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Investment appraisal of genetic improvement programs in Nile tilapia (*Oreochromis niloticus*)

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Abstract

The economic benefit derived from a genetic improvement program with Nile tilapia (*Oreochromis niloticus*) was examined from a national perspective. An industry structure was assumed whereby the genetic improvement program is conducted in a nucleus which provides brood stock to hatcheries, which in turn produce fry for farmers to grow out to market size. Discounting was used to express all returns and costs in terms of net present value. The economic benefit (discounted returns minus discounted costs, EB) and the benefit/cost ratio (BCR) were studied for a 10 year time horizon. The sensitivity of EB and BCR to a number of factors was examined, namely: (i) Biological (heritability values, accounting for feed intake), (ii) Economic (initial investment, annual cost, discount rate, price of fish), and (iii) Operational (year when first return occurs, reproductive efficiency). The risk involved was assessed by studying the anticipated variability in response to selection (and hence in EB and BCR). Heritability values had a moderate effect, whereas it was shown that the cost of increased feed intake as a correlated response to selection for greater growth rate should be considered to avoid gross over-estimations of EB and BCR. Initial investment, annual costs and choice of discount rate had a relatively small effect on EB and BCR, whereas the effect of the price of fish was substantial. Delays in obtaining the first returns in the program resulted in reduced EB and BCR. However, the greatest contribution to variations in EB and BCR came from improvements in the reproductive efficiency at the level of both the nucleus and the hatcheries. The risk of program's failure due to technical reasons was found to be extremely low. We conclude that even under the most conservative assumptions, genetic improvement programs are highly beneficial from an economic viewpoint, and that for the case studied they could result in EBs ranging from over four million US$ to 32 million US$, and corresponding BCRs of 8.5 to 60.
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1. Introduction

In terrestrial animal and plant species genetic improvement programs have made a substantial contribution to productivity increases and to industry viability. By contrast, most aquaculture stocks in current use in developing countries are genetically similar or inferior to wild, undomesticated counterparts (Eknath, 1991; Brummett et al., 2004). There is evidence that genetic improvement programs implemented in aquatic animal species can have the same positive effect they have had in livestock and crops (Gjedrem, 1998, 2000; Hulata, 2001). GIFT (Genetically Improved Farmed Tilapia; Gupta and Acosta, 2004) and Jayanti rohu (Mahapatra et al., 2006) are two examples in developing countries. They are improved strains of *Oreochromis niloticus* and *Labeo rohita*, respectively, very appealing and valuable

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to farmers due to their greater growth and survival rates. However, genetic improvement programs require an initial investment, as well as recurrent annual expenditure to run them. In view of these costs, government institutions may remain unconvinced about the wisdom to invest in such programs unless clear benefits to the nation can be confidently anticipated.

Annual responses to selection often look negligible when compared with the gains that may be achieved through expansion, improved nutrition and intensification of the production system. However, response to selection measured in one population does not provide a good measure of the potential impact of genetic gains. With an adequate industry structure, the small but cumulative responses to selection achieved in a nucleus undergoing genetic improvement, can be passed over to a multiplier tier of hatcheries and in turn, from hatcheries to farmers (Fig. 1). This potential for expression of small accumulated changes in thousands or millions of animals is what makes genetic improvement programs one of the most powerful and cheapest means of increasing the efficiency of aquaculture.

In this paper we examine the economic benefits of genetic improvement programs from a national perspective for a broad range of situations. Using Nile tilapia (*O. niloticus*) as an example, we conclude that even under the most conservative assumptions they are highly beneficial from an economic viewpoint.

2. Materials and methods

2.1. Assumed industry structure

In animal production, genetic improvement typically takes place in a very small fraction of the population. The genetic improvement achieved in that 'elite' or 'nucleus' of superior animals is multiplied and disseminated to the production systems. The flow of genes is graphically illustrated in Fig. 1. Fish are very well placed, with their high reproductive efficiency, to develop cost effective structures for the dissemination of genetic gain. The implementation of a genetic improvement program in a relatively small number of
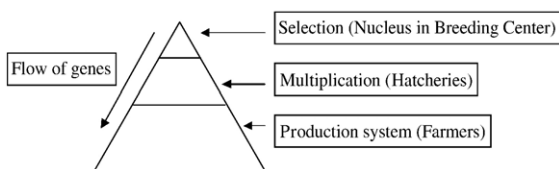

Fig. 1. Flow of genes from the nucleus in the breeding center to the production system.

animals can be enough to service a very large population involved in production. In this study we assume that a government department invests in the establishment and running of a nucleus. The nucleus supplies brood stock to hatcheries, annually replacing all the fish so that hatcheries always use the latest generation, with the greatest amount of genetic gain. It is further assumed that all the brood stock produced in the nucleus that is surplus to its own replacement needs, can be utilized by the hatcheries. Similarly, it is assumed that all the fry produced by hatcheries can be grown out in the production sector.

