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Estimation of genetic change in the GIFT strain of Nile tilapia (*Oreochromis niloticus*) by comparing contemporary progeny produced by males born in 1991 or in 2003

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Abstract

Genetic change in the Genetically Improved Farmed Tilapia (GIFT) Nile tilapia (*Oreochromis niloticus*) was estimated by comparing the performance of the progeny produced from cryopreserved spermatozoa from the base population with that produced by freshly collected spermatozoa from the ninth generation. The comparison involved artificial fertilization of 13 males from each generation (base and ninth) with a random sample of 18 female brood stock. The progeny produced went through a 120 day grow-out period, after which live weight, standard length, body depth and survival were recorded. The estimated total genetic change in live weight was 64% over nine generations, or 7.1% generation. The genetic change was lower than the estimate reported by Eknath et al. [Eknath, A.E., Dey, M.M., Rye, M., Gjerde, B., Abella, T.A., Sevilleja, R., Tayamen, M.M., Reyes, R.A., Bentsen, H.B., 1998. Selective breeding of Nile tilapia for Asia. 6th World Congress on Genetics Applied to Livestock Production (vol. 27). University of New England, Armidale, Australia, pp 89–96.], but in the present experiment the time span included generations in which there was no selection. We conclude that GIFT is a superior Nile tilapia strain, from which farmers can benefit due to its fast growth rate. The improvement in the latter trait was achieved without any deterioration in survival rate, which has remained high.
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Keywords: Nile tilapia; *Oreochromis niloticus*; Genetic change; Repeat mating; Cryopreservation

1. Introduction

Tilapia is an African fish widely cultured in nearly 100 countries in the world (Romana-Eguia et al., 2004). It has become popular because it is easy to breed, hardy, tolerates a wide range of water quality, salinity and temperature, it has versatile food habits, and it is highly marketable and affordable (Pullin, 1985; Shelton, 2002). In the 1970s tilapia was labeled as the 'aquatic chicken' (Maclean, 1984) and recently it was dubbed "foodfish of the 21st century" (Shelton, 2002). Fitzsimmons (2000) claims that tilapia has the potential to become the world biggest aquaculture species in the coming decades.

Over 98% of the tilapia farming is outside the species' native African range (Shelton, 2002). Asian countries accounted for 80% of the total farmed tilapia production in 2004 (FAO, 2006). Mozambique tilapia (*Oreochromis mossambicus*) was the first tilapia species introduced to Asian countries, but due to its poor growth performance and early sexual maturation it was replaced by Nile tilapia (*Oreochromis niloticus*) in the early 1970s (Mair, 2002). Nile tilapia has become the principal species cultured in Asia and it accounts for about 80% of the total farmed tilapia production (FAO, 2006).

Due to economic pressures and market requirements, farmers have been forced to look for productive strains that efficiently utilize the resources in their production system. The Genetically Improved Farmed Tilapia, known as GIFT, was developed through a selective breeding program conducted from 1988 to 1997. The base GIFT population was established by crossing eight different strains of Nile tilapia, four sampled from Africa, and another four domesticated Asian stocks (Eknath and Acosta, 1998; Eknath et al., 1998). During five generations of

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Table 1
Number of sires, dams and number of progeny recorded at tagging (day 0), at 30, 60 and 90 days after tagging, and at harvest, by sire generation

Sire generation	Sires	Dams	0	30	60	90	Harvest
Base population	13	18	1144	1065	409	401	985
Ninth generation	13		1144	1013	527	479	943
Total	26	18	2288	2078	936	880	1928

Out of a total of 18 females, 10 were mated to two males, and eight to four males.

selection for growth performance in the Philippines, GIFT achieved between 12 and 17% of genetic gain in growth rate per generation (Eknath and Acosta, 1998; Eknath et al., 1998). However, Eknath et al. (1998) comment that the accumulated response based on these estimates did not agree with the results obtained when the comparison was made with progeny of founder stock (the former estimates were greater than the latter). The sixth generation of GIFT was introduced to Malaysia in 2002. During the phase of selection in Malaysia, GIFT experienced 10 to 15% gain per generation over five generations (unpublished data). Details about the GIFT introduction to Malaysia were reported by Ponzoni et al. (2005).

During the selective breeding work in the Philippines, cryopreservation of sperm samples collected from males of the founder stocks and subsequent generations was carried out. In this paper, we compare the performance of the progeny produced from using cryopreserved spermatozoa of the base population (generation zero produced in Philippines) with the progeny of freshly collected spermatozoa from the ninth generation produced in Malaysia (three generations after it was received from Philippines). The results of this comparison are reported for five sampling periods taking individual live weights, standard length and body depth, as well as survival between stocking and harvesting.

