Crossbreeding effects on carcass traits in crossing Red Tilapia and Nile Tilapia fishes

Mohamed M. Soudy*, Maher H. Khalil, Mahmoud M. Iraqi, and Mohamed S. Hassaan
Department of Animal Production, Faculty of Agriculture at Moshtohor, Benha University, 13736, Egypt.
Corresponding author * Email: maher.khalil@fagr.bu.edu.eg

ORCID

Mohamed Mofreh Soudy https://orcid.org/0009-0000-9871-2441
Maher Hassab El-Nabi Khalil https://orcid.org/0000-0002-6929-3011
Mahmoud Maghraby Iraqi https://orcid.org/0000-0001-5633-9191
Mohamed Shaban Mohamed Hassaan https://orcid.org/0000-0002-6725-1715

Running Head (Short title): **Heterotic effects on carcass traits in crossing Red Tilapia with Nile Tilapia fishes**

Abstract:

A three years crossbreeding experiment was conducted between males of Red Tilapia fish (RT) and females of Nile Tilapia fish (NT) to obtain F_1 crossbred (½RT½NT), followed by *inter-se* mating to produce F_2 crossbred $(½RT½NT)^2$. A total number of 40 sires, 120 dams and 1206 fishes at slaughtering at 28 week of age were used to estimate heritabilities, breeding values (EBV), direct additive genetic effects (G^I), maternal effects (G^M), direct heterosis (H^I) and maternal heterosis (H^M) for carcass traits in terms of slaughter weight (SW), carcass weight (CW), trunk weight (TW), viscera weight (VW), head weight (HW), fillet weight (FW) and fillet yield (FY). Heritability estimates were moderate and ranging from 0.24 to 0.36. The crossbred fishes of ½RT½NT and $(½RT½NT)^2$ had favourable means in carcass traits than purebred fishes (RT and NT). Fishes of interse crossbred $(½RT½NT)^2$ have shown the highest ranges in EBV for carcass traits, while the other three groups (RT, NT and ½RT½NT) have shown inconsistent trends. The percentages of G^I were in favor of NT fish relative to RT fish by 9.8, 11.5, 23.6, 5.6, 3.9, 23.5 and 13.7 % for SW, CW, TW, VW, HW, FW and FY traits, respectively ($P \leq 0.01$), while the percentages of G^M were in favor of RT fish by 3.9, 5.8, 5.1, 7.3, 7.2, 6.5 and 4.4 % for the corresponding traits ($P \leq 0.01$). The estimates of H^I and H^M were positive and significantly moderate or high with H^I superiority ranging from 19.9 to 43.7 % and favourable H^M percentages ranging from 4.1 to 16.2 %.

Keywords: **Tilapia *fish*, *crossbreeding*, carcass traits, BLUPF90, *direct additive and maternal effects, direct and maternal heterosis***

