Aquaculture 285 (2008) 47–55

Contents lists available at ScienceDirect

Aquaculture

journal homepage: www.elsevier.com/locate/aqua-online

Accounting for genotype by environment interaction in economic appraisal of genetic improvement programs in common carp *Cyprinus carpio*

Raul W. Ponzoni [a,*], Nguyen Hong Nguyen [a], Hooi Ling Khaw [a], Nguyen Huu Ninh [b]

[a] *WorldFish Center, Jalan Batu Maung, 11960 Batu Maung, Bayan Lepas, Penang, Malaysia*
[b] *Research Institute for Aquaculture No. 1, Dinh Bang, Tu Son, Bac Ninh, Vietnam*

ARTICLE INFO

Article history:
Received 9 May 2008
Received in revised form 11 August 2008
Accepted 16 August 2008

Keywords:
Common carp
Cyprinus carpio
Genetic improvement
Selective breeding
Economic benefit
Genotype by environment interaction

ABSTRACT

In this study we examine effects of genotype by environment (G×E) interaction due to re-ranking and scaling effects on economic benefit (EB) and benefit to cost ratio (BCR) from a genetic improvement program in common carp at a national level in Vietnam. A discount approach was used for the economic evaluation over a 10 year time horizon. G×E interaction resulting from scaling effects generally had a negligible impact on EB and BCR. However, both EB and BCR decreased with the magnitude of the G×E (i.e. with the decrease in the genetic correlations between homologous traits in the selection and production environments). Furthermore, both EB and BCR from the genetic improvement program depend on other factors, which can be categorized in three groups: i) biological (heritability and feed intake), ii) economic (initial investment, annual recurrent cost, discount rate, price of fish and feed cost) and iii) operational (year when first return is realized, adoption rates of the improved fish by the production sector). The level of heritability affected EB and BCR, with greater heritability being associated with greater EB and BCR. Accounting for feed intake in breeding objectives avoided an overestimation of EB and BCR. Generally, the economic efficiency of the breeding program was almost insensitive to initial investment and annual cost. Increasing the discount rate by three times reduced EB and BCR by a factor of only 1.4 and 2.0, respectively. The price of fish and feed costs had a substantial effect on EB and BCR. However, the greatest contribution to variations in EB and BCR came from increases in adoption rates of the improved fish by the industry. The risk program failure due to technical reasons was extremely low. We conclude that even under the most conservative assumptions, and in the presence of G×E interaction, genetic improvement programs are highly beneficial from an economic viewpoint, and that for the situations studied they could result in EBs ranging from 11 to 226 million US$, and corresponding BCRs of 22 to 420.

1. Introduction

Investment in breeding programs can provide a high rate of economic return since genetic gain is cumulative, permanent and sustainable. Nearly all the genetic gain is contributed to the national economy, especially in countries where a pyramid breeding structure is well established to disseminate improved genotypes from the nucleus either directly or indirectly to commercial production. Although genetic gain is never lost if the population is well maintained, its value needs to be discounted to express all returns and costs in terms of net present value (Hill, 1971). The benefits of improved breeds or varieties (strains) through genetic selection have been widely demonstrated in terrestrial animal and plant species. For example, the wheat breeding program at CIMMYT yielded returns of greater than US$ 50 for every dollar invested (Lantican et al., 2005). Mitchell et al. (1982) also demonstrated that the genetic improvement carried out for economically important traits in pigs brought about 101×10^6 lb, with a benefit to cost ratio of 50 for Great Britain. Many other studies reported substantial economic benefits in livestock such as dairy cattle (Wickham et al., 1977) and beef cattle in New Zealand (Morris, 1980), Merino sheep in Australia (Atkins, 1993; Greeff, 1997).

Recently, Ponzoni et al. (2007) evaluated investment in a genetic improvement program in tilapia and reported that the economic benefit (EB) ranged from 4 to 32 million US$, and corresponding benefit to cost ratio (BCR) of 8.5 to 60. The substantial returns clearly indicate that it is wise for government institutions to invest in breeding programs. In order to gain further confidence in such benefits for other aquaculture species, we conducted an economic assessment of the investment in breeding programs in carp species, with particular reference to common carp (*Cyprinus carpio*) in Vietnam.

A selection program for common carp at Research Institute for Aquaculture No. 1 (RIA1), Vietnam, has been conducted over the past 22 years (Thien et al., 2001). Initially, a synthetic population was assembled from three base stocks: Vietnamese white carp, Hungarian scale carp and Indonesian yellow carp. Mass selection for high body weight was carried out over five generations (1985 to 1991). Growth

* Corresponding author. Tel.: +60 4 620 2159; fax: +60 4 626 5530.
E-mail address: r.ponzoni@cgiar.org (R.W. Ponzoni).

0044-8486/$ – see front matter © 2008 Elsevier B.V. All rights reserved.
doi:10.1016/j.aquaculture.2008.08.012

rate of the selected fish increased by 33% relative to the base population, but the genetic gain declined in the fifth generation. Family selection was then followed with a genetic gain of approximately 7% during the period of 1998 to 2001. Since 2004, the breeding program has been strengthened by incorporating six carp populations available at RIA1, and a combined within and between family selection using best linear unbiased prediction (BLUP) method was applied. The program is in the second generation of selection. Genetic gain per generation ranged from 7 to 21% (Ninh et al., unpublished results).

Based on parameters estimated from this program in common carp, we derived the economic benefit and benefit to cost ratio under different biological, economic and operational scenarios, following the approach used by Ponzoni et al. (2007). The approach was extended to account for different adoption rates of the improved fish by the production sector and for the effects of genotype by environment (G×E) interaction. We concluded that even under the most conservative assumptions, the genetic improvement program in carps was highly beneficial from an economic viewpoint.

2. Materials and methods

2.1. Breeding structure

A typical breeding structure for any given aquaculture species consists of three main tiers: the nucleus, the multiplication, and the production populations. Research institutions or government agencies usually take the lead in establishing and running the genetic improvement programs to develop the nucleus populations at the top of the pyramid. The improved fish from the nucleus are then transferred to hatcheries in lower tiers to be multiplied and distributed to farmers for commercial production as food fish. In this study, we assumed that after each generation of selection, all brooders in hatcheries were replaced by fish from the latest generation in order to obtain the greatest expression of genetic gain in the production tier.

It was further assumed that surplus brood stock (after selection and replacement requirements were satisfied) in the nucleus were made available to be utilized by the hatcheries, and that only a portion of the fish produced by hatcheries were grown out for sale.

2.2. Reproductive efficiency

Assume that the nucleus consists of N females. The number of progeny (Prg_{Nu}) produced in the nucleus is a function of

$$Prg_{Nu} = N \times F_{Nu} \times Spw_{Nu} \times (1-Wst_{Nu})$$

where F_{Nu} is the number of fry produced per spawning per female, Spw_{Nu} is number of spawnings per year, and Wst_{Nu} is the wastage of fry from spawning to sexual maturity.

