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Differences in sexual size dimorphism among farmed tilapia species and strains undergoing genetic improvement for body weight

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ABSTRACT

Many tilapia (*Oreochromis* spp.) farmers produce all-male populations because of the superior growth rate of males compared to females. To investigate differences in body weight at harvest of males and females among different tilapia strains, we analyzed data from 62,787 individuals collected from pedigreed breeding programs of *O. niloticus* (GIFT from Malaysia, the Abbassa line from Egypt, and the Akosombo line from Ghana), *O. shiranus* (the Bunda College-Domasi selection line), *O. aureus* (a selection line under development in Abbassa, Egypt, and a selection line from Israel) and a synthetic selection line of Red tilapia under development in Jitra, Malaysia, derived from stock from Malaysia, Taiwan and Thailand (*O.* sp.). Mixed models were separately fitted to the data from each selection line. There was a significant sex effect in all strains ($P < 0.001$). A significant ($P < 0.001$) sex by generation interaction was observed in all strains (scale effect, not reversal of rankings), except Red tilapia and *O. shiranus*. Least squares means showed a large range in the magnitude of body weight differences between sexes across the seven strains. The largest percentage difference between females and males was in *O. aureus* from Egypt (female body weight was 52.2% that of males at harvest), whereas the smallest difference was observed in the GIFT strain of *O. niloticus* (female body weight 84.7% that of males). Female to male body weight percentages for Red tilapia, *O. shiranus*, Egypt *O. niloticus*, Israeli *O. aureus* and Ghana *O. niloticus* were 81.3, 81.0, 69.1, 61.7 and 61.0, respectively. We discuss the results in relation to the potential productivity improvements due to superior growth rates of all-male culture compared to mixed-sex culture in tilapia populations differing in the female to male body weight ratio.

1. Introduction

Growth rate is a focal production trait in commercial aquaculture. Differences in individual growth due to sex have important consequences for production, such as large variation in harvest weight or unsalable small fish. In tilapia (*Oreochromis* spp.), one of the most important aquaculture species, males are on average larger than females (Lorenzen, 2000; Turner and Robinson, 2000). Because of the superior growth rate of males and availability of sex-reversal techniques, large sectors of the tilapia aquaculture industry produce all-male populations to improve productivity and control reproduction (Beardmore et al., 2001). The growth rate advantages of mono-sex over mixed sex populations of tilapia are dependent on the magnitude of sexual size dimorphism (SSD). With the additional expenses or facilities involved in producing all-male fish, mixed-sex populations having low SSD could be more profitable than mono-sex populations. It has been demonstrated that mono-sex tilapia culture is not always superior to mixed-sex culture (Kamaruzzaman et al., 2009; Little and Edwards, 2004). To

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Table 1
Summary of tilapia strains and their origin.

Species	Strain name	Generations of selection	Nucleus location	Reference(s)
Oreochromis aureus	Abbassa	4	Egypt: 30°32′27.22″ N 31°44′13.50″ E	WorldFish Unpublished data
O. aureus	Dor	4	Israel: 32°36′29.19″ N; 34°55′48.27″ E	Zak et al. (2014)
O. niloticus	Abbassa	8	Egypt: 30°32′27.22″ N 31°44′13.50″ E	Ibrahim et al. (2013); Rezk et al. (2009)
O. niloticus	Akosombo	6	Ghana: 6°16′57.04″ N 0°03′30.54″ E	CSIR-Water Research Institute, Ghana, Unpublished data
O. niloticus	GIFT	9[a]	Malaysia: 6°15′27.55″ N 100°25′54.01″ E	Bentsen et al. (1998); Eknath et al. (2007); Ponzoni et al. (2005)
O. sp.[b]	Red tilapia	2	Malaysia: 6°15′27.55″ N 100°25′54.01″ E	Hamzah et al. (2008); Nguyen et al. (2011), WorldFish Unpublished data
O. shiranus	Bunda-Domasi	3	Malawi: 15°18′31.33″ S 35°23′37.72″ E	Maluwa and Gjerde (2006); Maluwa and Gjerde (2007)

[a] At current location in Malaysia, see Ponzoni et al. (2011) for details of strain history after transfer from Philippines.
[b] A hybrid strain derived from *O. niloticus*, *O. mossambicus* and *O. aureus.*

predict the likely benefits of all-male populations it is important to determine if SSD for body weight differs among tilapia species or strains and by how much. Reported estimates of tilapia body weight indicate variation in the magnitude of SSD among strains or species (Palada-de Vera and Eknath, 1993; Rezk et al., 2002). Among these only a few utilize large datasets (e.g., Bentsen et al., 1998; Bentsen et al., 2012; Nguyen et al., 2007; Ponzoni et al., 2005). Furthermore, comparative studies are rare. Recent implementation of structured breeding programs in Asia and Africa has generated large datasets where individual tilapia growth rates are recorded. In this study multigenerational pedigreed data sets from seven tilapia breeding programs were analyzed to investigate the magnitude of SSD for body weight in a range of tilapias, and how this may influence the potential benefits of mono-sex culture.