1. Introduction

Fish meat is rich in high quality protein, essential amino acids, essential fats (omega-3), vitamins (D, A and B) and minerals (e.g. calcium, iodine, zinc, and selenium). However, fish meat is one of the most perishable and vulnerable to handling and processing because it has fragile and easily degraded muscle tissue **(Cheng et al., 2015).** Tilapia fish is a healthy food choice for consumers because it is a relatively low-fat fish that is rich in proteins and minerals. On worldwide bases, Tilapia is the second most cultivated freshwater fish, typically yielding between 30-40% fillet yield leaving 60-70% processing waste commonly referred as offal **(El-Sayed, 2006, 2020; Silva et al., 2014).** Around the world, tilapia fillets represent the preference in the form of meat consumption for this species **(El-Sayed, 2020).** The producers of Nile tilapia in the European market are paid according to the fillet weight and their characteristics are truly important for the commercialization process **(Rutten et al., 2005).** The requirement for the weight of fillets sold worldwide is directly linked to the consumer's eating habits: in the USA, Brazil, European Union and China, tilapias are slaughtered with average weights of 600, 800, 1000 and 1200 g, respectively **(Prabu et al, 2019).** According to what mentioned before, the most important traits in Nile tilapia fish are body weights and carcass traits and these traits represent the primary breeding objectives in genetic improvement programs for tilapia and other aquaculture species **(Garduño Lugo et al., 2003; Rezk et al, 2009; El-Zaeem, 2012; Gjerde et al., 2012; Said and Mekkawy, 2016; Said, 2017; Portillo-Salgado et al, 2025)**. However, these carcass traits in Tilapias fish have shown moderate heritability values ranging from 0.16 to 0.33 (**Rutten et al., 2004, 2005; Charo-Karisa et al., 2007; Bentsen et al., 2012**; **Gjerde et al., 2012; Trọng et al., 2013; Garcia et al., 2017; Joshi et al., 2018; Yoshida et al., 2019; Joshi et al., 2020).** Also, carcass quality traits (e.g. carcass and fillet yield) are considered as key traits in the breeding goal for tilapias genetic improvement programs **(Nguyen et al. 2010; Ponzoni et al. 2011**; **Khaw et al, 2016)**.

Across worldwide, most fish crossbreeding experiments have shown significant direct additive genetic effects, maternal effects and heterotic effects on carcass traits and therefore crossbreeding programs among fish breeds and lines are used to increase the efficiency of fish meat production **(Garduño-Lugo et al., 2003; Maluwa and Gjerde, 2006a&b**; **Nguyen et al., 2009; Pongthana et al., 2010; Neira et al., 2016; Thoa et al., 2016**; **Das, 2019**). In

Egypt, the studies concerning the evaluation of heterotic effects on carcass traits in crossbreeding experiments involving Tilapia fishes are scarce (**El-Zaeem et al., 2012; El-Zaeem and Salam, 2013; Said and Mekkawy, 2016**). The main objectives of the present study were to evaluate a crossbreeding experiment involving Red Tilapia fish (RT) as sires and Nile Tilapia fish (NT) as dams to produce F_1 crossbred (½RT½NT), followed by one generation of *inter-se* mating to obtain F_2 crossbred $(½RT½NT)^2$. This experiment was used to evaluate some carcass traits in terms of genetic groups comparisons, heritabilities, estimated breeding values, direct additive effects, maternal effects, direct heterosis and maternal heterosis.

2. Materials and Methods

2.1. Base fish populations and crossbreeding experiment performed

A three years crossbreeding experiment was conducted during the period from January 2021 to October 2024 between males of Red Tilapia (RT) and females of Nile Tilapia (NT) to obtain F_1 crossbred (½RT½NT), then *inter-se* mating to produce F_2 crossbred $(½RT½NT)^2$. Therefore, four genetic groups were obtained in this study (RT, NT, ½RT½NT, $(½RT½NT)^2$. This crossbreeding experiment was performed in fish farm, Faculty of Agriculture at Moshtohor, Benha University, Egypt. The Nile tilapias fishes used in this study were obtained from Kafr Al sheikh governorate, Egypt, while Red tilapias were brought from fish hatchery at kilo 21, Alexandria Government, Egypt.

2.2. Mating system, housing and feeding regime

Mating of ripe males and females was performed in 40 families, 10 families in each genetic group of Nile Tilapia, Red Tilapia, F_1 and F_2. A total of 40 Hapas (2 x 1 x1 m) were used, 10 hapas for each genetic group. The females were housed in Hapas (2 x1x 1 m) with mating ratio of one male: three females. Hapas were cleaned and disinfected regularly after each hatch. The concrete ponds were siphoned every three days to get rid of feces and ammonia. On 21st day after mating, the fries were collected from the mouse of the hatched females. Then, the fries were taken from each female and stocked in Hapa (1x1x1 m). Fries were tagged at 84 days from hatching then weighted and then random sample of 50 fry per female were taken and tagged individually in Hapas (1×1×1 m in length × width × height). The tagging of fingerlings was performed using thin plastic thread fixed in dorsal muscle of fish, this plastic thread fixed with different colors and shapes. The Fries were mashed fed

until they weighted 10 g at 12 weeks after hatching, then random samples of 50 fries were taken and tagging individually per female.

