Genetic Improvement Programs For Aquaculture Species In Developed Countries

M. Rye[*], B. Gjerde[†], and T. Gjedrem[†*]

Introduction

Throughout the last decades, farming of aquaculture species has continued to represent the fastest growing animal-food producing sector of the world, reaching a reported total of 52 million tonnes with a value of US$ 78.8 billion in 2006 (FAO (2009)). World aquaculture productions are largely dominated by the Asian- Pacific region, with China by far the largest producing country for many major species (e.g. cyprinids). For species like Atlantic salmon and tilapias, systematic genetic improvement work has been one of the main forces driving the development of resource effective and sustainable productions. On the larger scale, however, world aquaculture productions are still based on genetic material that has not yet undergone systematic genetic improvement (Gjedrem and Baranski (2009)), representing a major constraint for sustained growth and profitability in the sector. This paper reviews the status and current trends with respect to the implementation of applied selection programs, with focus on relevant programs in the developed countries in North America and Chile, Europe and Oceania. The scope for further improvement of the design of applied selection programs in aquaculture species is discussed, as well as constraints for wider industry uptake and use of improved seed. For the status of breeding programs in developing countries, see other paper presented in same session.

Aquaculture productions

Aquaculture productions in developed countries are generally characterized by being intensive, technically advanced and strongly focused on high-value carnivorous species (e.g. salmonids, marine fish species and marine shrimp), or high-value filter-feeding molluscs (e.g. abalone, oyster). For most species the reproductive cycle is closed, facilitating controlled reproduction in captivity and systematic genetic improvement by selective breeding. Furthermore, many aquaculture species are characterized by a very high fecundity and external fertilization following separate collection of eggs and milt, which opens for a wide range of alternative mating designs. Considering these characteristics and knowing that many important traits in aquaculture display large genetic variability, it is no surprise that selection responses reported per generation for aquaculture species tend to be much higher than corresponding estimates obtained for conventional livestock species (for review see Gjedrem and Baranski (2009)). Several species do also become sexually mature at younger ages, allowing the generation intervals to be kept relatively short (typically from one to four years) when the animals are bred in captivity. Hence most farmed aquaculture species easily lend themselves to systematic genetic improvement work. However, technology uptake has

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[*] Akvaforsk Genetics Center, N-6600 Sunndalsøra, Norway
[†] Nofima Marin, P.O. Box 5010, N-1432 Ås, Norway

been surprisingly slow in many areas; it is estimated that less than 10% of the current world aquaculture production is based on improved genetic material (Gjedrem and Baranski (2009)). Although the corresponding statistics for aquaculture in developed countries are likely higher, aquaculture productions are generally lagging far behind the agriculture sector when it comes to application of science and technology. Hence aquaculture still has a tremendous untapped potential for improvement in all aspects of production, not least through application of selection.

Applied genetic improvement programs

Selective breeding is widely recognized as a key factor for the development of resource efficient, sustainable and economically profitable aquaculture productions (FAO (1995); Worldbank (2006)). Pioneering programs for Atlantic salmon and rainbow trout in Norway initiated in the early 70'ies (Gjøen and Bentsen (1997); Gjedrem (2010)) clearly documented the potential for substantial selection responses for growth and other traits of key economic importance, and triggered implementation of selection programs for a number of other farmed species world wide. Numerous publications report on substantial selection response for growth rate, some indicating doubling the growth rate of the target populations over five to six generations. Scientific documentation of genetic gains for other traits is still surprisingly few. Although extensive analyses on the economic returns from investments in genetic improvement programs are still scarce, highly favourable benefit to cost ratios ranging from 8 to 400 are reported (Gjedrem (1997); Ponzoni, Nguyena and Khaw (2007); Ponzoni, Khaw and Ninh (2008)). Gjerde et al. (2007) estimated the accumulated gains of eight generations of selection in the Norwegian breeding program for Atlantic salmon to amount to at least NOK 15 (~EUR 1.80 at current exchange rate) per kg fish produced, corresponding to an economic gain per generation of NOK 0.50.