Table 1
Reproductive rate of common carp with different spawning systems

Spawning systems	N	F_{Nu}	Spw_{Nu}	Wst_{Nu}	0.5 Prg_{Ha}	Prg_{Pot}
1. Natural spawning (low efficiency)	100	14,000	1	0.65	245,000	1,200,500,000
2. Induced spawning in pools or tanks	100	21,000	1	0.50	525,000	5,512,500,000
3. Induced breeding and artificial incubation in the nucleus only, pools in hatcheries	100	28,000	1	0.50	700,000	7,350,000,000
4. In vitro fertilization in both nucleus and hatcheries	100	28,000	1	0.50	700,000	9,800,000,000

N = number of females in the nucleus; F_{Nu} = number of fry produced per spawning per female; Spw_{Nu} = number of spawnings per year; Wst_{Nu} = wastage of fry from spawning to harvest; 0.5 Prg_{Ha} = number of progeny produced by hatcheries with 50% females; Prg_{Pot} = total potential fish produced by hatcheries.

Table 2
Number of marketable fish annually (Nmkt) with different adoption rates by the industry

Adoption rate (%)[a]	Nmkt
10 (base)	60,658,280
30	181,974,840
60	363,949,680
100	606,582,800

[a] Percentage of improved fish cultured by the commercial sector.

It is also assumed that 50% of the progeny (0.5 Prg_{Nu}) are females. Then, the number of progeny produced by hatcheries (Prg_{Ha}) can be calculated as:

$$Prg_{Ha} = 0.5Prg_{Nu} \times F_{Ha} \times Spw_{Ha} \times (1-Wst_{Ha})$$

where F_{Ha}, Spw_{Ha}, and Wst_{Ha} are as defined above, but for hatcheries (not nucleus). Prg_{Ha} is the total potential fish produced by hatcheries which can be grown out for sale by the production sector. It is also denoted as Prg_{Pot} (potential number of progeny).

In order to calculate Prg_{Pot}, we considered four different systems of reproduction in common carp: 1) representing a very low reproduction rate of females spawned in natural environments, 2) induced breeding using hypophysation technique, followed by the release of the injected fish into pools for natural spawning, 3) induced breeding followed by collection of fertilized eggs for artificial incubation, and 4) in vitro fertilization (strip eggs and sperm, then mix to fertilize and transfer the fertilized eggs to incubators) (Table 1). In all cases, we used N=100, a normal size of a nucleus herd in carps. Calculations of fry number for different systems of reproduction were based on a very conservative fecundity of females. Systems of reproduction 1, 2, 3 and 4 correspond to 50,000, 75,000, 100,000 and 100,000 eggs per kg body weight of female, respectively. System 1 (natural spawning) represents poor management and low reproduction efficiency. System 2 (induced spawning in pools) is commonly practiced by carp hatcheries. System 3 combines both induced breeding and artificial incubation in the nucleus, but spawning in pools still occurs in hatcheries. System 4 (in vitro fertilization and artificial incubation) is applied in both the nucleus and hatcheries.

Results reported in the literature indicate that the fertility rate in carps averages 80%, and that 70% of the fertilized eggs are hatched. Survival of larvae to fry stage is 50%. In addition, we assumed that females spawn only once per breeding season and are on average 1 kg at spawning.

Based on the above values, the potential number of progeny (Prg_{Pot}) that could be produced by hatcheries is presented in Table 1.

Even under the most conservative reproduction scenarios, there is an abundant quantity of fish to supply to the production sector. Total common carp production in Vietnam was of the order of 303,291.4 tons in 2005. If we assume that the market weight of the fish is 0.5 kg (actual range 0.3 to 0.7 kg), then the total production population consists of 606,582,800 fish heads. This is the maximum number of marketable fish annually (Nmkt), if the industry cultured 100% improved fish from the breeding program. In reality, the common carp genetic improvement program at Research Institute for Aquaculture No. 1 (RIA1) supplies about 10% of the market requirements for production in the form of larvae, fry, fingerlings and brood stock. Hence, the number of market fish was considered to be 10% of the total current carp population in the country, and used as the base value in all analyses. In addition, we tested different adoption rates by the production sector, ranging from 10% (the actual level of dissemination) to 30, 60 and 100% adoption, which would be expected to increase in later years as the program unfolds (Table 2).

2.3. Breeding objective

Defining the breeding objective in common carp involves two main steps: i) choice of traits of economic importance, and ii) derivation of their economic values.

The breeding objective for common carp included the following traits: body weight at harvest (BW), survival rate from stocking to harvest (SR) and total feed consumption (FI) during the grow-out period. They were chosen because of their large impact on income and expense at farmers or producers level. Fish are generally priced based on their live weight at harvest and the bigger fish fetch greater prices. Survival rate affects the number of fish harvested and marketed. Feed is a major production cost, accounting for 60–70% of total costs.

The economic values for BW, SR and FI were derived from the following profit equation, which consists of the difference between Return and Cost.

$$\text{Profit}\,(P) = \text{Return}\,(R) - \text{Cost}\,(C)$$

Expressing this equation as a function of biological traits and scaling it up to a production unit of 1000 fish we may write:

$$P = 1000[(\text{BW})(\text{SR}/100)(\text{price per unit } W \text{ of fish}) - \text{FI}(\text{price per unit weight of feed})] - K$$

where BW and FI are expressed in grams, whereas SR is expressed as a percentage. K represents fixed costs. Fixed costs are those that a producer incurs in no matter what the level of production is, and can be ignored when deriving the economic value for each trait. The assumed values for BW, SR, price per g of fish, and a feed cost are shown in Table 3.

The economic value of each trait can be obtained from the partial derivative of the profit equation by differentiation with respect to the trait in question, treating other traits as constants (Harris, 1970). Thus, inserting actual values we can derive the economic value (EV) of each trait in the following manner:

$$\text{EV}_{\text{BW}} = \partial P/\partial W = (1000)(0.85)(\text{US\$0.001}) = \text{US\$0.85}$$

$$\text{EV}_{\text{SR}} = \partial P/\partial S = (1000)(500\,\text{g})(1/100)(\text{US\$0.001}) = \text{US\$5.00}$$

$$\text{EV}_{\text{FI}} = \partial P/\partial FI = -(1000)(\text{US\$0.00056}) = -\text{US\$0.56}.$$

The breeding objective can now be formally written as:

$$H = (\text{US\$0.85})(\text{EBV}_{\text{BW}}) + (\text{US\$5.00})(\text{EBV}_{\text{SR}}) - (\text{US\$0.56})(\text{EBV}_{\text{FI}})$$

where EBV stands for the estimated breeding value (genetic merit) for each trait.

For the sensitivity analyses involving variations in fish price, the economic values for BW and for SR were re-derived using the appropriate price per g, namely US$0.0015 or US$0.002. The effect of different feed costs was dealt with in a similar manner, and the economic values for FI for lower and greater costs were −US$0.37 and −0.84, respectively.