All the fishes were kept in the same hatchery under the same environmental and managerial conditions throughout the experimental period. Ripe fishes were housed for each sex individually in concrete pond. All the ponds were supplied with well aerated; the air was compressed to each pond via air stones by air pumps during the experimental period. Water volume (20 %) in each pond was daily replaced by new freshwater after removing the accumulated excreta of uneaten feeds and feces through outlets. Water quality parameters were monitored every week throughout the experiment. Water temperature was recorded daily with a mercury thermometer suspended at 15 cm depth, while *pH* was determined by using a *pH* meter (Orion *pH* meter, Abilene, Texas, USA). Dissolved oxygen (mg L^{-1}) was measured using YSI model 56 oxygen meters (YSI Company, Yellow Springs Instrument, Yellow Springs, Ohio, USA).

The larvae after yolk sac absorption after hatch were stocked in hapa and fed mashing feed Allar Aqua-Egypt (40 % crude protein) 10 times daily ad-libitum according to **NRC (2011)**. While fingerlings of fish after one month of fed pelleted feed (35% crude protein) three times daily 9.00 am, 11.00 am and 3.00 pm ad-libitum (**NRC, 2011**). Water exchange was done regularly to remove uneaten feeds and feces. About 25% of the culture water was always replaced every morning.

2.3. Slaughtering experiment and carcass evaluation

After 28 weeks of growth, the fishes were slaughtered and measured for the following carcass traits: slaughter body weight (SW) defined according to **Rutten et al. (2005**), carcass weight (CW) defined according to **Haffray et al. (2018)**, trunk weight (TW) defined according to **Cardoso et al. (2021**), viscera weight (VW) defined according to **Charo-Karisa et al. (2007)** and fillet weight (FW) and fillet yield (FY) defined according to **Rutten (2004)** and **Joshi et al. (2020)**. A clean fillet is defined as a fillet without skin, bones and fat that is ready to go to the market. After filleting, FW was weighted using the same weighing balance expressed in grams (g). The fishes were decapitated, gutted, and skinned manually, and then filleted. The fillets were rinsed and dried, and fillet weights (FW) were recorded by weighing the fillets from both sides. Fillet yield (FY) was calculated as: (FW/SW) X 100 reported by **Garcia et al. (2017).** A total of 1206 fishes obtained from 20 sires and 55 dams were slaughtered to be evaluated for carcass traits **(Table 1)**.

Table 1. The numbers of fishes slaughtered, categorized according to sires and dams and genetic groups

Sire genetic group	Dam genetic group	Fishes slaughtered
NT (5)	NT (15)	NT (303)
RT (5)	RT (13)	RT (301)
RT(5)	NT (13)	½RT½NT (301)
½RT½NT (5)	½RT½NT (14)	(½RT½NT)² (301)
Total No = 20	Total No = 55	Total No = 1206

NT= Nile Tilapia (*Oreochromis niloticus L.*), RT=Red Tilapia (*Oreochromis spp.*), ½RT½NT= F_1 cross (RTXNT), (½RT½NT)² = F_2 interse cross (½RT½NTX½RT½NT); The number of sires, dams and fishes slaughtered are given in brackets.