2.2. Reproductive efficiency

Part of the nucleus' progeny in one spawning is required as candidates from which the parents of the next generation will be selected. This number is negligible in relation to the total that can be produced, and surplus fish from this spawning, as well as all fish from other spawnings in the year are destined to hatcheries. We examined the consequences of different reproductive efficiencies, ranging from low, as with natural spawning in ponds, to high, as with spawning in tanks or hapas coupled with egg collection and artificial incubation. The reproductive efficiency in the nucleus will determine how many females can be made available to hatcheries. The nucleus consists of N females and the number of progeny (Prg_{Nu}) they can produce annually is a function of:

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

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

Assume that $0.5Prg_{Nu}$ are females. Then, the number of progeny produced by the hatcheries (Prg_{Ha}) can be calculated as:

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

where F, Spw and Wst have the same meaning as above, but for hatcheries.

Note that when all the fish produced by the hatcheries are grown out for sale by the production sector, Prg_{Ha} becomes the number of fish marketed annually (Mkt in Table 4).

Based on information collected at the Aquaculture Extension Center, Jitra, Malaysia (Azhar Hamzah — unpublished results) and a literature review (Appendix A) we assumed F, Spw and Wst values corresponding to

different operational systems. N was set to 100 females. Table 1 shows the number of progeny that would be harvested from the different systems. We chose a range of 'levels' of reproductive efficiency that is encountered in practice. Level 1 corresponds to poor management and natural spawning in ponds; Level 2 is as Level 1 but with good management; Level 3 uses reproduction in hapas, egg collection from the mouths of females and artificial incubation in the nucleus, and natural spawning with good management in hatcheries; Level 4 assumes that reproduction in hapas (as described for Level 3) is used in both the nucleus and in hatcheries.

2.3. The breeding objective

In the assumed industry structure (Fig. 1) farmers produce virtually all the fish for consumption. Hence, the breeding objective was defined according to farmers' interests, considering the nucleus and the dependent hatcheries as sectors servicing farmers. The biological traits included in the breeding objective are shown in Table 2. They were chosen because of their impact on income and expense at the farm level. The simple profit equation has the form:

Profit $(P) = $ Income $-$ Expense.

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

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

where W is weight at harvest, S is the survival rate (expressed as a percentage) to harvest time, FI is the total amount of feed consumed per fish to harvest time, and 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 W, S, price per g of fish, and a feed cost are shown in Table 4.

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:

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

$$\text{EV}_S = \partial P/\partial S = (1000)(300\text{g})(1/100)(\text{US } 0.001) = \text{US } 3.00$$

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

The breeding objective can now be formally written as:

$$H = (\text{US } 0.85)(\text{BV}_W) + (\text{US } 3.00)(\text{BV}_s) - (\text{US } 0.56)(\text{BV}_{\text{FI}})$$

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

For the sensitivity analyses involving variations in fish price the economic values for W and for S were re-derived using the appropriate price per g, namely US $0.0015 or US$0.002.

2.4. The selection index

We assumed that the nucleus consisted of 50 males and 100 females (each male mated to two females), and that 40 progeny per full sib group were recorded. The information available to estimate the breeding value of each trait and the overall index is shown in Table 3. Note that feed intake was included in the breeding objective, but it was not considered as a selection criterion because its measurement in fish is presently extremely difficult and imprecise.

Table 1
Levels of reproductive efficiency with different operational systems[a]

Level and operational system	Nucleus				Hatchery				
	N	F_{Nu}	Spw$_{\text{Nu}}$	Wst$_{\text{Nu}}$	0.5Prg$_{\text{Nu}}$	F_{Ha}	Spw$_{\text{Ha}}$	Wst$_{\text{Ha}}$	Prg$_{\text{Ha}}$
1. All pond, low efficiency	100	70	6	0.5	10,500	70	6	0.5	2,205,000
2. All pond, moderate efficiency	100	80	7	0.35	18,200	80	7	0.35	6,624,800
3. Hapa in nucleus, pond in hatcheries	100	250	16	0.35	130,000	80	7	0.35	47,320,000
4. Hapa in nucleus and hatcheries	100	250	16	0.35	130,000	250	16	0.35	338,000,000

[a] See definition of symbols in Section 2.2.

Table 2
Biological traits included in the breeding objective

Effect on profit	Trait	Logic for inclusion
Income	Harvest weight (W)	Fish are marketed on a weight basis, heavier fish generally fetch a greater price. Fast growing fish will reach a particular weight faster than slow growing fish.
	Survival rate (S)	Greater survival results in a greater number of fish available for consumption or for sale.
Expense	Feed intake (FI)	Feed is a major production cost. Greater growth rate may result in greater feed consumption.

2.5. Phenotypic and genetic parameters

Appendix Table A2 shows the phenotypic and genetic parameters used in the present work. Values were chosen from Eknath et al. (1998), Ponzoni et al. (2005), and unpublished estimates from the GIFT (Genetically Improved Farmed Tilapia) population jointly maintained by The WorldFish Center and the Department of Fisheries in Malaysia. There were no estimates available for feed intake. The mean was calculated assuming a feed conversion ratio of two during last two thirds of the growth period (i.e. the last 200 g, from 100 to 300 g) of the fish, hence the average cumulative feed intake of 400 g. The phenotypic standard deviation of feed intake was calculated assuming a coefficient of variation of 0.3. Very high correlation values were assumed between feed intake and harvest weight. The correlations between feed intake and survival were assumed to be approximately of the same magnitude as between the latter trait and harvest weight. The logic for including feed intake as a trait in the breeding objective is discussed in another section of this paper. The resulting variance–covariance matrices were tested and found to satisfy the 'permissibility' criteria described by Foulley and Ollivier (1986).