2. Materials and methods

2.1. The environment

The study was carried out at the National Freshwater Fisheries Technology Center (NFFTC), Bureau of Fisheries and Aquatic Resources (BFAR), located in the Science City of Muñoz, Nueva Ecija, about 152 km north of Manila, Philippines. The province of Nueva Ecija has two very distinct seasons; a wet season which lasts from May to November, and a dry season from December to April. Pond water temperatures range from 25° to 33.5 °C and from 23.5° to 36 °C in the wet and dry seasons, respectively.

2.2. The fish and data structure

The base population of GIFT was established following three rounds of matings. In the first one, eight strains of founder stock were used to produce purebred progeny to conduct a comparison among them and to estimate genotype by environment interaction (ICLARM, 1993). In the second one, progeny were produced in a complete 8×8 diallel crossing design in order to estimate the magnitude of heterosis or hybrid vigor (ICLARM, 1993). This was followed by a third round of reproduction of inter se matings of the progeny. The resulting progeny (born in 1991) were then considered the base population for GIFT. The frozen sperm used in this study was collected from the GIFT base population during the selective breeding program in the Philippines, and was cryopreserved during February and March 1995 when the base population fish were about four-year-old. The 'best' males for growth rate were sampled for this purpose from the base population. In order to conduct the comparison, 13 male progeny of the ninth generation with an average weight of 300 g were sent from Malaysia to Philippines in December 2004. The males sent from Malaysia were not the 'best' for growth rate (the best males were selected as potential breeders to produce the following generation in Malaysia). They were close to the average for all males that were available in that generation. The 18 female brood stock used in this study consisted of a random sample from stock available at BFAR-NFFTC (a mixture of the GET EXCEL strain developed by BFAR-NFFTC, a population that was being selected for cold tolerance, and fish derived from the 8th generation of GIFT). Because each female was mated to at least one male of each of the two generations there is no opportunity for any confounding between sire generation and female origin. All the brood stock (females and males) were identified with Passive Integrated Transponders (PIT tags). The data structure, including the number of sires, dams and progeny harvested at the end of experiment, by male parent generation (i.e. base population or ninth generation), is shown in Table 1.

2.3. Artificial fertilization

2.3.1. Collection of eggs

The females were checked for signs of pre-spawning behavior every morning. The readiness of the female to spawn was ascertained by the swelling of the genital papilla. Premature release of eggs by these females was avoided by holding the fish in a scoop net while preparing the experiment. Eggs from each spawning female (150–300 g) were stripped manually by applying a gentle downward pressure with the thumb across the abdomen in an anterior–posterior direction. The eggs collected in this way were kept in a covered petri-dish until required, one for each female.

2.3.2. Collection of sperm from the ninth generation males

The same procedure was used to collect sperm from males of both generations (1991 and 2003). In order to collect good quality sperm (without urine and fecal contamination), the bladder of each male was manually stripped of its urine and the genital area was dried with absorbent paper. A 100 µl capillary tube was held at the tip of the genital papilla to draw the sperm into the tube by capillary attraction. The collected sperm was transferred into labeled microcap vials, one for each male, and stored in a refrigerator at 4 °C.

2.3.3. Thawing of cryopreserved sperm from the base population

Males of the base population were randomly selected from the master list of cryopreserved sperm, giving preference to those with the greatest number of samples and good after freezing motility score. The frozen sperm was thawed by immediate transfer of the sample from a dewar to a plain water bath at a temperature of 40–41 °C, and shaken briskly for 8 s. The thawed sample was kept at 4 °C until used for fertilization.

Table 2
Number of observations, simple mean, minimum and maximum, standard deviation and coefficient variation (%) of live weight (g), standard length (cm), body depth (cm), age (days) at harvesting and survival

Variable		*n*	Mean	Min	Max	Standard deviation	Coefficient variation (%)
Live weight	Initial	2288	6.4	2	17	1.4	22
	30 days	2078	36.2	6	80	11.3	31
	60 days	936	74.9	13	153	24.5	33
	90 days	880	136.0	27	275	43.2	32
	Harvest	1928	162.7	37	385	55.7	34
Standard length	Initial	2288	5.5	3	8	0.4	8
	Harvest	1928	16.5	9	51	1.9	12
Body depth	Initial	2288	2.1	1	4	0.3	13
	Harvest	1928	6.9	4	10	1.0	14
Age at harvest		1928	212	200	227	7.3	3
Survival		2288	0.84	0	1	0.4	43

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Table 3
Analysis of variance of initial, 30 day, 60 day, 90 day and harvest live weight: tests of fixed effects using PROC MIXED

