Norwegian University of Life Sciences
Faculty of Biosciences
Department of Animal and Aquacultural Sciences

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Establishment of a base population for long-term genetic improvement of Nile tilapia in Ethiopia

Etablering av en basepopulasjon for et langsiktig avlsprogram for Niltilapia i Etiopia

Kassaye Balkew Workagegn

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Dedication

To my lovely father Balkew Workagegn, who I missed you just before the end of my PhD study. YOU are always in my heart. I will forever CHERISH. God place you on his right, “Amen” (Matthew 25:33).

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Ås, December 2018

Kassaye Balkew Workagegn

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SUMMARY

The success of genetic improvement obtained in fish breeding programs depends on the genetic diversity of the founder populations and how the base population is constructed, as they influence the genetic variation of the traits in the breeding goal. Therefore, the current study was initiated to establish a base population for long-term genetic improvement of Nile tilapia, *Oreochromis niloticus,* in Ethiopia. To this end, the base population was produced by a complete diallel cross of three Nile tilapia strains collected from three Ethiopian Rift Valley Lakes, Ziway, Koka and Chamo. For this study, 81 and 99 full-sib families were produced in the F_1 and in the F_2 generations, respectively. From each full-sib family, 20 to 30 fingerlings were randomly selected and tagged using Passive Integrated Transponder tags and reared in low and high input production systems. Genetic parameters for different body traits, such as body weight recorded at 5 months age in F_1 and F_2 and body weight and fillet traits recorded at 7 months in F_1were studied (Paper I-III). Fillet traits were also predicted using body measurements recorded on live fish (Paper II). Lastly, genetic gain and correlated responses for those traits were estimated (Paper III) using a bivariate animal model.

Most of the crossbreed had better growth performance than the purebreds (Paper I), and the total/direct heterosis effect for the different strain combinations ranged from 4.9% - 26.5%, with the largest values in the low input production system. Most of the total heterosis effects were significantly different from zero ($P < 0.05$). But, there were no significant differences ($P > 0.05$) among strains and strain combinations with respect to the additive, general reciprocal or total heterosis effects. The estimates of heritability for harvest body weight, defined as separate traits in the two production systems, were moderate; 0.16 and 0.37 in the low and in the high input production systems, respectively. The estimated genetic correlation between the traits were 0.96, which does not initially motivate environmental specific breeding programs in Ethiopia (Paper I).

The results presented in paper II revealed that body measurements on live Nile tilapia is well suited to predict fillet weight, but not fillet yield (R^2= 0.945 and 0.209, respectively). Body weight, fillet weight and predicted body weight were all estimated with a heritability around 0.25, and with very high internal genetic correlations ($\geq$ 0.82), but for fillet yield the heritability (0.05) and genetic correlations to the other traits were low ($\leq$0.39). No significant differences among strains and strain combinations were found for their additive, general reciprocal or heterosis effects, although the total heterosis effect for body weight, fillet weight and predicted fillet weight were significantly different from zero ($P < 0.05$).

The results presented in Paper III showed that body weight and fillet weight were considerably heritable ($\geq$0.33) with internally high positive genetic correlations ($\geq$ 0.96), while fillet yield had a low heritability (0.04) and low genetic correlation with other traits (-0.018). Moderate genetic gain (7.1%) was obtained for increased body weight over one generation of selection. The correlated responses in fillet weigh was also relatively moderate (6.8%) as compared with the value for fillet yield (0.09%). For all the traits included in this study, the estimates of strain additive and general reciprocal effects were not significantly different from zero ($P > 0.05$). However, most of the heterosis effects for body weight, fillet weight and predicted fillet weight were significantly different from zero ($P < 0.05$), but not significant for internally differences.

In conclusion, body measurements from live Nile tilapia is well suited to predict fillet weight, giving acceptable heritability. Moderate estimates of heterosis for body weight and fillet weight of Nile tilapia were achieved using the described selection breeding strategy. In this regard, crossbreeding program for Nile tilapia based on individuals from the existing population utilising non-additive genetic effects seem favourable, although pure breeding scheme should also be considered. However, the decision of what breeding program to choose should be based on a cost-benefit analysis.

SAMMENDRAG

Avlsmateriale av høy kvalitet er avgjørende for å sikre produktivitet, lønnsomhet og god ressursbruk i enhver akvakulturproduksjon. For å oppnå dette ble det samlet inn Niltilapia (Oreochromis niloticus) for å etablere en solid basepopulasjon og starte et avlsprogram for denne arten i Etiopia. Basepopulasjonen ble etablert ved å først testkrysse tre stammer av Niltilapia: Ziway, Koka og Chamo. Disse var samlet fra tre ulike innsjøer i Riftdalen. I hver av de to generasjonene som til nå har blitt produsert fra denne basen ble det laget 180 familier tilsammen, 81 i F_1 og 99 i F_2. Fra hver familie ble ca 30 yngel valgt ut og merket ved hjelp av elektroniske merker (PIT-tags) og satt ut i to ulike produksjonssystemer, et med intensiv fôring og et med mindre intensiv fôring.

Det har i denne studien blitt beregnet genetiske parametere for en rekke egenskaper hos Niltilapia (Artikkel 1-3). I tillegg ble det laget prediksjonsligninger for filetegenskaper, basert på målinger som kan gjøres på levende fisk (Artikkel 2), og til slutt ble genetisk fremgang og korrelert respons for de ulike egenskapene beregnet (Artikkel 3).

Det ble det funnet signifikante forskjeller i tilvekst, både for de ulike rene Niltilapiastammene og for de ulike stammekombinasjonene. Hybrid/krysningsavkom hadde bedre tilvekst enn de som ikke var krysningsavkom (Artikkel 1). Heterosis for de ulike stammekombinasjonene var i gjennomsnitts på 13.6%, men varierte fra 6 til 26 %. Kun i krysningene mellom Ziway og Koka var denne effekten ikke signifikant. Det var heller ingen signifikante forskjeller mellom stammene, hverken med hensyn til additive genetiske effekter eller resiproke effekter, dvs. forskjellen på om en stamme er brukt som mor eller far. Arvbarhetsestimatene for egenskapen tilvekst var på 16 % ved mindre intensiv fôring og 37 % ved intensiv fôring. Den genetiske korrelasjonen for tilvekst i de to testmiljøene var meget høy (0,99), noe som tilsier at det ikke er nødvendig med separate avlsprogram for de to driftsformene som her ble testet.

I artikkel 2 er det laget prediksjonslikninger for filetvekt og filetutbytte. For filetvekt fant en at den beste modellen forklarte hele 94,5% av den observerte variansen, mens den beste modellen bare kunne forklare 21% av variansen for filetutbytte. Arvbarhetsestimatene for tilvekst, filetvekt og predikert filetvekt var på 23 til 28 %, med svært høye genetiske korrelasjoner mellom egenskapene ($\geq$ 0,93), mens estimatene var svært lave for filetutbytte, med en arvbarhet på kun 5 % og genetiske korrelasjoner under 0,39. Ingen signifikante forskjeller mellom stammer ble funnet for additive genetiske-, resiproke- eller heterosis-effekter i denne første generasjonen, selv om total heterosis var signifikant forskjellig fra null ($p < 0,05$).

Målt genetiske framgang for økt tilvekst etter en generasjons seleksjon var på 7,1 % (artikkel 3). Det er også beregnet korrelert genetiske fremgangen for filetegenskapene når en kun selekterer for egenskapen økt tilvekst, og denne var som forventet svakere, fra 0 til 5,4 %. Bortsett fra for filetutbytte (4 %), viste egenskapene god arvbarhet, fra 24 til 37 %. Det ble funnet signifikante forskjeller mellom stammene mht. resiproke krysningseffekter, mens de additive stammeeffektene ikke var signifikant forskjellige. Flere av heterosiseffektene var signifikant forskjellig fra null også i denne studien.

Det kan konkluderes med at det er mulig å bruke målinger fra levende Niltilapia til å predikere filetvekt, noe som er viktig for å kunne selektere effektivt for denne egenskapen. Filetutbytte er derimot ikke en velegnet egenskap for seleksjon, først og fremst fordi den har lav arvbarhet. Det ble oppnådd godseleksjonsrespons for tilvekst og filetvekt i Niltilapia vha. den avlsstrategien som er beskrevet og brukt. De heterosiseffektene som er funnet kan tyde på at det er grunn til å starte et krysningsavlsprogram for Niltilapia, dvs. med henblikk på å utnytte både additive og ikke-additive genetiske effekter, slik det gjøres for fjørfe og gris. Alternativt kan en basere programmet på såkalt renavl, der en kun utnytter den additive genetiske variasjonen, slik det gjøres f.eks. for laks, storfe og sau.

LIST OF PAPERS

I. K. B. Workagegn, G. Klemetsdal, E. Dadebo and H. M. Gjøen. **Additive, reciprocal and heterosis effects for harvest body weight in a complete diallel cross of three Nile tilapia (*Oreochromis niloticus*) strains.** *(Submitted to Aquaculture)*

II. K. B. Workagegn, G. Klemetsdal, E. Dadebo and H. M. Gjøen. **Prediction of fillet weight and fillet yield from body measurements and genetic parameters in a complete diallel cross of three Nile tilapia (*Oreochromis niloticus*) strains.** *(Submitted to Aquaculture)*

III. K. B. Workagegn, G. Klemetsdal, E. Dadebo and H. M. Gjøen. **Selection response over one generation of selection for increased body weight of Nile tilapia in Ethiopian.** *(Manuscript)*

1. GENERAL INTRODUCTION

The growth of aquaculture production in many developing countries has served as an incentive for the development of superior strains of different fish species through selective breeding programs, e.g. Komen & Trong (2014) reported that Nile tilapia has large number of breeding programs, with a remarkable genetic progress. One of the most recognised fish breeding programs for tilapia is the Genetic Improvement of Farmed Tilapias (GIFT), producing one of the best performing tilapia strains available (Eknath *et al.,* 1993; Bentsen *et al.,* 1998). The base population of the GIFT strain was produced from a complete diallel cross of eight Nile tilapia strains collected from African and Asian countries (Eknath *et al.,* 1993). Nowadays, the GIFT-strain is widely distributed in Asia, America and Africa. The GIFT and its derived strains have contributed to dramatic increase in global tilapia production particularly in Asia (Komen & Trong, 2014). For instance, the GIFT and its derived strains contributed for nearly 70% of tilapia seed production in Philippines, 46% in Thailand and 37% in Vietnam (Eknath & Hulata, 2009). Many GIFT-derived strains are produced by other breeding programs, such as the GenoMar Supreme Tilapia program (Gjøen, 2003) using GIFT genetic materials.

Although tilapia is originating from Africa, the continents production is relatively low compared to the global tilapia production (Neira, 2009). Some of the main challenges to increased tilapia production in Africa, particularly in Ethiopia, are lack of improved brood stock, lack of quality fish diet, lack of skilled manpower and often poor production management (Lind *et al.,* 2012; Rothuis *et al.,* 2012).

Therefore, it becomes important to develop strains that can maintain optimal production performance under a wide range of production environments. This requires quantifying the magnitude of their additive, reciprocal and heterosis effects as well as evaluation of genotype

by environment interaction to use as basis for long-term selective breeding program in Ethiopia.

1.1. Aquaculture in Ethiopia

Aquaculture production in Ethiopia is still very low, although the country is highly suitable for developing this sector (MoARD, 2009; Rothuis *et al.*, 2012). For the last few decades, aquaculture practices in Ethiopia have been limited to introduce freshwater fish to several water bodies. Due to the adaptability to a wide range of environments and consumer preferences, Nile tilapia has been stocked in many natural and man-made water bodies (FAO, 2005). In the last few years, there has been significant increase in the total fish production, from 15,134 tons in 2001 (FAO, 2004) to more than 50,148 tons in 2015 (Alebachew *et al.*, 2016; Muluken, 2017), in which half of the production comes from aquaculture (Rothuis *et al.*, 2012).

Among all fish species produced in Ethiopia from both aquaculture and fisheries, Nile tilapia is the most widely captured/cultured fish, contributing to about 50% of the total fish production, followed by African catfish and common carp (Muluken, 2017). Despite the increase in fish production, the gap between fish demand and supply has been increasing over the years. This increase demand results from change in fish eating habits with time, increase meat price and human population growth (Rothuis *et al.*, 2012).

Recently, extensive and semi-intensive pond-based culture systems have become common practices. In most cases, the ponds are normally fertilised with animal manure, with or without supplementary feed, resulting in suboptimal production. To enhance productivity and profitability of aquaculture production, farmers need not only cost-effective production systems and quality fish feed, but also reliable sources of fingerlings that perform well under a wide range of production environments (Camara & Symonds, 2014).

1.2. Selective breeding schemes

A selective breeding program is a tool through which the genetic potential of a population can be enhanced, one generation after the other through selection. Selection are able to improve economically important traits of cultured fish species, by selecting desirable quantitative traits in a population (Gjedrem *et al.*, 2012; Xu *et al.*, 2015).

A well-defined selective breeding strategy should, therefore, target to maximise genetic gain for traits of interest for a certain number of production cycles, at a predefined rate of inbreeding and with a given capacity of the testing facilities (Sonesson & Meuwissen, 2000). The simplest selection method, phenotypic or individual selection, requires the least, in terms of ponds, equipment and organisation, to start a breeding program. Whereas family and combined selections required more infrastructure, such as breeding hapas, nursery hapas and tagging

Identifying an appropriate selection method together with appropriate mating design, number of family and number of individuals per families which they are mentioned later in this thesis are fundamental to effectively utilise the available resources. Knowledge of reproductive biology and fecundity, as well as genetic characteristics of target fish species are also crucial before designing selective breeding program (Gjedrem, 2005; Kristjánsson &Arnason, 2014). For instance, the reproductive biology of fishes with external fertilisation with a capacity to produce large number of eggs and the possibility to strip and collect eggs and milt makes it possible to obtain a wide variety of mating designs. In many fish species a high male and female fecundity, typically resulting in large maternal and parental full-sibs families (Ødegård *et al.*, 2014).

1.2.1. Breeding goal

Breeding goal is defined with respect to traits of interest for a given species undergoing genetic improvement. In many cases selective breeding programs can focus on cumulative short-term

genetic improvement of the traits, directed by market economic values. Alternatively, for sustainable genetic improvement of traits, long-term selective breeding goal can be set (Hamzah *et al.*,2014). To achieve the latter breeding goal, breeders need to focus on long-term biological, ecological and sociological conditions. In both cases, traits included in the breeding goal must be heritable and measurable (Gjedrem, 2005).

Several studies have shown that Nile tilapia production systems have focused on improving growth traits to increase production efficiency and thus are using body weight as the main breeding trait in the breeding goal (Ponzoni *et al.*,2005; Thodesen *et al.*,2011; Bentsen *et al.*,2012; Hamzah *et al.*,2014; Garcia *et al.*, 2017). In addition, with a tendency of fillets becoming the main commodity, fillet weight has now also grown in popularity as a target trait (Nguyen *et al.*, 2010; Garcia *et al.*, 2017). Improvement of flesh quality traits and feed utilisation efficiency traits are also of great interest in Nile tilapia, but since they are difficult to measure, especially on the breeding candidates themselves, they are more likely to be included only in more advanced breeding programs (Hamzah *et al.*,2016; Niera *et al.*, 2016).

In Ethiopia, whole-fish is preferable market product, and thus body weight is the main trait of interest, while fillet traits are the second most important breeding goal traits. Therefore, in the present study body weight and fillet traits were the main breeding goal traits.

1.2.2. Establishment of base a population

The number of strains contributing to the base population together with the type of mating strategy used, selection method and types of model used for genetic parameter estimation influence the magnitude of genetic progress in the subsequent generations (Eknath *et al.*, 2007; Gjedrem *et al.*, 1991; Bentsen *et al.*, 1998; Holtsmark *et al.*, 2006).

As reported by Bentsen *et al.* (1998), mating of fish from different strains before starting the regular selection program was done in order to form the base population for the GIFT breeding

program in the Philippines. In this program, low selection intensity was applied during the production of the first generation to maintain a broader genetic variability, allowing moderate long-term genetic progress and stepwise inclusion of new breeding goal traits. Gjedrem *et al.* (1991) reported that the genetic material for Atlantic salmon was collected from 40 Norwegian rivers. However, during production of the F_1generation, no restriction was applied with respect to the contribution of each of the strains. This gave opportunities to select the best strains or strain combinations, but at some expense of the genetic variation. Therefore, the structural design of the base population must consider the number of individuals to be sampled from larger founder strains, their mixing ability and the intensity of selection to be applied during the production of the initial generations (Gjedrem, 2005).

The main purpose of establishing the base population is, thus, to increase the genetic variation of the newly established mixed population through a complete diallel cross. This is because mixing of un-related populations is expected to increase heterogeneity as segregating genes affecting the trait selected and, thus, long-term genetic progress is expected. Secondly, when large number of potential candidates can be selected from all the tested families, it will help to increase selection intensity, and the additive performance of the base population will be improved. Thirdly, in mixing populations, some possible heterosis effects between the populations may be incorporated as a permanent internal heterosis in the synthetic populations. Therefore, a larger number of founder strains with a minimum representation of genes from all the initial strains can produce synthetic population with a broader additive genetic variance that can be used for long-term genetic improvement of the targeted body traits (Bentsen *et al.*, 1998; Holtsmark *et al.,* 2006; Eknath *et al.*, 2007). However, in the present study, only three Nile tilapia strains were used due to lake of infrastructures such as ponds, hapas and tagging materials.

1.2.3. Breeding strategies for genetic improvements

Breeding strategy is designed to change the genetics performance of a population to improve productivity and profitability of target species. It describes how to best mate parental breeders that allows to utilise genetic variation, i.e. additive and/or non-additive genetic variation found in a population, and thus, optimise response to selection in the subsequent generations. In this regard, the additive variance can be utilised in long-term genetic improvement through pure breeding program, whereas the non-additive effect can be utilised in short-term production improvement by mating of different lines to obtain favourable heterosis effect for a target trait(s) through crossbreeding (Gjerde *et al.* 1994; Rye and Mao, 1998; Joshi *et al.*, 2018).

In many breeding programs, pure breeding is one of the most common breeding strategies that offers the opportunity of continued genetic progress. It allows exploitation of the additive genetic effect. In this regard, individuals that possess the highest breeding values are selected to be parents for the next generation. The breeding values of animals can be primarily estimated using phenotypic record from offspring and pedigree information of the breeding candidate themselves and their relatives.

