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Performance of the Genetically Improved Farmed Tilapia (GIFT) Strain Over Ten Generations of Selection in Malaysia

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ABSTRACT

A selective breeding programme of Nile tilapia (*Oreochromis niloticus*) based on a fully pedigreed population of the GIFT (Genetically Improved Farmed Tilapia) strain has been carried out using Best Linear Unbiased Prediction (BLUP) method for genetic evaluation and selection. Two lines were created from the 2002 progeny; one selected based on high breeding values (selection line) and another one was selected for average breeding values (control line) for live weight (LW). The estimate of heritability for live weight at harvest was 0.24 ± 0.031, indicating that there is still abundant genetic variation and scope for further genetic improvement. The accumulated response was 107% in the latest generation of 2011, averaging 11.9% per generation. It can be concluded that although the selection programme in the nucleus of the GIFT strain in Malaysia resulted in significant improvement in harvest weight, there still exists an abundant genetic variation thus providing the scope for further enhancement in performance of this population.

Keywords: Nile tilapia, GIFT strain, selective breeding, BLUP, heritability, selection response

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INTRODUCTION

Genetic improvement has the potential to improve the productivity of cultured aquatic species (Gjedrem, 1998, 2000; Hulata, 2001). The Genetically Improved Farm Tilapia (GIFT) strain is an example where selective breeding has resulted in a

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high quality strain of fish for freshwater aquaculture. The strain was developed through a collaborative research programme between The WorldFish Centre, the Institute for Aquaculture Research, Norway (AKVAFORSK), Bureau of Fisheries and Aquatic Resources and Freshwater Aquaculture Centre (BFAR) of Central Luzon State University, Philippines in 1988 to 1997 (Bentsen *et al*., 1998; Eknath *et al*., 1993; Eknath & Acosta, 1998). A selection index combining information on individual, full sib and half sib live weights at harvest was used. The selection programme successfully resulted in an average response of 13% in growth rate and an accumulated response of 85% after six generations of selection (Eknath *et al*., 1998). Considering its fast growth and high yield, the GIFT strain was released in 1994 for an on-farm evaluation in Bangladesh, China, Thailand and Vietnam (ADB, 2005). In the Philippines, 70% of farmed tilapia is either GIFT strain or of GIFT- derived origin, whereas GIFT strain accounts for 46% of the total tilapia seed production in Thailand (ADB, 2005).

In Malaysia, tilapia (*Oreochromis* spp.) and catfish (*Clarias gariepinus*) are the major fish species for freshwater aquaculture. Aquaculture production of tilapia in Malaysia increased from 28,401 in 2005 to 38,642 tonnes in 2010, exhibiting 36% increase in its production during this period (DOF, 2005; 2010), valued approximately RM249 million. Due to the large-scale availability of diverse freshwater bodies such as lakes, reservoirs, ex-mining pools and irrigation canals, the potential for tilapia production in Malaysia is high. This species is widely cultured in ponds, cages and tanks, as well as in pen culture systems. However, most production is based on unimproved tilapia strains. Consequently, poor growth, high mortality, losses due to diseases and low economic return are quite common in tilapia grow-out farms. Therefore, in order to achieve sustainably high yields, a breeding programme to develop genetically improved tilapia strain seems imperative.

A selection programme using Best Linear Unbiased Prediction (BLUP) method for the estimation of genetic merit was implemented by the Department of Fisheries Malaysia (DOF) in collaboration with the WorldFish Centre. This collaborative programme provided opportunities for further improvement of the GIFT strain in Malaysia. To date, ten generations of a selection line (SL) and control line (CL) of GIFT strain have been produced and evaluated, and are maintained at the Aquaculture Extension Centre, DOF at Jitra, Kedah, Malaysia. The overall aim of the present study was to evaluate the performance of GIFT strain during the long-term selection programme in Malaysia. The specific objectives of the study were to: (i) examine the systematic fixed effects on growth performance traits, (ii) estimate genetic parameters for growth-related traits, and (iii) measure the direct response of the selection on harvest weight.

MATERIALS AND METHODS

The Genetic Lines

The initial population of the GIFT (Genetically Improved Farmed Tilapia) strain established in Malaysia was initiated using 63 full sib groups of 35 fish each, which were progenies from single pair-mated parents (i.e., 63 males each mated to a different female) provided by the GIFT Foundation International Inc., Philippines. They were used as the base population for the present genetic improvement programme. The fish were reared until they reached an average live weight of about 250 g before mating was initiated. A mating design to produce full and half sib groups of progeny was conducted by using hapas, where a male was allowed to mate with two different females in each mating hapa. The mating produced progenies in 2002. Two lines were formed from the progenies; one selected for high breeding value for live weight (selection line, SL), and another for average breeding values (control line, CL). The number of sires, the number of dams and the number of progeny harvested in each spawning season and line are shown in Table 1. Best Linear Unbiased Prediction (BLUP) procedures were used to estimate breeding values of all progeny in each generation. The full sib families and individuals within full sib families were then ranked on breeding values within each sex. Each male was

TABLE 1
Number of sires, dams and progeny, by spawning season and line.

