Heritability and Genotype-by-Environment Interaction for Harvest Weight of Nile Tilapia, *Oreochromis niloticus*, Fed with Fish Meal- and Non-Fish Meal-Based Diets

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ABSTRACT

While aquaculture of Nile tilapia *Oreochromis niloticus* is expanding worldwide, fish meal as a major protein source has become limited due to declining supply and environmental concerns. The aims of this research were to evaluate the magnitude of genotype-by-environment interaction (G×E) effect on harvest weight in commercial tilapia populations that were raised with fish meal-based and non-fish meal-based diets, and the impact of complete fish meal replacement on genetic parameters. Heritability estimates for body weight at harvest of Nile tilapia fed with fish meal and non-fish meal diets were based on data obtained from 120 full-sib and 50 half-sib families. A mixed linear animal model was used for data analyses, and variance components were estimated using an average information restricted maximum likelihood procedure. The heritability estimates for harvest weight (h^2_{HW}) of Nile tilapia fed with fish meal (0.23±0.03) and non-fish meal (0.22±0.03) diets were moderate. The correlation between family means of the estimated breeding values (EBV) for growth using fish meal and non-fish meal diets was 0.99, which implied no significant evidence for G×E. These genetic parameter estimates indicate good prospects for selective breeding to improve body weight at harvest for both fish groups fed fish meal and non-fish meal diets. Lack of G×E implied that each genotype was affected at a similar magnitude. Therefore, best fish selected for growth with fish meal diet would also perform well with non-fish meal diets. These results imply that changing from fish meal to non-fish meal diets would not affect the genetic improvement program for Nile tilapia.

Keywords: Fish meal diet, Genotype-by-environment interaction, Heritability, Nile tilapia, Non-fish meal diet

INTRODUCTION

Aquaculture of Nile tilapia is practiced worldwide, and this species supports the highest annual production among freshwater fishes (more than 4,500,000 tonnes globally in 2018; FAO, 2020). Increasing productivity and reducing the cost of production are important to the tilapia farming industry, and these goals have motivated selective tilapia breeding programs (Gjedrem, 2005). A classic example of success is the genetically improved farmed tilapia (GIFT) strain of Nile tilapia (Eknath *et al*., 1993; Eknath and Acosta, 1998; Eknath *et al*., 2007); global Nile tilapia production increased by 268 % (748,040 in 1998 from 203,198 in 1989; Asian Development Bank, 2005) due, in part, to higher yields from the GIFT strain.

Currently, tilapia farming largely depends on pelleted feed, which traditionally requires fish meal as the main protein source. As the price of fishmeal is steadily increasing (Edwards *et al*.,

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2004; Dani, 2018) due to declining supply and environmental concerns (Nguyen *et al*., 2009; Schmidt *et al*., 2016), it is necessary to explore alternative protein sources. In this context, the possibility of substituting fishmeal with alternative sources without affecting fish performance has been discussed with regard to alternative dietary protein sources. It was found that complete or partial replacement of fish meal with animal by-products such as fishery by-products (including fish protein concentrate and hydrolysates, shrimp meal, krill meal and squid meal), terrestrial animal by-products, poultry by-product meal, feather meal, blood meal, and meat and bone meal (Tacon and Jackson 1985; El-Sayed, 1999), while mixing complementary protein by-product meals to obtain the desired essential amino acid profile, did not affect the performance or feeding efficiency of Nile tilapia (Davies *et al*., 1989; El-Sayed, 1998). When soybean meal was substituted for fish meal in Nile tilapia fingerlings feed diets with supplementing essential amino acids (lysine, methionine and threonine) and dicalcium phosphate supplementation, it was found that diets with whole plant protein sources from soybean meal supplementation with essential amino acids according to the amino acid profile in tissues can completely replace FM in the diet for tilapia without negative effects on growth efficiency, carcass yield and composition (Furuya *et al*., 2004).