2.4. Models of analyses

The data were renumbered and recoded using the **renumf90** software **(Misztal et al., 2018)**. The pedigree file was checked for relationship issues using the **CFC v.1.0** software **(Sargolzaei et al., 2006)**. The variance components for random effects and heritabilities for carcass traits were estimated based on a Bayesian Inference of Gibbs Sampling Algorithm using **TM** software **(Legarra et al., 2008)**, The Gibbs Sampler Algorithm comprised 200,000 iterations, discarding the first 20,000. The estimated variance components were used to solve the mixed model equations using the **PEST** software **(Groeneveld, 2006),** getting the solutions for different genetic groups and the other fixed effects as well as their error variance-covariance matrix. Data of carcass traits were analyzed using the following single-trait animal model:

$$\boldsymbol{y = Xb + Z_a u_a + e} \qquad (\boldsymbol{Model\ 1})$$

Where y = vector of observed carcass trait for the fish; b = vector of fixed effects of genetic group of the fishes slaughtered (four levels: RT, NT, ½RT½NT cross and interse cross $(½RT½NT)^2$), sex, year-season of slaughtering (12 levels: four seasons and three years); u_a = vector of random additive effects; X and Z_a= incidence matrices relating carcass records to the fixed effects and additive genetic effects, respectively; e = vector of random residual effects. The BLUPF90 software **(Misztal et al., 2018)** was used to estimate the breeding values (EBVs) for each trait adopting single-trait animal model mentioned previously.

2.5. Estimation of crossbreeding effects

The CBE software **(Wolf, 1996)** was used to estimate the crossbreeding effects on carcass traits in terms of direct additive genetic effects (G^I), maternal effects (G^M), direct heterosis (H^I) and maternal heterosis (H^M). The solutions for the crossbreeding genetic group

effects were obtained according to Dickerson model **(Dickerson, 1992)**, using the procedure of Generalized Least Squares (GLS) and applying the following linear model:

$$y = X\mathbf{b} + \mathbf{e},\ \text{Var}(y) = V \quad \text{(Model 2)}$$

Where: y = vector of the estimated genetic groups solutions of carcass trait; X = incidence matrix of fixed effects; **b** = vector of estimable crossbreeding genetic effects; **e** = vector of random error; **V**= the error variance-covariance matrix of y. Then, crossbreeding parameters, representing the differences between the genetic groups in growth or carcass trait were estimated in terms of direct additive effects ($G^I = G^I_{RT} - G^I_{NT}$), maternal effects ($G^M = G^M_{RT} - G^M_{NT}$), direct heterosis ($H^I$) and maternal heterosis (H^M). Thus, four parameters were estimated according to **Dickerson (1992)** and **Wolf (1996)** as a vector called **b**-vector:

$$\boldsymbol{b} = [(\boldsymbol{G^I_{RT}} - \boldsymbol{G^I_{NT}}) \quad (\boldsymbol{G^M_{RT}} - \boldsymbol{G^M_{NT}}) \quad \boldsymbol{H^I} \quad \boldsymbol{H^M}]$$

The solutions of **b** were calculated by the method of Generalized Least Squares (GLS) using the following equation: $\hat{b} = (X'V^{-}X)^{-1}X'V^{-}y$ Where **X** was the matrix of coefficients of estimable crossbreeding effects, V^{-} = the generalized error variance–covariance matrix, with the variance–covariance matrix of the estimate of **b** being, $\text{Var}\,\hat{b} = (X'V^{-}X)^{-1}$. The coefficients of the matrix relating to the means of the genetic groups with crossbreeding effects are presented in **Table 2.**

Table 2. Genetic groups of fishes slaughtered, their sires and dams and coefficients of the matrix relating the means of fish genetic groups with crossbreeding effects

Genetic group			Mean	Coefficients of the matrix of the estimable crossbreeding effects					
Sire	Dam	Fishes slaughtered		G^I_{RT}	G^I_{NT}	G^M_{RT}	G^M_{NT}	H^I	H^M
RT	RT	RT	1	1	0	1	0	0	0
NT	NT	NT	1	0	1	0	1	0	0
RT	NT	½RT½NT	1	0.5	0.5	0	1	1	0
½RT½NT	½RT½NT	(½RT½NT)^2	1	0.5	0.5	0.5	0.5	0.5	1

RT=Red tilapia; NT=Nile tilapia and ½RT½NT= F_1 cross resulted from crossing Red tilapia sires and Nile tilapia dams and (½RT½NT)^2 = F_2 or interse cross resulted from inter-se mating between sires and dams of the F_1 crossbred. G^I_{RT} and G^I_{NT} = Direct additive genetic effects for Red tilapia and Nile tilapia, respectively; G^M_{RT} and G^M_{NT} = Maternal effects for Red tilapia and Nile tilapia lines, respectively; H^I = Direct heterosis; H^M = Maternal heterosis.