Spawning Season	Line	Sire	Dam	Progeny
2002	Base Population	52	54	1684
2003	Selection	35	65	2560
	Control	19	19	1150
2004	Selection	54	84	3714
	Control	17	22	957
2005	Selection	42	76	1763
	Control	13	20	480
2006	Selection	49	88	3134
	Control	10	15	513
2007	Selection	41	71	4238
	Control	15	15	859
2008	Selection	52	76	2735
	Control	14	14	583
2009	Selection	51	69	2674
	Control	9	11	458
2010	Selection	52	70	2366
	Control	8	8	367
2011	Selection	55	66	3098
	Control	10	10	479
Total		598	853	33812

mated to two different females in the SL, whereas one male was mated to one female in the CL. The mate allocations in the SL were conducted by assigning the best available male from the best full sib family to mate with the best available female from the best family, and also the female from the second best family. As the intention was to keep low inbreeding rate (3% or less), the inbreeding coefficient of the potential progeny was checked. Matings resulting in greater inbreeding were rejected and another male and female combination was sought among families lower in rank. In each spawning season, mate allocation involved fifty or more sires. However, due to the death of females or failure to mate among some pairs, a few sires in the SL produced progeny from only one female. None of the parents used in each spawning season was reused in the next spawning seasons (i.e., generations were discrete).

Progeny Production and Performance Testing

Progeny Production

The production of families was conducted in one cubic meter breeding hapas installed in 0.05 ha pond according to the mating plan prepared for the SL (one male mated to two females) and CL (single pair mating) lines. Two weeks before mating, the male and female breeders were conditioned in separate cages (installed in breeding ponds). A total of 140 breeding hapas were used in each mating cycle. The female breeders were transferred into the breeding hapas before the males. Only the most 'ready to spawn' (Longalong *et al*., 1999) females were paired with the male in the hapa. After a week of mating, fertilized eggs were collected from the mouth of the female and immediately transferred to hatching jars. The date of spawning was recorded for each individual pair mated. The male was then paired to the second female in another hapa. The male and female breeders were mated again if they produced less than 200 fry. The breeders were not fed when the females were expected to spawn in order to prevent them from swallowing their eggs. The eggs that were collected from the female breeder's mouth were transferred into hatching jars made of fibreglass. The design and system of the jars acted as an artificial incubator (or artificial breeder's mouth) for the fertilized eggs with a constant flow through of filtered water to optimize the environment for the eggs. Meanwhile, the eggs from each female were stocked in the respective jar for three to five days until hatching. The hapa number was recorded on the jar for family identification. In order to ensure a good hatching rate, the water temperature was maintained in the range of 26^{o}C to 30^{o}C.

Rearing of Fry

The hatched fry from the incubators were transferred into the nursery hapas (1 m x 1 m x 1 m with 2 mm mesh size) according to their parents or family number at a density of 200 fry per cubic meter. The total live weight and quantity of fry were recorded before transferring them into the hapas. At least three replicates of nursery hapas

for each family were installed in the same pond to reduce environmental differences between families. They were reared for 21 days in the nursery hapas and then transferred into the bigger mesh size (8 mm) hapas (1 m x 1 m x 1 m) called B-net cages. The stocking density in the B-net was reduced to 120 fry per cubic meter. The purpose of using B-net was to allow better water circulation. Rearing in the B-net took another 21 days until the fry live weight reached 5 to 10 gm and were ready to be tagged. The complete procedure was repeated over ten generations. Fig.1 and Table 2 show the production summary and scheduled periods of reproduction over the generations.

Breeding Data

Data of body and reproduction traits were collected for each step of the breeding activity to estimate genetic parameters of the strain; beginning with the mating of breeders, egg collection, nursing of fry and tagging. The live weight of all breeders was recorded before and after mating. Recording was also done on the number of eggs per female breeder, number, total live weight and date of fry hatching, number of fry per nursery hapas and number of fry transferred and collected from B-net cages.

Progeny Identification (Tagging)

Accurate testing of the fish in farm environments requires individual or group identification. As the full and half sibs were placed in the various separate compartments until tagging time, maintenance of a fully pedigreed population was ensured. When the fingerlings reached an average weight of 5 g, twenty to one hundred individuals per family were randomly sampled, anesthetized using tricaine methanesulphonate (MS 222) solution (1 g per litre) and tagged.

