Recent advances in animal breeding theory and its possible application in aquaculture

Toro M.A., López Fanjul C.G.

in

Bartley D.M. (ed.), Basurco B. (ed.).
Genetics and breeding of Mediterranean aquaculture species

Zaragoza : CIHEAM
Cahiers Options Méditerranéennes; n. 34

1998
pages 31-45

Toro M.A., López Fanjul C.G. **Recent advances in animal breeding theory and its possible application in aquaculture.** In : Bartley D.M. (ed.), Basurco B. (ed.). *Genetics and breeding of Mediterranean aquaculture species.* Zaragoza : CIHEAM, 1998. p. 31-45 (Cahiers Options Méditerranéennes; n. 34)

Recent advances in animal breeding theory and its possible application in aquaculture

M.A. Toro* and C. López-Fanjul**
*Area de Mejora Genética (CIT-INIA) - Carretera la Coruña km. 7
28040 Madrid, Spain
**Departamento de Genética, Facultad Ciencias Biológicas, Universidad Complutense
28040 Madrid, Spain

SUMMARY - The genetic change of the population mean of a quantitative trait is the outcome of the action of two antagonistic forces: artificial or natural selection and genetic drift. The latter may generate inbreeding depression and erosion of the genetic variance, both for production and fitness traits. Inbreeding changes are cumulative and inversely proportional to the effective population size. To keep undesirable inbreeding effects in check, a minimum number of selected parents larger than that required to produce the desired offspring number should be used. Moreover, the variability of selection response is also inversely proportional to the effective size. Thus, a reasonable chance of success of achieving some response can only be attained by further increasing the effective size. In parallel, the magnitude of short-term selection response depends linearly on the accuracy of selection. Efficient selection methods rely on the use of family information through BLUP evaluation. This procedure induces a closer genetic relationship between selected individuals, increasing the rate of inbreeding. Therefore, a compromise should be reached by using optimizing strategies considering: (i) the number of selected individuals and their respective contribution of offspring; (ii) the selection criterion used; and (iii) the mating system imposed. When members of a family must be reared together until they reach sufficient size to be individually identified, family information may also be of use to detect indirect genetic effects on growth rate shared by all members of a family.

Key words: Aquaculture, breeding programmes, selection and inbreeding, group selection.

RESUME - *"Développements récents en théorie de la génétique animale et possible application à l'aquaculture". Le changement génétique dans une population de la moyenne d'un caractère quantitatif est le résultat de l'action de deux forces antagonistes : la sélection artificielle ou naturelle et la dérive génétique. Celle-ci peut produire une dépression par consanguinité et une érosion de la variance génétique tant sur la production que sur les caractères d'efficacité reproductive. Les changements de la consanguinité sont cumulatifs et inversement proportionnels à la taille effective de la population. Pour contrôler les effets nocifs de la consanguinité, un nombre minimum de parents selectionnés, plus grand que celui nécessaire pour produire la descendance désirée, doit être utilisé. En plus, la variabilité de la réponse à la sélection est aussi inversement proportionelle à la taille effective. Parallèlement, la grandeur de la réponse à la sélection à court terme depend linéairement de la précision de la sélection. Les méthodes de sélection efficientes reposent sur l'utilisation de l'information familiale au moyen de l'évaluation BLUP. Cette procédure mène à une augmentation de la relation génétique parmi les individus sélectionnés, en augmentant le taux de consanguinité. Il faut donc trouver un compromis à l'aide des stratégies optimisées prenant en considération : (i) le nombre d'individus sélectionnés et leurs contributions respectives à la descendance ; (ii) le critère de sélection employé ; et (iii) le système d'accouplement imposé. Lorsque les membres d'une famille doivent être élevés ensemble jusqu'à ce qu'ils aient une taille suffisante pour être identifiés individuellement, l'information familiale peut aussi être utile pour détecter des effets génétiques indirects sur le taux de croissance partagé par tous les membres d'une famille.*

Mots-clés : *Aquiculture, programmes d'amélioration, sélection et consanguinité, sélection en groupe.*

Rate of genetic progress in farm livestock and economic gain

The possible rates of genetic change for commercial traits and overall economic performance in the four main species of farm livestock have been calculated by Smith (1985). He also confirms that these rates have been frequently achieved in practice both in selection experiments and commercial breeding programmes. The outcome of modern breeding programmes has been quite impressive, the yearly rates of change ranging from one to three percent of the mean. Relative to the returns, the cost of genetic improvement is small and, therefore, the benefit is very large. For pig breeding in the UK, Mitchell *et al.* (1982) estimated annual returns of some £100 million for annual costs of £2 million. Although the rates of genetic gain may seem small compared to the improvement brought about by nutrition or management they are, however, continuous, cumulative and permanent given the same selection environment. In dairy cattle achieved rates of genetic improvement in milk yield over the past two decades have been substantial and are estimated at 1-1.5% or even 2% (Smith and Burnside, 1990). In broilers, Havenstein *et al.* (1994) evaluated the relative contribution of genetic selection and dietary regimen to the performance, using a randombred control founded in 1957 and a 1991 selected strain and feeding them with "typical" 1957 and 1991 diets. The 1991 diet increased body weight by an average of 19% but the body weight of the 1991 strain was 210% greater than that of the 1957 strain. Nevertheless, the mortality and the incidence of tibial dyschondroplasia were greater in the improved strain. This illustrate how extreme genetic progress for some economic important traits may have undesirable correlated consequences on fitness traits.