Table 3
Parameter values

Parameter	Abbreviation or symbol (units)	Value(s)
Discount rate	d (fraction)	**0.05**, 0.10, 0.15
Discount factor	$r = 1/(1+d)$	Computed from d values
Year when first returns are obtained	y (years)	**4**, 5, 6
Number of years over which scheme is evaluated	T (years)	10
Selection intensity in females	i_F	1.554
Selection intensity in males	i_M	1.887
Standard deviation of the index	σ_I (US$)	14.3, **22.8**, 41.9 37.5, 43.1; 69.9
Generation interval in females	L_F (years)	2.0
Generation interval in males	L_M (years)	2.0
Number of fish marketed for slaughter/year	Mkt (million)	**60.66**; 121.32; 181.98; 242.63; 303.29; 606.58
Initial investment in program	I (US$)	50,000, **75,000**, 100,000
Annual (recurrent) costs	C (US$)	30,000, **60,000**, 90,000
Harvest weight	W (g)	500
Survival rate	S (%)	85
Cumulative feed intake	FI (g)	745
Price of fish (farm gate)	Fish price (US$/g)	**0.001**, 0.0015, 0.002
Cost of feed	Feed cost (US$/g)	0.00037, **0.00056**, 0.00084

2.4. Genetic parameters

Means, phenotypic standard deviations and heritabilities for weight were estimated by Ninh et al. (unpublished results). Parameters for survival rate and the genetic correlation between body weight and survival were taken from the average of 14 studies reviewed in the literature. Feed intake was calculated assuming a feed conversion ratio of two during the grow-out period. A coefficient of variation of 30% was assumed to calculate the phenotypic standard deviation for feed intake. Heritability for feed intake and its correlations with body weight and survival are not available for any aquaculture species, and hence they were adapted from a literature review of 30 studies in pigs. Appendix Table A1 shows the genetic parameters used in the present study.

2.5. Selection index

The expected genetic gain in the traits in the breeding objectives and standard deviation of the index (σ_I) were calculated using the above genetic parameters and economic values using the SelAction program (Rutten et al., 2002). The breeding goal aimed at improving live weight and survival at harvest while accounting for feed intake. Different selection indices were constructed, which corresponded to a range of heritability levels and to economic values based on alternative fish prices and feed costs. In all cases the following data structure was assumed: i) the pedigree consisted of 100 families (50 sires and 100 dams), ii) there were 20 female and 20 male progeny tested per family that were potential selection candidates, iii) the proportions of selected animals were 15% in females and 7.5% in males, and iv) selection was based on BLUP utilizing full pedigree information. Note that feed intake was included in the breeding objective, but it was not considered as a selection criterion due to a lack of practical methods of measurement.

The annual genetic gain (Δ_G) was calculated as:

$$\Delta_G = [(i_F)(\sigma_I) + (i_M)(\sigma_I)]/(L_F + L_M)$$

where σ_I is the standard deviation of the index, i is the selection intensity ($i_F = 1.554$ and $i_M = 1.887$), and L is the generation interval (two years in both sexes). We assume that in each generation, a total of 4000 fish are recorded (100 families times 40 individuals per family), out of which an equal proportion of males and females is expected. The proportion of selected females and males was 0.15 and 0.075, corresponding selection intensities of 1.554 (i_F) and 1.887 (i_M), respectively. This assumes that the number of selected females and males was three times (i.e. 300 females and 150 males) greater than that actually needed, to allow for losses and unsuccessful matings.

2.6. Genotype by environment interaction

Selection of the nucleus' replacements is generally carried out in a well controlled environment. By contrast, commercial production takes place in a variety of farming systems ranging from small farmers to intensive large scale commercial operations. This may result in a G×E interaction, affecting the ranking of genotypes (called re-ranking effect) or causing a reduction in genetic variance of traits (called scaling effect).

One way of approaching the study of G×E interactions due to the re-ranking effect is by treating the expressions of a trait in alternative environments as if they were different traits. Then, the estimates of genetic correlations between performances in different environments can be used as a measure of the G×E interaction (Falconer, 1952). A literature review across farmed aquaculture species indicates that the re-ranking G×E effect is not of biological significance for body traits (reviewed by Nguyen and Ponzoni, 2006), but it may be important for traits with low heritabilities (e.g. survival rate). In this study, we assumed

genetic correlations of 0.5, 0.7 and 0.9 between homologous traits recorded in the selection (nucleus) program and in the production environment. They represent varying degrees of G×E interaction (severe, moderate and insignificant). A genetic correlation approximating unity (0.99) was assumed between homologous traits for the base situation representing no G×E effect (0.99 instead of 1.0 was used to enable computation using SelAction). For heterologous traits, the genetic correlations between the two environments were also reduced by 50, 30 and 10%, respectively. Since the traits were assumed to be measured on animals in different environments, there is no environmental covariance between them. The phenotypic correlations do not exist because any individual fish will only express the trait in one environment. From a computational viewpoint we treated the traits in the production environment as correlated traits, and we calculated the correlated response to the selection taking place at the nucleus level (see Appendix B for parameters and trait structure).

The other type of G×E interaction we studied was the scaling effect. In this case there is a reduction in the additive genetic variances of the traits, but there is no change in the ranking of individuals between environments. We assumed that there was a reduction of 10, 20, 30 and 40% in the heritability for all traits in the production environment compared with the nucleus, corresponding to 0.27, 0.24, 0.21 and 0.18 for body weight, 0.23, 0.20, 0.18 and 0.15 for feed intake, and 0.09, 0.08, 0.07 and 0.06 for survival rate respectively. The genetic correlations between homologous traits in the nucleus and production environments were assumed to be near unity (0.99). The genetic correlations for heterologous traits within each environment and between the two environments were as given in Appendix A.

The effects of G×E interaction were modeled using selection index theory, with the same assumptions as described above (Section 2.5). The breeding objectives were selected for in the nucleus. The economic values for the traits in the breeding objectives are presented in Section 2.3. Correlated responses in traits (expressed in the production system) to the selection for the breeding objectives in the nucleus were used to calculate total economic gain, standard deviation of the index and accuracy of selection at the production system level. The total economic gain is the sum of the product of genetic gain in each trait times its economic values. The total genetic gain divided by the average selection intensity (Section 2.5) is the standard deviation of the index (σ_I). The accuracy of selection (r_{IH}), or correlation between the index and breeding objective, is the ratio of σ_I on σ_H, where σ_H is standard deviation of the aggregate genotype.

Table 4
Genetic gain per generation for each trait, standard deviation of the index (σ_I) and of the breeding goal (σ_H), accuracy of selection[a] and overall gain per generation in economic units

Breeding objective	Harvest weight (g)	Survival rate (%)	Feed intake (g)	σ_H (US$)	σ_I (US$)	Accuracy of selection	Overall gain in economic units (US$)
Base	39.4	6.8	50.7	66.7	22.8	0.34	39.0
Economic value of feed intake set at 0.0	53.3	5.3	62.1	84.7	41.9	0.49	71.6
Lower heritabilities[b]	38.1	4.4	45.6	51.0	14.3	0.28	28.7
Greater heritabilities[c]	44.0	11.7	56.8	85.4	37.5	0.44	64.0
Fish price US$1.50/kg	46.7	6.1	57.0	101.4	43.1	0.42	73.7
Fish price US$2.00/kg	49.0	5.9	58.9	140.4	63.9	0.46	109.3
Feed cost US$0.37/kg	46.8	6.1	57.1	67.7	28.9	0.43	49.3
Feed cost US$0.84/kg	14.5	7.6	27.0	75.7	16.1	0.21	27.5

[a] Accuracy of the index = $r_{IH} = \sigma_I / \sigma_H$.
[b] Equal to 0.2, 0.05 and 0.16 for harvest weight, survival, and feed intake, respectively.
[c] Equal to 0.4, 0.20 and 0.3 for harvest weight, survival, and feed intake, respectively.