The base population was identified using passive integrated transponder (PIT) tag. Twenty individuals per family were tagged before the culture trials. In the 2002 and 2003 spawning seasons, Floy® tags were used to tag 100 individuals per family. The third spawning season (2004) was marked with Floy® tags (100 individuals per family) and T-bar anchor tags (20 individuals per family). Due to the low retention rate of the Floy® and T-bar tag, PIT tags were used (70 individuals per family) in the fourth spawning season (2005) onwards. In all generations, the tag number, live weight (LW), body length (L), body depth (D) and body width (W) were recorded before stocking. The tagged fingerlings were pooled in a conditioning tank for two days without feeding before stocking in the test environments. Dead fingerlings were recorded and replaced by new ones from the respective family.

Testing Environments

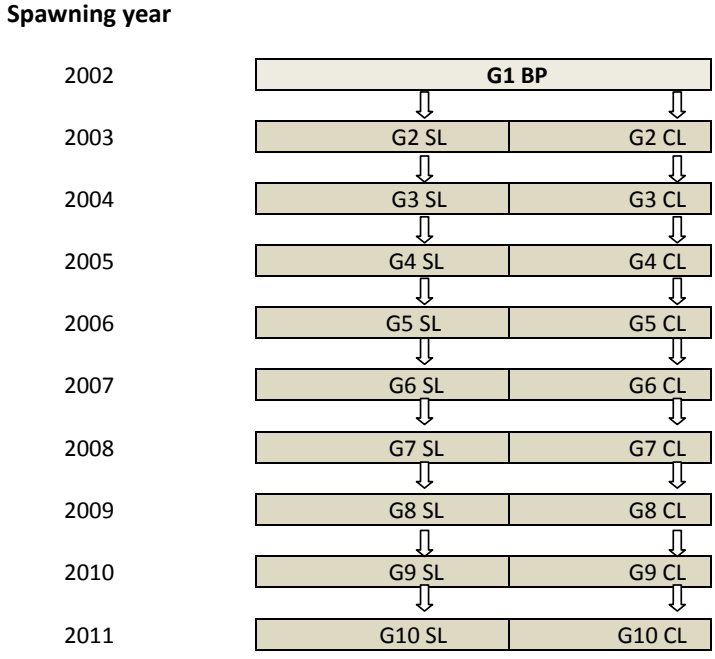
The tagged fish were grown either in cages or in earthen ponds. The cages were deployed in irrigation canal at Kodiang, Kedah, 22 km away from Jitra. Eight cages (3 m long by 3 m wide and 3 m depth) were positioned adjacent to each other, and the fish were assigned at random to

TABLE 2
Reproduction and management schedule

Activities	Spawning season									
	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
Mating	Feb - Mar 02	Jan - Feb 03	Nov 03 - Feb 04	Dec 04 - Feb 05	Nov 05 - Jan 06	Oct 06 - Mar 07*	Oct 07 - Feb 08*	Jan - Apr 09	Jan - Mar 10	Nov 10 - Apr 11
Nursing	Feb - Apr 02	Jan - Mar 03	Nov 03 - Feb 04	Dec 04 - Mar 05	Dec 05 - Feb 06	Nov 06 - Apr 07	Nov 07 - Mar 08	Feb - May 09	Jan - Apr 10	Dec 10 - May 11
Transfer to B-net	Mar - May 02	Feb - Apr 03	Dec 03 - Mar 04	Jan - Mar 05	Jan - Mar 06	Dec 06 - May 07	Dec 07 - Jun 08	Mar - Jun 09	Feb - May 10	Jan - Jun 11
Stocking	Apr - May 02	Mar - Apr 03	Feb - May 04	Mar - May 05	Mar - Apr 06	Feb - Jun 07	Mar - Jun 08	May - Jun 09	01-27 Jun 10	Mar - May 11
Grow-out	Apr - Nov 02	Mar - Sep 03	Feb - Sep 04	Mar - Sep 05	Mar - Sep 06	Feb - Aug 07	Mar - Nov 08#	May - Dec 09	Jun - Oct 10	Mar - Oct 11
Harvest	28 Oct - 13 Nov 02	18 Aug - 17 Sep 03	14 Aug - 22 Sep 04	18 Aug - 08 Sep 05	10 Aug - 04 Sep 06	14 Jun - 02 Aug 07	17 Sep - 05 Nov 08	10 Nov - 10 Dec 09	10-20 Oct 10	03 Aug - 10 Oct 11