The second strategy is crossbreeding in which mating is performed between breeds, strains or inbred lines to increase heterozygosity and exploit non-additive genetic variance through heterosis (Camara & Symonde, 2014). When lines are produced by selection, their crosses are expected to produce heterosis, in which offspring exhibits superior performance over the average of the parental breeds (Hedgecock & Davis, 2007). Crossbreeding should, therefore, be looked upon as a supplement to additive genetic improvement. It can be also used effectively to improve the whole production system by crossing complementary breeds, produce intermediate performance from extreme parental phenotypes, upgrade a different purebred, introduce a single novel gene into an existing breed, take advantages of heterosis or line specific

maternal effects and/or protect the genetic properties of the breeder through F_2 breakdown (Joshi *et al.,* 2018).

Clutter (2010) defined and partitioned heterosis in the F_2 generation into individual, maternal and parental heterosis effects, of which the individual heterosis effect is the more important, able to improve production traits in crossbreeding programs. The second most important effect is the maternal heterosis which is related to reproduction traits, such as maternal effect. The third effect listed is the paternal heterosis, which is a result of heterosis effect in the sire, but its benefit for the breeding program is usually limited as long as the male fertility in sufficient (Bidanel, 2010).

The third alternative breeding strategy is hybridisation. It is a mating of two related species or highly differentiated and/or inbreed strains (Bartley *et al.,* 2001). When a hybrid is characteristically superior to both the parents it is showing what it called over-dominance, but this is rarely found in animals. Hybrids can also have some special characteristics. Thus, such strategies have been practiced in various fish breeding program to increase growth rate, improve flesh quality, produce sterile fish and/or increase specific disease resistance (Bartley *et al.,* 2001; Rahman, *et al.,* 2013). For instance, Hickling (1960) reported that mating between male *O. Urolepis hornorum* and female *O. mossambicus* produced nearly 100% male offspring. Crosses between *O. aureus* and *O. Spilurus* as well as *O. mossambicus* and *O. niloticus* showed 22% and 25% heterosis for body weight, respectively (Tayamen *et al.,* 2002).

1.2.4. Selection and mating design

In many fish breeding programs, growth is one of the main trait to be improved through selection. Among the different selection methods, individual or phenotypic selection is apparently successful for short-term genetic improvement. It is one of the simplest and cheapest to setup under practical conditions. However, response to selection can be severely reduced

after a few generations due to high accumulation of inbreeding (Huang & Liao, 1990; Farias *et al.*, 2017). This method is also not efficient for low heritable traits, e.g. survival or meat quality (Gjerde, 2005).

Another selection method is family selection, although it is seldom used as the method in a breeding program. It refers to selection among families, based on the rank of the mean performance of each family. It is preferable for traits that cannot be measured on the breeding candidate themselves (Farias *et al.*, 2017). Thus, to use family information in the selection decisions, full-sib family are reared separately until tagging size or by individual genotyping. Separate rearing of families requires large facilities and also introduces environmental effects common to full-sib family, whereas, the genotyping is costly to use in a breeding programs in many developing countries. However, this method is the only method that can be used when the trait(s) cannot be measured on the breeding candidate themselves, such as invasive traits or disease resistance; unless genomic selection is applied.

The selection method that combines, the two selection methods above is the use of an index method where different sources of information relevant to the selection decision is weighted together. It implies using all available sources of information recorded on the breeding candidate themselves and their relatives (Gjedrem & Thodesen, 2005). The preferred method used to predict breeding values with this method is known as best linear unbiased prediction (BLUP). Such information will maximise the rate of genetic gain from one generation to the next (Gjerde, 2005). This method also requires that full-sib families have to be reared separately until tagging size or by individual genotyping. One of the main drawbacks of BLUP selection is that it will lead to high rate of inbreeding, especially if BLUP truncation selection is applied. To overcome this problem, appropriate selection restrictions can be applied, preferably the optimum contribution method, where each breeding candidate is given a contribution factor

allowed to maintain a certain inbreeding level. Such individual contribution factors are difficult to apply in fish breeding designs, where is selected parent is allowed to produce a large family, usually 50 – 100 if conventional tagging systems are used, or even thousands if genotyping is used for family assignment. However, Skaarud *et al.* (2011) have shown that these methods also can be applied with fish breeding designs and will be superior to the more commonly used method, which is restriction of number of breeding candidates used per family.

Genomic selection is already applied in some commercial salmon breeding programs, and it is shown that it can be very useful to obtain within family selection, even for invasively measured traits, such as fillet yield and resistance to specific disease (Meuwissen *et al.*, 2001; Nielsen *et al.*, 2009; Sonesson and Meuwissen, 2009; Vela-Avitúa *et al.*, 2015; Hosoya *et al*., 2017; Houston, 2017; Vallejo *et al*., 2017). However, this method requires extensive genotyping of many individuals within each family and will thus be costly to apply in Ethiopia at this stage.

Following selection of potential parents, applying appropriate mating design is vital, not only to create genetic tie between offspring and parents, but also to produce an optimum number of full- and half-sib families under the available breeding facilities. In Nile tilapia, production of full- and half-sib families are commonly performed in hapas or tanks applying a nested mating design, as reuse of the females in the same group of parents will cause too large time span between the first and the last family produced (Gjerde, 2005). It is the most commonly used mating design, involving mating of one male to two or more females; hence, both full- and half-sib families can be produced. This mating design allows to some degree the separation of the sire's additive genetic effect from maternal and the common environmental effects (Sonesson & Ødegård, 2016).

In this design, variance component of sire and dam parents accounts for one quarter of the additive genetic variance of each parent. However, the dam variance component may be

influenced by maternal, dominance and common environmental effects, the latter caused by separate rearing of full-sib families until tagging (Thanh *et al.,* 2010). Thus, female nested within male provides more accurate estimation of additive genetic variance than male nested within female (Gjerde, 2005). However, it is reported that among the different mating designs, factorial mating designs increases genetic gain by increasing the accuracy of breeding values and maintaining low rate of inbreeding (Berg & Henryon, 1998; Dupont-Nivet *et al.,* 2002; Busack *et al.,* 2007). The choice of the best mating design thus depends on several factors, such as tagging system, type of mating, availability of sexually matured breeders and unbiased and accurate prediction method (Sonesson & Ødegård, 2016).

In general, appropriate selection techniques and mating designs are tools used to improve genetic performance of a population, thereby increase productivity and profitability of many aquaculture species (Gjedrem & Robinson, 2014). For instance, in tilapia, about 85% genetic gain over five generations of selection was reported by Rye & Eknath (1999) for growth rate. Considerable variation in response to selection per generation for increased body weight in Nile tilapia has been reported by several studies (12% to 17% by Eknath *et al.,* 1998; 20% by Bentsen *et al.,* 2003; 8.4%-11.4% by Ponzoni *et al.,* 2005; 3.6% by Gjerde *et al.,* 2012). Such differences in genetic gain among breeding programs may be due to many factors, such as selection intensity, accuracy of selection and additive genetic variance resulting from differences in size of the breeding population, number of families and number of offspring per family, selection methods and mating design. Most Nile tilapia farming in Africa, particularly in Ethiopia, is small-scale pond-based production systems applying mainly poor management practices, often with poor broodstock performance as they are collected from the wild. The main goal of this study was, therefore, to produce genetic material that can be used for long-term genetic improvement of growth traits in Nile tilapia, that can be suitable to grow in wide range of environments in the country.

2. OBJECTIVES OF THE STUDY

Nile tilapia is one of the most dominant and promising candidate fish species for freshwater aquaculture in Ethiopia, but its production is very low. One of the main reasons is the absence of quality fingerlings in the country. In most cases, fingerlings are mostly collected from wild stocks. This leads to low productivity and profitability of fish farming in the country. Thus, the main goal of this study was to produce mixed genetic material that can be used for long-term genetic improvement for body traits of Nile tilapia. The main objectives of this study were to:

- estimate the additive genetic, reciprocal and heterosis effects for body weight of Nile tilapia produced in a complete diallel cross of three strains and to also determining the level of genotype by environment interaction;
- predict fillet traits based on body measurements and estimate genetic parameters for body weight and fillet traits produced in a complete diallel cross of three Nile tilapia strains; and
- estimate genetic gain over one generation selection and other parameters. such as additive genetic, reciprocal and heterosis effects for body weight of Nile tilapia, across the two generations.

3. GENERAL METHODOLOGY

3.1. Experimental framework

The base population used for this study was produced from three Nile tilapia strains collected from three Ethiopian Rift Valley Lakes: Ziway, Koka and Chamo. Both half- and full-sib families were produced using a hierarchical mating design. The overall experimental design of the study is presented in Figure 1.

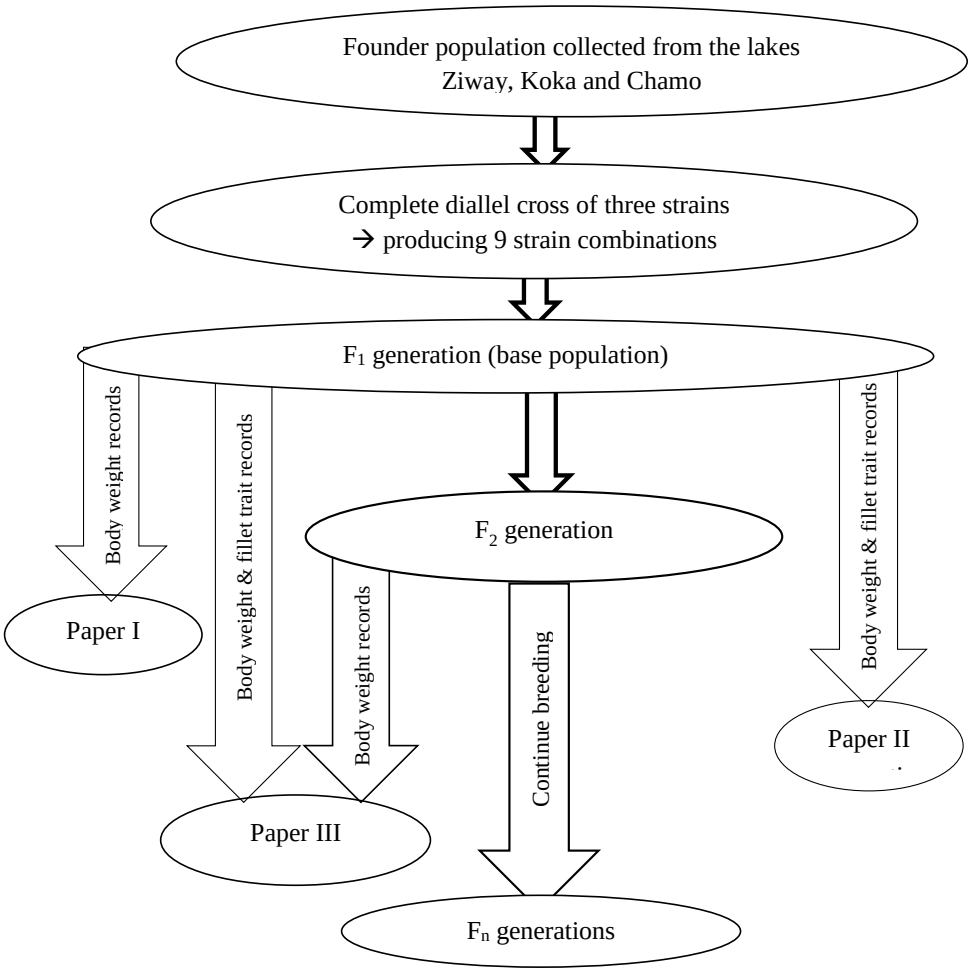

Figure 1. Schematic presentation of materials included in thesis relative to the present study

3.2. Breeding scheme and mating design

An overview of the breeding layout used in this study is shown in figure 2. Further details are given in papers I-III.

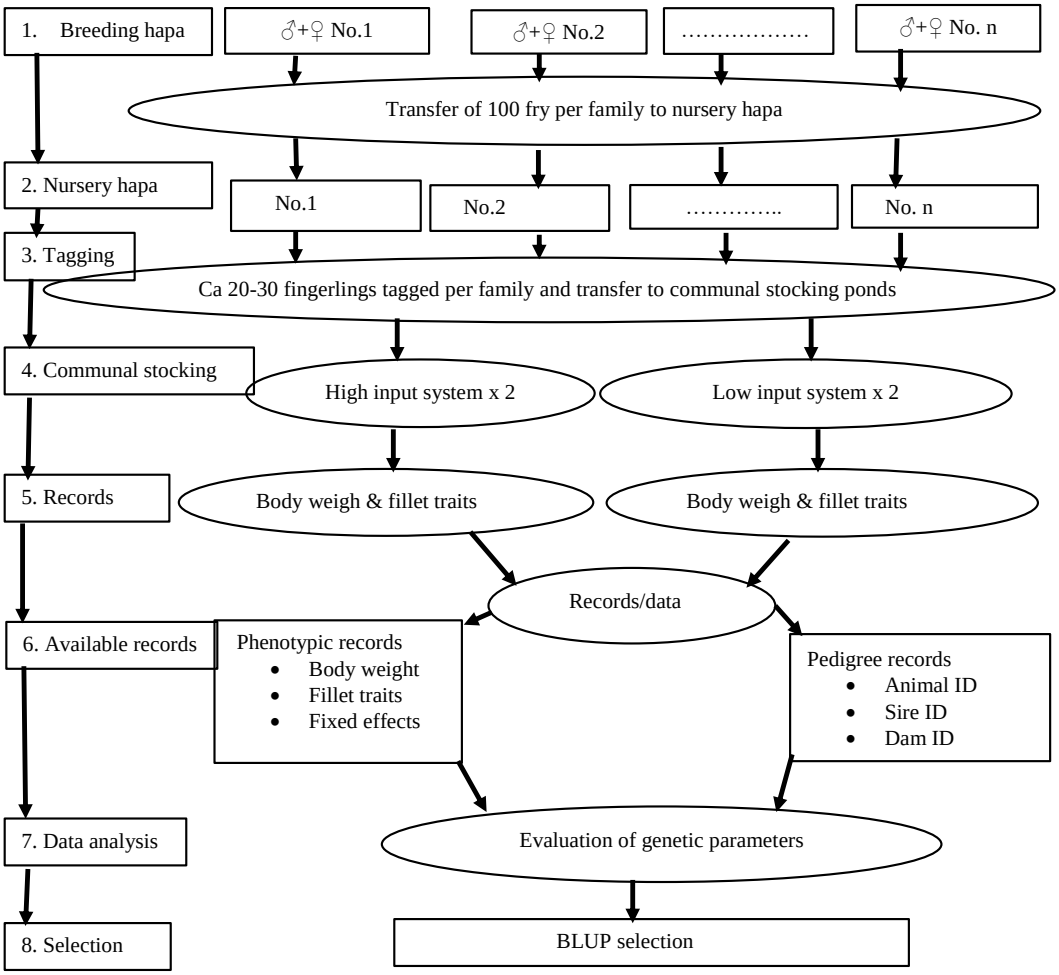

Figure 2. Overall production scheme used to produce ofspring in both the F_1 and F_2 generations, where n is a number of hapas used, n = 81 and 99 hapas for the F_1 and F_2 generation, respectively

4. A BRIEF SUMMARY OF PAPERS

4.1. Paper I

Additive, reciprocal and heterosis effects for harvest body weight in a complete diallel cross of three Nile tilapia (*Oreochromis niloticus*) strains

A complete diallel cross involving different strains of Nile tilapia is crucial to establish base population for further genetic improvement. Thus, the objectives of this study were to establish a base population for Nile tilapia breeding program, using a complete diallel cross of three local strains and to quantify the magnitude of additive, general reciprocal and heterosis effects for harvest body weight of three Nile tilapia strains.

Main results

The total heterosis effects for the different strain combinations ranged from 4.9% - 26.5%, with the largest value in the extensive production system. Except for heterosis effect, there were no significant differences among strains with respect to the additive genetic or general reciprocal effects. Across environments, the ZxC/CxZ strain combinations had a significantly ($P < 0.05$) higher harvest body weight than any other strain combinations. The estimates of heritability for harvest body weight, defined as separate traits in the two production systems, were 0.16 and 0.37 in the extensive and in the intensive environments, respectively. The estimated genetic correlation between the traits were 0.99, which does not motivate environmental specific breeding programs in Ethiopia.

Main conclusion

It is concluded that a crossbreeding program for Nile tilapia based on individuals from the base population utilising heterosis effect seems favourable, although pure breeding based on additive genetic performance is equally important. The decision of what breeding program to choose should however, be based on a cost-benefit analysis.

4.2. Paper II

Prediction fillet weight and fillet yield from body measurements and genetic parameter in a diallel cross of three Nile tilapia (*Oreochromis niloticus*) strains

Fillet traits cannot be measured on the selection candidate itself and ranking of live candidates is thus primarily based on information from slaughtered full-sibs. Thus, the objectives of this, study, were to investigate whether non-lethal method, utilising body measurements, could be used to efficiently predict fillet weight and fillet yield for Nile tilapia, and to estimate heritability, additive, general reciprocal and heterosis effects as well as genetic correlations between these traits.

Main results

The results revealed that body measurements on live Nile tilapia was well suited to predict fillet weight, but not fillet yield (R^2= 0.945 and 0.209, respectively). Body weight, fillet weight and predicted body weight were all estimated with a heritability around 0.25, and with very high genetic correlations, but not for fillet yield. The genetic correlation between traits were also high ($\geq$ 0.82), except for fillet yield ($\leq$ 0.39). No significant differences among strains as well as strain combination were found for their additive, general reciprocal or heterosis effects, although most of the total heterosis effect were significantly different from zero ($P < 0.05$).

Main conclusion

In conclusion, body measurements on live Nile tilapia is well suited to predict fillet weight, but not fillet yield. Body weight, fillet weight and predicted fillet weight were all estimated with a high heritability and high internal genetic correlations. Except for fillet yield and predicted fillet yield, the total heterosis effect contribute significantly to the differences in the total growth performance of the strains *($P < 0.05$).* but not for strain additive and the general reciprocal effects. Rather than to base selection on body weight and fillet yield, it should be selected for predicted fillet weight/body weight.

4.3. Paper III

Selection response over one generation of selection for increased body weight of Nile tilapia in Ethiopian.

Although Ethiopian aquaculture is at its enfant stage due to several constraints, its production is increasing. The absence of improved broodstock is probably the main bottleneck for the development of its production in the country. Thus, this study aimed at estimating the magnitude of genetic gain for body traits in a selective breeding program for Nile tilapia in Ethiopia, and estimating genetic parameters for these traits, including additive, general reciprocal and heterosis effects for harvest body weight across two generations.

