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Review

Genetic improvement for the development of efficient global aquaculture: A personal opinion review

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ABSTRACT

It has been exciting to follow the rapid development of aquaculture production in Norway, and internationally, since 1971. As an animal breeder I am particularly impressed with the genetic gain obtained for growth rate, and also for disease resistance in several aquatic species, which is five to six times higher than what has been achieved in terrestrial farm animals. This is illustrated in five selected projects I have been involved in. The sad story is, however, that only less than 10% of the world's aquaculture production is based on genetically improved stocks. The big challenge for the future is to develop more selective breeding programs for existing and new emerging aquaculture species in order to increase the production of this nutritious food source and to improve the efficiency of the use of feed, water, land and labor resources.

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1. Introduction

In 1972, Elsevier Science Publishers B.V. established a journal devoted to aquaculture. The total global production of cultured organisms at that time was less than five million tons while in 2008 it reached 52.5 million tons (FAO, 2010). Elsevier Science Publishers B.V. therefore showed great foresight when they established the journal *Aquaculture* which has been the key scientific journal in this field over the last 40 years.

It is difficult to determine when selective breeding and cross-breeding was first systematically applied to aquatic species as little published information is available. It is, however, most likely that individual (mass) selection was practiced at the time of domestication to improve growth rate together with body shape and external color. In this connection the high fecundity of fish can create problems because it increases the likelihood of selecting close relatives, unless the number of breeding candidates per family is equalized (Gjerde et al., 1996) or some type of walk-back selection is applied (Sonesson, 2005). It is well known that in the past farmers usually used only a few parents each year, and that after a few generations the animals became inbred and showed signs of depression of fitness and performance. With these experiences, some farmers lost confidence in selective breeding and continued to recruit breeders from wild stocks which were easily accessible and inexpensive.

The inheritance of qualitative traits in common carp (*Cyprinus carpio*) and aquarium fish species received attention early. Zhang (1994) describes the development of colored carp strains which began three hundred years ago when the Emperor sent red carps to Jiangxi province. Long term inbreeding and isolation resulted in large variation among strains. In ancient China, goldfish, which is an ornamental variety, was developed from crucian carp. Koi carp with its diverse color varieties were developed in Japan, also from common carp. Both fish types are now commonly found around the world and kept for decorative purposes. Later, genes for scale cover in common carp were described and named scaled, mirror, linear and leather (Kirpichnikov, 1937).

One of the first documented experiments investigating selection in fish was initiated in the USA in 1919 (Embody and Hyford, 1925), in which brook trout (*Salvelinus fontinalis*) were selected for increased survival to furunculosis. Over three generations survival rate increased from 2% to 69%. Large response to selection for increased survival to furunculosis in common carp was reported from Germany (Schaperclaus, 1962). Ilyassov (1987) summarized the results from selection of common carp against dropsy disease in the Ukrainian ropsha strain which began in 1953 by concluding that "Mass phenotypic selection within different breeds has given varying results". By the fourth and fifth generations of selection, the improvement in survival was 30 to 40% over non-selected control carp. The first work on common carp selection in USSR dates back to the 1920s and culminated in the 1950s with the development of two highly productive strains, Ukrainian scaly and frame carps (Kuzema, 1971). Moav and Wohlfarth (1963, 1973, 1976) applied individual selection for growth rate over five generations in common carp without obtaining any response when selecting for fast growth rate, but a positive response for slow growth rate. They concluded that overdominance played a role in the inheritance of growth rate in common carp and that there was no genetic variation in the trait. However, Kinghorn (1983) commented that 'the report of no response to selection for high growth rate is not conclusive in this case'.

Limbach (1969) reported response to selection for growth rate in rainbow trout (*Oncorhynchus mykiss*) and inbreeding depression for growth in progeny after mating close relatives. In 1932, Lauren R. Donaldson started to select rainbow trout for increased growth rate, increased number of eggs and early sexual maturation and achieved a remarkable response over many generations (Donaldson and Olson, 1955). Donaldson started selection on return rate in sea ranching with chinook salmon (*Oncorhynchus tshawytscha*) in 1949 and reported response to selection (Donaldson and Menasveta, 1961).

The heritability for fingerling weight in common carp was estimated to be 0.21 by Nenashev (1966), while in rainbow trout it was 0.16 at an age of 150 days and 0.32 at 280 days (Aulstad et al., 1972). In oyster (*Crossostrea gigas*), Lannan (1972) estimated a heritability of 0.33 for body weight.

2. Knowledge from livestock genetics

I was born in 1928 in Bjerkreim, Rogaland and my parents were farmers. I studied Animal Sciences at the Agricultural University of Norway (from 2005 the Norwegian University for Life Sciences), where I obtained my undergraduate degree in 1956, Licentiate degree in 1962 and later a Master of Science degree at University of Wisconsin, USA in 1963. At the Department of Animal Genetics and Breeding, Agricultural University of Norway, I led extensive breeding projects in sheep and studied phenotypic and genetic variation in production traits. I was responsible for developing a new breeding program for sheep based on progeny testing of rams in 'Ram circles' which still is used by the Norwegian sheep industry (Gjedrem, 1969a). The thesis for my doctorate degree, which I defended in 1970, was entitled: *Studies related to progeny testing of rams and selection indexes* (Gjedrem, 1969b).

In the early 1970s efficient breeding programs had been developed world wide for all main terrestrial farmed animal species (Hagedoorn, 1950) and it was generally accepted that selection was an efficient method to improve the productivity and production efficiency of farm animals, as it was for plants. The discussions were more directed towards which breeding and selection methods were most efficient and how they could be improved and best implemented.

3. Transfer to aquaculture research

3.1. Offer to move into a new research 'world'

In 1970, the late Prof. Dr. Harald Skjervold, then Head of Department of Animal Genetics and Breeding, asked me to take responsibility for research in aquaculture and the building of necessary facilities. With my background in agriculture and research in terrestrial farm animals, I felt that this task and position was difficult and challenging. At that time I had no experience and knowledge in aquaculture farming or about the culture of aquatic species. In spite of my father's advice, I decided to 'jump into the water' and accepted the offer and entered the field of aquaculture in February 1971.