2. Materials and method

Data were assembled from seven tilapia strains of three different species (Nile tilapia, *Oreochromis niloticus*; Blue tilapia, *O. aureus*; and Shiré tilapia, *O. shiranus*) and one hybrid strain (Red tilapia, *Oreochromis* spp.), developed and maintained at aquaculture field stations in Ghana, Malawi, Israel and Malaysia (Table 1). In all these strains genetic improvement programs to increase body weight are being implemented. No differential treatments were applied to the fish during the implementation of the breeding programs. All fish were reared and managed using standard industry practices (regular water exchange; acceptable stocking densities; use of anesthesia and antiseptics during tagging) to ensure appropriate care of animals.

2.1. Overview of selective breeding procedure and description of tilapia strains

2.1.1. General

The following general description of the breeding programs applies to all the strains studied, except the Israeli *O. aureus* selection program, which was conducted using a slightly different approach (see below). Genetic improvement programs for all other tilapia strains followed the general approach and recommendations for selective breeding of tilapias outlined in Thodesen and Ponzoni (2004). A "combined selection" approach utilizing information on individual fish and information coming from relatives was used to determine the genetic merit of potential brood stock. Animal model estimated breeding values (EBVs) of selection candidates were determined using Best Linear Unbiased Prediction (BLUP). Those with the greatest EBV for body weight at harvest were selected to be the parents of the next generation. To control inbreeding, mating of full- and half-sib relatives was avoided, and the number of individuals selected from each family was restricted in the manner described by Ponzoni et al. (2010). Selected brood stock were mated in mesh hapas suspended within earthen ponds, with a mating ratio of one male to two females in each hapa. Following successful mating, fertilized eggs were collected from females and full-sib families were reared separately in incubators, and subsequently in nursing hapas, until juveniles were large enough for individual tagging (approximately 3 to 5 g). Between 50 and 100 randomly selected juveniles from each full-sib family were tagged with Passive Integrated Transponder (PIT) tags (unless otherwise stated) each having a unique code. After tagging, fish were placed into communal (i.e., mixed families) grow-out ponds for a period of 4–6 months. Fish were fed a commercially available formulated feed throughout the nursing and grow-out periods at an amount equivalent to 3 to 5% of their body weight per day, unless stated otherwise below. The body weight of each fish was measured at the end of communal rearing period. Additional details about each strain are given below and in Table 1.

2.1.2. Blue tilapia (O. aureus), Abbassa strain

This strain is the subject of an ongoing genetic improvement program at the WorldFish Center Aquaculture Research Station at Abbassa, Egypt. A pedigreed base population was created in 2006 from a previous genetic improvement program based on mass-selection. The mass-selected line was derived from a combination of several cultured and wild populations. During winter months (December to March) average minimum water temperatures can drop to 10 to 15 °C (Rezk et al., 2009), which necessitates an "over-wintering" rearing stage using heated water to avoid excessive mortalities. During over-wintering, tilapia are transferred to earthen ponds or to cement tanks covered by greenhouse Like structures in order retain heat. The dataset used for this strain is from generations 2–4 of the selection line. Two 0.1 ha replicate ponds were used for communal rearing in generations 2 and 3, whereas four ponds were used in generation 4 because a greater number of families was produced that year.

2.1.3. Blue tilapia (O. aureus), Israeli strain

A detailed description of this selection program is outlined by Zak et al. (2014). The strain was derived from three populations collected from commercial hatcheries or previously stocked irrigation reservoirs in Israel. Families were created by strip spawning ripe females and fertilized with sperm collected from a single male per female. Families were reared separately in incubation jars, trays and then small net hapas suspended in tanks (progressively) until a mean weight of 0.2–0.5 g was attained. At this stage, 150–200 individuals per family were transferred into separate 400 L tanks, where they were reared until large enough to be individually tagged and sorted by sex (approx. 30 g). Numbered Floy tags (Floy Tag Inc., Seattle, WA) or color dye injections were used for the identification of individuals, but this was not conducted in generations 2 and 4 of the program because of limited resources. Hence, in these generations only families could be distinguished. After tagging, males and females of each family were separated and stocked at a rate of 1.5–1.75 fish per m^2 into two replicate earthen ponds per sex (350–400 m^2 pond size). Twenty families were stocked across four replicate ponds, after which an additional set of pond replicates were used until all families were stocked. A total of up to 12 ponds were used in each generation, depending on the number of families produced. Besides the separation of males and females into different ponds, there was no preferential treatment of either sex throughout the culture period. Fish were fed a commercial floating pellet feed at a rate according to a standard growth curve and feeding tables in generations 1 and 3, or adjusted according to a two-weekly weighing in generations 2 and 4. Communal rearing in ponds was carried out for 3–4 months until harvest, when body weight of all individuals was recorded. In each generation the heaviest 3–4 females and 2–3 males per family per replicate pond were selected and pooled together as the breeders of the next generation. Mating of related individuals was avoided when selecting brood stock pairs. Data collected from generations 2–4 were used for this study.

