Perspectives from Agriculture: Advances in Livestock Breeding - Implications for Aquaculture Genetics[1]

N.H. Nguyen and R.W. Ponzoni

Abstract

In this paper we present livestock breeding developments that could be taken into consideration in the genetic improvement of farmed aquaculture species, especially in freshwater fish. Firstly, the current breeding objective in aquatic species has focused almost exclusively on the improvement of body weight at harvest or on growth related traits. This is unlikely to be sufficient to meet the future needs of the aquaculture industry. To meet future demands breeding programs will most likely have to include additional traits, such as fitness related ones (survival, disease resistance), feed efficiency, or flesh quality, rather than only growth performance. In order to select for a multi-trait breeding objective, genetic variation in traits of interest and the genetic relationships among them need to be estimated. In addition, economic values for these traits will be required. Generally, there is a paucity of data on variable and fixed production costs in aquaculture, and this could be a major constraint in the further expansion of the breeding objectives. Secondly, genetic evaluation systems using the restricted maximum likelihood method (REML) and best linear unbiased prediction (BLUP) in a framework of mixed model methodology could be widely adopted to replace the more commonly used method of mass selection based on phenotypic performance. The BLUP method increases the accuracy of selection and also allows the management of inbreeding and estimation of genetic trends. BLUP is an improvement over the classic selection index approach, which was used in the success story of the genetically improved farmed tilapia (GIFT) in the Philippines, with genetic gains from 10 to 20 per cent per generation of selection. In parallel with BLUP, optimal genetic contribution theory can be applied to maximize genetic gain while constraining inbreeding in the long run in selection programs. Thirdly, by using advanced statistical methods, genetic selection can be carried out not only at the nucleus level but also in lower tiers of the pyramid breeding structure. Large scale across population genetic evaluation through genetic connectedness using cryopreserved sperm enables the comparison and ranking of genetic merit of all animals across populations, countries or years, and thus the genetically superior brood stock can be identified and widely used and exchanged to increase the rate of genetic progress in the population as a whole. It is concluded that sound genetic programs need to be established for aquaculture species. In addition to being very effective, fully pedigreed breeding programs would also enable the exploration of possibilities of integrating molecular markers (e.g., genetic tagging using DNA fingerprinting, marker (gene) assisted selection) and reproductive technologies such as in-vitro fertilization using cryopreserved spermatozoa.

Introduction

Genetic selection using quantitative and statistical methods has significantly increased productivity of several terrestrial animal species, especially chicken, dairy cattle, and pigs. Virtually all production in terrestrial livestock species is derived from improved strains and breeds. In all species, formal genetic improvement programs have been established. During the implementation of such programs, shortcomings or limitations have been identified and these have become pointers for further research, development and technology transfer. There are several successful examples in livestock breeding, for example, the developments in statistical procedures

---

[1] This paper originates from a presentation made at the Skretting Australasian Aquaculture Conference, 27-30 August 2006 in Adelaide, Australia.

to enable cross population genetic evaluation using Restricted Maximum Likelihood (REML) and Best Linear Unbiased Prediction (BLUP) under a framework of a mixed (animal) model, or the development of direct DNA tests for marbling or tenderness in beef cattle. It is, therefore, obvious that in aquaculture we also need to develop well designed, highly focused, sustainable genetic improvement programs for relevant species. As problems or new perspectives arise, we can accommodate them in the same way as has happened in livestock. Overall, a systematic breeding program in both terrestrial and aquatic species involves several steps (Ponzoni 2006; Ponzoni et al. 2006a). In the present paper, we discuss developments in the design of breeding programs, formulation of breeding objectives and the establishment of genetic evaluation and dissemination systems, with special reference to their application in tilapia and carps.

One or Several Programs?

