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ScienceDirect
Aquaculture
Aquaculture 272S1 (2007) S38 – S46
www.elsevier.com/locate/aqua-online

Can sexual dimorphism and body shape be altered in Nile tilapia (*Oreochromis niloticus*) by genetic means?

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Abstract

The objective of this study was to estimate genetic parameters in GIFT (Genetically Improved Farmed Tilapia), especially focusing on the genetic correlation between trait expressions in both sexes and among measurements of body size. Body weight, length, depth and width data at harvest from 12,308 individuals, progeny of 232 sires and 340 dams, were analyzed by restricted maximum likelihood methods fitting a multi-trait animal model. To explore the genetic variation in sexual dimorphism the trait expressions in the two sexes were treated as if they were different traits. Heritabilities and maternal and common environment effects for all the traits were very similar in females and males. The genetic correlations between sexes for all traits were close to unity (0.91 to 0.96), indicating that there was no sex by genotype interaction. When treated as a single trait the heritabilities (±SE) for body weight, length, depth and width were moderate to high, ranging from 0.20 to 0.35 (±0.04 to 0.05). The maternal and common environment effects accounted for 16 to 24% of the variance. Genetic correlations among the four body measurements were highly positive (0.94 to 0.99), suggesting the existence of little or no genetic variation independent of each other. We concluded that there was no need to treat trait expressions in the two sexes as different traits in genetic improvement programs. Furthermore, that the relative dimensions of the body were essentially controlled by the same genes, but that continued selection for live weight would result in relatively longer and thinner fish because of the greater correlated response in length relative to width and depth.

Keywords: Nile tilapia; *Oreochromis niloticus*; GIFT; Sexual dimorphism; Selective breeding, Genetic parameters

1. Introduction

Sexual size dimorphism is pervasive in both terrestrial and aquatic animal species, primarily as a result from natural or sexual selection pressurizing differently on males and females due to their contrasting roles in reproduction or competition for resource utilization (Darwin, 1874; Lande, 1980). In all species, the phenotypic difference between sexes is closely related to the commercial value of the animal. Hence, understanding the genetic basis of sexual dimorphism in aquaculture species, specifically in tilapia in this study, is of particular importance. It could provide parameters to enable the design of more effective breeding programs and genetic evaluation systems. If the expression of body traits in both sexes were determined to a large extent by different genes, female and male expressions should be treated as different traits. In extreme cases this could call for the conduct of separate selective breeding programs for females and males.

There are studies in which an absence of genotype by sex interaction has been found (e.g. in beef cattle by Van

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doi:10.1016/j.aquaculture.2007.08.013

Vleck and Cundiff, 1998, and in pigs by Crump et al., 1997; Zhang et al., 2000). By contrast, other results suggest that male and female body weight should be treated as different traits in breeding programs for beef cattle (e.g. Lee and Pollak, 1997) or sheep (Näsholm, 2004). These apparently conflicting results could be due to limitations of experimental design and size, or to differences in the performance testing environments between females and males. For farmed aquaculture species, Kause et al. (2003) reported that heritability estimates for body weight were of similar magnitude in male and female rainbow trout, and the between sex genetic correlation for body weight was close to unity. In tilapia, Rutten et al. (2005) reported greater heritability values for females (0.35) than for males (0.18) across measurement periods, but estimates had a relatively high standard error. The genetic correlations between the sexes for body weight at different ages were very high and close to unity. Although the general pattern observed across species is that genotype by sex interaction is of little or no significance for growth related traits, much remains to be learnt about the genetics of sexually dimorphic traits, especially in fish.

In addition to size or weight of the fish, shape may be also of importance. For instance, deeper and wider fish may be perceived as having a greater amount of edible flesh than those that are longer and slimmer, and hence be more attractive to consumers.

In this paper we present results on the heritability and genetic correlation of body weight between sexes, as well as among body measurements determining fish shape (i.e. depth, width and length) in the GIFT strain. Because the genetic correlation between sexes and among body measurements were close to unity, we conclude that either changing the female to male body weight ratio or the shape of the fish by genetic means is unlikely to be effective. We also speculate on the outcome of different selection strategies.

