Aquaculture 450 (2015) 154–161

Contents lists available at ScienceDirect

Aquaculture

journal homepage: www.elsevier.com/locate/aqua-online

Genetic and non-genetic indirect effects for harvest weight in the GIFT strain of Nile tilapia (*Oreochromis niloticus*)

Hooi Ling Khaw [a,b,*], Raul W. Ponzoni [c], Hoong Yip Yee [b], Mohd Aznan bin Aziz [b], Piter Bijma [a]

[a] Animal Breeding and Genomics Centre, Wageningen University, De Elst 1, 6708WD Wageningen, The Netherlands
[b] WorldFish, Jalan Batu Maung, 11960 Bayan Lepas, Penang, Malaysia
[c] Departamento de Produccion Animal, Facultad de Agronomia, 12900 Montevideo, Uruguay

ARTICLE INFO

Article history:
Received 17 February 2015
Received in revised form 14 July 2015
Accepted 29 July 2015
Available online 2 August 2015

Keywords:
Nile tilapia
Genetic improvement
Indirect genetic effect
Direct genetic effect
Maternal common environmental effect

ABSTRACT

Trait values of individuals are affected not only by their genetic makeup, but also by environmental factors and interactions with other individuals. The heritable effect of an individual on the trait values of other individuals it interacts with is known as an indirect genetic effect (IGE). Such IGEs may affect response to selection. Fish selected for high growth rate, for example, have been shown to be more aggressive and competitive, which may reduce the observed response in growth rate. The main objective of this study is to quantify the genetic and non-genetic indirect effects for harvest weight in the GIFT strain of Nile tilapia. A total of 6330 fish with harvest weight information were used to estimate genetic and non-genetic parameters. A bivariate analysis of harvest weight and survival was conducted by fitting different mixed models to investigate the presence of IGEs and other non-genetic effects. The full set of genetic parameters could not be estimated simultaneously with the inclusion of maternal common environmental effects. A confounding between maternal common environmental effects and direct genetic effects resulted from the mating strategy, where one sire was mated to only one or two dams. A 1 male to 2 females mating design is common in aquaculture, but it has limited power to estimate genetic parameters. Models without maternal common environmental effects showed significant IGE on harvest weight, which contributed 48% of total heritable variance. Models with maternal common environmental effects suggested the presence of IGE. The direct–indirect genetic correlation for harvest weight was negative (-0.38 ± 0.19), indicating that traditional selection, if performed in an environment where the fish have to compete with each other for the resources, will increase competition. A strongly negative genetic correlation between direct effects on survival and indirect effects on harvest weight (-0.79 ± 0.30) showed that individuals with better genes for survival suppressed growth rate of their social partners. Our results suggest that heritable competitive interactions affect harvest weight in Nile tilapia. Hence, breeding schemes may need to be adapted to avoid an increase in aggressiveness due to selection for growth rate in a competitive environment. Further studies are required to investigate the relevance of IGE and its implications on different systems of commercial aquaculture production.

Statement of relevance: Sociable fish will help to improve aquaculture production.

1. Introduction

Trait values of individuals within a population are not only affected by the genetic makeup of individuals, but also by the environmental conditions where the animals develop and socially interact with others (Hill et al., 2007; Waddington, 1960). With social interactions, the genotype of an individual may affect the trait values of other individuals that it interacts with (Bijma, 2012; Griffing, 1967; Moore et al., 1997; Muir, 1996). In the past, such social interactions have been ignored by animal breeders. However, in recent decades, social interactions have received increased attention by both evolutionary biologists and animal breeders. This has been mainly due to the increased evidence of heritable effects of individuals on trait values of other individuals, a phenomenon known as indirect genetic effects (IGE; examples: van Vleck et al., 2007; Ellen et al., 2008; Wilson et al., 2011; Peeters et al., 2012; Muir et al., 2013), coupled with advancements in genetic evaluation and statistical analysis for socially affected traits (Bijma, 2010, 2014; Muir, 2005). Because of their genetic basis, IGEs may affect the direction and magnitude of selection response and the amount of heritable variation available for response to selection (Bijma, 2011; Griffing, 1967; Muir et al., 2013).

For decades, aquaculture geneticists have argued that fast growing fish may be more aggressive and competitive for resources (Kinghorn,

* Corresponding author at: WorldFish, Jalan Batu Maung, 11960 Bayan Lepas, Penang, Malaysia.
E-mail address: h.khaw@cgiar.org (H.L. Khaw).

http://dx.doi.org/10.1016/j.aquaculture.2015.07.033

1983; Purdom, 1974). This association was demonstrated by Moyle (1969)and Swain and Riddell (1990), under limited resources conditions. By contrast, Ruzzante and Doyle (1991, 1993) have shown that with abundant resources, fast growing fish are less aggressive in a competitive environment. Tilapia aquaculture production systems encompass a range of environments from the viewpoint of among fish competition, including some where it is intense (e.g. cages at high density). In this paper we investigate the magnitude of social interactions or IGEs in an environment where competition for food is induced by the feeding regime.

World aquaculture production has increased at an average rate of 8.8% per annum, and Nile tilapia (*Oreochromis niloticus*) is one of the major freshwater cultured species in the world (FAO, 2012). Genetically Improved Farmed Tilapia (GIFT) is an improved Nile tilapia strain that until now has undergone 12 generations of selection for growth rate in Malaysia, managed by WorldFish. (WorldFish is an international, nonprofit organization that harnesses the potential of fisheries and aquaculture to reduce poverty and hunger; www.worldfishcenter.org). The coefficient of variation (CV) for harvest weight in GIFT or Nile tilapia in general is around 40 to 60% (Khaw et al., 2010; Nguyen et al., 2007; Ponzoni et al., 2005), which is considered large. Generally, an increase in the CV indicates inter-individual competition and dominance hierarchy (Adams et al., 2000; Jobling, 1995). Hence, the high CV suggests considerable competition in Nile tilapia. In order to reduce the competition and size variation in harvest weight of Nile tilapia or aquaculture species in general, we need to quantify and select for the IGEs on socially affected traits in those populations. Thus, the main objective of this study was to quantify the heritable variation for growth rate of GIFT, and the contribution of IGEs to this heritable variation. Here we describe the experiment conducted for this purpose, and present estimated parameters of genetic and non-genetic indirect effects on growth rate in the GIFT strain.

2. Materials and methods

2.1. The environment and the fish

The social interaction experiment began in 2009 and was conducted at the Aquaculture Extension Center (Department of Fisheries), located at Jitra in Kedah State of Malaysia. The first batch of experimental fish was produced from generation seven of the GIFT selection line in 2009. The other three batches were produced in subsequent years, with fish from generation eight, nine and ten. All the batches were named after the year in which the fish were stocked in the experimental ponds. Table 1 shows the reproduction and management schedule for the four batches of the experiment. Refer to Ponzoni et al. (2005, 2010) for further details on selection and mating process in the GIFT breeding program. Table 2 shows a list of abbreviations used throughout the paper.