As the first step of any breeding program, the question of having one or several genetic improvement programs is not simple. It depends. A genetic correlation approach and selection index theory can be used to assess the situation under different scenarios, that is, to examine the consequences of having a single program for a wide range of genetic and economic parameters. On the basis of soundly based results a decision can be made regarding whether or not a specific program is needed for a specific environment. For example, tilapia farming in Malaysia is mainly conducted in two production environments, namely, ponds and cages. Our multivariate analyses show that although genetic correlations between the expressions of body weight in the two environments are less than one, there is not enough evidence

to justify the conduct of separate genetic improvement programs for pond and cage environments in tilapia (Ponzoni et al. 2005a, 2005b). Similarly, further analyses show that there is no need to treat the expressions in females and males as separate traits because the between-sex genetic correlations for body traits (harvest weight, standard length, body width and depth) were all close to unity (Nguyen et al. 2006). Such research would not have been carried out if we had not had a genetic improvement program in the first place.

In other aquaculture species, such as Pacific white shrimp (Pérez-Rostro and Ibarra 2003; Gitterle et al. 2005) and rainbow trout (Fishback et al. 2002; Kause et al. 2003), the estimates of the genetic correlations for body weight between different environments ranged from 0.82 to 0.99, indicating that genotype by environment (G×E) interaction is not of biological importance for body weight. Jointly examining the available REML literature estimates together with our results, we may conclude that for the species and range of environments tested, separate selection and testing programs to improve body weight are not necessary. For other traits with lower heritability than growth-related traits (e.g. early sexual maturity), care should be taken since there appears to be G×E interaction in both Atlantic salmon (Wild et al. 1994) and rainbow trout (Kause et al. 2003).

Breeding Objectives

Defining breeding objectives is one of the most critical steps in the systematic development of genetic improvement programs. Major components in the establishment of breeding objectives include a choice of traits for genetic improvement and a derivation of economic weights (Ponzoni 1992). Breeding objectives

for aquatic animal species have almost exclusively focused on improving growth performance. Traits with low value of ah^2 (economic value of one phenotypic standard deviation unit x heritability) have rarely been considered as part of the breeding goals. Ideally, breeding objectives should include all traits of economic importance, but in practice only a limited number are used. A major reason for this is a lack of efficient methods to measure traits (e.g., feed intake, survival, flesh quality in aquatic animal species). This may have placed constraints on the estimation of genetic parameters for traits that are expensive or difficult to measure. Currently, in farmed aquaculture species, there is very limited knowledge about genetic variation and relationships among production, reproduction and adaptation traits. For instance, it is not possible to predict correlated responses in feed intake or food conversion efficiency, to selection for growth. Some estimates are not consistent. Gitterle et al. (2006) report that genetic correlations between growth and survival vary with batches, being both positive and negative, in *Penaeus vannamei*. In addition, economic values are seldom derived from profit equations. Researchers have simply assigned a certain ('social') value to a particular trait in the breeding goal. In general, there is still a paucity of data on variable and fixed production costs in aquaculture. All these factors hamper further expansion of the breeding objectives in fish.

By contrast, breeding goals for livestock are better defined, evolving from two or three production traits to 14 traits (production, reproduction, health and conformation traits) in dairy cattle (e.g. Miglior et al. 2005). In the past, the pig industry placed a strong emphasis on high efficiency of lean production (high lean growth, low fat and low feed conversion ratio). However, selection strategies

that emphasize efficiency rather than rate of lean growth are likely to result in a deterioration of meat and eating quality, predisposition to leg weakness, and impairment of sow reproductive performance (Nguyen et al. 2004). The breeding goals for pigs now include lean growth rate, number of piglets born alive, and meat quality index (or intramuscular fat). In all species, the breeding objectives are country specific, and in each country the programs are putting a different emphasis on each trait.

The breeding objective for GIFT tilapia is being broadened by considering a number of additional, important traits, such as fillet yield, flesh quality, sex ratio in response to thermal treatment, and may include disease resistance in the future. For rohu carp in India (Mahapatra et al. 2006), selection has been based on growth until recently, but the breeding goal is now being expanded to enhance disease resistance of the fish against *Aeromonas hydrophila* (K. Mahapatra pers. com.). There is evidence of genetic variation in this trait. The genetic correlation between survival and growth rate is slightly negative. A desired gains selection index approach can be used to simultaneously select for growth and resistance to *A. hydrophila.*

Genetic Evaluation

REML and BLUP applied to multi-trait mixed models have become the standard method for genetic evaluation in all terrestrial animal species. The main benefits of using this methodology include: (1) increasing accuracy of selection; (2) managing accumulation of inbreeding; (3) estimating genetic trend without a control; and (4) the possibility of conducting large scale genetic evaluation across populations.