Effect	Initial		30 days		60 days		90 days		Harvest	
	F value	Prob.>*F*	*F* value	Prob.>*F*	*F* value	Prob.>*F*	*F* value	Prob.>*F*	*F* value	Prob.>*F*
Sex (*S*)									666.2	<0.0001
Environment (*E*)	2.4	0.1228	3.1	0.0788	21.0	<0.0001	0.5	0.4704	59.2	<0.0001
Sire Generation (SG)	0.01	0.9397	17.4	0.0011	28.0	0.0001	34.6	<0.0001	37.4	<0.0001
*S***E*									1.6	0.2145
*S** SG									7.1	0.0077
*E** SG	0.01	0.9368	2.9	0.0874	1.4	0.2380	0.7	0.4158	0.5	0.4995
Age at harvest									1.6	0.2119
Fertilization date	4.5	0.0337	5.1	0.0248	2.2	0.1371	0.1	0.7974		
Residual variance	1.528		97.086		425.94		1273.19		1567.03	

2.3.4. Fertilization

The eggs from each female were divided into several aliquots with 200–250 eggs each, and fertilized by adding 200 μl of sperm, followed by 400 μl of water to activate the spermatozoa. Each female was fertilized by sperm from either two males (one from the base population and one from the ninth generation) or four males (two from the base population and two from the ninth generation). The sperm from both males in the base population and males from the ninth generation was used to fertilize eggs collected from two different females. In summary, each female was mated to two or to four males, and each male was mated to two females. After fertilization, the eggs were rinsed with UV treated water several times and transferred to a round-bottom incubator jar. After the eggs hatched, they were transferred to a container with minimum water flow until the yolk sac was fully absorbed. The identities of the sire and dam were kept for each batch of fertilized eggs. The mating procedure resulted in the creation of full and half sib families.

2.4. Rearing of fry

Each full sib family (progeny of the same sire and dam) of free swimming fry was reared in a fine mesh hapa at 100–125 pieces per square meter. After 3 weeks, the fingerlings of each full sib family were transferred to a B-net hapa, and stocked at 50–55 pieces per square meter until they reached tagging size (3–5 g).

2.5. The grow-out system

The mating design resulted in 52 full sib families, 26 maternal half sib families and 26 paternal half sib families. The number of families from sires of both generations was equal. Forty-four progeny from each full sib family produced were individually marked with Floy® tags. After tagging, the fish were sent for communal rearing in two ponds (labeled as pond 1 and pond 2, 600 m^2 each) at 1.9 pieces per square meter. Full sib families were equally represented in both ponds. One month after stocking, the Floy® tags were replaced with PIT tags to avoid loss of data as the fish grew bigger (the retention rate of PIT tags is much greater than for Floy® tags). The fish were harvested after 120 days of culture.

Table 4
Live weight (initial, 30 days, 60 days, 90 days and harvest) least squares means for sire generation

Live weight	Sire generation	Least squares means (g) (s.e.)
Initial	Base	6.4 (0.2)[A]
	Ninth	6.4 (0.2)
30 days	Base	33.1_a (1.1)
	Ninth	39.7_b (1.1)
60 days	Base	64.6_a (2.6)
	Ninth	83.6_b (2.5)
90 days	Base	117.0_a (4.9)
	Ninth	152.4_b (4.8)
Harvest	Base	140.9_a (5.8)
	Ninth	185.5_b (5.8)

[A]Within each time of live weight measurement, means with a different subscript are significantly different ($P<0.05$).

2.6. Records

All the fish were weighed at tagging time (initial weight at 0 day), at 30 days after stocking, and at harvest (120 days after stocking). A sample of fish was also weighed at 60 and 90 days after stocking. Standard length, body depth and sex were also recorded during harvesting. Body depth was measured at the mid-side of the fish, in a dorsal-ventral direction, where the dimension was greatest. Age at harvest was computed by using the harvesting date and fertilization date. Survival during the grow-out period was calculated from the difference between the number of fish stocked and the number harvested.

2.7. Data analysis

2.7.1. Theory

Genetic change was estimated by what is commonly known as the 'repeat mating' method. It consists of a comparison of contemporary of progeny produced by sires of different generations and it provides a means of estimating genetic change without use of a control population (Dickerson, 1969; Rye and Gjedrem, 2005). In the repeat mating design, a random sample of dams needs to be assigned to the sires of different generations. In the resulting progeny only half of the genes is contributed by the sires, hence the total genetic change can be measured, as (Dickerson, 1969; James, 1987; Rye and Gjedrem, 2005):

$$\Delta g = 2\left(\overline{X}_{\text{new}} - \overline{X}_{\text{old}}\right)$$

Where, $\overline{X}$ is the mean of performance for progeny produced by the new and by the old sires.