A slightly modified version of the computer program of Kunzi (1975) was used to calculate the genetic gain in each trait and in the overall breeding objective. Selection response was calculated as by truncation on the index value, but assuming that the proportion required of males and females was three times greater (i.e. 150 males and 300 females) than that actually needed, to allow for losses and unsuccessful matings.

A total of 4000 fish would be recorded (100 full sib groups times 40 individuals per group), out of which an equal proportion of males and females is expected (0.50). Thus, the proportion selected of females and males was 0.15 and 0.075, corresponding selection intensities of 1.554 (i_F) and 1.887 (i_M), respectively.

The annual genetic gain (gg/yr) in economic units (US$) was calculated as:

$$gg/yr = [(i_F)(\sigma_I) + (i_M)(\sigma_I)]/(gi_F + gi_M)$$

where σ_I is the standard deviation of the index and gi is the generation interval (one year in Nile tilapia).

2.6. Calculation of economic benefits

2.6.1. Rationale

We consider and calculate economic benefits from a national perspective. Government departments having to make investment decisions may legitimately ask the question: 'If we invest in a genetic improvement program for Nile tilapia, what sort of return to the nation can we expect, if any?'. There are other perspectives from which the economic benefit of a genetic improvement program can be calculated (Moav, 1973), but for a developing country government trying to improve the well being of the human population, the national perspective is the most appropriate.

2.6.2. Economic parameter values

Table 4 shows the economic parameters and the values used in the calculation of the economic benefit derived from the genetic improvement program. When several values are shown for a given parameter, the one in bold was used as a reference, other values being used in the sensitivity analysis.

2.6.3. Methodology

We calculated the economic benefit of the genetic improvement program using the discounting technique described by Hill (1971) and later by Weller (1994). In a genetic improvement program there are costs that occur early during implementation, whereas it will certainly be some time before returns are accrued. Hence, discounting is important because a monetary unit available now is worth more than one available at some later time. The discounting technique allows the expression of economic benefit in terms of 'net present value'.

Table 3
Characters used as selection criteria in the index and information available from relatives

Characters	Relatives
Harvest weight	Individual
	39 full sibs
	40 half sibs
Survival rate	46 full sibs 47 half sibs
Feed intake	No records available

Table 4
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)	**2**, 3, 4
Number of years over which scheme is evaluated	To (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$)	8.2188, **12.6283**, 17.7043, 28.3738, 33.3836, 44.8096
Generation interval in females	gi_F (years)	1.0
Generation interval in males	gi_M (years)	1.0
Number of fish marketed for slaughter/year	Mkt (million)	2.205; **6.6248**; 47.32; 338.0
Initial investment in program	I (US$)	50,000, **75,000**, 100,000
Annual (recurrent) costs	C (US$)	30,000, **60,000**, 90,000
Harvest weight	W (g)	300
Survival rate	S (%)	85
Cumulative feed intake	FI (g)	400
Price of fish (farm gate)	Fish price (US$/g)	**0.001**, 0.0015, 0.002
Cost of feed	Feed cost (US$/g)	0.00056

Using the definitions and notation presented in Table 4, the undiscounted annual return (R) from the genetic improvement program can be calculated as the product between the number of fish marketed per year and the genetic gain per year:

$$R = (\text{Mkt})(\text{gg/yr}).$$

The discounted return (dR) for the To years for which the program was evaluated was calculated as:

$$\begin{aligned} dR &= R[r^y + 2r^{y+1} + ... + (\text{To} - y + 1)r^{\text{To}}] \\ &= R\{(r^y - r^{\text{To}+1})/(1 \div r)^2 - [(\text{To} - y + 1) \\ &\quad \times (r^{\text{To}+1})]/(1 - r)\} \end{aligned}$$

The annual (recurrent) undiscounted cost is C (Table 4) and the discounted cost (dC) over To years was calculated as:

$$dC = C[r + r^2 + ... + r^{\text{To}}] = C\,r(1 - r^{\text{To})}/(1 - r).$$

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

$$EB = dR - dC - I$$

Similarly, the benefit/cost ratio was calculated as:

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

Calculations were carried out for a set of parameter values (base, indicated in bold type in Table 4) that were considered realistic, but very conservative and in some instances close to the lower limit. The results obtained using these base parameter values were used as a reference point in this study. The logic behind choosing conservative parameter values for the base was that if EB and BCR turned out to be favorable under such circumstances, they would be even better under improved (and quite likely) scenarios. We examined the sensitivity of the system by studying the consequences of deviations from the base values in a number of parameters. The total duration of the program (To) was set at 10 years. SAS code (SAS Institute Inc., 1990) was written (and manually checked for correctness) to carry out all the calculations.

2.6.4. Sensitivity analysis

There are many factors that can affect EB and BCR. For convenience they were grouped into three categories: (i) Biological (heritability values, accounting for feed intake), (ii) Economic (initial investment, annual cost, discount rate, price of fish), and (iii) Operational (year when first return occurs, reproductive efficiency).

2.6.5. 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:

$$CV = (gi_{F+}gi_M)^{0.5}/[Q(N_e\text{To})0.5]$$

where gi_F, gi_M and To are defined in Table 4, 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 response to selection may then be used to calculate upper and lower limits for EB and BCR.