Increasing accuracy of selection

BLUP increases the accuracy of estimated breeding values (EBVs), thus increasing genetic response to selection. This is so because the method can account for all systematic effects (e.g., batch, sex, production environment, age variation) that are often associated with traits of economic importance in farmed aquaculture species. The maternal and common environmental effects (c^2) due to separate rearing of full-sib families before tagging can also be effectively separated from the additive genetic variance in fully pedigreed populations of sufficient depth. The c^2 effects for body traits in fish often account for a large proportion of total variation; for example, from 14 to 24 per cent in Nile tilapia (Ponzoni et al. 2005c; Nguyen et al. 2006) and in Atlantic cod (Gjerde et al. 2004). By failing to account for the c^2 effects in the model, EBVs can be biased upward by 15 to 20 per cent (Nguyen et al. 2006). With BLUP analysis, all pedigree information (from ancestors, parents, family and individuals) is utilized through a numerator relationship matrix to account for changes in additive genetic variance due to inbreeding or assortative mating, and thus the EBVs are obtained without bias. Multi-trait BLUP is especially useful for selection on expensive or difficult to measure traits (e.g., flesh quality, disease resistance) which cannot be measured on live breeding candidates. The application of BLUP to selection in fish is exemplified by the GIFT tilapia program in Malaysia (Ponzoni et al. 2005c) and by the selection of indigenous tilapia species in Africa (Maluwa 2005). In these programs, the genetic gain has been from 6 to 12 per cent per generation and the fish have continued to show response after several generations of selection. So far, there is no evidence of a reduction in selection response in GIFT or any sign of

deterioration in fitness-related traits (e.g., reproduction or viability). The improved fish have remarkable vigor and high adaptation to different farming conditions in Asia. There are also no differences in flesh quality between GIFT and three local (and highly favored) strains of red tilapia in Malaysia (Khaw et al. 2006; Ponzoni et al. 2006b). Learning from this success, other breeding programs for carps in Asia (Freshwater Fisheries Research Center, Wuxi, China; Bangladesh Fisheries Research Institute; Central Institute of Freshwater Aquaculture, India; Aquatic Animal Genetics Research and Development Institute, Thailand; Research Institute for Aquaculture No.1, Vietnam) carried out in collaboration with the WorldFish Center are maintaining full pedigree records and fitting animal models, to achieve genetic progress and to enable a rigorous monitoring of inbreeding.

Control of inbreeding

Inbreeding is unavoidable in any closed nucleus of finite size. Control of inbreeding is important to secure long term genetic response to selection. Although BLUP, in comparison with individual mass selection, results in greater genetic gain, it is also associated with greater levels of inbreeding because the method uses family information, leading to co-selection of relatives. By maintaining full pedigree information, inbreeding can be monitored through combined between and within family selection, (i.e., selecting a limited number of individuals from each family and having representatives of as many families as possible in future generations). In addition, several mating strategies can be applied. Besides avoidance of closely related mating, (e.g., full and half sibs), pairs resulting in a greater level of inbreeding than a limit set by the experimenter (e.g., > 2 per cent) may not be allowed. A more effective

approach is minimum coancestry, involving the mating of males and females to produce offspring with the lowest level of inbreeding. In parallel with BLUP, optimal genetic contribution theory (weighting the genetic contribution of selected individuals to the next generation) can maximize genetic gain while minimizing the rate of inbreeding in the long run. The procedure can be implemented with packages such as EVA (Berg 2004) or TGMR (Kinghorn 2000).

