APPLICATION OF BREEDING AND SELECTION THEORY ON FARMED FISH

Hans B. Bentsen
AKVAFORSK (Institute of Aquaculture Research)
P.O. Box 10, N-1432 Ås-NLH, Norway

SUMMARY

The present production of farmed fish for human consumption represents a minor fraction of the total food supply. The prospects of increasing the production significantly are good. However, the genetic material available for fish farming is less domesticated and less genetically improved than in other farm animals. The need for long term genetic improvement programs for farmed fish is obvious. The long term breeding goal should be to establish specialized and high performing breeds for fish farming. The process of designing breeding programs for fish populations is discussed, and some solutions are suggested.

INTRODUCTION

The history of fish farming probably dates back as far as 2000 B.C., with the development of pond cultures in China, Japan, the Mediterranean and South America. Still, the farmed fish species has not gone through a process of genetic domestication comparable to that of the farmed species of mammals and birds. Most of the genetic material used in fish farming has not been definitively separated from the wild populations to form specialized domesticated breeds. Wild broodstock has often been used as a regular part of fish farming systems, either continuously or to "refresh" the cultivated stocks. Furthermore, selective breeding has rarely been successfully practiced in fish. The two main reasons for this has probably been the lack of controlled mating and reproduction and the problems of keeping individual records of the breeding candidates. Most farmed species have reproduced in captivity only when left undisturbed in an environment close to their natural habitat. The possibilities to maintain pedigree records have consequently been quite limited.

Mass selection has probably been attempted during broodstock recruitment in many farming systems. But the lack of life history records has excluded reliable corrections for systematic environmental sources of variation like age or season effects. The genetic component of the phenotypic variation may consequently have been rather low. The probability of selecting full sibs may also have been increased because of common environmental effects. In combination with the high selection intensities that may be applied in fish populations, and the small breeder numbers needed in commercial fry production (Eknath and Doyle, 1990), this may have resulted in high rates of inbreeding and inbreeding depression (Kincaid, 1983). The tradition of "refreshing" cultivated stocks with wild breeders may be understandable in such systems.

In 1986, finfish culture contributed about 5.5 million tons per year (FAO, 1989), or less than 7 percent of the total world fish supply. This is in a striking contrast to animal production on land, where the contribution from harvested or cultivated wild animal resources is marginal. The world supply of animal protein is totally dependent on the genetic modified farmed species. A large majority of today's fish culture is concentrated on herbivorous freshwater species fed on natural plancton and algae production in a fertilized environment. Carp culture probably accounts for more than 2 million tons per year, and another important species today is tilapia (Bardach et al., 1976). Marine fish farming is a rather new development which has brought several new species into culture.

PRESENT SITUATION

During the recent years, several attempts have been made to overcome the slow genetic development of specialized breeds of farmed fish. One major breakthrough has been the closing of controlled life cycles in captivity for important species as carps, tilapias, catfish and salmonids. Techniques for induced spawning, stripping of eggs and milt and incubation of fertilized eggs have been developed, and procedures for controlled matings have been established. This has speeded up the process of domestication and development of culture strains, and of course improved the prospects of performance testing and selective breeding. Today, several strains are defined for the most common cultured species, and strain hybrids are produced for commercial purposes (Kirpichnikov, 1981, 1987; Pullin and Lowe-McConnell, 1982; Jhingran and Pullin, 1985; Dunham, 1987; Kincaid, 1987; Márián, 1987; Wohlfarht et al., 1987).

The increased access to performance records in pedigreed stocks has greatly improved the knowledge about important parameters as genetic variation, heritabilities, genetic correlations etc. for a wide range of traits in farmed fish populations (rewiewed by Gjedrem, 1983; Kinghorn, 1983; Gjerde, 1986).

