DESIGN OF FISH BREEDING PROGRAMS

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INTRODUCTION

Even though fish farming has been widely practised for thousands of years, the farmed fish species have not gone through a process of genetic domestication comparable to that of farmed species of mammals and birds. Comparison tests show that wild fish stocks may perform as well as farmed stocks in culture (see eg. Eknath et al. 1993). Some of the farmed species have not been reproduced in captivity until recently or have only been common in culture for a few decades. In traditional farmed species, wild broodstock is often used to "refresh" culture stocks, probably because of the lack of controlled mating procedures to prevent inbreeding.

The genetic productivity of domesticated populations of mammals and birds is often at least 3-5 times higher than that of their wild progenitors, and substantial progress has been made during the last 40-50 years through the application of modern animal breeding theory. Attempts have been made to apply a variety of such strategies in populations of farmed fish (see eg. review by Bentsen, 1990). The main challenge of aquaculture geneticists today will be to develop domesticated breeds of fish for farming of a similar genetic superiority compared to their wild progenitors as in the traditional domestic animals.

It is obvious that the most realistic way to achieve this is to imply long term breeding programs to utilize the potential for improved additive genetic performance. Simply screening available stocks for superior strains or strain hybrids will not provide the industry with the kind of fish material it will need in the future. Most crossbreeding experiments with fish show low to moderate heterosis for performance traits (se eg. Gjerde & Refstie, 1984, Dunham, 1987, Márián, 1987, Wohlfarth, 1993), and heterotic gain may not be accumulated like additive gain. The prospects of improving the performance in applied fish farming by genetic engeneering to a level that may be compared to terrestrial farm animals are uncertain. The following will consequently focus on the design of programs for continuous additive genetic improvement. The costs of the programs will not be evaluated.

PROSPECTS OF ADDITIVE GENETIC PROGRESS

The important parameters determining additive genetic progress per generation in a breeding program are: The accuracy of selection (the correlation between true and estimated breeding values), the genetic variation in the population, the selection intensity, and the inbreeding depression. In addition, the progress per year will depend on the generation interval.

The components affecting the accuracy of selection are the heritabilities and the genetic correlations of the traits under selection and the family information (the number and the type of relatives tested). The heritability of growth and reproduction in heterogeneous fish populations seems to be comparable to traditional farm animals, and the genetic variability evaluated by the coefficient of variation often seems to be wider (see eg. reviews by Gjedrem, 1983, Kinghorn, 1983, Gjerde, 1986), even if heritability estimates close to zero have been reported in some experiments. The heritability of fitness related traits in a farm environment sometimes seems to be considerably higher in fish populations (see eg. Gjedrem et al. 1991, Gjedrem & Gjøen, 1994), probably reflecting a lack of genetic adaptation to the unfamiliar farm environment. Furthermore, the accuracy of selection may easily be improved substantially in fish breeding by utilizing family information from large groups of simultaneous full sibs and half sibs. Correlations between individual breeding values and mean performance of full sibs or half sibs may approach the maximum values of 0.71 and 0.50 resp., even

at low heritabilities (see eg. Falconer, 1989).

The generation interval in fish breeding programs may vary considerably depending on the species, from less than a year (tilapias) to 3-4 years (eg. some salmon and carp species). This is similar to the range of biological generation intervals in farmed animal species. However, the realized generation intervals in farm animals are often increased to collect post maturation records or to improve the accuracy of selection by accumulating records from younger relatives (eg. sibs or progeny). This is normally not required in fish breeding programs.

Because of the high fecundity, it is often argued that extremely high selection intensities may be applied in fish breeding programs. However, high selection intensities may easily result in high rates of inbreeding. Reduced productivity caused by inbreeding depression has been documented in fish populations (see eg. Kincaid, 1976a,b, Gjerde et al., 1983), and is widely considered to be a problem in commercial fish farming (see eg. Eknath & Doyle, 1990).

In a breeding program, where the broodstock is not randomly chosen, the rate of inbreeding will be determined not only by the number of spawners used, but also by the genetic relationship between them (Wray & Thompson, 1990). Because of the large sib groups and the wide genetic variability in many fish populations, the best performing individuals may easily all come from a low number of full sib families. Consequently, the number of individuals that may be selected from each sib group should be restricted to avoid inbreeding depression. This may reduce the selection intensity in fish breeding programs to a level that may be compared to intensive breeding programs with farm animals.