Estimation of genetic trends

Another advantage of BLUP is that it provides an opportunity to estimate genetic trends. Conventionally, genetic gain has been estimated as the difference in phenotypic mean between the selection line and a randomly bred control. However, breeding programs in aquaculture are often conducted within a very limited number of tanks or ponds. With limited resources, when we attempt to have both a selection and a control line, due to the reduced effective population sizes used, the estimate of genetic gain could be of limited value. Both the selection and control lines could be subject to genetic drift. By contrast, mixed model methodology can effectively separate genetic from environmental trends and thus obviates the need for a control population to estimate genetic responses to selection (Blair and Pollak 1984), especially in populations with overlapping generations (Nguyen and McPhee 2005). The theory of such methods is generally well understood, but its application to analysis of experimental selection data has so far been very limited in aquaculture species (Gall and Bakar 2002; Ponzoni et al. 2005c).

With the BLUP method, the genetic gain can be estimated by regression of individual EBVs on generations of selection or birth years of animal
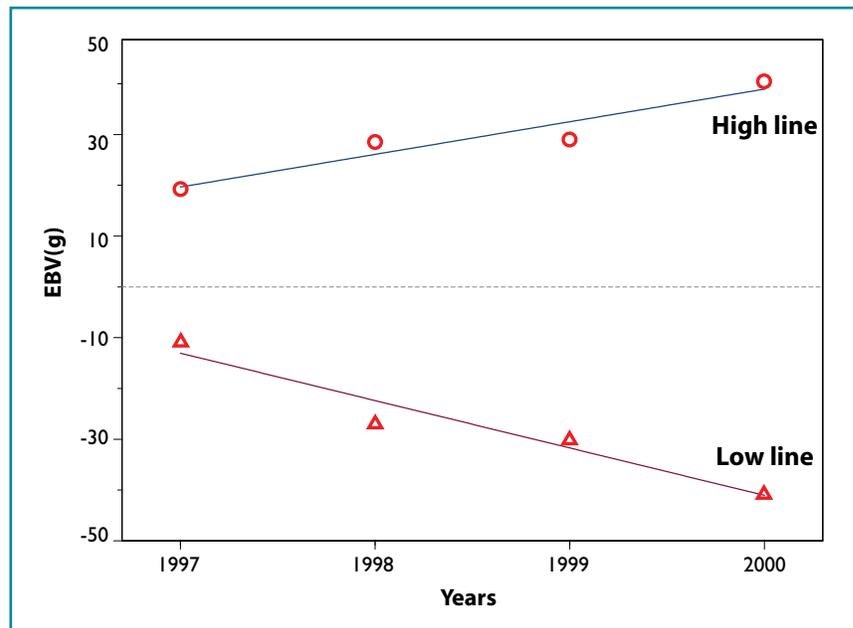

Figure 1. Genetic trend for growth rate in the high ○ and low △ growth line over four years of selection in Large White pigs (Nguyen and McPhee 2005).

(Fig. 1). The estimated genetic trend is unbiased if the relationship information on selected animals (tracing back to the base population) is included, and genetic parameters are estimated from REML based on models of best fit. In finfish species with long generation interval (e.g., carps), breeding programs are often designed with different year classes, and there is thus a need to create good genetic linkages between contemporary groups or generations. Other practical issues that should be taken into genetic evaluation include correctness of pedigree recording, precision and consistency of measurements, distribution of progeny of selected animals among contemporary groups, and systematic recording of all recognized environmental effects. In summary, although the establishment of a control population is desirable when facilities and resources are available, the estimation of genetic trends with mixed model methodology is an alternative of great practical value, especially in large scale genetic evaluation programs.

Large scale genetic evaluation

REML and BLUP methods also enable the conduct of large scale genetic evaluation across populations, years or countries. This can be done through genetic connectedness among populations (year classes or generations) using in-vitro fertilization or cryopreserved sperm. In this way, superior animals can be identified, widely used and exchanged to increase genetic progress in the population as a whole. In the case of GIFT tilapia, the fish have been requested by and distributed to different countries in Asia. In some cases, full pedigrees have been maintained and selection has been performed in a similar manner to the program that we have in Malaysia. Through genetic exchanges, the populations can be refreshed to reduce a risk of accumulated inbreeding. In the future, if proper genetic linkages among the populations were established, we would be able to perform large scale genetic evaluations.