3.2. General view on selective breeding in aquaculture

As I tried to build my competence in aquaculture and contacts with national and international researchers and experts in the field, I was shocked to learn about the generally negative views on selective breeding. The main arguments were as follows: Don't you know that selective breeding does not work for aquatic species? Don't you know that the well known professor in Israel, Rom Moav, did not get any response after many generations of selection for growth rate in common carp? Don't you know that he concluded that there is no genetic variation for growth rate in common carp? This was followed with reference to Deputy Director Colin E. Purdom in Lowestoft, England who repeatedly declared that selective breeding does not work in fish, because fish are different from terrestrial farm animals.

These views were discouraging and came at a time when the publications referred to above (Section 1) which had found positive responses to selection in fish species were not well known, at least not to me. However, for us at the Department of Animal Genetics and Breeding the results obtained from our own initial experiments with rainbow trout in freshwater during 1967–1970 (Aulstad et al., 1972) demonstrating genetic variation in body weight at 280 days of age, were convincing and stimulated further studies in quantitative traits in fish. Still, knowledge of the magnitude of the genetic variation for economically important traits in aquatic species was very limited and no estimates of genetic correlations between production traits were available.

3.3. Research facilities

In 1970–71, researchers at Department of Animal Genetics and Breeding were convinced that to ensure future success for the emerging Atlantic salmon (*Salmo salar*) and rainbow trout industries, the productivity of these species should be improved through domestication and selective breeding. How this could be done, and how to structure an effective breeding program were still open questions at the time when there was no systematic and efficient breeding program for aquatic species. In addition to reliable estimates of phenotypic and genetic parameters for traits of economic importance for each candidate species in question, we needed basic knowledge about reproduction characteristics. Some limited information was available for rainbow trout, but none for Atlantic salmon. To obtain this information we needed facilities to produce individual full-sib families, to keep the fertilized eggs of each family separated in a hatchery, and to separately rear the fry of each family until they could be physically tagged. Many questions needed answers, for example: which would be feasible tagging methods and what type of grow-out facilities and feeds would be needed both in the freshwater and the in the sea-rearing phase?

During 1971–73, a freshwater aquaculture research station was built at Sunndalsøra, located approx. 200 km south of Trondheim, Norway. The facility included a hatchery containing 300 trays, a barn for Atlantic salmon with 216 2 m^2 tanks and one barn for rainbow trout with 192 mostly 1 m^2 tanks, and 36 78 m^2 concrete ponds outdoors to rear the fingerlings before release into floating net cages in the sea. Sunndalsøra was selected as the site for the research station because it was close to a large hydroelectric power facility. The temperature of the large volumes of water used to cool the turbines was high enough during the winter for production of 1 1/2 year old smolts which could be transferred into sea water cages in May–June. In addition, the research station was located close to a river with freshwater and a fjord with sea water. In 1973–1974, a marine research station with floating net cages was established at Averøy (approx. 100 km west of Sunndalsøra). Looking back, it is impressive that Dr. Skjervold succeeded to raise enough money to build these large research stations in 1971 when Norwegian aquaculture production totaled only 100 t of Atlantic salmon and 540 t of rainbow trout. When the operations at the new facilities were initiated, only the manager Arne Kittelsen (who was trained by Prof. Lauren Donaldson at College of Fisheries, University of Washington, USA) had hands-on experience with fish culture. The rest of the team, researchers and field workers, had to learn on the road. There was little knowledge and experience and much skepticism, as can be seen from the following anecdote: Dr. Skjervold was once asked what the purpose of the 36 outdoor ponds was, and he replied that he was planning to produce 100,000 smolts. The reply was that he might succeed in that, but that he would never manage to sell them. Well, he did; in 2011 Norway produced 300 million smolts.

3.4. Problems to be solved

One of the first questions asked was which species would be best for farming in Norway. At that time we focused on salmonids and compared Atlantic salmon, brown trout (*Salmo trutta*) specimens from large lakes, rainbow trout, Arctic char (*Salvelinus alpinus*), pink salmon (*Oncorhynchus gorbuscha*) (Gjedrem and Gunnes, 1978) and crosses between these species except for pink salmon (Refstie, 1983). It was concluded that Atlantic salmon and rainbow trout had the highest potential for farming in Norway.

There were many challenges to overcome before we could produce the planned 200 Atlantic salmon and 200 rainbow trout families each generation. Atlantic salmon will be used as an example below. In 1971 a dry pellet became available for start feeding of fry and automatic feeders were attached to each of the tanks and worked satisfactory. However, at that time no dry pellets were suitable for grow out of salmon in the sea. A moist pelleted feed, which disintegrated easily in sea water and caused pollution problems, was produced during the 1970s. Identification of individual fish for determining genetic relationship was also a problem. Several methods were evaluated (Refstie and Aulstad, 1975), and freeze branding using liquid nitrogen combined with fin clipping was selected as the preferred tagging method. This allowed us to group-tag 120 different full-sib families. In the early 1980, this method was replaced with individual tagging using PIT-tags.

3.5. Organizing the work

Our group of scientists and technicians worked under various institutions with different names. In 1982 we became the Institute of Aquaculture Research (AKVAFORSK) under the Agricultural Research Council of Norway and ten years later, in 1992, we became a limited public research company. Finally, in 2008, AKVAFORSK merged with four other research institutes in Norway into the new research company named Nofima. Below I use the name AKVAFORSK to describe the organization through all of these periods.

4. Breeding program for Atlantic salmon

4.1. Experiments

Our research with Atlantic salmon started in the fall of 1971. In the first phase we studied phenotypic and genetic parameters for economically important traits and how to transfer this knowledge into the creation of a selective breeding program. It was considered to be of great importance to collect eggs from many wild Atlantic salmon strains to secure as much genetic variation as possible in the base population established for selection. No information about the relative performance for key production traits among the wild river strains in Norway was available at that time, except for age at sexual maturation in terms of one sea-winter (grilse) and multi sea-winter strains.

Since our main aim was to study the magnitude of genetic variation, we had to know the parentage of the eggs and the resulting

fry, fingerlings and grow-out animals. Since at that time mass spawning combined with DNA fingerprinting for parental assignment was not an option, a controlled mating design using artificial stripping had to be used. In 1971 we used a factorial design, typically mating 3 males × 3 females, to produce 9 full-sib groups and three paternal half-sib and three maternal half-sib groups. Later a nested mating design was used with each male mated to two or more females to produce full- and half-sib families.