3. Results and Discussion

3.1. Descriptive statistics for carcass traits

The main statistical parameters estimated by Gibbs Sampling Algorithm using TM software for carcass traits across the four genetic groups were shown in Table 3. The generalized least square means (GLM) for carcass traits at 28 weeks of age were 314, 211, 188, 56, 76.6, 166 and 52 g for SW, CW, TW, VW, HW, FW and FY, respectively (Table 4).

These means are in agreement with those estimates cited in literature for some carcass traits like carcass weight, visceral weight**,** head weight**,** fillet weight and fillet yield in Tilapia fish **(Rutten et al., 2005; Nguyen et al., 2010; Hamzah et al., 2016; Garcia et al., 2017; Joshi et al., 2018,2020; Yoshida et al., 2019; Cardoso et al., 2021; Yoshida and Yáñez, 2021; Todesco et al., 2022; Portillo-Salgado et al., 2025).** However, wide variations in these reviewed means for carcass traits were reported according to the slaughtering age used. For slaughter weight, fillet weight and fillet yield NT fish, the means reported were 787, 308 and 37.3 g at 61 weeks of age by **Rutten et al. (2005)**, 527, 176.7 and 34.4 g at 72 weeks of age by **Hamzah et al. (2016)**, and 647, 218 and 33.7 g at 41 weeks of age by **Garcia et al. (2017)**, respectively. **Yoshida and Yáñez. (2021)** stated that means for head weight, fillet weight and fillet yield at 53 weeks of age were 245, 300 and 31.7 g, respectively. **Todesco et al. (2022)** found that mean for slaughter weight at 47 weeks of age was 922 g. **Portillo-Salgado et al. (2025)** stated that means for carcass weight, head weight, visceral weight, fillet weight and fillet yield at 26 weeks of age were 363, 102, 57, 197 and 37.7 g, respectively.

Wide ranges between minimum and maximum values of carcass traits were detected since the percentages of variation (CV) were moderate and ranged from 15 to 34% (Table 3). **Todesco et al. (2022)** reported moderate coefficients of variation for carcass traits, ranging from 21 to 31 %. But, **Yoshida and Yáñez (2021)** and **Portillo-Salgado et al. (2025)** reported low or moderate coefficients of variation for carcass traits, ranging from 6.9 to 26.7 %.

Table 3: Descriptive statistics in terms of generalized least square means (GLM), standard deviations (SD), minimum and maximum values and percentages of variation (CV) for carcass traits across all fish genetic groups

Carcass trait (g)	GLM	SD	Minimum value	Maximum value	CV%
Slaughter weight (SW)	314	46.1	165	523	15
Carcass weight (CW)	211	42.9	70	415	20
Trunk weight (TW)	188	43.2	50	265	23
Visceral weight (VW)	36	12.4	13	79	34
Head weight (HW)	56	15.7	22	104	28
Fillet weight (FW)	166	39.8	35	241	24
Fillet yield (FY)	52	8.6	21	69	16

Number of slaughtered fishes = **1206**

3.2.Heritability estimates

Heritability estimates for carcass traits were moderate, being 0.33, 0.24, 0.36, 0.27, 0.29, 0.33 and 0.32 for SW, CW, TW, VW, HW, FW and FY, respectively (Table 4). The

heritability estimates obtained here are reliable since these estimates are associated with low standard errors, ranging from 0.04 to 0.09 and consequently the estimable accuracies were high. These heritability estimates for carcass traits are agreed with most estimates cited in several studies involving Tilapia fishes for slaughter and carcass weights, visceral weight, head weight, fillet weight and fillet yield **(Charo-Karisa et al., 2007; Nguyen et al., 2010; Haffray et al., 2018; Garcia et al., 2017; Joshi et al., 2020)**.