3. Results

3.1. Genetic gains

Table 5 shows the annual genetic gain in each trait in the breeding objective as well as the overall gain in economic units $\{[(i_F)(\sigma_I) + (i_M)(\sigma_I)]/(gi_F + gi_M)\}$. The overall gain in economic units can also be obtained as the sum of the economic value times the genetic gain for each trait.

3.2. Economic benefit with base parameter values

Table 6 shows the discounted return, the discounted cost, the economic benefit and the cost/benefit ratio from the program from years 0 to 10 for the base situation. 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, hence the EB is negative. In year 1 the negative value of EB increases further due to the

annual testing costs and absence of returns. Returns first appear in year 2, and the 'break even' point (when the value of EB changes from negative to positive) occurs between the second and the third year. By year ten EB was over four million US$ and BCR was 8.5.

3.3. Sensitivity analysis

The effect of different magnitudes of (i) Biological (heritability values, accounting for feed intake), (ii) Economic (initial investment, annual cost, discount rate, price of fish), and (iii) Operational (year when first return occurs, reproductive efficiency) parameters on EB and BCR are shown in Figs. 2, 3 and 4. Note that the BCR values are given at the top of the bars in each figure.

3.3.1. Biological parameters
Greater heritabilities resulted in greater EB and BCR, as one would expect (Fig. 2). However, values at both the lower and higher end of available estimates resulted in only relatively moderate departures from the base.

The way in which feed intake was handled in the breeding objective had an impact of greater magnitude than the heritability values. In the calculations for the base situation, feed intake was included as a trait in the breeding objective. In this way, we accounted for the increased production cost due to the assumed greater feed intake of faster growing fish. Setting the economic value of feed intake at zero is equivalent to assume that faster growing fish do not have greater feed intake or that the additional intake has no cost. The effect of this assumption was to greatly increase the EB, resulting in a BCR of 22.

3.3.2. Economic parameters
EB was not sensitive to the initial investment or to the annual cost of the program (Fig. 3). BCR showed greater variation in the case of the latter factor. Greater discount rates resulted in lower EB, but a three-fold increase of

Table 5
Annual genetic gain for each trait, standard deviation of the breeding objective (σ_H) and of the index (σ_I)[a], and overall gain in economic units

Breeding objective	Harvest weight (g)	Survival rate (%)	Feed intake (g)	σ_H (US$)	σ_I (US$)	Genetic gain in economic units (US$)
Base	48	3	50	36.1374	12.6283	21.73
Economic value of feed intake set at 0.0	69	0	69	56.4005	33.3836	57.44
Lower heritabilities [b]	23	3	25	29.0628	8.2188	14.14
Greater heritabilities [c]	47	6	49	44.0837	17.7043	30.46
Fish price US$1.50/kg	62	1	63	61.4829	28.3738	48.82
Fish price US$2.00/kg	65	1	65	88.5714	44.8096	77.10

[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, 0.12 and 0.3 for harvest weight, survival, and feed intake, respectively.

this factor resulted in only a 25% reduction in BCR (from 8 to 6). Of the economic factors examined, the farm gate price of the fish had the greatest impact, where doubling it increased BCR by a factor of 3.75.

3.3.3. Operational efficiency

The year in which first returns occur had a moderate effect on EB and BCR (Fig. 4). The magnitude of this effect pales into insignificance when compared with the consequences of different reproductive efficiency levels. The reproductive efficiency assumed in the base calculations was very conservative (Level 2 in Table 1). Further reducing the already low reproductive rate used to a lower level (Level 1 in Table 1) reduced the EB to a quarter of the base and BCR to 3. Note that this lowest level of reproductive efficiency would be unacceptably poor in a nucleus and in any associated hatcheries responsible for the dissemination of improved stock. By contrast, an improvement in the reproductive rate in the nucleus (Level 3 in Table 1), which would make more females available for hatcheries, increased EB by a factor of 8, and raised BCR to 60. A further improvement by introducing the hapa system in hatcheries (Level 4 in Table 1) caused an additional and astonishing increase in the EB, which resulted in a BCR of more than 400.
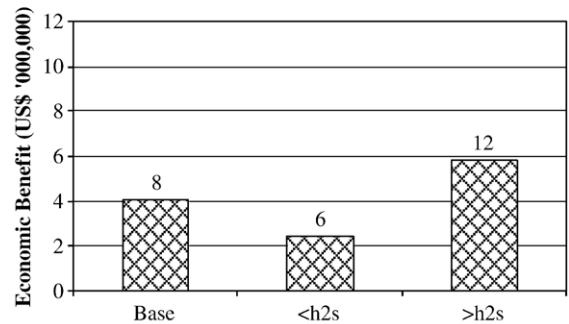
3.4. Chance of success

From the equation of Nicholas (1989), the coefficient of variation of response to selection corresponding to the size, design and time horizon of our program was 6.44%. 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
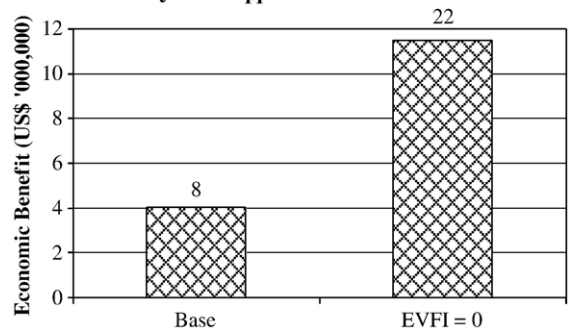

Fig. 2. Sensitivity to biological parameters (benefit/cost ratio at top of bar).

will fall within acceptable values, even for the lowest level of reproductive efficiency.