Advanced Statistical Methods

Often animals are measured more than once for a particular trait. Examples are, individual body weight of fish measured over different periods (e.g., every month), and reproduction of fish over different spawning seasons. In such cases, repeatability models assuming a unity genetic correlation between successive measurements can be applied to estimate both additive genetic effect of animal and the permanent environmental effect common to all observations on the same animal. Another approach to analyze repeated measures when there are heterogeneous (co)-variances, is to use random regression or covariance function analysis. The method enables calculation and comparison of (co)-variances within individuals between measures at different time points, or both the between and within individuals for each treatment group. In livestock species where systematic data recording (e.g., milk yield in dairy cattle) is available, the random regression approach has been used to replace the multi-trait model in genetic evaluation systems (Meyer 2004; Schaeffer 2004). However, both repeatability and random regression models are expected to have limited use in aquaculture species (at least in tilapia). First, the genetic correlations between successive measures of growth are close to one, such as in tilapia (Rutten et al. 2005). Second, repeated measures are time consuming, costly and labor intensive, and may cause stress in fish, thus depressing their growth rate and causing mortality. Hence, in practical breeding programs, in view of the absence of any evidence to the contrary, one (at harvest) or two (at stocking and at harvest) body weight measurements should suffice.

Recently, the development of threshold-linear models (Damgaard

and Korsgaard 2006) has enabled a combination of genetic evaluation of both continuous and categorical traits (e.g., growth and survival). Until now genetic evaluation of threshold traits has been carried out independently using a non-linear model with logit or probit link functions, or using a linear model assuming normal distribution for the traits. By using threshold-linear model, we could more effectively improve important traits such as survival and sexual maturity in fish.

Breeding Structure

In well structured animal industries, genetic improvement typically takes place in a small fraction of the population (called the nucleus). The improved animals in the nucleus are then multiplied and disseminated directly to farmers and producers or indirectly through hatcheries (Fig. 2). With the very high reproductive rate in fish, we can effectively service a large population involved in production with a relatively small nucleus. Unfortunately, aquaculture has developed without (or with very limited) breeding centers conducting well designed genetic improvement programs (Fig. 3). Due to limited resources and breeding experience, the assumed dual role of hatcheries in maintaining and breeding replacement brood stock, as well as producing large numbers of fry for farmers, has not worked in developing countries. The hatcheries should specialize in multiplication under strict technical protocols and legal commitments to ensure that superior genetic material reaches the producers.

In livestock, genetic evaluation has been principally based on performance records and pedigrees collected from individual seed stock breeders, often through breed
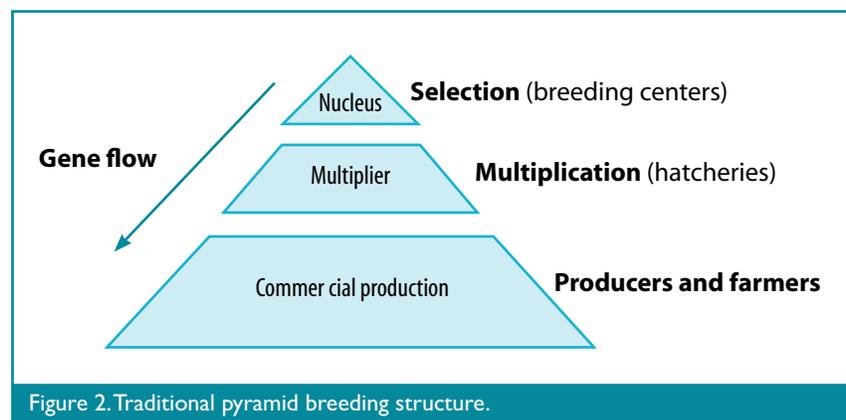
Figure 2. Traditional pyramid breeding structure.
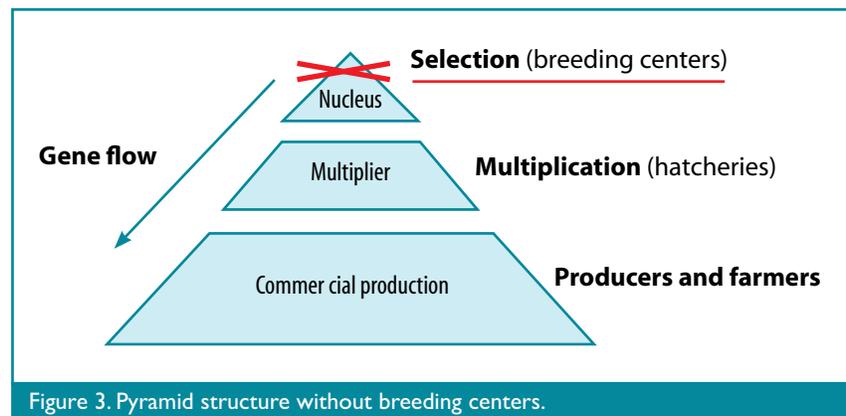