2. Materials and methods

2.1. The genetic lines

The present selection and control lines originate from a long-term genetic improvement project of farmed tilapia (GIFT) conducted over the past 18 years (Eknath et al., 1993; Bentsen et al., 1998). The initial population established in Malaysia consisted of 63 full sib groups, each represented by 35 fish from the sixth generation of selection of the GIFT strain in the Philippines (Ponzoni et al., 2005). The founder stock was transferred in batches from the GIFT Foundation International Inc., Philippines, to Jitra Research Station in Kedah, Malaysia, where they were reared to an average body weight of about 250 g before mating was initiated. In 2002, the progeny of the first spawning season was produced in Malaysia, thus creating what we call the base population. Two lines were formed with the 2002 progeny, one selected on high breeding value for live weight (selection line), and another one selected for average breeding values (control line). A combined between and within family selection was practiced in both lines. The average proportion of selected animals was 6.6% in females and 3.8% in males. Note, however, that selection was on breeding values but not by truncation (due to inability to reproduce of some selected breeders we had to resort to selecting lower ranking ones). On average, each generation was the progeny of 70 dams and 46 sires for the selection line, whereas they were the progeny of 20 pairs (20 full sib families) for the control line. This design and experimental size were followed throughout the period during which the data reported here were collected (Table 1). Ponzoni et al. (2005) provide a description of the genetic origin of the fish.

2.2. Progeny production and performance testing

2.2.1. Preparation of ponds and breeding hapas

Breeding ponds (1000 m^2) were completely drained and allowed to dry for one to two weeks before liming and refilling with water at a level of 0.8 m in depth. Hydrated lime was applied at a rate of 100 g per square meter. A fine mesh screen net was used to cover the pond inlet to prevent the entry of predators into the pond. Prior to stocking of breeders, the breeding pond was fertilized with an inorganic fertilizer (triple super phosphate, TSP) at a rate of 30 kg per ha. Breeding hapas (fixed net enclosures made of polyethylene netting with joints in nylon threads) were then installed in the pond in rows, 1.5 m apart from each other, to enable water circulation. The standard size of a hapa used for breeding was 1 m (width) × 1 m (length) × 1 m (depth) with a mesh size of 2 mm. Production and maintenance of full sib families were carried out in these hapas.

2.2.2. Stocking, mating and progeny production

The production of progeny was conducted in separate 1 m^3 breeding hapas according to the mating plan prepared for the selection (one male mated to two females) and control (single pair mating) breeders. Before mating, the female and male breeders were conditioned in separate tanks for one week. The females were then transferred to the breeding hapas before the

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

Spawning season	Line	Sires	Dams	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
Total		232	340	12308

males. Due to aggressive mating behavior of males, the male breeders were anesthetized using beta dine disinfectant solution (10%) and their upper lip was removed in the manner described by Thodesen and Ponzoni (2004) before transfer to the breeding hapas. This prevented males from biting females, thus reducing mortality and increasing mating success.

In each mating cycle, a total of 140 breeding hapas was used. Once females were 'ready to spawn' (Longalong et al., 1999), they were paired with the males in a breeding hapa. After one week, fertilized eggs were collected from the mouth of the female and immediately transferred to hatching jars, and labeled with a unique code identifying the eggs' dam and sire. The jars are made of fiberglass and designed as artificial incubators for hatching the fertilized eggs. The collected eggs from each female were stocked in an individual jar, and they hatched after three to five days. During hatching, the water temperature was maintained between 26 °C and 30 °C. The date of spawning was recorded for each mating pair. After mating with one female, males from the selection line were paired to the second female in another hapa. Any female-male pair that produced less than 200 fry was re-mated. When spawning was expected to occur, the female breeders were not fed to prevent them from swallowing their eggs.

In order to minimize stress of breeders and fry, an anesthetic was applied before handling (Tricaine methanesulfonate (MS 222) solution (1 ppt) and clove oil (1 ppt)).

2.2.3. Progeny rearing and tagging

The hatched fry from the incubators were then transferred to nursery hapas (1 × 1 × 1 m with 2 mm mesh size) retaining their parents' identity, and they were nursed at a density of 200 fry per m^3. The total live weight and quantity of fry were recorded before moving them to hapas. All hapas were in the same pond to reduce environmental differences between families. The hapas were laid out in rows inside the pond. Each full sib family was stocked in three replicates, adjacent nursery hapas installed in a row of hapas. The row of hapas was filled as new families were produced. This systematic procedure helped to keep track of the stocking date and the age of the fry, and it made tracing families for tagging easier. After 21 days of rearing in the nursery hapas, fry were transferred to the bigger mesh size (~6 mm) hapas (1 × 1 × 1 m) called B-net cages, which allow better water circulation. The stocking density in the B-net was reduced to 120 fry per m^3. Rearing in the B-net hapas, which was also conducted in three replicates, took another 21 days until the fry reached a live weight of 4 to 8 g to be physically tagged.

