Aquaculture 372–375 (2013) 137–148

Contents lists available at SciVerse ScienceDirect

Aquaculture

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

Heritability estimates for male proportion in the GIFT Nile tilapia (*Oreochromis niloticus* L.)

Carlos A. Lozano [a,b,*], Bjarne Gjerde [b,c], Jørgen Ødegård [b,c], Hans B. Bentsen [c]

[a] *Akvaforsk Genetics Center AS, N-6600 Sunndalsøra, Norway*
[b] *Department of Animal and Aquacultural Sciences, Norwegian University of Life Sciences (UMB), P.O. Box 5003, 1432 Ås, Norway*
[c] *Nofima, P.O. Box 5010, 1432 Ås, Norway*

ARTICLE INFO

Article history:
Received 23 June 2011
Received in revised form 25 September 2012
Accepted 6 October 2012
Available online 5 November 2012

Keywords:
GIFT
Nile tilapia (*Oreochromis niloticus*)
Heritability
Male proportion
Sex ratio

ABSTRACT

The main goal of this study was to estimate the heritability of the proportion of phenotypic males in progeny of Nile tilapia broodstock based on visually scored sex from six consecutive pedigreed generations from the GIFT project. Mean male proportion was 0.44 across all generations, ranging from 0.37 to 0.56 across generations and environments. Across all generations there was a low but significant "additive" genetic component for male proportion with heritability estimates of 0.12 ± 0.02 (observed scale) and 0.22 ± 0.04 (underlying liability scale). The within generation heritability estimates varied from 0.00 ± 0.03 to 0.25 ± 0.07 on the observed scale, and from 0.11 ± 0.02 to 0.32 ± 0.07 on the underlying liability scale. As expected, genetic correlations between male proportion in the different post-nursery test environments were in 16 out of 17 cases not significantly different from unity ($P > 0.05$) since sex was determined before fish were stocked in the different test environments, indicating no or the same degree of sex dependent mortality among the families in the different environments.

In general, the regression coefficient of raw family means on the estimated mean family breeding values is expected to be unity for a normal polygenic trait. The regression coefficient of observed full-sib family male proportions on the associated mid-parent estimated breeding values across generations (omitting the records of the 1st generation offspring of each breeder, one generation at a time) was significantly different ($P < 0.01$) from unity (0.64 ± 0.12). This suggests that the magnitude of the genetic variation in male proportion found in this study may be biased upwards by some parents having a phenotypic sex different from that determined by the major sex determining system (XX/XY).

Selection for increased male proportion based solely on family means may lead to an increased fraction of masculinized XX males. If a "normal" ($XX \times XY$) mating produces a significantly skewed sex ratio, this has to be a result of either 1) masculinizing/feminizing of XX/XY offspring, 2) differing viability of "male" and "female" sperm, or 3) sex-specific mortalities prior to recording of sex. Thus, selecting males from "high male" families may involve selecting XX sires, which will counteract the response to selection as all their offspring will be XX females. Genetic selection for increased male proportion in a purebred population (without the use of temperature treatment) is expected to be difficult.

1. Introduction

Early reproduction of tilapia in aquaculture causes stunted growth and large size variability (Little et al., 2003; Longalong et al., 1999). Unwanted reproduction in mixed sex populations may cause up to 70% of the total harvest weight to be small fish of no commercial value (FAO, 2010). The use of hormonal sex inverted male fry has been the industry standard for mono-sex culture in Nile tilapia as well as for other tilapia species. However, best aquaculture management practices (BAP) for tilapia encourage methods other than the use of hormones for the production of all-male fry (GAA, 2008), such as manual sorting (Beardmore et al., 2001), inter-specific hybridization (Desprez et al., 2006; Hulata et al., 1983, 1993; Pruginin et al., 1975; Wohlfarth, 1994), use of "super-males" (YY) (Mair et al., 1991a, 1997; Tuan et al., 1998, 1999) and selection for increased "male proportion" (MP) under temperature treatment (Wessels and Hörstgen-Schwark, 2011). However, manual sorting has proven to be labor intensive and subject to human error (Beardmore et al., 2001) and inter-specific hybridization has shown breakdowns due to contamination of the broodstock species with misidentified hybrids (Beardmore et al., 2001; Hulata, 2001). Furthermore, YY-male technology requires several generations of progeny testing and has shown deviations from the expected 100% male ratio based on a simple XX/XY sex determination system (Mair et al., 1997; Tuan et al., 1999). Production of all-male Nile tilapia through androgenesis and gynogenesis has been achieved on an experimental scale, but these techniques are not easily applied for commercial production