Selection experiments have been carried out, mostly based on mass selection for growth rate across, between or within families in experimental stocks. Results have been reported from carps (Moav and Wohlfarht, 1976; Kirpichnikov, 1987), tilapias (Hulata et al., 1986; Teichert-Coddington and Smitherman, 1988), catfish (Dunham, 1987) and rainbow trout (Lewis, 1944; Donaldson and Olson, 1955; Kincaid et al., 1977). The response to selection has been highly variable from one experiment to another, and possible explanations will be discussed later. Very few examples of selection programs utilizing combined selection for commercial breeding have been reported. Bondari (1983) combined between and within family selection for growth rate in channel catfish. Combined selection based on the performance of full sibs, half sibs and the individual itself has been applied in salmonids (Gjedrem, 1985; Hersberger, 1990; Refstie, 1990). A similar approach has recently been initiated for tilapia on the Philippines (Eknath, 1989).

Extensive research, mainly during the last few years, has shown that fish species are much more tolerant than higher animals to manipulations of the reproductive and early developmental processes. Viable and often fertile hybrids between related fish species are well known (reviewed by Chevassus, 1983; Dunham, 1986; Longwell, 1987; Nævdal and Dalpadado, 1987; Krasznai 1987). Interspecific hybridization increases the range of combinations that may be tested for commercial hybrid production. Induced polyploidy, gynogenesis (all maternal inheritance) and androgenesis (all paternal inheritance) has been reported from a large variety of fish species, and systems for commercial applications of such techniques have been developed (reviewed by Cherfas, 1981; Thorgaard 1986; Chourrout, 1987; Chevassus, 1987; Någy, 1987). Induced triploidy may be applied to prevent sexual maturation. Gynogenesis and androgenesis may be used for rapid development of inbred lines. A variety of techniques for sex manipulation of fishes has also been established (reviewed by Yamazaki, 1983). Phenotypic sex reversal may be induced in both males and females by hormone treatment. Monosex cultures may be produced by the use of sexual reversed homogametic parents, by the use of gynogenetic super females or androgenetic super males, or by certain interspecific crosses. Monosex cultures are highly relevant for several species showing large sex differences in productivity traits or to prevent breeding in culture.

FUTURE PROSPECTS

Several worldwide trends and opportunities are pointing towards a rapid increase in the fish farming industry, sometimes referred to as "the blue revolution". More than 70 percent of the earth's surface is covered by water. Still, the total output of nutrients for human consumption from land animals (including milk and eggs) is 4-5 times higher than the total output of fish products. As pointed out earlier, the high yields of land animal products are depending totally on genetically improved domesticated breeds and some level of controlled input, while the fish supply is mainly based on harvesting wild populations. The possibility to increase the supply of fish proteins by expanding traditional fisheries seems to be limited. FAO (1987) anticipates an annual increase as low as 0.3 percent in fisheries harvest. Several wild stocks are threatened by collapse because of heavy harvesting.

The major source of increased fish protein supply will consequently be various systems of fish culture and farming. According to FAO (1987), aquaculture products is expected to contribute about 25 percent of the total fisheries production by the end of the century. This may be achieved by improving the efficiency of the existing fish farming industry, and by expanding fish farming in environments or geographic areas not yet utilized. In both cases, animal breeding scientists will face great challenges. Genetic improvement programs will be needed both for traditional and new species of farmed fish. The process of applying breeding and selection theory in fish populations has been discussed by several authors (Gjedrem, 1983, 1985; Shultz, 1986; Gall, 1990; Refstie, 1990). The main elements of breeding planning in farm animals are recommended, starting with the formulation of breeding goals.

LONG TERM BREEDING GOALS

The long term breeding goal for farmed fish should probably be to establish domesticated fish breeds that possess a similar advantage in productivity and efficiency compared to their wild ancestors as the traditional farmed animals. The difference between the high performing domestic animal breeds and their genetic origin, measured in terms of genetic standard deviations, may probably be counted in tens. This is a result of thousands of years of accumulated selection, which has not taken place in most populations of farmed fish. In this perspective, the only way of approaching the long term breeding goal for farmed fish will probably be to utilize the additive genetic variation in a steady selection program, even if the immediate effects of hybrid programs, polyploidy, monosex cultures etc. may turn out to be impressive in some species.

The prospects of catching up some of the delay in the development of farmed breeds of fish by improving the additive genotype seems to be good. Modern breeding and selection theory may be applied from the early start of the domestication process. According to the previously cited papers on genetic parameters, the genetic variation in productivity traits seems to be substantial in most fish populations. The large reproductive capasity will facilitate high selection intensities and rapid dissemination of improved stocks. In some species (e.g. tilapia), generation intervals as low as 1/2 year may be realized.