** The prolonged mating period was due to insufficient families produced for the Control line and unfavourable climate.*
 # The prolonged grow out period and harvesting period were due to unfavourable weather condition, which affected the growth of the fish

them. The initial stocking density was 55 fish per square meter of surface water. The fish in both environments were fed an amount equivalent to 3 to 5% of their live weight on a commercial dry pelleted feed with 32% protein content twice a day (i.e. at 8.30 a.m and 5.00 p.m.). Water parameters (temperature, pH, dissolved oxygen) were monitored once a week. The culturing was conducted in cages and ponds in the spawning seasons of 2002, 2003 and 2004 whereas it was in earthen ponds only for 2005 and onward. The design was based on the findings of an earlier study which showed high genetic correlation (0.70 ± 0.113, Hamzah, 2006; Ponzoni *et al*., 2005 and 0.73 ± 0.092, Khaw *et al*., 2012) between environments leading to the conclusion that the live weight in ponds and cages were essentially the same trait. Earthen ponds (0.01 ha) located at the Aquaculture Extension Centre, DOF, Jitra, Kedah, were used for the experiments. The density in each pond was 3 fish per square meter of surface water. Water quality parameters (temperature, pH, dissolved oxygen and total ammonia) were also monitored once a week.



BP = base population, G = generation, SL = selection line, CL = control line

Fig.1: Schematic diagram summary of the selection and control lines produced in spawning season 2002 to 2011

Harvesting and Data Recording

Fish were harvested after 120 days of grow-out period. Those grown in cages were harvested by lifting up the net, transferred into aerated containers by using a scoop net, and later conditioned in brood stock tanks. A seine net was used for harvesting in the ponds by seining in three drags. The ponds were completely dried early the following morning. The fish were then transferred to the conditioning cages (3 m x 3 m x 1 m) installed in another pond. Data recording was done three days after conditioning. The individual tag numbers, sex, visual assessment of female sexual maturity, individual live weight (LW), body length (L), body width (W) and body depth (D) were recorded. Width and depth were measured at the mid-side of the fish, where they were the greatest. They were then transferred back to their respective conditioning cages and tanks until the estimation of their variance components and breeding values was completed. The age (in days) of each individual fish was computed based on the harvesting and hatching dates.

Statistical Analysis

Data Transformation and Standardization

The data were first examined using SAS (1990) to calculate simple statistics, remove anomalies (i.e. errors and outliers) and conduct a preliminary selection of the statistical models to be fitted. The procedure PROC MIXED (SAS Institute Inc., 1997) was used to estimate the fixed effects (spawning season, line, environment and sex) and the initial values of variance components, in which case sire (nested within spawning season and line) and dam (nested within sire, spawning season and line) were fitted as random effects. In a second phase, the computer programme ASReml was used (Gilmour *et al*., 2002). The models fitted included the fixed effects of spawning season (2002 to 2011), lines (SL and CL), environments (pond or cage) and sex, and their interactions.

Animal and dam (the non-genetic component) were fitted as random effects, whereas age of the fish was used as a covariate. The sub-set of effects fitted for different purposes varied and had been indicated in each particular case. This analysis enabled the estimation of breeding values (animal model) for all fishes, which were utilised in choosing the replacements for the SL and CL, and in estimating the genetic trend. The analysis also enabled the estimation of variance components, from which phenotypic and genetic parameters were calculated. Once the breeding values were estimated, all the fish in the respective family were ranked according to their estimated breeding values. Selection of brood stocks and mate allocation were based on the estimated breeding values of individuals and their relations to other animals in the pedigree.

Estimation of Phenotypic and Genetic Parameters

The ASReml programme (Gilmour *et al*., 2002) was used for variance component estimation. Spawning season, line, sex,

environment and their interactions were fitted as this was the model resulting in the greatest log likelihood value. Age at harvest was included as a covariate. The availability of a complete pedigree in the population enabled fitting a random animal model. Dam was fitted as another random effect, but solely accounting for the environmental effect on the progeny, without a genetic structure. In this case, the dam variance component (σ^2_D) is a combination of the maternal effect and the common environment (so $\sigma^2_D = \sigma^2_{M\_Ec}$) to which full sibs are exposed early in life (that is, while being hatched and while in the nursing and rearing hapas).

The animal variance component provided the estimate of the additive genetic variance (σ^2_A), whereas the phenotypic variance was estimated from the sum of all variance components ($\sigma^2_P = \sigma^2_A + \sigma^2_D + \sigma^2_E$). The heritability ($h^2$) was computed as the ratio between the additive genetic and the phenotypic variances ($h^2 = \sigma^2_A/\sigma^2_P$). The maternal and common environmental effect (c^2) was calculated as the ratio between the dam variance component and the phenotypic variance ($c^2 = \sigma^2_D/\sigma^2_P$ or $\sigma^2_{M\_Ec}/\sigma^2_P$). The data on LW were transformed to square root in all analyses to improve the distribution of residuals.