Main results

The results showed that body weight and fillet weight were considerably heritable ($\geq$0.33) with internally high positive genetic correlations ($\geq$ 0.96), while fillet yield had a low heritability (0.04). The genetic gain obtained for increased body weight over one generation of selection was 7.1% and correlated responses in fillet weigh was 5.0%, and even negative for fillet yield (-0.4%). The estimates of strain additive, and general reciprocal effects were not significantly different from zero ($P > 0.05$), but the estimates of individual heterosis effects were significantly different from zero ($P < 0.05$) and more important than the maternal heterosis effect.

Main conclusion

In conclusion, the results with considerable individual heterosis effects support a crossbreeding program for Nile tilapia in Ethiopia based on individuals from the composite population, but a "pure" breeding program would be easier to run and has already shown to result in considerable genetic progress. The decision of what breeding program to choose should be based on a cost-benefit analysis.

5. GENERAL DISCUSSION

Although Ethiopian aquaculture production is in its early development, its production is increasing. However, it is mostly based on small-scale pond production systems. The absence of improved broodstock is probably one of the main bottlenecks for the development of fish production in Ethiopia, although lack of quality fish feed and skilled manpower are also important constraints affecting aquaculture production. Thus, the overall goal of this PhD project was to establish a base population and start a selection program, including the estimation of different genetic parameters for different body traits and the development of methods to predict fillet traits (Papers I-III). The main findings are briefly discussed under the following subtitles.

5.1. Predictability and prediction power of body measurement

In Nile tilapia, the focus of genetic enhancement has mainly been on growth traits (Bentsen *et al.*, 1998; Eknath *et al.*, 1998; Gall and Bakar, 1999). Although fillet weight is an important trait in the breeding goal (Paper II), it is hampered by the fact that it is difficult to measure on the breeding candidates themselves. Therefore, genetic improvement for this trait has been addressed through different strategies, for which family selection have been used most frequently so far. However, this strategy only utilises half of the additive genetic variation, i.e. the between family variation, using records only from fullsibs, not the candidate themselves. Thus, ranking of live candidates is based on the family breeding values estimated from slaughtered siblings. The second strategy would be to use genomic selection, which would allow within family selection as well, but this requires relatively costly genotyping of both a reference and candidate population (Haffray *et al*., 2013). The third alternative strategy is an indirect selection based on body measurements that can be recorded on the live candidates. By developing non-invasive methods to predict fillet traits in Nile tilapia, this strategy was applied in the current study and is presented in Paper II.

The prediction model for fillet weight had five variables explaining ca 95% of the total phenotypic variation, whereas only 21% of the variation could be explained for fillet yield. Some reasons for this huge difference in predictability for the two traits are listed in paper 2. It should also be mentioned that the predictor variables in the fillet yield model, i.e. body thickness and head thickness, will be less accurately measured than the main variable in the fillet weight model; body weight (Rutten *et al.*, 2004). However, fillet yield is likely to remain a challenging trait to select for, as it is a ratio trait, stemming from two composite traits, body weight and fillet weight, with different biological, genetic and statistical characteristics.

5.2. Additive and non-additive genetic effects

High genetic variance is essential for the long-term genetic improvement also in Nile tilapia breeding programs (Thodesen *et al.*, 2011). Such genetic variation could be available both within and between strains. In order to combine and exploit both those genetic variations, BLUP based selection methods will normally be applied, as it also was in this study, both when analysing the data from the F_1 and the F_2 generation. In addition, the magnitude of additive, reciprocal and heterosis strain effects for body traits were quantified for both generations (Papers I-III).

The results presented in Papers I - III revealed that the strain additive and the general reciprocal effects did not contribute significantly *($P > 0.05$)* to the differences in the total growth performance of the strains. As discussed in paper III, this can be due to the use of a hierarchical design in our study, which is less able to capture this the source of variance, as it will be confounded with the common environmental effect associated with fullsibs. A better design in this respect is a partial factorial design, but this was difficult to apply in our case as it would have prolonged the mating period due to the need for reuse of the females, as also mentioned above.

On the other hand, the total heterosis effect contribute significantly to the differences in the total growth performance of the strain combinations ($P < 0.05$), which accounted for 10.6% and 11.4% of the total variation in body weight across test environments in average at 5 and 7 months of age, respectively (Papers I and II). This value is higher than the average value of 4.3% reported by Bentsen *et al*. (1998) and 1.8% reported by Lozano *et al*. (2011). The results from Paper II also revealed that the total heterosis effects for fillet weigh and predicted fillet weight had similar trend, with most of them being significantly ($P < 0.05$) different from zero.

The results from Paper III also revealed that the individual heterosis effect was more important than maternal heterosis effect, and significantly different from zero ($P < 0.05$). Maluwa & Gjerde (2006) also stated that higher individual heterosis effect could be obtained in the F_2 generation if selection can be done based on ranking of individuals by their breeding values from all families including low-ranking families. In this regard, a large proportion of heterosis effects in the F_2 generation could be created (Maluwa & Gjerde, 2006).

5.3. Genotype by environmental interaction

In fish breeding programs, selection and production of fingerings take place in a breeding nucleus, whereas normal production can take place in a wide range of environments or production systems, and thus genotype by environment interaction might be anticipated. The magnitude and the importance of genotype by environment interaction for body weight vary among different studies, which could depend on the level of differences between the types of production systems/environments or the selections history and intensity (Eknath *et al.,* 2007; Khaw *et al.,* 2009). Eknath *et al.* (2007) found a wide range of genetic correlations for body weight of fish reared in different pond production systems, 0.76 to 0.99, and between cage and pond production systems, 0.36 to 0.82. Our estimate of genetic correlation for harvest body weight between the two pond production systems was very high, 0.99, agreeing well with the

higher values reported by Eknath *et al.* (2007). This may imply that further estimation of genotype by environment interaction for wide range of test environments could be important, and GxE should anyhow be monitored as selection proceeds.

5.4. Heritability and genetic correlation

The estimates of heritability for different body traits in the two production systems were moderate in magnitude (0.16 in L and 0.37 in H) (Paper I), except for fillet yield (0.05). The heritabilities estimated for the weight traits in F_1 (0.19 – 0.28, Paper II) were lower than the ones estimated across F_1 and F_2 (0.24 – 0.37, Paper III). These results agree well with the estimates of heritability reported by e.g. Thodesen *et al.* (2011), in which the magnitude of estimated heritability for most of the traits were slightly lower within generations than across generations.

Fillet yield had low genetic correlation to the other body traits ($\leq$ 0.39), whereas the internal genetic correlations among the remaining traits were generally high ($\geq$ 0.82) (Paper II). This difference was even clearer when both generations were analysed (Paper III), as the estimates of genetic correlations between fillet weight and other traits were even higher ($\geq$ 0.96), whereas the genetic correlation between growth rate and fillet yield now was slightly negative (- 0.018).

5.5. Genetic gain

When using BLUP, genetic response to selection can be measured as the difference in estimated breeding values (EBVs), either between a candidate and control populations or those between successive generations. Hung *et al.* (2013) and Dong *et al.* (2015) found that the magnitudes of genetic gain obtained by the two methods were similar. Due to limited test capacity, the present experiment was carried out without control line, and thus the realised genetic gain was estimated as the difference in mean breeding values between the two successive generations.

The estimate of genetic gain over one generation selection for body weight was 7.1%. The current value compares to the lower values (8.4%-11.4%) reported by Ponzoni *et al.*, 2005) but higher than the value (3.6%) reported by Gjerde *et al.*, 2012). However, it is clearly lower compared with the values reported by Eknath *et al.* (1998) and Bentsen *et al.* (2017) for the same fish species, but their selection responses stems from the generations subsiding three generations of deliberate testing and mixing of the strains, i.e. they reported gain after they had finished the procedures and testing similar to what we have been reporting for our two first generations.

5.6. Optimising response to selection

In order to enhance fish production in Ethiopia, it is important to develop genetically improved Nile tilapia that can grow in a wide range of production environments. To this end, individuals with the highest breeding values were selected to be parents for the next generation, but the number of candidates selected per family was restricted to five or less; to control the rate of inbreeding. In addition, mating between full-sibs and half-sibs was also avoided. These measures were also taken to minimise the loss of genetic variation in the population.

The type of mating design applied in the present study was nested mating design, i.e. one male mated with two females, which, through the repeated use of sires, allows some correction for the environmental effects common to fullsibs (Gjedrem, 2005). One of the main drawbacks of such mating design is that keeping one male and one female breeder in the same spawning hapa often leads to injury or even death of the female breeder, as the male breeder is more aggressive. When the injured or dead breeder must be replaced with another one, the new breeder will often have a poorer breeding value, and the highest ranked individuals may thus not necessarily contribute offspring to the next generation. In addition, if the male breeder dies after mating only one female, then no half-sib family can be produced from that particular male. These incidences result in an unbalanced mating design and loss of genetic ties or contrast between

halfsibs-groups, which again creates confounding between the common full-sib and additive genetic effect (Trong *et al.,* 2013). Furthermore, the nested mating design is labour intensive, requires a large number of hapas and lengthens the time needed for family production.

As result of the second constraint mentioned above, the number of families in the present study were restricted to 81 in the F_1 and 99 in the F_2 generation. Moreover, the number of tagged candidates per family was restricted ca 30 or less. In addition, the time used for rearing of fingerlings until tagging in the present study was two and half months. This is still within or lower than the time span reported for different generations of the GIFT strain, i.e. from one and half to six months (Ponzoni *et al.,* 2011; Bentsen *et al.,* 2012; Khaw *et al.,* 2012; Trong *et al.,* 2013). Trong *et al.* (2013) reported that such long time for family production of Nile tilapia may reduce accuracy of selection, which directly reduces the genetic response to selection.

Instead of applying a fixed quota of selected candidates per family, as described above, some aquaculture programs claim that they recently have started applying a method that put a a pre-set constraint to the allowed rate of inbreeding per generation, known as optimum contribution (OC) selection (Meuwissen, 1997). Optimum contribution selection is maximising the genetic merit and controlling inbreeding by restricting the level of relatedness in a population and optimising the genetic contribution of each candidate to the next generation by use of the estimated breeding values and the additive genetic relationships among the contributing candidates (Hallander & Waldmann, 2009; Henryon *et al.,* 2015). The optimal genetic contribution of the selected candidates to the next generation is estimated as (Meuwissen, 1997):

$$G_{t+1}=C_t.EBV_t,$$

where EBV_t is a vector of estimated breeding value of the selection candidates in generation t and C_t is a vector of genetic contributions of the selection candidates to generation t+1.

As described in the introduction, the implementation of OC is not straight forward in fish breeding programs due to the large and equal number of fullsibs produced by each selected couple of parents. As shown by Skaarud *et al*. (2011), the best way to implement OC in such programs is by partial factorial designs, which however is practically challenging due to the required reuse of female breeders, prolonging the minimum mating period.

6. DISSEMINATION

An effective dissemination scheme is crucial to make selective breeding programs powerful means to enhance productivity and profitability of aquaculture (Ponzoni *et al.*, 2007). Thus, the success or benefit of the genetic improvement of the Nile tilapia strains obtained in the present study depends on an efficient multiplication and dissemination of fingerlings in order to potentially increase the productivity of tilapia production in Ethiopia.

Multiplication and dissemination of fingerlings can be done either in a centralised system or by a decentralised system. In the former, multiplication and dissemination of improved fingerlings is achieved through the construction of large hatcheries established at strategic locations, scaled to supply large number of farmers. However, due to cost and lenght of transportation, centralised system may fail to adequately deliver the seeds to farmers in remote areas. In contrast, a decentralised system that consists of many small hatcheries, located in different geographical area, could be able to reach farmers also in the remotest areas.

The current genetically improved Nile tilapia strain is so far produced only in one breeding station and disseminated to local farmers, and a total of 70,000 fingerlings were disseminated to surrounding such farmers. Since there was a positive feedback from those farmers, Hawassa University is convinced to continue the breeding program and, thus, a new fish breeding station is under construction at the university campus. The station will also be used for conducting further research, providing training, as well as producing better quality fingerlings to maximise fish production in the country.

7. CONCLUSION

Based on the findings of the present studies, the following concluding remarks are made:

⇒ Small differences in additive and general reciprocal effects among different strains were observed.

⇒ Moderate estimates of heterosis for body traits was obtained. In this regard, crossbreeding program for Nile tilapia based on individuals from the existing population utilising non-additive genetic effects seem favourable.

⇒ There was no evidence of genotype by environment interaction, as genetic correlation for body weight records of Nile tilapia reared in the two production systems was high, and hence does not motivate to establish distinct breeding program for each environment in Ethiopia.

⇒ Sufficient additive genetic variance and moderate estimates of heritabilities with reasonable genetic gain for increased body weight was obtained over one generation of selection, allowing to long-term genetic improvement for body traits from F_2 onward.

⇒ Body measurements could potentially be used as non-invasive predictor variables for fillet weight prediction.

⇒ Selection on improving body weight would likely improve fillet weight as well as its genetic correlation with body weight is high, but not for fillet yield.

⇒ In general, selective breeding program aimed at improving growth traits require identification of breeding strategies. Two points are emphasised here:

1. Additive genetic variance can be exploited for further genetic improvement of Nile tilapia using the present breeding scheme, with the existing facilities.
2. The moderate heterosis effect obtained for body weight of Nile tilapia can be exploted through crossbreeding scheme, but additional infrastructure required to maintain the two pure lines separately. However, the decision of what breeding program to choose should be based on a cost-benefit analysis.

8. FUTURE RESEARCH

Currently, fish supply and demand in Ethiopia is unbalanced due to low production in the country. The low fish production is due to lack of quality fingerlings, poor quality fish feed and low production management practices. Thus, providing better quality fingerlings, together with quality diet and production guidelines could enhance fish production in the country. In this regard, the current improved Nile tilapia strain will play a significant role to increase Nile tilapia production. Based on the results presented in this thesis, the following points are suggested for further research.

⇒ Papers I-II present estimates of additive genetic and heterosis effects for growth traits. Exploiting either additive or non-additive genetic effects for further genetic improvement of Nile tilapia is possible. The decision to choose the proper breeding program should be based on a cost-benefit analysis and such a study should be carried out rapidly.

⇒ Based on Paper II, re-evaluation of fillet trait prediction with larger number of records obtained from fish of a larges size is needed for better accuracy of fillet traits prediction, particularly for fillet yield.

⇒ Although the estimated genotype by environment interaction for body weigh was low, the magnitude and importance of genotype by environment interaction (GxE) could vary depending on the degree of differences between production environments. Thus, evaluation of GxE for a wide range of test environments is required and may help to produce more robust Nile tilapia strains for use throughout the country.

⇒ From F_2 onwards, optimal contribution procedures should be applied to maximise the genetic gain in the subsequent generations at a predefined rate of inbreeding though either a pure- or a cross-breeding program. Feed efficiency, late sexual maturity and disease specific resistant traits should be also evaluated.

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Paper I

Additive, reciprocal and heterosis effects of harvest body weight in a complete diallel cross of three Nile tilapia (*Oreochromis niloticus*) strains

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Additive, reciprocal and heterosis effects of harvest body weight in a complete diallel cross of three Nile tilapia (*Oreochromis niloticus*) strains

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Abstract

The aim of this study was to quantify the magnitude of additive, reciprocal and heterosis effects for harvest body weight in a complete diallel cross of three Nile tilapia (*Oreochromis niloticus*) strains collected from three Ethiopian Rift Valley lakes. The body weight of 1,564 male fish from 81 full-sib families, reared in two production systems were recorded at harvest. Percent heterosis for the different strain combinations ranged from 4.9% to 26.5%, with the largest values in the extensive production system. Except for heterosis effect, there were no significant differences among strains with respect to the additive genetic or general reciprocal effects. Across environments, the ZxC strain combinations had a significantly ($P < 0.05$) higher harvest body weight than many other strain combinations. The estimates of heritability for harvest body weight, defined as separate traits in the two production systems, were moderate; 0.16 and 0.37 in the extensive environment and in the intensive, respectively. The estimated genetic correlation between the traits were 0.99, which does not motivate environmental specific breeding programs in Ethiopia. The results are indicating that a crossbreeding program for Nile tilapia in Ethiopia based on individuals from the base population utilising non-additive genetic, heterosis, effects seems favourable, although pure breeding based on selection for additive genetic performance is equally important. The decision of what breeding program to choose should be based on a cost-benefit analysis.

Key Words: *Cross breeding; Genetic correlation; Genotype by environment interaction; Heritability; Maternal effect; Non-additive genetic effect*

1. Introduction

Tilapia is one of the most common cultured fish species in tropical and subtropical freshwater aquaculture, comprising approximately 5% of the total global fish farming (Ansah *et al.,* 2014). It can be reared in a wide range of farming systems, from small-scale extensive pond culture systems to large intensive systems, and in highly diverse environments. This adaptability of tilapia and the general intensification of modern aquaculture have resulted in a rapid expansion worldwide. Thus, the contribution of tilapia to the global aquaculture production has increased from 28,000 tons in 1970 (Silva *et al*., 2004) to more than 5.6 million tons in 2015 (Yue *et al.,* 2016), with more than 10% annual growth over the last four decades (Ansah *et al.,* 2014). It is the second most important cultured fish in the world, next to carp (FAO, 2014). In the last two decades, global tilapia farming has been dominated by three species: *Oreochromis niloticus, O. mossambicus,* and *O. aureus*. Of these, *O. niloticus*, or Nile tilapia, is by far the most widely cultured and accounted for 90% of the total tilapia production in 2014 (Fitzsimmons, 2016).

This expansion has been supported by several breeding programs being established and maintained worldwide, with the Genetically Improved Farming Tilapia (GIFT) program (Eknath *et al.,* 1993) as the most recognized. Subsequently, a complete diallel cross experiment with eight Nile tilapia strains was produced and the strains additive, general reciprocal and heterosis effects were estimated for harvest body weight of this fish (Bentsen *et al*. 1998; Lozano *et al.,* 2011). Similarly, the strains additive, general reciprocal and heterosis effects were estimated for harvest body weight by Maluwa & Gjerde (2006) for *Oreochromis shiranus*. Most of these programs aimed to develop fast growing strains under semi-intensive production environments, where production relies on formulated diets and growth is expected to be high. However, most *O. niloticus* farming in Africa, particularly in Ethiopia, are small-scale farming, relying on plankton produced by fertilising or manuring of ponds, with or without supplementary feed from locally available feed ingredients such as wheat bran, brewery by-products or even table leftovers, i.e. of low intensity.