During four years (1971–1974) fertilized eggs were sampled from a total of 40 Norwegian and one Swedish river. In total, 442 full-sib families, i.e. the offspring of 188 sires and 428 dams, were tagged and performance-tested at different private marine farms (test stations). Estimated heritabilities for survival in freshwater and resistance against vibriosis were low (Gjedrem and Aulstad, 1974; Kanis et al., 1976; Rye et al., 1990) but were found to be relatively high for harvest body weight (Gunnes and Gjedrem, 1978). The coefficient of variation for harvest body weight was high (around 30%, Gunnes and Gjedrem, 1978), but lower (around 25%) when the body weight records were adjusted for sex and sexual maturity (Gjerde and Gjedrem, 1984; Rye and Gjerde, 1996). Farm and strain interaction for harvest body weight was generally low and accounted for 1 to 4% of total phenotypic variance (Gunnes and Gjedrem, 1978). A diallel cross involving five river strains showed significant but low heterosis for both growth and survival (Gjerde and Refstie, 1984).

As I stepped down from leader position of AKVAFORSK in 1988, I was able to do more research. The Agricultural Research Council of Norway supported a project to establish challenge testing to study genetic variation in furunculosis resistance. Gjedrem et al. (1991) demonstrated by challenge tests that the resistance against this bacterial disease under standardized environmental conditions had high heritability (0.45). Today challenge testing is routinely used as the basis for selecting for increased resistance to a number of diseases and ectoparasites in breeding programs, and this has opened the possibility for developing more resistant strains. Recent work has demonstrated that the development of resistant strains for specific diseases may be reached even faster by including marker assisted selection for QTL in breeding programs (Housten et al., 2008; Moen et al., 2009).

4.2. Developing the breeding program

Being the first to farm Atlantic salmon in Norway, some of the aquaculture pioneers earned good money. Most successful were the brothers Sivert and Ove Grøntvedt, who in the spring of 1970 successfully stocked 20,000 smolts into the 'Grøntvedt cages' in sea at Hitra Island. Their success increased the interest for farming Atlantic salmon along the coast. The production of smolts was still low for several years, and since AKVAFORSK did not need all the smolts we produced for research purposes, we became a major supplier of smolts to the industry during the 1970s and 1980s. The sales of eyed eggs, smolts and market-sized salmon became an important source of funding for our research. This activity brought us in close contact with the farmers and we learned from each other. This collaboration with the industry was important for demonstrating the impact of our research, and enabled us to get a strong response to selection and rapid transfer of the genetic gains to the emerging industry.

Before we could start the breeding program, many questions had to be answered and a number of decisions had to be taken, e.g. which breeding methods to use. Crossbreeding of inbred lines was immediately ruled out, based on bad experiences in terrestrial farm animals and later also in rainbow trout (Gjerde, 1988). Crossbreeding of other strains was of potential interest, but our knowledge was limited and we decided to wait for more results. Low heterosis for growth and survival was later demonstrated when crossing different wild strains of Atlantic salmon (Gjerde and Refstie, 1984). However, the magnitude of heterosis when crossing domesticated strains (developed over several generations of selection) has not been studied. Selection within a nucleus population (pure breeding) was decided upon as the best choice.

Likewise, we had to decide which selection methods should be used? Individual selection was appealing, but could only be used efficiently for traits that could be recorded on living breeding candidates (at that time growth rate and age at sexual maturity), hence individual selection could not be the only solution. Progeny testing, which was used for most terrestrial farm animals, was considered, but because it usually doubled the generation interval it was not our first choice. Family (sib) selection was seen to have several advantages. It does not lengthen the generation interval, it allows recording of all economic traits, and it is a selection method that had successfully been used since the 1930s in poultry breeding (Lerner and Hazel, 1947).

We eventually decided to go for combined between families and within family selection to increase growth rate and reduce early sexual maturity, and family selection for improvement of disease resistance and product quality traits.

Further, as we estimated that the strain by farm interaction accounted for a small part of the total variation in growth rate in salmon, it was decided to develop one single improved strain of salmon for the whole Norwegian coast. However, for age at sexual maturity a substantial genotype by farm interaction has since been reported when using data from sibs reared at different farms (Wild et al., 1994), and genotype by farm interactions should therefore be investigated for other traits.

The initial breeding goal included the following traits:

- Body weight at harvest
- Age at sexual maturation—some salmon become sexually mature as parr in the freshwater phase and some after 1 year in the sea (grilse), at a body weight (1–2 kg at that time) of low economic value in the market. Therefore, to reduce the frequency of early sexual maturity, these early maturing fish were discarded as breeding candidates, and breeding candidates were not selected from families with a high proportion of such fish.
- Survival—this was difficult to include because the heritability of survival during the freshwater period was very low and the tagging method used did not allow identification of dead fish in the sea cages.
- Selection for specific diseases was included in the breeding objective after 1989 when controlled challenge tests for specific diseases were developed (Gjedrem et al., 1991)
- Meat quality—filet fat and filet color were included after 1990 as effective recording methods were developed (Gjerde, 1987; Rye, 1991).

4.3. Achievements

The first selection of breeders from the families produced in the fall of 1971 took place in the summer and fall of 1975. This was the first time selection using sib information was used for an aquatic species (Gjedrem, 2010). Selection continued for each of the four year classes (as the generation interval was four years) using combined between and within family selection for harvest body weight. We sold smolts from the first selected parents to the industry in June 1977 without receiving any specific feedback from the farmers, but when they received G_2 selected smolts in June 1981, the reaction was very positive. These second generation smolts were considered to be a different and faster growing fish. The positive response to selection continued in the following years and eliminated the earlier skepticism about selective breeding for aquatic species in Norway. Gjedrem (2010) described the process used to get the farmer organizations directly involved in the breeding program. After four generations of selection from a total of 16 different year classes this came to an end in 1992 when AquaGen AS was established as a limited

company and continued the breeding work based on the four breeding nucleus populations which were established by AKVAFORSK during the early 1970s. We had hoped that the breeding program could have been continued as a farmers' cooperative.

The achievements obtained through the 40 years of farming Atlantic salmon in Norway have been considerable in many ways. To date, the time to produce a standard market-sized 4 kg fish has been halved, and while 3 kg dry matter (in moist feed) was needed to produce 1 kg of salmon in the beginning this has been reduced to 1.15 kg (dry pellets) (Austreng, 1993). Survival rate has also been improved, particularly in the freshwater period.