2.2. The experimental design

The common strategy of mating one male to two females (nested mating design) in the GIFT breeding program was used in the production of the fish for this experiment. The offspring were placed in groups, each consisting of two distinct families. This is the optimal group composition for estimating the indirect genetic variance (Bijma, 2010). To allocate the families in groups, we implemented a design with blocks composed of 11 full-sib families per block (Fig. 1). For better statistical power of parameter estimation, the combination of two paternal half-sib families within the same block was avoided. With the block design, each family was combined precisely once with each of the other ten families in the block, yielding 55 different family combinations per block. For example, in Fig. 1, family A was combined with families B to K to form 10 different groups. Each group consisted of 16 fish, with both families each contributing eight randomly selected progeny (see Discussion section). After hatching, the fry were separately nursed by full-sib family until they reached the tagging size of 2 to 5 g. Then, for each experimental batch, 80 fish per family were individually identified with PIT (Passive Integrated Transponder) tags before stocking in the pond (Table 3).

Two earthen ponds of size 0.1 ha were used in this experiment, except in Batch 2010 for which only one pond was used. In Batch 2010 there was high mortality during nursing (fry were over-stressed by high temperature), so that there were not enough fry to fill two ponds. In each pond, an equal number of net-cages (sized 1 m × 1.5 m, and 1.0 m depth) were installed (per pond: 182 units for Batch 2009; 144 units for Batch 2010; 171 units for Batch 2011). Each net-cage contained a single group of 16 fish. Thus the number of net-cages equaled the number of groups stocked. Each group consisted of two distinct families, which was allocated according to the description in the previous paragraph of this section. With the block design, each group was a unique combination of two families. Table 3 shows the number of families, groups and fish involved in the experiment.

During the grow-out period, the fish were fed twice a day, an amount of 3 to 5% of their average live weight, using a commercial dry pellet feed containing 32% of protein. In order to allow competition to take place among the fish, the feed was administered at a corner of the net-cage, instead of spreading it all over the surface of the net-cage (see Discussion). The water temperature, pH and dissolved oxygen level were monitored once a week.

2.3. Records

The grow-out period in net-cages was about five to eight months to reach a harvest size of 200 to 250 g on average. The fish were harvested at the end of the grow-out period. Harvesting took about one to three days (Table 1). At that time, live weight, standard length, body width, body depth, sex, tag number, net-cage label, and pond number were recorded. The details of body measurement and sexing are described in Khaw et al. (2012). The survival was recorded as 1 and 0 for survived and dead fish, respectively, at the time of harvest relative to the initial stocking data after tagging.

The age at harvest of each fish was computed based on the recorded spawning date and harvesting date. A total of 6330 fish with phenotypic

Table 1
Reproduction and management schedule.

Activities	Batch		
	2009	2010	2011
Mating	January to April	January to March	December to April 2011
Nursing	February to Aug	February to July	January to June
Stocking	01 to 03 September 30 September to 01 October[a]	05 July	27 to 28 June
Grow-out	September to April 2010	July to December	June to November
Harvest	25 to 29 April 2010	08 December	21 to 23 November

[a] The fry for Batch 2009 were stocked in two batches.

Table 2
List of abbreviations.

Abbreviation	Definition
AIC	Akaike Information Criteria
CV	Coefficient of variation
DBV	Direct breeding value
DGE	Direct genetic effect
EBV	Estimated breeding value
GIFT	Genetically improved farmed tilapia
IGE	Indirect genetic effect
LRT	Likelihood ratio test
REML	Residual maximum likelihood
SBV	Social breeding value
SD	Standard deviation
TBV	Total breeding value

Family no.	B	C	D	E	F	G	H	I	J	K
A	A-B	A-C	A-D	A-E	A-F	A-G	A-H	A-I	A-J	A-K
B		B-C	B-D	B-E	B-F	B-G	B-H	B-I	B-J	B-K
C			C-D	C-E	C-F	C-G	C-H	C-I	C-J	C-K
D				D-E	D-F	D-G	D-H	D-I	D-J	D-K
E					E-F	E-G	E-H	E-I	E-J	E-K
F						F-G	F-H	F-I	F-J	F-K
G							G-H	G-I	G-J	G-K
H								H-I	H-J	H-K
I									I-J	I-K
J										J-K

Fig. 1. Example of the block design for assignment of two families to each group. For example, Group A–B was a combination of Family A and Family B.

information (harvest live weight) over the first three batches of the experiment was used in the statistical analysis. The pedigree data for generation one to ten of GIFT were combined with the data collected in this study for (co)variance component estimation. The full pedigree consisted of 37,670 individuals. To our knowledge, this is by far the largest experiment for the estimation of IGE in aquaculture to date.

2.4. Estimation of phenotypic and genetic parameters

Variance and covariance components were estimated by residual maximum likelihood (REML) fitting an animal model with full pedigree information, implemented in ASReml (Gilmour et al., 2009). Since harvest weight records were available only on the fish that survived, the individuals with harvest weight records may represent a selected subset of the entire population. With univariate analysis, parameter estimates can be biased when the data are a non-random subset of the entire population (Pollak et al., 1984). In such cases, bivariate analysis of the trait of interest together with the selection variable can be used to avoid such bias. Thus we used bivariate analysis of harvest weight and survival. In a preliminary analysis, univariate models were fitted to find the best model for both harvest weight and survival. To improve the distribution of residuals of harvest weight, we (natural) log-transformed harvest weight. In tilapia breeding programs, maternal common environmental effects are routinely included in parameters estimation to account for non-genetic covariances between full sibs due to the shared environment before communal rearing. However, we had difficulty in estimating the genetic parameters with the maternal common environmental effects in the model. The issue of maternal common environmental effects is further discussed below. Social interactions between group mates were accounted for by including IGEs in the model for harvest weight. For survival, the estimated variance of IGEs was fixed at the boundary of zero and the effect was therefore left out of the model.

For the bivariate analysis, we fitted five different models to investigate the presence of IGEs. Model 1 was a classical animal model extended with random group-effects and random group-by-family effects. The random group-effects account for non-genetic indirect effects between group mates; such non-genetic indirect effects create a covariance between group mates that takes positive values unless groups are very small (Bergsma et al., 2008). The group-by-family effects account for differential non-genetic interactions between members of the same family versus members of different families within a group. In the following, we refer to the group-by-family effects as non-genetic kin effects. The non-genetic kin effect is further elaborated on in the Discussion section. Thus model 1 was:

$$\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix} = \begin{bmatrix}\mathbf{X}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{X}_2\end{bmatrix}\begin{bmatrix}\mathbf{b}_1\\ \mathbf{b}_2\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_{1_D} & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_{2_D}\end{bmatrix}\begin{bmatrix}\mathbf{a}_{1_D}\\ \mathbf{a}_{2_D}\end{bmatrix} + \begin{bmatrix}\mathbf{V}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{V}_2\end{bmatrix}\begin{bmatrix}\mathbf{g}_1\\ \mathbf{g}_2\end{bmatrix} + \begin{bmatrix}\mathbf{W}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{W}_2\end{bmatrix}\begin{bmatrix}\mathbf{k}_1\\ \mathbf{k}_2\end{bmatrix} + \begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix},$$

where subscript 1 refers to harvest weight and subscript 2 to survival; $\mathbf{y}$ is the vector of phenotypic observations; $\mathbf{b}$ is the vector of fixed effects; $\mathbf{a}_D$ is a vector of direct random genetic effects, $\mathbf{g}$ is a vector of random group effects; $\mathbf{k}$ is a vector of random non-genetic kin effects, and $\mathbf{e}$ is a vector of random residuals. The $\mathbf{X}$, $\mathbf{Z}_D$, $\mathbf{V}$ and $\mathbf{W}$ are the known design matrices.