SHORT TERM BREEDING GOALS

The short term breeding goal (10-20 years) should be defined by a set of traits that are of economic importance, that are known to be inherited, and that may be recorded in an applied selection program. The short term breeding goal in farmed fish should of course, as in other farm animals, be chosen to improve the efficiency of the production or to minimize the input to output ratio. Efficiency may be partially quantified in terms of feed conversion ratio (FCR) or units of feed per unit of product. Even today, farmed fish populations compete well with other farm animals. FCR in farmed fish has been estimated to 1.5-2.0, while FCR in meat producing farm animals ranges from 2.5 (chickens) to 5.5 and above (grazing animals) according to Edwardson (1978). Still, there is no reason why efficiency should not be the reference trait in a selection program for farmed fish. Improved efficiency will secure a better utilization of the input resources, reduced costs for the producer, and eventually reduced market prices for the consumers.

Growth and quality

Direct records of individual efficiency of the breeding candidates are even less obtainable in fish than in traditional farm animals because of the poor control of individual feed consumption. This problem has been avoided in animal breeding by focusing on the improvement of the output in terms of meat, milk, eggs etc, which may easily be recorded. This has resulted in an automatic correlated response in efficiency because of reduced production time and maintenance costs per unit of yield. A similar approach will probably be useful in most species and farming systems of farmed fish. Consequently, the main breeding goal should be growth rate.

It may be argued that growth rate is of less importance in farming systems where feed is provided by the natural plancton and algae production in the pond environment, as in the most common carp and tilapia systems. Even if fertilization of the ponds is widely applied, some upper limit of the feeding intensity will be reached. In this situation, however, increased growth rate may be utilized by shortening the production cycles and by lower initial stocking densities. Supplementary feeding with agricultural waste products or by reallocation of feed resources for farm animal production should also be considered.

An additional trait affecting the output value may be product quality. Today, most of the market for farmed fish does not practice price differentiation for quality, except for size and colour in some species. Product quality may be included in the breeding goal if it is priced by the market.

Domestication

The application of selective breeding programs in farmed fish will frequently involve an element of genetic domestication. This may increase the importance of considering traits like mortality, disease resistance and stress susceptability in the breeding goal. Most farmed animal species have been through a historic process of natural genetic adaptation to farm environments. The genetic variability of such fitness traits is consequently quite low in most farm animal populations (heritabilities of 0.1 and below). In farmed fish, however, the process of genetic domestication has a shorter history, and may probably be speeded up in a selection program.

Considerable genetic variation in fitness traits of fish populations has been observed in farming environments, e.g. in disease resistance (reviewed by Ilyassov, 1987; Chevassus and Dorśon, 1990), mortality (Standal and Gjerde, 1987; Rye et al., 1990) and stress (Refstie, 1982). Selection for improved growth and productivity will probably result in a correlated response in domestication and fitness parameters because of better performance in adapted individuals. Furthermore, the prospects of direct testing and recording of fitness related traits are much better in fish than in less prolific species. Several parallels of large full sib groups may be produced simultanously, and challenge tests may be carried out outside the breeding nucleus. Indirect selection based on immunological, hormonal or other biochemical parameters should also be considered. Improved fitness will affect both output (improved survival and growth) and input (reduced stocking, feed and veterinary costs) of the production.

Reproduction

Reproductive performance is frequently included in the breeding goal for traditional farm animals because of the large marginal effects of dividing the maintenance costs of the parent stock on an increased number of offspring. In fish, however, the marginal effects of increasing the number of offspring per parent will be negliable because of the high initial fertility. Most farmed species produce thousands of eggs per year of even millions (carps and several marine species), and the mortality of eggs and fry may be controlled or significantly reduced in hatchery or farm environments. Fecundity may consequently be disregarded in the breeding goal for most species as long as reproduction is not affected by selection for other traits. Still, age at sexual maturity may be an important trait in some species. Early maturation may lead to overstocking (e.g. in tilapia) or to growth interruption and mortality (e.g. in salmon). In such species, age at maturity should be included in the breeding goal.