Response to Selection

The progeny resulting from the 2002 spawning season were selected as parents of the next generation in two different ways, to create the SL and to continue the base population as the CL. The parents for the SL were selected from among those with the greatest breeding values whereas the parents of the CL were selected among those with breeding values as close as possible to the average of the population. Inbreeding was restricted by avoiding mating of full sibs, half sibs or cousins. This mating strategy was applied to ensure the least possible inbreeding coefficient in the progeny. Furthermore, the effective population size in each generation could be maintained at a satisfactory level for sustainability of the selection programme (Ponzoni *et al*., 2011). The same procedure was followed to produce the subsequent generations throughout the programme. Estimation of the genetic change in LW was calculated using two different methods: (i) comparing the estimated breeding values for LW between the progeny of the Selection line in two spawning seasons, and (ii) comparing the estimated breeding values of the SL and CL in progeny of the same spawning season.

RESULTS

Statistical Analysis

Statistical analyses were carried out using univariate model where the detailed analyses of selection response for LW at harvest of the ten generations bred in Malaysia from 2002 until 2011 are presented in Tables 3 through 6.

Descriptive Statistics

The fish were harvested at average age of 238 days with the mean weight of 214.9 g. Coefficient of variation in LW and age at harvesting were generally greater in the

earlier spawning seasons than in the later seasons (Fig.2 and Fig.3).

Fixed Effects

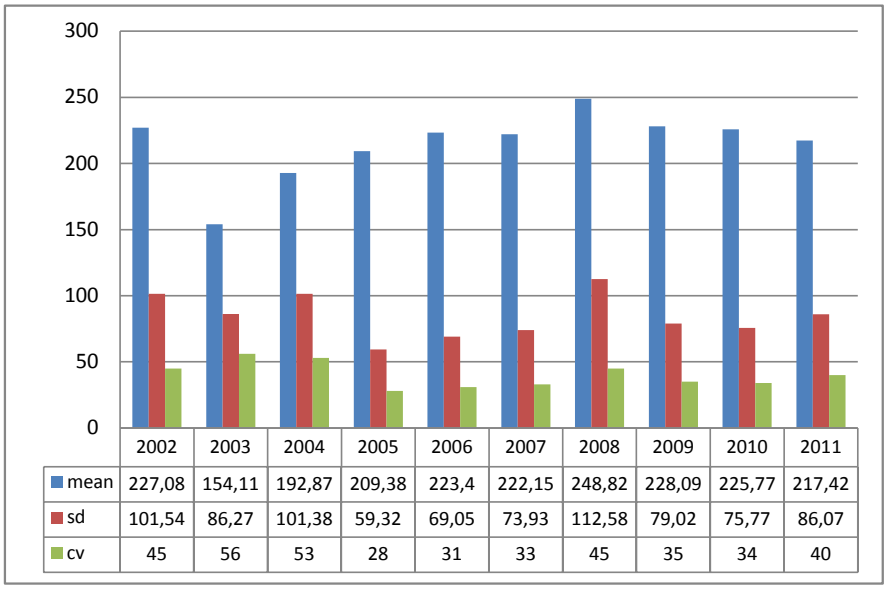
Table 3 shows the analysis of variance for $LW^{0.5}$. All effects fitted in the analysis of variance were statistically significant. The significant difference between lines suggests that there was response to selection. The significant spawning season by line by sex interaction (SS*L*S) can be explained by the fact that the between line difference in both males and females increased after each generation.

Heritability and Common Environmental Effects

Table 4 shows the estimates of variance components, heritability and maternal common environmental effect. The results indicate the presence of additive genetic variance and maternal common environmental effect in the population. The heritability for LW was moderate while the maternal common environmental effect was large.