Design of breeding programmes

The design of breeding improvement schemes for farm livestock should follow a well-established series of logical steps. The first is to define the breeding objective in the context of a given production-marketing system. The second step is to evaluate the available breeding stocks and crosses for economic merit. This allows the breeders to choose the best stocks and to establish breeding systems, such as cross-breeding, to exploit the genetic differences between them. The third step is to develop within-stock testing and selection systems for the further improvement of economic merit. The last step is to disseminate the improved stock to the industry, so that it profits from the breeders work.

Objective

The breeding objective includes the traits of interest weighted by their economic values, these representing the economic desirability of changes in these traits, as established by Hazel (1943). The experience in most domestic species has highlighted several problems that, sooner or later, will have to be faced in fish breeding (Newman and Ponzoni, 1994). First, the interests of seedstock producers, commercial producers and consumers will not always coincide. Second, there are instances in which the prices paid for a particular stock are grossly disproportionate with respect to its true genetic merit, due to marketing strategy coupled with earlier economic and social achievements of that stock. Third, the breeding objective is understood in a different way by different people. Geneticists and economists prefer to define it as an aggregate of breeding values weighted by economic values, while breeders usually think of it in terms of specific combinations of target levels for different traits. Fourth, as breeding programmes become successful, several important traits, specially those related to growth, will presently be in the optimal range or have attained an upper limit, whereas other traits such as reproduction, disease resistance or welfare and meat quality, will increase their economic importance.

Choice of stock

The choice of appropriate stock within a production marketing system requires previous knowledge of the comparative performance of the available stocks and their crosses. In most domestic species, this knowledge could already be available, except in the case of developing countries where this information is frequently lacking. There is evidence of large differences among strains of cultured fishes and also between domesticated and wild fishes. Domestic fishes usually grow faster, have greater survival rates and show a less nervous behaviour in hatchery environment (Dunham, 1986). In aquaculture, it seems therefore likely that a full programme of testing stocks and their crosses should probably take priority over selection within stocks, although these programmes are usually very costly if accurate information is sought.

Testing system

The next step is the development of a testing and selection system. Classically, truncation selection can be carried out on: (i) individual phenotypic values (individual or mass selection); (ii) phenotypic family means (family selection); or (iii) individual deviations from family means (within-family selection). Family data can also be combined in an index of individual, full- and half-sib information. Finally, an Animal model-BLUP selection (a generalized version of selection index that utilizes the information from all relatives and simultaneously correct for the environmental fixed effects) is carried out by selecting those individuals with highest estimated breeding values.

There is a general agreement that BLUP is the best available method for genetic evaluation. It was originally developed by Henderson (1948) in the dairy industry and now is being used routinely in dairy and beef cattle, pig, horse, poultry and, more recently, in fish. BLUP methodology has several advantages and consequently has had an impact on the breeding industry allowing to implement new selection programmes based on larger populations with lower cost per unit of genetic improvement due to increased accuracy and selection intensity. First, it facilitates the comparison among animals in different herds, under different management regimes or over different periods of time and also among animals on which different amount of information are available or that undergo a different amount of selection. For these reasons it makes it possible for the breeding programme to be based on a group of breeding herds with on-farm testing and genetically linked, mainly through artificial insemination or, in the future, by embryo transfer and cloning. Central testing stations have become unnecessary or they concentrate in monitoring traits (appetite, meat and fat quality) which cannot be recorded on farms. Second, BLUP uses family information from all known relatives and this has become increasingly important as reproductive and meat quality traits are included in the breeding goal. Finally, it partitions genetic and non-genetic effects on performance such that genetic progress over time can be assessed.

Dissemination

Finally, the fourth step is the dissemination of genetic progress from nucleus stocks to commercial stocks. Dissemination can be facilitated by the large reproductive capacity of farmed fishes in that one breeding nucleus could supply fry or eggs through multiplier stations. However, splitting the nucleus in several genetically connected or independent populations could be recommended: (i) for safety reasons; (ii) to cover the range of farming systems; (iii) to allow selection for different breeding goals. The final success of a breeding programme will depend on an efficient communication between the nucleus and the producers through fish farmer's organizations.

Animal breeding theory provides a general framework where: (i) the relative efficiency of different selection methods can be compared and; (ii) useful indications on the factors that the breeder can manipulate to maximize genetic gain can be obtained.