However, unfortunately there is not much reliable documentation on how much of these phenotypic improvements are due to genetic improvement. Gjedrem (1993) reports a genetic gain of 15% in growth rate from the first generation of selection. For growth until harvest size the predicted genetic gain over the first five generations of selection was in the order of 13–15% per generation and that for early sexual maturity 3% units per generations (Gjerde and Korsvoll, 1999). The only reported realized and correlated genetic gain is from comparing the 5th generation farmed salmon with wild salmon originating from one of the rivers (Namsen) from which many base population animals were obtained as summarized in Table 1 (Thodesen et al., 1999). The high genetic response for growth rate had led to a correlated response of 20% for feed conversion efficiency, and improved retention of both protein and energy. These correlated genetic responses are particularly welcomed since in practice it is very difficult and costly to directly and accurately record feed intake, and thus feed conversion efficiency, in fish in the grow-out phase (Kolstad et al., 2005).

Documentation of genetic gain for other economically important traits is scarce. Gjedrem (2004) documented that 97% of the total production of Atlantic salmon in 2003 was based on improved stocks, which is exceptional for an aquatic species. It could be argued that more resources should have been used to get more reliable estimates of genetic gain for the selected traits.

Sampling 41 salmon strains, to be sure to capture broad genetic variation for the species, was excessive. Holtsmark et al. (2006) concluded from a simulation study that sampling from more than eight populations did not significantly increase genetic gain any further. When tagging the fish we faced a problem because some fingerlings were too small for tagging and the frequency of these under sized fish varied between families. This pre-selection of size of fingerlings could affect our estimation of both phenotypic and genetic parameters. This problem was reduced in the following generations as growth rate was increased by selecting for harvest weight. A study of the dam component showed considerable effect on body weight at tagging (Refstie and Steine, 1978) while it was of minor importance at harvest size (Gunnes and Gjedrem, 1978).

5. Breeding program for Nile tilapia

In 1985, Dr. Roger Pullin from the International Center for Living Aquatic Resources Management (ICLARM, now the WorldFish Center) invited me to participate in a project for comparing different species and strains of tilapia in Africa. My initial response to this request was negative. However, I added that if ICLARM wanted to start a selective breeding project with tilapia we would be interested to cooperate. In 1986, I was invited, together with Dr. Gideon Hulata, to the Philippines to discuss a breeding project for tilapia. It was decided to develop a plan to focus on the genetic improvement of Nile tilapia (*Oreochromis niloticus*) and the Bureau of Fisheries and Aquatic Resources (BFAR)'s National Freshwater Fisheries Training and Research Center (NFFTRC) in Muñoz, Nueva Ecija, Philippines was selected as the location for the project. ICLARM applied to the United Nations Development Programme (UNDP) for financial support. UNDP's director Alva App decided to support the project after several discussions with ICLARM and myself, and he visited Sunndalsøra and Averøy to learn about our breeding work with Atlantic salmon and rainbow trout and the achieved selection responses. Later the Asian Development Bank (ADB) also supported the project. At AKVAFORSK we were excited to be involved with what, for us anyway, was a new tropical species, and to be able to apply and transfer our experience from salmonids.

Table 1
Genetic gain in Atlantic salmon over five generations of selection (from Thodesen et al., 1999).

Trait	Selected over wild (%)
Growth rate	+113*
Food consumption	+40*
Protein retention	+9
Energy retention	+14*
FCR[a]	−20*

[a] Feed conversion ratio or kg feed per kg body weight produced.
* $P<0.05$.

5.1. Status and general opinion in the field

The skepticism to apply selective breeding for fish species was still present. Now the message was as follows: 'Selective breeding seems to work for cold water fish' (referring to our work with salmonids), 'but it does not work for warm water species like tilapia and common carp'. The reasons for this continued skepticism was still Moav's former work with common carp, the lack of response in several selection projects based on performance testing for increased growth rate in tilapia (Hulata et al., 1986; Teichert-Coddington, 1980) and the demonstration of a low heritability (0.04) for 90-day body weight in tilapia (Tave and Smitherman, 1980). It was, therefore, encouraging that ICLARM initiated the UNDP financed project for selective breeding of Nile tilapia despite these concerns. ICLARM appointed Dr. Ambekar E. Eknath as project leader.

5.2. Experiments with tilapia

The preliminary project plan was prepared during 1986, and focused primarily on the estimation of phenotypic and genetic parameters for growth and documentation of response to selection for growth. The project plan was detailed at a meeting at AKVAFORSK, Ås, Norway in the spring of 1988 with participants from ICLARM, BFAR/NFFTRC, Marine Science Institute of the University of the Philippines (UPMSI) and Freshwater Aquaculture Center, Central Luzon State University (FAC/CLSU), Muñoz, Nueva Ecija. It was already clear that a couple of hundred full-sib families should be produced in each generation, but a major question was how should this be done? Artificial mating by stripping males and females was not commonly practiced for tilapia at that time. It was therefore decided to let the mating take place in 1 m^3 hapas installed in earthen ponds. Floy tags were selected for tagging in order to keep track of genetic relationships among animals. To ensure that we started out with broad genetic variability, broodstock were sampled from four farmed tilapia strains in Philippines (denoted Israel, Singapore, Taiwan and Thailand stocks) in addition to four wild stocks imported from Africa (Egypt, Ghana, Kenya and Senegal). The project was given the name GIFT (Genetic Improvement of Farmed Tilapias).

The most important results from the first three years of the project are as follows: The wild strains from Africa (except for the Ghana strain) outperformed the local farmed strains in the Philippines (Eknath et al., 1991). Extensive testing of the eight strains across 11 distinct and highly variable production environments revealed low strain by environment interaction, on average accounting for only ~1% of the total variation in harvest body weight (Eknath et al., 1991). A complete diallel cross including the eight tested strains

(8×8 cross) showed an overall level of heterosis of 2.3% for harvest body weight and survival from tagging to harvest (Pullin et al., 1991). A later study based on the same data reported heterosis of 4.5% for harvest body weight (Bentsen et al., 1998). Heritability for harvest body weight in the synthetic base population was estimated to be 0.15 with a relatively high effect common to full-sib families (c^2 effect) (Eknath et al., 2007).