4. Discussion

4.1. General

In conducting the economic appraisal of a genetic improvement program with Nile tilapia, we examined the problem a national perspective, focusing on the calculation of what additional wealth to the nation would emerge from the implementation of such a program. The results strongly suggest that very favorable returns on investment can be obtained from genetic improvement. The distribution of the newly created wealth, however, is a separate issue, and is not dealt with here. Note that the findings are also applicable to a vertically integrated firm controlling the three tiers described in Fig. 1, namely, the nucleus, the hatcheries and the production sector.

4.2. Base parameter values

The base parameter values were purposely chosen to represent a very conservative scenario. For instance, both

Table 6
Discounted cash flow ($d = 5\%$), economic benefit and benefit/cost ratio (monetary values are expressed in thousands of US$) for the base situation

Year	Discount factor	Discounted returns	Discounted costs	Economic benefit	Benefit/ cost ratio
0	1.0	0	0	−75	–
1	0.952	0	57.14	−132.14	0
2	0.907	130.56	111.56	−56.01	0.7
3	0.864	379.23	163.39	140.84	1.6
4	0.823	734.48	212.76	446.73	2.6
5	0.784	1185.60	259.77	850.83	3.5
6	0.746	1722.64	304.54	1343.10	4.5
7	0.711	2336.40	347.18	1914.21	5.5
8	0.677	3018.35	387.80	2555.56	6.5
9	0.645	3760.62	426.47	3259.15	7.5
10	0.614	4555.90	463.30	4017.60	8.5

a. Sensitivity to initial investment.

b. Sensitivity to annual cost.

c. Sensitivity to discount rate.

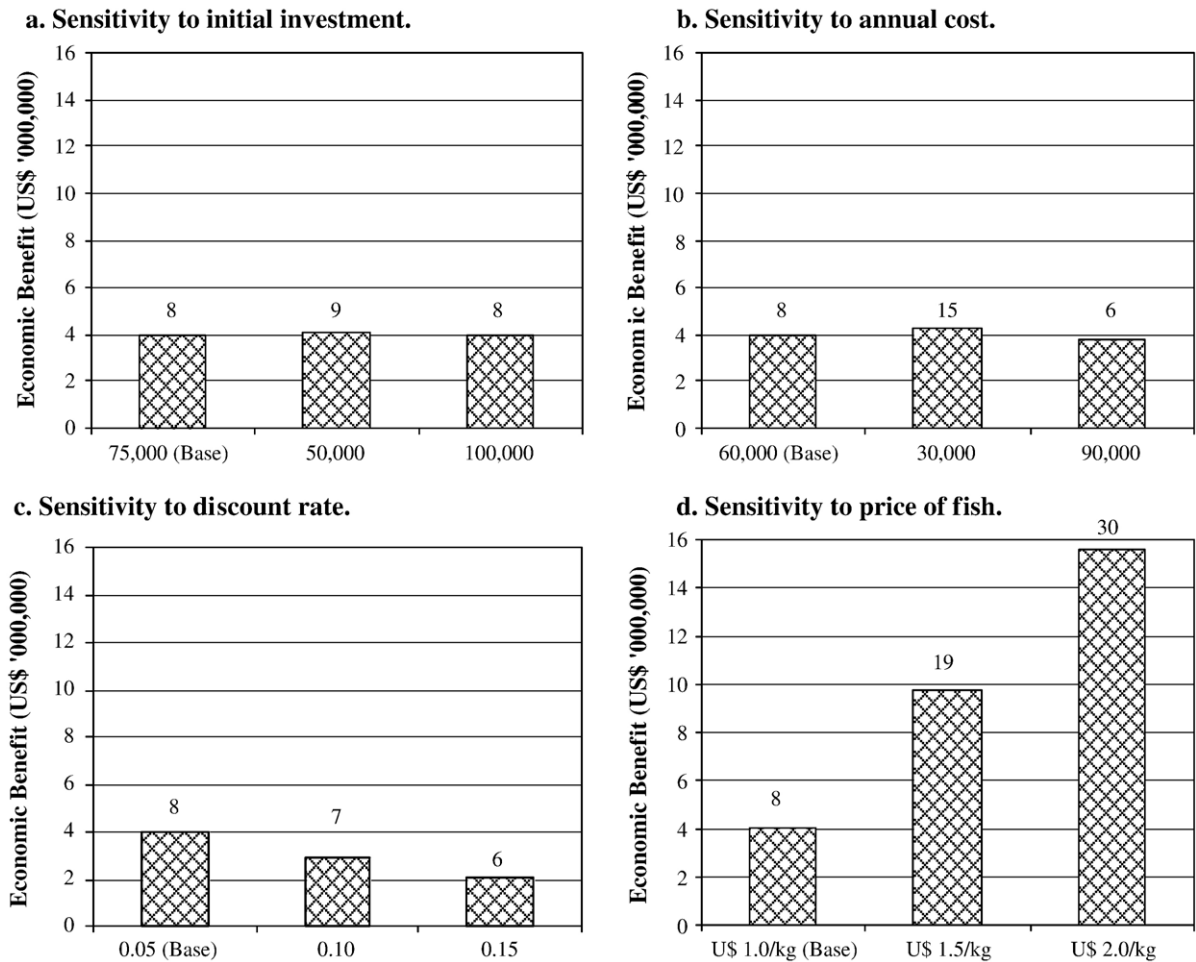**d. Sensitivity to price of fish.**

Fig. 3. Sensitivity to economic parameters (benefit/cost ratio at top of bar).