Concern has been raised that different diets might have interactions with genotypes (genotype by environment interaction effect; G×E), whereby a genotype performs differently when fed with different diets. This would adversely affect a selection program if the selected strain did not perform well when reared with different types of diets. Little evidence has been reported on this issue, where a G×E was apparent when Nile tilapia was fed with diets with varying lysine content (Leite *et al*., 2019). On the contrary, no G×E was observed when Nile tilapia were reared in low-input ponds compared to full feeding with commercial pellets (Khaw *et al*., 2009) and when tilapia was fed duckweed compared to pelleted diets with high protein content (Binyotubo, 2017). The objectives of this study were to evaluate the magnitude of G×E between fishmeal and non-fish meal diets and the impact of complete fish meal replacement on genetic parameters for Nile tilapia. Therefore, this study was conducted to estimate the G×E and the growth traits of Nile tilapia that were fed fish meal or non-fish meal pelleted feeds. In addition, the genetic parameters for harvest weight were estimated. The information obtained will be used to plan a selective breeding program for the improvement of harvest weight in Nile tilapia.

MATERIALS AND METHODS

Production of a base population (G0)

The study was conducted at Namsai Farm Co., Ltd., a commercial tilapia production farm (Lat 13.988569256004231, Long 101.21349581564893) in Prachinburi Province, Thailand. The broodstock population used in this study was from Namsai's commercial tilapia population. This population had previously been established using the Chitralada strain from Department of Fisheries, Ministry of Agriculture and Cooperatives acquired in 1994 from Asian Institute of Technology, Thailand, with three successive introductions of Big Nin (otherwise known as GenoMar's "Supreme Tilapia") developed from monosex fry purchased in 1995 and GIFT strain from National Aquaculture Genetics Research Institute (NAGRI) in 1997 and 2000. For this study, 400 brooders were used with ages of 1 to 1.5 years old and mean body weight of 343.54 g for females and 410.00 g for males.

A nested dams-within-sires mating design was used, whereby one male was paired with two to four females. The Tilapia Mating system (pettypatent No. 1803001978) developed by our group was used for the breeding. The Tilapia Mating system comprises a well-designed cage (2×2×1 m stocked with 1 male and 4 females) that provides sufficient space for mating as well as hiding spaces for female breeders to minimize attacks by aggressive males. This system was shown to improve successful mating to 50 % of females during one month of observation, compared with only 30 % success using a standard cage (Meekaew, 2019).

Overall, a total of 60 males and 240 females were used, resulting in 120 full-sib families and 50 paternal half-sib families within one month (from 25 May to 24 June 2018). Three weeks after the initial pairing, the female breeders were checked for fertilized eggs in the mouth every six days. Fertilized eggs from each female were transferred to an incubation tray. Hatching commenced after 3 to 7 days, when 300-500 swim-up fry from each family were nursed for a month in separate 1×1×1 m hapas (28 May to 27 June 2018). Later, the families were moved to 2×2×1 m hapas fixed in a fertilized earthen pond and raised separately from 28 June to 3 August 2018, until tagging. The fry were fed three times daily with the fish meal for two weeks, fish meal mixed with rice bran (1:1) for six weeks, and 35 % protein pelleted feed (with fish meal as a protein source) until tagging.

Experimental set-up

When the fish reached a size of approximately 10 g (ages ranged from 66 to 96 days after hatching [average age of 86.94±8.02 days]; average BW of 10.48±4.43 g), 50 fish from each family (6,000 total fish) were individually tagged (from 1 to 8 September 2018) using a PIT tag (Free Vision Technologies Co., Ltd.), and body weight was recorded. Subsequently, the tagged fish were communally stocked in a 120 m^2 hapa for six weeks (starting 1 September 2018). They were fed twice daily with 30 % protein commercial pelleted diet (Hexa Calcination Co., Ltd.). After six weeks of rearing, a total of 4,361 tagged fish (from all families) survived and were used for the feeding trial.

Grow-out and feeding experiment (fish meal and non-fish meal pelleted)

At commencement of the experiment (9 to 12 October, 2018) the fish had an average age of 128.07±8.01 (range 107-137) days. A random sample of two fish per family were communally stocked in each of 18 cages sized 14.4 m^2 (4×3× 1.2 m), which resulted in a stocking rate of 240 fish per cage (2 fish×120 families). Then, each cage was randomly assigned to different feed types (30 % protein, with or without fish meal as detailed in Table 1). The average body weights of the experimental fish were 29.60±12.30 g and 29.90±12.00 g, respectively, for the groups fed with fish meal and non-fish meal diets. Feeding to satiation was done twice daily at 8 a.m. and 4 p.m., for three months during November 2017-January 2018.