5.3. Achievements

I insisted that the initial selection should focus on growth rate only, in order to demonstrate that genetic improvement can be obtained also in a tropical fish species, and thus convince producers, researchers and authorities that selective breeding was an efficient way to increase productivity in Nile tilapia. The base population was formed by breeders selected from all purebred and crossbred groups in the diallel. When producing the first selected generation the selection intensity was kept low in order to let all strains be represented in future generations of selection. Through five generations of selection conducted during the life span of the GIFT project, the accumulated selection response for growth rate was 86% (corresponding to an average of 17% per generation) (Fig. 1).

According to Neira (2010) and Rye et al. (2010), at least 20 family-based breeding programs are now in operation for Nile tilapia around the world. This is more than for any other aquatic species. The base populations in 10 of the 20 tilapia breeding programs are known to be derived from the GIFT strain (Neira, 2010) and mainly with breeders from the 5th selected generation. It is interesting to observe that the production of Nile tilapia is expanding fast, increasing from 127,000 t in 1988 to 2.3 million tons in 2008, making tilapia the fish species with the highest increase in production (FAO, 2010). According to Fitzsimmons et al. (2011) tilapia have the potential to become the most important aquaculture species in the world. According to Ponzoni et al. (2010) the GIFT project has had a world-wide impact on aquaculture. In 2005, Nile tilapia represented 84% of total tilapia production compared with 42% in 1988. Frozen tilapia filets, mainly derived from Asia and Latin-America, and exported to USA, Europe and other countries, are now a world-wide commodity. The continuation of the GIFT project is described by Eknath and Hulata (2009).

Selection for harvest weight of the fish was at around 100 g, which was a common size desired by local markets at the start of the experiment. However, as the developing export markets for frozen filets were developed during the 1990s, desired harvest weights increased to 600–800 g, an increase in harvest body weight during the project would therefore have been preferable. Tagging at an early age and a more standardized testing environment would increase the genetic gain.

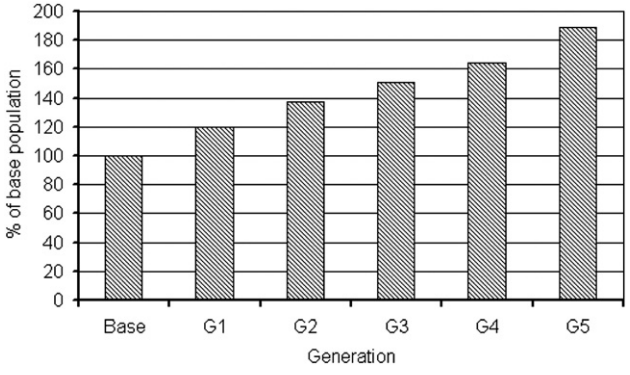

Fig. 1. Selection response in the GIFT project for increased body weight at harvest, measured as the percentage of the base population mean. For each generation, the response is calculated by comparing progeny of selected parents and progeny of parents with average breeding values (from Bentsen et al., 2003).

Already in December 1995, I urged the board of ICLARM to do their outmost to secure economic support for continuation of this successful project and to develop a selective breeding program with a broader breeding goal, if necessary with support of AKVAFORSK. AKVAFORSK regret that ICLARM did not find financial support to develop a breeding program after termination of the GIFT project in 1997. Regretfully, not all results from this project have so far been published.

6. Breeding program for rohu carp

In August 1990 I met Dr. S.D. Tripathi the director of Central Institute of Freshwater Aquaculture (CIFA), Bhubaneswar, India at a meeting in Muñoz, Philippines. During the meeting we discussed the possibility to start a selective breeding project with rohu (*Labeo rohita*) at CIFA. We agreed to apply to NORAD (Norwegian Agency for Development Cooperation) for economic support. On a visit to CIFA in May 1991 the experiments were detailed and NORAD decided to support a three year project (1992–1994). Due to the encouraging results obtained during these three years (Anonymous, 1996) the project was extended first to 1996, then to 2001, and finally to 2003 with the objective of developing a commercial selective breeding program for rohu.

6.1. Status and general opinion in the field

Rohu carp was selected among the three Indian major carp species (rohu, mrigal and catla) because it was considered to have the best quality. The biology and reproduction were well known but there was no information about genetic parameters for important economic traits. According to Eknath and Doyle (1985; 1990) the hatchery practices for carps in India at that time were counter-productive, most likely caused by an undesirable tendency to breed a limited number of individuals which results in inbreeding depression for important economic traits, and thus the need to introduce new wild breeders.

6.2. Experiments with rohu

To form a base population one local farmed stock together with five wild river strains were selected (Reddy et al., 2002). For each strain both full-sib as well as maternal and paternal half-sib families were produced. Fertilized eggs of each fullsib family were transferred to hatchling hapas (2 m×1 m×1 m) and the resulting fry reared in 100 m^2 earthen ponds until tagging. Since rohu in India is farmed both in monoculture and polyculture it was of interest to estimate the magnitude of genotype by production system interaction for growth in particular. After tagging each family was therefore stocked both in (three) mono and (two) polyculture ponds together with catla (*Catla catla*) and mrigal (*Cirrhinus mrigala*).

The estimated heritability for harvest weight was of medium size ($h^2=0.23$) while the effect common to full-sibs was very high ($c^2=0.32$). This was most likely caused by separate of the full-sib families in ponds prior to tagging in which the environmental conditions were difficult to standardize. The effect would have been accentuated because fish were tagged at a much higher body weight than planned for in most year-classes (Gjerde et al., 2003). The genetic correlation between harvest body weight in monoculture and polyculture varied greatly between the four year classes (−0.4, 0.75, 0.30 and 0.84) thus resulting in substantial to minor re-ranking of families in the two production systems.

To study the magnitude of heterosis for growth and survival two 3×3 diallel crosses with five strains were produced and tested both in earthen ponds using either monoculture or polyculture. For harvest weight, total heterosis for each of the six stock crosses was low or negative and average heterosis was also low, and in most cases, not

significantly different from zero. For survival, total and average heterosis was negligible and not significantly different from zero.

For both harvest weight and survival total heterosis for each of the five stock crosses was low or negative (Gjerde et al., 2002). It was concluded that genetic improvement of growth and survival through crossbreeding of different rohu carp stocks has little practical application (Anonymous, 2003).