Sea ranching and polycultures

Even if efficiency is maintained as the reference trait for definition of breeding goals, some specialized culture systems may require modifications of the breeding goal compared to the most common systems.

Sea ranching is based on intensive culture during early life stages to avoid bottlenecks limiting the population size in the natural habitat at a later stage. If the natural grow-out habitat may support an increased number of individuals, productivity may be improved by releasing fry or juveniles from culture. However, the efficiency of such systems will largely be determined by the recapture frequency of the released individuals, even if growth rate and other traits may be important as well. A breeding plan for sea ranching where recapture frequency is included in the breeding goal has been suggested by Gjedrem (1986), and is presently tested in a sea ranching program with Atlantic salmon in Iceland and the Faroe Islands.

Polycultures involving several species are quite common. e.g. in carps. Polyculture performance may be defined by total input to output ratio. Total output should be determined by weighing the yield from each species by their market value. Selective breeding within each species to maximize the total efficiency or the total output may be quite difficult because of interspecies interaction. A testing scheme for improved interaction will be extremely complicated. An alternative may be within species selection based on performance in a well defined polyculture, but aiming at the same breeding goals in each species as described for monocultures. The effect of selection on the total polyculture performance should then be continuously checked. The genetic correlations between performance in polyculture and in monoculture should also be determined, to evaluate the possibility of utilizing the same improved strains in both systems.

Combined rice-fish cultures utilizing paddyfields during the flooded seasons may represent a large potential for fish culture. Rice-fish cultures are practiced with carps and tilapia, and should be regarded as a polyculture system where the combined productivity of rice and fish should be maximized. The breeding goal should probably be defined as described above. However, if the rice culture may be regarded as homogenous, the interaction between rice crop yields and performance of diffierent full sib groups of fish may be tested in separate replicated test units, and interaction may be included in the breeding goal.

CHOICE OF GENETIC BASE

The importance of considering the genetic base when starting selective breeding for additive genetic performance in fish has been demonstrated in several selection experiments. Mass selection for improved growth rate in experimental populations of tilapia and carps has frequently failed to show response (Moav and Wohlfarth, 1976; Hulata et at., 1986; Teichert-Coddington and Smitherman, 1988). Even if some response has been observed for downwards selection, the authors suggest that genetic bottlenecks and high levels of inbreeding in such closed, experimental populations may have reduced the genetic variation significantly by start of the experiments. The genetic variability in the base population may be secured by forming a synthetic population (Skjervold 1982). Bondari (1983) derived a genetic base of channel catfish by crossing six different cultured stocks and obtained significant response to selection for growth rate. The national Norwegian breeding program for salmon was started by collecting and testing breeding candidates from a large number of wild populations (Gunnes and Gjedrem, 1978). Even if cultured strains are available, wild populations may be possible contributors to a synthetic population because of the moderate genetic differences between wild and cultured stocks. Testing should be carried out in a common, commercial farming environment. The founder stock of a synthetic population should then be formed by selecting the best individuals across populations. Some minimum level of representation from the tested populations may be demanded, to ensure the genetic variability of the synthetic population.

If a wide variety of farming environments is applied in commercial farming, the testing should be carried out in several representative environments to check for genotype-environment interaction. Most fish populations appear to be robust to moderate variability in environmental conditions, but this may only be checked by testing (Gjedrem, 1985). If the ranking of the tested stains or populations is highly variable from one farming system to another, specialized populations may be established.

The choise of parent strains in a hybrid program is determined by the non additive genetic interaction in the crossbred offspring. This may only be tested by crossing the strains. The hybrid performance should not only exceed the best parent strain, but also all other available purebred stocks. In general, crossbred offspring after highly inbred strains may express considerable heterosis, while heterogeneous parent strains normally produce less heterosis. If culture strains of fish are considered to be generally more inbred than wild populations, this picture seems to be valid for fish crossbreeding (reviewed by Gjedrem, 1985; Dunham, 1986; Bakos, 1987), even though the genetic gain from crossbreeding often seems to be moderate in both situations. If heavily inbred strains are required to benefit from a hybrid program in fish, the prospects of improving the additive genotype in the parent strains will be poor. A hybrid program without selection for improved additive performance will probably be a blind alley compared to the long term breeding goal.