Based on the considerations above, the prospects of additive genetic progress is at least as good in fish breeding programs as the progress achieved in farm animals during the latest decades. Progress rates of 10-20% per generation have been achieved in several selection experiments and programs (see eg. Bondari, 1983, Gjerde, 1986, Dunham 1987, Hershberger et al. 1990)

BREEDING PROGRAM STRUCTURES

The extremely high fecundity of most fish species facilitates concentration of available resources in a limited number of breeding centres (nucleus breeding). Genetic gain in the breeding nucleus may be disseminated throughout the entire industry with a minimum delay through one or two level(s) of multipliers. Additive genetic gain may also be utilized efficiently outside the breeding system through on-farm reproduction. Whatever achieved in the breeding nucleus may consequently have an extensive and immediate impact on the industry, and the cost to benefit ratio will be low.

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

Firstly, a single, closed breeding nucleus may always be subject to long term accumulation of inbreeding and random loss of genetic variability. The genetic variability is critical not only for the response to selection in each generation, but also for the long term limits of response (see eg. 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. In traditional farm animals, the problems of loss of genetic variation may be solved by introducing broodstock from other well performing populations (open breeding strategies). However, present and future fish breeding programs 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 breeding program increases. Splitting the breeding program in two or more separate populations will provide opportunities to exchange broodstock between populations. This may reestablish variability within populations and neutralize accumulated inbreeding.

Secondly, a single breeding nucleus will be vulnerable to accidents. The nucleus broodstock

may be lost in a technical breakdown or disease outbreak. 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 this will not secure eg. against infections acquired before separation. Splitting the breeding program in parallel, independent populations will provide a higher level of security.

Thirdly, the range of farming systems, climatic conditions etc. to be covered by the breeding program should always be tested for genotype by environment interactions. If the genetic correlations between performance in different environments is low, the breeding program may be split in several populations with performance in different farm environments as breeding goals. Significant genotype by environment interactions have been estimated in populations of farmed fish (Sylvèn et al., 1991, Romana-Eguia and Doyle, 1992, Eknath et al.,1993). However, the interactions often seems to be proportional, not resulting in extensive re-ranking of breeding candidates from one test environment to another. This will of course depend on the range of farm environments to be covered by the breeding program.

FAMILY DESIGNS

The reproductive biology of fishes (external fertilization) and the possibility in many species to strip and collect eggs and milt makes it possible to obtain a wide variety of family designs. A large number of maternal and/or paternal half sib groups may be produced in hierarchal or factorial designs from a set of simultaneously stripped spawners, and spawning may often be synchronized or induced. In some species (eg. tilapias), natural single pair matings in cages may be used to produce sib families.

As previously stated, the number of selected individuals per sib family should be restricted to control the rate of inbreeding. Under a given testing capacity, the optimum number of tested individuals per family may be determined by repeated computer predictions or simulations using variable family sizes, family designs and restrictions on the rate of inbreeding. Increasing the number of tested individuals per family will result in a decreased number of families in the test, if the number of individuals that may be tested in the breeding nucleus is limited.

Generally, if the rate of inbreeding is to be kept constant, the number of individuals that may be selected per family will be reduced as the number of families in the test decreases. This will reduce the intensity of selection between families, since the average number of selected individuals per family has to be fixed to maintain the family design in the next generation. On the other hand, reducing the number of families in the test will result in increased family sizes and higher selection intensities within families (the maximum number of individuals that may be selected from each family will represent a lower proportion of the family).

PERFORMANCE TESTING

The breeding candidates should be stocked for performance testing in an environment as close as possible to commercial farm environments. Even if genotype by environment interactions may be of limited importance in heterogeneous fish populations across a certain range of applied farming systems (see above), the use of highly specialized experimental facilities for performance testing reduce the validity of the test results. This may be even more important in fish breeding than in farm animals, since farmed fish populations probably have been less affected by natural domestication selection. Strong genetic correlations may occur eg. between farm environment adaptation and performance, if wild type behaviour, stress sensitivity etc. has been maintained in the stocks presently used in aquaculture.