Before tagging, fingerlings were anesthetized using MS 222 solution (1 ppt). Floy tags were used for the progeny of the first and second spawning seasons (2002 and 2003), and T-bar tags were tried for the third spawning season (2004). The retention rate of both Floy and T-bar tags were, however, not satisfactory in these seasons. Therefore, PIT (Passive Integrated Transponder) tags are being used from the 2005 spawning season onwards. PIT tags were implanted in the visceral cavity of the fish, using a standard syringe (or implanter). All the tagged fingerlings (100 individuals per family in generations one, two and three, and 40 individuals per family in generations four and five) were pooled in a conditioning tank for two days without feeding before stocking in the test environments. Dead fingerlings were recorded and replaced by other fingerlings from the same family. The tag number and body measurements (weight, depth, length, width) of each fish were recorded before growing-out.

2.2.4. Testing environments

After tagging the fish were grown out in both cages and earthen ponds, which constitute the two main production environments in Malaysia. The cages were located in an irrigation canal at Kodiang, Kedah, 22 km away from Jitra station. Eight (3 m long by 3 m wide) cages adjacent to each other were established, and the fish were assigned at random to these cages. The initial stocking density was 55 fish per m^2 of surface water. The fish were fed (twice daily, at 8.30 am and 5.00 pm) a commercial pellet with a 32% protein content, at the rate of 3–5% of body weight. Water quality (temperature, pH, dissolved oxygen) were monitored once a week.

The earthen pond was 0.1 ha large, located at Jitra station. The initial density in the pond was three fish per m^2 of surface water. The feeding, culturing and management practices, and water monitoring procedures were the same as used for the cages.

2.2.5. Harvesting and data recording

Following a grow-out period of approximately 120 days, all the test fish in cages and pond environments were harvested. In cages, fish were captured by lifting up the net, transferred into aerated tanks by using a scoop net, and transported to Jitra station where they were conditioned in tanks. A seine net was used in the ponds, seining in three drags. To complete the harvest, the ponds were completely dried the following day, early in the morning. All the pond fish were then stocked in conditioning cages (3 m × 3 m × 1 m) installed in a different pond.

After conditioning the fish in tanks or cages for two or three days, individual measurements were taken of live weight, standard length, body width and body depth. Body width and depth were measured at the mid-side of the fish. The tag number and sex of each fish were recorded, and a visual assessment of female sexual maturity was made. When data recording was completed, the breeders were returned to their respective conditioning cages.

2.3. Statistical analyses

2.3.1. Determination of fixed and random effects

To identify systematic effects of environmental factors related with the phenotypic performance of body traits (harvest weight, standard length, body width and body depth), we conducted general linear model analyses (SAS Institute Inc., 1997). Selection line, production environment, sex and spawning year were fitted as fixed effects. There were significant differences in all traits ($P < 0.001$) between selection lines (selection and control), production environments (cages and ponds), sexes (males and females) and spawning years (2002, 2003, 2004 and 2005). Age at harvest showed a linear

Table 2
Basic statistics for live weight, length, depth and width in female and male tilapia

Traits	Sexes	Records (number)	Mean	SD	CV (%)
Weight (g)	Female	6582	168.3	82.35	48.9
	Male	5726	206.8	99.73	48.2
	All	12308	188.9	94.02	59.8
Length (cm)	Female	6582	16.2	2.87	17.7
	Male	5726	17.3	3.01	17.4
	All	12308	16.8	2.99	17.8
Width (cm)	Female	6582	6.7	1.34	20.0
	Male	5726	7.3	1.43	19.7
	All	12308	7.0	1.42	20.2
Depth (cm)	Female	6582	3.0	0.72	23.8
	Male	5726	3.2	0.67	21.0
	All	12308	3.1	0.70	22.4

relationship with body traits, and thus was fitted as a linear covariate in the model. In a further analysis, we examined all the possible interactions among these effects and discarded those which negligibly contributed to goodness of fit in the model. Regarding terms in the random structure, we assessed significance of the additive genetic, and maternal and common environmental effects (c^2) by using likelihood ratio test (LRT). The LRT is the natural logarithm of the ratio between the full and reduced model multiplied by the coefficient of −2. Asymptotically, the LRT is approximately distributed as a chi-square with the number of degrees of freedom equal to the difference in number of parameters fitted between the two models. Alternatively, variance component estimates for both the additive genetic and c^2 effects were greater than 2 times their standard errors, indicating that the effects to be significant (Gilmour et al., 2002).