SELECTION STRATEGIES

Mass selection has been the traditional selection strategy in fish. As pointed out prevously, the moderate sucess of this strategy, both historically and in several recent selection experiments, may be caused by large, uncontrolled systematic environmental variation (e.g. age differences) and by uncontrolled inbreeding. Social competition may be another systematic source of variation, e.g. in growth rate. Even if competing ability is assumed to be partially genetic, it is not expected that a correlated response in competing ability will improve growth rate (Kinghorn, 1983; Doyle and Talbot, 1986a). Social competition may also magnify age dependent variation.

Several strategies have beed suggested to avoid these problems, e.g. age standarizing (Tave and Smitherman, 1980), size standardizing (Doyle and Talbot, 1986b), within family selection procedures (Uraiwan and Doyle, 1986) etc. However, the standard strategy in other farm animals has been to test breeding candidates in a common environment without severe restrictions on resources affecting performance, and to maintain individual life history records. The testing environment should be as similar as possible to a representative, commercial farming environment. This strategy has been successfully applied to fish (Gjedrem, 1979; Bondari, 1983; Hersberger et al. 1990). The main requirement of this strategy is individual tagging or branding of all breeding candidates. A variety tagging and branding systems has been used (Gjedrem, 1983). In fish, tagging or branding may only be applied after a certain growth period because of the small sizes of fry by hatching. The obvious solution in a selection program is to keep full sib groups in separate units during this period. The tagging or branding system may then be extended to include pedigree information. The period of separate rearing should be minimized to avoid large common environmental effects in the full sib groups.

Pedigree records will allow for combined selection strategies, utilizing the performance of relatives to determine individual breeding values. The large numbers of full sibs and half sibs (maternal as well as paternal) that may be produced simultaneously in a fish breeding program will increase the accuracy of the individual breeding value estimates substantially. The use of sib records is also of great importance when selecting for traits that may not be recorded in the breeding candidates (e.g. sex limited traits, carcass quality traits etc.) or traits that may only be quantified in frequencies (e.g. mortality, disease, seasonal sexual maturation etc.). Further testing of relatives (e.g. progeny testing) will usually not contribute much in a fish breeding program.

In most cases, more than one trait will be included in the breeding goal. To rank the breeding candidates, a breeding value reflecting the total performance should be estimated. The well established methods in animal breeding theory for computing total breeding values should be applied (e.g. selection index methology or mixed model methology). Commercial fish breeding programs utilizing combined selection for several traits has been practised for salmon and rainbow trout since 1976 in Norway (Gjedrem, 1985; Refstie, 1990).

The selection strategies described above are focusing on the improvement of the average additive genetic performance in the population. According to the long term breeding goal, this should be the main objective in a selection program for farmed fish. However, selection strategies have been developed for simultaneous improvement of additive and non-additive genetic performance. If selection within two different heterogenous populations (e.g. synthetic populations of different origin) is carried out based on progeny testing after crossbreeding, the spesific combining ability between the two populations may be improved as well as the additive genetic performance in both populations. This reciprocal recurrent selection strategy (RRS) may be of some interest in fish breeding, where each male and female may be stripped and artificially mated to a large number of mating partners from the other population. Until now, no examples of applications of RRS in fish breeding have been reported. RRS will slow down the progress in additive genetic performance because of prolonged generation intervals, and the strategy is quite resource demanding because of the large requirements for progeny testing. RRS may only be applied in multiple spawning species.

BREEDING STRATEGIES

According to the long term breeding goal, the only suitable breeding strategy for a breeding nucleus will be some type of purebreeding approach. Assuming that the additive genetic variability has been secured, e.g. by forming a synthetic population, systematic breeding for improved additive genetic performance within the population is a well proved strategy for long term improvement. However, even if bottlenecks in the effective population size and mating of close relatives are avoided, inbreeding will accumulate in the breeding nucleus. An important property of a synthetic population is the possibility to benefit from a permanent heterotic component by maintaining high levels of heterozygosity in the population. The breeding nucleus should consequently not be regarded as a closed population. Breeders from other populations should be allowed to enter the nucleus according to their performance.