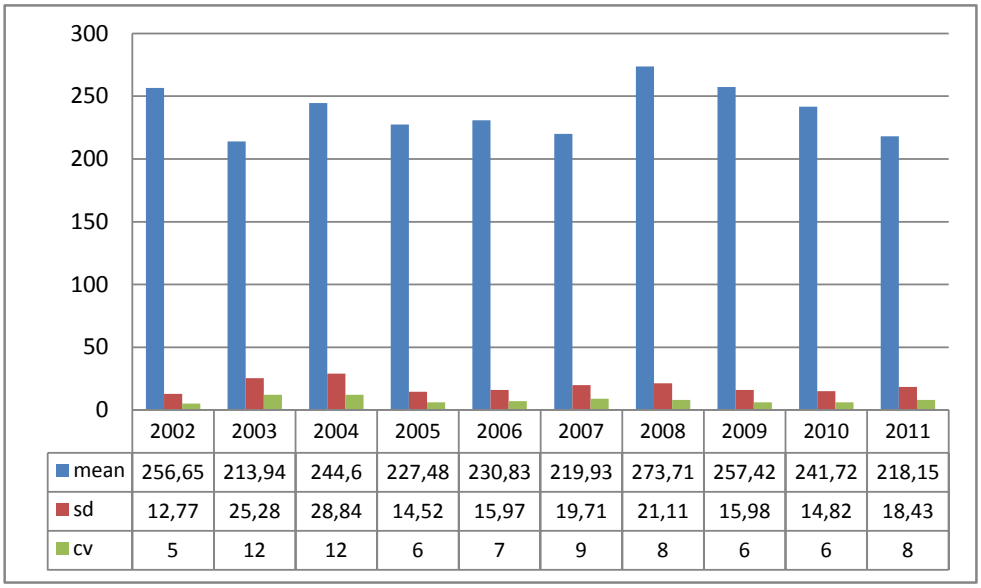
Response to Selection

The selection response in $LW^{0.5}$ during the ten generations was expressed in three different ways, namely, in actual units, as a percentage of the mean, and in genetic standard deviation units (Tables 5 and 6). Response to selection was estimated by using two methods. In the first method, the estimated breeding values were compared in consecutive generations. The second method involves the comparison of the estimated breeding values between the SL and CL in each spawning season. There was continued



	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
mean	227,08	154,11	192,87	209,38	223,4	222,15	248,82	228,09	225,77	217,42
sd	101,54	86,27	101,38	59,32	69,05	73,93	112,58	79,02	75,77	86,07
cv	45	56	53	28	31	33	45	35	34	40

Fig.2: Mean, standard deviation and coefficient of variation of LW (g) at harvesting



	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
mean	256,65	213,94	244,6	227,48	230,83	219,93	273,71	257,42	241,72	218,15
sd	12,77	25,28	28,84	14,52	15,97	19,71	21,11	15,98	14,82	18,43
cv	5	12	12	6	7	9	8	6	6	8

Fig.3: Mean, standard deviation and coefficient of variation of age at harvesting

TABLE 3
Analysis of variance for $LW^{0.5}$: Tests of fixed effects using PROC MIXED.

Effects	F Value	Prob. > F
Spawning Season (SS)	29.22	< 0.0001
Line (L)	22.34	<0.0001
Sex (S)	45.28	< 0.0001
Environment (E)	7.80	0.0052
SS*L*S	3.86	<0.0001
Age (SS, S, E)	152.32	< 0.0001
Residual Variance	2.8313	

***Remark**: This is the model with the best fit statistic (BIC: 84709.7). The random effects fitted were sire within spawning season and line, and dam within sire, spawning season and line.*

TABLE 4
Variance components, heritability and maternal common environment effect for $LW^{0.5}$.

Parameter	REML Estimate
Additive genetic variance (σ^2_A)	1.60
Maternal and common environmental variance ($\sigma^2_D = \sigma_{M\_Ec}$)	2.71
Phenotypic variance (σ^2_P)	6.58
Heritability (standard error) [h^2 (s.e.)]	0.24 (0.0311)
Maternal common environment (standard error) [c^2 (s.e.)]	0.41 (0.0169)

TABLE 5
Response to selection estimated by comparing the estimated breeding value for live weight (LW) between progeny from selection line of two subsequent spawning seasons

Method (between spawning season)	Model (effects)	Selection Response ($LW^{0.5}$)[A]		
		Actual units ($g^{0.5}$)	%	Genetic Standard Deviation Units (Actual/σ_A)
2002 and 2003	Fixed: SSxLxSxE	1.060	8.09	0.838
2003 and 2004		0.954	8.08	0.754
2004 and 2005	Covariate: Age at harvest (SS, L, S, E)	0.852	7.22	0.673
2005 and 2006		0.647	5.48	0.512
2006 and 2007	Random: spline(age_hv), uni(sex,2), animal and DAM	0.812	6.88	0.642
2007 and 2008		0.518	4.39	0.409
2008 and 2009		0.587	4.97	0.464
2009 and 2010		0.559	4.73	0.442
2010 and 2011		0.604	5.12	0.478

[A] Actual units are $LW^{0.5}$ difference in mean breeding values for methods (i) and (ii); percentage refers to actual units, in relation to the least squares means of $LW^{0.5}$ for the control population ($11.8023 g^{0.5}$); Genetic standard deviation equals the square root of the additive genetic variance in Table 4 ($_A$ = $1.2649 g^{0.5}$).

response over the period examined, as well as good agreement between the two methods used (55.85% vs 53.77% for the first and second methods, respectively).