Performance testing in an applied farm environment will normally imply large test units (ponds, cages etc.). Mass selection may easily be carried out in such units. Within family selection with

untagged fish will require one test unit per family. With tagged or branded fish, the families may be mixed and communally stocked for performance testing in almost any type of test environment, and the performance of relatives may be utilized to improve the accuracy of selection (combined selection).

Tagging or branding will require hatching of eggs and rearing of fry in separate family containers or cages until the fingerlings reach taggable size. A variety of techniques like ink or freeze branding, fin clipping, external tags or implanted electronic tags have been used. The period of separate rearing should be minimized to avoid large environmental correlations of performance within sib families.

The high fecundity of farmed fish species permits testing of large numbers of simultaneous full sibs, and the sib groups may be split after tagging and tested in a variety of test environments in addition to the breeding nucleus. Field tests may be carried out in a number of representative commercial farms or test stations to ensure a valid ranking of the families. Parallel family materials may also be submitted to disturbing or destructive tests that can not be carried out in the breeding nucleus (eg. disease or stress challenge tests, slaughter quality tests etc.)

MASS SELECTION DESIGNS

Mass selection designs may be considered if the family identity of the breeding candidates may not be maintained during testing. The main problem of mass selection in fish breeding is probably to keep inbreeding under control. If large full sib groups are stocked for testing, the wide genetic variability and common non-genetic full sib effects (eg. maternal effects or age effects) may easily result in a high representation of individuals from the same sib families among the selected broodstock. Restrictions on the number of selected individuals per family may not be implemented after testing unless the family identity is maintained eg. by tagging.

In the absence of family identity records, restrictions on the number of individuals that may be selected per family must be implemented before the families are mixed. Testing a restricted number of individuals per full sib family from a large number of families will reduce the rate of inbreeding (see above). However, this will also reduce the intensity of selection. A restriction resulting in an average number of eg. 20 mature individuals per family at the end of the test will imply a selection intensity of 5-10% (depending on the sire to dam ratio), if the same number of families is to be tested in every generation.

Inbreeding depression may also be counteracted in a mass selection program by maintaining two or several separate populations in the program and by crossing breeders from different populations to produce commercial fingerlings. The genetic progress within the two populations may be reduced by inbreeding depression, but as long as survival and fertility are not to severely affected, the additive genetic gain may be exploited in the outbred offspring. However, random loss of genetic variation within the selected populations because of low effective population sizes may depress the long term limits of additive genetic gain.

The accuracy of single trait mass selection designs will be equal to the square root of the heritability of the trait selected for. The accuracy of simultaneous mass selection for several traits (eg. based on a selection index) will be determined by the heritabilities of the traits and the genetic correlation between them. Systematic non-genetic effects (eg. maternal effects or age effects) that may not be corrected for in a mass selection design will reduce the heritabilities.

WITHIN FAMILY SELECTION DESIGNS

Family identification of the test fish may be maintained without tagging if the families are stocked and performance tested in separate units (tanks, cages etc.). However, records of the mean

performance of non-replicated families may not be utilized for selection between families because of confounding effects between the family performance and the environmental effects of the test units. A fixed number of spawners will then have to be selected from each family (eg. one male and one female per family under a full sib design). This means that the genetic variation between families will not be exploited by the selection program. The effective additive genetic variation will then be reduced by 50% (full sib families) or 25% (half sib families).

On the other hand, high within family selection intensities may be applied without increasing the rate of inbreeding. The within family selection intensity will depend entirely on the number of tested individuals per family, and the rate of inbreeding may be controlled eg. by applying rotational mating systems. The number of tested families will then determine the lower limit of the rate of inbreeding.

The accuracy of within family selection (the within family heritability) will also be reduced compared to mass selection, if the phenotypic correlation within sib families under mass selection is lower than the coefficient of relationship within sib families, ie. if strong non-genetic correlations are not occuring within sib families under mass selection (see eg. Falconer, 1989).