* Corresponding author at: Akvaforsk Genetics Center AS, N-6600 Sunndalsøra, Norway. Tel.: +47 95816815; fax: +47 64949502.
E-mail address: carlos.lozano@afgc.no (C.A. Lozano).

0044-8486/$ – see front matter © 2012 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.aquaculture.2012.10.029

(Beardmore et al., 2001). The use of mixed sex sterile triploid populations of Nile tilapia (Hussain et al., 1996) to control unwanted reproduction has been constrained by the ability to produce large amount of triploids at a reasonable cost.

Nile tilapia has a complex sex determination system where the phenotypic sex is determined by major genetic factors (i.e., XX/XY), several autosomal genetic factors, as well as rearing water temperature during early development stages (Baroiller et al., 2009). The hypothesized "sex chromosome" (XX/XY) exhibits male heterogamety (Jalabert et al., 1971; Mair et al., 1991a). Using synaptonemal complex analysis, Carrasco et al. (1999) observed an incompletely paired segment in the XY genotype providing cytological evidence for a XX/XY sex determination system, and recently sex-linked markers have been identified for Nile tilapia in linkage group 1 (LG1) (Cnaani et al., 2008; Lee et al., 2003). Markers found by Lee et al. (2003) predicted sex correctly for 95% of individuals in two of the three families studied; however in the third family there was no association between LG1 and sex. Cnaani et al. (2008) suggested that two different linkage groups (LG1 and LG3) may contribute to sex determination in some families, explaining the results obtained by Lee et al. (2003). Eshel et al. (2010) found that indeed two linkage groups (LG1 and LG23) had an association with sex, but it was LG23 that showed the strongest association. Nevertheless "sex chromosomes" in Nile tilapia appear to be at an early evolutionary stage of differentiation (Cnaani et al., 2008; Lee et al., 2003). The occurrence of females in progeny of YY males has been attributed to the action of several autosomal sex modifying genes (Mair et al., 1997). Large between-family variance for sex ratio among progeny of Nile tilapia (Tuan et al., 1999) and large variation in crosses between Nile and blue tilapias (Mair et al., 1991b) also suggest an autosomal polygenic mechanism for sex determination. Autosomal genes in the Thai-Chitralada strain seem to have a greater influence on sex determination than in the Egypt-Swansea strain of Nile tilapia (Tuan et al., 1999).

Temperatures above 32 °C applied during the period of sex differentiation (from 10 to 20 days post fertilization) can masculinize progeny overriding the influence of both major genetic factors and autosomal sex determining genes (Baroiller et al., 1995, 2009; Tessema et al., 2006; Wessels and Hörstgen-Schwark, 2007, 2011). Both significant parental sire and dam effect have been found for temperature sensitivity during sex differentiation (Baroiller and D'Cotta, 2001; Tessema et al., 2006). High realized heritability for temperature sensitivity with respect to sex determination was observed in a selection experiment with two divergent lines selected for high ($h^2 = 0.63$) or low ($h^2 = 0.84$) response to temperature treatment over three generations (Wessels and Hörstgen-Schwark, 2011). Temperature sensitivity with respect to sex determination also responds to selection, since after three generations of selection the temperature treated group (36 °C) selected for high response increased from 65% males in the base population to 93% males, whereas at normal temperatures (28 °C) MP remained almost unchanged (52% males in the base population to 54% males in G3) (Wessels and Hörstgen-Schwark, 2011).