fish price and reproductive efficiency were set close to the lower limit of the values that can be expected. Even under this sort of circumstance EB turned from negative to positive by the third year of program implementation (Table 6), and by year 10 the BCR was 8.5. In practice, the fish price is likely to be greater, and using very simple and inexpensive technology the reproductive efficiency of the fish can be greater. Hence, the EB and BCR obtained with the base parameter values should be taken as the minimum that can be expected from a genetic improvement program such as the one in question.

4.3. Sensitivity analysis

4.3.1. Biological parameters

We studied the effects of two biological factors, namely, the heritability values for the traits in the breeding objective, and the approach taken regarding feed intake. With regards to the former, greater heritabilities resulted in greater genetic gain and consequently in greater EB and BCR. Partly, the heritability value is a property of the trait and the population in question, but it may be improved by reducing the environmental variance by managerial means. Although EB and BCR were only moderately sensitive to rather large variations in the heritabilities, management practices that may lead to reduced environmental variance should be adopted whenever possible. The production of progeny from synchronized spawnings and its grow out in standard and uniform conditions are examples of such practices.

With regards to feed intake, despite a lack of genetic parameters for this trait in tilapia, it was included in the breeding objective because generally feed is a major cost in aquaculture production. The parameter values used for feed intake were based on a number of assumptions, but note that ignoring feed intake involves more radical assumptions, namely, that feed requirements do not increase with greater growth rate, or that the cost of the additional feed is

a. Sensitivity to year in which first returns occur.
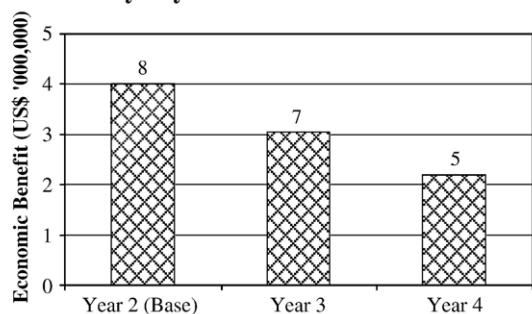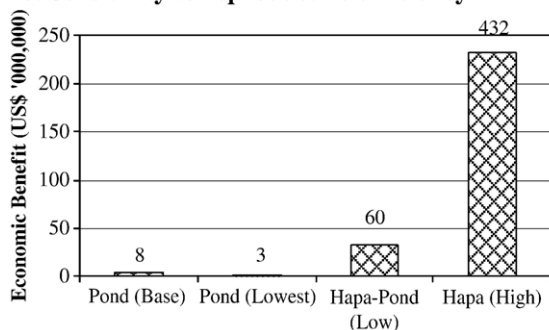

b. Sensitivity to reproductive efficiency.

Fig. 4. Sensitivity to operational efficiency (benefit/cost ratio at top of bar).

zero. We can be sure that the latter assumption is not correct. With regards to the former, there is experimental evidence indicating that in Atlantic salmon (*Salmo salar*) there is a correlated response in feed intake, as well as in feed efficiency, to selection for growth rate (Thodesen, 1999). Mambrini et al. (2006) found that in brown trout (*Salmo trutta*) there is a correlated response in feed intake, but that there is no change in the efficiency of feed utilization. These experimental results, coupled with the importance of feed costs in the production system, provide ample justification for the inclusion of the trait in the breeding objective. Setting the economic value of feed intake at zero greatly increased EB and BCR. If the correlated responses reported by Thodesen (1999) and by Mambrini et al. (2006) were confirmed in tilapia, ignoring feed intake in the breeding objective would result in a gross over-estimate of the benefit of a genetic improvement program emphasizing growth rate. This result is consistent with what is observed in terrestrial animal species (e.g. Ponzoni, 1992). Although it is unlikely that feed intake will ever be measured in practical tilapia breeding programs in developing countries, the estimation of phenotypic and genetic parameters for this trait by research institutions would be highly desirable so that we can be more confident about the appropriate parameter values to be used in predicting responses to selection, and not entirely rely on assumed ones (Doupe and Lymbery, 2003).

4.3.2. Economic parameters

EB and BCR were both insensitive to the magnitude of the initial investment (Fig. 3), whereas the annual cost of the program had a greater effect on BCR than on EB. By contrast, discount rate had a greater effect on EB than on BCR. The choice of a discount rate in a study such as this is always open to debate. In the present context the costs and benefits are being assessed from the viewpoint of society as a whole (as distinct from an individual firm or person), and the discounting technique is used to express such costs and benefits in terms of net present value. This net present value can then be compared to that obtained from alternative uses of the limited resources a nation may presently have for investment. Bird and Mitchell (1980) discuss the choice of discount rate in the context of animal breeding programs and conclude that it should be of the order of 3 to 5%. Greater discount rates may be used as a way of accounting for risk. In our case, Fig. 3 shows that despite the assumed low reproductive rate (Level 2 in Table 1), even at a high discount rate of 15% EB remained highly positive and BCR was about 75% of that for the base situation.