Model 2 contained IGE for harvest weight, but without non-genetic kin effects,

$$\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix} = \begin{bmatrix}\mathbf{X}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{X}_2\end{bmatrix}\begin{bmatrix}\mathbf{b}_1\\ \mathbf{b}_2\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_{1_D} & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_{2_D}\end{bmatrix}\begin{bmatrix}\mathbf{a}_{1_D}\\ \mathbf{a}_{2_D}\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_{1_S}\mathbf{a}_{1_S}\\ \mathbf{0}\end{bmatrix} + \begin{bmatrix}\mathbf{V}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{V}_2\end{bmatrix} \times \begin{bmatrix}\mathbf{g}_1\\ \mathbf{g}_2\end{bmatrix} + \begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix},$$

where $\mathbf{a}_S$ is a vector of indirect random genetic effects, and $\mathbf{Z}_{1_S}$ is the corresponding design matrix.

Model 3 contained both IGE for harvest weight and non-genetic kin effects,

$$\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix} = \begin{bmatrix}\mathbf{X}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{X}_2\end{bmatrix}\begin{bmatrix}\mathbf{b}_1\\ \mathbf{b}_2\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_{1_D} & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_{2_D}\end{bmatrix}\begin{bmatrix}\mathbf{a}_{1_D}\\ \mathbf{a}_{2_D}\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_{1_S}\mathbf{a}_{1_S}\\ 0\end{bmatrix} + \begin{bmatrix}\mathbf{V}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{V}_2\end{bmatrix} \times \begin{bmatrix}\mathbf{g}_1\\ \mathbf{g}_2\end{bmatrix} + \begin{bmatrix}\mathbf{W}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{W}_2\end{bmatrix}\begin{bmatrix}\mathbf{k}_1\\ \mathbf{k}_2\end{bmatrix} + \begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix}.$$

Analyses of models with maternal common environmental effects resulted in estimates of the direct genetic variance that were not significantly different from zero. Model 4, therefore, contained maternal common environmental effects, group effects and non-genetic kin effects, but no genetic effects,

$$\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix} = \begin{bmatrix}\mathbf{X}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{X}_2\end{bmatrix}\begin{bmatrix}\mathbf{b}_1\\ \mathbf{b}_2\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_{1_C} & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_{2_C}\end{bmatrix}\begin{bmatrix}\mathbf{c}_1\\ \mathbf{c}_2\end{bmatrix} + \begin{bmatrix}\mathbf{V}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{V}_2\end{bmatrix}\begin{bmatrix}\mathbf{g}_1\\ \mathbf{g}_2\end{bmatrix} + \begin{bmatrix}\mathbf{W}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{W}_2\end{bmatrix}\begin{bmatrix}\mathbf{k}_1\\ \mathbf{k}_2\end{bmatrix} + \begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix}$$

where $\mathbf{c}$ is a vector of random maternal common environmental effects, and $\mathbf{Z}_{1_C}$ is the corresponding design matrix.

Table 3
Number of sires, dams and groups used, and the number of fish stocked and harvested, by batch.

Batch	Number of sires	Number of dams	Number of groups		Number of fish	
			Stocked	Harvested	Stocked	Harvested
2009	50	66	212	209	3350	2565
2010	30	33	45	45	720	509
2011	60	68	248	239	3958	3256
Total	140	167	505	493	8028	6330

Model 5 contained IGE, maternal common environmental effects, group effects and non-genetic kin effects, but no direct genetic effects (DGE),

$$\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix}=\begin{bmatrix}\mathbf{X}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{X}_2\end{bmatrix}\begin{bmatrix}\mathbf{b}_1\\ \mathbf{b}_2\end{bmatrix}+\begin{bmatrix}\mathbf{Z}_{1_S}\mathbf{a}_{1_S}\\ 0\end{bmatrix}+\begin{bmatrix}\mathbf{Z}_{1_C} & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_{2_C}\end{bmatrix}\begin{bmatrix}\mathbf{c}_1\\ \mathbf{c}_2\end{bmatrix}+\begin{bmatrix}\mathbf{V}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{V}_2\end{bmatrix}\times\begin{bmatrix}\mathbf{g}_1\\ \mathbf{g}_2\end{bmatrix}+\begin{bmatrix}\mathbf{W}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{W}_2\end{bmatrix}\begin{bmatrix}\mathbf{k}_1\\ \mathbf{k}_2\end{bmatrix}+\begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix}.$$

A comparison of models 4 and 5 indicates whether IGE are significant in models with maternal common environmental effects.

The fixed effects fitted for harvest weight were the interaction of batch (2009, 2010, 2011), sex (male and female) and pond (1 and 2). The linear covariate age at harvest was fitted within this interaction. In addition, we also fitted the non-nested quadratic effect of age at harvest (to accommodate the non-linear relationship between harvest weight and age) and the linear regression on social age at harvest. Social age at harvest was the average age at harvest of the group mates of an individual. This effect was included to account for age-dependent social interactions. For example, when an individual is accompanied by older group mates it may initially be smaller than its group mates, which may subsequently reduce its growth rate. For survival, we fitted the same fixed effects, except for sex, which was unknown for the dead fish, and the quadratic effect of age at harvest and social age at harvest which were not statistically significant.

The total heritable variance for response to selection in harvest weight, σ^2_{TBV}, for models 2 and 3 was calculated as, $\sigma^2_{TBV}=\sigma^2_{A_D}+2(n-1)\sigma_{A_{DS}}+(n-1)^2\sigma^2_{A_S}$, where, $\sigma^2_{A_D}$ and $\sigma^2_{A_S}$ denote the direct and indirect genetic variance, respectively; $\sigma_{A_{DS}}$ the direct–indirect genetic covariance, and n the group size (16 individuals in the present experiment) (Bijma, 2011). For model 5, total heritable variance was calculated as $\sigma^2_{TBV}=(n-1)^2\sigma^2_{A_S}$. The heritability, h^2, for harvest weight in model 1 and for survival in all models was calculated as the ratio of $\sigma^2_{A_D}$ and phenotypic variance, σ^2_P. For models 2, 3 and 5, the ratio of total heritable variance and phenotypic variance was calculated, $T^2=\sigma^2_{TBV}/\sigma^2_P$. Phenotypic variances were calculated as,

$$\begin{aligned}&\text{model 1},\sigma^2_P=\sigma^2_{A_D}+\sigma^2_g+\sigma^2_k+\sigma^2_e;\\ &\text{model 2},\sigma^2_P=\sigma^2_{A_D}+(n-1)\sigma^2_{A_S}+\sigma^2_g+\sigma^2_e;\\ &\text{model 3},\sigma^2_P=\sigma^2_{A_D}+(n-1)\sigma^2_{A_S}+\sigma^2_g+\sigma^2_k+\sigma^2_e;\\ &\text{model 4},\sigma^2_P=\sigma^2_c+\sigma^2_g+\sigma^2_k+\sigma^2_e;\\ &\text{model 5},\sigma^2_P=(n-1)\sigma^2_{A_S}+\sigma^2_c+\sigma^2_g+\sigma^2_k+\sigma^2_e.\end{aligned}$$

In principle, phenotypic variance for models 2, 3 and 5 has a term depending on relatedness among group members. However, for the purpose of comparison of phenotypic variances across different studies, we used the standardized phenotypic variance with zero relatedness, following suggestions of Bijma (2012) and Nielsen et al. (2014). Likelihood ratio tests (LRT) were used for comparison of nested models, and Akaike Information Criteria (AIC) for comparison of non-nested models.

