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Genetic improvement of farmed tilapias: Response to five generations of selection for increased body weight at harvest in *Oreochromis niloticus* and the further impact of the project

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A B S T R A C T

Selection for increased body weight at harvest in Nile tilapia (*Oreochromis niloticus*) was carried out for five generations from 1991 to 1996, as a part of the project Genetic Improvement of Farmed Tilapias (GIFT). The base population for selection was composed of a mixture of various three- and four-way cross individuals descending from four wild African strains and four farmed Asian strains. Methods for single pair mating, separate rearing of full-sib groups and individual tagging and pedigree recording were developed. The parents for a new generation were selected based on a selection index including their own age corrected-body weight at harvest as well as that of their full- and half-sibs. Across generations, a total of 512 males were mated in a nested mating design to 941 females to produce 81,429 tagged progenies. Of those, 56,633 progeny had their body weight recorded at harvest after grow-out testing in a diverse range of farming environments. Estimates of the within generation realized response to selection across farming environments were obtained as the difference between the least squares mean performance of offspring of selected parents and of offspring of parents with average values of the selection index. The average realized response to selection per generation was 13.6% (range 9.0 to 20.1%), resulting in an accumulated response over five generations of 88% relative to the base population. A genetic trend analysis based on BLUP breeding values estimated across generations after the termination of the project suggested an accumulated response of 67%. The genetic composition of the synthetic population also changed during selection. The proportion of ancestors from three of the wild African founder strains increased from 59.7 to 76.3%. The accumulated coefficient of inbreeding was 7.1%. After the termination of the GIFT project, selection was continued in the GIFT population. The population has also been used as a genetic source in a number of similar public and private selection programs. A status review of the presently recorded dissemination of the genetic material and methodology is presented.

Statement of relevance: The GIFT project showed that five generations of repeated selection based on testing of individually tagged and pedigreed individuals from a synthetic farmed population of Nile tilapia gradually increased the body weight at harvest. The total increase was 67–88%. Reports from several descending populations shows that the selection response has continued during >10–15 additional generations.

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1. Introduction

An international collaborative project to improve the genetic performance of farmed Nile tilapia (*Oreochromis niloticus*) was initiated at the Bureau of Fisheries and Aquatic Resources/Freshwater Aquaculture Center (BFAR/FAC) facilities in Muñoz, Philippines in 1988 (Gjedrem, 2012; Pullin et al., 1991). The project, commonly known by the name Genetic Improvement of Farmed tilapias (GIFT), lasted for 10 years until 1997 and was based on the experiences from the pioneering Norwegian salmon selection program initiated in 1971 (reviewed by Gjedrem, 2010). The initial objective of the project was to apply up to date farm animal breeding and selection technology to improve the performance of tropical farmed finfish. Nile tilapia was chosen as a test case because of the short generation interval of the species, and for its significance for a wide range of fish farming operations, including small-scale and backyard farmers. Growth performance was chosen as the selection goal because of its economic importance for the target farmers and because it may easily be recorded in the live test fish. The GIFT project was started by collecting genetic material from eight different sources, four wild populations in Africa and four farmed populations in Asia, that were reproduced in Muñoz and tested for growth performance as pure strains in eleven different farming environments (Eknath et al., 1993). A complete diallel cross experiment with all eight strains was then carried out to study possible heterosis effects on growth performance in seven different farming environments (Bentsen et al., 1998). It was concluded that genotype by environment interactions and non-additive gene effects were of minor importance for growth performance. Consequently, it was decided to form a synthetic population composed of three and four way crossed individuals involving all eight founder strains, and genetic parameters for growth performance in seven different farming environments were estimated (Eknath et al., 2007). The estimates suggested a low to moderate heritability for growth performance and high genetic correlations between growth performances in different farming environments (possibly somewhat lower correlations for one intensive cage farming environment). The parameter estimates were later confirmed by an analysis across five generations descending from the synthetic base population (Bentsen et al., 2012). Since the possible genetic gain from developing multiple environment specific strains or specialized hybrid parent strains seemed to be marginal, it was decided to focus on selection for improved additive genetic growth performance within the genetically diverse synthetic population, based on testing in mainly semi-intensive farming environments. Five generations of selection for improved growth performance were then carried out.