The price of fish had a large effect on both EB and BCR. Although prices are most often beyond planners' and farmers' control, bigger fish often fetch greater prices in the market, so an added (and not accounted for) benefit of the selection program could be better prices in the future.

4.3.3. 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 stock to hatcheries. 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. 4).

Table 7

Upper and lower limits (95% probability) for EB and BCR for the different levels of reproductive efficiency

Reproductive efficiency [a]	Limit for EB and BCR	EB (millions US$)	BCR
Level 1	Upper	1.17	3.17
	Lower	0.79	2.46
Level 2	Upper	4.60	9.53
	Lower	3.44	7.40
Level 3	Upper	36.11	68.08
	Lower	27.90	52.82
Level 4	Upper	261.25	486.32
	Lower	202.56	377.30

[a] See Table 1 for definition of Levels 1 to 4.

The reproductive efficiency assumed for the base situation (Level 2 in Table 1) was what may be considered the lowest level at which a genetic improvement program should be entertained, and one that can be easily improved with readily available and affordable technology. Despite this it resulted in a very favorable EB and a BCR of 8.5. Note that in the research facilities at the Aquaculture Extension Center, Jitra, in the GIFT stock jointly managed by the Department of Fisheries (Malaysia) and WorldFish, using hapas, egg collection from the mouths of tilapia females, and artificial incubation, the reproductive efficiency is at least equivalent to that shown for the nucleus in Level 3 of Table 1. Because this level of reproduction can be achieved with simple and inexpensive technology it should be the one targeted in a national genetic improvement program. When the hapa technology was assumed to be used in the nucleus (Level 3 in Table 1), EB increased by a factor of 8 and BCR changed from 8.5 in Level 2, to 60. In Level 4 it was assumed that the hapa technology was used in both the nucleus and the hatcheries, and both EB and BCR increased in an extraordinary manner. It may be argued that to achieve a greater reproductive rate in hatcheries an additional government investment would be required to transfer the hapa technology to hatchery managers. We made calculations assuming that an additional US$200,000 was invested annually for that purpose. After allowing for such increased cost of the program, EB and BCR were US$30.5 million and 16, respectively, for Level 3, whereas they were US$230 million and 112 for Level 4. So despite substantial additional investment to train hatchery personnel, EB and BCR were still very favorable.

4.3.4. Summary of sensitivity analysis

Management practices in the nucleus that may reduce environmental variance and thus increase heritabilities are likely to have a moderate effect.

The cost of increased feed intake as a correlated response to selection for greater growth rate should be taken into consideration to avoid gross over-estimations of the EB and BCR of the program.

Initial investment, annual costs and choice of discount rate are likely to have a relatively small effect on EB and BCR, whereas the effect of the price of fish can be substantial.

The earlier the first returns are achieved the greater EB and BCR will be. However, the greatest contribution to EB and BCR came from improvements in the reproductive efficiency at the level of both the nucleus and the hatcheries. This last factor, reproductive efficiency, is the one likely to have the greatest impact on EB and BCR.

4.4. Chance of success

The present study is deterministic (it uses mathematical equations to predict results) implicitly assuming a total certainty of outcomes. However, we know that genetic improvement by selection is a stochastic process, involving sampling of genes when the parents of each generation are chosen and when those parents produce progeny. A way of assessing the probability of success of a genetic improvement program is by looking at the anticipated variability in response to selection (Nicholas, 1989). We found that the coefficient of variation of selection response was low enough to inspire confidence in the program's outcome, and that if confidence limits were set for EB and BCR (Table 7) these fell within favorable values even for the lowest level of reproduction studied. Hence, we conclude that the risk of failure due to technical reasons is extremely low. Of course, failure due to natural disasters or to lack of continuity of purpose can occur but it is very difficult to deal with this kind of causes in a systematic manner.

5. Concluding remarks

The methodology used illustrates the multiplicity of factors that can influence the impact of a genetic improvement program. The results point to the factors to which the economic benefit and the benefit/cost ratio are most sensitive, thus assisting in the identification of areas worthy of the greatest attention. We found that both EB and BCR were most sensitive to reproductive efficiency in the nucleus and in hatcheries, a factor that determines the number of fish upon which the genetic improvement is expressed. This quantitative finding is consistent with the generalized perception that multiplication and dissemination of improved strains or breeds is of paramount importance in a comprehensive approach to genetic improvement. The model can be used to investigate other factors that one may suspect will influence the outcome of a genetic improvement program (e.g. less frequent transfer of brood stock to hatcheries, expression of only a fraction of the selection response in the nucleus in the production environment due to genotype by environment interaction). It can be used 'in reverse', to examine the wisdom of setting up a genetic improvement program for hatchery and production sectors of specific sizes. Also, it can be easily adapted to programs with other species. Note that in the model, the undiscounted return is equal to: $R = (Mkt)(gg/yr) = (Mkt)[(i_F)(\sigma_I) + (i_M)(\sigma_I)]/(gi_F + gi_M)$, so any proportional change in the contributing factors to R will have the same effect. This enables a quick (albeit only approximate) examination of many scenarios.