*2.1.4. Nile tilapia (*O. niloticus*), Abbassa strain*

This strain is maintained at the WorldFish Aquaculture Research Station, Abbassa, Egypt. The strain was founded in 2002 from a 4 × 4 diallel cross of wild and domesticated Egyptian tilapia populations, producing a composite base population (Rezk et al., 2009). The dataset analyzed here comprises the 6th, 7th and 8th generations of selection. Two 0.1 ha ponds were used for communal grow-out in generation 6 and 7, and four replicate ponds were used in generation 8 because a greater number of families were produced that year.

2.1.5. Nile tilapia, Akosombo strain

The Akosombo Nile tilapia strain was developed by the CSIR-Water Research Institute at the Aquaculture Research and Development Center, Akosombo, Ghana. The strain is derived from a 4 × 4 diallel crossing of three populations of *O. niloticus*, collected from three different agro- ecological zones within the Volta system in Ghana and a farmed strain from a local producer (Attipoe, 2006; Attipoe and Abban, 2004; Ponzoni and Brummett, 2008). Data collected from generations 4–6 of the selection line are used for this study.

2.1.6. Nile tilapia, Malaysian GIFT strain

The GIFT strain (Bentsen et al., 1998; Eknath et al., 2007) has been maintained by WorldFish and the Malaysian Department of Fisheries at the Jitra Aquaculture Extension Center, Malaysia since being transferred from the Philippines in 2000 and 2001 (Ponzoni et al., 2005; Ponzoni et al., 2011). Each generation, two 0.1 ha grow-out ponds were stocked with tagged juveniles at a density of 3–4 fish per m^2. Juvenile fish are distributed between the ponds so that each receives representatives from all families. Data analyzed in this study are from the 7th, 8th and 9th generations of selection conducted in Malaysia (7th generation corresponds to the 2009 spawning season reported in Ponzoni et al., 2011).

*2.1.7. Red tilapia (*O. sp*), Malaysian strain*

This selection line is in the early stages of development, initiated in 2008 at the Jitra Aquaculture Extension Center, Malaysia by WorldFish and the Malaysian Department of Fisheries. It is derived from a complete 3 × 3 diallel cross of red tilapia populations from Malaysia, Taiwan and Thailand (Hamzah et al., 2008). The founder Malaysian lines were chosen from the top four ranked in a growth evaluation experiment involving 16 stocks collected from different hatchery locations in the country. Communal growth evaluations were conducted for approximately 4 months in a single 0.1 ha earthen pond. During this period, fish were fed with a standard commercial feed (32% protein) twice daily. A description of the selection procedures and genetic gain in initial generations in this population is given in Nguyen et al. (2011).

*2.1.8. Shiré tilapia (*O. shiranus*), Bunda-Domasi strain*

The base population of this strain was derived from the 4 × 4 diallel cross of wild *O. shiranus* populations described by Maluwa and Gjerde (2006). Paired matings were conducted at the National Aquaculture Center in Domasi, Malawi, in hapas suspended in earthen ponds. Following successful spawning, full-sib families were transferred to separate 1 m^3 concrete tanks where each family was reared until large enough for tagging with individual Floy tags (tagging age between 76 and 131 d). Tagged juveniles were split among three different geographic locations across Malawi where they were communally reared in a single 500 m^2 earthen pond for 180 d (Maluwa and Gjerde, 2007; Maluwa et al., 2006). Initial stocking densities were 3 fish per m^2. Representatives from all families were reared at each site. Data used in the analysis are from generations 1–3 of the breeding program (corresponding to F1, F2 and F3 from Maluwa and Gjerde, 2007).

2.2. Statistical analyses

The data were analyzed using ASReml (Gilmour et al., 2009). The mixed models fitted to each dataset were of the general form:

$$y = \mathbf{Xb} + \mathbf{Za} + \mathbf{Wc} + \mathbf{e}$$

where $\mathbf{y}$ is the vector of observations, $\mathbf{b}$, $\mathbf{a}$, $\mathbf{c}$ and $\mathbf{e}$ are the vectors of fixed effects, random animal effects, random common environmental and dam effects, and random residual effects, respectively. Note that the rearing method in all populations entailed maintaining full sib groups together until they could be physically identified, so that what we estimate in $\mathbf{Wc}$ is the combination of common environmental and dam effects. $\mathbf{X}$, $\mathbf{Z}$ and $\mathbf{W}$ are the incidence matrices relating records to fixed effects, additive genetic effects and common environmental effects, respectively. The number of levels of each fixed effect and the number of dams and sires contributing progeny within each strain are shown in Table 2. Depending on the dataset in question, management group (either generation, generation by pond, or generation by environment) and sex were fitted as fixed effects; animal and common environment plus dam were fitted as random effects. Age at harvest was fitted as a covariate within management group. In the Israeli *O. aureus* selection line, pond effects were confounded with sex because the sexes were reared separately. To overcome this in the analysis, a nested design fitting the replicated pond effect within sex within generation enabled the differences between males and females (i.e., an estimation of the sex effect) to be tested against the mean square of pond within sex. The square root transformation of body weight at harvest improved the distribution of residuals in all datasets, and was used in all analyses. All possible interactions between fixed effects were initially tested in each model, and non-significant interactions were removed from the final models. For each strain, least squares means

Table 2
Data structure for each strain.

Strain	No. of progeny	Sires	Dams	No. of generations	Culture environments	Pond replicates[a]
O. aureus, Egypt	8845	166	250	3	1	2 or 4
O. aureus, Israel	14093	185	201	3	1	5 or 6[b]
O. niloticus, Egypt	10164	173	285	3	1	2 or 4
O. niloticus, Ghana	12190	184	221	3	1	2
O. niloticus, GIFT	9182	176	235	3	1	na
Red tilapia	6119	190	208	3	1	1
O. shiranus	2194	102	130	3	3	1

[a] Within a generation.
[b] Replicate ponds per sex per generation.

Table 3
Number of observations (n) and simple statistics of harvest weight (g) for different tilapia strains.

Strain	Sex	*n*	Minimum	Maximum	Simple mean	SD	CV (%)
O. aureus, Egypt	Female	4496	9.0	119.0	36.6	13.2	36
	Male	4349	10.0	154.0	64.7	18.1	28
	Both	8845	9.0	154.0	50.4	21.2	42
O. aureus, Israel	Female	7082	47.0	628.0	204.3	80.8	40
	Male	7011	54.0	819.0	320.0	108.7	34
	Both	14093	47.0	819.0	261.8	111.8	43
O. niloticus, Egypt	Female	4871	13.0	291.0	93.2	46.9	50
	Male	5293	18.0	414.0	136.9	62.6	46
	Both	10164	13.0	414.0	115.9	59.7	52
O. niloticus, Ghana	Female	5587	16.0	165.0	43.0	13.1	30
	Male	6603	21.0	192.1	68.8	22.3	32
	Both	12190	16.0	192.1	57.0	19.4	34
O. niloticus, GIFT	Female	4208	33.1	546.3	217.5	80.7	37
	Male	4974	19.7	670.0	249.6	98.8	40
	Both	9182	19.7	670.0	234.9	92.3	39
Red tilapia	Female	2689	21.2	593.7	178.5	84.2	47
	Male	3430	22.9	595.0	222.8	99.7	45
	Both	6119	21.2	595.0	203.3	95.7	47
O. shiranus	Female	1195	36.0	146.0	75.2	17.5	23
	Male	999	24.0	198.0	92.9	24.0	26
	Both	2194	24.0	198.0	83.3	22.5	27

for sex and sex by generation were predicted at the average harvest age and back transformed to original measurement units (g).

Female weight as a percentage of male weight at harvest was calculated as an indicator of SSD using the least squares means of each sex. Confidence intervals for the mean female weight as a percentage of male weight were calculated for each strain following the method of Fieller (1954).

3. Results

3.1. Descriptive statistics

Table 3 shows the number of records, minimum and maximum harvest weight, simple mean, SD and CV within each strain. A large range in harvest weight was observed within all populations. The smallest individuals were not always female. Coefficient of variation ranged from moderate to high across the seven strains, with *O. shiranus* showing the lowest (27%) and *O. niloticus* from Egypt the greatest (52%). Within a strain, males had a smaller CV than femalesin *O. aureus* (from Egypt and Israel), in *O. niloticus* from Egypt, and Red tilapia. In the other strains the CV was greater for males.

3.2. Tests for fixed effects

The significance level of fixed effects in each strain is shown in Table 4. Sex effect was significant ($P < 0.001$) in all strains. Sex by generation (S × G) interaction was also significant ($P < 0.001$) in all strains except *O. shiranus* and Red tilapia (S × G in Israeli *O. aureus* could not be tested). Significant S × G interactions only affected the magnitude of the superiority of male over female and not the ranking. Across generations the average harvest weight of males was always greater than for their female counterparts.

Table 4
Effects fitted in the models for the analysis of harvest weight in different tilapia strains. Nested effects were fitted within the effects shown in brackets. Significance of fixed effects and the covariate are indicated by the superscripts. Animal and common environment plus dam were fitted as random effects in all cases.