Table 5
Discounted cash flow (d=5%), economic benefit and benefit to cost ratio (monetary values are expressed in thousands of US$)

Year	Discount factor	Discounted returns	Discounted costs	Economic benefit	Benefit to cost ratio
0	1.0	0	0	−75	0
1	0.952	0	57.1	−132.0	0
2	0.907	0	111.6	−186.6	0
3	0.864	0	163.7	−238.4	0
4	0.823	978.8	212.8	691.0	3.4
5	0.784	2,843.2	259.8	2,508.4	8.5
6	0.746	5,506.6	304.5	5,127.0	14.5
7	0.711	8,888.6	347.2	8,466.5	21.1
8	0.677	12,914.9	387.8	12,452.1	27.9
9	0.645	17,516.4	426.5	17,014.9	34.9
10	0.614	22,629.2	463.3	22,090.9	42.0

2.7. Economic evaluation of breeding programs

Economic benefits were evaluated from a national perspective. Table 3 shows the economic parameters and values used in the calculations. For a given parameter, the value in bold was used as a reference. Other values were used in the sensitivity analyses. A SAS code (SAS Institute Inc., 1990) was written to carry out all the calculations.

We calculated the economic benefit of the genetic improvement program using the discounting cash flow technique described by Hill (1971) and later by Weller (1994). Genetic gain is permanent, but its value in future years must be discounted to a net present value. Thus, cumulative discounted return can be computed as the sum of a progression of the form:

$$dR = R\left[r^y + 2r^{y+1} + \ldots + (T-y+1)r^T\right].$$

where R is the undiscounted annual return from the genetic program, calculated as the product of the number of fish marketed per year and the genetic gain per year ($R = Nmkt \times \Delta_G$), $r = 1/(1+d)$, d = the discount

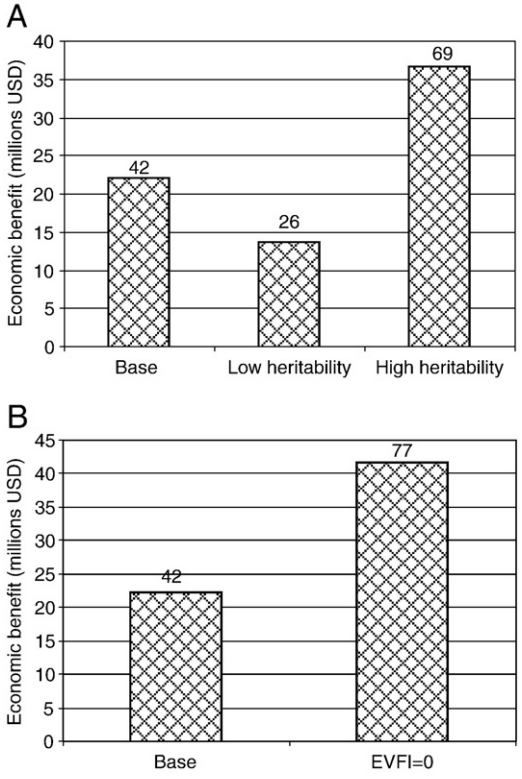

Fig. 1. A) Sensitivity to levels of heritability (benefit to cost ratio at top of bar). B) Sensitivity to economic values of feed intake (EVFI).

rate, T = number of years for which the program was evaluated, and y = years until first returns are realized. The sum of this progression is computed as follows (Hill, 1971):

$$dR = \frac{r^{y} - r^{T+1}}{(1-r)^{2}} - \frac{(T-y+1)r^{T+1}}{1-r}.$$

The annual (recurrent) undiscounted cost is C (Table 3) and the discounted cost (dC) over T years was calculated as:

$$dC = C\left[r + r^{2} + \ldots + r^{T}\right] = \frac{Cr(1-r_{T})}{1-r}$$

The economic benefit (EB) of the program accumulated over T years can be calculated as:

$$EB = dR - dC - I$$

where I is the initial investment in establishing the genetic improvement program.Similarly, the benefit to cost ratio was calculated as:

$$BCR = dR/(dC + I).$$

2.8. Chance of success: risk

For both those making investment decisions and those whose livelihoods depend on the productivity of their fish, achieving a response to selection consistent with that predicted by the commonly used formulae (e.g. Falconer and Mackay, 1996) is vital. For a given size and design of a selection program Nicholas (1989) provides equations that enable the estimation of the coefficient of variation (CV) of selection response:

$$CV = (L_{F+}L_{M})^{0.5} / \left[Q(N_{e}T)^{0.5}\right]$$

where L_F, L_M and T are defined in Table 3, Q is the average of the product of selection intensity and accuracy of selection for females and males, and N_e is the effective population size. CV can be calculated inserting the appropriate values for our case in the equation above. Because CV is the ratio of the standard deviation on the mean, re-arranging the equation to calculate the standard deviation is straightforward, which may then be used to set confidence limits (CL) on the response to selection:

$$CL = \text{mean response} \pm (t)(\text{standard deviation})$$

where t is the appropriate table value for the chosen confidence level (e.g. 1.96 for 95% confidence). The upper and lower limits of the