COMBINED SELECTION DESIGNS

If family identification is maintained by branding or tagging, all families may be communally stocked for testing, and selection may be based on a combination of individual and family performance (selecting the best individuals from the best families based on eg. a selection index or on BLUP breeding values). The entire additive genetic variation will then be utilized, and families may be ranked on a continuous scale even for discontinuous traits like mortality. Sib records may be utilized to select for traits that are not expressed in the breeding candidate (eg. selection in the opposite sex for sex limited traits). In fish breeding programs, where proper designs may provide records from large groups of full and half sibs, the accuracy of selection may often be increased to 0.70-0.75. This is equivalent to a heritability of about 0.5 in a single trait mass selection program.

The accuracy of the breeding value estimates (ie. the accuracy of selection) is affected by the definition of the breeding goal. To compare the accuracy achieved in different breeding program designs, the breeding goal should be kept constant. In a combined selection design, selection may be based on economically important traits that may not be recorded in each individual breeding candidate (see above). If these traits are included in the breeding goal of a mass selection or within family selection program, the accuracy of selection will be lower than indicated by the heritabilities of the traits used for selection (the accuracy of selection for the remaining traits in the breeding goal will depend on the genetic correlation with the recorded traits). Combined selection designs may consequently improve the accuracy of selection substantially depending on the breeding goal.

Individual tagging may provide complete pedigree records of all selected broodstock, and matings may be planned to obtain minimum inbreeding coefficients in the progeny. This may prevent large differences in inbreeding depression from one sib group to another in the next generation or during dissemination, and it may also delay the accumulation of inbreeding during the initial phase of the breeding program. However, the long term rate of inbreeding will depend on the effective population size rather than the mating design (see eg. Falconer, 1989).

The factors determining the long term rate of inbreeding in a combined selection program will consequently be similar to those described for mass selection programs. Since sib family records are used to estimate the individual breeding values, individuals from the same sib family will tend to have more similar breeding values than under mass selection. The probability of selecting large numbers of sibs from a limited number of families will then be even higher.

Consequently, the need to restrict the number of selected individuals from each family is even more important in a combined selection program than under mass selection. However, with tagged fish, the restriction may be implemented after performance testing in stead of at stocking, allowing

for selection of the best performing individuals within the top ranked families.

If the number of spawners per family is restricted in a combined selection program, the selection intensity may not be computed in terms of the fraction of the breeding candidates used as broodstock. High performing individuals may be rejected because they come from families that have already exceeded the restriction. Different designs may be compared based on the realized or predicted selection differential on the scale of breeding values.

Theoretically, combined selection may also be applied to untagged fish if the families are tested separately in replicates. However, if more than a limited number of families shall be tested, this will require tremendous testing facilities, in particular if the performance is to be recorded in an approximate applied farm environment.

FAMILY SELECTION DESIGNS

If the possibilities to utilize sib group records are fully exploited, the impact of individual records collected in the breeding nucleus on the estimated breeding values may easily be substantially reduced. This will certainly be the case if important traits in the breeding goal may not be recorded in the breeding candidates or in the breeding nucleus (eg. records on sex limited traits and records from field tests, disease challenge tests, carcass quality tests etc.).

The selection within families in the breeding nucleus will then contribute less to the genetic progress relative to the selection between families. As the importance of sib records increases, a combined selection design may automatically approach a family selection design (random individuals from the top ranked families may be used as broodstock without substantial loss in accuracy of selection and selection intensity).

In a family selection design, the number of full sibs per family that needs to be stocked in the breeding nucleus may be reduced considerably. The only requirement is that the number of surviving, mature spawners per family available at the end of the test period should not be lower than the number of individuals that may be selected per family. If the stocking capacity in the breeding nucleus is limited, the number of families that may be tested will be increased compared to a combined selection design. This will also increase the number of spawners that may be used per family without increasing the rate of inbreeding, and consequently increase the intensity of the selection between families.

A possible future family selection design may be that all records are collected from parallel full sib materials outside the breeding nucleus. The breeding nucleus may then focus entirely on the production, tagging and distribution of large numbers of test fingerlings from a large number of families, and on securing the necessary broodstock to carry out the family selection based on the collected records. The management of the breeding nucleus may concern more about protecting the broodstock against accidents, diseases etc. than about providing a representative applied farm environment.

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