Figure 3. Pyramid structure without breeding centers.
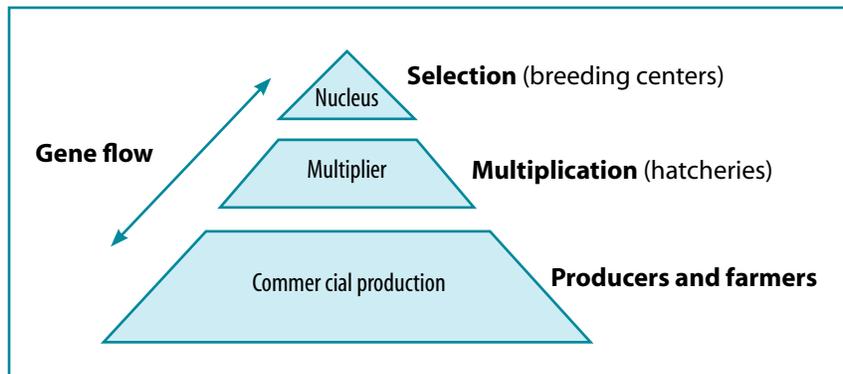
Figure 4. Open breeding structure.

societies. Data from commercial herds (e.g., crossbreed data) is also recorded through a number of breed society databases. Furthermore, by applying an open breeding structure, the gene flow may not only be from the upper to the lower layers, but also in the opposite direction (Fig. 4). This can help to reduce the genetic lag from the nucleus to commercial populations and alleviate any effects of inbreeding in the nucleus. Nevertheless, the traditional breeding system with a unidirectional flow of genes (Fig. 2) is likely to remain the most important one in aquaculture. Although there are examples of genetic improvement programs that include on-farm performance recording, such as in Atlantic salmon (Guy and Hamilton 2005), it is unlikely that such a system will be applied in the foreseeable future in developing countries where resources and experience are generally limited. In addition, the risk of disease transmission from farms to the nucleus would have to be taken into consideration.

Conclusions

The application of livestock selection theory to the improvement of farmed aquaculture species is still at a very early stage. There are ample opportunities for genetic improvement in aquaculture. The effectiveness of genetic improvement programs can be improved by refining or developing virtually every

step in a systematic and logical manner as described earlier. There are many benefits to be derived from well established breeding programs, an important one being helping to identify weaknesses for further research, development and technology transfer. The establishment of sound breeding programs would also allow the exploration of possibilities of integrating new reproductive techniques and molecular genetics information. Note, however, that resources are often very limited in developing countries. Ponzoni et al. (2006a) discuss in detail the issue of matching the complexity of the program to available resources.

References

Berg, P. 2004. User's Guide EVA version 1.5. Danish Institute of Agricultural Science, Denmark.

Blair, H.T., and E.J. Pollak. 1984. Estimation of genetic trend in a selected population with and without the use of a control population. Journal of Animal Science 58:877–886.