For such systems, the above-mentioned strains may not perform as well, e.g. due to possible genotype by environmental interaction (GxE), that can be occurred if the test environment differs much from the actual farm environment (Sae-Lim *et al.,* 2016). Testing of local strains should be performed, since differences between strains originating from different geographical locations have been found by Eknath *et al.* (1993), Bentsen *et al.* (1998), Lozano *et al.* (2011) and Workagegn and Gjøen (2012). Initially, such a program also should examine

the performance of the different strains under both low and high production intensity to decide whether specialised strains for each farm environment will be necessary (Eknath *et al.,* 1993). Estimates of strain additive, strain general reciprocal and heterosis effects for body weight is also lacking. These parameters are of importance in deciding upon the types of breeding strategy that are best suited for improving the genetic performance of a species (Gjerde *et al.,* 2002). Thus, the aim of this study was to do a diallel cross of three local *O. niloticus* strains in two environments to estimate additive, reciprocal and heterosis effects for harvest body weight (HBW), and to determine the level of genotype by environment interaction, with the end goal to establish a selective breeding strategy for genetic improvement of Nile tilapia in Ethiopia.

2. Materials and methods

2.1. Origin and rearing of experimental fish

The three *O. niloticus* strains (generation 0) were sampled at random in February 2013 from three Ethiopian Rift Valley Lakes located more than 100 km apart: Lake Ziway (Z), Lake Koka (K) and Lake Chamo (C). Fish were transported to Ziway Fisheries Resource Research Centre (ZFRRC) and stocked separately in 40 m^2 concrete ponds (with a water depth of 100 cm) at a density of 3 to 4 fish/m^2. After four months of rearing, the fish were sorted by sex and separated by a net in the same type of pond, at a density of 2 to 3 fish/m^2. When the fish reached 100 to 200 g, they were transported to Hawassa Agricultural Research Centre (HARC). At this breeding centre, 80 male and 160 female breeders were randomly sampled and stocked, by sex, in 1 m^3 hapas installed in 250 m^2 pond, at a stocking density of 2 to 3 fish/m^2, for further conditioning. In both breeding centres, the fish were fed three times a day with a diet containing 40% bone-meat meal, 15% fish meal, 15% soybean meal, 15% wheat flour, 10% corn flour and 5% niger press cake, in total 35% crude protein, at a daily rate of 3% of body weight.

2.2. Preparation of breeding hapas

One medium sized breeding pond (250 m^2) was drained and then dried for two weeks before being refilled with water. One week prior to stocking, the pond was fertilised with 38 kg poultry manure per month. In this pond, 90 breeding hapas (1 m^3) were installed, with one female per hapa. Five rows of breeding hapas, i.e. each of 18 hapas, were installed side-by-side to enable easy transfer of the male breeder between its two female breeders. The distance between each row of hapas was 1.5 meter, to ensure sufficient water circulation in the pond production system.

2.3. Mating design and number of parents and offspring

A diallel cross of the three *O. niloticus* strains was carried out, using 45 sires and 90 dams from the three strains. A hierarchical mating design with 1 male mated with 2 females was applied, producing nine strain combinations; three purebreds and six crossbreds in generation 1 (F_1 generation), where neither male nor female breeders were used across the nine strain combinations. Among 90 mated, only 81 mated families were successfully produced. The number of families produced along with their number of offspring, per strain combination, is shown in Table 1.

2.4. Production and rearing of fry

Among the two females used for each male, priority for mating was given to the female breeder that was readiest to spawn. To minimize stress and mortality of female breeders during mating, the upper lip of the male breeders was removed after anaesthetisation with 0.02% clove oil. Natural mating and spawning were carried out from the beginning of November 2013 to mid-January 2014. Fry produced in the first 15 days of November 2013 was classified as hatching group or batch one, while fry produced from January 1 to 15, 2014 was classified as batch five. All breeding hapas were inspected twice a week for appearance of swim-up fry, at which the male breeder was transferred to the hapa with the second female breeder. The female breeder was also removed when its buccal cavity remained free of fry. To produce the required amount of full-sib families, any dead breeder was replaced with a new one. A female that produced too few fry was re-conditioned in a separate hapa and re-mated with the same male to produce an adequate number of fry. From each full-sib family, about 200 fry were stocked in a $1m^3$ breeding hapa (Eknath *et al.*, 2007). They were fed four times a day with the diet that contained 35% crude protein, at a daily rate of 30% of their body weight. After a month, about 100 fry were randomly sampled per family and reared in individual nursery hapas until they reached an average size of about 23 g, at which tagging took place. In the nursery hapas, the rate of feeding was first reduced to three times a day at a daily rate of 20% of their body weight; eventually ending up with a rate of 10% of their body weight per day. About 20 to 30 randomly sampled fingerlings per full-sib family were tagged using Passive Integrated Transponder (PIT) tags.

2.5. Production environments

All the tagged fingerlings were divided equally among four rectangular ponds: a low input production system (L) in two ponds of $250m^2$ each and a high input production system (H) two ponds of $125m^2$ each. In L, the average stocking density was 2.5 fish/m^2 fertilized with

poultry manure. In addition, the fish were fed twice a day with a supplementary diet consisting of 70% wheat bran, 15% niger press cake and 15% bone-meat meal, 21% crude protein in total, at a daily rate of 3% of their body weight. The stocking density in H was 5.2 fish/m^2, and the fish were fed three times a day with pelleted diet consisting of 40% bone-meat meal, 20% roasted soybean meal, 20% wheat flour, 15% maize flour and 5% niger press cake, 28% crude protein in total, at a daily rate of 3% of their body weight. The water level of the ponds was maintained at a depth of 80-100 cm with a water renewal for L and H of 2.5% and 7.2% of the pond volume per day, respectively.

2.6. Data recording and analyses

2.6.1.Data recording and phenotypic variance correction

After a five months grow-out period, harvest body weight (HBW) of 2,421 fish was recorded. It was observed that in females, early sexual maturation had occurred frequently. Thus, it was decided to only utilise data from male fish in the analyses, 913 fish in H and 651 fish in the L. Prior to analyses, HBW was pre-corrected for phenotypic variance differences in batch subclasses using a multiplicative correction factor, i.e. cHBW = $Y_{ij} = y_{ij}(\sigma_y/\sigma_{yi})$, where Y_{ij} and y_{ij} are, respectively, the variance corrected and the observed harvest body weight for animal *j* in level *i* of the subclasses, σ_y is the weighted mean standard deviation of harvest body weight across all batch subclasses and σ_{yi} is the standard deviation of harvest body weight in level *i* of the subclass (Hill, 1984; Jere *et al.*, 2003).

2.6.2. Estimation of additive, reciprocal and heterosis effects

The strain additive genetic effects ($b_{A(m)}$), the general reciprocal effects ($b_{R(m)}$) and the total heterosis effect ($b_{D(n)}$) for harvest body weight, both across and within the two production systems, were estimated using mixed animal model, ASReml version 4.1 (Gilmour *et al*, 2015). Compared with a fixed model, the mixed animal model is assumed to reduce sampling effects, relative to the number of offspring per family that contributed in the diallel cross, by correcting for the variance caused by individual animals (Overton, 1998). The family effect was also tentatively included in the model, however, the estimated variance for the random full sib family effect was zero. This is likely due to confounding between the random full sib effect and the strain general reciprocal effect. Thus, the random full sib family effect was excluded both in univariate model, Model 1, and bivariate model, Model 2. The univariate model used to analyse the F_1-data across the two environments was (Model 1, after Fimland, 1984 used by Maluwa & Gjerde, 2006):

$$Y_{ijkmno} = \mu + B_i \cdot Rep_j \cdot E_k + \sum b_{Am} A_m + \sum b_{Rm} R_m + \sum b_{Dn} D_n + a_o + e_{ijkmno}$$

where Y_{ijkmno} is the variance corrected HBW (cHBW) of the o^{th} individual, μ is the overall mean, B_i is the fixed effect of the i^{th} batch (i = 1-5), Rep_j is the fixed effect of the j^{th} pond (replicate) (j = 1,2), E_k is the fixed effect of the k^{th} production system (k = 1,2), b_{Am} is the regression coefficient of the additive genetic effect of the genes originating from the m^{th} strain (m = 1-3), A_m is the proportion of genes in the o^{th} individual originating from the m^{th} strain (A_m = 0, 0.5 or 1, and $\sum A_m = 1$; Table 2), b_{Rm} is the regression coefficient of the reciprocal effect of the m^{th} strain, R_m is the proportion of genes of the dam of the o^{th} individual originating from the m^{th} strain (R_m = 0 or 1 and $\sum R_m = 1$; Table 2), b_{Dn} is the regression coefficient of the mean heterosis effect of both reciprocals of the n^{th} cross between two different strains (n = 1-3), D_n is the proportion of the total heterosis effect of the n^{th} strain cross expressed in the o^{th} individual, (D_n = 0 or 1, and $\sum D_n = 1$ for crossbreeds or $\sum D_m = 0$ for pure-breeds; Table 2), a_o is the random additive genetic effect of the o^{th} individual fish ~ $N(0, \mathbf{A}\sigma^2_a)$ where **A** is the additive relationship matrix among all fish (1564 fish in F1 and 124 parents) and σ^2_a is the additive genetic variance, and e_{ijkmno} is the random residual error of the o^{th} individual. Data was also analysed within each of the two production systems by omitting the environmental effect from the model above.

In Table 2 $\sum A_m = 1$ and $\sum R_m = 1$. This implies dependencies in the columns of either effect, and the need for imposing restrictions to obtain solutions. For the total heterosis effects, no restriction was needed, and the solutions were used as estimated. All the three effects were estimated simultaneously. Constraints were imposed upon the strain additive and strain general reciprocal effects, i.e. $\sum b_{Am} = \sum b_{Rm} = 0$ (Lozano *et al.*, 2011).

The least-squares means (LSMs) for cHBW were calculated following Fimland (1983) and Bentsen *et al.* (1998). First, the contribution from the fixed effects was calculated as:

LSM (contribution from fixed effects) = $\mu + B_i.Rep_j.E_k/n_{Bi} \cdot n_{Rep} \cdot n_E$, where $n_{B,}$ n_{Rep} and n_E are number of classes for batches, replicates and test environments, respectively. Thereafter, the additional contribution of the m^{th} strain, when used either as a sire (s) ($LSM(A+R)_{s=m}$) or as a dam (d) ($LSM(A+R)_{d=m}$) were computed as follows, respectively:

$$LSM(A+R)_{s=m} = \tfrac{1}{2}LSM(\text{contribution from fixed effects}) + \tfrac{1}{2}b_{Am}$$

$$LSM(A+R)_{d=m} = \tfrac{1}{2}LSM(\text{contribution from fixed effects}) + \tfrac{1}{2}b_{Am} + b_{Rm}$$

Still following Bentsen *et al.* (1998), the least-squares means of cHBW for the offspring of sires from strain m = x and dams from strain m = y, ($LSM(A+R)_{xy}$), altogether 9 combinations, were calculated as:

$$LSM(A+R)_{xy} = LSM(A+R)_{s=x} + LSM(A+R)_{d=y}$$

Adding the total heterosis effects (b_{Dxy}), assuming that $b_{Dxy} = 0$ when x = y, i.e. for purebreds and that one mean value were estimated for both reciprocals, allowed the least-squares means for each of the 9 strain combinations to be computed as:

$$LSM_{xy} = LSM(A+R)_{xy} + b_{Dxy}$$

Then, percentage total heterosis was calculated as:

$$H\%_{xy} = (b_{Dxy}/LSM(A+R)_{xy})100$$

Finally, average general heterosis for each strain was calculated as the average of the total heterosis effects involving that strain, while average heterosis was obtained as an overall mean of the total heterosis effects (Gjerde *et al.*, 2002).

2.6.3. Estimation of heritabilities and genotype by environment interaction

Genetic parameters were estimated by a bivariate animal model; considering cHBW in the two production systems as two different traits and otherwise expanding Model 1 with a random additive genetic effect. The magnitude of the genotype by environment interaction was expressed as the genetic correlation between cHBW in environments L and H. The model was (Model 2):

$$\begin{bmatrix} \boldsymbol{Y_L} \\ \boldsymbol{Y_H} \end{bmatrix} = \begin{bmatrix} \boldsymbol{X_L} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{X_H} \end{bmatrix} \begin{bmatrix} \boldsymbol{b_L} \\ \boldsymbol{b_H} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_L} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{Z_H} \end{bmatrix} \begin{bmatrix} \boldsymbol{a_L} \\ \boldsymbol{a_H} \end{bmatrix} + \begin{bmatrix} \boldsymbol{e_L} \\ \boldsymbol{e_H} \end{bmatrix}$$

where $\begin{bmatrix} \boldsymbol{Y_L} \\ \boldsymbol{Y_H} \end{bmatrix}$ is the vector of observations for cHBW in the two environments, $\begin{bmatrix} \boldsymbol{b_L} \\ \boldsymbol{b_H} \end{bmatrix}$ is a vector of environment specific fixed effects, and $\begin{bmatrix} \boldsymbol{X_L} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{X_H} \end{bmatrix}$ is design matrix relating the observations to the fixed effects, $\begin{bmatrix} \boldsymbol{Z_L} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{Z_H} \end{bmatrix}$ is the design matrix relates observations in the two environments to the additive genetic effects, $\begin{bmatrix} \boldsymbol{a_L} \\ \boldsymbol{a_H} \end{bmatrix}$ is a vector of the two traits, the two test environments treated as two separate traits, $\begin{bmatrix} \boldsymbol{A\sigma^2 a_L} & \boldsymbol{A\sigma a_L a_H} \\ \boldsymbol{sym.} & \boldsymbol{A\sigma^2 a_H} \end{bmatrix}$ is the (co)variance structure, where **A** is the additive relationship matrix among all fish, and $\begin{bmatrix} \boldsymbol{e_1} \\ \boldsymbol{e_2} \end{bmatrix}$ is a vector of random residual effects for

the two traits, with their covariance set to zero as an individual is reared in one of the two environments, only.

3. Results

3.1. Additive, reciprocal and heterosis effects

Table 3 shows estimates of the additive and the general reciprocal strain effects for cHBW, both across and within production systems, as obtained with Model 1. For both the strain additive and general reciprocal effects, no significant ($P < 0.05$) differences were obtained among strains and none of them were significant different from zero. However, re-ranking of both effects was observed, in which Koka and Chamo strains ranked first in the L and in the H, respectively, for general reciprocal effects. For additive genetic effect, Ziway strain ranked first in both production systems, while Koka and Chamo strains ranked last in the H and the L, respectively. In both within and across production systems, Ziway strain was inferior in terms of general reciprocal effect and superior in terms of additive genetic effect.

The least-squares means for cHBW of sires and dams of each strain (LSM $(A+R)_{s=m}$ and LSM$(A+R)_{d=m}$, respectively) are plotted in Figure 1, both within and across production systems. The results show that dams from Ziway origin had higher contribution to the least squares means of harvest body weight of their offspring than sires, whereas dams and sires from Koka and Chomo origin had more or less similar contribution to the least squares means of harvest body weight of their offspring.

For purebreds, the least-squares mean of cHBW for the three purebred combinations from fixed, additive and reciprocal effects (LSM$(A+R)_{xy}$ = LSM_{xy}) are shown in Table 5 for across production systems, and in Tables 6 and 7 for H and L, respectively. Generally, the Tables 5 and 6 show that the total performance was not significantly ($P > 0.05$) different among all the three strains. However, the total performance of Koka strain was significantly higher than the other two strains in L ($P < 0.05$) (Table 7).

The total heterosis estimates for cHBW, both within and across production systems, are presented in Table 3. The three total heterosis effects for each combination/cross were positive, but none of them were internally significant different ($P > 0.05$). However, most of the total heterosis effects were significantly different from zero *($P < 0.05$)*. The result showed that the total heterosis effects on harvest body weight across production systems ranged from 6.2g for KxC/CxK in H to 26.0g for ZxC/CxZ in L. On average, the effects of total heterosis on harvest body weight was 10.6%, 6.3% and 13.8% points across, in H and in L, respectively.

Regarding the strain average general heterosis, i.e. the average of the total heterosis effects involving that particular strains, the three strains did not differ significantly ($P > 0.05$) across the two environments (Table 4). However, the magnitude of the estimates was largest in L and least in H, as were the overall heterosis estimates (Table 4). Among the three strains, Ziway strain had the highest average general heterosis effect, while Koka strain and Chamo strain had the lowest in across and H, and in L, respectively.

3.2.Total performance

The joint effect of fixed, additive, reciprocal and heterosis effects of crossbreds are summed up as least-squares mean estimates for cHBW, in Tables 5, 6 and 7, across production systems, in H and in L, respectively. Both across and within production systems, the total performance was highest for CxZ, followed by KxZ. Especially in the extensive environment and across the production systems, these two combinations performed significantly ($P < 0.05$) better than many of the other strain combinations. Also, in the extensive and intensive environments both these strain combinations performed significantly ($P < 0.05$) better than the purebred CxC and ZxZ, while for most of the remaining strain combinations, no significant ($P > 0.05$) differences were obtained. The overall phenotypic means of cHBW of the male fish reared in the two environments were similar, 136.3 g in H and 133.8 g in L, with 30.7% and 28.6% coefficient of variation, respectively.

3.3. Heritabilities and genotype by environment interaction

The genetic parameters for cHBW when analysed with Model 2, i.e. considered as separate traits in the intensive and in the extensive environments, are shown in Table 8. The genetic correlation between cHBW recorded in the two test environments was high, 0.99, and the estimates of heritability in the two test environments were considerable; 0.16 and 0.37 in the extensive and in the intensive environments, respectively, whereas the heritability was 0.28 ± 0.06 when both environments where analysed with the single trait model.

4. Discussion

The comparison of the strain combinations for growth, which was done by least-squares means averaged over fixed effects and incorporating additive, general reciprocal and, for crossbreds, also the total heterosis effect, generally showed that purebred Koka (K) strain was superior to purebred Chamo (C) and Ziway (Z) strains, at least in L (Table 7), and this differences among strains are similar to those reported by Eknath *et al.* (1993), Bentsen *et al.* (1998), Lozano *et al.* (2011) and Workagegn and Gjøen (2012). However, the highest harvest

body weight was obtained by crossbreds, with considerable variation in growth among the various combinations, also compatible with the results of Eknath *et al.* (1993) and Bentsen *et al.* (1998).