3. Results

3.1. General

A total of 6330 fish with phenotypic information collected over three batches were included in the statistical analysis. Table 4 shows the descriptive statistics. The phenotypic means of these three batches were relatively similar (166.55 g for batch 2009, 140.34 g for batch 2010, and 169.66 g for batch 2011). We found a smaller CV of harvest weight, 36%, compared to previous studies of the GIFT strain where fish were communally reared (48% by Ponzoni et al., 2005; 59.8% by Nguyen et al., 2007; 40% by Khaw et al., 2010).

Survival was 77% for batch 2009, 71% for batch 2010 and 82% for batch 2011. This is similar to the survival observed in the ordinary GIFT population in Malaysia, which is around 80% on average (Khaw et al., 2010). Survival was calculated based on the number of fish stocked and number of fish present at harvest time with identification. The unidentified fish were excluded from the data analysis since we were unable to trace back their family. In addition, we could not be sure that those unidentified fish were the experimental fish or their progeny. Unidentified fish accounted for about 6% on average of the total number of fish harvested.

Social age at harvest was fitted as a linear covariate in all the models. In all cases the estimated regression coefficient of social age at harvest was −0.001 g per day and was statistically significant, $p < 0.01$. The negative regression coefficient indicates that the older the group mates, the greater the reduction in growth rate of an individual within the group. In standard deviation (SD) units for age at harvest (Table 4), the magnitude of the social age effect at harvest was −0.058 g (calculated as −0.001 g per day × 58.21 days), indicating that this effect was small. Hence, in spite of being statistically significant, the effect of social age at harvest resulted in negligible differences in harvest weight.

To test for robustness of the estimates, we investigated the effect of removing outliers. Outliers were defined as residuals that are more than 3.5 standard deviation in magnitude (Gilmour et al., 2009). After the removal of outliers, the parameter estimates either remained very similar (mainly for survival) or changed by 1% to 10%. There was no change in the sign of estimated correlations. Because overall the changes were negligible, all analyses presented here used the complete data set.

3.2. Estimation of phenotypic and genetic parameters

Table 5 shows the bivariate REML estimates for all the five models and their log-likelihood. Bivariate analysis significantly better fitted the data than univariate analysis, as the difference in log-likelihood of, for example, model 3 versus model 3 with all between-trait correlations fixed at zero equaled 37 (likelihood ratio test, $\chi^2_5=74$, $p<0.0001$). Therefore results are only shown for the bivariate analysis.

We had difficulty in estimating the genetic parameters when maternal common environmental effects were included in the models. When maternal common environmental effects were included, the direct and indirect genetic variances were not properly estimated and marked as "liable to change from positive definite to fixed at a boundary". Several different models with maternal common environmental effects included were tested. The ASReml outputs of all the tested models showed the log-likelihood converged. But all the genetic parameters (with or without IGEs) were not properly estimated (parameters did not converge; results not shown).

First we focus on the significance of IGE in models without maternal common environmental effects, which follows from a comparison of model 3 with model 1. A LRT showed that model 3 had a better goodness of fit than model 1 (Table 5, $\chi^2_2=12.52$, $p=0.0019$). Hence, when maternal common environmental effects were omitted, there was evidence for IGEs on harvest weight. Including IGEs in the model caused a slight increase in the direct genetic variance for both traits (model 3 versus 1 in Table 5). Although the estimated indirect genetic variance may seem small, its contribution to the total heritable variation was substantial, about 48% ($\frac{(n-1)^2\sigma^2_{A_S}}{\sigma^2_{TBV}}\times 100\%=48\%$). However, the negative

Table 4
Number of observations (N), simple mean (μ), minimum and maximum, standard deviation (σ) and coefficient variation (CV, %) of harvest weight (g), standard length (cm), depth (cm), width (cm) and age (days) at harvest for batches 2009, 2010 and 2011 combined.

Variable	N	μ	Min	Max	σ	CV
Harvest weight	6330	166.04	28.9	579.8	58.97	36
Standard length	6330	15.99	8.9	26.0	1.87	12
Depth	6330	6.96	3.9	10.5	0.96	14
Width	6330	2.91	1.4	4.4	0.42	14
Age at harvest	6330	348.62	252	450	58.21	17

Table 5
REML estimates (s.e.) from bivariate models of log-transformed harvest weight [log(hw)] and survival.

Parameters	Model 1		Model 2		Model 3		Model 4		Model 5	
	log(hw)	Survival	log(hw)	Survival	log(hw)	Survival	log(hw)	Survival	log(hw)	Survival
$\hat{\sigma}^2_{A_D}$	0.032 (0.006)	0.003 (0.002)	0.050 (0.008)	0.016 (0.004)	0.036 (0.007)	0.004 (0.002)	–	–	–	–
$\hat{\sigma}^2_{A_S}$	–	–	0.00012 (0.00004)	–	0.00007 (0.00003)	–	–	–	0.00004 (0.000026)	–
$\hat{\sigma}_{A_{DS}}$	–	–	−0.0013 (0.0004)	–	−0.0006 (0.0004)	–	–	–	–	–
$\hat{\sigma}^2_c$	–	–	–	–	–	–	0.011 (0.002)	0.003 (0.001)	0.011 (0.002)	0.003 (0.001)
$\hat{\sigma}^2_g$	0.017 (0.002)	0.025 (0.003)	0.021 (0.002)	0.032 (0.003)	0.016 (0.002)	0.025 (0.003)	0.017 (0.002)	0.025 (0.003)	0.017 (0.002)	0.025 (0.003)
$\hat{\sigma}^2_k$	0.010 (0.002)	0.016 (0.002)	–	–	0.010 (0.001)	0.015 (0.002)	0.010 (0.001)	0.014 (0.002)	0.010 (0.001)	0.014 (0.002)
$\hat{\sigma}^2_e$	0.043 (0.003)	0.109 (0.002)	0.037 (0.004)	0.109 (0.003)	0.040 (0.004)	0.108 (0.002)	0.058 (0.001)	0.110 (0.002)	0.057 (0.001)	0.110 (0.002)
$\hat{\sigma}^2_{TBV}$	–	–	0.036 (0.010)	–	0.033 (0.010)	–	–	–	0.009 (0.006)	–
$\hat{\sigma}^2_P$	0.103 (0.004)	0.153 (0.003)	0.109 (0.004)	0.157 (0.004)	0.103 (0.004)	0.153 (0.003)	0.097 (0.003)	0.153 (0.003)	0.096 (0.003)	0.153 (0.003)
$\hat{T}^2$			0.33 (0.09)		0.32 (0.09)		–	–	0.099 (0.06)	–
$\hat{h}^2$	0.31 (0.05)	0.02 (0.01)		0.10 (0.02)		0.03 (0.01)				
$\hat{c}^2$	–	–	–	–	–	–	0.12 (0.02)	0.02 (0.007)	0.12 (0.02)	0.02 (0.008)
$\hat{g}^2$	0.16 (0.02)	0.17 (0.02)	0.19 (0.02)	0.21 (0.01)	0.16 (0.02)	0.17 (0.02)	0.18 (0.02)	0.17 (0.02)	0.17 (0.02)	0.17 (0.02)
$\hat{k}^2$	0.10 (0.02)	0.10 (0.01)	–	–	0.09 (0.01)	0.10 (0.01)	0.11 (0.02)	0.09 (0.01)	0.10 (0.02)	0.09 (0.01)
$\hat{r}_{A_{D_{hw}} s_{hw}}$	–		−0.56 (0.14)		−0.38 (0.19)		–		–	
$\hat{r}_{A_{D_{hw}} D_{surv}}$	−0.28 (0.26)		−0.08 (0.13)		−0.05 (0.24)		–		–	
$\hat{r}_{A_{D_{surv}} s_{hw}}$	–		−0.46 (0.17)		−0.79 (0.30)		–		–	
LogL	9122.97		9018.34		9129.23		9135.27		9137.08	
AIC	1778.06		1987.32		1771.54		1753.46		1751.84	