Data recording and analyses

Growth was measured at harvest, when the fish were individually weighed to the nearest milligram. Prior to the measurements, the fish were anaesthetized with clove oil. All the procedures were approved by the Maejo University Animal Care and Use Committee (Approval ID: MACUC 0105/2560), which regulates animal ethics for scientific proposes for the National Research Council of Thailand.

The weight gain was calculated by subtracting individual stocking weight from individual harvest weight.

Statistical analyses

Descriptive statistics were performed using the SAS University (SAS, 2020) program. Least Squares Means of harvest weight and weight gain for the two feed-type groups were computed by PROC GLM.

The data were subjected to variance component estimation of harvest weight and weight gain using a mixed linear animal model. The model is written in matrix notation as follows:

$$y = Xb+Za+e$$

where y is a vector of the observations (harvest weight and weight gain) in different environments; relates to fish meal diet and non-fish meal diet; a is a vector of animal additive genetic effects; b is a vector of fixed effects (i.e., 27 stocking ages, 18 cages, and 2 sexes); e is a vector of residual effects; X and Z are incidence matrices assigned the observations to levels a or b, respectively.

Table 1. Composition of the experimental diets formulated for tilapia during the grow-out stage.

Feed ingredient	Fish meal diet $g{\cdot}100\ g^{-1}$ (%)	Non-fish meal diet $g{\cdot}100\ g^{-1}$ (%)
Tuna fish meal 55 % (TC Union)	11.64	0.00
Meat and bone meal	10.18	16.00
Protosan	3.88	4.85
Squid meal	1.75	2.72
Corn meal	29.58	28.61
Cassava meal	5.82	4.85
Soybean meal (solvent extracted)	30.07	35.87
Salt	0.68	0.68
Calcium carbonate	1.94	1.94
Fish oil	3.88	3.88
Vitamin and mineral	0.23	0.23
Lysine	0.35	0.37
Proximate analysis		
Crude protein (%)	30.96	30.53
Fat (%)	8.44	8.39
Crude fiber (%)	2.87	3.39
Ash (%)	9.34	9.83
Energy ($kcal{\cdot}kg^{-1}$)	2,774.79	2,703.73

The variance components were estimated following an animal model using a restricted maximum likelihood procedure employing an Average Information algorithm. Subsequently, the variance component estimates were used to calculate heritability (h^2) according to the formula:

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2+\sigma_e^2}$$

where σ_a^2 is additive genetic variance and σ_e^2 is residual variance. Individual Estimated Breeding Values for each trait of each fish were predicted using the best linear unbiased prediction. The calculation was facilitated by the ASREML computer software (Gilmour *et al*., 2002). The estimated genotypic correlation for a particular trait between Nile tilapia fed with fish meal or non-fish meal diets was considered for G×E. The correlation between rankings of each family's mean EBV for the traits of Nile tilapia fed with the two feed types was also estimated.

RESULTS AND DISCUSSION

Descriptive statistics

The ages and body weights of Nile tilapia at tagging and harvest reared with fish meal- and non-fish meal diets are shown in Table 2. Notably, the average harvest weight of the fish that were fed the fish meal diet was 485.07±126.19 g, while harvest weight of those fed with the non-fish meal diet was 457.96±123.73 g. Least Squares Means (LS Mean±SE) of harvest weight and weight gain of tilapia in the fish meal treatment (484.89±2.41 g; 455.39±2.38 g for harvest weight and weight gain, respectively) were higher ($p<0.01$) than in the non-fish meal diet (457.01±123.73 g; 426.88±2.35 g).

Genetic parameters

The heritability (h^2) estimates for harvest weight and weight gain of Nile tilapia fed a diet with or without fish meal are presented in Table 3. The heritability values for body weight at harvest and weight gain were moderate to high (0.22±0.03 to 0.39±0.01), and they were similar for the two treatments (fed with or without fish meal).

The heritability values for harvest weight obtained in this study fell within the range reported for Nile tilapia (0.25-0.50, Rutten *et al*., 2005; Charo-Karisa *et al*., 2006; Hans *et al*., 2012; Trọng *et al*., 2013). Notably, the heritability for harvest weight of Nile tilapia fed the fish meal diet was slightly higher than for the non-fish meal diet, whereas heritability for weight gain showed the opposite trend (h^2 of non-fish meal treatment > h^2 for the fish meal treatment).

