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## Comparative study of the breeding performances of five populations of Nile tilapia (*Oreochromis niloticus*) (F1) in an experimental ongrowing system in Benin (West Africa)

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#### ABSTRACT

In order to investigate the breeding performances of five F1 populations of *Oreochromis niloticus* originated from wild brood-stock of Nangbéto, Sohoumè and Togbadji in the Mono basin, Gobé in the Ouémé basin and Gbassa in the Niger basin, breeding tests were conducted for 10 weeks in an ongrowing experimental system. All tested populations were checked daily in order to collect spawn and to compare the reproductive performances. Compared with others, Sohoumè, Togbadji, and Gobé populations significantly (P < .05) displayed the best breeding performances in terms of rate of multi-spawning females (89.3 ± 15.2-92.3 ± 10.8%); mean relative fecundity (4 ± 2–6 ± 3 eggs/g of female), mean gonadosomatic index (3.1 ± 2–4.8% ± 2.6); mean absolute fecundity rates (865 ± 339–989 ± 547 eggs); mean fertilization rates (98 ± 4.3–99.3 ± 1.1%); and mean hatching rates (83.7 ± 10–88.9 ± 9.1%).

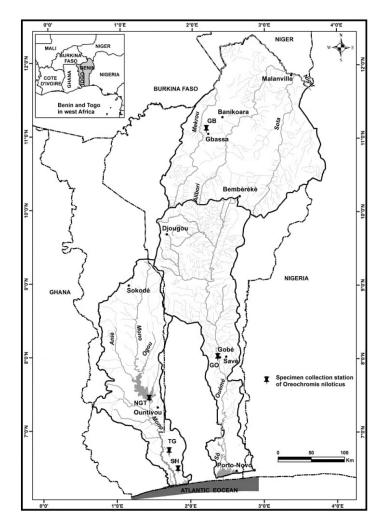
#### KEYWORDS

Oreochromis niloticus; basin; spawning; West Africa

#### Introduction

In 2016, global tilapia production was estimated at more than 5.90 million tons with a projected growth rate of 3.4% annually (Kolding et al. 2017; OCDE/FAO 2019; Tacon and Metian 2008). This growth is due to rising farming systems that need large quantities of fry accordingly. High-quality tilapia fingerlings production is therefore important due to the low fecundity of broodstock (El-Sayed and Kawanna 2008; Mires 1982). In Benin, *O. niloticus* is the most produced species because of its fast growth, precocious sexual maturity, rusticity, excellent flesh quality, and good market acceptance (Rurangwa et al. 2014). Increased global demand for tilapia requires optimization of hatchery efficiencyFigure 1.

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**Figure 1.** Hydrographic map of the Mono (NGT: Nangbéto, SH: Sohoumè, TG: Togbadji), Ouémé (GO: Gobé) and Niger (GB: Gbassa) basins showing collection stations for wild breeders stocks. The choice of localities was based on the presence of the species in the environment. The chips on the map indicate the collection points in the different localities.

The ability to control sexual maturation and spawning to get highquality fingerlings is a key issue to aquaculture production success (Migaud et al. 2013). Broodstock productivity is the most significant constraint in commercial tilapia farming. A knowledge of the factors regulating broodstock productivity (Coward and Bromage 1999) and a better choice of the initial strains for the fry production are therefore of great importance for the development of tilapia culture. *Oreochromis niloticus* is the major farmed species which exhibits high parental care. The female is a mouth-breeder which produces a relatively low number of 309 to 1158 eggs per female (Rana 1988). The issue of the mass production of tilapia seed is further exacerbated because of the low degree of female spawning synchrony and the reduction in spawning effort with time (El-Sayed and Kawanna 2008; Mires 1982; Campos-mendoza et al., 2004; Ng and Wang 2011). The different geographic strains of this species may have genetic, physiological, behavioral, and/ or other traits that modulate biological performances, such as growth rate and fecundity according to local environment (Khater 1986; Smitherman et al. 1988; Tave et al. 1990).