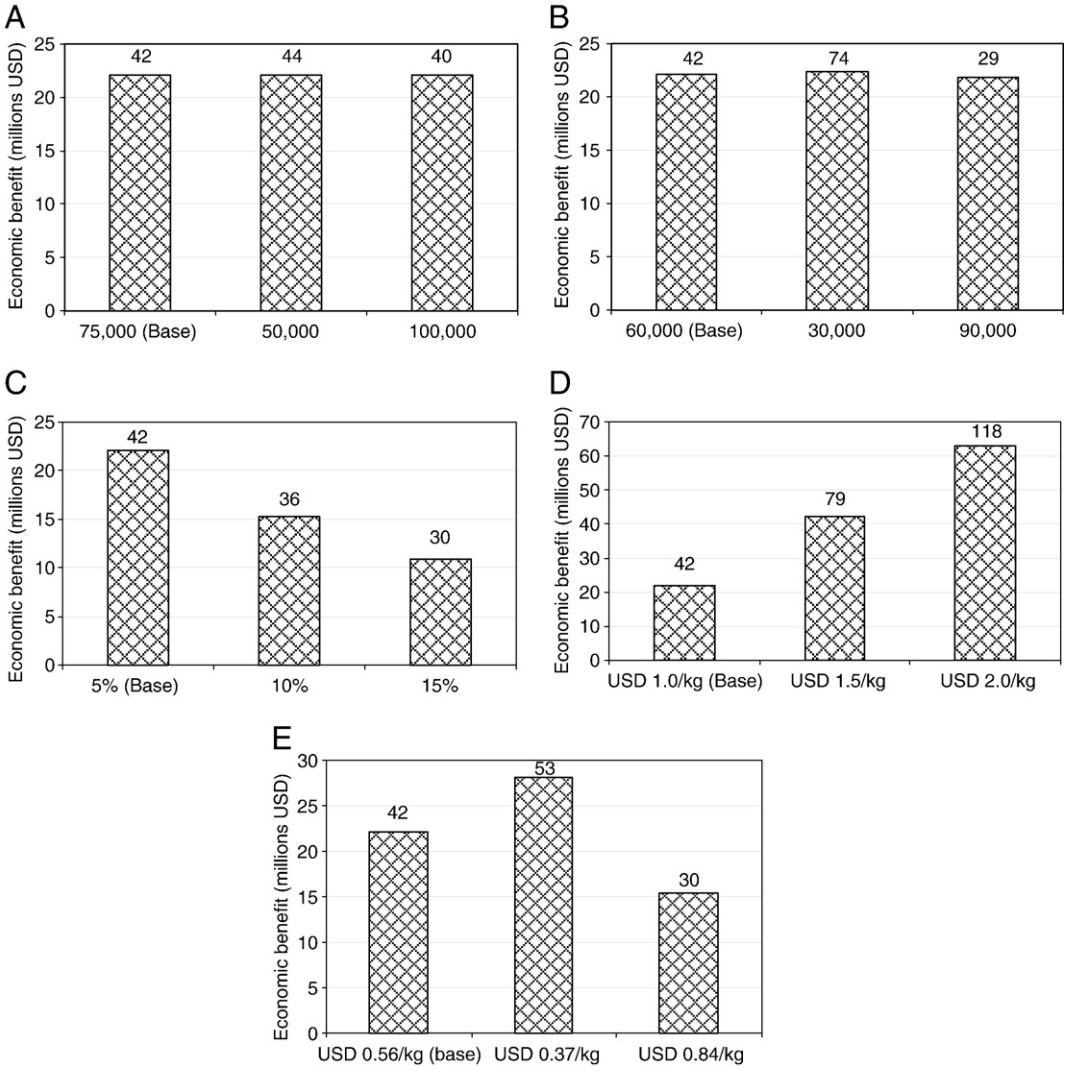

Fig. 2. A) Sensitivity to initial investment. B: Sensitivity to annual cost. C) Sensitivity to discount rates. D) Sensitivity to price of fish. E) Sensitivity to feed costs.

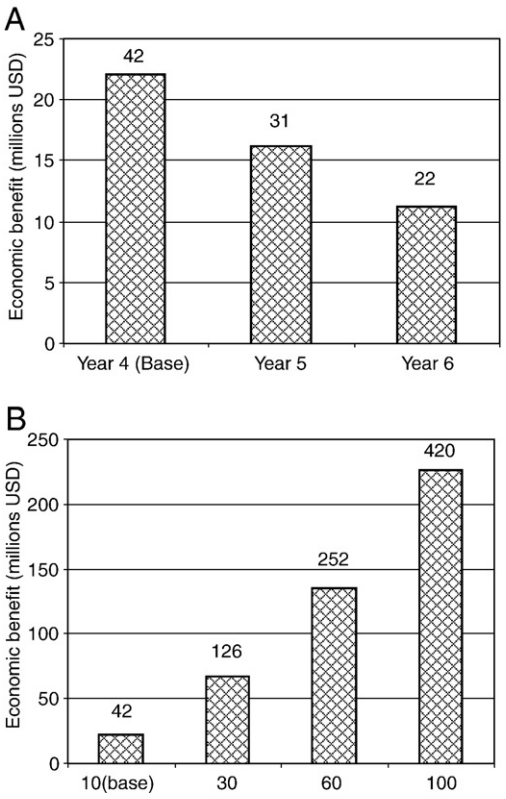

Fig. 3. A Sensitivity to number of years before first return is realized. B) Sensitivity to adoption rates (%).

response to selection may then be used to calculate upper and lower limits for EB and BCR.

3. Results

3.1. Genetic gain

Table 4 presents genetic gains per generation for individual traits in the breeding objectives, standard deviation of the index and of the breeding goal, accuracy of selection, and overall gain in economic units. Genetic gains in BW, SR and FI are as expected from their heritabilities and genetic correlations. The magnitude of responses in all traits did not vary greatly with parameter inputs, except that lower heritability and high feed cost resulted in smaller responses than in other cases. Both standard deviations of the index and breeding goal were greatest when price of fish was US$2.00 per kg. By contrast, they were smallest at the lower end of heritabilities. Overall gain in economic units also increased with heritability and price of fish. By contrast, it decreased with increases in feed costs.

3.2. Economic benefit with base values

Table 5 shows the discounted return, the discounted cost, the economic benefit and the benefit to cost ratio from the program from years 0 to 10. In year 0 there is no revenue or annual testing costs, but it is the year in which the initial investment for the program is made. There is also no return in year 1. From year 2 the negative value of EB increases further due to the annual testing costs and absence of returns, hence the EB is negative. Returns first appear in year 4, and the 'break even' point (when the value of EB changes from negative to positive) occurs between the third and fourth year. By year ten EB was about 22.1 million US$ and BCR was 42.0.

3.3. Sensitivity analysis

3.3.1. Biological parameters

Both EB and BCR were highly sensitive to levels of heritability (Fig. 1A). Greater heritabilities for traits almost doubled EB and BCR, whereas lower heritabilities resulted in a slight reduction in both EB and BCR.

Feed intake also had a large impact on EB and BCR. An exclusion of feed intake in the breeding objective (i.e. setting economic values of feed intake to zero) resulted in overestimates of EB and BCR (Fig. 1B).

3.3.2. Economic parameters

EB and BCR were insensitive to initial investment (Fig. 2A). Similarly, EB remained unchanged with variations in current annual cost (Fig. 2B). However, reducing to a half the annual cost increased BCR almost by two-fold. In breeding programs, annual costs are mainly incurred in data recording, feed and breeding stock replacement. Generally, costs were small relative to the value of genetic gain (Fig. 2B).

Discount rates had a moderate effect on EB but little impact on BCR (Fig. 2C). Despite the relatively high discount rates used, there was only a slight reduction in BCR. Using high discount rate (>5%) in the

Table 6
Genetic gain per generation for each trait (direct and correlated responses), standard deviation of the index (σ_I), accuracy of selection (r_{IH}) and overall gain per generation in economic units

Genotype by environment interaction[a]	Direct responses (nucleus)[b]			Correlated responses (production system)[c]			σ_I (US$)	Accuracy of selection	Overall gain in economic units (US$)
	BW (g)	SR (%)	FI (g)	BW (g)	SR (%)	FI (g)			
(i) Base									
r_g=0.99	39.4	6.8	50.7	39.0	6.7	50.7	22.2	0.33	38.3
r_g=0.9	39.4	6.8	50.7	35.4	6.1	45.6	20.4	0.31	35.1
r_g=0.7	39.4	6.8	50.7	27.6	4.8	35.5	16.0	0.24	27.6
r_g=0.5	39.4	6.8	50.7	19.7	3.4	25.3	11.4	0.17	19.6
(ii)Reduction in h^2 value									
10%	39.4	6.8	50.7	37.0	6.4	48.6	21.1	0.32	36.2
20%	39.4	6.8	50.7	34.9	6.0	45.3	19.9	0.30	34.3
30%	39.4	6.8	50.7	32.7	5.6	42.9	18.5	0.28	31.8
40%	39.4	6.8	50.7	30.2	5.2	39.3	17.5	0.26	30.2

[a] Genotype by environment interaction was due to: (i) re-ranking effects as measured by three levels of genetic correlations (r_g=0.9, 0.7 and 0.5); (ii) scaling effect, i.e. reduction in the heritabilities of traits by 10, 20, 30 and 40% in the production relative to the selection environment. Genetic parameters in the selection (nucleus) environment are shown in Appendix Table A1.