The additive and the general reciprocal effects did not contribute significantly to the differences in the least-squares means of the nine combinations since the differences in average additive and general reciprocal effects, neither across or in any of the two production systems, were no significant difference among the strains; and none of these effects were different from zero ($P > 0.05$; Table 3). Bentsen *et al*. (1998) also studied additive genetic and general reciprocal strain effect differences in the growth trait of Nile tilapia, but contrary to us, they did find significant ($P < 0.05$) differences in these effect among strains, possibly since as much as eight strains were compared.

Several authors, e.g. Gjerde and Refstie (1984), Gjerde (1988), Bentsen *et al.* (1998), Gjerde *et al.* (2002) and Thanh *et al.* (2010), reported considerable differences between strain general reciprocal effects. Such differences in strain general reciprocal effect could be largely attributed to the non-additive maternal effects, including relative egg size and egg quality, relative maternal body size in caring for eggs or fry or cytoplasmic inheritance (Thanh *et al*., 2010), and common environmental effects caused by separate rearing of full-sib families until tagging (Gjerde, 2005). The later one was not estimated in our study because reciprocal/maternal effect and communal environmental effect were confounded (Thanh *et al.*, 2010), resulting in zero variance for communal environmental effect when included in the model. Thus, the random communal environmental effect was dropped from the model used for genetic parameter estimation.

The last contribution to the least-squares means of the crossbred comes from the total heterosis effects; largest and significant ($P < 0.05$) for the ZxC/CxZ combinations in the extensive environment. In percent of the least-squares means, calculated from fixed, additive and reciprocal effects, the ZxC/CxZ heterosis in the extensive environment amounted to 26.5/23.6%, respectively (Table 7). This value was larger than those obtained by Bentsen *et al.* (1998). Moreover, all heterosis percentages were larger in the extensive than in the intensive environments, indicating an effect of the environment on heterosis, as also reported by Bentsen *et al.* (1998).

Among the six strain combinations ZxC/CxZ expressing the most heterosis, in percent across environments, the corresponding crosses had significantly larger least-squares means than most

other strain combinations ($P < 0.05$). These results are in support of a future breeding program for growth with Nile tilapia in Ethiopia having two lines, one based on the Chamo strain and one based on Ziway strain. However, the number of families for these two purebred strains found in the F_1 generation are very few, ranging from 8 to 10 families per strain, to use as a base line population. This likely will lead to insufficient additive genetic variation and consequently low long-term genetic gain. However, if crossbreeding program is more economically viable, ways to compensate for this may be sought, e.g. by sampling more individuals from the preferred lakes. An alternative approach is thus to put all the best individuals from the three strains into a common composite population to capitalise on a large proportion of the non-additive genetic variance and thus utilise an average heterosis produced from the three strain combinations. As also suggested by Maluwa & Gjerde (2006) states that selection of individuals based on their ranking for additive genetic effect/breeding values/ from all strains whether the strain is high or low ranking, rather than their ranking for strains additive genetic effect only could be maintained a composite population in which a large proportion of total heterosis effect could be utilised in the next generation. The decision of which breeding program to choose should be based on a cost-benefit analysis.

When adjusting for the genetic group effect by regressing on the additive breeding value of strains in Model 2, the additive genetic variance across the two populations became substantial (Table 8), and the heritability estimates were 0.16 and 0.37 in the extensive and in the intensive environments, respectively. The estimates of heritability for harvest body weight were well within the range of other estimates reported by several authors for the same fish species reared in a range of different pond production systems; such as 0.01-0.59 by Charo-Karisa *et al.* (2006), 0.06-0.68 by Bentsen *et al.* (2012) and 0.26-0.34 by Rutten *et al.* (2005). Our estimates are of a size for which one can expect a considerable genetic improvement of harvest body weight of Nile tilapia to occur through selection.

Another pre-requisite when starting a breeding program is to have knowledge on whether genotype by environment interaction might be anticipated. We estimated this as a genetic correlation between the same trait in the extensive and intensive environment and found an estimate of 0.99. This estimate is larger than the critical threshold of 0.8 suggested by Robertson (1959) and 0.86 by Sae-Lim *et al*. (2016). Thus, GxE is not expected to lead to substantial re-ranking and hence does not motivate distinct breeding schemes for each environment in Ethiopia.

This experiment revealed that fish grown in L had comparable HBW to that of fish grown in H, which indicates that the extensive environment fits these strains, but with lower coefficient of variance. With an improved diet in the intensive environment, one should expect the fish to grow better, but the stocking density was higher and thus likely led to increased energy expenditure and reduced growth, likely as a result of antagonist behavioural interaction, competition for food and living space, reduced dissolved oxygen level and/or stress, as also described in Kapinga *et al.* (2014) and El-Said & Hussein (2015). However, the total production in the H is expected to be higher than in the L as it has higher stocking density.

Batch and age are systematic effects that are known to affect growth of Nile tilapia (e.g. Bentsen *et al.,* 2012), and are thus adjusted for in the models used, although they were significant ($P < 0.05$) in across and within test environments. Regardless of the possibility of correcting for this effect, special focus should be given to reduce its impact by shortening the time used for family production (Rutten *et al.,* 2005; Bentsen *et al.,* 2012).

Conclusion

The results support that a breeding program can be established for Nile tilapia in Ethiopia. The results are to some extent in favour of establishing a crossbreeding program for Nile tilapia in Ethiopia based on individuals from the base population utilising non-additive genetic, heterosis, effects, although pure breeding program based on selection for additive genetic performance is equally important. The decision of what breeding program to choose should be based on a cost-benefit analysis.

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Table 1

Number of families (N_F) and number of offspring (N_O) per family for each of the nine strain combinations in the first generation (F_1), resulting from crossing parental fish from three Nile tilapia strains (Z = Ziway strain, K = Koka strain and C = Chamo strain)

Strains ♂	Z	K	C
♀	N_F/No	N_F/No	N_F/No
Z	10/314	10/291	9/252
K	8/271	10/312	9/245
C	10/329	6/177	9/230

Table 2

Coefficients assigned in the complete diallel cross in the first generation (F_1), for additive genetic (A_m), reciprocal (R_m) and total heterosis strain cross (D_n) effects

Strain cross	A_m			R_m			D_n		
♀x♂	Z	K	C	Z	K	C	ZxK/KxZ	ZxC/CxZ	KxC/CxK
ZxZ	1	0	0	1	0	0	0	0	0
ZxK	0.5	0.5	0	1	0	0	1	0	0
ZxC	0.5	0	0.5	1	0	0	0	1	0
KxK	0	1	0	0	1	0	0	0	0
KxZ	0.5	0.5	0	0	1	0	1	0	0
KxC	0	0.5	0.5	0	1	0	0	0	1
CxC	0	0	1	0	0	1	0	0	0
CxZ	0.5	0	0.5	0	0	1	0	1	0
CxK	0	0.5	0.5	0	0	1	0	0	1

Table 3

Estimates of additive genetic, reciprocal and total heterosis effects of variance corrected harvest body weight (g) in crosses of three *O. niloticus* strains (Z = Ziway strain, K = Koka strain and C = Chamo strain), both within and across the High (H) and Low (L) input production system, as obtained with Model 1. No internal difference was observed for all the three estimates within and across production systems.

Effects	Production system		
Additive genetic	H+L	H	L
Z	12.8[a1)]	2.5 [a]	16.6 [a]
K	6.9 [a]	-4.2 [a]	14.7 [a]
C	0.0 [a]	0.0 [a]	0.0 [a]
Reciprocal			
Z	-15.5 [a]	-17.5 [a]	-11.8 [a]
K	-1.1 [a]	-2.7 [a]	4.2 [a]
C	0.0 [a]	0.0 [a]	0.0 [a]
Total heterosis			
ZxK/KxZ	10.3 [a]	8.4 [a]	11.8 [a*]
ZxC/CxZ	17.4 [a *2)]	9.4 [a]	26.0 [a**]
KxC/CxK	13.0 [a]	6.2 [a]	15.3 [a *]

1) Equal letters indicate that no significant differences were found among strain/strain combinations ($P < 0.05$).

2) * $P < 0.05$ *and* ** $P < 005$ for test of being different from zero.

Table 4

Estimates of average general and overall heterosis for variance corrected harvest body weight (g) in a diallel cross of three *O. niloticus* strains (Z = Ziway strain, K = Koka strain and C = Chamo strain), both within and across the High (H) and Low (L) input production system, as obtained with Model 1.

Average general heterosis	H + L	H	L
Z	13.9[a1)]	8.9 [a]	18.9 [a]
K	11.7 [a]	7.3 [a]	13.6 [a]
C	13.3 [a]	7.1 [a]	16.5 [a]
Average heterosis	13.6	8.0	17.7

[1)] Equal letters indicate that no significant differences were found among strain/strain combinations ($P < 0.05$).

Table 5

Least-squares means (LSMs) of variance corrected harvest body weight (g) for the nine strain combinations resulting from crossing three *O. niloticus* strains (Z = Ziway strain, K = Koka strain and C = Chamo strain), percent heterosis (H%, in parenthesis), as obtained with model 1, and P-values for the contrasts of least-squares means. The results are obtained for the combined data set**, across the high and low input production systems**.

Strain combination		P-values for the contrasts between pairs of LSMs								
♀x♂	LSMs (H%)	ZxZ	ZxK	ZxC	KxK	KxZ	KxC	CxC	CxZ	CxK
ZxZ	110.9 (0.0%)	-	0.201	0.106	0.176	0.007	0.021	0.386	0.004	0.015
ZxK	118.3 (9.6%)		-	0.319	0448	0.033	0.129	0.305	0.038	0.066
ZxC	121.9 (16.7%)			-	0.390	0.127	0.189	0.184	0.033	0.189
KxK	119.4 (0.0%)				-	0.070	0.145	0.268	0.035	0.113
KxZ	132.7 (8.5%)					-	0.316	0.020	0.288	0.386
KxC	128.9 (11.2%)						-	0.049	0.218	0.444
CxC	113.6 (0.0%)							-	0.009	0.034
CxZ	137.4 (14.5%)								-	0.186
CxK	130.0 (11.1%)									-

Table 6

Least-squares means (LSMs) of variance corrected harvest body weight (g) for the nine strain combinations resulting from crossing three *O. niloticus* strains (Z = Ziway strain, K = Koka strain and C = Chamo strain), percent heterosis (H%, in parenthesis), as obtained with model 1, and P-values for the contrasts of least-squares means. The results are for the **high input production system**.

Strain combination		P								
♀x♂	LSMs (H%)	ZxZ	ZxK	ZxC	KxK	KxZ	KxC	CxC	CxZ	CxK
ZxZ	115.2 (0.0%)	-	0.316	0.221	0.224	0.030	0.061	0.097	0.018	0.045
ZxK	120.2 (7.5%)		-	0.371	0.386	0.058	0.156	0.189	0.061	0.067
ZxC	123.3 (8.3%)			-	0.499	0.149	0.195	0.274	0.047	0.164
KxK	123.4 (0.0%)				-	0.136	0.221	0.278	0.078	0.149
KxZ	135.1 (6.7%)					-	0.359	0.334	0.291	0.472
KxC	131.6 (5.0%)						-	0.448	0.252	0.390
CxC	130.2 (0.0%)							-	0.203	0.356
CxZ	140.9 (7.2%)								-	0.264
CxK	134.3 (4.9%)									-

Table 7

Least-squares means (LSMs) of variance corrected harvest body weight (g) for the nine strain combinations resulting from crossing three *O. niloticus* strains (Z = Ziway strain, K = Koka strain and C = Chamo strain), percent heterosis (H%, in parenthesis), as obtained with model 1, and P-values for the contrasts of least-squares means. The results are for the **low input production system**.

Strain combination		P								
♀x♂	LSMs (H%)	ZxZ	ZxK	ZxC	KxK	KxZ	KxC	CxC	CxZ	CxK
ZxZ	106.4 (0.0%)	-	0.066	0.008	0.039	0.0001	0.0012	0.264	0.0002	0.0056
ZxK	117.2 (11.2%)		-	0.138	0.337	0.005	0.07	0.015	0.016	0.127
ZxC	124.1 (26.5%)			-	0.323	0.115	0.248	0.001	0.042	0.492
KxK	120.5 (0.0%)				-	0.049	0.154	0.009	0.035	0.309
KxZ	133.3 (9.7%)					-	0.227	<0.0001	0.352	0.108
KxC	128.5 (13.5%)						-	0.0001	0.203	0.251
CxC	101.6 (0.0%)							-	<0.0001	0.006
CxZ	135.9 (23.6%)								-	0.042
CxK	124.3 (14.1%)									-

Table 8
Estimates and their standard errors (±S.E.) of additive genetic (σ_a^2), residual (σ_e^2), phenotypic (σ_p^2) variances and heritability (h^2) of variance corrected harvest body weight in a cross of three *O. niloticus* strains reared in two production systems (High input (H) and Low input (L)), and the estimated genetic correlation between the traits in the two environments (r_g).

	σ_A^2 ±S.E.	σ_e^2 ±S.E.	σ_p^2 ±S.E.	h^2±S.E	r_g ±S.E.
H	651 ± 174	1095 ± 116	1745 ± 107	0.37 ± 0.08	
L	216 ± 98	1117 ± 93	1334 ± 80	0.16 ± 0.07	0.99 ± 0.15

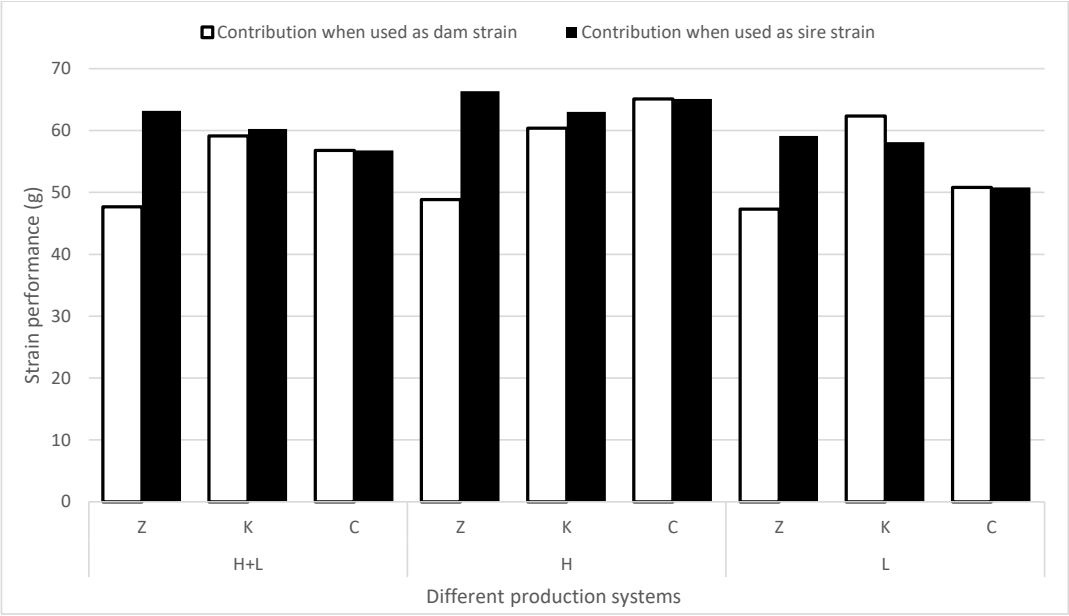

Figure 1 Least-squares means of variance corrected harvest body weights (g) of progeny of three *O. niloticus* strains (Z = Ziway strain, K = Koka strain and C = Chamo strain) when the strains were used as sire or dam, within and across production systems, High input (H) and Low input (L), as obtained with Model 1.

Paper II

Prediction of fillet weight and fillet yield from body measurements and genetic parameters in a complete diallel cross of three Nile tilapia (*Oreochromis niloticus*) strains

Kassaye Balkew Workagegn, Gunnar Klemetsdal, Elias Dadebo and Hans Magnus Gjøen

Manuscript

Prediction of fillet weight and fillet yield from body measurements and genetic parameters in a complete diallel cross of three Nile tilapia (*Oreochromis niloticus*) strains

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Abstract

In this study, the first objective was to investigate whether non-lethal or non-invasive methods, utilizing body measurements, could be used to efficiently predict fillet weight and fillet yield for three Nile tilapia strain combinations. The second objective was to estimate heritability of body weight, actual and predicted fillet traits as well as genetic correlations between these traits. A third goal was to estimate additive, reciprocal and heterosis effects for body weight and the various fillet traits. The fish used in this experiment originated from a complete diallel cross of three Nile tilapia strains. In females, early sexual maturation was widespread, and it was decided to only utilize data from male fish. Thus, only 958 male fish from 81 full-sib families were used, both for prediction of fillet traits and in genetic analysis. The prediction equations from body measurements were established by a stepwise forward regression analysis, choosing models with the least predicted residual error sums of squares (PRESS). The results revealed that body measurements on live Nile tilapia is well suited to predict fillet weight, but not fillet yield (R^2= 0.945 and 0.209, respectively), but both models were seemingly unbiased. The genetic analyses were carried out with bivariate, multibreed models. Body weight, fillet weight and predicted body weight were all estimated with a heritability around 0.25, and with very high genetic correlations. Contrary, fillet yield was only to a minor degree heritable, while predicted fillet yield obtained a heritability of 0.19, being a resultant of two body weight variables, known to have a high heritability. The latter trait was estimated with genetic correlations to body weight and fillet weight traits larger than 0.82. No significant differences among strains were found for their additive genetic, reciprocal or heterosis effects, while total heterosis effects were estimated positive and significant ($P < 0.05$). Rather than to base selection on body weight and fillet yield, it should be selected for predicted fillet weight/body weight.

Key words: *Additive; Fillet traits; Genetic correlation; Heritability; Heterosis; Prediction; Reciprocal*

1. Introduction

Tilapia is one of the most popular freshwater aquaculture species, particularly in Asia and Latin America (FAO, 2012). Among tilapia species, Nile tilapia, *Oreochromis niloticus*, is commercially the most important and has been improved through various breeding programs around the world, with the primary aim to improve growth traits (Eknath *et al.*, 1993; Gjøen, 2003; Bentsen *et al.*, 2012). Since Nile tilapia has relatively low fillet yield, genetic improvement of fillet traits, i.e. fillet weight and fillet yield, have been studied over the last few decades (Rutten *et al.*, 2005a; Nguyen *et al.*, 2010; Gjerde *et al.*, 2012; Peterman & Phelps, 2012).