Recent advances on the prediction of selection response

The following analysis has been derived from that presented by Wei *et al.* (1996). It focus on the dependence, at different time horizons, of the response to artificial selection and its variability on the effective population size.

Consider a panmictic population with nested mating structures (several dams per sire) and effective population size N_e that are both constant through discrete generations. Under the infinitesimal model, the expected response to artificial selection R_t at generation t for a neutral quantitative trait, is given by:

$$R_t = i\rho_t\sigma_{At} - D/2N_e$$

where i is the selection intensity, ρ_t is the accuracy of selection (i.e., the correlation between the selection criterion and the individual breeding values), σ^2_{At} is the additive genetic variance and D is the inbreeding depression expressed per unit of inbreeding.

For a given selection method, ρ and σ^2_A change through time, due to genetic drift and mutation. The cumulative response after t generations of selection can be approximately ($t < N_e$) given by:

$$CR_t \sim R_o[t - \beta(1-\alpha)t^2/4N_e] - Dt/2N_e$$

where $\beta = d \log R / d \log \sigma^2_{AW}$ expresses the reduction of the within-family additive variance σ^2_{AW} due to drift, $\alpha = N_e \sigma^2_m/\sigma^2_{AW}$ takes into account the increase in σ^2_{AW} due to the introduction of new variation through mutation, at a rate of σ^2_m per generation, and R_0 is the asymptotic response after the genetic variance has attained an equilibrium value (Bulmer, 1971). This expression allows the analysis of the relative importance of different factors concerning CR_t. Of course, i, ρ,σ^2_A, α, β and D depend both on the trait selected and on the population structure.

The above equation clearly shows how the magnitude of N_e affects the net cumulative response. The initial response depends mainly on accuracy but, as selection progresses, factors α, β and D can only be disregarded if $t<<N_e$. Moreover, R_0 also depends on N_e as it is directly proportional to i.

The intensity of selection diminishes with the number of families tested, the reduction being greater with increasing values of the correlation between breeding values for the selected trait among selected individuals. Therefore, i values will be substantially reduced when family information is used (Hill, 1976).

In addition, there is also an antagonistic relationship between ρ and N_e. Increasing ρ using family information leads to larger short-term responses but reduces N_e, because of coselection of family members. Consequently, β increases, as $\sigma^2_{AWt} \sim \sigma^2_{AWo}/2N_e$, and its value is about 0.65 under BLUP and index selection, with large family sizes. However, α increases, as larger N_e values allow one to exploit the mutation variance more efficiently. Summarizing, these changes result in smaller long-term responses than predicted assuming a constant rate of progress per generation.

Variability of selection response

Following Nicholas (1980) the simplest scheme is that of individual selection, where the response is measured as deviation from a control. The number of parents and of scored individuals are assumed to be the same in the control and the selected line, and both sexes are assumed equally represented. Assuming that parameters do not change with selection and that generations are discrete, the response will accumulate linearly, but inbreeding will reduce its expected value by a fraction δ. Therefore, the following calculations only apply to short-term responses (~4-5 generations, approximately). Thus, the cumulated response after t generations is:

$$CR_t = (1-\delta)t\,i\,h\,\sigma_A$$

Assuming drift is the most important source of variation in response to artificial selection, the coefficient of variation of the response $CV(R_t)$ is given by:

$$CV(R_t) = \sqrt{2}\ /\ (1-\delta)\,i\,h\sqrt{N_e t}$$

Thus, if a coefficient of variation of 10% is thought to be adequate and ih is approximately 1 (for example, $i = 2$ and $h^2 = 0.3$), $N_e = 200/t$ with no inbreeding depression ($\delta = 0$) or $N_e = 312/t$ for ($\delta = 0.2$) (for example, when R = 3% per generation and inbreeding depression occurs at a rate of 0.6% per 1% ΔF).

Alternatively, if we wish to find the value of N_e required to obtain, with probability γ, an observed response that is greater than a proportion π of the expected response, the value Z_γ of the standard normal deviate for γ is given by:

$$Z_\gamma = (\pi - 1) / C_V(R_t)$$

If $\gamma = \pi = 0.9$ and, again, ih = 1, $N_e = 328/t$ with no inbreeding depression or $N_e = 512/t$ for $\delta = 0.2$.

Therefore, the second criterion (chance of success) is more demanding than the first (coefficient of variation of response) and, in the examples, the corresponding value of N_e is 56% larger. Moreover, inbreeding depression substantially increases the effective size required to meet the above criteria (by 64% in our example). Summarizing, the above criteria will be met (in our example), with effective population sizes ranging from 40 to 130.

Effective population sizes in breeding programmes

Effective population size is one of the most pervasive concepts in animal breeding. In the short term, it affects selection response through its influence on the selection intensity, the inbreeding depression and the loss of genetic variance and it also affects the variation in response. In the long term, it affects selection limits and the response from new mutation.