2.3.2. Estimation of (co)-variance components

Variance and covariance components of the body measurements were estimated using average information algorithm-restricted maximum likelihood method applied to a multi-trait mixed model in ASReml (Gilmour et al., 2002). First, measurements in females and males were considered as one trait, and the model included all the significant fixed and random effects described in Section 2.3.1. Second, the female and male expressions of the body measurements were treated as different traits, and analyses were carried out separately in females and males in order to examine whether there were differences between sexes. The model was basically as described above, except that the effect of sex was dropped. In these analyses, genetic correlations between the expression of body traits in females and males were estimated through genetic relationships in the full pedigree. There were no environmental covariances between the homologous traits since they were phenotypically measured on different animals.

We tested whether heritability, maternal and common environmental effects and correlation estimates were significantly different from each other, or zero, and whether the genetic correlations between sexes were significantly different from one by using z-scores:

$$z = \frac{x_i - x_j}{\left(\sigma_i^2 + \sigma_j^2\right)^{0.5}}$$

where x_i and x_j are the estimates of heritability, maternal and common environmental effects, or genetic correlations for the two traits (or the two sexes), and σ_i and σ_j are their respective standard errors. Both x_j and σ_j were set to zero or one when we tested whether an estimate was significantly different zero or one, respectively. The resulting z-scores were then tested against a large sample normal distribution.

2.4. Modeling changes in body traits

Selection index theory using the genetic parameter estimates in both sexes from the present study (summarized in Appendix A)

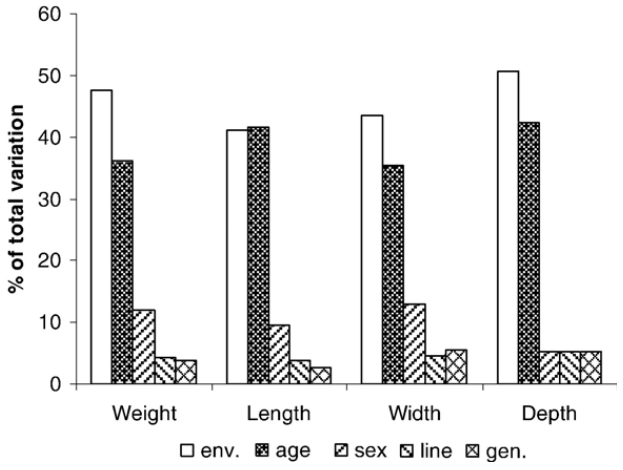

Fig. 1. Percentage of variation explained by systematic effects for body traits.

Table 3
Genetic (σ_A^2) and maternal and common environmental (σ_C^2) variances, heritabilities (h^2), and the maternal and common environmental effects (c^2) in females, males and both sexes

Traits	Sexes	σ_A^2	σ_C^2	h^2	c^2
Weight †	Female	1.8555	0.9261	0.36 (0.054)	0.18 (0.023)
	Male	2.0889	1.2546	0.33 (0.054)	0.20 (0.024)
	All	1.9971	1.0208	0.35 (0.049)	0.18 (0.020)
Length	Female	1.0458	0.6036	0.29 (0.050)	0.16 (0.022)
	Male	1.2584	0.6978	0.30 (0.052)	0.16 (0.022)
	All	1.1928	0.6431	0.30 (0.045)	0.16 (0.019)
Width	Female	0.2688	0.1545	0.26 (0.047)	0.15 (0.020)
	Male	0.2938	0.2022	0.26 (0.052)	0.18 (0.023)
	All	0.3002	0.1693	0.29 (0.043)	0.16 (0.018)
Depth	Female	0.0561	0.0789	0.14 (0.037)	0.19 (0.019)
	Male	0.0504	0.0762	0.17 (0.046)	0.26 (0.025)
	All	0.0605	0.0730	0.20 (0.039)	0.24 (0.021)

†Weight$^{0.5}$ (square root transformation for weight).
Standard errors are in parentheses.