[b] Direct responses do not vary because it is assumed that selection takes place at the nucleus for the defined breeding objective.

[c] Correlated responses vary according to: (i) the assumed genetic correlation between nucleus and production environment, or (ii) according to the heritability of the traits when expressed in the production system.

evaluation of genetic improvement plan can account for risk, but tends to underestimate the value of returns and discourages investments in programs with long term results. In the context of breeding programs, the discount rate should be of the order of 3 to 5% (Bird and Mitchell, 1980).

EB and BCR were highly sensitive to the price of fish (Fig. 2D). Both EB and BCR increased by almost two-fold with a half dollar increment in fish price. A decrease in feed cost increased EB and BCR by a factor of 1.27 (Fig. 2E). A change in the opposite direction was observed when feed cost was increased.

3.3.3. Operational efficiency

The year when first returns occur is likely to be a reflection of how soon the program gets fully underway, including the distribution of the improved stock from the nucleus to hatcheries and producers. There may be delays in the latter activities despite on-going genetic gain in the nucleus. The results indicate that the earlier returns occur, the better, but that even with a delay of two years EB and BCR were still highly favorable (Fig. 3A).

The sensitivity analysis of EB and BCR to different adoption rates is presented in Fig. 3B. Both EB and BCR increased by a factor consistent with the adoption rates of the improved fish by the production sector.

3.4. Sensitivity to genotype by environment interaction

3.4.1. Effect of G×E on genetic gain

Table 6 shows the effect of G×E interaction on the underlying components of genetic gain. The G×E that results in ranking differences had a large effect on the accuracy of selection (r_{IH}), standard deviations of the index (σ_I) and total economic gain in the production environment. Changes in the genetic gain for all traits were proportional to the decrease in the genetic correlation from one to 0.5. A decrease in accuracy of selection was the main source of loss in genetic gain. Generally, the presence of G×E interaction due to scaling effect resulted in little change in the underlying components of genetic gain.

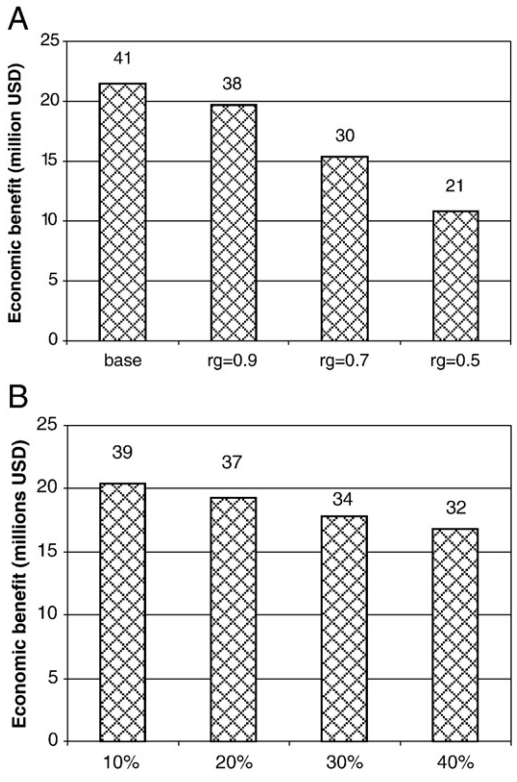

Fig. 4. A) Sensitivity to different levels of genetic correlations. B) Sensitivity to percentage reduction in heritability for traits in production environment.

Table 7
Upper and lower limits (95% probability) for EB and BCR for the different levels of adoption rates

Adoption rate (%)[a]	Limit for EB and BCR	EB (million US$)	BCR
10	Upper	26.1	49.7
	Lower	18.0	34.3
30	Upper	79.7	149.1
	Lower	55.0	102.9
60	Upper	160.1	298.2
	Lower	110.4	205.8
100	Upper	267.2	497.1
	Lower	184.3	342.9

[a] See Table 2 for definition of adoption rates.

3.4.2. Sensitivity of EB and BCR to G×E interaction due to ranking or scaling effects

G×E interactions resulting from either re-ranking or scaling effects had a different impact on EB and BCR. In the case of re-ranking effects (Fig. 4A), both EB and BCR were reduced by 8 to 50% as levels of genetic correlations between the same traits in the nucleus and production environments decreased. A reduction in EB and BCR also occurred, even when the genetic correlation was very high (r_g=0.9). For scaling effects (Fig. 4B), only small changes in EB and BCR were observed even when there was a reduction of 40% in the heritabilities of the traits in the production environment. A reduction of the heritabilities by 10% did only marginally change EB and BCR.

3.5. Chance of success

From Nicholas' (1989) equation, the coefficient of variation of response to selection corresponding to the size, design and time horizon of our program was 9.36%. The 95% confidence limits for EB and BCR are shown in Table 7. The results indicate that the probability of success is extremely high, with a 95% chance that EB and BCR will fall within acceptable values, even for the lowest level of adoption rate.

4. Discussion

We evaluated the economic consequences of implementing a genetic improvement program in common carp at a national level in Vietnam. The return from the investment in such a program was high, with an EB of 11 to 226 million US$, and corresponding BCRs of 22 to 420. The present study also indicates that the efficiency of the breeding program may be influenced by various biological, economic, operational and environmental parameters. These are discussed in the following sections.

4.1. Biological parameters

In this category we considered heritability and feed intake. The effect of variations in heritability values on both EB and BCR was moderate. In contrast, feed intake had a strong influence on EB and BCR. The exclusion of feed intake from the breeding objective (i.e. setting economic values of feed intake to zero) resulted in over-estimates of EB and BCR (Fig. 1B). In general, selection for high growth rate is associated with an undesirable increase in feed intake and maintenance requirements of the animals if harvested at a fixed age (Thodesen, 1999; Mambrini et al., 2006). This is possibly due to the accompanying increase in fatness with a larger body size. Genetic correlations between body weight, feed intake and measures of fat are well documented to be moderately to highly positive under *ad libitum* feeding (e.g. in pigs, Lo et al., 1992). In common carp, Kocour et al. (2007) have recently reported genetic correlations of 0.59 to 0.71 between body traits and fat percentage. Generally, genetic control of

body fat as an indirect way to increase efficiency of feed utilization has been ignored in fish. If reliable genetic parameters for measures of body fat and feed intake were available, a selection index approach could be used to model alternative selection schemes. Nevertheless, the benefits of including fatness in breeding objectives may not be fully justified unless the fish are priced for flesh quality. In any case, our study highlights the lack of efficient methods of recording feed intake, that would enable the development of strategies to increase the efficiency of energy utilization. Correlated increases in feed consumption (to selection emphasizing growth rate) add costs to the breeding program and production systems.