Table 4: Estimates of heritability (h^2±SE), common environmental effects (c^2±SE) and random error (e^2±SE) estimated by Threshold Model software (TM) for carcass traits across all fish genetic groups

Carcass trait	h^2±SE	e^2±SE
SW	0.33±0.04	0.66±0.04
CW	0.24±0.04	0.75±0.04
TW	0.36±0.09	0.63±0.09
VW	0.27±0.06	0.72±0.06
HW	0.29±0.08	0.70±0.08
FW	0.33±0.09	0.66±0.09
FY	0.32±0.06	0.67±0.06

[+]The traits are defined in Table 3; Number of slaughtered fishes = **1206**

2.4. Genetic groups comparisons

The generalized least square means (GLM) given in Table 5 have shown that ½RT½NT and $(½RT½NT)^2$ crossbred fishes were higher than RT and NT purebred fishes in slaughter weight at 28 weeks of age (351.2 and 325.6 g in crossbreds vs 259.8 and 317.6 g in purebreds), carcass weight (238.6 and 229.8 g in crossbreds vs 164.9 and 207.9 g in purebreds), trunk weight (224.6 and 210.3 g in crossbreds vs 121.1 and 196.0 g in purebreds), visceral weight (32.0 and 34.7 g in crossbreds vs 41.6 and 37.0 g in purebreds), head weight (51.1 and 53.5 g in crossbreds vs 63.5 and 58.1 g in purebreds), fillet weight (200.6 and 187.3 g in crossbreds vs 106.0 and 171.5 g in purebreds) and fillet yield (57.5 and 57.5 g in crossbreds vs 41.1 and 54.3 g in purebreds). **Garduño-Lugo et al. (2003)** found that means of carcass traits in Stirling Nile tilapia (SNT) and Red hybrid tilapia (RHT) were 384 g in SNT and 496 g in RHT for body weight at slaughter at 14 weeks age. **Rutten et al. (2004)** reported that means of Chitralada, AIT and GIFT tilapias fish were 784, 715 and 705 g for slaughter weight at 52 weeks of age, 271, 252 and 267 g for fillet weight and 34.5, 35.2 and 37.8 g for fillet yield, respectively. **Peterman and Phelps (2012)** stated that means of four strains of Nile Tilapia (Oreochromis niloticus) in Egypt, Ivory Coast, Lake Victoria, and Sagana were 413, 406, 403 and 434 g for body weight at slaughter at 17 weeks of age and 30.8, 33.1, 31.8 and 29.6 g for fillet yield, respectively. **El-Zaeem et al. (2012)** found that

means for carcass traits in four strains of Manzalah, River Nile, Edku lake and Cultured Nile tilapia fish were 23.1, 22.1, 25.0 and 23.5 g for head weight and 12.5, 12.8, 9.8, and 12.2 g for viscera weight, respectively.

Table 5: Generalized least square means and their standard errors (GLM±SE) for carcass traits in different fish genetic groups

Carcass trait (g)	Genetic group											
	NT			RT			½RT½NT			(½RT½NT)²		
	N	GLM	SE	N	GLM	SE	N	GLM	SE	N	GLM	SE
SW	303	259.8^{d}	12.1	301	317.6^{c}	11.7	301	351.2^{a}	4.4	301	325.6^{b}	19.6
CW	303	164.9^{c}	12.1	301	207.9^{b}	11.7	301	238.6^{a}	4.4	301	229.8^{a}	19.7
TW	303	121.1^{d}	5.9	301	196.0^{c}	5.8	301	224.6^{a}	2.2	301	210.3^{b}	9.7
VW	303	32^{c}	4.6	301	34.7^{b}	4.5	301	41.6^{a}	1.9	301	37^{b}	7.5
HW	303	51.06^{c}	5.7	301	53.5^{c}	5.6	301	63.5^{b}	2.1	301	58.11^{a}	9.3
FW	303	106.0^{d}	5.9	301	171.5^{c}	5.8	301	200.6^{a}	2.2	301	187.3^{b}	9.7
FY	303	41.1^{c}	2.0	301	54.3^{b}	1.9	301	57.5^{a}	0.7	301	57.5^{a}	3.3