Table 4
Multi-trait estimates of phenotypic (r_p above), genetic (r_g, below the diagonal), residual (r_e, above) and common environmental correlations (r_c, below the diagonal) for body traits in both sexes

Parameters		Traits			
		Weight	Length	Width	Depth
r_p and r_g	Weight		0.92 (0.003)	0.87 (0.005)	0.69 (0.011)
	Length	0.97 (0.008)		0.85 (0.005)	0.64 (0.011)
	Width	0.99 (0.008)	0.94 (0.018)		0.56 (0.015)
	Depth	0.96 (0.027)	0.92 (0.038)	0.95 (0.048)	
r_e and r_c	Weight		0.87 (0.007)	0.80 (0.010)	0.59 (0.020)
	Length	0.98 (0.005)		0.81 (0.010)	0.55 (0.019)
	Width	0.85 (0.022)	0.84 (0.025)		0.53 (0.020)
	Depth	0.65 (0.044)	0.60 (0.050)	0.19 (0.076)	

Standard errors in parentheses.

was applied to evaluate the expected response to selection in the breeding goal as well as the correlated traits and accuracy of selection. The breeding goal aimed at improving live weight at harvest, and its economic value was set to one. Different selection indices were constructed, which included either one or several (two, three and four) characters as selection criteria. In all indices, the following data structure was assumed: i) the pedigree consisted of 100 families (50 sires and 100 dams), ii) there were 40 female and 40 male progeny tested per family and that were potential selection candidates, iii) the proportions of selected animals were 2.50% in females and 1.25% in males, and iv) selection was based on BLUP utilizing full pedigree information. All the selection index calculations were carried out using SelAction (Rutten et al., 2002).

3. Results

3.1. Basic statistics and fixed effects

Table 2 shows the mean, standard deviation and coefficient of variation for all body measurements. The mean for body traits of males was 7–23% greater than for females. The coefficients of variation for live weight were remarkably greater than for other traits. Exploratory analyses indicated that the square root transformation improved the distribution of residuals for live weight but not other traits, and hence was used for live weight only in all analyses.

All systematic effects of selection lines, production environments, gender and spawning years (or generations), as well as the linear covariate age at harvest, were highly significant ($P<0.001$) for all traits. The R^2 values determined by the general linear model analysis indicated that a large proportion of the variation in body traits was related to the testing environments (from 41.2 to 52.6% for all traits) (Fig. 1). Age at harvest was also an important source of variation in body measurements, accounting for 35.3 to 42.2% across the traits. Despite the highly significant effects of sex, selection line and spawning season, they explained only a small part of the total variation in the model, ranging from 5.3 to 12.8, 3.9 to 5.3 and 2.7 to 5.5%, respectively. Further, the goodness of fit of the model improved when the significant interactions among all effects were included in the analyses. The percentage increase in R^2 values ranged from 23.7 to 26.4 across traits.

3.2. Heritability, and maternal and common environmental effects

The heritabilities for body traits (whether jointly or separately estimated in females and males) were moderate to high, ranging from 0.14 to 0.36 (Table 3). All the estimates of heritability were significantly different from zero ($P<0.05$ to

Table 5
Phenotypic (r_p above), genetic (r_g below), residual (r_e above) and maternal and common environment effect (r_c below the diagonal) correlations for body traits in females and males

Correlations	Traits	Females				Males			
		Weight	Length	Width	Depth	Weight	Length	Width	Depth
r_p and r_g	Weight		0.92 (0.003)	0.86 (0.006)	0.67 (0.013)		0.92 (0.003)	0.87 (0.005)	0.71 (0.010)
	Length	0.98 (0.008)		0.83 (0.007)	0.62 (0.014)	0.97 (0.011)		0.86 (0.005)	0.67 (0.012)
	Width	0.99 (0.011)	0.95 (0.021)		0.52 (0.018)	0.99 (0.011)	0.93 (0.026)		0.61 (0.014)
	Depth	0.93 (0.041)	0.91 (0.049)	0.91 (0.070)		0.99 (0.033)	0.91 (0.055)	0.97 (0.060)	
r_e and r_c	Weight		0.98 (0.007)	0.80 (0.034)	0.57 (0.061)		0.97 (0.008)	0.90 (0.020)	0.77 (0.037)
	Length	0.85 (0.011)		0.79 (0.038)	0.52 (0.067)	0.88 (0.008)		0.89 (0.022)	0.71 (0.046)
	Width	0.79 (0.014)	0.78 (0.015)		−0.003 (0.098)	0.82 (0.011)	0.83 (0.010)		0.45 (0.072)
	Depth	0.57 (0.028)	0.52 (0.027)	0.50 (0.028)		0.60 (0.022)	0.58 (0.022)	0.55 (0.022)	

Standard errors in parentheses.

0.001). When expressions in both sexes were treated as a single trait, the heritabilities for all traits were slightly greater than those estimated separately in females and males. However, the magnitude of the separate estimates in females or males was not significantly different from that in the single trait analyses ($z=-1.12$ to 0.14, $P>0.26$). Also, there were no statistically significant differences in heritabilities between females and males in any of the traits ($z=-0.03$ to 0.51, $P>0.61$). The additive genetic and common environmental variances for all traits were almost identical in females and males.