Strain	Fixed effects[a]	Covariate[a]
O. aureus, Egypt	$S^{‡}, G^{‡}, P(G)^{‡}, S \times G^{‡}$	$Age\ (G, P)^{‡}$
O. aureus, Israel	$P(G, S)^{‡}, S$	$Age\ (G, S, P)^{‡}$
O. niloticus, Egypt	$S^{‡}, G^{‡}, P(G)^{†}, S \times G^{‡}$	$Age\ (G, P)^{‡}$
O. niloticus, Ghana	$S^{‡}, G^{‡}, P(G)^{‡}, S \times G^{‡}$	$Age\ (G, P)^{‡}$
O. niloticus, GIFT	$S^{‡}, G^{‡}, S \times G^{‡}$	$Age\ (G)^{‡}$
Red tilapia	$S^{‡}, G^{‡}, S \times G^{ns}$	$Age\ (G)^{‡}$
O. shiranus	$E^{ns}, S^{‡}, G^{*}, S \times E^{ns}, S \times G^{ns}, E \times G^{‡}$	$Age\ (G, E)^{‡}$

ns: non-significant.
[a] Sex (S); Generation (G); Pond (P); Environment (E).
[*] $P < 0.05$.
[†] $P < 0.01$.
[‡] $P < 0.001$.

3.3. Differences between females and males

Least squares means of harvest weight for both sexes and the ratio of female to male least squares means expressed in percentage term in each strain are presented in Table 5. A large variation in the weight of females relative to males was observed among strains. Average differences between females and males was greatest in the *O. aureus* line from Egypt, whereas it was smallest in the GIFT strain. Within Nile tilapia strains, the weight of females relative to males ranged from 61.0% in the Akosombo strain to 84.7% in the

Table 5
Mean harvest age, least squares means (LSM) for male and female body weight (BW) at harvest and ratio of female to male harvest weight with 95% confidence limits for different tilapia strains.

Strain	Mean age at harvest (d)	Sex	BW LSM[a] (g)	Female/ Male (%)	Female/ Male 95% CI[b]
O. aureus, Egypt	297	Female	27 ± 1.7	52.2	45, 61
		Male	51 ± 2.3		
O. aureus, Israel	287	Female	196 ± 6.9	61.7	57, 67
		Male	317 ± 8.3		
O. niloticus, Egypt	331	Female	106 ± 4.2	69.1	63, 77
		Male	153 ± 5.0		
O. niloticus, Ghana	284	Female	43 ± 1.0	61.0	57, 64
		Male	71 ± 1.2		
O. niloticus, GIFT	260	Female	152 ± 5.6	84.7	77, 94
		Male	179 ± 6.1		
Red tilapia	263	Female	256 ± 10.9	83.4	75, 93
		Male	307 ± 10.0		
O. shiranus	284	Female	74 ± 1.3	81.0	78, 85
		Male	91 ± 1.4		

[a] Retransformed values; analysis conducted on square root transformed harvest weights. Standard errors are in brackets. LSM predicted for mean age at harvest.
[b] Confidence interval calculated following method of Fieller (1954).

GIFT strain. The 95% confidence intervals are almost completely non-overlapping across all three *O. niloticus* strains (Table 5).

No clear pattern was observed among strains in the magnitude of sex differences across generations, that is, sex differences did not consistently become smaller each generation or vice versa (Fig. 1). In some cases, such as *O. aureus* from Egypt, the fluctuation in SSD across generation was large, whereas in other cases, such as GIFT and *O. shiranus*, the differences between females and males were relatively constant (Fig. 1).

4. Discussion

This study is unique, we present the results from analyses of seven large datasets, each corresponding to a different tilapia strain, but that have all been bred using a similar approach. We analyzed the data using a consistent methodology across strains, and we report female/male relative harvest weights for the different strains. We examine and discuss the extent of SSD among the strains, as well as the ramifications for the tilapia industry. Note that the aim of our study was to show and document differences among strains, not to explain the underlying mechanisms causing them. Nevertheless, to put our results in context, a brief review of possible explanations is relevant.

All reference to tilapia size in this paper relates to body weight, as it is one of the key measurements defining overall production of an aquaculture operation (the other one being survival rate). SSD is likely to be similar in tilapia for length, height and other size measurements, but for clarity we only discuss SSD for body weight and report this as the ratio of average female weight to average male weight, expressed as a percentage.

4.1. Possible causes of sexual size dimorphism in tilapia

The degree to which SSD varies within or among cultured tilapia species or strains is not clearly understood. Parker (1992) outlines several arguments for the evolution of SSD in fish. He generalizes that in mass spawning species, sperm competition is the major factor for reproductive advantage rather than body size and will generally result in males being the smaller sex, up to 100-fold different in some instances. For non-mass spawning species that gain reproductive advantage through male-male “combat”, selective pressure will generally favor larger males. In these species, males can be larger than females but rarely more than double their size (Parker, 1992). Tilapias fall into the latter category, being paired spawners with males often highly aggressive toward rivals in seeking out potential female mates.