[+]The traits are defined in Table 3.
[a,b,..] The estimates with the same letters in each row are not significantly different (P≤0.05).

2.5. Estimated breeding values

The ranges in estimated breeding values (EBV), their standard errors (SE) and accuracy of estimation (r_A) for carcass traits of each separate genetic group are presented in Table 6. In general, the interse cross group $(½RT½NT)^2$ recorded the highest ranges in EBVs for all traits, while the other three groups (RT, NT and ½RT½NT) have shown inconsistent EBV trends. The ranges in EBV for carcass traits in interse $(½RT½NT)^2$ group were 98.5 g for SW, 79.6 g for CW, 34.0 g for TW, 29.8 g for VW, 28.3 g for HW, 29.0 g for FW and 13.5 g for FY. The accuracies of estimation ($\mathbf{r_A}$) in EBV were high and ranged from 0.62 to 0.71 (Table 6). These high accuracies may be due to that estimates of heritability were highly associated with more available pedigree information for all fishes in different genetic groups (**Haffray et al, 2018**).

Table 6: The ranges in breeding values (EBV) estimated by BLUPF90 software for carcass traits in each separate fish genetic group

Carcass trait (g)	Genetic group							
	NT		RT		½RT½NT		$(½RT½NT)^2$	
	N	Range in EBV	N	Range in EBV	N	Range in EBV	N	Range in EBV
SW	303	87.9	301	77.9	301	81.9	301	98.5
CW	303	74.3	301	65.5	301	68.0	301	79.6
TW	303	28.9	301	32.7	301	28.6	301	34.0
VW	303	26.1	301	23.4	301	24.2	301	29.8
HW	303	24.1	301	23.0	301	23.1	301	28.3
FW	303	26.1	301	31.2	301	25.7	301	39.0
FY	303	10.8	301	9.9	301	9.6	301	13.5

[+]The traits are defined in Table 3.
The accuracies of estimation in EBV (R_A) were high and ranged from 0.62 to 0.71.

2.6. Direct additive genetic and maternal effects

The generalized least square solutions (GLS) of direct additive genetic effects (G^I) for carcass traits were significantly in favour of NT fish relative to RT fish (Table 7). The percentages of G^I effects for carcass traits were significantly in favour of NT fish by 9.8, 11.5, 23.6, 5.6, 3.9, 23.5 and 13.7 % for SW, CW, TW, VW, HW, FW and FY traits, respectively (P≤ 0.01). Oppositely to G^I effects, the GLS for maternal effects (G^M) were significantly in favour of RT fish by 3.9, 5.8, 5.1, 7.3, 7.2, 6.5 and 4.4 % for SW, CW, TW, VW, HW, FW and FY traits, respectively (P≤0.01). The findings of direct additive and maternal effects obtained here are consistent with those cited in fish crossbreeding studies, which showed that direct additive and maternal effects were of considerable importance for the majority of carcass traits in Nile or Red tilapia fish breeds/lines in Malawi (**Maluwa and Gjerde, 2006a&b),** Malaysia (**Nguyen et al., 2009),** Thailand (**Pongthana et al., 2010),** Vietnam (**Thoa et al., 2016),** Philippine (**Joshi et al, 2018),** and Norway **(Das, 2019**).