Santiago and Caballero (1995) have given a general equation that illustrates the effect of selection and different systems of mating on population size:

$$N_e = 4N/(2(1-\alpha_I)+(S_K^2+4\, i^2\, r_E\, t+4Q^2\, i^2\, r_G)(1+\alpha_I+2\alpha_0)),$$

where α_0 is the correlation of genes between mates, α_I is the inbreeding coefficient, S^2_K is the variance of family size under random selection, i is the intensity of selection, r_E and r_G are the correlations of sibs due to non-inherited (common environmental variance) and to inherited causes, respectively, and Q^2 accounts for the cumulative effect of selection (Robertson, 1961).

The choice of population size for animal breeding programmes depends on the time horizon of the breeder: as this horizon increases, so does the ideal population size. In more practical terms it will depend on the inbreeding and/or the coefficient of variation of response that breeders can accept.

Tolerable rates of inbreeding may differ among populations and among traits, depending on the importance of inbreeding depression in production and in fitness traits, as well as on the magnitude of the reduction in genetic variance. Those rates may therefore differ among breeding programmes, but figures of the order of 0.5% per year are usually considered acceptable. On the other hand, desirable coefficients of variation of response will depend on the degree of risk aversion. When national breeding schemes are considered, taking some precautions appears reasonable but, in competitive situations, a breeding company could prefer to run a high risk selection scheme trying to outperform the competitors. Values from 5 to 10% after 10 years of selection (implying coefficients of variation of annual selection response of 16% to 32%) are considered acceptable in order to be confident that most of the expected response will actually be achieved in practice.

Meuwissen and Woolliams (1994) followed a different approach. They consider that, in livestock populations, fitness may decrease either as consequence of inbreeding depression or from a negatively correlated response to artificial selection but, on the other hand, fitness may increase due to natural selection. They calculated that in order to prevent an undesirable decline in fitness, effective sizes should range from 31 to 250 per generation.

Selection schemes for traits of economic importance in aquaculture

As the mass of information increased, it has become clear that the genetic properties of production (growth rate) and reproductive traits in fish and shellfish are similar to those previously established for comparable traits in traditional domestic animal species and that the prospective for improving productivity in aquaculture by applying selection and crossbreeding is very good (see review by López-Fanjul and Toro, 1990; López-Fanjul, 1990; Bentsen and Gjerde, 1994; Hulata, 1995). Thus, the heritability of growth rate is intermediate (about 0.3) and that of reproductive traits and disease resistance are lower (about 0.1). Data on inbreeding depression are generally based on a small number of families and, therefore, are subjected to large sampling errors. In rainbow trout and carp, inbreeding depressions for growth rate are about 0.5 - 1%, per unit (1%) increase in inbreeding coefficient. In spite of the high fecundity rate of fishes, large selection intensities cannot be applied as they will result in inbreeding side-effects undesirable large. Furthermore, the generation interval in salmon and carp is about 3-4 years. Those two later factors are also similar to those operating in other farm animals.

In aquaculture, the effective population size is likely to be much smaller than the number of parents, due to the lack of strict control on mating and reproduction. In natural populations the ratio of effective to actual population size over taxonomic groups averaged 0.10 (Frankham, 1995), in agreement with estimates from hatchery stocks of Kuruma prawn and black seabream (see López-Fanul and Toro (1990) for a review). Sbordoni *et al.* (1987) analysed 20 isoenzymes during the first seven generations of the introduction of the Kuruma prawn *Penaeus japonicus* in Italy and they found a drastic reduction in the heterozygosity, from 0.115 to 0.032. If we accept that selection was absent and that this reduction of the was only a consequence of the reduction of the effective population size, this parameter can be estimated to be about 4 despite that the number of potentially breeding individuals was always about 600. In parallel, there was a reduction of viability, from 50% to 10%.

Maintaining large N_e and monitoring inbreeding in domestication programmes is, therefore, of paramount importance to efficiently preserve genetic variability in domesticated populations, from which genetically superior breeds of fish will be eventually developed.

Mass selection has been the traditional selection strategy in fish. It is simple to apply and has the advantage that individuals from different families can be mixed in the same environment just after fertilization, although it has the limitation that only traits that can be recorded on live breeding candidates can be selected for. On the other hand, inbreeding will be difficult to keep under control and we can only act through the election of the number of breeding individuals or, perhaps, by maintaining two or several populations and crossing them to assure that, at least in the commercial animals, inbreeding effects could be mitigated.

Efficient selection methods such as BLUP rely on the use of family information to increase accuracy (ρ). BLUP requires complete pedigrees and, therefore, individual or family identification is needed. In communally stocked fish, family identification can be implemented by tagging. Due to their very small size, newly hatched fish cannot be marked and, therefore, families must be reared in separate tanks during the first months of life, until they reach sufficient size to be branded or tagged. This is costly and only a limited proportion of offspring can be identified. Moreover, this practice introduces environmental effects on selected traits common to all members of a family. On the other hand, inbreeding can be kept under control using some of the methods that will be described below. BLUP selection could also be implemented on untagged fish if families are stocked and tested separately in replicates, to avoid the confounding effects between the family performance and the environmental effects of tanks and cages, but this would probably be too costly. If families are not replicated, only within-family selection could be practised, reducing accuracy but facilitating the control of inbreeding.