Several studies were conducted with tilapia in order to select productive traits (Fülber et al. 2009; Ponzoni et al. 2005), genetic traits (Fortes-Silva et al. 2010), nutritional (Nakaghi et al. 2009; Tsadik and Bart 2007) and reproductive traits (Mataveli et al. 2007; Yoshida et al. 2017). Scientific literature on reproductive traits, such as the percentage of spawning females/week, interval between spawns, hatching rate, and other variables, is scarce. Getting accurate data about these traits can help to better select the breeders with desirable characteristics in order to improve the productivity of the species (Almeida et al. 2013).

Tilapia species differ markedly from one another in many traits of evolutionary importance, which also reflect on their suitability for aquaculture. Intraspecific variation among stocks / strains were evaluated only in O. niloticus. The works of Osure and Phelps (2006) allowed the assessment of reproductive performances of four O. niloticus strains from Ivory Coast, Victoria Lake, Egypt, and Sagana. These studies have shown variability between the reproductive performances of these different strains. Almeida et al. (2013) also showed reproductive performances variability between three different strains of O. niloticus. Smitherman et al. (1988) found differences in reproductive performances of three strains of O. niloticus from Egypt, Ivory Coast and Ghana. The selection of an appropriate strain for a given set of conditions can significantly improve performances (Eknath and Hulata 2009). In this context, the quantity and quality of eggs, larvae, and juveniles are of great importance in monitoring tilapia culture (Almeida et al. 2013), since these factors are the basis of the production chain (Meurer et al. 2005).

This study aimed to compare the breeding performances of different populations of *O. niloticus* collected in the Mono, Ouémé, and Niger basins in Benin in order to select the population that exhibits the best reproductive performances in an experimental ongrowing system.

#### **Material and methods**

## **Ethics Statement**

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

#### Origin of broodstock and production of F1 stock

In order to obtain a first generation (F1) of the captive broodstock from different basins in Benin, 100 wild breeders were collected with seine and trap fishing in five localities: Nangbéto in Togo (near the border with Benin), Sohoumè and Togbadji from the Mono basin; Gobé from the Ouémé basin and Gbassa from the Niger basin. The wild broodstocks were transported in the experimental ongrowing system at the University of Abomey-Calavi and acclimatized in 1.9 m<sup>3</sup> fiberglass tanks for 10 months.

From January to March 2018, the broodstocks were stocked in five 1.9 m<sup>3</sup> breeding tanks (28.5  $\pm$  1.3°C) with a sex ratio of 1 male to 4 females for a total of 20 fish per tank. Once a week, eggs were collected from the mouth of the females and incubated in zug bottles until hatching. For each population, at least three spawns with a minimum of 150 larvae per spawn were grouped and reared in 50 L aquariums before being transferred into 0.4 m<sup>3</sup> plastic tanks for ongrowing. Finally, a minimum of 300 individuals were harvested and used as the stock of the first generation (F1) of the captive breeders.

#### Breeding and eggs harvesting

From February to April 2019, the 17-months old F1 broodstocks were selected in each population according to the sexual characteristics of males (milt emission) and females (oocytes emission). A sex ratio of 1 male to 4 females was applied to all populations. Thus 32 females (mean weight of  $209.4 \pm 9.3$  g) and 8 males (mean weight  $262 \pm 17.4$  g) were selected in each population. They were separately distributed into ten 1.9 m<sup>3</sup> tanks in a recirculating aquaculture system. For each population, a replicate was set up at the rate of 16 females and 4 males per 1.9 m<sup>3</sup> tanks. The broodstocks were fed every morning at 5% of the total biomass (Santiago and Laron 2002) for two weeks with an extruded commercial food (35% proteins, 6% lipids, and crude energy = 17.4 MJ/kg). Then, males were introduced into the females tanks for natural mating. The broodstocks were maintained under a 12L:12D photoperiod and each tank was checked daily by lowering the height of water in the tank to collect the spawns. The incubating females were identified and fished in a plastic bucket to retrieve the eggs. All females were Pit-Tagged to determine their individual spawning frequency and fecundity.