4.2. Economic parameters

Among the economic parameters we studied (initial investment, annual running cost, discount rate, fish and feed prices), the price of fish and feed costs had large effects on EB and BCR. The price of fish is beyond farmers' control, but this result shows that in order to capture full economic benefit from genetic improvement programs, planners and policy makers should develop synergistic strategies to market aquaculture products. As production increases, the price of fish may go down. Thus in order to remain competitive, fish farmers and producers need to increase efficiency of production through adopting better genetics along with improved nutrition and management practices.

Feed often accounts for 60 to 70% of the total production costs. As demonstrated in this study, EB and BCR from the breeding program were highly sensitive to feed costs. In farmed common carp complete industrial feed is mostly used, thus elevating costs per unit of production. In order to sustain aquaculture and to increase profit of fish farmers, research in the area of nutrition should focus on the development of balanced low cost diets through efficient utilization of local feedstuff resources.

4.3. Operational factors

With the high reproductive rate of common carp, EB and BCR are expected to be substantial, even under the most conservative circumstances of spawning in natural environments (system 1). Our assumption of the reproduction rate is much lower than the average literature value of 100,000 eggs per kg of body weight (Huet, 1986). The long term data on induced breeding of common carp at a large scale hatchery in Hungary showed that the average number of stripped eggs per kg body weight of fish was between 114,100 and 163,000 (Szabo et al., 2000). In common carp, induced breeding coupled with fry collection has become a common spawning practice in hatcheries to produce fry to supply farmers. This system was considered as the standard procedure. By using hypophysation technique combined with in vitro fertilization and artificial incubation, both EB and BCR are remarkably increased (results not presented here). In general, the techniques are relatively simple and the cost of setting up an incubator system is low. Other expenses in terms of training hatchery personnel can be compensated for by the great economic return from the improvement in brood stock reproduction.

As the potential progeny produced across reproduction scenarios far exceeds the current production capacity of the country, we assumed that a realistic number of improved fish was transferred from the breeding program to farmers for commercial production as the base value in all analyses. At present, the adoption rate is approximately 10% of the total national population, but the proportion of improved fish used by the industry is expected to increase in coming years since the culture area for common carp is expanding. In addition, local producers are interested in the improved carp of RIA1 because of their superiority over available strains under a wide range of on farm testing environments, with respect to growth rate, survival and yield per unit area (Ninh, unpublished results). Fig. 3B shows that EB and BCR increased linearly with the adoption rate, indicating that in order to fully capture the economic benefit from genetic improvement programs, the dissemination of the improved fish to commercial production should be carried out in a systematic manner to ensure that high quality of seed reaches farmers and producers. Ponzoni (2006) and Nguyen and Ponzoni (2006) discuss strategies for effective dissemination of improved fish strains.

Despite using the lower limit of only 10% improved fish contributing to the current total national production, EB and BCR ranged from 11 to 226 million and 22 to 420, respectively. Both EB and BCR would increase by a factor of 10 if the production sector cultured 100% of improved fish from the breeding program in the country (606 million fish heads marketed annually).

4.4. Genotype by environment interactions

The G×E interaction due to the ranking effect had a greater impact on the efficiency of the breeding program than the interaction due to a scaling effect. Both EB and BCR were reduced by 8 to 50% (Fig. 4A). Under this circumstance, separate genetic improvement programs could be considered for different environments. However, such a course of action is recommended only when there is a severe G×E effect (e.g., r_g=0.5 in our study). In that case, for instance, the annual losses in production calculated as the difference in economic benefit from the base situation (approximately 2 million US$) are greater than the cost of running a new program (as given in Table 3). Nevertheless, in farmed aquaculture species, a single breeding program is virtually always implemented for a wide range of environments especially in developing countries where resources and experience in managing breeding programs are limited. The selection program in common carp in RIA 1, Vietnam, has been carried out under a standard pond environment. Most likely, there will be a little loss in genetic gain in other prevailing environments, at least for growth performance. The estimates of genetic correlations between expressions of body traits in a range of environments reported in the literature are close to unity (ranging from 0.70 to 0.99) across a number of species such as rainbow trout (Sylven et al., 1991), tilapia (Ponzoni et al., 2005a,b), rainbow trout (Fishback et al., 2002; Kause et al., 2003), white shrimp (Gitterle et al., 2005) and pacific oysters (Swan et al., 2007). In order to minimize G×E effects in breeding schemes, a number of strategies can be applied. First, G×E effects can be reduced through the choice of a selection environment that is as close as possible, or identical to, practical production. For instance, one form of G×E interaction is between genotype and dietary protein and energy levels. Quantification of such interaction is necessary to establish the optimal selection environment for commercial production systems. Choosing the correct performance testing environments in the nucleus has the power to maximize profit through improved performance of their descendants in commercial production. Second, the measurement of traits should be standardized to avoid G×E as a consequence of differences in trait definition. Third, breeding schemes could record performance of relatives in the production environment, and a combined genetic evaluation of the data recorded in both environments may alleviate G×E effects, thus reducing the loss in genetic gain (Mulder and Bijma, 2005). Note however, that the traditional breeding structure with unidirectional flow of genes from the nucleus to multipliers and grow out is still predominant in aquaculture, and that data recording at the commercial level is technically difficult in aquatic animals and often impossible in developing countries.

5. Conclusions

The economic benefits from a genetic improvement program in carps are substantial, indicating that it is worth while investing in such activities from a national perspective. Furthermore, expanding to other farmed aquaculture species of economic importance would be justified. The efficiency of the program, however, depends on several factors. Of particular importance are reproduction rate of female breeders and adoption rate by the production sector, which determine

the number of fish of the improved strain that reach the production systems and are later available for sale. For carp species, improvement in reproduction rate can be easily implemented by taking advantage of induced breeding together with artificial incubation in both the nucleus and hatcheries. Dissemination of the improved fish is a key component in fully capturing all economic benefits from genetic improvement. The high sensitivity of the economic benefits to biological parameters (heritability and feed intake) and to genotype by environment interaction due to re-ranking effects also suggest that the design of breeding programs should aim to minimize systematic effects, choosing appropriate testing environments.

Appendix A

Phenotypic and genetic parameters for harvest weight (BW), survival rate (SR) and feed intake (FI)

	BW (g)	SR (%)	FI (g)
Mean	500	85	745
h^2	0.30	0.10	0.25
σ_P	136	35.7	224
Phenotypic (above) and genetic (below) correlations			
BW		0.20	0.70
SR	0.20		0.30
FI	0.70	0.30	
Common environmental effects and correlations			
c^2	0.15	0.08	0.15
BW			
SR	0.20		
FI	0.70	0.20	

Appendix B

Heritabilities (h^2) and genetic correlations (r_g) for body weight (BW), survival rate (SR) and feed intake (FI) in the nucleus (_n) and production (_p) environments

G×E	Scenarios	Parameters	BW (g)	SR (%)	FI (g)
		Mean	500	85	745
		σ_P	136	35.7	224
Scaling effect	Base	h^2_n	0.30	0.10	0.25
	10%	h^2_p	0.27	0.09	0.23
	20%	h^2_p	0.24	0.08	0.20
	30%	h^2_p	0.21	0.07	0.18
	40%	h^2_p	0.18	0.06	0.15
			BW_n	SR_n	FI_n
Re-ranking effect	Base	BW_p	0.99		
	(r_g=0.99)	SR_p	0.20	0.99	
		FI_p	0.70	0.30	0.99
	r_g=0.90	BW_p	0.90		
		SR_p	0.18	0.90	
		FI_p	0.63	0.27	0.90
	r_g=0.70	BW_p	0.70		
		SR_p	0.14	0.70	
		FI_p	0.49	0.21	0.70
	r_g=0.50	BW_p	0.50		
		SR_p	0.10	0.50	
		FI_p	0.35	0.15	0.50

References

Atkins, K.D., 1993. Benefits of genetic improvement to the Merino wool industry. Wool Technol. Sheep Breed. 41, 257–268.