direct–indirect genetic covariance fully canceled the contribution of IGE to total heritable variation ($\frac{2(n-1)\sigma_{A_{DS}}}{\sigma^2_{TBV}} \times 100\% = -55\%$). As a consequence, total heritable variance was nearly identical to the ordinary direct genetic variance, so that the T^2 from model 3 (0.32 ± 0.09) was approximately equal to the h^2 from model 1 (0.31 ± 0.05). Beware that the lack of impact on σ^2_{TBV} does not mean that IGE do not affect response to selection. Instead, the negative direct–indirect genetic correlation will decrease response to ordinary mass or BLUP selection (see Discussion).

The negative direct–indirect genetic correlation for harvest weight of -0.38 ± 0.19 indicates a moderate, yet statistically significant, competitive phenomenon in the GIFT population. The estimated direct genetic correlation between harvest weight and survival did not differ significantly from zero, -0.05 ± 0.24. However, the estimated correlation between the direct genetic effect for survival and indirect genetic effect for harvest weight was strongly negative (-0.79 ± 0.30). Thus, better survival was observed for animals with group mates showing a poor growth. This result suggests the presence of competition. The estimated parameters for survival were similar to those estimated from model 1.

Subsequently we investigated the evidence for IGEs in models including maternal common environmental effects (models 4 and 5; Table 5). A comparison of likelihoods and AIC of models 3 and 4 shows stronger evidence for maternal common environmental effects than for genetic effects. Since the full set of genetic parameters could not be estimated from models including maternal common environmental effects, we only investigated the evidence for IGE (model 5 versus 4). Based on the AIC for models 4 and 5, model 5 has the smallest AIC and was likely the best model. To test for the significance of IGEs, a LRT was performed between models 4 and 5. The test, $\chi^2_1 = 3.62$ with $p = 0.057$, suggests the presence of IGEs on harvest weight. The non-genetic random effects were robust to the inclusion or exclusion of genetic effects from the model. We also tested for the presence of social maternal common environmental effects, which were effects of the maternal environment of individuals on the growth rate of their group mates, but this effect was not significant (results not shown). Therefore, it was excluded from all models.

Based on models 3 and 5, group and non-genetic kin effects were highly significant, and contributed about 17% and 10% of the phenotypic variance for both traits, respectively. The comparison of models 2 and 3 served the purpose of testing the non-genetic kin effect. The LRT between models 2 and 3 indicated that model 3 was statistically much better than model 2 ($\chi^2_1 = 221.78$, $p < 0.0001$). The same result was found when comparing model 5 to model 2 ($\Delta AIC = AIC_2 - AIC_5 = 235.48$). Thus non-genetic kin effects were highly significant. This result demonstrates that family members in the same group were more similar than family members in different groups, even after correction for group and family effects (see discussion). The elimination of non-genetic kin effects from the model caused a substantial increase in almost all the (co)variances, except the residual variance for harvest weight. This implies that the genetic parameters may be biased when excluding non-genetic kin effects.

Table 6 shows the Spearman rank correlations between estimated breeding values from the different models. For harvest weight, the correlations between direct breeding values (DBV) and total breeding values (TBV; calculated as $TBV = DBV + (n-1)SBV$) were relatively high, ranging from 0.83 to 0.98. Whereas, the correlations between social breeding values (SBV) and TBV were moderate (0.43 for both model 2 versus model 5 and model 3 versus model 5), and a very low correlation was found between SBV and DBV, which was 0.14. For the survival trait, no IGE was fitted in models 1, 2 and 3. Therefore, all the correlations presented are between DBVs of two different models, i.e. for models 1, 2 and 3. All these correlations were moderate to high, being 0.83 (model 1 versus model 2), 0.67 (model 1 versus model 3) and 0.79 (model 2 versus model 3). These results show that model 5 in particular, produces different EBVs for harvest weight than the other models.

4. Discussion

4.1. Overall findings

When maternal common environmental effects were excluded from the model, our results show evidence for IGEs on harvest weight in Nile

Table 6
The Spearman rank correlation[a] for estimated breeding values between different models for harvest weight[b,c] (above diagonal) and survival trait[d] (below diagonal).

	Model 1	Model 2	Model 3	Model 5
Model 1		0.83	0.86	0.14
Model 2	0.83		0.98	0.43
Model 3	0.67	0.79		0.43

[a] All the correlations have p-value of <0.0001.
[b] For harvest weight, the EBVs obtained from model 1 were direct breeding values (DBV), from models 2 and 3 were total breeding values ($TBV_i = DBV_i + 15SBV_i$), and from model 5 were social breeding values (SBV).
[c] No genetic component was included in model 4 for harvest weight.
[d] Estimated breeding values obtained from models 1 to 3 for survival were DBV; no genetic component was included in models 4 and 5 for survival trait.

tilapia. However, we were unable to estimate all the direct and indirect genetic, and non-genetic parameters simultaneously. Though the estimated indirect genetic variance may seem very small, the relevant quantity is the contribution of IGE to heritable variation, which is given by $(n-1)^2\sigma^2_{A_S}$, and was large (48% of total heritable variance). Similar results were found in the few other studies on IGE in aquaculture (Brichette et al., 2001; Monsen et al., 2010; Nielsen et al., 2014). Therefore, a very small estimate of the indirect genetic variance should not be interpreted as unimportance of IGEs, particularly when group sizes are large. Based on the results, with exclusion of maternal common environmental effect from the model, we could expect that there will be a very slight change (by decimal) in almost all the random effects, except the direct genetic variance that will change in an upward direction and may be overestimated. We did not find IGEs for survival, irrespective of the inclusion or exclusion of maternal common environmental effect in the model. This may indicate the absence of such effects, but may also be due to the limited statistical power because of the low heritability of survival.

4.2. Estimation of direct and indirect genetic effects with nested mating design

In fish breeding programs, it is common practice to include maternal common environmental effect in the animal model for harvest weight (examples, Ponzoni et al., 2005; Nguyen et al., 2007; Rezk et al., 2009). The newly hatched fry are too small for individual identification and the fish from the same full-sib family are therefore nursed together until they reach tagging size. However, we were unable to estimate the genetic parameters when maternal common environmental effects were included in the models. Our results suggest that maternal common environmental effects were confounded with the DGEs, because previous analysis of larger data sets of the same GIFT population, where the fish reared communally, indicated significant direct genetic and maternal common environmental effects (Khaw et al., 2010). Furthermore, we found suggestive evidence of IGEs from model 5 that included maternal common environmental effects ($p = 0.057$). These results suggest that the difficulty of separating genetic from maternal common environmental effects was most likely due to the nested mating design, rather than the group structure used for studying IGEs.

