selection. Individual selection is currently the most frequently applied selection method in fish, mainly because it is relatively easy to perform. However, it can only be applied for traits that can be recorded on the breeding candidates while alive. The method is thus difficult to practice for carcass quality traits and will also be inefficient at low or high frequencies for binary traits like survival and age at sexual maturity. Advances in cryopreservation and cold storage of gametes may mean that animals can contribute gametes when they are no longer alive.

Individual selection requires substantial precautions in order to avoid inbreeding. Such norms are often violated or not known by seed producers. Stocking of large families for testing may easily result in a high representation of individuals from few groups only among the selected broodstock. This effect may be further strengthen by large systematic environmental effects (e.g., age and tank/cage differences). As a result seed quality become poor due to the negative effect of inbreeding, expressed as poor survival and growth. Introduction of individuals from a different stock will counteract the negative effects of inbreeding, but may at the same time prohibit improvement of the genetic level in the cultured stocks relative to the genetic level of introduced stock.

To prevent accumulation of inbreeding when applying individual selection, the selection of large numbers of sibs from a limited number of families must be avoided. This can be solved by pooling a restricted number of individuals from each family at fertilization or shortly thereafter (Gjerde *et al.*, 1996).

Family selection

Several important economic traits in aquaculture species cannot be recorded on live individuals (e.g., carcass quality traits) and at high or low frequencies for binary traits, such as survival and sexual maturity, mass selection become inefficient. For such traits family selection may be successfully applied. Breeding candidates are ranked on the basis of records made on its full- and half-sibs. Information on relatives can be used because the breeding candidate and its relatives share common genes. Records on relatives of more remote relationships than half-sibs will contribute little to the accuracy of the estimated breeding values.

The high fecundity in aquatic species permits testing of sub-samples of each family in a variety of test environments and for different traits. Sub-samples may also be submitted to tests that can not be carried out in a commercial test environment (e.g., challenge tests for diseases).

The efficiency of family selection rests on the fact that the random environmental effects affecting individual animals tend to cancel each other out when the mean phenotypic value of the family is calculated. The phenotypic mean of the family will therefore reflect its genotypic mean. The advantage of family selection compared to individual selection is greater when environmental deviations constitute a large part of the phenotypic variance and when family sizes are large. Thus, the chief circumstances under which family selection is to be preferred are when the trait selected for has a low heritability and when large families can be produced. The high fecundity in aquaculture species make family selection important for these species. To obtain an acceptable rate of genetic gain and to keep the rate of inbreeding low, however, the number of family groups tested when applying family selection must be high (>100). This becomes increasingly important when additional traits are included in the breeding objective.

Systematic environmental effects common to members of a family may severely impair the efficiency of family selection schemes. If this component becomes large, it will mask the genetic differences between the families and prohibit accurate ranking of the families according to their genetic values. Under such circumstances family selection will become ineffective. To reduce the common environmental component to a minimum, the environment for all family groups should be standardised as much as possible in the period the groups are kept separate. In addition, individuals from all groups should be tagged as early as possible and subsequently reared together in the same tank, pond or cage.

In a future family design all records may be collected from parallel full- and half-sib groups tested outside the breeding nucleus. The breeding nucleus may then focus entirely on the production, tagging and distribution of fingerlings from a large number of families, and on securing the necessary broodstock to carry out family selection.

The management of the breeding nucleus may focus more on protecting the broodstock against accidents, diseases etc. than on providing a commercial farm environment. However, the lower selection intensity in such a design have to be compensated for by a higher number of tested family groups.

Combined selection

By combining family and within-family selection, the additive genetic variance both between and within families will be utilised in an optimal way. This will maximise the rate of genetic gain and is therefore considered as the optimal selection method when applicable.

When sib records are used to estimate the breeding values, the siblings will tend to have more similar breeding values than under individual selection. The probability of selecting large numbers of sibs from a limited number of families will then be higher. Consequently, the need to restrict the number of selected individuals from each family is more important when applying combined selection as compared to individual selection. However, in a population where family identity can be attained through tagging, this restriction may be implemented after the performance test instead of at fertilisation or shortly thereafter as for individual selection.

For a given population size and a given restriction on the rate of inbreeding, the optimum design when applying truncation selection will therefore have to consist of more and smaller full- and half-sib groups than is the case for optimum mass selection designs (Gjerde *et al.*, 1996).

One or several breeding programmes

The extremely high fecundity in fish species facilitates concentration of available resources in a limited number of breeding centres (nucleus breeding). Genetic gain in the nuclei may be disseminated throughout the entire industry with a minimum delay through one or two level(s) of multipliers. Whatever achieved in the breeding nucleus may consequently have an extensive and immediate impact on the industry. High returns on the investments are therefore to be expected in fish breeding programmes (Gjedrem, 1997) as compared to programmes for farmed animals (Mitchell *et al.*,1982; Barlow, 1992).