The use of DNA fingerprint could improve the selection schemes in fish. Physical tagging could be substituted by DNA tagging but the actual cost of the technique might make it prohibitively expensive. More interestingly, DNA fingerprint can be carried out only on previously mass-selected animals, allowing to control inbreeding. The largest animal in the population would be DNA fingerprinted and chosen as parent of the next generation, then the second-largest animal would be fingerprinted and accepted as parent if it comes from a different family and so on ("walk back-selection", Doyle *et al*., 1994).

Methods of evaluation of breeding values and inbreeding

As it has been previously indicated, there is a general consensus on BLUP being the best available method for genetic evaluation. However, BLUP includes information from all known relatives of an individual and, therefore, its use results in higher rates of inbreeding than selection based on the phenotype or on an index. This phenomenon could be specially important in some situations: (i) small nucleus herds making intensive use of new reproductive technologies such as MOET (Multiple Ovulation and Embryo Transfer), where a small number of parents can make large contributions of offspring; (ii) selection for sex-limited traits of low heritability, implying that high weight is given to family information; and (iii) selection for economically important traits showing dominance such as prolificacy in pigs.

As an illustration of how high rates of inbreeding can substantially reduce the expected genetic gain from BLUP we will use the results of pilot experiment with *Drosophila* (Pérez-Enciso and Toro, 1992). The goal of the experiment was to check the use of family indices proposed to improve litter size in pigs. Selection was carried out for pupae number and three family indices were considered: (i) Id, based simply on dam records; (ii) Ihd, including records from the dam's full-sibs and half-sibs; and (iii) Ihs, further including records from the sire's full-sibs and half-sibs. Despite theoretical expectations based on infinite population theory, the simplest index Id was consistently better than the more complex indices due, at least partially, to the higher inbreeding depression induced by using the latter.

For those reasons Quinton *et al.* (1992) suggested that selection methods should be compared at the same level of inbreeding. This would allow more intense selection (fewer males selected) using less accurate methods. They showed by stochastic simulation that, at the same level of inbreeding, differences between methods are much smaller than in the case of unrestricted inbreeding. If low to moderate inbreeding levels are targeted, as in closed lines of limited effective size, selection on phenotype can yield higher responses than selection on BLUP.

Compromise between selection and maintenance of genetic variability

In recent years, considerable work has been done on the design of strategies to maintain genetic diversity in selection programmes. These strategies are aimed to simultaneously optimize genetic gain and inbreeding, either by reducing the rates of inbreeding (or the variance of response) while keeping genetic gains at the same level, or by increasing selection response under a restriction on inbreeding (or on the variance of response).

Following Toro and Pérez-Enciso (1990) the success of these strategies rely on 3 factors: (i) the number of selected individuals and their contribution to the next generation; (ii) the selection criterion used; and (iii) the mating system imposed. Here we do not intend a complete review of all possible strategies but to pay attention to those that could be more easily implemented in fish breeding.

The first factor involves those strategies intending to optimize the number of selected males to achieve maximum genetic gain whilst constraining the rate of inbreeding (or the variability of response). Gjerde *et al.* (1996) gave an application to a fish breeding programme. They consider phenotypic selection during 15 generations and an optimization procedure, finding by stochastic simulation the number of sires (for a fixed scored population size N, mating ratio d, and heritability h^2) giving the highest genetic gain while the rate of inbreeding is maintained at a specified level. As an example, for d=2 and h^2=0.2 and rate of inbreeding of 2%, the optimum number of sires is 16 if N=1800 and 21 if N=9600 but, if the inbreeding restriction is stronger, e.g., a rate of 0.25%, the sire's number would be 103 and 155,. respectively. Obviously, the largest breeding scheme will produce 15-20% greater genetic response.

To the same group belong the strategies aimed to modify the contribution of the selected individuals of a generation to the selected individuals of the next generation, by practising some form of within-family selection with respect to the phenotypic or the BLUP value. For a fixed number of families, within family selection results in zero variance of family size and maximum effective population size but, with family selection, both the rate of inbreeding and the variance of family size will be maxima. Nevertheless, it should not be overlooked that there is a wide range of intermediate selection methods which differ in the magnitude of the variance of family size. All possible distributions of family size are equivalent to all possible forms of arranging k marbles (the selected individuals) among k boxes (families), each of capacity n (maximum family size). These arrangements follow a multi-hypergeometric distribution. Following Wei and Lindgren (1995), consider a breeding population comprising k families of infinite size. The breeding value of an individual can be partitioned into a family component b_i and a within-family component w_{ij}. If the proportion of the i-th family in the selected population is p_i and the within-family selection intensity is $i(w_i)$, the predicted selection gain will be:

$R = \Sigma p_i b_i + \Sigma p_i \, i(w_i)$ and the effective population size can be given as $N_e = 1/\Sigma p^2_i$

Following a mathematical optimization method, the optimal contribution of the families can be calculated to maximize genetic gain for a fixed effective population size.