#### **Experimental design**

Spawns were individually weighted and photographed, and the eggs in the pictures were counted using Image J 1.45S software. Spawns were incubated in Zug bottles in a recirculating system ( $30.6 \pm 0.4^{\circ}$ C) up to 10 days post fertilization (10 dpf). All larvae were counted.

For each population, two batches of 500 10-dpf-old larvae originating from four different spawns were constituted in order to assess the evolution of the sexual maturity of F2 fry. They were first transferred into 0.1 m<sup>3</sup> happas placed in 1.9 m<sup>3</sup> tanks ( $29 \pm 0.8^{\circ}$ C), and released into the tanks at 75 dpf. From 119 dpf, 50 individuals per tank were sampled every 15 days, weighted, measured, and individually checked by abdominal stripping to control milt or oocytes emission. Water temperature, dissolved oxygen, and pH were measured daily early in the morning in the sump tank of hatchery and in the breeding tanks.

Fecundity parameters, as absolute fecundity (AF), relative fecundity (RF), number of spawns per female (NS/f), the rate of multi-spawning females (MSf), mean spawn weight (WSa), mean eggs weight (WEa) gonadosomatic index (GSI) and the fertility parameters, such as fertilization rate (FR) and hatching rate (HR), were calculated as follows:

#### $GSI = 100^{*}(Ws/Wt)$

where GSI is the gonadosomatic index (%), Ws is the total weight of spawn (g), and Wt is the total body weight (g).

### $\mathbf{RF} = \mathbf{AF}/\mathbf{Wt}$

where RF is the relative fecundity (egg/g), Wt is the total body weight (g), and AF is the absolute fecundity (egg number).

#### FR = (AF-NUE)/AF \* 100

where FR is the fertilization rate (%), AF is the absolute fecundity (eggs number), and NUE is the number of unfertilized eggs.

## $HR = NL_{10Dpf} / (AF-NUE) * 100$

where HR is the hatching rate (%),  $NL_{10Dpf}$  is the total number of larvae at 10 dpf, AF is the absolute fecundity, and NUE is the number of unfertilized eggs.

#### MSf (%) = NMs/NS \*100

where MSf (%) is the rate of females spawning more than one time, NMs is the number of multi-spawning females, and NS is the number of spawning females

#### NS/f = TNS/NSf

where NS/f is the number of spawns per female, TNS is the total number of spawn collected per population, and NSf is the total number of spawning females per population.

#### Statistical analysis

Results were expressed as mean  $\pm$  standard error. Data normality was checked with the Shapiro–Wilk test. When data were heterogeneous or did not have a normal distribution, a log-transformation of the data was applied and the analysis was performed on the transformed data. Once the data were transformed, the Shapiro–Wilk normality test was performed again. When the distribution of the transformed data was normal, the one-way analysis of variance (ANOVA 1) was performed and when the difference was significant, the Post-Hoc Tukey test was performed in the "Ismeans" R package to find the differences. When the distribution of the transformed data was not normal, the Kruskal–Wallis nonparametric test was performed and when the difference was significant, the Dunn test was performed in the R package "dunn. test" to find the differences according to the Bonferroni method. The differences observed were defined as statistically significant at the 5% level. All analyses were performed with R version 3.5.1 Software (Team R Core 2018).

#### Results

#### Hatchery and tank water quality

The mean physicochemical parameters in the hatchery water during the different incubations were  $30.6 \pm 0.4$  °C for temperature,  $6.5 \pm 0.1$  mg/L for dissolved oxygen and  $6.8 \pm 0.7$  for pH.