The nested mating design of one male to two females has been the common mating strategy in GIFT and other tilapia breeding programs (for examples, Rezk et al., 2009; Attipoe et al., 2013). A classical animal model with maternal common environmental effects yields large standard errors of genetic (co)variances when a 1:2 mating design is used (Bijma and Bastiaansen, 2014). In addition, we did often not succeed in having a 1:2 mating ratio in this study. This was because not all sires successfully mated with two dams by the end of the reproduction period. Of the 140 sires that reproduced in the experiment, only 27 sires successfully mated with two dams and produced progeny for the experiment. Hence, the majority of records came from 1:1 matings, in which genetic and maternal common environmental effects are fully confounded. This increased the difficulty to separate both effects. Furthermore, we should be aware that with the 1:1 mating ratio, the maternal common environmental effect also contained the dominance covariance between full-sibs. In the ordinary GIFT breeding program population, the number of sires succeeding in mating with both dams was about 12% higher than in this study, and the data set is much larger.

In model 5 with maternal common environmental effects, the only genetic term included were IGEs, because direct effects were omitted. Hence, since IGEs were the only genetic term, this may suggest that they capture direct genetic variance and therefore be overestimated. However, in our block design (Fig. 1), each family was combined with another specific family only once. Consequently, presence of direct genetic variance does not create a covariance between the members of families with which a family is combined into groups. Hence, in the block design, IGE cannot account for covariances among records that originate from direct genetic effects. Instead, the direct genetic variance will contribute to the variance of maternal common environmental effects. Thus we do not expect that omission of direct genetic effects leads to overestimation of IGE in model 5.

To solve the problem with confounding of genetic and maternal common environmental effects, a more powerful mating structure may need to be implemented. For example, a mating ratio of 1:5 or a factorial mating design. Most tilapia breeding programs are using a natural reproduction technique, with a pair of "ready to spawn" parents placed in a hapa (for examples, see Rezk et al., 2009; Attipoe et al., 2013; A hapa is a fixed net enclosure which is made out of polyethylene netting with joints in nylon thread). For implementing a more complex mating structure, in vitro fertilization (IVF) and hormone induction techniques could be used (Fernandes et al., 2013). Alternatively, a group mating design could be used, where one male mates to multiple females under natural spawning conditions (Trọng et al., 2013).

Irrespective of the mating technology used, however, a persistent problem is that designs optimal for parameter estimation may be undesirable for long term genetic improvement. In aquaculture breeding programs, limited facilities often restrict the number of full sib families that can be used. Hence, the use of, for example, a 1:5 mating ratio instead of 1:2 would result in fewer sires per generation, substantially decreasing effective population size and threatening long-term genetic improvement. The 1:2 mating ratio is used in the GIFT program because the main aim is to produce a superior strain, rather than accurate genetic parameters.

The Spearman rank correlations (0.43; Table 6) obtained from estimated TBV and SBV for harvest weight indicated that the ranking of the fish based on these two estimated breeding values differ. On the other hand, the correlations obtained between estimated DBV and TBV for harvest weight were relatively high, which indicates that the ranking of the fish on EBV is similar with both models. In addition, the ranking of fish based on DBV and SBV was very different. For survival, the correlations between DBV of two different models indicated that the ranking of fish were more similar between models 1 and 2 compared to between models 2 and 3. The low correlation between EBVs from models 1, 2 and 3 versus model 5 indicate that inclusion of IGEs may have substantial effects on selection decisions. Hence, knowledge of IGEs is important for the GIFT breeding program.

4.3. Heritable competition

Based on model 3, the estimated direct–indirect genetic correlation for harvest weight indicated moderate competition in the GIFT population. This competition almost completely canceled the heritable variation contributed by IGE. The fact that presence of IGEs did not alter

total heritable variation, $\sigma^2_{TBV} \approx \sigma^2_{A_D}$, does not imply that response to selection is unaffected by IGEs. The negative direct–indirect genetic covariance will reduce the accuracy of selection, which in turn reduces response. For mass-selection, for example, the true accuracy is given by

$$\rho = \frac{\sigma^2_{A_D} + (n-1)\sigma_{A_{DS}}}{\sigma_{TBV}\sigma_P} = 0.46$$

when fish are reared in groups composed at random with respect to family (Ellen et al., 2007; Griffing, 1967). The perceived accuracy when IGEs are ignored equals $\sqrt{h^2} = 0.59$, which is 29% higher than the true accuracy. Hence, when ignoring IGEs, response to selection will be over-predicted by 29%. Moreover, the negative direct–indirect genetic correlation indicates that selection for individual performance will increase competition when fish are kept in groups composed at random with respect to family (Ellen et al., 2007), at least, in competitive environments. This increase in competition can be avoided by using groups composed of related individuals (Ellen et al., 2007; Griffing, 1967).

Results of model 3 suggest competition in the competitive environment studied here. Besides reducing the performance of the fish, competition may also reduce the welfare of the fish. With the empirical evidence from livestock, selection on total breeding values (which includes IGEs) could simultaneously improve productivity and welfare of the animals (Camerlink et al., 2012; Ellen et al., 2008; Muir, 1996; Muir et al., 2013; Nielsen et al., 2014). In addition, Nielsen et al. (2014) demonstrated that accounting for IGEs in Atlantic cod breeding will improve selection response for welfare traits. Note, however, that they did not demonstrate a similar phenomenon for growth traits. Further study is needed to investigate whether this also applies to Nile tilapia.

4.4. Group effects and non-genetic kin effects

Our results showed that group effects contributed about 16 to 21% of the phenotypic variance. This is high compared to other genetic and non-genetic effects in the models. This indicates that group mates have similar trait values, which is probably a result of the common social environment experienced by group mates, as net-cages were physically identical. In addition, we found that the exclusion of group effects inflated the estimated heritable variation for both traits (results not shown). This is consistent with previous studies showing that the removal of group effects from the model causes an upward bias in the genetic estimates (Bergsma et al., 2008; van Vleck and Cassady, 2005). Hence, allowing for random group effects in the model is essential when fitting IGE (see also Cantet and Cappa, 2008 for a discussion on group effects).

In this study, we also fitted a random effect for the interaction of group by family to account for non-genetic kin effects. This effect was highly significant and explained about 9 to 11% of the phenotypic variance. This result indicates that family members in the same group show similar trait values, even after correction for group effects and family effects. This suggests that individuals interact differently with their family members than with the members of the other family in the same group, suggesting kin-recognition (Brown and Brown, 1993; Olsén, 1989; Olsén et al., 1998). From an evolutionary perspective, preferential behavior towards kin is expected because it increases an individual's so-called inclusive fitness (Hamilton, 1964). Kin recognition has been found before in salmonids (Brown and Brown, 1993; Olsén, 1989), and also in tilapia (*Sarotherodon melanotheron* samples from a wild population; Pouyaud et al., 1999). The presence of kin-specific behavior may complicate the selection for IGE, because IGEs on kin may differ from those on unfamiliar individuals (Alemu et al., 2014). Alternatively, the non-genetic kin effect may originate from environmental variation between groups together with differential sensitivity of families to such environmental variation. In other words, genotype by environment interaction could cause the non-genetic kin effects we found here. Furthermore, the results showed that the exclusion of non-genetic kin effects caused an upward bias for almost all estimated parameters. Thus, the inclusion of non-genetic kin effects in the model was essential.