DISCUSSION

Heritability

The heritability for $LW^{0.5}$ (0.24) was moderate. This estimate is in good agreement with those reported by Charo-Karisa *et al*. (2005), Gall and Bakar (2002), Maluwa *et al.* (2006), Ponzoni *et al*. (2005), and Rutten *et al*. (2005) fitting an animal model to the data. However, higher values have been reported in studies where the heritability estimate was based on full sib analysis. For instance, Kronert *et al*. (1989) and Oldorf *et al*. (1989) report heritabilities of 0.65 and 0.51, respectively, from full sib analyses. The greater values are likely to be biased upwards due to effects common to full sibs other than additive genetic effects (e.g., environmental effects due to the separate rearing of the families in hapas until tagging, maternal effects and components of non-additive genetic effects common to full-sibs). Similarly, Bolivar and Newkirk (2002) also report a high heritability (0.56) in Nile tilapia selected for growth rate over twelve generations, possibly due to the fact that the maternal and common environmental effect (c^2) was not accounted for in the model fitted.

In other aquaculture species, heritability estimates have also been mostly reported for LW. Hetzel *et al*. (2000) reported that the average realized heritability for weight at six months of age of *Penaeus japonicus* was 0.24 whereas that of the common carp

TABLE 6
Response to selection estimated by comparing the estimated breeding value for live weight (LW) between progeny from control line and selection line of the same spawning season

Method (within spawning season)	Model (effects)	Selection Response ($LW^{0.5}$)[A]		
		Actual units ($g^{0.5}$)	%	Genetic Standard Deviation Units (Actual/σ_A)
2003	Fixed: SSxLxSxE	1.387	11.75	1.096
2004		2.395	20.29	1.893
2005	Covariate: Age at harvest (SS, L, S, E)	3.044	25.79	2.406
2006		3.548	30.06	2.805
2007		4.354	36.89	3.442
2008	Random: spline(age_hv), uni(sex,2), animal and DAM	4.826	40.89	3.815
2009		5.430	46.00	4.293
2010		5.904	50.02	4.667
2011		6.346	53.77	5.017

[A] Actual units are $LW^{0.5}$ difference in mean breeding values for methods (i) and (ii); percentage refers to actual units, in relation to the least squares means of $LW^{0.5}$ for the control population ($11.8023g^{0.5}$); Genetic standard deviation equals the square root of the additive genetic variance in Table 4 ($_A$ = $1.2649g^{0.5}$).

(*Cyprinus carpio* L.) was in the range of 0.31 to 0.41 (Vandeputte *et al*., 2008). In redclaw crayfish (*Cherax quadricarinatus*), estimates of realized heritibilities for harvest weight varied from 0.13 to 0.38 (McPhee *et al*., 2004). In addition to its great importance in the breeding objective, the high heritability for LW across species had justified its selection as the sole criterion in many breeding programmes. The focus on LW is also related to the current market practice that is based on whole live fish weight. Compared to other body trait measurements (length, depth and width), harvest weight is the most efficient criterion to improve overall performance of the fish (Nguyen *et al*., 2007), and the best predictor of fillet weight, a carcass trait of great importance in fish (Nguyen *et al*., 2010).

Maternal and Common Environmental Effects

The maternal and common environment effects (c^2) estimated from the dam variance component (0.41) was larger than other estimates reported in the literature. Ponzoni *et al*. (2005) reported a c^2 value of 0.15 whereas Rutten *et al*. (2005) and Maluwa *et al*. (2006) found c^2 value of 0.09 and 0.21, respectively. The lower c^2 reported by Rutten *et al*. (2005) could be attributed to the larger LW at harvest compared to this current study (609 vs. 215 g). The smaller size of fish at harvest in this study (200 to 400 g) is the mature size for mating and preferred by consumers in Malaysia. As the harvested size was small, the c^2 remains an important consideration in order to obtain unbiased estimation of parameters. Nguyen *et al*. (2010) noted that the maternal and

common environmental effects diminished with a longer grow out period and greater weight at harvest. Charo-Karisa *et al*. (2005) reported a high c^2 (0.61) for LW at 49 days. Vandeputte *et al*. (2002) also noted that estimates of c^2 effects in traits measured at early development stages often include large maternal effects. As the estimate of c^2 in the current GIFT breeding programme was high, this effect was included in the statistical model to estimate the genetic parameters. The high estimate of c^2 in the GIFT selection programme in Malaysia is related to keeping the full sibs together in their respective nursery hapas until reaching size for safe tagging (at 5 g on average). By then, they have been maintained in hapas for 60 days in order to record full pedigree information. However, practical attempts to reduce the c^2 value have been carried out by transferring the fry to larger mesh size hapas after a month of rearing period as well as by reducing the stocking density from 200 to 120 fry per hapa. This technique had abbreviated the rearing period before tagging and produced a uniform size fry. Therefore, the c^2 effect can be reduced by better management techniques, but the maternal effects could still remain due to the egg size and the mouth brooding nature of Nile tilapia (Khaw *et al.*, 2008). In general, genetic evaluation of growth related traits should account for common effects other than additive genetic effects in the statistical model (Johansson *et al*., 1993; Nguyen & McPhee, 2005; Roehe & Kennedy 1993).