In the fish-breeding tanks, the physicochemical parameters of water ranged from  $28.9 \pm 0.8^{\circ}$ C to  $29.0 \pm 0.8^{\circ}$ C for temperature, from  $6.2 \pm 0.5$  mg/L to  $6.4 \pm 0.5$  mg/L for dissolved oxygen and from  $6.5 \pm 0.5$  to  $6.7 \pm 0.8$  for pH. The ANOVA test displayed no significant difference (P > 0.05) between these physicochemical parameters.

### Fecundity of populations

#### Spawning performances of females

At the end of the experiment, the female spawning rate ranged from  $59.4\% \pm 13.3$  (Gbassa) to  $84.4\% \pm 13.3$  (Togbadji) (P > 0.05). The number of spawns per female ranged (P < 0.05) from  $1.3 \pm 0.4$  to  $3.3 \pm 0.5$  spawns/female for the Nangbéto and Gobé populations, respectively (Table 1). Compared to Togbadji ( $3.0 \pm 0.1$  spawns/female and  $90\% \pm 14.1$  of multi-spawning females), Gobé and Sohoumè exhibited a similar number of spawns per female ( $3.3 \pm 0.5$  and  $2.9 \pm 0.9$  spawns/female, respectively) with a rate of multi-spawning females of  $92.3\% \pm 10.8$  and  $89.3\% \pm 15.2$ , respectively. The Gbassa and Nangbéto populations recorded the lowest rates of multi-spawning females with  $54\% \pm 12.1$  and  $37\% \pm 11.9$ , while the Gobé and Togbadji populations recorded the highest rates of multi-spawning females ( $92.3\% \pm 10.8$  and  $90\% \pm 1$ 

Parameters	Gbassa	Gobé	Nangbéto	Sohoumè	Togbadji
Total number of females	32	32	32	32	32
Mean weight of females	$204.4 \pm 9.8^{a}$	213 ± 12.1 <sup>a</sup>	196 ± 15.3 <sup>a</sup>	219.7 ± 13 <sup>a</sup>	214.1 ± 21.4 <sup>a</sup>
Rates of spawning (%)	59.4 ± 13.3 <sup>a</sup>	$75 \pm 8.8^{a}$	78.1 ± 13.3 <sup>a</sup>	78.1 ± 13.3 <sup>a</sup>	84.4 ± 13.3 <sup>a</sup>
Number of spawns per female (Spawns/Female)	$1.9 \pm 0.2^{ab}$	$3.3 \pm 0.5^{b}$	$1.3 \pm 0.4^{a}$	$2.9 \pm 0.9^{ab}$	3 ± 0.1 <sup>ab</sup>
Rate of multi-spawning female (%)	$54 \pm 12.1^{ab}$	92.3 ± 10.8 <sup>b</sup>	37 ± 11.9 <sup>a</sup>	89.3 ± 15.2 <sup>b</sup>	90 ± 14.1 <sup>b</sup>
Time interval between two spawns (Days)	$14 \pm 4^{a}$	$17 \pm 6^{a}$	22 ± 15 <sup>a</sup>	$17 \pm 10^{a}$	14 ± 3 <sup>a</sup>
Mean gonadosomatic index (%)	2.6 ± 1.8 <sup>a</sup>	4.1 ± 1.7 °	$2.8 \pm 1.3^{ab}$	3.1 ± 2 <sup>b</sup>	$4.8 \pm 2.6^{d}$
Mean absolute fecundity (Eggs)	676 ± 453 <sup>a</sup>	$944 \pm 302^{b}$	627 ± 375 <sup>a</sup>	989 ± 547 <sup>b</sup>	865 ± 339 <sup>b</sup>
Mean relative fecundity (Eggs/g of female)	3 ± 3ª	6 ± 2 <sup>cd</sup>	$5 \pm 3^{bc}$	$4 \pm 2^{\mathbf{b}}$	6 ± 3 <sup>d</sup>
Mean fertilization rate (%)	$97.5 \pm 5.4^{ab}$	$98 \pm 4.3^{a}$	87.8 ± 14.2 <sup>b</sup>	$98.6 \pm 2.6^{a}$	99.3 ± 1.1 <sup>a</sup>
Mean hatching rate; (%)	81.4 ± 12.5 <sup>a</sup>	83.8 ± 10.9 <sup>a</sup>	$59 \pm 19.8^{b}$	$83.7 \pm 10^{a}$	88.9 ± 9.1 <sup>a</sup>
Mean weight of egg (mg)	$8 \pm 4^{a}$	8 ± 3 <sup>a</sup>	$8 \pm 5^{a}$	$7 \pm 2^{a}$	$9 \pm 4^{a}$
Cumulated absolute fecundity (Eggs)	20948	51917	13784	46474	35479