In the same direction, it is also possible to modify the contribution of the selected individuals to the evaluated individuals of the next generation (instead to the selected individuals), by a strategy called weighted selection (Toro and Nieto, 1984). In a typical selection process, the top N individuals of each sex are selected and each pair makes an identical contribution to the individuals scored in the next generation (w_i= constant). In the weighted selection method, a larger number of pairs (N') may be selected, with each pair making unequal offspring contributions, while maintaining the same selection differential. Of all possible values of N' and w_i, we must choose those resulting in the maximum effective size. Because this parameter is inversely proportional to Σw^2_i, the problem reduces to minimize the last quantity, subject to the restriction of a fixed selection differential. This can be accomplished by using quadratic programming techniques or by a linear approximation that makes offspring contributions of the selected individuals linearly proportional to the breeding values of the selected individuals. Similar algorithms have been proposed to choose a variable number of both sires and of dams/sire (Wray and Goddard, 1994). These are currently used in tree breeding to choose the proportion of k clones to be planted, in order to maximize yield but with a restriction on the known risk of having too many trees of the same genotype in a forest (Lindgren, 1991).

The second group of strategies propose the use of a sub-optimal selection criterion to select the individuals. The use of family information in an index or BLUP evaluation has been shown to increase inbreeding with respect to phenotypic selection. To avoid this several strategies have been proposed based on the idea of reducing the weight given to family information (Villanueva *et al.*, 1994). An even simpler method that can also be applied to BLUP evaluations is to use a heritability upward biased. With such a simple method, the inbreeding can be reduced up to 30% with only a small reduction in response.

The above procedures can produce some psychological dissatisfaction, as they seem to imply that ignorance or false information could be better than true knowledge. Similar results can be obtained using strategies more intuitively appealing, as those including inbreeding considerations in the objective of selection. Brisbane and Gibson (1995) consider that the selection objective to maximize is:

$$O = G_t - D\,F_t,$$

where G_t and F_t are, respectively, the genetic merit of animals born in generation t and their inbreeding coefficient, and D is the inbreeding depression. They show that the selection criterion that maximizes this objective includes the genetic relationship among the selected animals and is of the form:

$$M = 0.50\ EBV_s + 0.50\ EBV_d - 0.50\ k\ a,$$

were k is a constant that depends on the desired restriction on inbreeding, and EVB_s and EVB_d the mean breeding value of selected sires and dams, respectively, and a is the average genetic relationship among selected animals.

The third group of strategies propose to act on the mating system. These include factorial mating designs, minimum coancestry matings using linear programming and compensatory matings (see review by Caballero *et al.*, 1996). If factorial mating designs can be achieved, these are likely to be as effective, or even more effective, than hierarchical mating schemes. For example, in a complete factorial design such that each female mates to all males and has only one offspring, there is a total avoidance of full-sib offspring. It should be noted, however, that the use of factorial mating should be restricted to organism with high reproductive rate. If this is low, factorial mating implies an increase in the generation interval and a corresponding loss in response. For this reason, there is a good prospect for the use of factorial mating in fish breeding as has been shown in simulation studies (Engstrom *et al.*, 1994). In minimum coancestry mating, the average pairwise coancestry coefficient in the selected group is minimized. This can be implemented using linear programming techniques, although more simplified versions, such as avoidance of full-sib mating, are possible. Under this system of mating, the asymptotic rate of inbreeding will be generally reduced with respect to that obtained under random mating, except in those situations where family sizes are equal or approximately so. In the compensatory mating system, selected individuals of each sex are ranked according to their mean coancestry with all other selected individuals and highest ranking males are mated to lowest ranking females. Under this system of mating, negative correlations between drift caused by selection and drift caused by sampling are induced, partly o completely counteracting the cumulative effect of selection.

Finally, mate selection strategies potentially include most of the desirable properties of the above methods. Mate selection is defined as the simultaneous selection of parents and the formation of mating pairs, erasing the distinction between selection and mating activities that has been classical in animal breeding. It is useful in several contexts, one of them being the joint regulation of genetic gain and inbreeding. This method computationally relies on techniques of linear or quadratic programming (Toro *et al.*, 1991).

Group selection and competition effects

Competition has often been recognized as one of the most important components of productivity for some species, specially in cultivated plants. In poultry egg production, multiple-bird cages can result in injuries through aggression such that beak trimming is required.