4.5. Implications for aquaculture production

Social interactions for aquaculture species at commercial level are not documented and their effect is unknown. This could be because direct observation of fish behavior is costly, and behavior is difficult to record in large groups of fish. Nevertheless, it is reasonable to postulate that competition varies with the production system and feeding regime. For instance, fish are kept at high densities in floating cages, cement tanks and re-circulating systems, but at lower densities in earthen ponds. In this study, one of the key questions is whether IGEs found here are representative of IGEs occurring in commercial farms, where fish are usually reared communally in very large groups and high density.

At commercial farms, the feeding is always unrestricted in terms of amount and accessibility. This is with the purpose to prevent any competition for resources that may happen in the population. In our experiment, the nutrient composition and amount of feed were the same as in the GIFT selective breeding population (no restriction on feeding quantity, examples, Ponzoni et al., 2005). The difference was that fish were kept in small net-cages where feed was deposited at the corner of the cage, which provided a competitive environment. In communal rearing for GIFT population, the feed is spread over the surface of the pond, which may provide a less competitive environment (similar to commercial farm). Note, no auto-feeder is used and the feed is usually not spread over the entire surface. Therefore, it is difficult to judge whether our set-up increased or decreased competition compared to a communal rearing environment. However, based on the CVs for harvest weight in both environments (competitive and less competitive), the size of fish in communal rearing environment varies more than those in the net-cages (examples, 48% by Ponzoni et al., 2005; 59.8% by Nguyen et al., 2007; 40% by Khaw et al., 2010). This suggests that the feeding method did not further increase the competition which may already exist in the population. Thus, further experiments with no restriction on the access to feed using the same experimental design may be useful to validate the above assumption.

Besides the feeding regimes, the stocking density at commercial farms is higher than in this study. For example, a commercial farm with intensive system may stocks 1500 fish per square meter (FAO, 2014). In our experiment, the stocking density was about 11 fish per square meter. For socially affected traits, the total genetic variance and selection response depend on the relationship between group size and the IGEs (Bijma, 2012). In a larger group, the social interaction between a particular pair of animals may be less and this phenomenon is named 'dilution' (Bijma, 2012). So far, from our knowledge, there have been no studies on the degree of dilution for aquaculture species under commercial level. This is mainly because IGEs can only be estimated with data coming from many groups (Bijma, 2012), similar to the experimental design presented in this study. Hence, more experiments and validations need to be done before we can draw any conclusion on the relevance of IGE on commercial aquaculture industry.

5. Conclusions

Our study is the first large-scale IGE experiment in an aquaculture species. Unfortunately, confounding between maternal common environmental and genetic effects prevented simultaneous estimation of all parameters. Models without maternal common environmental effects showed significant evidence for IGE on harvest weight in Nile tilapia, while a model with such effects suggested the presence of IGE

($p = 0.057$). In models without maternal common environmental effects, the estimated genetic correlation between direct and indirect genetic effects on harvest weight was negative, indicating that traditional selection will increase competition among individuals in the environment of our study. We also found a strongly negative genetic correlation between direct effects on survival and indirect effects on harvest weight, indicating that individuals with better genes for survival had group mates with lower growth rate in the competitive environment that prevailed in our experiment. The confounding between maternal common environmental effects and DGEs indicated that the one male to two females nested mating design has limited power to estimate the genetic parameters. We have to be aware that other mating designs may allow more accurate estimation of genetic parameters, but may be suboptimal for long-term genetic improvement in schemes where the number of families is limited. Furthermore, more investigation is needed on the implications of IGEs on commercial aquaculture industry, where competition among fish varies depending of the production system and feeding regime.

Acknowledgments

The contributions of PB and HLK were funded by the Technology Foundation STW of the Netherlands Organisation for Scientific Research (NWO). The GIFT breeding program in Malaysia is funded by the European Union and contributes to the CGIAR Research Program on Livestock and Fish.