Table 1. Reproductive parameters of breeders from the five (F1) populations of Oreochromis niloticus in Benin.

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14.1, respectively,) (Table 1). All populations were compared 2 by 2. With the exception of the rates of multi-spawning females in pairs (NGT, GO), (NGT, TG), (NGT, SH) for which we noted a significant difference (P < 0.05, Tukey test), all other possible pairs displayed no significant difference (P > 0.05, Tukey test). Also, considering the number of spawns per female, except for the pair (GO, NGT) which displayed a significant difference (P < 0.05, Tukey test), all other pairs displayed no significant difference (P < 0.05, Tukey test), all other pairs displayed no significant difference (P < 0.05, Tukey test), all other pairs displayed no significant difference (P < 0.05, Tukey test), all other pairs displayed no significant difference (P < 0.05, Tukey test), all other pairs displayed no significant difference (P < 0.05, Tukey test), all other pairs displayed no significant difference (P < 0.05, Tukey test), all other pairs displayed no significant difference (P < 0.05, Tukey test), all other pairs displayed no significant difference (P < 0.05, Tukey test), all other pairs displayed no significant difference (P < 0.05, Tukey test), all other pairs displayed no significant difference (P < 0.05, Tukey test), all other pairs displayed no significant difference (P < 0.05, Tukey test), all other pairs displayed no significant difference (P < 0.05, Tukey test), all other pairs displayed no significant difference (P < 0.05, Tukey test), all other pairs displayed no significant difference (P < 0.05, Tukey test), all other pairs displayed no significant difference (P < 0.05, Tukey test), all other pairs displayed no significant difference (P < 0.05, Tukey test), all other pairs displayed no significant difference (P < 0.05, the pair (P < 0

The mean interval time (TI) between the two spawns ranged from  $14 \pm 3$  to  $22 \pm 15$  days for Togbadji and Nangbéto, respectively, and was not significantly different (P > 0.05) between populations (Table 1).

#### Gonadosomatic index and mean weight of egg

The females gonadosomatic index (GSI) ranged (P < 0.05) at the end of the experimental period from 2.6% ± 1.8 to 4.8% ± 2.6 (Table 1) for Gbassa and Togbadji, respectively. No significant difference (P > 0.05, Tukey test) was noted between the mean GSIs of the population pairs (NGT, GB) and (NGT, SH), while all GSIs of the other population taken in pairs showed a significant difference (P < 0.05, Tukey test) (Table 1).

The mean egg weight ranged from  $7 \pm 2$  to  $9 \pm 4$  mg for Sohoumè and Togbadji populations, respectively, and was not significantly different (P > 0.05) between the populations (Table 1)

## Absolute and relative fecundity

Mean absolute fecundity significantly varied (P < 0.05) from 627 ± 375 to 989 ± 547 eggs for Nangbéto and Sohoumè, respectively. The populations of Sohoumé, Gobé, and Togbadji displayed the best absolute fecundity with 989 ± 547 eggs, 944 ± 302 eggs, and 865 ± 339 eggs, respectively (Table 1). The mean absolute fecundity of the Gbassa and Nangbéto populations displayed no significant difference (P > 0.05, Tukey test). However, the mean absolute fecundity of these two populations were significantly different (P < .05, Tukey test) from those of the Gobé, Sohoumè, and Togbadji populations, which between them, did not show any significant difference (P > 0.05, Tukey test).