Damgaard, L.H., and R.I. Korsgaard. 2006. A bivariate quantitative genetic model for a linear Gussian trait and a survival trait. Genetics Selection Evolution 38:45-64.

Fishback, A.G., R.G. Danzmann, T. Sakamoto, M.M. Ferguson and J.P. Gibson. 2002. Estimates of genetic parameters and genotype by environment interactions for growth traits of rainbow trout (*Oncorhynchus mykiss*) as inferred using molecular pedigrees. Aquaculture 206:137-150.

Gall, G.A.E., and Y. Bakar. 2002. Application of mixed-model techniques to fish breed improvement: analysis of breeding-value selection to increase 98-day body weight in tilapia. Aquaculture 212:93-113.

Gitterle, T., M. Rye, R. Salte, J. Cock, H. Johansen, C. Lozano, J.A. Suárez and B. Gjerde. 2005. Genetic (co)variation in harvest body weight and survival in Penaeus *(Litopenaeus) vannamei* under standard commercial conditions. Aquaculture 243:83-92.

Gitterle, T., B. Gjerde, J. Cock, M. Salazar, M. Rye, O. Vidal, C. Lozano, C. Erazo and R. Salte. 2006. Optimization of experimental infection protocols for the estimation of genetic parameters of resistance to White Spot Syndrome Virus (WSSV) in *Penaeus (Litopenaeus) vannamei*. Aquaculture. In press.

Gjerde, B., B.F. Terjesen, Y. Barr, I. Lein and I. Thorland. 2004. Genetic variation for juvenile growth and survival in Atlantic cod *(Gadus morhua)*. Aquaculture 236:167-177.

Guy, D.R., and A. Hamilton. 2005. Genetic parameters for harvest and processing traits in Landcatch strains of Atlantic salmon, *Salmo salar*. Aquaculture 247:17.

Kause, A., O. Ritola, T. Paananen, E. Mäntysaari and U. Eskelinen. 2003. Selection against early maturity in large rainbow trout *Oncorhynchus mykiss*: the quantitative genetics of sexual dimorphism and genotype-by-environment interactions. Aquaculture 228:53–68.

Khaw, H.L., R.W. Ponzoni, A. Hamzah, K.R.A. Bakar, N. Kamaruzzaman, N. Ismail, H. Jaafar and N.H. Nguyen. 2006. A comparison of GIFT and red tilapia for fillet yield and sensory attributes of flesh quality assessed by a trained panel. In: Proceedings of the 8th

World Congress on Genetics Applied to Livestock Production. 13-18 August 2006. Brazil. Web access at http://www.wcgalp8.org.br/wcgalp8/articles/paper/9_98-2120.pdf

Kinghorn, B.P. 2000. The tactical approach to implementing breeding programs. p291-308. In: B.P. Kinghorn, J.H.J. Van der Werf and M. Ryan (eds.) Animal breeding- use of new technologies. The Post Graduate Foundation in Veterinary Science of the University of Sydney, Australia.

Mahapatra, K.D., P.K. Jana, J.N. Saha, B. Gjerde and N. Sangi. 2006. Lessons from the breeding program in Rohu. p34-40. In: R.W. Ponzoni, B.O. Acosta, A.G. Ponniah. (eds.) Development of Aquatic Animal Genetic Improvement and Dissemination Programs. WorldFish Center, Penang, Malaysia.

Maluwa, A.O.H. 2005. Genetic selection for growth of a Malawian indigenous tilapia, *Oreochromis shiranus*. PhD thesis. Norwegian University of Life Sciences.

Meyer, K. 2004. Scope for a random regression model in genetic evaluation of beef cattle for growth. Livestock Production Science 86:69-83.

Miglior F., B.L. Muirand B.J. Van Doormaal. 2005. Selection indices in Holstein cattle of various countries. Journal of Dairy Science 88:1255-1263.

Nguyen, N.H., C.P. McPhee and M.D. Claire. 2004. Genetic selection strategies for efficient lean growth in pigs. Pig News and Information. 25(4):149-163N.