Fillet traits are not directly measurable on selection candidates and ranking of live candidates thus has to be based on information on relatives, mainly from slaughtered full-sibs. This requires a number of animals to be slaughtered and fillet traits accurately recorded, which can be laborious and costly. With full-sibs information, one only utilises half of the additive genetic variation, that between families. In contrast, genomic selection would also utilise within family variation, but this requires relatively costly genotyping of both a reference and the candidate populations (Haffray *et al*., 2013). A third option would be to base selection on predicted phenotypes of the fillet traits for the breeding candidates, based on their body measurements. This could be the only information criteria for these traits or be combined with actual fillet traits from slaughtered full-sibs.

Several studies on improvement of fillet traits by use of body measurements have been conducted in different fish species (e.g. Cibert *et al.*, 1999; Sang *et al*., 2009; Hung & Nguyen, 2014). In this study, the first objective was to investigate whether non-lethal or non-invasive methods, utilising body measurements, could be used to efficiently predict fillet weight and fillet yield for three Nile tilapia strain combinations. The second objective was to estimate heritability of body weight, actual and predicted fillet traits as well as genetic correlations between these traits. A third goal was to estimate additive, reciprocal and heterosis effects for body weight and various fillet traits.

2. Material and methods

2.1. Genetic material and rearing conditions

The fish used in this experiment originated from a complete diallel cross of three Nile tilapia strains. The parental fish (F_0) were collected randomly from three Ethiopian Rift Valley Lakes, i.e. Lake Ziway (Z), Lake Koka (K) and Lake Chamo (C). A total of 81 full-sib families were produced in breeding hapas in 2013/2014 by natural mating (Workagegn *et al.*, 2018). From each full-sib family, about 200 fry were stocked in a $1m^3$ breeding hapa. Fry produced in the first 15 days of November 2013 was classified as hatching group or batch one, while fry produced from January 1 to 15, 2014 was classified as batch five. After one month, 100 fry were randomly chosen and reared separately in nursery hapas until they reached an average size of 23g, at which tagging took place (Workagegn *et al.*, 2018). Subsequently, about 20-30 fingerlings per full-sib family were chosen at random and tagged using Passive Integrated Transponder (PIT) tags.

The tagged fingerlings were randomly distributed into four groups and then stocked into two production systems, in duplicates; two ponds for a low input production system (L) and two other ponds for a high input production system (H). In L, the average stocking density in the two replicate ponds was 2.5 fish/m^2, and both ponds were fertilized with poultry manure at a rate of 1,500 kg per hectare per month. The fish were fed twice a day with a supplementary diet consisting of 70% wheat bran, 15% niger press cake and 15% bone-meat meal, having 21% crude protein in total, at a daily rate of 3% of their body weight. The stocking density in the H replicates was 5.2 fish/m^2, and the fish were fed three times a day with a pelleted diet consisting of 40% bone-meat meal, 20% roasted soybean meal, 20% wheat flour, 15% maize flour and 5% niger press cake, having 28% crude protein in total, at a daily rate of 3% of their body weight. The water level of the ponds was maintained at a depth of 80-100 cm with a water renewal for L and H of 2.5% and 7.2% of the pond volume per day, respectively.

2.2. Data collection and measurement

At five months of age all 2421 fish from the 81 full-sib families were weighted (BW5, mg). Further, at seven months of age, 1348 fish were randomly sampled for slaughter and filleting. Before slaughter, the following body measurements were recorded: body weight (BW7, mg) by a digital weight, standard body length (SL, mm) and head length (HL, mm) by a ruler as well as body thickness (BT, mm), body depth (BD, mm) and head thickness (HT, mm) by a calliper. The

positions for measuring the body measurments are indicated in Figure 1. Subsequently, the fish were manually filleted by two trained persons, and skin-off fillet weight (FW) was recorded. All fish were recorded within two weeks. In addition, fillet yield in percent (FY=FW/BW7)100) and corrected standard body length (CL=SL-HL) were calculated.

2.3. Data analysis

In females, early sexual maturation was widespread, and it was decided to only utilise data from male fish. Thus, only 958 male fish were used, both for prediction of fillet traits and genetic analysis.

2.3.1. Prediction of fillet traits

This was carried out by use of PROC GLMSELECT in SAS®, with forward selection and 5-fold cross-validation after checking for possible outliers. The model used to obtain a prediction equation for fillet trait was (Model 1):

$$Y_i = \mu + \beta_1 BW7_i + \beta_2 BT_i + \beta_3 HT_i + \beta_4 HL_i + \beta_5 BD_i + \beta_6 CL_i + \beta_7 SL_i + e_i$$

where Y_i denotes either fillet weight or fillet yield on individual i, μ is the intercept, β are the regression coefficients for BW, BT, HT, HL, BD, CL, SL and e_i is a random residual for the i^{th} individual.

The SAS-procedure chooses the model with the least predicted residual error sum of squares, PRESS, obtained from cross-validation. In addition, the models' fit statistics, i.e. the coefficient of determination (R^2) and Akaike information criterion (AIC) are given. For the preferred model, bias was calculated as follows:

$$bias = \left(\frac{\sum_{i=n}^{n}(Yi - \ddot{Y}i)}{n}\right)$$

where Y and Ÿ are observed and predicted values of each of the two traits (fillet weight or fillet yield), and n is the number of fish with data (958). Similarly, for the chosen model the coefficient of determination in prediction was obtained as:

$$R^2_p = \left(1 - \frac{PRESS}{TSS}\right)$$

where TSS is the total sums of squares.

2.3.2. Genetic analyses

All six traits were pre-corrected for phenotypic variance differences in batch subclasses using a multiplicative correction factor, i.e. with $Y_{ih}(\sigma_Y/\sigma_{Yh})$, where Y_{ih} is the trait phenotype for animal *i* in level *h* of the batch subclass, σ_y is the weighted mean standard deviation of predicted fillet traits in all data, and σ_{yh} is the standard deviation of prediction fillet traits in level *h* of the subclass (Hill, 1984; Jere *et al.*, 2003).

The genetic parameter estimation for body weight (BW5 and BW7), fillet weight, fillet yield, predicted fillet weight and predicted fillet yield was carried out using bivariate animal models in ASReml, version 4.1 (Gilmour *et al.*, 2015). The model used for estimation of genetic parameter for the two traits was (Model 2):

$$\begin{bmatrix} \boldsymbol{Y_1} \\ \boldsymbol{Y_2} \end{bmatrix} = \begin{bmatrix} \boldsymbol{X_1} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{X_2} \end{bmatrix} \begin{bmatrix} \boldsymbol{b_1} \\ \boldsymbol{b_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_1} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{Z_2} \end{bmatrix} \begin{bmatrix} \boldsymbol{a_1} \\ \boldsymbol{a_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{e_1} \\ \boldsymbol{e_2} \end{bmatrix}$$

where: $\begin{bmatrix} \boldsymbol{Y_1} \\ \boldsymbol{Y_2} \end{bmatrix}$ is a vector of observations for traits 1 and 2, respectively, $\begin{bmatrix} \boldsymbol{b_1} \\ \boldsymbol{b_2} \end{bmatrix}$ is a vector of fixed effects for the two traits, $\begin{bmatrix} \boldsymbol{X_1} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{X_2} \end{bmatrix}$ is a design matrix relating the observations of the two traits to the fixed effects. For each trait the fixed effects considered were μ, (the intercept), B_h (the interaction between the fixed effect of the h^{th} batch (h = 1-5)) x Rep_j, (the fixed effect of the j^{th} pond (repetition) (j = 1, 2)) x E_k (the fixed effect of the k^{th} production system (k = 1, 2)), and P_l, the effects of filleters. Other fixed effects were; $b_{A(m)}$, the regression coefficient of the additive genetic effect of the genes originating from the m^{th} strain (m = 1-3) with the regression variable A_m, the proportion of genes in the i^{th} individual originating from the m^{th} strain (A_m = 0, 0.5 or 1, and $\sum A_m = 1$); $b_{R(m)}$, the regression coefficient of the reciprocal effect of the m^{th} strain, with the regression variable R_m, the proportion of genes of the dam of the i^{th} individual originating from the m^{th} strain (R_m = 0 or 1 and $\sum R_m = 1$) and $b_{D(n)}$, the regression coefficient of the individual heterosis effect of the n^{th} cross between two different strains (n = 1-3), with the regression variable D_n, the proportion of the individual heterosis effect of the n^{th} strain cross expressed in the i^{th} individual, (D_n = 0 or 1, i.e. $\sum D_n = 1$ for crossbreds or $\sum D_n = 0$ for purebreds. The design matrix $\begin{bmatrix} \boldsymbol{Z_1} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{Z_2} \end{bmatrix}$ relates the observations of the two traits to their random effects, $\begin{bmatrix} \boldsymbol{a_1} \\ \boldsymbol{a_2} \end{bmatrix}$. For the latter, the (co)variance structure was: $\begin{bmatrix} \boldsymbol{A\sigma^2 a_1} & \boldsymbol{A\sigma a_1 a_2} \\ \boldsymbol{sym.} & \boldsymbol{A\sigma^2 a_2} \end{bmatrix}$, where **A** is the additive relationship matrix

among all fish (958 fish in F_1 and 124 parents), and $\begin{bmatrix} \boldsymbol{e_1} \\ \boldsymbol{e_2} \end{bmatrix}$ is a vector of random residual effects for the two traits. The common environmental effects caused by separate rearing of full-sib families until tagging was not included in the model because the reciprocal/maternal effect and communal environmental effect were confounded, resulting in zero variance for the communal environmental effect.

For calculation of additive genetic, general reciprocal and heterosis effects of each strain and strain combinations, independent of other traits, a univariate version of Model 2 was used, denoted Model 3.

3. Results

The prediction equations for fillet weight and fillet yield were established with fish having on average 176 g body weight, 58.3 g fillet weight and 33.1% fillet yield. For fillet weight, the preferred model (Model 5; Table 1) contained five predictor variables; body weight, body thickness, head thickness, head length and body depth. This model had the lowest PRESS-value, was seemingly unbiased (0.008) and had a R^2_p of 0.94, meaning that the model in prediction explained 94% of the phenotypic variance. This was only slightly lower than for model fit (R^2 = 0.945). Body weight and body thickness were estimated with positive regression coefficients (0.38 and 8.5, respectively) whereas the regression coefficients for head thickness, head length and body depth were negative (Table 1).

The preferred prediction model for fillet yield contained two variables (Model 2; Table 2); body thickness and head thickness. This model was also seemingly unbiased (0.0018) but did not predict well since the R^2_p value was only 18.3%. Likewise, with respect to model fit the phenotypic variance explained by the model was small, only 20.9% (R^2). The regression coefficients were 5.7 for body thickness and -2.9 for head thickness (Table 2).

The estimates of genetic parameters for body weight and the various fillet traits are presented in Table 3. The estimated heritability of body weight at five and seven months of age, fillet weight and predicted fillet weight were of similar size (0.23-0.28; Table 3), with high internal genetic correlations ($\geq$ 0.93). In contrast to this, the estimated heritability for fillet yield was found very low (0.05), and fillet yield was estimated with a low genetic correlation to the former traits ($\leq$ 0.39). However, the estimate of heritability for predicted fillet yield was considerably higher

(0.19), with a low positive genetic correlation to fillet yield (0.10), but with a higher genetic correlation to the other traits ($\geq$ 0.82).

The estimates of additive, general reciprocal and individual heterosis effects of strains and strain combinations for the various traits across the two production systems are presented in Table 4. No significant differences ($P > 0.05$) were found between strains or strain combinations for any of the three effects. However, the total heterosis effects were significantly larger than zero ($P < 0.05$) for body weight, fillet weight and predicted fillet weight (Table 4). This was also reflected in the significant average general heterosis effect of the Koka strain for body weight (Table 5).

3. Discussion

The results revealed that the preferred model for prediction of fillet weight, with body weight, body thickness, head thickness, head length and body depth as predictors, had high coefficient of determination ($R^2 = 0.945$; Table 1). This R^2 value agrees well with the value of 0.95 reported by Rutten *et al.* (2004) in tilapia for fillet weight. Rutten *et al.* (2004) also found body weight, body thickness and body depth to be important in addition to standard body length and corrected body length, which were also included in this study. This indicates that body weight, body thickness and body depth are the most potent predictor variables for fillet weight.

For fillet yield, the preferred prediction model, with two predictor variables; body thickness and head thickness, only explained 20.9% of the variation in this trait (Table 2). The R^2 value obtained in the present study compares to, and was even somewhat higher than, the values reported by Rutten *et al.* (2004) (15%) and Pires *et al.* (2011) (16%). Of the two predictor variables, body thickness was the most important predictor variable as also reported by Rutten *et al.* (2004), although these authors stated that this variable might be less accurately recorded than the other body measurements.

In other fish species, much higher R^2 values have been obtained for fillet yield, e.g. Sang *et al.* (2009) (R^2=0.77), who found volume to be the most important predictor. Volume was not considered in this study, demonstrating that there should still be scope for some improvement of the prediction model for fillet yield in tilapia. One should also consider reducing the measurement error and increase the filleting accuracy by training of filleters and recorders. Despite these

possible improvements, it seems that it is harder to obtain a sufficiently accurate prediction equation for fillet yield in tilapia.

The estimates of heritability for fillet weight and predicted fillet weight were moderate, with a relatively high internal genetic correlation (Table 3). Size of the heritability estimates for fillet weight compares to the estimates reported by Rutten *et al.* (2005a) (0.24) but was higher than the estimates reported by Gjerde *et al.* (2012) (0.16). The genetic correlations between fillet weight and predicted fillet weight were found to be very high also in their studies (> 0.98).

The average fillet yield (33.1%) of *O. niloticus* obtained in this study was moderate, and similar to the values found on equally sized tilapia reported by Nguyen *et al.* (2010) (33.6%), Pires *et al.* (2011) (32.03%) and Peterman & Phelps (2012) (31.3%)), but lower than the values reported on larger tilapia by Rutten *et al.* (2004) (35.7%), Rutten *et al.* (2005a) (37.3%) and Gjerde *et al.* (2012) (42.6%). It is thus reasonable to assume that the lower value in the present study was mainly due to a relatively small body size of the fish (176 g); as demonstrated by Gjerde *et al.* (2012), who found 45.1% fillet weight in 1200 g fish, 42.2% in 860 g fish and 41.3% in 650 g fish.

The estimate of heritability for fillet yield was low (0.05; Table 3), similar to the estimates reported by Gjerde *et al.* (2012) (0.06) and Thodesen *et al.* (2012) (0.08). In contrast, Nguyen *et al.* (2010) found a considerably higher estimate (0.25) in larger fish (> 527 g). Thus, the low estimates of heritability for fillet yield in the present study could also be a consequence of the low body weight (176 g) in this study, as also argued by Gjerde *et al.* (2012). Likewise, Rutten *et al.* (2005b) and Mello *et al.* (2016) reported that the size of estimates of heritability are affected by the age of the fish.

Powell *et al.* (2008) argued that fillet yield, being a ratio trait, *i.e.* fillet weight per body weight, is expected to have a low genetic variance; leading to low heritability and low genetic correlations, as also obtained in this study. Controlling the various factors that influence fillet yield are required to increase its predictability and to obtain reasonable genetic correlation and heritability (Nguyen *et al.*, 2010; Reis Neto *et al.*, 2014). Further, Nguyen *et al.* (2010) stated that the genetic correlation between fillet yield and its predicted value was low, whereas those between fillet weight and its predicted value was generally high. This statement corresponds well with the results obtained in this study, and the higher heritability of predicted fillet yield is likely a consequence of being a

resultant of two body weight variables, known to have high heritability. In general, fillet yield being a ratio trait, with a mixture, and perhaps divergent genetic control mechanism and no known statistical distribution, is not well suited in a breeding context.

The main result obtained is that prediction works well for fillet weight, but not for fillet yield. If fillet weight is set as the breeding goal, the way ahead should either be to select directly for predicted fillet weight alone or, alternatively, to select for body weight as an indirect trait, since it has a high genetic correlation to fillet weight (0.93-0.99; Table 3). Of these two traits, body weight has a practical advantage since it is easiest to record.

In this limited material, with only 958 fish, it was found no significant ($P < 0.05$) differences among strains additive genetic and reciprocal effects as well as among strain combinations' total heterosis effect. These results are consistent with Workagegn *et al.* (2018) who in the same material analysed body weight recorded at 5 months of age utilising altogether 1564 fish, i.e. two months earlier than in this study. In contrast to us, several studies have shown significant ($P < 0.05$) differences between additive genetic, reciprocal and individual heterosis effects among strains and strain combinations, likely due to a larger number of strains being compared and no correction for the random animal effect in the analysis (Bentsen *et al.*, 1998; Gjerde *et al.*, 2002; Thanh *et al.*, 2010; Lozano *et al.*, (2011)). In our study, the ZxK/KxZ combinations produced the most expressed total heterosis effect across the two production systems. The overall average heterosis effect for body weight at 7 months of age (11.4%) was more or less similar to that of the corresponding value obtained at 5 months of age (10.6%) of the same fish (Table 5 and Workagegn *et al.*, 2018), with slightly higher at later age. In correspondence to this, the average general heterosis estimates of strains also increased with age (Table 5), indicating that heterosis in tilapia is age dependent. In general, these estimates were larger than those obtained by Bentsen *et al.* (1998), Maluwa *et al.* (2006) and Lozano *et al.* (2011).

Conclusion

Body measurements on live *O. niloticus* is well suited to predict fillet weight, but not fillet yield ($R^2 = 0.945$ and 0.209, respectively). Body weight, fillet weight and predicted body weight were all estimated with a heritability around 0.25, and with high internal genetic correlations. Rather than to base selection on body weight and predicted fillet yield, the results suggest selecting for predicted fillet weight/body weight.

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Table 1

The regression variables entering the prediction equation for fillet weight (at 7 months of age) through the first six steps of forward selection.