Mean relative fecundity (P < 0.05) ranged from  $3 \pm 3$  (Gbassa) to  $6 \pm 3$  eggs/ g of female (Gobé and Togbadji) (Table 1). No significant difference (P > 0.05, Tukey test) was noted between the mean relative fecundities of the population pairs (NGT, GO), (NGT, SH) and (GO, TG). On the other hand, between the mean relative fecundities of Gbassa and all other populations taken in pairs, we note a significant difference (P < .05, Tukey test).

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 Table 2. Values of the size of sexual maturing.

	Size of sexual	Size of sexual maturing (cm)		
Populations	Males	Females		
Gbassa	13.3 ± 1	14.0 ± 1.5		
Gobé	15.0 ± 0.8	15.5 ± 1.5		
Nangbéto	12.4 ± 1.1	12.2 ± 1.7		
Sohoumè	13.7 ± 1.1	13.3 ± 1.5		
Togbadji	13.7 ± 0.8	13.5 ± 1.8		

#### Fertility

#### Fertilization and hatching rates

The median values of fertilization rates ranged (P < 0.05) from 87.8%  $\pm$  14.2 to 99.3%  $\pm$  1.1 for Nangbéto and Togbadji, respectively (Table 1). A significant difference (P < 0.05, Dunn test) was noted between the median values of the fertilization rates of Nangbéto and the Gobé, Sohoumè, and Togbadji populations. On the other hand, the median values of the fertilization rates of the Nangbéto and Gbassa populations did not display any significant difference (P > 0.05, Dunn test).

The hatching rates ranged (P < 0.05) from 59%  $\pm$  19.8 to 88.9%  $\pm$  9.1 for Nangbéto and Togbadji, respectively (Table 1). The median value of the hatching rate of the Nangbéto population was significantly different (P < 0.05, Dunn test) from that of the other populations, which between them, did not display any significant difference (P > 0.05, Dunn test) (Table 1).

#### Size of sexual maturing individuals

The first sexually maturating individuals were observed at 114 dpf in Gbassa and Togbadji populations. 3% and 4% of maturing individuals were recorded at mean lengths of  $85 \pm 5$  mm and  $74 \pm 5$  mm, respectively.

The females of Nangbéto started gonad maturation early compared to the other populations; 50% of the females of Nangbéto began by carrying the first oocytes at a size of 12.2 cm, while those of Gbassa, Gobé, Sohoumè, and Togbadji began at 14.0 cm, 15.5 cm, 13.5 cm, and 13.3 cm, respectively (Table 2). Also, 50% of males from Nangbéto already started emitting milt at a size of 12.4 cm, while those of Gbassa, Gobé, Sohoumè, and Togbadji started at 13.3 cm, 15 cm, 13.7 cm, and 13.7 cm, respectively (Table 2 and Figure 2). Comparing females and males within the same population, the sizes of maturing individuals (L50), which expresses in our study the size at which 50% of individuals begin gonad maturation, showed no significant difference (P > 0.05). Similarly, no significant difference (P > 0.05) was noted between the sizes of maturing individuals in the five populations.



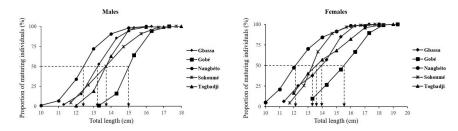


Figure 2. Evolution of the rate of individuals in the phase of sexual maturation as a function of size during the test.