The heritability estimation in this study indicated a sufficient additive genetic effect for a selection program to improve growth, even though the higher common environmental effect due to common rearing of each family before tagging; c^2 were observed in the early stage of growth in this population (Meekaew, 2019; Meekaew and Kitcharoen, 2019). The estimated additive genetic variance tended to increase with age: at two months of age, h^2 was low for body weight (BW; 0.01± 0.19); at three months, h^2 for body weight (BW; 0.20±0.14) was higher than at two months (data shown in Meekaew, 2019); and there was a further increase at 120 days.

Table 2. Sample size, age, and body weight (BW) of Nile tilapia at tagging, stocking (commencement of the feeding trial) and harvest.

		Sample size	Age (days)			BW (g)		
			Mean	**SD**	**CV (%)**	**Mean**	**SD**	**CV (%)**
Tagging	Overall	6,000	86.94	8.02	9.22	10.48	4.43	42.27
Stocking	Overall	4,361	128.07	8.01	6.25	29.70	11.80	39.73
	FM	2,158	128.10	8.00	6.25	29.60^a	12.30	41.55
	NFM	2,203	128.00	8.01	6.26	29.90^a	12.00	40.13
Harvest	Overall	4,295	214.28	9.75	4.55	471.16	126.74	26.90
	FM	2,156	212.60	11.30	5.32	485.07^a	126.19	26.01
	NFM	2,139	215.80	7.68	3.56	457.96^b	123.73	27.02
Weight gain	Overall	4,111	121.50	20.51	16.88	411.88	311.69	75.67
	FM	2,033	128.15	7.94	6.20	451.11^a	142.84	31.66
	NFM	2,078	128.02	8.04	6.28	431.38b	122.54	28.41

Note: Mean body weights of FM and NFM groups superscripted with different lowercase letters are significantly different ($p<0.01$); FM, NFM = groups fed fish meal diet and non-fish meal diet, respectively

Table 3. Genetic variance (σ_a^2), phenotypic variance (σ_p^2) and heritability (h^2) estimates for harvest weight and weight gain of Nile tilapia fed artificial diets with or without fish meal.

Traits	Fish meal diet			Non-fish meal diet		
	σ_a^2	σ_p^2	h^2±SE[1]	σ_a^2	σ_p^2	h^2±SE[1]
Harvest weight	2,459	10,830	0.23±0.03	3,788	14,240	0.22±0.03
Weight gain	2,287	10,180	0.27± 0.01	3,855	9,741	0.39±0.01

Note: [1]SE = standard error

The estimates of heritability for harvest weight and weight gain were precise based on small standard errors and because the size of the dataset and numbers of full-sibs and half-sibs were sufficient. Additionally, the Best Linear Unbiased Prediction (BLUP) method (Henderson, 1975) was used to estimate systematic environmental effects, additive genetic effect, and breeding values simultaneously (Gjedrem and Baranski, 2009). When compared to the early stages of this population, the standard error of heritability estimates was lower in the present study. From tagging to harvest, all fish from 120 full-sib families were communally reared; thus, the common environmental effect in this study during grow-out and the feeding experiment did not affect harvest weight. For example, in Refstie and Steine (1978), the tank effect, accounted for as common environmental effect on body weight, was estimated to be 5 % of the total phenotypic variance in Atlantic salmon *Salmo salar*. However, the tank effect was lower than 1 % of harvest weight during the portion of the experiment where the salmon were in cage culture.

Genotype-by-environment interaction (G×E)

The genotypic correlations for harvest weight and weight gain between tilapia fed with fishmeal diets and those fed with non-fish meal diets were high (0.99±0.03 and 0.99±0.01 for harvest weight and weight gain, respectively). Likewise, the correlation was also high (0.99) between rankings of mean estimated breeding values (EBV) of the families fed with the two diets. Correlations of the top 20 families (Figure 1) indicated that there was no genotype-by-environment interaction (G×E) effect on harvest weight of Nile tilapia fed with fish meal or non-fish meal diets. Mean EBV of the harvest weight from tilapia fed with fish meal (0.13 g) and non-fish meal (0.12 g) diets were similar.