6.3. Achievements

Four generations of selection were performed in mono- and polyculture for growth rate. The overall selection response was extremely high and reached 29.6% per generation. The response was higher in monoculture (30.6) compared with polyculture (27.0%) (Mahapatra et al., 2004). The genetic correlation between body weight at 14 months of age and harvest weight (20 months) was close to unity (Anonymous, 2003).

To develop a plan for a breeding program, and the dissemination of genetic gain to the Indian carp industry, a working group was appointed for the purpose of establishing a foundation called the Genetic Improvement of Farmed Carp (GIFC) and was scheduled to report its findings to ICAR (Indian Council of Agricultural Research) by the end of year 2000. As far as I know this has not been done.

At a final workshop in 2003 a plan for a large-scale breeding program for rohu in India was developed based on the results obtained from the project (Rye et al., 2003). However, until now this ambitious plan has not materialized. CIFA continue the breeding program and select for growth rate and resistance to *Aeromonas hydrophila* but with a reduced number of families. Still some of the data from the project has not been published.

7. Breeding program for *Litopenaeus vannamei*

In 1993 I was contacted by Dr. Gary Pruder of Oceanic Institute, Hawaii about problems with their Specific Pathogen Free (SPF) project with *Penaeus (Litopenaeus) vannamei*. During several generations of reproduction using closed shrimp populations their animals had become highly inbred with reduced performance. After discussing the matter it was decided to start a breeding experiment within their SPF project.

7.1. Status and general opinion in the field

No family based breeding program was known in shrimp and the knowledge of genetic parameters was sparse. The estimated heritability for growth in *P. vannamei* using a full-sib design ranged from 0 to 1 and consequently with large errors (Lester, 1988). Methods for artificial reproduction were well known in *P. vannamei* while they were not fully known in the major species *Penaeus monodon*, for which the industry therefore relied on the catch of wild mother shrimp bearing eggs. My experience with the industry in the early 1990s was that their view on selective breeding and the expectation of its benefit was rather indifferent.

7.2. Experiments with shrimp

The base population consisted of four stocks, of which two had a narrow genetic base. From these stocks a synthetic population was produced. Full-sib families were produced by artificial insemination and the broodstock were marked with eye-tags. Each family was reared in an individual bucket until about a size of 1 g when they were tagged with a colored elastomer polymer (Godin et al., 1996). During 1995 and 1996, five cohorts (batches) of 294 full-sib families in total (the offspring of 63 females and 294 males) were produced and tested in six different environments (Fjalestad et al., 1997). A significant genetic variation was found for harvest weight ($h^2 = 0.76$) and survival during challenge with Taura syndrome virus ($h^2 = 0.22$). The genotype by environment interaction for harvest weight was very low and not significant.

AKVAFORSK was involved in the project for three years (1995–1997) and took part in later breeding projects with *P. vannamei* in cooperation with CENIACUA in Columbia (Gitterle et al., 2005) and with Aquatec in Brazil.

7.3. Achievements

Genetic gain after one generation of simultaneous selection for increased growth and resistance to TSV was 4.4% for harvest body weight and 12.4% for TSV survival (Fjalestad et al., 1997). According to Neira (2010), four breeding programs are presently running for *P. vannamei*, and Rye et al. (2010) report three breeding programs for *P. monodon*.

It is interesting to observe that in 1993 the production of *P. vannamei* accounted for 13% of the world production of shrimp and has increased to 45% in 2008, as compared to *P. monodon* which accounted for 59% of the production in 1993 and only 14% in 2008. What effect the first selective breeding program for *P. vannamei* which was started in Hawaii in the mid 1990s has had on these changes is not known?

8. Breeding program for sea ranching of Atlantic salmon

8.1. Background

One of my first tasks in aquaculture was to work out plans for a breeding project for sea ranching of Atlantic salmon in 1971. At that time several hatcheries were established to increase the productivity in major salmon rivers through production and release of fry, or in some cases smolts, of the local stock. According to McNeil (1980) sea ranching of Pacific salmon (*Oncorhynchus* spp.) dates back to 1872 in the McCloud River in California. A major breakthrough came in the 1950s with improved feed technology and the work of Professor Dr. Lauren R. Donaldson at The College of Fisheries in Seattle, USA. He initiated research into sea ranching of Chinook salmon (*O. tshawytscha*) (Isaksson, 1988). In 1949 Donaldson released 23,000 fry from a pond on the campus and got 23 returns four years later (Hines, 1976). During several generations of selection the return rate increased, while age of the returning fish was reduced (Donaldson and Menasveta, 1961). Today, sea ranching of Pacific salmon species is extensive, particularly in Alaska, Canada, Japan and Russia. In 1972 a private company, Oregon Aqua-Foods, started sea ranching in Newport, Oregon (Isaksson, 1988). Iceland was in a special situation since the sea fishery of Atlantic salmon in Icelandic waters had been forbidden for over 50 years (Isaksson, 1988). In 1963 Kollafjørdur Experimental Fish Farm was established, later followed by several private companies set up for the purpose of sea ranching. The return rate of salmon to Kollafjørdur varied from 2 to 9% (Isaksson, 1988). In Sweden the flow of most of the main rivers had been regulated to facilitate production of hydro electric power, and the power companies were ordered to produce and release smolts to compensate for the losses of natural spawning. Carlin (1969) reported significant variation in return rate of 17 full-sib families from the Baltic Sea which ranged from 0.5 to 17%, averaging 7%. Thus there was some indication of genetic variation in return rate of an anadromous fish species.

8.2. Experiments in sea ranching

In 1981 The Norwegian Directorate for Nature Management appointed a working group to discuss a number of issues related to sea ranching of Atlantic salmon. One of the main propositions was to study the effect of selective breeding for obtaining increased return rates. Detailed plans for such a project were already prepared, but the

project had not yet been implemented due to lack of financial support. The solution came some years later when a joint Nordic project was financed by the Nordic Council of Ministers and the Nordic Industrial Fund. Iceland was selected to host the project because of its generally high return rate of salmon and because the Icelandic Government also supported the project with additional funding. A Nordic board was established and Dr. Jonas Jonasson was appointed as the project leader.

During four years (1988–1991) broodstock were sampled from seven rivers in Iceland. In total 247,272 smolts representing 512 full-sib families, the offspring of 194 sires and 512 dams, were released from five sites. The return rate varied from 1% to 3% between years. Differences in return rates between sites of release were significant.