In all traits, the maternal and common environmental effect (c^2) accounted for a large proportion of total variance (15 to 24%) when jointly estimated for both sexes as well as when separately estimated in females and males (Table 3). For live weight, standard length and body width the c^2 values did not differ between sexes ($z=0$ to 0.98, $P>0.33$). The maternal and common environment variance and the c^2 estimate for body depth were, however, significantly greater in males than in females (0.26 vs. 0.19, $z=2.23$, $P<0.01$).

3.3. Correlations among body traits fitting sex as a fixed effect

Table 4 presents the estimates of genetic, phenotypic, residual, and maternal and common environmental correlations when the data were pooled across sexes. The high genetic correlations (0.95 to 0.99) among body traits suggest that they are essentially controlled by the same genes. The phenotypic, maternal and common environment, and residual correlations of live weight and standard length with body width were greater than those of live weight and length with body depth (Table 4). Among the maternal and common environmental correlations, the estimate between body width and depth was low (0.19± 0.08), but it was statistically different from zero ($P<0.05$).

3.4. Correlations among body traits within females and males

Table 5 presents phenotypic, genetic, residual, and maternal and common environmental correlations for body traits estimated within females and males. They all followed the same trend and had the same magnitude ($P>0.05$) as those estimated treating the expression in both sexes as a single trait (Table 4). The genetic correlations among body traits were all positive and high, almost being unity (0.91 to 0.99, $P<0.001$). There were no significant differences ($z=-0.74$ to 1.14, $P>0.26$) in the genetic correlation between females (0.91 to 0.99) and males (0.91 to 0.99). Similarly, differences in the phenotypic correlations (r_p) between the sexes were not statistically significant ($z=0.83$ to 1.39, $P>0.17$). The r_p values ranged from 0.52 to 0.92 in females and 0.61 to 0.92 in males. For maternal and common environmental correlations, statistical differences between females and males were significant only for some pairs of traits, namely, between body weight and standard length ($z=2.21$, $P<0.05$), and between standard length and body width ($z=2.77$, $P<0.01$). However, most between-sex differences in residual correlations were significant ($z=2.34$ to 3.73, $P<0.05$ to 0.01), except between body weight and standard length ($z=-0.94$, $P>0.35$).

Table 6
Genetic and common environment correlations for body measurements between the traits expressed in the two sexes

Pairs of traits between sexes	Genetic correlation (standard error) [r_g(s.e.)]	Common environment correlation (standard error) [r_c(s.e.)]
Female weight–male weight	0.96 (0.033)	0.90 (0.034)
Female length–male length	0.96 (0.039)	0.89 (0.039)
Female width–male width	0.92 (0.047)	0.92 (0.036)
Female depth–male depth	0.91 (0.062)	0.94 (0.023)

3.5. Between sex correlations for body traits

Table 6 shows the genetic and common environmental correlations of live weight, standard length, body width and body depth between the expressions in both sexes. The genetic correlations were very high (0.91 to 0.96) and were not significantly different from unity ($z=-0.04$ to -0.08, $P>0.97$). Ditto for the maternal and common environmental correlations (0.89 to 0.94, $z=-0.06$ to -0.11, $P>0.91$). The near unity genetic correlations suggest that the expressions of body traits in females and males are controlled by the same genes.

3.6. Predicted responses to selection in body traits

Table 7 shows the predicted response over ten years and accuracy of selection for body traits when either only one or all

Table 7
Predicted genetic change over ten years and accuracy of selection for different indices evaluated for the breeding goal aiming to improve live weight at harvest

Selection criteria	Genetic gain in the actual units				Accuracy
	Weight (g)	Length (cm)	Width (cm)	Depth (cm)	
Weight	458	12.7	6.5	2.8	0.552
Length	434	12.8	6.0	2.6	0.517
Width	439	11.9	6.3	2.7	0.524
Depth	370	10.1	5.2	2.5	0.428
Weight+length	458	12.7	6.5	2.8	0.553
Weight+width	461	12.7	6.6	2.8	0.557
Weight+depth	459	12.7	6.5	2.8	0.553
Length+width	450	12.6	6.4	2.8	0.540
Length+depth	442	12.8	6.1	2.7	0.528
Width+depth	452	12.3	6.5	2.9	0.545
Weight+length+width	462	12.8	6.6	2.8	0.558
Weight+length+depth	459	12.8	6.5	2.8	0.554
Weight+width+depth	466	12.7	6.7	2.9	0.565
Length+width+depth	457	12.6	6.5	2.7	0.551
All four traits	467	12.9	6.7	2.9	0.567