A more uniform nursing environment provided to the fry before they reach the tagging size or by genotyping the fingerlings to ascertain parentage could also reduce c^2 (Fjalestad *et al*., 2003). Therefore, microsatelite marker techniques for genetic identification of parentage is one of the options since all the fry from different families can be cultured together in one pond until harvest. Thus, nursing at the fry stage in separate hapas could be eliminated. Ninh (2009) reported that maternal and common environmental effects were close to zero in communal rearing of common carp fry (*Cyprinus carpio*) using seven microsatellite loci for parentage assignment. Although genetic tagging could reduce the c^2, the application of this technique in fish improvement programmes should be weighed against the costs and its benefits.

Selection Response

The GIFT selection programme in Malaysia yielded about 55% of selection response. James (2007) showed that the selection response expressed as a percentage after square root transformation is a fraction 0.501 of that in actual units. This means that in actual units the response was of the order of 107% (an average about 11% genetic gain per generation). The responses were large enough to suggest that genetic change was being achieved and in the intended direction. This response to selection is comparable to the estimate reported by Eknath *et al*. (1998) for Nile tilapia and for Atlantic salmon (Kinghorn, 1983). For instance, the gain obtained in the Egyptian Nile Tilapia was 5.8% (Rezk *et al*., 2009), 6.6% in *Oreochromis shiranus* (Maluwa & Gjerde,

2007), 12.45%, 3% and 13.3% in Nile tilapia reported by Bolivar and Newkirk (2002), Basiao and Doyle (1999) and Gall and Bakar (2002), respectively. The genetic gain per generation achieved in the current breeding programme of GIFT in Malaysia was in line with Gjedrem's (2000) estimation of 10% to 20% genetic gain per generation in aquatic animals in general.

To date, there has been no evidence of any slowing down of the rate genetic gain in the GIFT population. This may be partly explained by the genetic variation assembled in the base population (sample of eight different Nile tilapia strains (Eknath *et al*., 2007) and the mating strategy to constrain the accumulation of inbreeding and maintain a relatively high effective population size (Ponzoni *et al*., 2010). The selection and mate allocation of fish can affect the genetic variance and consequently the genetic gain. The level of inbreeding in the latest generation of GIFT in Malaysia was 2.14%. FAO (1998) and Hall (2004) suggest a minimum effective population number of 50 whereas a range of 100 to 150 was proposed by Smitherman and Tave (1987). Bijma (2000) suggested values of 50 to 100, and added that with these values inbreeding can be contained and heritabilities maintained. The effective population in the GIFT population size in Malaysia was 88 (Ponzoni *et al*., 2010), above the critical number for maintaining the genetic variation, auguring well for selection response in future generations.

Results of this breeding programme reflected that a sustained improvement of harvest weight was achieved. Thus, the methodology adopted by GIFT breeding programme could be used as a guideline to initiate similar genetic improvement programmes for other important aquaculture species in Malaysia.

Since the gain achieved by selective breeding is permanent, the improved GIFT strain must be managed and disseminated for sustainable benefits. The estimated per capita annual fish consumption in Malaysia was about 56 kg in 2010 (Dasar Pertanian Negara ke-3, 2006) and the total consumption is increasing in concomitant with the growing population. Meanwhile, the declining fish catch from capture fisheries and overfishing has increased the gap between fish demand and supply. Hence, the use of genetically improved strains in aquaculture gains significance in order to bridge this gap and to supply the cheap protein food. As the GIFT strain performs well in both pond and cage culture environments (the main culture systems for tilapia) thus providing an attractive option for the Malaysian aquaculture industry.

CONCLUSION

Analyses of the GIFT breeding programme data collected over 10 years (2002-2011) in Malaysia indicated that there has been significant genetic improvement in harvest weight in this population. The GIFT strain is thus a valuable genetic resource for the aquaculture industry. Therefore, a systematic approach of brood stock management and dissemination should be implemented to ensure an effective use and

sustainability of this strain. Furthermore, the strain offers ample scope for further genetic improvement.

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