Bolivar et al. (1993) showed that the distribution of female spawning status (categorized by early spawners, late spawners or virgin) within a population will influence the observed sex differences in body weight of *O. niloticus* at 210 d old. They also showed that least squares means of virgin female body weight can be equal or even greater than that of males at 210 d old. The inference made by the authors is intuitive, reasoning that females that have not spawned will be heavier than those that have, therefore a delay in spawning will reduce population-wide SSD at harvest, if body weight is the metric used to determine this. However, this result should be interpreted with caution because of the small sample sizes ($n = 16–20$) in the study. Given the large CV for body weight observed in tilapia (Table 3), results from small samples may be very different from what may be observed in a similar trial of, say, 1000 individuals. Rutten et al. (2005) showed that the F/M % for body weight in *O. niloticus* steadily decreased from 75% at approximately 110 d, to 56% at approximately 290 d. The authors note that female growth curve trajectories continued linearly and did not plateau after the point at which sexual maturity is expected, when energy is often thought to be diverted toward reproduction and not somatic growth. They suggested environmental conditions that may suppress breeding (such as high stocking densities) might have been a reason that females continued to grow. Age at sexual maturity is reported to differ substantially within and among tilapia species (reviewed in El-Sayed, 2006). Although currently it is not well known how much of this variation is due to environmental or to genetic influences, is likely to be an important factor to consider when conducting studies on SSD in tilapias. Sexual maturity or spawning status was not routinely recorded in any of the populations in the present study, however, early or unwanted reproduction in communal rearing ponds during grow-out periods was often observed among several of the strains. In our analyses variation due to sexual maturity is considered a component of the residual variance. Because of the possible difficulties of accurately assessing the sexual maturity of tilapia by eye, we suggest that the assistance of experienced technicians be utilized if this is to be incorporated in future studies investigating its influence on SSD.

The effect of social interactions between male and female tilapias may also influence the degree of SSD. Schreiber et al. (1998) reported *O. niloticus* females grew significantly larger ($P < 0.05$) than males when reared individually and the potentially agonistic influences of males on females are removed. The authors conclude that the usual observation of females being smaller than males in mixed sex environments is probably caused by behavioral factors rather than physiological factors. In addition, it has been suggested that the differential expression of a thyroid hormone (T3) is a contribut-

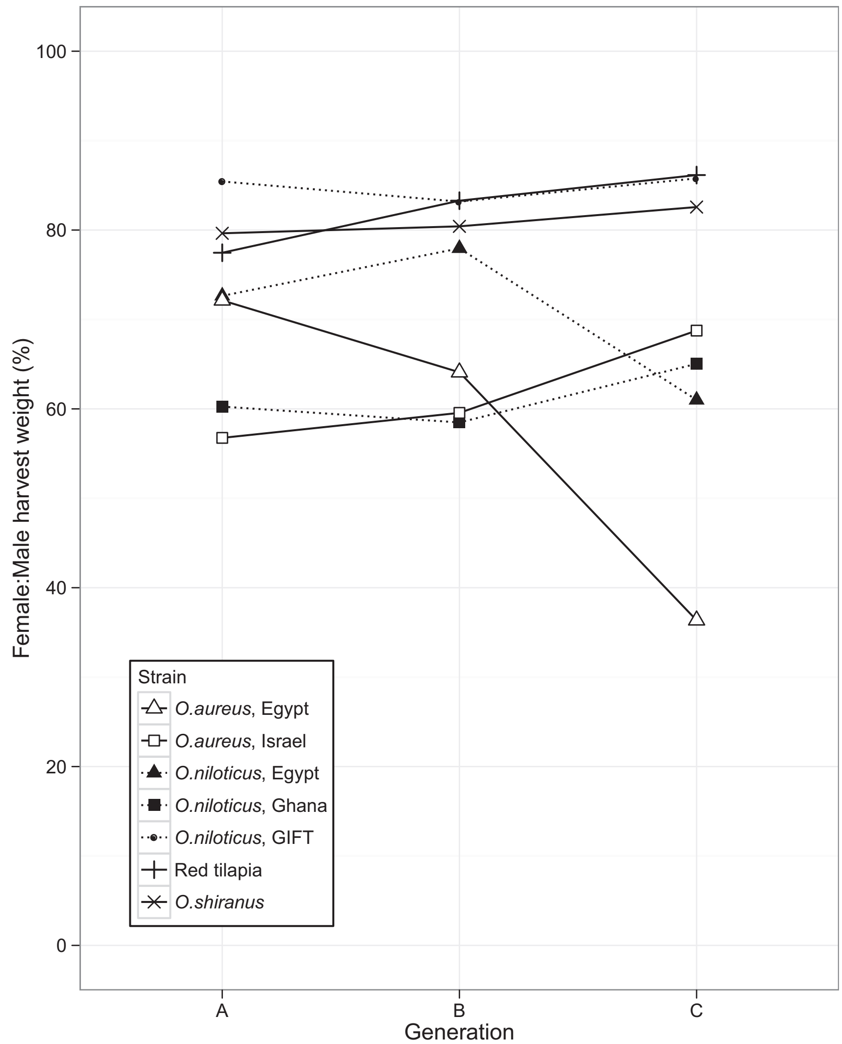

Fig. 1. Across generation changes in sexual size dimorphism of different tilapia strains measured by the ratio of female to male least squares means for harvest weight.