In Appendix C we present a summary of studies on the economic consequences of genetic improvement programs. The species and circumstances of those studies are very different from ours, which makes a rigorous comparison impossible. We found only one study with fish (Gjedrem, 1997). Overall, the studies report favorable economic outcomes from genetic improvement programs, but this could be biased due to non-reporting negative or less favorable cases.

Our results indicate that with elementary reproductive technology (Level 2 in Table 1), attractive EB and BCR values of over four million US$ and 8.5, respectively, can be obtained. Implementing available, proven, and inexpensive reproductive technology (Level 3 in Table 1) EB and BCR increased to over 32 million US$ and 60, respectively. Because of its feasibility and impact the latter level of reproductive efficiency should be the initial target in national genetic improvement programs, with a view to upgrading to Level 4 (Table 1) as skills in hatcheries are enhanced.

Appendix A

Table A1
Summary of studies on the female reproductive potential of Nile tilapia

References	No. of eggs per gram of female	Range of spawning interval (mean)
Gunasekera et al. (1996)	4.0	16–30 (18)
De Graaf et al. (1999)	6.0	
Al Hafedh et al. (1999)	6.8	
Bhujel et al. (2001)	7.3	
Campos-Mendoza et al. (2004)	6.6	
Perterson et al. (2004)	4.6	
Average	6.0	
	No. of fry per gram of female	
Watanabe and Kuo (1985)	8.4	17–31 (22)
Santiago et al. (1988)	8.0	
El-Sayed et al. (2003)	10	7–39 (20)
Ridha and Cruz (2003)		25–38 (27)
Biswas et al. (2005)	6.0	
Osure and Phelps (2006)	8.2	
Average	8.0	
Overall mean	7.0[A]	21.8

Watanabe and Kuo (1985): average fry production per gram of female at various levels of salinities: 0, 5, 10, 15 and 32 ppt in laboratory aquaria.

Santiago et al. (1988): across diets containing 0, 20, 40 and 80% leucaena leaf meal.

El-Sayed et al. (2003): average spawning performance of females fed different crude protein levels (25, 30, 35 and 40%) and reared at three levels of salinities (0, 7 and 14 ppt).

Biswas et al. (2005): average number of eggs per gram of female exposed to different photoperiods over three spawnings.

Osure and Phelps (2006): mean of Egypt, Ivory Coast, Sagama and Lake Victoria strains.

Gunasekera et al. (1996): average of three different protein levels (10, 20 and 35% over four spawnings).

De Graaf et al. (1999), Al Hafedh et al. (1999), Bhujel et al. (2001), Campos-Mendoza et al. (2004) are adapted from Perterson et al. (2004).

[A]Example calculation: assume that the average body weight of females at spawning is 250 g, that the spawning interval is three weeks, and the number of successful spawnings per female is 10 times per year. The total number of fry produced per female per year would be $250 \times 7 \times 10 = 17,500$. If survival rate of fry to harvest were 60%, there would be 10,500 fish for slaughter per female per year.

Appendix B

Table A2
Phenotypic and genetic parameters for harvest weight (W), survival rate (S) and feed intake (FI)

	W (g)	S (%)	FI (g)
Mean	300	85	400
h^2	0.3	0.08	0.25
σ_P	90	35.7	120
Phenotypic (above) and genetic (below) correlations			
W		0.2	0.85
S	0.2		0.3
FI	0.85	0.3	
Common environmental effects and correlations			
c^2	0.15	0.1	0.15
W			
S	0.6		
FI	0.85	0.6	

Appendix C

Table A3
Summary of economic appraisal studies of animal genetic improvement studies

References	Species	Country	Benefits	Costs	Benefit/cost ratio
Wickham et al. (1977)	Diary cattle	New Zealand	11.326×10^6	3.282×10^6	~4

Table A3 (continued)

References	Species	Country	Benefits	Costs	Benefit/ cost ratio
Morris (1980)[A]	Sheep	New Zealand	732	200	~4
Morris (1980)[A]	Beef cattle	New Zealand	720	400	~2
Mitchell et al. (1982)[A]	Pig	Great Britain	100×10^6	2×10^6	50
Atkins (1993)	Merino sheep	Australia	3500		
Greeff (1997)[A]	Merino sheep	Australia	500,000	60,000	8
Gjedrem (1997)	Salmon	Norway	45×10^6	3×10^6	15

[A]Discounting applied (5 to 10%).

Costs and benefits in local currency of respective countries (NZ $ in New Zealand, AUD$ in Australia and Pounds in Great Britain).

Wickham et al. (1977): estimates in 1974–1975 from the national herd of 2 millions dairy cattle.

Morris (1980): cost and net returns for a flock of 200 ewes or cows in 1979–1980. Average gain per ewe or cow per year is $ 1.

Mitchell et al. (1982): annual cost to benefit ratio was estimated from the genetic improvement program for six economically important traits over 15 years (1975 to 1980) in Great Britain.

Atkins (1993): selection on greasy fleece weight and fibre diameters (flock size of 1000 breeding ewes and 800 adult wethers). Predicted benefits over 30 years.

Greeff (1997) assumed that only annual cost was from buying 300 rams. Annual benefit was estimated from a commercial herd of 40,000 animals.

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