Step	Prediction equation[1)]	R^2	R^2-adj	AIC	PRESS	R^2_p	Bias
1	-5.4+0.36BW	0.936	0.935	2728.7	12378.1		
2	-18.4+0.32BW+7.7BT	0.940	0.940	2654.1	11503.6		
3	-7.1+0.35BW+9.5BT-8.1HT	0.943	0.943	2611.6	11153.3		
4	0.74+0.37BW+9.5BT-6.6 HT-2.9HL	0.944	0.944	2591.1	11100.5		
5[2)]	1.74+0.38BW+8.5BT-5.7HT-2.0HL-1.1BD	0.945	0.945	2579.8	11016.5	0.940	0.008
6	6.3+0.39BW+8.6BT-5.1HT-2.4HL-1.3BD -0.44CL	0.945	0.945	2579.4	11062.0		

At each step, the statistics relevant for model fit (coefficient of determination (R^2), adjusted R^2 and the Akaike Information Criterion (AIC)) and for the quality of model prediction (predicted residual error sums of squares (PRESS), coefficient of determination in prediction (R^2_p) and bias.

[1)]Variables being those indicated in Figure 1 and in addition; body weight (BW) and corrected body length (CL=SL-HL).

[2)]Preferred model.

Table 2

The regression variables entering the prediction equation for fillet yield (at 7 months of age) through the first six steps of forward selection.

Step	Prediction equation[1)]	R^2	R^2-adj	AIC	PRESS	R^2_p	Bias
1	23.3+3.6BT	0.178	0.178	1595.9	3863.6		
2[2)]	25.4+5.7BT-2.9HT	0.209	0.207	1562.0	3754.5	0.183	0.0018
3	26.2+6.2BT-2.5HT-0.6HL	0.211	0.209	1560.5	3771.9		
4	29.6+0.01BW+5.7BT-3.3HT-1HL	0.216	0.213	1556.5	3795.1		
5	30.2+0.02BW+5.7BT-3.3HT-0.9HL-0.32BD	0.218	0.214	1556.2	3801.8		
6	29.5+0.01BW+5.5BT-3.2HT-1.04HL-0.32BD+0.11SL	0.219	0.214	1557.8	3809.1		

At each step, the statistics relevant for model fit (coefficient of determination (R^2), adjusted R^2 and the Akaike Information Criterion (AIC)) and for the quality of model prediction (predicted residual error sums of squares (PRESS), coefficient of determination in prediction (R^2_p) and bias.

[1)]Variables being those indicated in Figure 1 and in addition; body weight (BW) and corrected body length (CL=SL-HL).

[2)]Preferred model.

Table 3

Estimates with standard errors (± s.e.) of genetic parameters for variance corrected body weight at 5 and 7 months of age (BW5 and BW7, respectively), fillet weight (FW), predicted fillet weight (PFW), fillet yield (FY) and predicted fillet yield (PFY) (all at 7 months of age) with phenotypic variances (σ^2_p), heritability on diagonal and additive and phenotypic correlations above and below the diagonal, respectively. in the parenthesis.

Traits	σ^2_p [1)] ± s.e.	BW5 ± s.e.	BW7 ± s.e.	FW ± s.e.	PFW ± s.e.	FY ± s.e.	PFY ± s.e.
BW5	1578 ± 72	**0.28** ± **0.06**	0.98 ± 0.04	0.93 ± 0.05	0.98 ± 0.05	0.04 ± 0.3	0.86 ± 0.10
BW7	1815 ± 98	0.49 ± 0.04	**0.27** ± **0.07**	0.99 ± 0.01	<1.0 ± 0.00	0.26 ± 0.3	0.86 ± 0.08
FW	257 ± 14	0.44 ± 0.04	0.96 ± 0.00	**0.23** ± **0.07**	0.99 ± 0.07	0.39 ± 0.2	0.82 ± 0.08
PFW	242 ± 13	0.47 ± 0.04	0.99 ± 0.00	0.96 ± 0.04	**0.26** ± **0.07**	0.26 ± 0.1	0.88 ± 0.06
FY	6.3 ± 0.3	0.09 ± 0.04	0.33 ± 0.04	0.57 ± 0.03	0.36 ± 0.04	0**.05** ± **0.04**	0.10 ± 0.30
PFY	1.3 ± 0.1	0.19 ± 0.05	0.64 ± 0.03	0.70 ± 0.03	0.71 ± 0.02	0.49 ± 0.04	**0.19** ± **0.06**

[1)]Estimates for BW7 when analysed bivariately with FW, otherwise in bivariate analysis with BW7.

Table 4

Estimates of additive genetic, reciprocal and individual heterosis effects of variance corrected body weight at 7 months of age (BW7), fillet weight (FW), predicted fillet weight (PFW), fillet yield (FY), and predicted fillet yield (PFY) (all at 7 months of age) in a cross of three *O. niloticus* strains (Z = Ziway, K = Koka and C = Chamo), obtained with Model 3.

Effects	BW7	FW	PFW	FY	PFY
Additive genetic					
Z	-7.1	-3.2	-2.9	-0.20	-0.07
K	5.9	2.1	2.6	0.37	0.56
C	0.0	0.0	0.0	0.0	0.0
Reciprocal					
Z	-10.1	-2.4	-3.6	0.47	-0.13
K	-8.6	-1.6	-2.8	0.65	-0.16
C	0.0	0.0	0.0	0.0	0.0
Individual heterosis					
ZxK/KxZ	23.2$^{**1)}$	9.1**	8.2**	0.59	0.24
ZxC/CxZ	9.1	4.1	3.3	0.71	0.14
KxC/CxK	22.2**	7.2*	7.5*	0.17	0.16

None of the contrasts between strains or strain combinations were significantly different from each other ($P < 0.05$).

[1)] * P <0.05, ** P <0.01, for test of being different from zero.

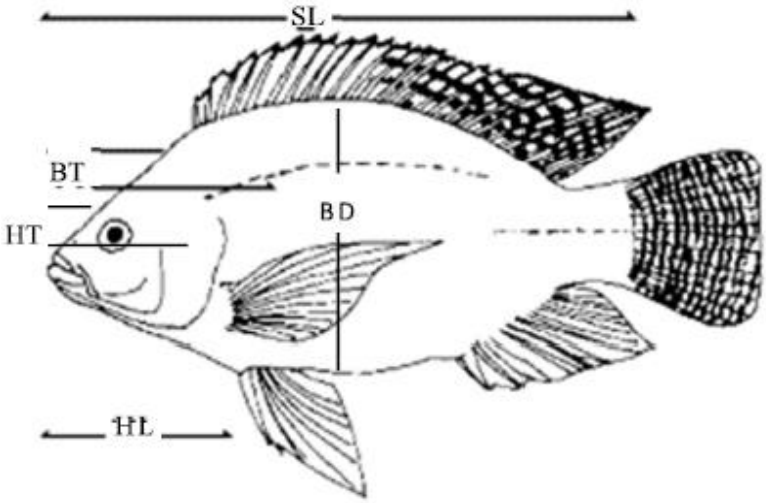
Table 5

Estimates of average general heterosis for each stain and the overall average heterosis of all strains for body weight at 7 months of age (BW7), fillet weight (FW), predicted fillet weight (PFW), fillet yield (FY) and predicted fillet yield (PFY) (all at 7 months of age) in a cross of three *O. niloticus* strains (Z = Ziway, K = Koka and C = Chamo), obtained from Model 3.

General heterosis	BW7	FW	PFW	FY	PFY
Z	16.2	6.6	5.8	0.65	0.19
K	22.7[*1]	8.2	7.9	0.38	0.20
C	15.7	5.7	5.4	0.44	0.15
Overall heterosis	18.1	6.3	6.3	0.49	0.18

None of the contrasts between strains were significant different from each other ($P<0.05$).

[1)]* $P<0.05$, for test of being different from zero.



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378 **Figure 1.** Body measurments: head length (HL), head thickness (HT), body thickness (BT), body
379 depth (BD), and standard body length (SL).

Paper III

Selection responses over one generation of selection for increased body weight in Nile tilapia in Ethiopia

Kassaye Balkew Workagegn, Gunnar Klemetsdal, Elias Dadebo and Hans Magnus Gjøen

Manuscript

Selection responses over one generation of selection for increased body weight in Nile tilapia in Ethiopia

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Abstract

The aim of this study was to estimate the magnitude of genetic gain for six traits in a selective breeding program for Nile tilapia in Ethiopia, and to estimate genetic parameters for these traits, including additive, reciprocal and heterosis effects for harvest body weight, across two generations. Body weight at 5 months of age was recorded over two generations, while the following traits were recorded at 7 months of age in the F_1 generation: body weight, fillet weight, predicted fillet weight, fillet yield and predicted fillet weight. In females, early sexual maturation was widespread, and it was thus decided to only utilise data from male fish in the analysis. Body weight was recorded at harvest at 5 months of age for 3,051 male fish from 81 and 99 full-sib families from the F_1 and F_2 generation, respectively. In addition, 958 records for the other body traits were obtained at 7 months of age in the F1 generation. The genetic analysis was carried out with bivariate, multibreed animal models. Body weight and fillet weight traits were highly heritable ($h^2 \geq 0.33$) and with internally high positive genetic correlations (≥ 0.96), while fillet yield had a low heritability ($h^2 \geq 0.04$) and low genetic correlation to body weight at 5 months of age (-0.018). When selecting on estimated breeding values for body weight at 5 months of age, the selection response obtained over one generation of selection for body weight was 7.1% and correlated responses in fillet weigh was 5.0%, and a slightly negative response for fillet yield (-0.4%). Estimates of *a priori* significant ($P < 0.05$) total/direct heterosis effect on body weight at 5 months of age were verified when utilising both F_1 and F_2 data, with altogether 3,051 fish. The results with considerable individual heterosis effects support a crossbreeding program for Nile tilapia in Ethiopia based on individuals from the composite population, but a "pure" breeding program would be easier to run and has already shown to result in considerable genetic progress. The decision of what breeding program to choose should be based on a cost-benefit analysis.

Key words: *Additive genetic; Genetic gain; Genetic parameters; Reciprocal; Heterosis*

1. Introduction

Farmed Nile tilapia (*Oreochromis niloticus*) production has increased substantially worldwide over the last few decades. Genetic improvement programs of this species, such as the Genetically Improved Farmed Tilapia (GIFT) and the GenoMar Supreme Tilapia (GST), have contributed significantly to this success (Komen & Trong, 2014). These and other breeding programs have been implemented in different parts of the world, with varying responses to selection per generation for increased body weight in Nile tilapia, e.g. 12% to 17% by Eknath *et al.* (1998); 20% by Bentsen *et al.* (2003), 8.4% to 11.4% by Ponzoni *et al.*, (2005) and 3.6% by Gjerde *et al.* (2012). Variation in genetic gain among breeding programs may be due to several factors, such as selection intensity, accuracy of selection and/or lack of additive genetic variance resulting from differences in size of the breeding population, number of families, number of offspring per family, selection methods and mating strategies.

Although the aquaculture production in Ethiopia is growing, it is still in its early stage (Rothuis *et al.*, 2012). The absence of improved broodstock is probably one of the main bottlenecks for sustainable development of fish production in the country. Recent national research has compared growth performance of various Nile tilapia strains by calculating their average phenotypic performance and specific growth rate in pond culture systems, at the Sebeta Fisheries and Aquatic Life Research Centre (SFARC) and the Ziway Fisheries Resource Research Centre (ZFRC). In one of these tests, growth performance of four Nile tilapia strains, E.g. the Koka, Awassa, Ziway and Hora strains were evaluated for their growth rates over a two months period, and no significant difference among the strains were found, although the Koka strain was ranked best (Workagegn & Gjøen, 2012). Still, the Hora strain is used as the main source for fingerling production. Also, evaluation of reproductive traits and early fingerling growth in some selected Nile tilapia strains have been initiated at the Ziway and Sebeta research centres. However, there is no well-organized selective breeding program aiming at long-term genetic improvement in the country up till now.

Establishment of a Nile tilapia base population for long-term genetic improvement of growth traits from locally available strains is thus indispensable. Initially, additive, reciprocal and heterosis effects of strains have been estimated in a diallel cross with 3 strains. This is essential information when designing the future breeding scheme (Workagegn *et al.*, 2018a). Data from the following generation (F_2) will allow us to quantify the magnitude of genetic gain from selecting for increased body weight at 5 months of age in F_1. Estimates of additive, general reciprocal and heterosis effects for growth in the F_2 generation would add useful information

for the best choice of the future breeding program, as also reported by Bentsen *et al.,* (1998) and Maluwa and Gjerde (2006). Additionally, a prediction equation for fillet weight has been established (Workagegn *et al.,* 2018b) that will allow us to shift from traditional selection for increased body weight to fillet weight, which is the more valuable product. Thus, the present study aims at estimating the magnitude of genetic gain for body weight and fillet weight as well as fillet yield traits in a selective breeding program for Nile tilapia in Ethiopia, and to estimate genetic parameters for these traits, including additive, general reciprocal and heterosis effects for harvested body weight, across two production systems of different intensity.

2. Materials and methods

2.1. Description of experimental site and origin of Nile tilapia

The experiment was carried out at Hawassa Agricultural Research Centre (HARC), located 275 km south of Addis Abeba, Ethiopia. The base population of this selective breeding program was established with a complete diallel cross of three wild Nile tilapia strains collected from three Ethiopian Rift Valley Lakes, *i.e.* Lake Ziway (Z), Lake Koka (K) and Lake Chamo (C), in 2013. Each strain was stocked separately in 40 m^2 concrete ponds at a stocking density of 3-4 fish/m^2 and reared until they reached sexual maturation. Both the F_1 and F_2 generations were produced using a hierarchical mating design, in which a single sire was mated with up to two dams (Workagegn *et al.,* 2018a). To avoid high rate of inbreeding, the number of selection candidates per full-sib family was restricted to 5.

2.2. Production and rearing of fry

Natural mating and spawning were carried out in 1m^3 breeding hapas. For both the F_1 and F_2 generation, full- and half-sib families were produced, in 2013/2014 for the F_1 generation and in 2015 for the F_2 generation. Fry produced in the first two weeks of each generation was classified as hatching group or batch one of that generation, while fry produced the two last weeks was classified as batch five. After a month, 100 fry per family were transferred from the breeding hapa to a nursery hapa. When the fish reached an average size of 25g, about 20 to 30 fingerlings per full-sib family were randomly sampled and tagged using Passive Integrated Transponder (PIT) tags. The tagged fingerlings were randomly distributed into four groups and then stocked into two production systems in duplicates; two ponds mimicking a low input production system and two other ponds a high input production system (Workagegn *et al.,* 2018a).

2.3. Grow-out in two environments

The tagged fingerlings were communally stocked in the two grow-out ponds, termed *low*- (L) and *high*- (H) input production systems. The L had a stocking density of 2.5 fish/m^2, and the ponds were fertilised with poultry manure at a rate of 1,500 kg per hectare per month. In L, the fish were fed twice a day with supplementary diet containing 21% crude protein, at a daily rate of 3% of their body weight. The stocking density of fish in H were 5.2 fish/m^2. The fish were fed three times a day with pelleted diet containing 28% crude protein at a daily rate of 3% of their body weight (Workagegn *et al.*, 2018a).

2.4. Data recording and analyses

2.4.1. Data recording and preliminary analysis

Harvest body weight of 3,051 fish from 180 families of both generations, 81 full-sib families in F_1 and 99 in F_2, was recorded. The number of families and number of offspring produced per strain combination is shown in Table 1. It was observed that in females, early maturation was widespread, and it was thus decided to only utilise data from male fish for the data analyses, i.e. altogether 1564 fish with body weight at 5 months of age (BW5) in F_1, while 1487 fish had BW5 recorded in F_2. Further, a total of 958 fish in F_1 had records at 7 months of age; body weight (BW7), fillet weight (FW), predicted fillet weight (PFW), fillet yield (FY) and predicted fillet yield (PFY).

Since it is known that variance in body weight of aquaculture spices is size dependent (e.g. Jere *et al.*, 2003), it was decided to do a correction for this prior to the statistical analyses. Thus, all the six traits were pre-corrected for phenotypic variance differences within each batch subclass using a multiplicative correction factor, i.e. by calculating a derived record,

$\hat{y}_{ih} = y_{ih}(\sigma_y/\sigma_{yh})$, where y_{ih} is the observed trait phenotype for animal *i* in level *h* of the batch subclass, σ_y is the weighted mean standard deviation of the trait in all data and σ_{yh} is the standard deviation of the trait in level *h* of the subclass (Hill, 1984).

2.4.2. Estimation of genetic parameters

To estimate genetic parameters for all the six traits and their genetic correlations, the analysis was carried out using bivariate animal models in ASReml, version 4.1 (Gilmour *et al.*, 2015). The model used was (Model 1):

$$\begin{bmatrix} \boldsymbol{Y_1} \\ \boldsymbol{Y_2} \end{bmatrix} = \begin{bmatrix} \boldsymbol{X_1} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{X_2} \end{bmatrix} \begin{bmatrix} \boldsymbol{b_1} \\ \boldsymbol{b_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_1} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{Z_2} \end{bmatrix} \begin{bmatrix} \boldsymbol{a_1} \\ \boldsymbol{a_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{e_1} \\ \boldsymbol{e_2} \end{bmatrix}$$

where $\begin{bmatrix} \boldsymbol{Y_1} \\ \boldsymbol{Y_2} \end{bmatrix}$ is a vector of variance corrected observations for traits 1 and 2 , $\begin{bmatrix} \boldsymbol{b_1} \\ \boldsymbol{b_2} \end{bmatrix}$ is a vector of fixed effects for the two traits, $\begin{bmatrix} \boldsymbol{X_1} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{X_2} \end{bmatrix}$ is a design matrix relating the observations of the two traits to the fixed effects. For each trait, the fixed effects were μ (the intercept), B_h (the fixed effect of the h^{th} batch (h = 1-5)) x Rep_j (the fixed effect of the j^{th} pond (replicate) (j = 1, 2)) x E_k (the fixed effect of the k^{th} production system (k = 1, 2)), and P_l, the fixed effect of the l^{th} filleter (l = 1, 2). Other fixed effects were: $b_{A(m)}$, the regression coefficients of the additive genetic effect of the genes originating from the m^{th} strain (m = 1 - 3), with the regression variables being A_m, the proportions of genes in the i^{th} individual originating from the m^{th} strain (A_m = 0, 0.25, 0.5 0.75 or 1 and $\sum A_m = 1$), $b_{R(m)}$, the regression coefficients of the reciprocal effect of the m^{th} strain, with the regression variables being R_m, the proportions of genes of the dam of the i^{th} individual originating from the m^{th} strain (R_m = 1.0 for pure breed, 0.5 when a dam is a cross between two strains) and $b_{D(n)}$ is the regression coefficients of the individual heterosis effect of the n^{th} strain–cross, with the regression variables being D_n, the proportions of the individual heterosis effect of the n^{th} strain-cross expressed in the i^{th} individual (D_n = 0, 0.25, 0.5 0.75 or 1). Some examples of the use of the various regression variables are shown in Table 2. Further, $\begin{bmatrix} \boldsymbol{Z_1} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{Z_2} \end{bmatrix}$ is a design matrix relating the observations of the two traits to their random effect vector $\begin{bmatrix} \boldsymbol{a_1} \\ \boldsymbol{a_2} \end{bmatrix}$. For the latter, the (co)variance structure was: $\begin{bmatrix} \boldsymbol{A\sigma^2 a_1} & \boldsymbol{A\sigma a_1 a_2} \\ \boldsymbol{sym.} & \boldsymbol{A\sigma^2 a_2} \end{bmatrix}$ where **A** is the additive relationship matrix among all fish (124 in F_0, 1564 in F_1 and 1487 in F_2) and $\begin{bmatrix} \boldsymbol{e_1} \\ \boldsymbol{e_2} \end{bmatrix}$ is a vector of random residual effects for the two traits, i.e. with the environmental covariance between the two environments set to zero. The common environmental effects caused by separate rearing of full-sib families until tagging was not included in the model because the reciprocal/maternal effect and the common environmental effects are totally confounded when using a hierarchical mating design.