Nguyen, N.H., and C.P. McPhee. 2005. Genetic parameters and responses in performance and body composition traits in pigs selected for high and low growth rate on a fixed ration over a set time. Genetics Selection Evolution 37: 199-213.

Nguyen, N.H., H.L. Khaw, R.W. Ponzoni, A. Hamzah and N. Kamaruzzaman. 2006. Can Sexual Dimorphism and Body Shape be altered in Nile Tilapia by Genetic Means? Submitted to Aquaculture.

Pérez-Rostro, C.I., and A.M. Ibarra. 2003a. Heritabilities and genetic correlations of size traits at harvest size in sexually dimorphic Pacific white shrimp (*Litopenaeus vannamei*) grown in two environments. Aquaculture Research 34:1079-1085.

Ponzoni, R.W. 1992. Genetic improvement of hair sheep. FAO Animal Production and Health Paper No. 101. FAO, Rome, Italy.

Ponzoni, R.W., A. Hamzah, N. Kamaruzzaman and H.L. Khaw. 2005a. Live weight genetic parameters in two production environments in the GIFT strain of Nile tilapia, *Oreochromis niloticus*. In: Proceedings of the 16th Conference of Association for the Advancement of Animal Breeding and Genetics, 25-28 September, Noosa, Queensland, Australia. 16, 202-205.

Ponzoni, R.W., A. Hamzah, N. Kamaruzzaman and H.L. Khaw. 2005b. Response to selection in two production environments in the gift strain of Nile tilapia, *Oreochromis niloticus*. In: Proceedings of the 16th conference of Association for the Advancement of Animal Breeding and Genetics, 25-28 September, Noosa, Queensland, Australia. 16, 206-208.

Ponzoni, R.W., A. Hamzah, T. Saadiah and N. Kamaruzzaman. 2005c. Genetic parameters and response to selection for live weight in the GIFT strain of Nile Tilapia (*Oreochromis niloticus*). Aquaculture 247:203-210.

Ponzoni, R.W. 2006. Genetic improvement and effective dissemination: keys to prosperous and sustainable aquaculture industries. p1-6. In: R.W. Ponzoni, B.O. Acosta and A.G. Ponniah (eds.) Development of Aquatic Animal Genetic Improvement and Dissemination Programs. WorldFish Center, Penang, Malaysia.

Ponzoni, R.W., H.N. Nguyen and H.L. Khaw. 2006a. Importance and implementation of simple and advanced selective breeding programs for aquaculture species in developing countries. In: Proceedings of the 8th World Congress on Genetics Applied to Livestock Production. 13-18 August 2006, Brazil. Web access at http://www.wcgalp8.org.br/wcgalp8/articles/paper/9_683-1814.pdf

Ponzoni, R.W., H.L. Khaw, A. Hamzah, K.R.A. Bakar, N. Kamaruzzaman, N. Ismail, H. Jaafar and N.H. Nguyen.2006b. A comparison of GIFT and red tilapia for fillet yield and sensory attributes of flesh quality assessed by an untrained panel. In: Proceedings of the 8th World Congress on Genetics Applied to Livestock Production. 13-18 August 2006, Brazil. Web access at http://www.wcgalp8.org.br/wcgalp8/articles/paper/9_99-2121.pdf

Rutten, M.J.M., H. Komen and H. Bovenhuis. 2005. Longitudinal genetic analysis of Nile tilapia (*Oreochromis niloticus L.*) body weight using a random regression model. Aquaculture 206:101-113.

Schaeffer, L.R. 2004. Application of random regression models in animal breeding. Livestock Production Science 86:35-45.

Wild, W., H. Simianer, H.M. Gjøen and B. Gjerde. 1994. Genetic parameters and genotype×environment interaction for early sexual maturity in Atlantic salmon (*Salmo salar*). Aquaculture 128:51–65.

N.H. Nguyen and **R.W. Ponzoni** are from The WorldFish Center, Jalan Batu Maung, 11960 Bayan Lepas, Penang, Malaysia.
Email: n.nguyen@cgiar.org and r.ponzoni@cgiar.org