possible combinations of two, three or four characters were used as selection criteria. Overall, the responses were consistent in magnitude across all indices used, and as expected given the high and positive genetic correlations among traits (Table 4). The four character selection index slightly increased responses in harvest weight, but only marginally increased correlated responses in standard length, body width and body depth. The accuracy of selection was also greater for the four character than for the single character indices (0.57 vs. 0.43 to 0.55). We also found that the two and three character indices including harvest weight resulted in greater responses for standard length, body width and depth (2 to 6%) than those from which harvest weight was excluded. A similar trend was observed for the accuracy of selection (Table 7). Both the magnitude of the response and the accuracy of selection from the multi character indices were similar to that from selection for harvest weight as the sole criterion. This may be explained by the large genetic variation in this trait and its high genetic correlation with standard length, body width and depth, and it indicates that length, width and depth had very little to add to the indices examined to improve harvest weight. By contrast, if selection for harvest weight were solely based on length, width or depth there would be a loss of accuracy (5 to 22%) and hence a reduction in selection response (10 to 20%) across traits.

4. Discussion

4.1. Heritabilities

There was considerable genetic variation in the body traits observed in GIFT, indicating that the fish would continue to respond to selection for these traits in future generations. The heritability for live weight was generally consistent with the REML estimates recently published for tilapia (e.g. Gall and Bakar, 2002; Rutten et al., 2005; Charo-Karisa et al., 2005; Ponzoni et al., 2005). We found no other reports on parameter estimates for standard length, body width and body depth in the literature.

The similarity in the estimates of heritability and the amount of additive genetic (or phenotypic) variance for all traits in the two sexes (Table 3) indicates that female and male expressions of body traits will respond to selection in the same way. As a corollary, it also indicates that there were no differences in the sensitivity to the environment between females and males. A number of studies (e.g. Lee and Pollak, 1997) hypothesize that between sex differences in parameter estimates are mainly attributable to differences in accuracy and intensity of selection in females and males. This is, however, not consistent with our findings in the present study.

In search of further support for the hypothesis of no sex-specific response to selection, we calculated the conditional additive genetic variance ($V_{A(y/x)}$) for each trait in sex y that is conditioned upon the genetic variance of the same trait in the other sex x and their genetic covariance, following Hansen et al. (2003):

$$V_{A(y|x)} = V_{A(y)} - \frac{\left(\mathrm{Cov}_{A(xy)}\right)^2}{V_{A(x)}}$$

where $V_{A(y)}$ and $V_{A(x)}$ denotes the additive genetic variance in sexes y and x, respectively, and $\mathrm{Cov}_{A(xy)}$ is the additive genetic covariance between the sexes. We calculated the conditional additive genetic heritabilities for harvest weight, standard length, body width and body depth using the parameter estimates of the present study. They were small relative to the actual values and almost identical between females (0.146, 0.080, 0.041 and 0.004) and males (0.164, 0.098, 0.045 and 0.004), respectively. The amount of the additive genetic variance in one sex which was independent of the other sex was small and thus the potential of a trait to respond in one sex independently of the other is very low. Our results suggest that gender-specific response or evolution has not occurred for body traits during the course of selection in GIFT. The conclusion drawn here was, nevertheless, tested with the multi-trait analyses of the genetic correlations for the expressions of body traits between sexes (Section 4.4).

4.2. Maternal and common environmental effects

As reported in other studies (e.g. Rutten et al., 2005; Ponzoni et al., 2005), the proportion of variance due to common family effects for body traits in GIFT was large, accounting for 16 to 26% of the total variance. If they were omitted from the statistical models, estimated breeding values for body measurements could be biased upwards, consequently reducing the accuracy of selection. Using the present parameter estimates in selection index theory showed that the predicted response in harvest weight to selection was overestimated by about 15% when the effects of maternal and common environment were ignored. The accuracy of selection was also reduced by approximately 17%. It is therefore recommended that in genetic evaluation systems for aquaculture species, where the common environmental effects caused by separate rearing of full and half-sibs until the fish reach a suitable size to be physically tagged (e.g. 4 to 8 g in tilapia) may be present, maternal and common environment effects must be included.