2.7.2. Statistical analysis and model fitted

The data were analyzed using SAS software (SAS Institute Inc., 1990) and a small number of outlier data were deleted. We analyzed records for five live weights (initial, 30 days, 60 days, 90 days and harvest), standard length and body depth (at the time of taking initial and harvest weights), and also survival rate using PROC MIXED (SAS Institute Inc., 1997).

Table 5
Analysis of variance of survival: tests of fixed effects using PROC MIXED and PROC CATMOD

Effect	PROC MIXED		PROC CATMOD	
	F value	Prob.>*F*	Chi-square	Pr>ChiSq
Environment (*E*)	6.0	0.0143	6.6	0.0100
Sire Generation (SG)	2.3	0.1511	0.3	0.5752
*E** SG	15.8	<0.0001	11.7	0.0006
Residual variance	0.128		24.4	0.4394

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Table 6
Survival least squares means and standard errors (s.e.) for sire generation

	Sire generation	Least squares means (s.e.) (g)
Survival	Base	0.86 (0.02)
	Ninth	0.83 (0.02)

Table 7
Analysis of variance of initial and final standard length: tests of fixed effects using PROC MIXED

Effect	Initial		Final	
	F value	Prob.>*F*	*F* value	Prob.>*F*
Sex (*S*)			408.9	<0.0001
Environment (*E*)	12.4	0.0004	0.0	0.9667
Sire Generation (SG)	0.9	0.3491	31.3	<0.0001
*S***E*			2.5	0.1144
*S**SG			0.2	0.6922
*E**SG	0.8	0.3750		
Age at harvest			2.0	0.1550
Fertilization date	6.8	0.0091		
Residual variance	0.135		2.343	

The statistical models for initial weight, 30, 60 and 90 day weights, standard length and body depth included environment (pond 1 or 2), sire generation (base population or ninth generation) and their two-way interaction as fixed effects. Sire (nested within sire generation), dam, and the interaction between sire and dam were fitted as random effects. In all models, fertilization date was fitted as covariate.

Measurements taken at harvest time (live weight, standard length and body depth) included sex in the model, as well as environment, sire generation and the two-way interaction between sex and the other two fixed effects. Instead of fertilization date, age at harvest was fitted as covariate. Note that because in all instances records were taken within one or 2 days, the use of 'fertilization date' or of 'age at measurement' yield the same result, the latter variable being equal to the former plus a constant. The same random effects as for the other traits were fitted for the traits measured at harvest time.

The model fitted to survival rate was the same as for initial weight, but without fertilization date as a covariate. Because survival rate is dichotomous trait it was also analysed using the procedure CATMODE in SAS (1990), which is specifically for categorical traits. Survival was coded as 0 for a dead fish, and as 1 for a live fish at harvest time.

3. Results

3.1. Descriptive statistics

The number of observations, simple means, minimum and maximum, standard deviation and coefficient of variation for all the body measurements, age at harvest and survival are presented in Table 2. Live weights measured at 60 days and 90 days after stocking are from sampling that consisted of about 40% of the initial number of fish stocked. The survival rate was inferred from the number of fish stocked and the number harvested.

Table 8
Analysis of variance of initial and final body depth: tests of fixed effects using PROC MIXED

Effect	Initial		Final	
	F Value	Prob.>*F*	*F* value	Prob.>*F*
Sex (*S*)			723.2	<0.0001
Environment (*E*)	16.9	<0.0001	30.3	<0.0001
Sire Generation (SG)	3.1	0.1018	42.7	<0.0001
*S***E*			0.5	0.4757
*S**SG			1.2	0.2648
*E**SG	27.3	<0.0001		
Age at harvest			2.4	0.1188
Fertilization date	9.6	0.0019		
Residual variance	0.0459		0.464	

Table 9
Standard length (initial and harvest) least squares means for sire generation

Standard length	Sire generation	Least squares means (cm) (s.e.)
Initial	Base	5.5 (0.05)[A]
	Ninth	5.5 (0.05)
Harvest	Base	15.8_a (0.21)
	Ninth	17.1_b (0.21)

[A]Within each time of measurement, means with a different subscript are significantly different ($P<0.05$).