Although it has been suggested that complete fish meal replacement in tilapia feeds can be achieved using soybean meal, squid meal or meat and bone meal (Tacon and Jackson, 1985; El-Sayed, 1998; 1999), concern has been raised that the yield of fish is compromised. Furthermore, in the present study we observed slightly higher variation in harvest weight within families reared with non-fish meal diet than in those fed fish meal diet.

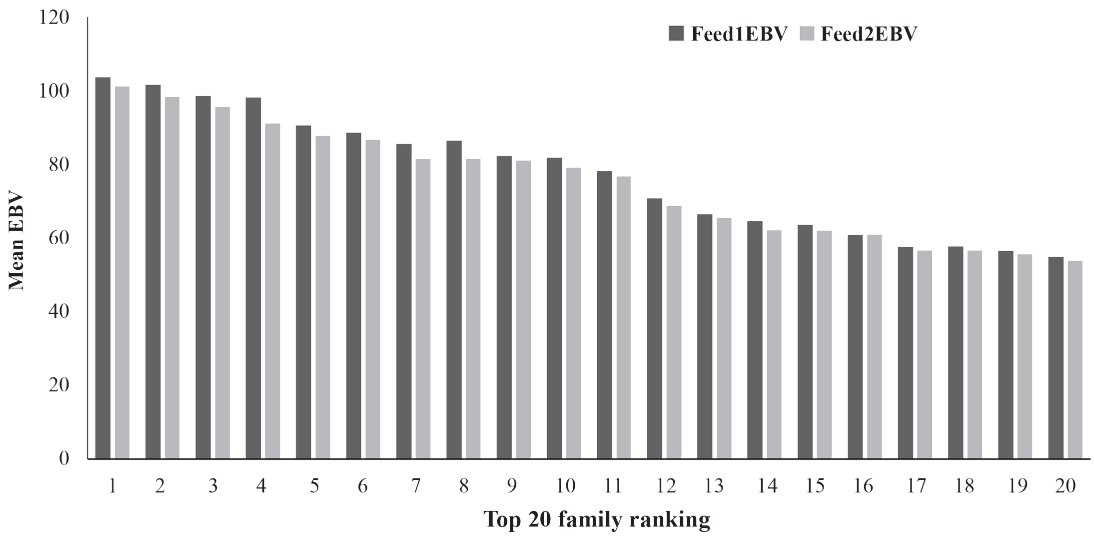

Figure 1. Mean EBV of top 20 families reared with fish meal (Feed1 EBV) and non-fish meal (Feed2 EBV) feeds.

The objective of this study was not only to focus on harvest weight, but also to assess the G×E effects between fishmeal and non-fish meal diets and the impact of complete fish meal replacement on genetic parameters. Heritability and G×E are important parameters that should be considered when setting up a breeding program. The results obtained in the present study are in line with most reports on Nile tilapia. A G×E effect on growth traits was not found, for example, among fish reared in ponds and cages (Thodesen *et al*., 2011; Khaw *et al*., 2012; Trọng *et al*., 2013); in the GIFT base population of Nile tilapia cultured in low- or high-input environments (Khaw *et al*., 2012); or in Nile tilapia fed on duckweed or pelleted feed (Binyotubo, 2017). Only certain rearing conditions (all-male *vs*. mixed sex) showed significant G×E effects (Omasaki *et al*., 2016). Lack of G×E implies that each genotype was affected at a similar magnitude. Therefore, selection for genetic improvement of Nile tilapia fed with fish meal diet, which has been done in many commercial operations, would give similar results in tilapia fed with non-fish meal diets. Our results are highly relevant to and support the current global trend to gradually reduce the use of fish meal in fish diets. Importantly, the replacement of fish meal would not affect the selection response for harvest weight of Nile tilapia.

CONCLUSION

The heritability estimates of harvest weight and weight gain were similar for Nile tilapia fed diets with or without fish meal. The heritabilities were moderate, and hence are favourable for selective breeding. The most important finding of the present study is that diets with or without fishmeal can be used in a selective breeding program to improve harvest weight of Nile tilapia without of G×E interaction and the performance of genetic gain on harvest weight and weight gain. This finding is beneficial since it justifies the current trends of reducing of the amount of fish meal in fish diets and of enhancing the utilization of processing wastes (e.g., squid meal).

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