Mass selection vs. use of sib information

Relatively simple and low cost individual (mass) selection programs can be highly effective for improving traits that can be recorded on the live breeding candidates, e.g. growth rate (Gjerde, Gjøen and Villanueva (1996); Bentsen and Olesen (2002); Gjøen and Gjerde (1998); Sonesson, Gjerde and Meuwissen (2005)) and binary traits of low frequency (Falconer and Mackay (1996)). However, to keep the rate of inbreeding at acceptable levels full-sib groups from individual pairs of parents must be reared separately through initial periods with high mortality, before a restricted number of animals from each group are pooled and reared communally until time of selection. The rate of inbreeding in mass selection programs may also be controlled by implementing some type of a walk-back selection procedures which involves genotyping of animals preselected based on phenotypic value (Doyle and Herbinger (1994)). The method may be combined with optimum contribution selection (Sonesson (2005)). A major obstacle for the practical implementation of efficient mass selection programs is the limited number of traits that presently can be recorded on live breeding candidates. Nevertheless such low cost programs should be seriously considered for species with low current production levels, and eventually be transformed into more advanced programs later when additional costs can be justified by increased production output or market share.

More complex programs facilitating the use of sib information (with general structure as illustrated in Figure 1), often referred to as family based programs, are established as the industry standard in most industrialized aquaculture productions. These programs enable effective selection for all types of traits including those that can be recorded only through destructive tests (e.g. carcass quality) or disturbing tests (e.g. disease challenge).

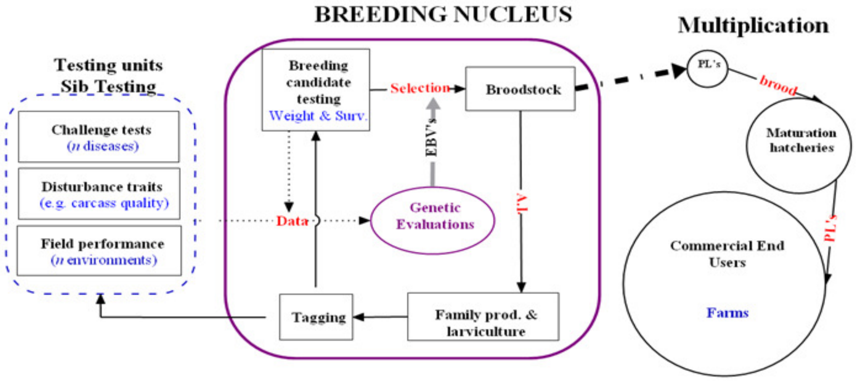

Figure 1: Structure of family based breeding programs (exemplified for shrimp)

As compared to mass selection schemes, programs utilizing sib information also provide increased selection accuracy for traits of medium (e.g. growth) and low (e.g. survival) heritability, but are more costly to implement and operate as they require complete pedigrees obtained either through separate rearing of families until the animals can be physically tagged, or by tagging and subsequent DNA fingerprinting of breeding candidates at later stages in case animals of different families are pooled early and communally reared. Since the additive genetic relationship among the breeding candidates are known family based programs allow for close monitoring of the rate of inbreeding, which can easily be controlled by restricting the number of selected breeders from the top ranked families or by the use of optimum contribution selection procedures (Meuwissen (1997)), preferably adapted to species with a large number of breeding candidates (Hinrichs, Wetten and Meuwissen (2006)). A substantial disadvantage of family based selection schemes is that selection intensity may be low for traits that are selected based on sib information only (e.g. restricted to between-family selection), in particular if the number of tested full-sib families is low and the number of traits selected for is high. This situation may often be encountered for programs that initially target improved growth when the marginal economic importance of other traits increases and performance data for these new traits are available only from sibs. For supporting such programs, in particular those serving small volume sectors and hence with limited options to defend increased operational costs, theoretical studies are needed on how combined walk-back and optimum contribution selection (Sonesson (2005)) can be extended to included sib information for some of the traits selected for and thus lower infrastructure investments (e.g. no. of tanks) and operational costs (e.g. physical tags and/or DNA fingerprinting). It should be noted that since only the most superior animals are measured using walk-back selection, estimated BLUP breeding values (Henderson (1984)) are biased (Sonesson (2005)).