In this case, Griffing (1967) showed that one should consider that the individual's genotype has a direct (*d*) effect on its own phenotype and associate (*a*) effects on the phenotypes of other individuals of the group sharing the same medium, due to competition for the same fixed resources. Consequently, the response to individual selection of intensity *i* for a trait with phenotypic standard deviation σ is:

$$R = (i/\sigma)\ ({}_{d}\sigma^{2}_{A} + {}_{(da)}\sigma_{A})$$

where ${}_{d}\sigma^{2}_{A}$ is the additive variance of the direct effects and ${}_{(da)}\sigma_{A}$ is the additive covariance between direct and associate effects. This covariance may even be negative, as expected when those individuals phenotypically superior for the selected trait are, at the same time, the most aggressive ones. This problem may perhaps be avoided in a breeding nucleus (by eliminating competition), although it will be present, however, in commercial farms. Therefore, part of the genetic progress achieved in the nucleus cannot be transmitted to the industry.

If the group is defined as the unit of selection,

$$R = (i/\sigma)({}_{d}\sigma^{2}_{A} + 2\ {}_{(da)}\sigma^{2}_{A} + {}_{a}\sigma^{2}_{A})$$

where ${}_{a}\sigma^{2}_{A}$ is the additive variance for associate effects. Thus, transferring the selection pressure from the individual to the group ensures that the population mean will not decrease. Griffing (1976) pointed out that the efficiency of the process can be improved with the use of non-random groups, i.e., families. In this situation, group selection would be operatively equivalent to family selection. However the rationale is different: a family selection scheme can be of use, not because the selection criterion (family means) allows the elimination of random environmental differences between families, but because it detects useful indirect genetic effects shared by all members of a family. In essence, this is the mechanism that favours altruistic behaviour through natural selection (Hamilton, 1964). Experimental evidence supporting Griffing's theory was obtained in *Tribolium castaneum* (García and Toro, 1990) and in poultry, where group selection in multiple-bird cages resulted in a dramatic increase in liveability (Muir, 1994).

One of the best documented fish selection experiments is that carried out by Moav and Wohlfarth (1976) for growth rate in carp. No response to upward mass selection was achieved during the initial five generation period. However, a clear response to downward selection was observed in that period, showing the existence of genetic variation for the selected trait in the base population. Subsequently, family selection was practised in the upward line, resulting in considerable progress. These results were interpreted in terms of direct and associate effects on growth rate, the later being ascribed to within-family competition.

References

Bentsen, H.B. and Gjerde, B. (1994). Design of fish breeding programmes. *Proc. 5th World. Congr. Genet. Appl. Liv. Prod.,* 19: 353-359.

Brisbane, J.R. and Gibson, J.P. (1995). Balancing selection response and rate of inbreeding by including genetic relationships in selection decisions. *Theor. Appl. Genet.,* 91: 421-431.

Bulmer, M.G. (1971). The effect of selection on genetic variability. *Am. Nat.,* 105: 201-211.

Caballero, A., Santiago, E. and Toro, M.A. (1996). Systems of mating to reduce inbreeding in selected populations. *Anim. Sci.,* 62: 431-442.

Doyle, R.W. and Herbinger, C., Smith, C., Gavora, J.S., Benkel, B., Chesnais, J., Fairfull, W., Gibson, J.P., Kennedy, B.W. and Burnside, E.B. (1994). The use of DNA fingerprinting for high intensity, within-family selection in fish breeding. *Proc. 5th World. Congr. Genet. Appl. Liv. Prod.,* 19: 364-371.

Dunham, R.A. (1986). Selection and crossbreeding responses for cultured fish. *Proc. 3rd World. Congr. Genet. Appl. Liv. Prod.,* 10: 391-400.

Engstrom, G., McMillan, I., McKay, L., Quinton, M., Smith, C., Gavora, J.S., Benkel, B., Chesnais, J., Fairfull, W., Gibson, J.P., Kennedy, B.W. and Burnside, E.B. (1994). Comparison of mating systems in a fish population - A simulation study. *Proc. 5th World. Congr. Genet. Appl. Liv. Prod.,* 19: 360-363.

Frankham, R. (1995). Effective population size/adult population size ratios in wildlife: A review. *Genet. Res.,* 66: 95-107.

Garcia, C. and Toro, M.A. (1990). Individual and group selection for productivity in Tribolium castaneum. *Theor. Appl. Genet.,* 79: 256-260.

Gjerde, B., Gjoen, H.M. and Villanueva, B. (1996). Optimum design for fish breeding programmes with constrained inbreeding. Mass selection for a normally distributed trait. *Livest. Prod. Sci.,* 47: 59-72.

Griffing, B. (1967). Selection in reference to biological groups. I. Individual and group selection applied to populations of unordered groups. *Aust. J. Biol. Sci.,* 20: 127-139.

Griffing, B. (1976). Selection in reference to biological groups. V. Analysis of full-sib groups. *Genetics,* 82: 703-722.

Hamilton, W.D. (1964) The genetic evolution of social behavior. *J. Theor. Biol.,* 7: 1-16.