ing factor to differential growth rates in male and female *O. niloticus* (Toguyeni et al., 1996; Toguyeni et al., 2009) and *O. aureus* (Mol et al., 1994). These studies suggest that T3 levels are correlated with a hormone (11-KT) that is linked to aggressive social behavior, which may be contributing to growth rate suppression in females. Separation of males and females during the grow-out period in the Israeli *O. aureus* strain analyzed here shows that a considerable SSD could still be observed even when potential effect of male-female social interaction is removed. Although the sex-separated Israeli *O. aureus* showed lower SSD than the mixed-sex *O. aureus* from Egypt, it is inappropriate to infer such differences are due to the suppression of female growth from aggressive interactions with males. Such a conclusion would require a controlled, side-by-side trial.

Genetic factors have also been previously considered as a potential influence on SSD in tilapias. Lester et al. (1989) report zero heritability for variation in SSD in *O. niloticus*, inferring that all variation is due to environmental factors. In the GIFT strain, Nguyen et al. (2007) report high genetic correlations (not significantly different from unity) when the expression of body dimension characteristics (weight, length, depth) in males and females are treated as different traits. They conclude that the various body dimensions are essentially under control of the same genes in both sexes, and that the relative proportions of these traits are unlikely to be altered through deliberate selection in this strain. Maluwa and Gjerde (2006) report similar but slightly lower genetic correlations between male and female body weight in *O. shiranus*, with $r_g = 0.85 \pm 0.15$ (not significantly different from unity). The same study also reports greater heritability for body weight in males than females ($h^2 = 0.40 \pm 0.13$ and 0.27 ± 0.08, respectively). These studies were conducted on the same *O. shiranus* strain analyzed here. A recent analysis of the GIFT strain based on five generations of data collected between 1991 and 1996 showed a lower genetic correlation between male and female harvest weight in ponds compared to cages (Bentsen et al., 2012). They suggested this may indicate a low to moderate genotype by sex interaction in pond environments that may not occur when rearing is done in intensive cage environments.

Several studies report changes in the magnitude of SSD in tilapias when reared under different culture environments (e.g., Maluwa and Gjerde, 2006; Pongthana et al., 2010). This supports the hypothesis that environment has a significant effect on the magnitude of SSD in tilapias. However, across three generations of data in *O. shiranus*, we found no significant sex by environment interaction. We found significant sex by generation interactions (due to changes in the between strain differences, not reversal of ranking) in four of the seven tilapia strains (Table 4). Note that the effect of generation cannot be entirely attributed to genetic changes in a population, and that the effect of environmental fluctuations from year to year (such as rainfall, ambient temperature) will also contribute to the generation effect, albeit confounded with genetic changes in this case. All strains included in our study were cultured in different climates with the exception of GIFT and Red tilapia in Malaysia, and Egyptian *O. niloticus* and *O. aureus* in Abbassa. Where possible, it would be valuable to compare strains such as those described here in side-by-side growth trials. Alternatively, repeated mating of brood stock pairs across multiple years would also provide valuable information on the environmental effect on SSD. This would help to clarify (and quantify) the contribution made to SSD by the strain itself and by environmental factors such as those related to year to year conditions (environment as a random effect). Furthermore, recording the performance of a strain in different locations would enable estimate the effect of prevailing conditions in a particular location on SSD (environment as a fixed effect) (James, 1975).

4.2. Implications for tilapia culture and strain selection

Our results and published literature suggest that the magnitude of SSD can vary substantially within and among tilapia species. This variation is likely to have important consequences on decisions to pursue mono-sex tilapia culture or not. Note, however, that the benefits of all-male tilapia culture are not limited to potential improvements in growth rate (Beardmore et al., 2001; El-Sayed, 2006). Eliminating reproduction in tilapia ponds has been a driving factor in the adoption of mono-sex culture in the tilapia aquaculture sector (Mair and Little, 1991; Wohlfarth and Hulata, 1983). The productivity benefits of all-male tilapia culture are likely to be attributable to a combination of both the superior growth rate of males and minimizing reproduction; however, there are reports showing that mono-sex tilapia culture is not always more productive than mixed-sex culture (Dan and Little, 2000; Kamaruzzaman et al., 2009; Little et al., 2003). Whereas mono-sex tilapia culture has had undoubted success at limiting unwanted reproduction, and thus reducing unmarketable small fish or poor productivity, Kamaruzzaman et al. (2009) have suggested that this may be of less importance when faster growing strains are used and the duration of the culture period is reduced. A faster growth rate of males is the primary reason for mono-sex culture in systems where reproduction is inhibited, such as in floating cages, tanks or when stocking densities are high. Whilst recognizing the potential benefits of eliminating unwanted reproduction in some tilapia culture systems, this study highlights that if the anticipated increase in growth rate is an important factor in choosing mono-sex over mixed-sex tilapia, it would be pertinent to consider the magnitude of SSD in the strain(s) and location(s) cultured.