Primary target traits

The number of selection programs utilizing sib-information for farmed species of fish, crustaceans and molluscs in North America and Chile, Europe and Oceania today exceeds 60 (Table 1). Most programs target salmonid species, reflecting the high level of industrialization and the relatively well documented history of selection in salmonids. As a result, close to 100% of the current world aquaculture production of Atlantic salmon is based on stocks undergoing systematic genetic improvement.

Table 1: Family based breeding programs for aquaculture species in North America and Chile, Europe and Oceania

Species	# of programs	Average (range) # of families tested per generation	Average (range) # of traits in breeding goal	Traits included in the breeding goal (in addition to growth rate)				World prod. 2005* (x 1000 tons)
				Disease resistance	Carcass quality	Age at sexual mat.	Other	
Atlantic salmon	13	280 (100-800)	5.4 (3-13)[1]	10	9	9	4	1 236
Rainbow trout	13	206 (100-400)	5.2 (2-11)	5	7	2	2	487
Coho salmon	4	133 (40-300)	2.7 (1-6)	1	1			117
Chinook salmon	2	100	1.5		1	1		24
Common carp	4	?	3.7	1	2	1	6	3 043
Channel catfish	1	200	4	1	1			380
White fish	1	70	2		1			1
Atlantic cod	3	110 (50-200)	4 (2-8)	2	1	2	1	8
Turbot	2	60	1					7
Sea bass	3	100	5	1	1		1	346
Sea bream	4	100	6	1	1		1	242
Tilapia	1	?	3	3	1		1	2 026
Oysters	5	48 (30-60)	4.3 (4-5)	2	3			4 615
Mussel	1	60	3		1			1 786
Marine shrimp	3	212 (150-300)						2 675
Abalone	2	70 (59-100)	3.5 (3-4)		2			334
Sum	62	125	3.8					

* FAO statistics 2007

The corresponding number for other key aquaculture species worldwide is dramatically lower, but is picking up as the respective aquaculture sectors mature and becomes more industrial. A clear trend is evident; when production increases and the competition in main markets intensifies resulting in reduced prices for end-products and hence reduced operational margins, the demand for seed of high genetic merit and quality increases as use of poorly performing stocks no longer is economically viable. It is also in the most industrialized aquaculture productions the use of improved stocks is highest. Growth rate is of principal importance in virtually all aquaculture operations, and therefore targeted for improvement in almost any genetic improvement program irrespective of species. Increased growth rate leads to shorter production cycles and thus reduced economical and biological risks of aquaculture operations. However, as growth rate is improved, the marginal economic importance of improving other traits such as age at first maturation, disease resistance, fillet yield or characteristics related to the quality of the final product increases. This is exemplified by the expansion of Norwegian based Aqua Gen's breeding goal for Atlantic salmon; from targeting only growth rate during the initial period 1975–80, its current complex breeding goal at present includes 10 traits (growth rate, age at sexual maturation, flesh pigmentation, fat content and distribution, robustness, and resistance to furunculosis, infectious salmon anaemia (ISA), infectious pancreatic necrosis (IPN) and piscirickettsiose (SRS).