4.3. Genetic correlations among body traits

The genetic correlations among harvest weight, standard length, body width and body depth were very

high and near to unity, consistent in both sexes, and also with the results obtained when the analysis that treated body traits in both sexes as a single trait. The very high and positive genetic correlations between live weight and standard length (>0.90) in the present study were also consistent with literature results in other farmed aquaculture species, such as rainbow trout (Gunnes and Gjedrem, 1981; Elvingson and Johansson, 1993), Atlantic salmon (Gjerde and Gjedrem, 1984), and tilapia (Rutten et al., 2005). For all traits, the genetic and phenotypic correlations did not differ ($P>0.05$) between the sexes, indicating that there was little or no independent additive genetic (co)-variance between females and males.

4.4. Genotype by sex interaction

The genetic correlations for homologous traits between the two sexes were all close to one (0.91 to 0.96), indicating that there was no genotype by sex interaction for body traits in GIFT. Hence, female and male expressions of body traits in tilapia can be safely treated as the same trait in practical breeding programs. However, caution should be exercised in cases in which the traits exhibit heterogeneous variances between the sexes. These should be accounted for in the genetic evaluation by an appropriate transformation, using linear regression of phenotypic standard deviation (or variance) to a mean value (Hill, 1984), multiplicative (anti-log) mixed model (Meuwissen et al., 1996), or a log-linear model (Urioste et al., 2001).

The near unity genetic correlations for the expressions of body traits between sexes impose a constraint to selection for sexual dimorphism. The response to selection for sexual dimorphism (R_{SD}) is defined as the difference of male and female response (e.g. Cheverud et al., 1985):

$$R_{SD} = \frac{1}{2}[h_M^2\sigma_{PM}i_M - h_F^2\sigma_{PF}i_F + h_M h_F r_G(\sigma_{PM}i_F - \sigma_{PF}i_M)] \quad (1)$$

where subscripts M and F refer to male and female parameters, h^2 represents heritability, while h is the square root of heritability, σ_P is the phenotypic standard deviation, i is the selection intensity and r_G is the genetic correlation between the trait expression in the two sexes.

By substituting the genetic parameters given in Table 3 for females and males into Eq. (1), the responses to selection for sexual dimorphism for all traits were close to zero, assuming that the same selection intensity was applied in both sexes ($i_M=i_F=1$). When using the selection proportions of females and males corresponding to our present breeding program, the R_{SD} values ranged from −0.009 to 0.105 σ_P. Further, sensitivity analyses to more extreme differences in the selection intensity of females (10%) and males (1%) also gave a small R_{SD} (−0.006 to 0.128 σ_P across traits). It can be concluded that in GIFT there is very limited opportunity for selection for sexual dimorphism.

4.5. Body shape

The response in body dimensions of the fish as a consequence of using a range of indices shows that live weight is the most effective selection criterion to improve overall performance of the fish. However, for situations in which live weight could not be recorded, the use of length, width and depth resulted in virtually the same accuracy as recording weight alone. Hence, if weight recording is not an option, the three body measurements examined here provide an alternative.

A differential change between the different body dimensions as a consequence of using different combinations of the selection criteria would indicate a change in shape of the fish. The relative genetic change in each of these characters varies very little with the different indices, but the gain is always greater for length than for width and depth. The difference in favor of the former character at the expense of width and depth is greatest when it is the sole selection criterion. In practical terms, this means that, albeit at a slow rate, fish undergoing selection for live weight would gradually become longer, relative to their width and depth, with respect to those in the original population.

5. Conclusion

Because of the very high genetic correlation between the expression of body traits in the two sexes, we conclude that in GIFT there is very limited scope for selection for sexual dimorphism. With regards to body shape there is also limited scope for change, but the results obtained with all the selection alternatives we examined indicate that selection for greater harvest will slowly result in relatively longer and thinner fish.

Acknowledgements

This project is funded by European Union. The contributions made by personnel and resources from the Department of Fisheries, Malaysia are highly appreciated.

Appendix A

Phenotypic variances (σ^2_P), heritabilities (h^2), common environmental effects (c^2), phenotypic (above) and genetic (below), and common environmental (below the diagonal) correlations for traits included in selection indices

Traits	Weight	Length	Width	Depth
σ^2_P	4453.50	3.98	1.04	0.30
h^2	0.33	0.30	0.29	0.20
c^2	0.19	0.16	0.16	0.24
Weight		0.92	0.87	0.69
Length	0.97		0.85	0.64
Width	0.99	0.94		0.56
Depth	0.96	0.92	0.95	
Weight				
Length	0.98			
Width	0.85	0.84		
Depth	0.65	0.60	0.19	

σ^2_P, h^2 and c^2 for weight estimated in the original (untransformed) unit, g.

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