Consider the following hypothetical scenario. Assume a tilapia farmer produces a mixed-sex population with equal proportion of males and females, having an overall mean size of 300 g and total yield of 3.00 t (i.e., 10,000 fish). If the farmer's strain shows a SSD the same as the lower limit of 95% CIs presented in this study (F/M weight of 45%, Table 5), it can be shown that average weights of males and females would be 414 g and 186 g, respectively. If the females of this strain had been masculinized using a standard hormone sex-reversal technique and therefore had a mean weight the same as males, we could anticipate a total yield of 4.14 t. This represents a production boost of 1.14 t by producing an all-male population compared to the mixed sex population described earlier. Applying similar logic for a strain showing SSD at the upper limit presented here (F/M of 95%), average male and female weights would be 309 g and 291 g, respectively. If these females had been masculinized, a total yield of 3.09 t would be predicted, representing an increase of only 90 kg over the mixed sex population. Of course, this is a simplified example with several broad assumptions (e.g., unwanted reproduction is a minor issue), but nevertheless demonstrates that the magnitude of SSD can have a large influence on the relative benefits of producing all-male tilapia populations. When considering the additional costs required to produce all-male mono-sex populations, it is reasonable to assume that there is a particular point at which it is no longer beneficial to produce all-male over mixed-sex populations. This notion is supported by field trials that show that mixed-sex populations can be just as productive as mono-sex male populations produced by different approaches (Dan and Little, 2000; Kamaruzzaman et al., 2009; Little et al., 2003). Further to this, some consumer markets, such as the European Union, are forbidden to produce or import tilapia products for human consumption that have been subjected to hormonal treatment (following Directive 2003/74/EC). Consumer preferences against hormone treated animals have also given rise to the emergence of organic certification standards that do not permit the use of hormones during rearing or reproduction (e.g., Naturland, 2005). We suggest that the degree of SSD could have an important role in tilapia production where the use of hormonally induced all-male populations is undesirable. A more detailed simulation study incorporating factors such as the magnitude of SSD, market price structures and sex reversal efficiencies could be of particular interest when investigating the benefits of mixed- vs. mono-sex tilapia aquaculture.

A logical, practical consideration is whether it is possible for a culturist to choose a particular tilapia strain and have confidence that its degree of SSD is constant (or at least predictable within certain limits). Similarly, is it likely that a fingerling producer is able to confidently market their product as having low SSD? This study demonstrates that SSD can be relatively consistent over extended periods for some strains (e.g., the GIFT strain presented here and in Nguyen et al., 2007; Ponzoni et al., 2005), and less consistent for other strains. Unfortunately, the question of whether this is due to genetic characteristics of the strain itself, or the environmental conditions it is cultured under, still remains unanswered. For instance, differences observed among the *O. niloticus* strains from Egypt, Ghana and Malaysia are relatively constant over three generations. However, it is impossible, with the data available, to conclude that this is because of genetic differences among strains, differences in climatic conditions in the location of culture, or a combination of both. Only side-by-side controlled trials will help disentangle these factors. Such trials have not been performed to date and this further echoes the importance of multi-species and multi-strain comparisons of tilapia emphasized by Rezk et al. (2002).

5. Conclusion

We showed that the magnitude of SSD varied substantially across tilapia species and strains each reared in a different environment. There are indications that SSD for body weight may be relatively stable within a given population or genetic group over an extended time period, although in other instances it may vary substantially from generation to generation. We observed significant sex by generation interactions in several tilapia strains, indicating that the magnitude of SSD may vary depending on generation. We found little evidence to suggest that selection for greater body weight may consistently reduce (or increase) the difference between sexes over a period of three generations. Further investigation on factors affecting SSD in tilapia is required to better gauge the relative benefits of mono-sex male culture over mixed-sex culture, and whether it is worthwhile to culture mono-sex populations in some instances. Research investigating environmental factors that could contribute toward changes in the magnitude of SSD in tilapia may also provide pointers to management strategies that could help minimize the disadvantages of large weight differences between males and females. The magnitude of SSD is often overlooked in tilapia aquaculture, yet variation in SSD of the order identified in this study may have substantial impact on productivity. We anticipate the results of this study will provide sound justification for further investigation of this topic in one of the most important aquaculture species throughout the world.

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