Havenstein, G., Ferket, P.R., Scheideler, S.E. and Rives, D.V. (1994). Carcass composition and yield of 1991 vs 1957 broilers when fed 'typical' 1957 and 1991 broiler diets. *Poult. Sci.,* 73: 1795-1804.

Hazel, L.N. (1943). The genetic basis for constructing selection indexes. *Genetics,* 28: 476-490.

Henderson, C.R. (1948). *Estimation of general, specific and maternal combining abilities in crosses among inbred lines of swine*. Ph.D. Thesis, Iowa State University, Ames.

Hill W.G. (1976). Order statistics of correlated variables and implications in genetic selection programmes. *Biometrics,* 32: 889-902.

Hulata, G. (1995). A review of genetic improvement of the common carp (*Cyprinus carpio,* L) and other cyprinids by crossbreeding, hybridization and selection. *Aquaculture,* 129: 143-155.

Lindgren, D. (1991). Optimal utilization of genetic resources. *Forest Tree Improvement,* 23: 49-67.

López-Fanjul, C. (1990). The tools of genetics in aquaculture: Introductory remarks. In: *Mediterranean Aquaculture*, Flos, R., Tort, L. and Torres, P. Ellis Horwood, New York, pp. 162-166.

López-Fanjul, C. and Toro, M.A. (1990). *Mejora Genética de Peces y Moluscos*. Mundi-Prensa. Madrid.

Moav, R. and Wohlfarth, G.W. (1976). Two-way selection for growth in the common carp (*Cyprinus carpio,* L.) *Genetics,* 82: 83-101.

Meuwissen, T.H.E. and Woolliams, J.A. (1994) Effective sizes of livestock populations to prevent a decline in fitness. *Theor. Appl. Genet.,* 89: 1019-1026.

Mitchell, C., Smith, C., Makower, M. and Bird, P.J.W.M. (1982). An economic appraisal of pig improvement in Great Britain. Genetic and production aspects. *Anim. Prod.,* 35: 215-224.

Muir, W.M. (1994). Group selection for adaptation to multiple-hen cages: Selection program and direct responses. *Poultry Sci.,* 75: 447-458.

Newman, S. and Ponzoni, R.W. (1994). Experience with economic weights. *Proc. 5th World. Congr. Genet. Appl. Liv. Prod.,* 17: 217-223.

Nicholas, F.W. (1980). Size of population required for artificial selection. *Genet. Res.,* 35: 85-105.

Pérez-Enciso, M. and Toro, M.A. (1992). Classical and mixed-model analysis of an index selection experiment for fecundity in Drosophila melanogaster. *J. Anim. Sci.,* 70: 2673-2681.

Quinton, M., Smith, C. and Goddard, M.E. (1992). Comparison of selection methods at the same level of inbreeding. *J. Anim. Sci.,* 70: 1060-1067.

Robertson, A. 1961. Inbreeding in artificial selection programmes. *Genet. Res.*, 2: 189-194.

Santiago, E. and Caballero, A. (1995). Effective size of populations under selection. *Genetics,* 139: 1013-1030.

Smith, C. (1985). Rates of genetic change in farm livestock. *Research & Development in Agriculture,* 1: 79-85.

Smith, C. and Burnside, E.B. (1990). Effective genetic improvement in dairy cattle. *Proc. 4th World. Congr. Genet. Appl. Liv. Prod.,* 14: 50-57.

Sbordoni, V., La Rosa, G., Mattoccia, M., Cobolli Sbordoni, M., de Mattheis, E. (1987). Genetic changes in seven generations of hatchery stock of the Kuruma prawn, *Penaeus japonicus* (Crustacea, Decapoda). *Proc. World Symp. Selection, Hybridization, and Genetic Engineering in Aquaculture,* 1: 144-155.

Toro, M.A. and Nieto, B. (1984). A simple method for the response to artificial selection. *Genet. Res.,* 44: 347-349.

Toro, M.A. and Pérez-Enciso, M. (1990). Optimization of response under restricted inbreeding. *Genet. Sel. Evol.,* 22: 93-107.

Toro, M.A. and Silió, L. and Pérez-Enciso, M. (1991). A note on use of mate selection in closed MOET breeding schemes. *Anim. Prod.,* 53: 403-406.

Villanueva, B., Woolliams, J.A. and Simm, G. (1994). Strategies for controlling rates of inbreeding in MOET nucleus schemes for beef cattle. *Genet. Sel. Evol.,* 26: 517-535.

Wei, M., Lindgren, D. (1995). Optimal family contributions and a linear approximation. *Theor. Pop. Biol.,* 48: 318-332.

Wei, M., Caballero, A. and Hill, W.G. (1996). Selection response in finite populations. *Genetics,* 144: 1961-1974.

Wray, N.R. and Goddard, M.E. (1994). Increasing long-term response to selection. *Genet. Sel. Evol.,* 26: 431-451.