8.3. Achievements

The estimated heritability for return rate was 0.12 and that for body weight at return 0.36 (Jonasson, 1994). The most interesting result was the estimated response in return rate from one generation of selection. At all five release sites, the selected group had a higher return rate as compared with control groups, averaging 27% genetic gain (Jonasson, 1994). These results were promising and opened the possibility for improving the return rate through selective breeding. In earlier years relatively high return rates were seen in Iceland, but return rates declined because of environmental conditions in the sea, making it unprofitable for the established private companies to practice sea ranching, and thus implement selective breeding to improve the return rate.

Besides anadromous fish species, sea ranching is possible for molluscs, algae and marine and diadromous fish species. This is a potential means of harvesting the organisms responsible for primary production in sea which become feed for fish and shellfish species.

9. Documentation and education

In 1972 the salmon industry was new and based on very limited knowledge and experience. In Norway we had some knowledge about farming of rainbow trout, but the practice involving cage culture in the sea was new. Most salmon farmers had a background in fishing and agriculture farming. At the time there was no formal education in fish farming and no textbook on the topic was available in Norwegian. To meet the need for information we offered a course at the Agricultural University of Norway entitled “Introduction to fish farming”, and lecture notes were published (Austreng and Hvidsten, 1974; Gjedrem, 1975; Gjerde, 1991). In 1979 our group published the book Oppdrett av laks og aure (Farming Salmon and Trout) (Gjedrem, 1979) which was revised in Gjedrem (1986) and Gjedrem (1993). Later, several books covering specific topics related to aquaculture production were published. These books received positive responses from the farmers.

Experimental results were generally published in international peer reviewed journals, many of them in *Aquaculture*. In addition, we wrote popular articles in trade journals such as Norsk Fiskeoppdrett (Norwegian Fish Farming) summarizing major results.

A number of textbooks on quantitative genetics and selective breeding with a focus on farm animals were on the market, but none focused on selective breeding and applied breeding programs for aquatic species. In 2005 our group wrote the book ‘Selection and Breeding Programs in Aquaculture’, published by Springer (Gjedrem, 2005), which in 2009 was followed by the book ‘Selective Breeding in Aquaculture: An introduction’ also published by Springer (Gjedrem and Baranski, 2009). These books are mainly based on results and experience during our 40 years of research.

10. Prospects for future aquaculture production

10.1. The good news

There is a large need for increased production of animal protein in the future (Diouf, 2009; Kutty, 2010). The expansion of meat-producing farm animals is low and fisheries have stabilized at around 90 million tons. Today aquaculture is the fastest growing industry for food production with a growth rate of 7.7% per year during the period 1998–2007 (FAO, 2009), and there is a growing recognition

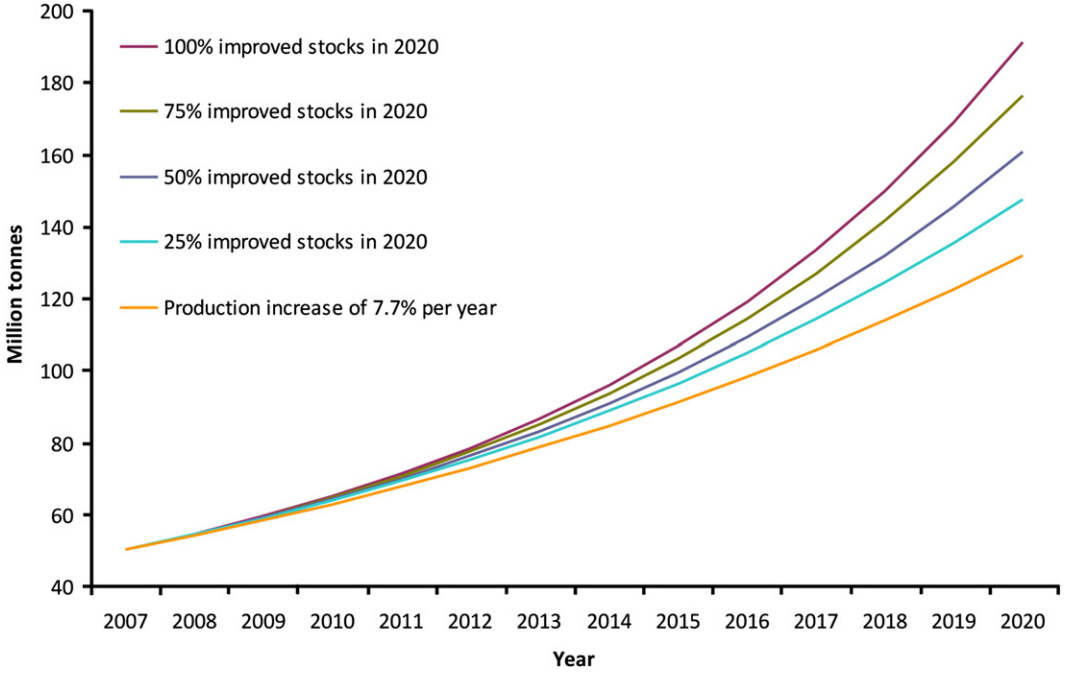

Fig. 2. Expected future aquaculture production of fish and shellfish with 7.7% increase per year and adding genetic gain of 12.5% per generation of selection considering a generation interval of 2.3 years with varying increased frequency of improved stocks.

worldwide that in coming years we have to turn to waters for additional production of animal protein (Kutty, 2010).

The lower line in Fig. 2 illustrates the expected increase in production with the present expansion of 7.7% per annum. As the use of improved stocks increases, the production is predicted to reach 190 million tons in 2020 if 100% of fish and shellfish are genetically improved. This would, however, be unrealistic to achieve, due to the high number of species farmed and that this scenario implies that at least one breeding program is established per species. In 2005, aquaculture production was reported for more than 241 fish and shellfish species, and 124 with more than 1000 t (FAO, 2007). However, Fig. 2 shows how production would be supplemented if we could increase numbers of stock sourced from efficient breeding programs.

In general, the possibility to increase aquaculture production in the future seems to be very high. For illustration, Gjedrem et al. (2012) estimated marine production per km coastline and freshwater production per km^2 land area in some main aquaculture producing countries. In 2005 China had the highest marine production of 1721 t/km coastline while world average marine production was 103 t/km. If the rest of the world was able to achieve half of China's marine production, 310 million tons of marine fish could be produced. Bangladesh had the highest freshwater aquaculture production per km^2 land area of 5.96 t compared with a world total production of 0.17 t/km^2. If production reaches half of Bangladesh's current levels around the world it would be possible to produce 176 million tons of freshwater species. These figures show that there is a very significant potential for aquaculture expansion.