For calculation of genetic parameters for BW5 using data from either the F_1 or F_2 generation, a univariate version of Model 1 was used, denoted Model 2.

2.4.3. Estimation of response to selection

Realised genetic gain (ΔG_R) for BW5, which was recorded in both generations, as well as correlated responses (ΔGc_R) in the other traits, which were only recorded in the F_1 generation, was calculated as the difference between estimated breeding values in the F_2 and the F_1

generation. The breeding values for the traits recorded in only one generations were predicted using the bivariate animal model (Model 1), including BW5 from both generations.

The genetic gain expressed in percentage was calculated relative to the least-squares means (LSM) of the respective trait in the F_1 generation, i.e. $\Delta G_R\% = (\Delta G_R/LSM_{F1})100$ or $\Delta Gc_R\% = (\Delta Gc_R / LSM_{F1})100$ (Liu *et al.*, 2015).

2.4.4. Estimation of additive, reciprocal and heterosis effects

Since BW5 was recorded over two generations, the data allowed the addition of maternal heterosis effects to the univariate Model 1, which will be denoted Model 3. The following terms were added: b_{MDn}, the regression coefficients of the maternal heterosis effect with the regression variable D_n, assigning the incidents of potential maternal heterosis occurring in the n^{th} strain-cross expressed in the mother of the i^{th} individual (D_n = 0 for purebreds and 1 for crossbreds). An overview of the coefficients used as regression variables in Models 1-3 is shown in Table 2.

3. Results

The phenotypic means and the coefficient of variation for all the traits recorded within each generation are presented in Table 3. The average body weight of the male tilapia fish at five months of age increased from 135.3g in the F_1 generation to 145.5g in F_2, while the coefficient of variation was 29.9% in F_1 and 27.2% in the F_2 generation. At seven months of age, the average body weight was 176.0g in F_1, while the coefficient of variation was 26.6%. The coefficients of variation for fillet yield and predicted fillet yield were much lower than for the other traits (8.0% and 6.3%, respectively). The average values for actual and predicted fillet weight corresponded well, with 58.3g and 58.2g, respectively.

The estimates of phenotypic variance components, heritabilities, genetic and phenotypic correlations for the six traits are presented in Table 4. The magnitude of the estimated heritabilities for body weight and fillet weight traits ranged from 0.33 to 0.37, while the heritability estimate for predicted fillet yield was 0.24, but much lower for actual fillet yield (0.04). The estimates of the genetic correlation between body weight and fillet weight traits/predicted fillet yield were high ($\geq$ 0.96), whereas it was close to zero for fillet yield (-0.02).

In Table 5, the estimates of variance components and heritabilities for BW5, when using data from either F_1 or F_2 generation, are given. Both the estimates of the additive genetic variance and of heritability increased noticeably from the F_1 to the F_2 generation.

From the difference in mean EBVs between the two generations for BW5, the selection response was calculated as 7.1% (Table 6). The correlated selection responses when selecting for BW5 were 5.0% for FW and 5.4% for PFW, whereas it was close to zero for FY (-0.4%) and PFY (0.5%).

The estimates of the additive, reciprocal as well as individual and maternal heterosis effects for BW5, as obtained with Model 3 across the two generations, are presented in Table 7. Neither additive nor the general reciprocal effect of strains were significantly different from each other ($P < 0.05$). Similarly, none of the contrast between individual or maternal heterosis effects of strain combinations were significantly different. The individual heterosis effects for BW5 of the strain combinations were all positive and significantly different from zero ($P < 0.05$), while the same was not obtained for the maternal heterosis effects.

4. Discussion

Utilising data from both the F_1 and F_2 generations for BW5 showed no significant ($P < 0.05$) maternal heterosis effect (Table 7). As Workagegn *et al*. (2018a) had found the direct or individual heterosis effect to be significant in F_1, the analysis was in main carried out with Model 1, which include only this heterosis effect. The analysis revealed that the estimates of heritability for increased body weight in the present study were higher than those reported by Workagegn *et al.* (2018b) in F_1 for BW7, and in the high end compared with the estimates reported by several authors in tilapia (0.15-0.41 by Khaw *et al.*, 2009; 0.34 by Ponzoni *et al.*, 2005). The higher estimates result from higher additive genetic variation found in the F_2 generation than in the F_1 generation (Table 5). Similarly, Maluwa & Gjerde (2007) reported that the additive genetic variance in the F_2 generation was slightly higher than in F_1, as did Thodesen *et al.* (2013) who obtained higher estimates of heritability in F_2 (0.60) than in F_1 (0.43) in tilapia. The higher additive genetic variance and lower residual variance in F_2 in our study could be due to increased domestication and better production environment in F_2 than in F_1, leading to stronger expression of the genetic potential in F_2.

Not only did the heritability of BW5 increase from F_1 to F_2, but so did in general the heritability of the jointly analysed data with the bivariate model, i.e. BW7, fillet weight traits as well as fillet yield trait, although data for the latter were recorded in the F_1 generation only. As reported by Workagegn *et al.* (2018b), the estimated genetic correlations between body weight and fillet weight traits were high ($\geq$ 0.93), while the genetic correlation to fillet yield, with a heritability of only 0.05, was low (0.04). In addition, fillet yield was predicted very

inaccurately from body measurements (Workagegn *et al.*, 2018b), which further questions its value in a breeding context.

Selection in F_1 was carried out on basis of BLUP breeding values for body weight at 5 months of age, predicted with a model containing fixed effects of sex, batch x replicate x environment, and a random effect of animal. Still, the present study shows only moderate genetic improvement for increased body weight over one generation of selection (7.1%; Table 6). This estimate is lower than the 8.4% to 11.4% obtained for Nile tilapia by Ponzoni *et al.* (2005), the 9.0% to 20.1% obtained Bentsen *et al.* (2017), but slightly higher than the 6.1% reported by Hamzah *et al.* (2014) and the 3.6% reported by Gjerde *et al.* (2012). Moreover, the genetic response to selection in the present study falls within the range, 5% to 15%, obtained for many other farmed aquaculture species (Nguyen, 2016). The main reasons for the somewhat low selection response in the present study are likely the restriction applied to the number of selected per family (5) and the deliberate mixing and testing of strains continued in the F2 generation.

The additive and the reciprocal effects did not contribute significantly *($P > 0.05$)* to the differences in BW5 among the strains (Table 7). This is in line with the results in the F_1 generation reported by Workagegn *et al*. (2018a). Maluwa and Gjerde, (2006) also studied additive genetic and reciprocal strain effect differences for body weight of Nile tilapia, but contrary to us, they did find significant ($P < 0.05$) differences in these effect among strains, possibly since as much as eight strains were compared. Likewise, Joshi *et al.* (2018), found a significant maternal effect in a complete reciprocal cross between two genetic lines developed over a few generations. This may indicate that our design was not fully able to capture this variance source due to the hieratical structure, which is a weakness with this design, as also pointed in their study.

The size of dataset used to estimate additive genetic, reciprocal and individual heterosis effect across the two generations was close to doubled compared to the dataset analysed by Workagegn *et al.* (2018a), and the current analysis verified the previous results of positive and significant *($P < 0.05$)* total/direct heterosis effects. The results also revealed that direct heterosis was more important than maternal heterosis. The F_2 design for estimation of the individual heterosis effect will be much improved over that in F_1, with improved cross-classification of not only the regression coefficients but also with related animals used across the 9 sub-cells of the diallel cross. A similar improvement in F_1 could have been achieved if

sires had been mated across females from the different sub-cells of the cross, but this would have prolonged the required mating period too much. Another effect of the animal model relative to a fixed model in analysis of the data is the ability to shrink eventually overestimated values and to reduce the effect of sampling, i.e. in comparison of breeds there will always be a chance that an eventual difference between breeds is a result of randomly chosen superior individuals representing the breed (sampling) and not the breed itself. Obviously, the probability for this sampling effect will be larger the smaller the sub-cell sizes becomes, and the animal model will reduce this effect by only allowing a part of it to be subscribed to the fixed effects of the model, i.e. to the additive genetic, reciprocal and heterosis effects.

An alternative way to analyse data across the two generations when estimating the fixed effects, i.e. the additive genetic, the general reciprocal and total heterosis effects, would have been to only use data from the last generation. However, Fikse *et al.* (1997) have shown that this data structure with data only for the last generation in an animal model has the ability to inflate the fixed effect estimates if there exists genetic trend for the trait investigated when pedigree data include all generations, also the base. Therefore, our choice was to analyse data across the two generations.

Workagegn *et al.* (2018a) carried out a proper comparison of strains on basis of least-squares means, considering jointly additive genetic, reciprocal and heterosis effects, giving a preference to the Chamo and Ziway strains. Based on this, the authors proposed that one approach for a future breeding program would be to establish a two-line design, aiming at utilising heterosis. An alternative, simpler approach is a composite breeding program, which initially also will capitalize on a substantial amount of heterosis. As stated by Workagegn *et al.* (2018a), the decision of which strategy to follow should be based on a cost-benefit analysis.

Despite, and after correcting for, the significant ($P < 0.05$) individual heterosis effect when calculating breeding values in F_1, a reasonable genetic gain was produced over one generation of selection. If choosing to base future selection on a composite population, breeding value estimation in F_2 could well be carried out with the same model as utilised in the F_1 generation. However, one should aim at incorporating also the common environmental effect into the evaluation model by reuse of dams as well as sires. Then, even with this scheme, with a composite population made up of the three strains, considerable amounts of heterosis will still be expressed (Bourdon, 1997).

The diallel cross was rather balanced (Workagegn *et al.*, 2018a), and close to maximises the available genetic variance from the three strains in F_1. To not reduce the genetic variance to much from F_1 to F_2, the number of selection candidates per full-sib family was restricted to five. In F_2, however, it is rather recommended that optimal contribution selection should be carried out (e.g. Skaarud *et al.*, 2011).

Conclusion

Body weight and fillet weight traits were estimated with heritability over 33% and with internally high positive genetic correlations ($\geq$ 0.96), while fillet yield was estimated with a low heritability (0.04). When selecting on estimated breeding values for body weight at 5 months of age, considerable genetic gain was obtained over one generation of selection for both body weight and fillet weight traits, but with close to no response for fillet yield. Estimates of *a priori* significant ($P < 0.05$) heterosis effect on body weight at 5 months of age was verified when utilising F_1 and F_2 with altogether 3,051 fish. The results, with considerable individual heterosis effects, support a crossbreeding program for Nile tilapia in Ethiopia based on individuals from the composite population, but a "pure" breeding program would be easier to run and has generally shown to result in considerable genetic progress. The decision of what breeding program to choose should be based on a cost-benefit analysis.

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Table 1

Number of families (N_F) and number of offspring (N_O) per family for each of the different crosses in the F_2 generation, resulting from crosses or pure strain parents from the F_1 generation (Z = Ziway strain, K = Koka strain and C = Chamo strain, i.e. for instance the F1-parent denoted ZZ is a cross of ZxZ, ZK is a cross of ZxK etc.).

Cross ♀	ZZ	ZK	ZC	KK	KZ	KC	CC	CZ	CK
♂	Nf/No	Nf/No	Nf/No	Nf/No	Nf/No	Nf/No	Nf/No	Nf/No	Nf/No
ZZ	0	1/7	0	1/20	2/27	2/21	1/14	1/9	1.20
ZK	2/33	5/55	2/23	2/25	0	1/17	1/14	2/17	0
ZC	2/34	4/62	1/14	0	1/16	1/16	0	0	1/11
KK	3/62	1/14	2/30	1/3	0	2/26	2/37	1/23	0
KZ	3/46	2/33	0	0	2/35	3/51	1/15	1/18	3/46
KC	0	0	4/79	1/9	0	0	1/16	2/27	1/19
CC	5/77	0	1/16	1/18	0	1/15	1/18	1/19	0
CZ	0	1/9	3/49	0	0	2/22	1/12	0	0
CK	5/78	1/17	0	1/12	2/39	0	1/9	1/8	1/9

Table 2

Examples of coefficients assigned for additive genetic, reciprocal, individual heterosis and maternal heterosis effects in F_2 generation, in pure breeding (1), between purebreds (2), purebred x cross (3), cross x same cross (4) and cross x different cross (5).

Strain cross[1)]	Strain additive and reciprocal effects						Heterosis effects					
	Additive genetic			Reciprocal			Individual			Maternal		
♀x♂	Z	K	C	Z	K	C	ZxK	ZxC	KxC	ZxK	ZxC	KxC
1. ZZxZZ	1	0	0	1	0	0	0	0	0	0	0	0
2. ZZxKK	0.5	0.5	0	0	1	0	1	0	0	0	0	0
3. ZZxZK	0.75	0.25	0	0.5	0.5	0	0.5	0	0	1	0	0
4. ZKxZK	0.5	0.5	0	0.5	0.5	0	0.5	0	0	1	0	0
5. ZKxZC	0.5	0.25	0.25	0.5	0	0.5	0.25	0.25	0.25	0	1	0

[1)] Z, K and C represent the three strains, Ziway, Koka and Chamo, respectively

Table 3

Mean and coefficient of variation (CV) for body weight at 5 and 7 months of age (BW5 and BW7), fillet weight (FW), fillet yield (FY), predicted fillet weight (PFW) and predicted fillet yield (PFY) (all at 7 months of age), in F_1 and F_2 generations.

	BW5		BW7		FW		FY		PFW		PFY	
Generation	Avg.(g)	CV (%)	Avg.(g)	CV (%)	Avg.(g)	CV (%)	Avg.(%)	CV (%)	Avg.(g)	CV (%)	Avg.(%)	CV (%)
F1	135.3	29.9	176.0	26.6	58.3	29.5	33.1	8.0	58.2	28.9	33.5	6.3
F2	145.5	27.2										

Table 4

Estimates of genetic parameters for variance corrected body weight at 5 and 7 months of age (BW5 and BW7, respectively), fillet weight (FW), predicted fillet weight (PFW), fillet yield (FY)), and predicted fillet yield (PFY) (all at 7 months of age) with phenotypic variance (σ^2_p), heritability (h^2) and additive and phenotypic correlations (r_{G1G2} and $r_{P1,P2,}$ respectively) across generations. The standard errors (± s.e) are also given. Estimate for BW5 is obtained from a bivariate analysis with FW, else genetic correlations are from bivariate analysis with BW5.

Trait	σ^2_p ±s.e.	h^2 ± s.e.	Correlations with BW5	
			r_{P1P2} ± s.e	r_{G1G2} ± s.e.
BW5	1640 ± 58	0.37 ± 0.05	-	-
BW7	2312 ± 121	0.37 ± 0.06	0.54 ± 0.04	0.99 ± 0.02
FW	313 ± 17	0.33 ± 0.06	0.49 ± 0.04	0.96 ± 0.04
PFW	304 ± 16	0.37 ± 0.07	0.52 ± 0.04	0.99 ± 0.02
FY	6.4 ± 0.3	0.04 ± 0.03	0.10 ± 0.05	-0.02 ± 0.30
PFY	1.6 ± 0.09	0.24 ± 0.06	0.23 ± 0.05	0.91 ± 0.07

Table 5

Estimates of additive genetic (σ_A^2), residual (σ_e^2) and phenotypic variances (σ_p^2), as well as the heritability (h^2) with their standard error (± se) for body weight at 5 months of age utilising data in the F_1 and F_2 generation.

Generation	σ_A^2 ± se	σ_e^2 ± se	σ_p^2 ± se	h^2 ± se
F_1	441 ± 110	1137 ± 77	1577 ± 72	0.27 ± 0.06
F_2	631 ± 139	990 ± 89	1621 ± 82	0.39 ± 0.07

Table 6

Estimates of realised genetic gain, in actual units and as a percent, for body weight at 5 months of age (BW5; ΔG_R and ΔG_R%, respectively) and the correlated selection responses, in actual units and as a percent (ΔGc_R and ΔGc_R%, respectively), for body weight at 7 months of age (BW7), fillet weight (FW), predicted fillet weight (PFW), fillet yield (FY) and predicted fillet yield (PFY). Estimate for BW5 is obtained from a bivariate analysis with FW, else genetic correlations are from bivariate analysis with BW5.

Traits	ΔG_R	ΔG_R%[1)]	ΔGc_R	ΔGc_R%[1)]
BW5	9.0 (g)	7.1 (%)		
BW7			8.7 (g)	5.2 (%)
FW			2.9 (g)	5.0 (%)
PFW			3.1 (g)	5.4 (%)
FY			-0.12 (% point)	-0.4 (%)
PFW			0.17 (% point)	0.5 (%)

[1] Genetic gain expressed in percentage was calculated relative to the least squares means of body weight obtained from F_1 generation.

Table 7

Estimates of additive genetic, reciprocal as well as individual and maternal heterosis effects for body weight at 5 months of age (g) in a cross of three Nile tilapia strains (Z = Ziway, K = Koka and C = Chamo) utilising data both from the F_1 and F_2 generations, as obtained with Model 3. No significant differences among the strain/strain combinations were found for neither of the four effects.

Strain	Additive genetic	Reciprocal
Z	5.5	-2.0
K	-4.5	1.1
C	0.0	0.0
Heterosis effects	**Individual**	**Maternal**
ZxK	16.0**	5.4
ZxC	11.7*	-3.5
KxC	14.1**	-3.5

*$P < 0.05$ and ** $P < 0.01$, for test of being different from zero.

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