In most fish species, the amount of commercial eggs or fry that may be supplied from a single breeding nucleus through multipliers will probably be more limited by technical and organisational constraints than by biology. However, splitting the breeding program in two or several independent populations may be desired for several reasons.

Firstly, a single, closed breeding nucleus will always be subject to long term accumulation of inbreeding and random loss of genetic variability. Genetic variability is critical not only for the response to selection in each generation, but also for the long term limits of response (e.g., Falconer, 1989). Securing a wide genetic variability in the founder population of a breeding program is of course crucial, but

strategies to maintain the variability through generations of selection are also required. Due to the much lower reproductive capacity in farm animals, the problems of loss of genetic variation is less than in fish species and may also be solved by introducing broodstock from other well performing populations (open breeding strategies). However, present and future fish breeding programmes may easily run for generations as the only program for a given species and breeding goal. As response to selection accumulates, the negative effects of introductions from outside the program increases. Splitting the program in two or more separate populations will facilitate exchange of broodstock between populations to re-establish variability within population and to neutralise accumulated inbreeding.

Secondly, a single breeding nucleus is vulnerable to accidents due to technical breakdown or diseases. Infectious diseases may also require stamping out procedures in the nucleus to prevent dissemination of infected fingerlings to the industry. A backup of the nucleus families may be stocked in a separate facility, but will not be immune to infections acquired before separations. Splitting the breeding program in parallel, independent programmes provides a higher level of security

Thirdly, the farming of aquaculture species is widespread and takes place under different climatic conditions and in a wide range of production systems. If the rank correlation of genetic groups tested in different environments is low, the breeding program may be split in two or more populations with performance in each environments as breeding objectives.

Results from studies on genotype by environment interaction in fish vary. Low genotype by environment interaction is found in Nile tilapia raised in a variety of freshwater systems (Eknath *et al.*,1993), Atlantic salmon (Gunnes and Gjedrem, 1978), rainbow trout (Gunnes and Gjedrem, 1981) and rohu carp (Reddy *et al.*, 1996) while significant interaction is reported both for common carp (Moav *et al.*,1975; Wohlfarth *et al.*,1983) and rainbow trout (Sylvèn *et al.*, 1991). Consequently, the need for specialised stocks can only be evaluated based on performance data obtained in the actual range of production environments.

Forthly, transport of live animals involves the risk of transfer of parasites or diseases to new geographic areas. There may be legal concerns and practical limitations when it comes to regulation and control of such transports. Without efficient local breeding programmes, it will be more difficult to withstand the pressure for introduction of new stocks. Selective breeding of local species should therefore be encouraged and supported by transfer of knowledge in quantitative genetics and applied fish breeding (Bentsen, *et al.*, 1992). If these improved species are desired for export, several codes of practice and guidelines may be consulted (Bartley *et al.* 1996).

It may also be argued that competition between several independent breeding units may benefit the efficiency of the breeding programmes. However, the long term efficiency of a breeding program may hardly be evaluated on a year to year basis. Market competition may consequently be a poor guide for the breeding units, and the costs of maintaining several parallel breeding programmes will be considerable. On the other hand, the quality of commercial eggs or fry may be highly variable due to different management procedures, e.g., on the multiplier level. Market competition

may then be beneficial to encourage optimal management procedures in the dissemination of the improved stock (Bentsen, 1990).

Constraints

Currently available tagging systems represents a major restriction for further development of family selection programmes in aquaculture, since family groups have to be reared separately until individuals are large enough for tagging. This requires costly multi-tank facilities, and may also introduces systematic environmental effects common to sibs. This may severely reduce the efficiency of family selection schemes. For some species (e.g., molluscs and crustaceans) no reliable physical tagging method is available.

The development of microsatelitte DNA profiling techniques for family identification represents a milestone in selective breeding of aquatic species. These techniques allows different family groups to be kept in a common tank from fertilisation onwards, substantially reducing the rearing costs involved and eliminating problems related to common environmental effects. It also enables larger numbers of families to be tested and thus facilitates the use of higher selection intensities without rapid accumulation of inbreeding.

As genetic identification obviates the need for physical tagging, only surviving individuals need to be identified. This is particularly valuable in species where culture is undertaken only for part of the life cycle and the harvested fish constitute a rather small proportion of the total number released. The wire tags presently used in sea ranching programmes (Jonasson *et al.*, 1997) can not be read on live individuals and imposes severe constraint on the use and mating of the best individuals.

Lack of methodology to record traits on live breeding candidates represents another important constraint. In the breeding program for Atlantic salmon in Norway, as an example, only one out of the seven traits selected for can be recorded on live individuals. If such methodology was available a much higher selection intensity could be applied and thus a higher genetic gain be obtained. Alternatively, today's genetic gain could be obtained by testing a lower number of family groups. The development of such methodology should be encouraged.

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