Selective breeding experiments and programs have been carried out with Nile tilapia to improve traits such as growth, carcass quality, fillet yield, cold tolerance and early sexual maturation (Bolivar and Newkirk, 2002; Charo-Karisa et al., 2005, 2006; Longalong et al., 1999; Neira, 2010; Ponzoni et al., 2005; Rutten et al., 2005; Rye et al., 2010). One of these programs is the widely recognized "Genetic Improvement of Farmed Tilapias" (GIFT), a collaborative research project which started in the Philippines in 1988 (Bentsen et al., 1998; Eknath et al., 1993, 2007). Using data from the GIFT diallel cross experiment, a significant strain additive genetic, strain reciprocal and strain total heterosis effects were found for MP (Lozano et al., 2011a), suggesting that strain genetic effects are present in the determination of the phenotypic sex in Nile tilapia. However, the genetic variation in MP between families within this population has not been assessed. Lester et al. (1989) reported a heritability of medium magnitude ($h^2 = 0.26$) for MP in Nile tilapia on the underlying liability scale, using half-sib families produced with 18 sires and 37 dams. So far, this is the only reported heritability estimate for MP in tilapia under normal rearing temperatures.

In general, estimates of additive genetic variance are inferred from the covariance among full- and half-sibs. Preferably, also the genetic relationships among the parents should be taken into account. For species with a sex determination system completely controlled by a single major genetic sex determination factor (e.g., the XY system in most mammals), the major genetic sex determination factor will not contribute to between-family variation in MP (i.e., as all individuals will be offspring of XX females and XY males). If so, no genetic variation in MP should be expected, which is in accordance with results from studies in mammals such as humans (Maynard Smith, 1980) and pigs (Toro et al., 2006). However in species such as Nile tilapia, where the sex-determination system is more complex and the phenotypic sex may deviate from the major genetic sex determination factor (XX/XY), genetic variation in phenotypic sex (e.g. male proportion) may be expected. The occurrence of natural sex reversion in Nile tilapia has been suggested for XX males (Bezault et al., 2007), XY females (Bezault et al., 2007; Mair et al., 1991a), and reproduction of such females will necessarily produce a fraction of YY males. When such deviations occur, the major sex determining factor will to some extent act as major segregating QTL in the population, contributing to the between-family variation and potentially also to the estimated additive genetic variance. If "genetic sex" (i.e. sex determined by XX/XY system) of one or both parents is different from the phenotypic sex of that parent, this may give substantial deviations from the expected MP of the offspring in the first and to some extent second generation, but is not expected to have any lasting effects on future generations (Appendix 1). The XX males will produce normal XX female offspring, XY females will produce 75% normal (i.e., XX female and XY male) and 25% YY offspring, while YY males will produce normal XY male offspring, assuming that all these are mated with normal partners. Nevertheless, deviations between genetic and phenotypic sex may appear spontaneously in all subsequent generations and therefore consistently contribute to the between-family variation in MP.

Genetic variation may exist with respect to how likely individual sex phenotypes are to deviate from their major genetic sex determination system (XX/XY). Temperature dependent sex determination may also be controlled by several genes expressed at the embryo stage as seen in Nile tilapia (Wessels and Hörstgen-Schwark, 2007). Some of the genetic variation in MP may be attributed to female behavior through their different temperature preference, as seen for variation of maternal choice of nest temperature in turtles (Bulmer and Bull, 1982). To the extent that such factors (if present) have a genetic background, they will also contribute to the estimated additive genetic variance in the observed MP. In all cases where other factors (both genetic and environmental) override the effect of the major sex determination factor, the latter factor will necessarily contribute to between-family variation in MP in the following generations and may thus add to the estimated additive genetic variance for MP.

Theoretically, genetic variation in observed MP may also arise for reasons outside the sex determination system, i.e., due to genetic variation in fertilization rate of "male" and "female" sperm or sex dependent variation in survival of offspring.

The main goal of this study was to estimate the magnitude of the additive genetic variance for MP in six consecutive pedigreed generations of Nile tilapia from the GIFT project.

2. Material and methods

2.1. Genetic material

Data from six generations of Nile tilapia from the GIFT project was used. The project started with a performance comparison test of four wild African strains (Egypt, Ghana, Kenya, and Senegal) and four Asian farmed strains (known as Israel, Singapore, Taiwan and