Table 7: Generalized least square solutions and percentages of direct additive effects (G^I), maternal effects (G^M) and their standard errors (SE) estimated by Dickerson model for carcass traits in crossing Red tilapia with Nile tilapia fish

Carcass trait (g)	Direct additive genetic effects (G^I)				Maternal effects (G^M)		
	N	$G^I=G^I_{RT}-G^I_{NT}$ (in units)	SE	G^I as %$^{++}$	$G^M= G^M_{RT}-G^M_{NT}$ (in units)	SE	G^M as %$^{++}$
SW	1206	-28.2**	0.24	9.8	11.4 **	0.18	3.9
CW	1206	-21.5**	0.24	11.5	10.9 **	0.18	5.8
TW	1206	-37.4**	0.12	23.6	8.2**	0.09	5.1
VW	1206	-2.8 **	0.09	5.6	3.6**	0.07	7.3
HW	1206	-2.6 **	0.12	3.9	4.9**	0.08	7.2
FW	1206	-32.6**	0.12	23.5	8.6**	0.09	6.5
FY	1206	-6.5**	0.04	13.7	3.6 **	0.04	4.4

$^{+}$The traits are defined in Table 3.

$^{++}$Percentage computed as [Estimate of G^I or G^M in units/(RT+NT)/2]x100; NS= Not Significant, *=P⩽ 0.05 and **=P⩽ 0.01.

2.7. Direct and maternal heterosis

The GLS of direct heterosis (H^I) as well as their percentages for carcass traits were positive and significantly moderate or high for all traits, with heterotic percentages ranged from 19.9 to 43.7 % (P≤0.01; Table 8). These estimates fall within the ranges cited in most of fish crossbreeding studies in Malawi **(Maluwa and Gjerde, 2006a&b)**, Egypt **(Essa and Haroun, 1998; El-Zaeem et al., 2012; El-Zaeem and Salam, 2013),** Vietnam **(Thoa et al., 2016)**, and Costa Rica **(Neira et al., 2016).** The GLS of maternal heterosis (H^M) as well as their percentages for carcass traits indicated that the estimable solutions of H^M were significantly moderate for all traits where the maternal heterotic percentages ranged from 3.8

to 16.2 % (P ≤ 0.01; Table 8). However, the positive estimates of H^M for carcass traits indicate that crossbred dams of fishes had valuable heterotic maternity over their purebred dams for these carcass traits. However, the estimates of H^M obtained here are in accordance with those estimates cited in some Tilapia fish studies (e.g. **Maluwa and Gjerde, 2006a&b; Neira et al., 2016).**

Table 8: Generalized least square solutions and percentages of direct heterotic effects (H^I), maternal heterotic effects (H^M) and their standard errors (SE) estimated by Dickerson model for carcass traits in crossing Red tilapia with Nile tilapia fish

Carcass trait[+]	N	Direct heterotic effects			Maternal heterotic effects		
		H^I (in units)	SE	H^I as %[++]	H^M (in units)	SE	H^M as %[++]
SW	1206	60.4**	0.3	21.0	13.4 **	0.15	4.1
CW	1206	51.1**	0.27	27.4	10.9 *	0.16	5.8
TW	1206	64.9**	0.13	40.9	6.1 **	0.29	3.8
VW	1206	11.2**	0.1	22.6	8.1 **	0.23	16.2
HW	1206	14.1**	0.13	20.5	9.2 **	0.28	13.4
FW	1206	60.7**	0.13	43.7	6.9 *	0.29	4.9
FY	1206	9.5**	0.04	19.9	2.5 **	0.10	5.3

[+]The traits are defined in Table 3.
[++]Percentage computed as [Estimate of H^I or H^M in units/(RT+NT)/2]x100; *=P≤ 0.05 and **=P≤ 0.01.

Conclusions

The desired heterotic consequences obtained in the present study have shown that crossing Red Tilapia males with Nile Tilapia females could be beneficial to improve carcass traits in fish industry. In Egypt, new synthetic meat-type fish lines could be established by crossing Nile and Red Tilapia fishes based on their estimated direct additive, maternal and heterotic effects.

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