Bird, P.J.W.N., Mitchell, G., 1980. The choice of discount rates in animal breeding investment appraisal. Anim. Breed. Abst. 48, 499–505.

Falconer, D.S., 1952. The problem of environment and selection. Am. Nat. 86, 293–298.

Falconer, D.G., Mackay, T.F.C., 1996. Introduction to Quantitative Genetics, 4th edition. Longman Group Ltd., Harlow, U.K. 464 pp.

Fishback, A.G., Danzmann, R.G., Sakamoto, T., Ferguson, M.M., Gibson, J.P., 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.

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

Greeff, J.C., 1997. Cost–benefit analysis of realized genetic improvement of wool production in an open nucleus breeding scheme. Wool Technol. Sheep Breed. 45, 157–166.

Harris, D.L., 1970. Breeding for efficiency in livestock production: defining the economic objectives. J. Anim. Sci. 30, 860–865.

Hill, W.G., 1971. Investment appraisal for national breeding programmes. Anim. Prod. 13, 37–50.

Huet, M., 1986. Breeding and cultivation in cyprinids, Fish Culture Breeding and Cultivation of Fish, Fishing News Books Ltd; 2nd Ed., pp. 111–150. Oxford, UK.

Kause, A., Ritola, O., Paananen, T., Mäntysaari, E., Eskelinen, U., 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.

Kocour, M., Mauger, S., Rodina, M., Gela, D., Linhart, O., Vandeputte, M., 2007. Heritability estimates for processing and quality traits in common carp (*Cyprinus carpio* L.) using a molecular pedigree. Aquaculture 270, 43–50.

Lantican, M.A., Dubin, H.J., Morris, M.L., 2005. Impacts of International Wheat Breeding Research in the Developing World, 1988–2002. CIMMYT, Mexico D.F.

Lo, L.L., McLaren, D.G., McKeith, F.K., Fernando, R.L., Novakofski, J., 1992. Genetic analyses of growth, real-time ultrasound, carcass, and pork quality traits in Duroc and Landrace pigs: II. Heritabilities and correlations. J. Anim. Sci. 70, 2387–2396.

Mambrini, M., Labbe, L., Randriamanantsoa, F., Boujard, T., 2006. Response of growth selected brown trout (*Salmo trutta*) to challenging feeding conditions. Aquaculture 252, 429–440.

Mitchell, G., Smith, C., Makower, M., Bird, P.J.W.N., 1982. An economic appraisal of pig improvement in Great Britain. 1. Genetic and production aspects. Anim. Prod. 35, 215–224.

Morris, C.A., 1980. Some benefits and costs of genetic improvement in the New Zealand's sheep and beef cattle industry. II. Discounted costs and returns on a farm basis following selection. N.Z. Agric. Sci. 8, 341–345.

Mulder, H.A., Bijma, P., 2005. Effects of genotype×environment interaction on genetic gain in breeding programs. J. Anim. Sci. 83, 49–61.

Nguyen, N.H., Ponzoni, R.W., 2006. Perspectives from agriculture: advances in livestock breeding — implications for aquaculture genetics. NAGA. WorldFish Center Quarterly, vol. 29, pp. 39–45. No. 3 & 4 Jul–Dec 2006.

Nicholas, F.W., 1989. Incorporation of new reproductive technology in genetic improvement programmes. In: Hill, W.G., Mackay, T.F.C. (Eds.), Evolution and Animal Breeding. CAB International, Wallingford, U.K., pp. 203–209.

Ponzoni, R.W., 2006. Genetic improvement and effective dissemination: keys to prosperous and sustainable aquaculture industries. In: Ponzoni, R.W., Acosta, B.O., Ponniah, A.G. (Eds.), Development of Aquatic Animal Genetic Improvement and Dissemination Programs. WorldFish Center, Penang, Malaysia, pp. 1–6.

Ponzoni, R.W., Hamzah, A., Kamaruzzaman, N., Khaw, H.L., 2005a. Live weight genetic parameters in two production environments in the GIFT strain of Nile tilapia, *Oreochromis niloticus*. Proc. 16th conf. Assoc. Advance. Anim. Breed. Genet. 25–28 September, Noosa, Queensland, Australia, vol. 16, pp. 202–205.

Ponzoni, R.W., Hamzah, A., Kamaruzzaman, N., Khaw, H.L., 2005b. Response to selection in two production environments in the gift strain of Nile tilapia, *Oreochromis niloticus*. Proc. 16th conf. Assoc. Advance. Anim. Breed. Genet.25–28 September, Noosa, Queensland, Australia, vol. 16, pp. 206–208.

Ponzoni, R.W., Nguyen, N.H., Khaw, H.L., 2007. Investment appraisal of genetic improvement programs in Nile tilapia (*Oreochromis niloticus*). Aquaculture 269, 187–199.

Rutten, M.J.M., Bijma, P., Woolliams, J.A., van Arendonk, J.A.M., 2002. SelAction: software to predict selection response and rate of inbreeding in livestock breeding programs. J. Heredity 93, 456–458.

SAS Institute Inc., 1990. Fourth Edition. SAS/STAT® User's Guide, Version 6, vols. 1 and 2. Cary, NC, USA.

Sylven, S., Rye, M., Simianer, H., 1991. Interaction of genotype with production system for slaughter weight in rainbow trout *(Oncorhynchus mykiss)*. Livest. Prod. Sci. 28, 253–263.

Swan, A., Thompson, P.A., Ward, R.D., 2007. Genotype×environment interactions for weight in Pacific oysters (*Crassostrea gigas*) on five Australian farms. Aquaculture 265, 91–101.

Szabo, T., Szabo, B., Urbanyi, B., Horwath, L., 2000. Review of the results of common carp (*Cyprinus carpio*) breeding at a large scale hatchery. Rep. Domest. Anim. 35, 89–94.

Thien, T.M., Dan, N.C., Tuan, P.A., 2001. Review of fish genetics and breeding research in Vietnam, 91–96. In: Gupta, M.V., Acosta, B.O. (Eds.), Fish Genetics Research in Member Countries and Institutions of the International Network on Genetics in Aquaculture. ICLARM Conf. Proc., vol. 64. 179 pp.

Thodesen, J., 1999. Selection for Improved Feed Utilization in Atlantic Salmon. Doctor Sci. Thesis, Agricultural University of Norway, 108 pp.

Weller, J.I., 1994. Economic Aspects of Animal Breeding. Chapman & Hall, London. 244 pp.

Wickham, B.W., Belsey, M.A., Jackson, R.G., Rumball, W., 1977. Genetic improvement: some aspects of costs and benefits to the New Zealand livestock industry. 1. Dairy Cattle. N.Z. Agric. Sci. 11, 54–64.