3.2. Estimation of genetic gain

Table 3 shows the statistical significance for the fixed effects and the covariates fitted to the five live weights. Analysis of variance of live weights revealed that from 30 days after stocking onwards, there were significant differences between sire generations in live weight. The interaction between sex and sire generation for harvest weight was also statistically significant. This was because the difference between sexes (males were heavier than females) was greater (54 g *vs.* 44 g) for the progeny produced by sires from ninth generation than for progeny of those from the base population, and not due to between sex rank reversal. Table 4 shows the least squares means for live weights by sire generation. The genetic change estimated from the difference in least squares means of harvest weight, between the progeny of base population and ninth generation sires was 64%.

Tables 5 and 6 show the results of the analysis of survival rate. The results obtained from PROC Mixed and CATMODE were in agreement. No significant differences were observed between the progeny of the base population and ninth generation sires. There was a significant sire generation by environment interaction. This was due to a reversal of the ranking for survival in the two ponds. Survival was greater for the progeny of sires from the Base population in one pond, whereas the opposite was true in the other pond.

The analysis of variance tables for standard length and body depth are presented in Tables 7 and 8, respectively. The sire generation effect was highly significant for both harvest measurements. The least squares means (Tables 9 and 10) show that progeny produced by sires from generation ninth were longer and deeper compared with those produced by sires from the base population.

4. Discussion

The total genetic change in harvest weight for GIFT between the base population and the ninth generation was 89.2 g (i.e.

Table 10
Body depth (initial and harvest) least squares means for sire generation

Body depth	Sire generation	Least squares means (cm) (s.e.)
Initial	Base	2.0 (0.04)[A]
	Ninth	2.1 (0.04)
Harvest	Base	6.5_a (0.09)
	Ninth	7.3_b (0.09)

[A]Within each time of measurement, means with a different subscript are significantly different ($P<0.05$).

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twice 44.6 g), or 64%. If we compute the genetic change per generation from this latter figure, for nine generations, is only 7.1%, considerably lower than the estimate reported by Eknath et al. (1998). However, for the reasons we detail below, ours may be an underestimate of the true genetic gain, whereas Eknath's may be an overestimate.

After five generations of selection, Eknath et al. (1998) reported an annual genetic gain of 12–17%, which is considerably higher than our estimate for nine generations. Eknath et al. (1998) did not establish a separate control population and maintain it throughout these five generations, but rather, they recreated a new control in each generation by mating a sample of average individuals for that generation. There may have been inadvertent selection of the fish to be mated as controls, and sampling problems accumulated during the selection could have caused an over estimation of the genetic gain that reported by Eknath et al. (1998).

By contrast, our estimate of genetic gain may actually be biased downwards. Firstly, the frozen sperm was collected from the best growing males in the base population, whereas the sires used from the ninth generation were not the best (they were close to the average of that generation). Secondly, the formal GIFT selection program ended at the fifth generation, and there was no selection when matings were conducted to produce the sixth and seventh generations. The sixth generation was sent to Malaysia and was used there to establish the population now located in Jitra Aquaculture Extension Center, Kedah state. That means in between these nine generations, we have two in which no selection of superior individuals for growth rate or any other trait was conducted. If allowance were made for this when calculating genetic gain per generation, a figure (9%) closer to that reported by Eknath et al. (1998) would be obtained.

The genetic gain in actual units (cm) was greater for standard length than for body depth, consistent with the predictions made by Nguyen et al. (2007). The consequences of the genetic relation among body dimensions are discussed in detail in the latter paper. In practical terms, this means that, albeit at a slow rate, fish undergoing selection for live weight gradually became longer, relative to their body depth, with respect to those in the base population.

Note that the 64% of genetic change estimated for harvest weight in this study was achieved without any deterioration in survival rate.

5. Conclusion

The present study confirms that GIFT is a superior tilapia strain that has accumulated at least 64% of genetic gain in growth rate since the base population was established. Dey and Gupta (2000) predict that the adoption of the GIFT strain can improve the productivity and profitability of tilapia production in Asia, and that this would bring about lower fish prices, thus benefiting the lower income groups. In Africa, where very little has been done in terms of genetic improvement of Nile tilapia, one may safely assume that the productivity of the current stock is at the level of the GIFT base population or lower (Brummet et al., 2004). Hence, one may also safely assume that the introduction of GIFT to Africa would improve growth by at least 64%. This is not a trivial gain, and it could greatly benefit emerging aquaculture industries in many Sub Saharan African countries.

GIFT is also suitable for more demanding markets. Recent findings on flesh quality of GIFT compared with red tilapia in Malaysia indicate that GIFT has a very high acceptability by local consumers (Ponzoni et al., 2006; Khaw et al., 2006). Its reproductive rate, growth rate, survival, fillet yield and highly rated flesh quality, make GIFT a very attractive and promising strain capable in increasing production for domestic and export markets in developing countries.

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