The breeding strategies that may be applied to produce grow-out fry for commercial fish farming are less restricted than when breeding within the nucleus. Any kind of crossbreeding, ploidy manipulations, sex manipulations, etc. may be applied if the productivity of the commercial fry is improved. As pointed out earlier, any breeding strategy for commercial fry production that impose limitations on the progress in additive genetic performance in the nucleus should be avoided. One example is the use of highly inbred strains in a hybrid program. The resources and time needed to produce, maintain and replace inbred lines will be better utilized by increasing the efforts to improve the additive genetic performance of a purebred nucleus (Gjedrem, 1985; Gjerde, 1988).

COMMERCIAL APPLICATIONS

The large reproductive capasity of farmed fish species facilitates a sentralized breeding system. In most cases, one breeding station may produce sufficient commercial fry or eggs to supply the entire fish farming industry on a national level, either directly or through a network of multiplier stations. For safety reasons, the breeding nucleus may be split on two or more localities, but a controlled exchange of breeders should be practised to expand the effective population size and increase the selection intensity. It may be argued that competition between several independent breeding units may benefit the efficiency of the breeding programs. 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 programs will be considerable. On the other hand, the quality of commercial fry or eggs 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.

Still, a sentralized breeding system will be of no importance to commercial fish farming if the improved genetic material is not appreciated and utilized by the fish farmers. In most species, the farms may easily be restocked by producing any broodstock available. To ensure a close communication between the breeding nucleus and the fish farms, some level of integration of the two activities should be established. It is of crucial importance that a fish farmers' organisation is established, and that the organisation participates in the formulation of breeding goals and strategies. Commercial fish farms may also participate in the breeding program as test stations. Several tagged or branded parallels of the full sib groups in the breeding nucleus may be produced and stocked for testing in commercial farms, to ensure valid test results for the selection in the nucleus. The ultimate integration is of course a farmer owned breeding system.

REFERENCES

BAKOS, J. 1987. Proc. EIFAC-Symp.*, Bordeaux, I: 303-311.

BARDACH, J.E., RYTHER, J.H. and McLARNEY, N.O. 1976. Aquaculture. John Wiley and Sons, 868 pp.

BONDARI, K. 1983. Aquaculture 33: 73-81.

CHERFAS, N.B. 1981. In: V.S. Kirpichnikov, Genetics Bases of Fish Selection. Springer-Verlag, 255-273.

CHEVASSUS, B. 1983. Aquaculture 33: 245-262.

CHEVASSUS, B. 1987. Proc. EIFAC-Symp.*, Bordeaux, II: 145-161.

CHEVASSUS, B. and DORSON, M. 1990. Aquaculture 85 (in press).

CHOURROUT, D. 1987. Proc. EIFAC-Symp.*, Bordeaux, II: 111-126.

DONALDSON, L.R. and OLSON, P.R. 1955. Trans. Am. Fish. Soc. 85: 93-101.

DOYLE, R.W. and TALBOT, A.J. 1986a. Can. J. Fish. Aquat. Sci. 43: 1059-1064.

DOYLE, R.W. and TALBOT, A.J. 1986b. Aquaculture 57: 27-35.

DUNHAM, R.A. 1986. Proc. 3rd World Congress on Genetics Applied to Livestock production X: 391-400.

DUNHAM, R.A. 1987. Proc. EIFAC-Symp.*, Bordeaux, II: 407-416.

EDWARDSON, W. 1978. Rep. no. 6, System analysis research unit. Univ. of Strathclyde, Glasgow.

EKNATH, A.E. 1989. Genetic Improvement of Farmed Tilapia. Progress report, ICLARM, Manila.