Scope for technical optimization

On the technical side, applied breeding programs must constantly strive to improve its efficacy by producing increased selection responses at defendable costs. The design of optimum fish breeding programs have been discussed in general terms (Bentsen and Gjerde (1994); Gjerde et al. (2002)), but detailed studies on optimum designs for aquaculture species are few and limited to mass selection schemes (Gjerde, Gjøen and Villanueva (1996); Villanueva, Gjerde and Woolliams (1996); Sonesson, Gjerde and Meuwissen (2005)), choice of mating designs for the inference on genetic parameters (Berg and Henryon (1998)), and selection and mating strategies at the multiplier level (Skagemo et al. (2010)). No studies are published for programs that use sib information. Studies on breeding nucleus designs should be conducted reflecting the need to restrict the rate of inbreeding to a predefined level.

As mentioned, implementation of technologies offering records on live breeding candidates for an increasing number of traits may substantially increase selection responses. Likewise, recent developments in the field of molecular genetics now offer means of improving selection accuracies as well as selection intensities for many traits. Selection for increased resistance to diseases based on controlled challenge tests provides an excellent example in this context. Substantial additive genetic variation in innate resistance to bacteria and viruses has been documented for a number of species of fish and marine shrimp (for a review see Ødegård et al. (2010a)). For biosecurity reasons, however, animals surviving challenge tests are usually not considered as breeding candidates, hence limiting selection to the between-family component which constitutes only half of the additive genetic variance. Extensive studies on benefit vs. biosecurity (taking into account the accuracy of present PCR methods available for screening survivors) of introducing survivors into to the breeding nucleus are needed. It should be noted that these survivors ideally should be tested also for other traits included in the breeding nucleus in order to avoid that the benefit gained by increased selection intensity and accuracy for disease resistance is outweighed by reduced selection intensity and accuracy for other traits selected for.

Methodology for obtaining records on live breeders is also much needed for a key trait like feed conversion efficiency, which at present neither can be recorded on family groups nor on individuals at an acceptable cost. Consequently, genetic improvement of feed efficiency relies on correlated responses through selection for increased growth rate (Thodesen, Grisdale-Helland and Gjerde (1999); Thodesen et al. (2001); Ogata, Oku and Murai (2002); Silverstein, Hostuttler and Blemings (2005)), or by changing the composition of the end product e.g. lowering body fat content (Quillet et al. (2007)). Near-infrared spectroscopy (NIR) can now be used to obtain records of fat content in the fillet on the live breeding candidates of Atlantic salmon with acceptable accuracy (Folkestad et al. (2006)). For most carcass quality traits decisions are still based on sib information only, or the actual traits are not directly selected for due to lack of appropriate recording technologies. The need for new technologies to obtain records on new traits, and preferably on live animals, is obvious.

The availability of genomic information now offers new possibilities for selective breeding for disease resistance. Information on quantitative trait loci (QTL) may be implemented in breeding programs either through gene- or marker-assisted selection (GAS and MAS, respectively). By these methods candidates may be selected based on individual markers or actual causative genes (QTL), rather than phenotypes of sibs only. The widely accepted assumption that disease resistance in aquaculture species is a complex, polygenic trait has been challenged by results seen for resistance to viral diseases in marine shrimp (Cock et al. 2009) as well as for infectious pancreas necrosis (IPN) in Atlantic salmon. A major QTL that explains the most of the genetic variance for resistance to IPN has been identified in independent studies in Scottish (Houston et al. (2008)) and Norwegian (Moen et al. (2009)) populations of Atlantic salmon. In both populations, this QTL has been narrowed down to a relatively small chromosomal region and is estimated to explain 80-98% of the genetic variance for resistance, with a similar effect detected both on the fry and post-smolt stages. Commercial breeding companies in Norway and Scotland are currently incorporating QTL information for resistance to IPN in nucleus selection as well as production of commercial roe sold to their customers, representing a milestone for the application of molecular information in applied selection work in aquaculture. The rapid drop in genotyping costs facilitates obtaining dense genome-wide marker information which may serve as basis for genomic selection. Genomic selection utilizes data on individual phenotypes linked with genomic data from genome wide dense marker maps (Meuwissen, Hayes and Goddard (2001)), opening for replacing current pedigree relationship information by genomic similarities estimated through information on genetic markers. Genomic selection does not require any prior knowledge about the effect and location of specific QTL, and has the potential to increase the accuracy of selection beyond the maximum value that can be obtained from using sib records only (0.71), or own and sib records combined (~0.75) (Sonesson and Meuwissen (2009)). Importantly, there is seemingly little to gain by including individual records on selection candidates in addition to considerable amount of data on full-sibs (20/family) (Ødegård et al. (2009)). Thus data on full-sibs may largely replace the need for individual data on the breeding candidate, which is never the case in classical selection (Ødegård et al. (2009)). Moreover, accurate individual breeding values may be obtained for all traits as soon as the fish are genotyped, implying a potential for shortening the generation interval, depending on the reproductive characteristics of the species. However, simulations confirmed that the association between marker alleles and phenotypes should be re-estimated every second-third generation (Sonesson and Meuwissen (2009)). Thus high cost of genotyping may limit its practical application in the short term. Although a chip is available for Atlantic salmon (www.cigene.no), SNP arrays required for genomic selection are presently unavailable for the vast majority of aquaculture species. It is expected that genotyping costs may be substantially reduced if high-density SNP allele effects within families can be tracked using co-segregation information from evenly-spaced low-density SNPs across the genome (Habier, Fernando and Dekkers (2009)).