From a resource point of view, fish are much more efficient utilizers of feed resources than farm animals (Austreng, 1993). In addition, Thodesen et al. (1999) estimated that feed conversion efficiency has improved by 20% after five generations of selection (Table 1).

A summary of measured responses to selection has shown estimated genetic gains of 10–20% per generation for growth rate when growth rate is the main, or only, trait selected (Gjedrem and Baranski, 2009). Genetic gain has also been obtained for other economically important traits, particularly disease resistance (Fjalestad et al., 1997).

As early as in 2002, 97% of the world's Atlantic salmon production was based on genetically improved stocks (Gjedrem, 2004), which demonstrates that it is possible to base the entire production of a key aquaculture species on improved material.

Besides fisheries, aquaculture is the only way to harvest the large world-wide resource of plankton and algae existing in the sea (through the production of fish, shellfish, seaweed and sea ranching of anadromous and catadromous species, as well as species living in coastal areas and brackish waters). By intensifying production through the selective breeding of species used in aquaculture and sea ranching, a major change in productivity and resource efficiency would be obtained.

10.2. The bad news

The use of genetically improved stocks in aquaculture production is very low and has increased slowly during the last years. Gjedrem (1997) estimated that only 1% of production was based on genetically improved stocks in 1993, 5% in 2002 (Gjedrem, 2004) and 8.2% in 2010 (Gjedrem et al., 2012; Neira, 2010; Rye et al., 2010). To me this represents a tragic situation because the benefits from selective breeding are not reaching about 90% of the production. This loss affects farmed animals, producers and consumers. Wild animals under farming conditions are stressed. It is well documented that selection speeds the rate of domestication which increases the welfare of animals (Vandeputte and Prunet, 2002). As shown above for Atlantic salmon and Nile tilapia, it is possible to double growth rate in 6–7 generations by selection, which means that the farmer can double the production with only some expansion of existing facilities, which means improved use of land and water resources. In addition (at least for carnivorous fish), conversion rate may be improved by about 4% per generation (Thodesen et al., 1999) because it is correlated to selection for growth rate. Selective breeding could greatly benefit consumers by lowering prices (as a result of reduced cost of production/kg) and by improving product quality and the world supply of animal protein.

I do not understand the reason for the lack of confidence in selective breeding for aquatic species. It is well documented that it is possible to obtain a genetic gain of 10–20% for growth rate per generation, which is 5 to 6 times higher compared with what is usually obtained for farm animals (Gjedrem and Baranski, 2009).

For agriculture, education and research had an early focus, and schools for farmers, research stations and agriculture universities were also established in most countries with breeding and genetics as important topics. This has been completely lacking for aquaculture in most countries, and researchers and advisory personnel have mostly been biologists educated at universities without any teaching in quantitative genetics and applied selective breeding. Even now, education in aquaculture has a low priority in most countries, both at undergraduate and graduate levels. This difference in education between agriculture and aquaculture may be one explanation why there has been such little application of selective breeding.

I do not know how to convince the industry to start selective breeding programs. I did hope that the successes of breeding programs in Atlantic salmon, rainbow trout, Nile tilapia, shrimp and other species would change opinions, but so far this has not occurred. The best we can do is to ask the farmers (particularly the bigger ones), the farmer's organizations, aquaculture authorities in each country and even international aquaculture organizations to push for the establishment and use of stock from selective breeding programs. I should not forget the researchers in aquaculture. Their job is primarily to document what genetic improvements can be obtained, and to raise awareness for the possibilities of further development of selective breeding programs. The documentation of the realized responses to selection should be a primary objective of the breeding companies as such information will benefit their market share and can also be used as an internal control to ensure that their program is working according to their intentions, plans and predictions.

Maybe farmers, aquaculture authorities and aquaculture organizations are waiting for 'miracles' from biotechnological methods to change the animals completely in one generation. I want to stress that even if the promises of new biotechnologies are/will be fulfilled, conventional selective breeding programs should remain the basis for genetic improvement in the future, and that hopefully such new technologies can be efficiently incorporated into these programs in order to further increase genetic gains. Today, after 40 years of international research in many countries, there are few examples of valuable inputs to genetic improvement of aquatic species from biotechnology research.

The fact that 90% of the global aquaculture industry is based on wild, undomesticated and unproductive stocks, while genetic improvement has the potential to greatly increase the efficiency of our dwindling feed, land and water resources, tarnishes the reputation of our industry.

11. My advice

I urge the aquaculture community to organize themselves and to contact those with expertise in selective breeding in order to develop plans for the implementation of effective selective breeding programs for aquaculture species. Relevant public authorities must step up and provide necessary funds for infrastructure and operational costs during the initial phase until such programs can be economically sustainable. Furthermore, the education and training in quantitative genetics and selective breeding in aquaculture species must be strengthened.

The lack of qualified personnel poses a significant obstacle for the implementation of selective breeding technology in most regions of the world.

I am convinced that the improved efficiencies derived from the application of selective breeding programs for aquatic species will be crucial to meet the world's future increasing demands for animal proteins.

Acknowledgments

My transfer to the new 'world' of aquaculture 41 years ago has been challenging and very rewarding and I do not regret leaving the sheep. During these years world production has increased around 12 fold which means that we are producing more high quality food for mankind. Today there is more interest to apply selective breeding to improve productivity of animals and plants, but compared with the large potential for genetic gain, the development of selective breeding programs, and use of genetically improved aquatic species, are surprisingly slow and disappointing. However, I have been very fortunate to work together with able and creative colleagues. I am particularly grateful and impressed with my colleagues who took the leadership in the projects described above: Mr. Terje Refstie in Atlantic salmon in Norway, Dr. Hans B. Bentsen in the GIFT project in the Philippines, Dr. Bjarne Gjerde in the rohu project in India and Dr. Kjersti T. Fjalestad in the shrimp project in Hawaii. I would also like to thank Nofima and AFGC who still encourage me and give me the possibility to continue work on this important sector of food production and Drs. Morten Rye, Nick Robinson and Bjarne Gjerde for reading the manus. I also owe thanks to Section Editor Gideon Hulata who challenged me to write this personal opinion review.

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