References

Adams, C.E., Huntingford, F.A., Turnbull, J.F., Arnott, S., Bell, A., 2000. Size heterogeneity can reduce aggression and promote growth in Atlantic salmon parr. Aquac. Int. 8, 543–549.
Alemu, S.W., Berg, P., Janss, L., Bijma, P., 2014. Indirect genetic effects and kin recognition: estimating IGEs when interactions differ between kin and stranger. Heredity 112, 197–206.
Attipoe, F.Y.K., Blay Jnr, J., Agyakwah, S., Ponzoni, R.W., Khaw, H.L., Abban, E.K., 2013. Genetic parameters and response to selection in the development of Akosombo strain of the Nile tilapia, *Orechromis niloticus*, in the Volta Basin, Ghana. Proceedings From 10th International Symposium on Tilapia Aquaculture: 6–10 October 2013; Jerusalem. Israel.
Bergsma, R., Kanis, E., Knol, E.F., Bijma, P., 2008. The contribution of social effects to heritable variation in finishing traits of domestic pigs (*Sus scrofa*). Genetics 178, 1559–1570.
Bijma, P., 2010. Estimating indirect genetic effects: precision of estimates and optimum designs. Genetics 186, 1013–1028.
Bijma, P., 2011. A general definition of heritable variation that determines the potential of a population to response to selection. Genetics 189, 1347–1359.
Bijma, P., 2012. Socially affected traits, inheritance and genetic improvement. In: Meyers, R.A. (Ed.), Encyclopedia of Sustainability Science and Technology. Springer, New York, pp. 9358–9394.
Bijma, P., 2014. The quantitative genetics of indirect genetic effects: a selective review of modeling issues. Heredity 112 (1), 61–69.
Bijma, P., Bastiaansen, J.W.M., 2014. The standard error of the genotype-by-environment genetic correlation: how much data do we need to estimate a purebred-crossbred genetic correlation? Genet. Sel. Evol. 46, 79.
Brichette, I., Reyero, M.I., García, C., 2001. A genetic analysis of intraspecific competition for growth in mussel cultures. Aquaculture 192, 155–169.
Brown, G.E., Brown, J.A., 1993. Social dynamics in salmonid fishes: do kin make better neighbours? Anim. Behav. 45, 863–871.
Camerlink, I., Bijma, P., Kemp, B., Bolhuis, J.E., 2012. Relationship between growth rate and oral manipulation, social nosing, and aggression in finishing pigs. Appl. Anim. Behav. Sci. 142, 11–17.
Cantet, R.J.C., Cappa, E.P., 2008. On identifiability of (co)variance components in animal models with competition effects. J. Anim. Breed. Genet. 125, 371–381.
Ellen, E.D., Muir, W.M., Teuscher, F., Bijma, P., 2007. Genetic improvement of traits affected by interactions among individuals: sib selection schemes. Genetics 176, 489–499.
Ellen, E.D., Visscher, J., van Arendonk, J.A.M., Bijma, P., 2008. Survival of laying hens: genetics parameters for direct and associative effects in three purebred layer lines. Poult. Sci. 87, 233–239.
FAO, 2012. The State of World Fisheries and Aquaculture 2012. Publishing Policy and Support Branch, Rome.
FAO, 2014. Diversification of aquaculture activities and production methods. Available, http://www.fao.org/fileadmin/templates/SEC/docs/Fishery/cage/3DAAPM_en.pdf (Consulted on July 30th, 2014).
Fernandes, A.F.A., Alvarenga, É.R., Oliveira, D.A.A., Aleixo, C.G., Prado, S.A., Luz, R.K., Sarmento, N.L., Teixeira, E.A., Luz, M.R., Turra, E.M., 2013. Production of oocytes of Nile tilapia (*Oreochromis niloticus*) for in vitro fertilization via hormonal treatments. Reprod. Domest. Anim. 48, 1049–1055.
Gilmour, A.R., Gogel, B.J., Cullis, B.R., Welham, S.J., Thompson, R., 2009. ASReml User Guide, Release 3.0. VSN, Hemel Hempstead, UK.
Griffing, B., 1967. Selection in reference to biological groups I. Individual and group selection applied to populations of unordered groups. Aust. J. Biol. Sci. 20, 127–139.
Hamilton, W.D., 1964. The genetic evolution of social behaviour. I. J. Theor. Biol. 7, 1–16.
Hill, W.G., Mulder, H.A., Zhang, X.S., 2007. The quantitative genetics of phenotypic variation in animals. Acta Agric. Scand. Sect. A 57, 157–182.
Jobling, M., 1995. Simple indices for the assessment of the influences of the social environment on growth performance, exemplified by studies on Arctic charr. Aquac. Int. 3, 60–65.
Khaw, H.L., Ponzoni, R.W., Hamzah, A., Nguyen, N.H., Abu-Bakar, K.R., Yee, H.Y., 2010. Genetic analysis of the GIFT strain (Nile Tilapia, *Oreochromis niloticus*) in Malaysia. Proceedings From 9th World Congress on Genetics Applied to Livestock Production, 1–6 August 2010. Leipzig. Germany (no. 0920).
Khaw, H.L., Ponzoni, R.W., Hamzah, A., Abu-Bakar, K.R., Bijma, P., 2012. Genotype by production environment interaction in the GIFT strain of Nile tilapia (*Oreochromis niloticus*). Aquaculture 326–329, 53–60.
Kinghorn, B.P., 1983. A review of quantitative genetics in fish breeding. Aquaculture 31, 283–304.
Monsen, B.B., Ødegård, J., Nielsen, H.M., Arnesen, K.R., Toften, H., Damsgård, B., Bijma, P., Olesen, I., 2010. Genetics of social interactions in Atlantic cod (*Gadus morhua*). Proceedings From 9th World Congress on Genetics Applied to Livestock Production: 1–6 August 2010; Leipzig. Germany (no. 910).
Moore, A.J., Brodie III, E.D., Wolf, J.B., 1997. Interacting phenotypes and the evolutionary process: I. Direct and indirect genetic effects of social interactions. Evolution 51, 1352–1362.
Moyle, P.B., 1969. Comparative behavior of young brook trout of domestic and wild origin. Prog. Fish Cult. 31, 51–59.
Muir, W.M., 1996. Group selection for adaptation to multiple-hen cages: selection program and direct responses. Poult. Sci. 75, 447–458.
Muir, W.M., 2005. Incorporation of competitive effects in forest tree or animal breeding program. Genetics 170, 1247–1259.
Muir, W.M., Bijma, P., Schinckel, A., 2013. Multilevel selection with kin and non-kin groups, experimental results with Japanese quail (*Coturnix japonica*). Evolution 67–6, 1598–1606.
Nguyen, N.H., Khaw, H.L., Ponzoni, R.W., Hamzah, A., Kamaruzzaman, N., 2007. Can sexual dimorphism and body shape be altered in Nile tilapia by genetic means? Aquaculture 272S1, S38–S46.
Nielsen, H.M., Monsen, B.B., Ødegård, J., Bijma, P., Damsgård, B., Toften, H., Olesen, I., 2014. Direct and social genetic parameters for growth and fin damage traits in Atlantic cod (*Gadus morhua*). Genet. Sel. Evol. 46, 5. http://dx.doi.org/10.1186/1297-9686-46-5.
Olsén, K.H., 1989. Siblings recognition in juvenile artic charr, *Salvelinus alpinus* (L.). J. Fish Biol. 34, 571–581.
Olsén, K.H., Grahn, M., Lohm, J., Langefors, Å., 1998. MHC and kin discrimination in juvenile Arctic charr, *Salvelinus alpinus* (L.). Anim. Behav. 56, 319–327.
Peeters, K., Eppink, T.T., Ellen, E.D., Visscher, J., Bijma, P., 2012. Indirect genetic effects for survival in domestic chickens (*Gallus gallus*) are magnified in crossbred genotypes and show a parent-of-origin effect. Genetics 192, 705–713.
Pollak, E.J., van der Werf, J., Quaas, R.L., 1984. Selection bias and multiple trait evaluation. J. Dairy Sci. 67, 1590–1595.
Ponzoni, R.W., Hamzah, A., Tan, S., Kamaruzzaman, N., 2005. Genetic parameters and response to selection for live weight in the GIFT strain of Nile tilapia (*Oreochromis niloticus*). Aquaculture 247, 203–210.
Ponzoni, R.W., Khaw, H.L., Nguyen, N.H., Hamzah, A., 2010. Inbreeding and effective population size in the Malaysian nucleus of the GIFT strain of Nile tilapia (*Oreochromis niloticus*). Aquaculture 302, 42–48.
Pouyaud, L., Desmarais, E., Chenuil, A., Agnese, T.F., Bonhomme, F., 1999. Kin cohesiveness and possible inbreeding in the mouthbrooding tilapia *Sarotherodon melanotheron* (Pisces Cichlidae). Mol. Ecol. 8, 803–812.
Purdom, C.E., 1974. Variation in fish. In: Harden Jones, F.R. (Ed.), Sea Fisheries Research. Elek Science, London, pp. 347–355.
Rezk, M.A., Ponzoni, R.W., Khaw, H.L., Kamel, E., Dawood, T., John, G., 2009. Selective breeding for increased body weight in a synthetic breed of Egyptian Nile tilapia, *Oreochromis niloticus*: response to selection and genetic parameters. Aquaculture 293, 187–194.
Ruzzante, D.E., Doyle, R.W., 1991. Rapid behavioral changes in Medaka (*Oryzias latipes*) caused by selection for competitive and noncompetitive growth. Evolution 45 (8), 1936–1946.
Ruzzante, D.E., Doyle, R.W., 1993. Evolution of social behavior in a resource-rich structured environment: selection experiments with Medaka (*Oryzias latipes*). Evolution 47 (2), 456–470.
Swain, D.P., Riddell, B.E., 1990. Variation in agonistic behavior between newly emerged juveniles from hatchery and wild populations of coho salmon, *Oncorhynchus kisutch*. Can. J. Fish. Aquat. Sci. 47, 566–571.
Trọng, T.Q., van Arendonk, J.A.M., Komen, H., 2013. Genetic parameters for reproductive traits in female Nile tilapia (*Oreochromis niloticus*): I. Spawning success and time to spawn. Aquaculture 416–417, 57–64.
van Vleck, L.D., Cassady, J.P., 2005. Unexpected estimates of variance components with a true model containing genetic competition effects. J. Anim. Sci. 83, 68–74.
van Vleck, L.D., Cundiff, L.V., Koch, R.M., 2007. Effect of competition on gain in feedlot bulls from Hereford selection line. J. Anim. Sci. 85, 1625–1633.
Waddington, C.H., 1960. Experiments on canalizing selection. Genet. Res. 1, 140–150.
Wilson, A.J., Morrissey, M.B., Adams, M.J., Walling, C.A., Guinness, F.E., Pemberton, J.M., Clutton-Brock, T.H., Kruuk, L.E.B., 2011. Indirect genetics effects and evolutionary constraint: an analysis of social dominance in red deer, *Cervus elaphus*. J. Evol. Biol. 24, 772–783.