In standard challenge test survival models all individuals are typically assumed to be at risk. This assumption does not hold if a fraction of the population is non-susceptible (cure fraction) and consists of tolerant or completely resistant individuals (Farewell, 1982). Non-susceptible individuals are likely preferred over individuals with high degree of endurance (time until death), as selection for the latter is more likely to postpone the mortality rather than avoiding it in the longer run. However, the test period is often limited due to practical consideration, and survivors are thus expected to be a mixture of truly non-susceptible individuals and susceptible ones having censored lifespans. A mixture cure model is a survival model accounting for a non-susceptible fraction within the population (Farewell, 1982), and recently a cure model allowing prediction of breeding values for non-susceptibility has been developed (Ødegård et al. 2010b)

Another debated issue is whether vaccinated or non-vaccinated animals should be used in challenge test experiments for pathogens for which vaccines are available. Results from a challenge test to furunculosis (caused by *A. salmonicida*) with vaccinated and non-vaccinated Atlantic salmon indicate a positive genetic correlation of only moderate magnitude between recorded survival rates in the two groups (Drangsholt et al. (2009)). Whether testing should be performed with vaccinated or non-vaccinated fish thus largely depends on the relative emphasis on the short vs. long term breeding goal (i.e. if commercial fish are expected to be vaccinated or not).

Protection of investments

Running advanced breeding programs involves highly complex and costly operations, and is associated with substantial biological and financial risks. Hence, besides the technical issues addressed above, the long term sustainability of breeding programs for aquaculture species in developed countries critically rely on adequate biological and/or legal measures to ensure recuperation of costs of research and development, and fair revenues on investments in this sector. Various levels of biological protection against unauthorized reproduction and use of improved stocks may be achieved by measures such as ensuring significant and stable genetic progress encouraging only use of the most recent generation of selected material; dissemination of highly selected material from a strictly limited number of families making the commercial product not suited for reproduction; or by dissemination of sterile animals such as triploids. Relevant literature on the complex legal aspects related to balancing the need for protection of vs. access to genetically improved material in livestock (Ogden and Weigel (2007)) and aquaculture is still scarce (for issues related to Atlantic salmon, see Rosendal et al. (2006)). Further work on these issues is encouraged.

Conclusions

A number of applied selection programs are contributing to the development of biologically effective and sustainable aquaculture productions for key species of fish, marine shrimp and molluscs in North America and Chile, Europe and Oceania. Family based programs using sib information represent the industry standard for most species. Substantial scope exists for technical optimization of current breeding program designs, including simpler mass selection schemes, and for the implementation and optimal use of molecular tools. Improved legal and/or biological protection measures may be needed to ensure sufficient investments in further research and development work.

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