The GIFT project resulted in a faster-growing, synthetic aquaculture stock of Nile tilapia (Acosta and Gupta, 2010; ADB, 2004; Dey et al., 2000; Yosef, 2009) that has later been an important genetic source for a variety of public and private genetic improvement and/or dissemination programs (Eknath and Hulata, 2009; Ponzoni et al., 2010a). Although continuous genetic response to selection for growth performance has been reported in a number of descending populations (Gjedrem et al., 2012; Hussain et al., 2011; Luan, 2010; Ponzoni et al., 2005; Thodesen et al., 2011), the initial selection response during the GIFT project has only been preliminary reported (Bentsen et al., 2003; Eknath and Acosta, 1998; Eknath et al., 1998), and not yet been fully and scientifically documented. At the time of the GIFT project, the world aquaculture production of Nile tilapia was about 0.5 million metric tons and the focus was on small scale and backyard farmers. Since then, production has increased to 3.7 million tons in 2014 (as compared to 2.3 million tons of Atlantic salmon, FAO, 2016), and much of the production has evolved into large scale, commercial operations. The GIFT strain has been widely available and disseminated since the first generations of selection, and a significant proportion of the present production of Nile tilapia is likely to be based on genetic materials with some degree of GIFT ancestry (see Section 4.4 below). In this paper the procedures used and the results obtained during the first five generations of selection for increased body weight at harvest in the GIFT project are documented, and the impact of the GIFT strain and technology is reviewed.

2. Materials and methods

2.1. The GIFT population

The initial generation of the GIFT population subjected to selection (G0) was composed of full- and half-sib progeny groups from a nested mating design (each male mated to two or more females). It involved 50 male breeders and 123 female breeders chosen from the best performing strain combinations (Eknath et al., 2007), out of the 64 combinations from the 8 × 8 complete diallel cross study (Bentsen et al., 1998). The genetic material used in the diallel cross study represented four wild African strains (Egypt, Ghana, Kenya, and Senegal) and four farmed Asian strains (Israel, Singapore, Taiwan, and Thailand) (Eknath et al., 1993). The parents of the G0 population were systematically mated to produce progeny that were various three- or four-way strain crosses between the eight strains. The genetic ancestry proportions from the founder strains to the G0 population varied from 3 to 27% depending on the growth performance of the strains, but under the restriction that all eight strains should be represented among the ancestors (confer Table 6). In subsequent generations, breeders were selected and mated according to a nested mating design without considering the pure strain ancestry of the breeding candidates, but matings between full and half-sibs were avoided. The number, age and harvest body weight of male and female parents used to produce the G0 population families and the families of the five following generations are given in Table 1. The performance and genetic characteristics of the base population (G0) were reported by Eknath et al., 2007 and of the following five generations (G1 – G5) by Bentsen et al., 2012.

2.2. Mating and rearing of fry and fingerlings

A detailed description of the methods applied for single pair mating and tagging of progeny was given by Eknath et al. (2007). In summary, the selected breeders of each sex were conditioned in separate net enclosures (called 'hapas') within a pond at a stocking density of 2 to 5 fish per m^2 for 1 to 2 days. They were then transferred to 1 m^3 hapas at a stocking density of 3 to 5 males or 5 to 7 females per hapa for two weeks. During this period, breeders were fed ad libitum twice daily with a mixture of 70% rice bran and 30% fish meal. Once the breeding pond was prepared and fertilized, each female breeder was transferred to a separate 1 m^3 breeding hapa installed within the pond. The spawning condition of all female breeders was evaluated at stocking by examining the female genital papilla (Longalong and Eknath, 1995; Longalong et al., 1999). Females with the most swollen papillas were given priority for mating by stocking a male of similar body weight into the breeding hapa, avoiding mating of full or half-sibs. After 10 to 14 days, fry were collected from each breeding hapa and stocked in separate 1 m^3 fine mesh nursery hapas at a density of 150 to 200 fry/m^3. The male was transferred to another breeding hapa to be mated with a new female. After 21 days of rearing, the fingerlings were transferred to 1 m^3 hapas with larger mesh size (B-net hapas) at a stocking density of 100 to 150 fish per hapa. Supplementary feeding was provided in the fry and fingerling hapas. All full-sib families were reared separately until tagging at a live weight of 3 to 5 g. Following a rearing period of 6 to 13 weeks, all the fingerlings were tagged within a three-week period, using modified Floy® external fingerling tags as described by Longalong et al. (1999). Equal numbers of tagged fingerlings from all full-sib families were pooled together and conditioned in a separate tank for each test environment for 1 to 2 days without feeding before communal stocking in the different test environments.