EKNATH, A.E. and DOYLE, R.W. 1987. Aquaculture 85 (in press).
FAO 1987. ADCP/REP/87/25.
FAO 1989. FAO Fisheries Circulator No. 815.
GALL, G.A.E. 1990. Aquaculture 85 (in press).
GJEDREM, T. 1979. Z. Tierz. Züchtungsbiol. 96: 56-59.
GJEDREM, T. 1983. Aquaculture 33: 51-72.
GJEDREM, T. 1985. GeoJournal. 10.3: 233-241.
GJEDREM, T. 1986. Aquaculture 57: 77-80.
GJERDE, B. 1986. Aquaculture 57: 37-55.
GJERDE, B. 1988. Aquaculture 75: 71-87.
GUNNES, K. and GJEDREM, T. 1978. Aquaculture 15: 19-23.
HERSBERGER, W.K., MYERS, J.M., IWAMOTO, R.N., McAULEY, W.C. and SAXTON, A.M. 1990. Aquaculture 85 (in press).
HULATA, G. WOHLFAHRT, G.W. and HALEVY, A. 1986. Aquaculture 57: 177-184.
ILLYASSOV, Y.I. 1987. Proc. EIFAC-Symp.*, Bordeaux, I: 455-469.
JHINGRAN, V.G. and PULLIN, R.S.V. 1985. A Hatchery Manual for the Common, Chinese and Indian Major Carps. ADB/ICLARM, Manila. 191 pp.
KINCAID, H.L. 1983. Aquaculture 33: 215-227.
KINCAID, H.L. 1987. Proc. EIFAC-Symp.*, Bordeaux, II: 417-430.
KINCAID, H.L., BRIDGES, W.R. and Von LIMBACK, B. 1977. Trans. Am. Fish. Soc. 106: 621-628.
KINGHORN, B.P. 1983. Aquaculture 31: 283-304.
KIRPICHNIKOV, V.S. 1981. Genetic Bases of Fish Selection. Springer-Verlag, 410 pp.
KIRPICHNIKOV, V.S. 1987. Proc. EIFAC-Symp.*, Bordeaux, II: 449-460.
KRASZNAI, Z.L. 1987. Proc. EIFAC-Symp.*, Bordeaux, II: 35-45.
LEWIS, R.L. 1944. Calif. Fish. Game 30: 95-97.
LONGWELL, A.C. 1987. Proc. EIFAC-Symp.*, Bordeaux, II: 3-21.
MÁRIAN; T. 1987. Proc. EIFAC-Symp., Bordeaux*, II: 383-392.
MOAV, R. and WOHLFAHRT, G.W. 1976. Genetics 82: 83-101.
NÁGY, A. 1987. Proc. EIFAC-Symp.*, Bordeaux, II: 163-173.
NÆVDAL, G. and DALPADADO, P. 1987. Proc. EIFAC-Symp.*, Bordeaux, II: 23-33.
PULLIN, R.S.V. and LOWE-McCONNELL, R.H. 1982. The Biology and Culture of Tilapias. ICLARM, Manila. 433 pp.
REFSTIE, T. 1982. Dev. Comp. Immunol., Suppl. 2: 205-209.
REFSTIE, T. 1990. Aquaculture 85 (in press).
RYE. M., LILLEVIK, K.M. and GJERDE, B. 1990. Aquaculture (in press).
SHULTZ, F.T. 1987. Aquaculture 57: 65-76.
SKJERVOLD, H. 1982. Arch. Tierzucht 25: 1-12.
STANDAL, M. and GJERDE, B. 1987. Aquaculture 66: 197-207.
TAVE, D. and SMITHERMAN, R.O. 1980. Trans. Am. Fish. Soc. 109: 439-445.
TEICHERT-CODDINGTON, D.R. and SMITHERMAN, R.O. 1988. Trans. Am. Fish. Soc. 117: 297-300.
THORGAARD, G.H. 1986. Aquaculture 57: 57-64.
URAIWAN, S. and DOYLE, R.W. 1986. Aquaculture 57: 93-98.
WOHLFAHRT, G.W., MOAV, R. and HULATA, G. 1987. Proc. EIFAC-Symp.*, Bordeaux, II: 393-405.
YAMASAKI, F. 1983. Aquaculture 33: 329-354.

* Proc. EIFAC-Symposium, Bordeaux, 1987: Tiews, K. (ed.). Selection, Hybridization and Genetic Engeneering in Aquaculture. Vol I-II. Schriften der Bundesforschungsanstalt für Fischerei, Hamburg.