#### Discussion

In our study, Gobé population (Ouémé basin) and Sohoumè and Togbadji populations (Mono basin) displayed a higher number of spawns per female and a higher rate of multi-spawning females, suggesting that these three populations are more prolific than the other populations studied. Nangbéto and Gbassa populations were the less productive in terms of eggs production. These results show that the eggs productivity of a population depends not only on the number of exploited females but also on the biological and genetic traits of the population. Moreover, the females of the Togbadji population (Rate of spawning =  $84.4\% \pm 13.3$ , NS/F =  $3 \pm 0.1$  spawns/female, Msf =  $90\% \pm 14.1$  and the mean absolute fecundity =  $865 \pm 339$  eggs) breed much more than females of all other populations. These results could be explained by a possible link between the origin and genetic traits of this population which exhibits genetic differences compared to the other populations in the same basin (Fagbémi et al. 2021). The rates of spawning females in our study are similar to those obtained by Almeida et al. (2013) in happas installed in tank but remained better than those obtained by Osure and Phelps (2006) for four strains of O. niloticus from Ivory Coast, Egypt, Sagana, and Lake Victoria (Kenya). The multi-spawning females data in our experiments remained better than those obtained by Almeida et al. (2013). Overall, the mean interval time between two spawns recorded in our study shows that oocytes maturation for the Nangbéto population takes much longer and varies much more compared to other populations. This result could be linked to the low adaptation of this population to rearing conditions and to genetic traits specific to this population. In contrast to Nangbéto, the mean interval time between two spawns for the Togbadji population remained more stable throughout our study.

The Togbadji population displayed the best mean gonadosomatic index (4.8%  $\pm$  2.6), whereas that of Gbassa and Nangbéto got the lowest one (2.6%  $\pm$  1.8 and 2.8%  $\pm$  1.3, respectively,). As all broodstocks received the same food at the same ratio (5%) this difference suggests that population

of Togbadji could have a genetic wherewithal to make better use of the food and thus to devote more energy to the production of oocytes. Since *O. niloticus* is a multiple spawner that has oocytes at different stages of maturation in the ovaries and only mature oocytes are released at each spawning (Babiker and Ibrahim 1979; Yun et al. 1983), this result also suggests that Togbadji population has a large pool of simultaneously maturing oocytes in the ovaries which would allow for a large quantity of oocytes to be obtained at each spawning event compared to other populations.

The Sohoumè, Gobé, and Togbadji populations displayed the highest mean absolute fecundities. For the Gobé and Sohoumé populations, with fewer spawning females over the trial period, we obtained the highest cumulative number of eggs than that of Togbadji, which recorded the highest rate of females that laid. The mean absolute fecundities data obtained were better than those obtained by Mair et al. (2004) and Charo-Karisa et al. (2007) but remained lower than those reported by De Oliveira et al. (2014) (from  $2860 \pm 811$  eggs to  $3757 \pm 970$  eggs). This performance of these populations could be linked to the weight of females since Silva and Torres (1997) reported that absolute fecundity increases with the size and weight of females. However, in our study, the females of Sohoumé, Togbadji (from Mono basin) and Gobé (from Ouémé basin) had similar mean weights to each other and similar mean weights to that of Gbassa (from Niger basin), who had significantly lower mean absolute fecundity than these populations. (Gómez-Márquez et al. 2003; Komolafe and Arawomo 2007) reported that the weight of females has a greater influence on the total number of eggs per spawn than age at maturation. However, our results showed that beyond this parameter, the diversity of origins is likely to influence the reproductive performance in a given environment. This variability could be probably explained by the age, origin of the spawners, and by the genetic traits of each population (El-Sayed, Mansour, and Ezzat 2005).

The mean fertilization rates recorded could be explained by the specific genetic traits of the populations that had the best fertilization rates due to the diversity of their origins. Indeed, it has been reported that the difference between strains and their spawning history is important factors that could contribute to the overall success of spawning in terms of eggs collection and successful incubation (Osure and Phelps 2006). The high fertilization rates of these populations could be related to the reproductive behavior of this species in general and of males in particular. The breeding competition between males would favor the dominant ones (DeWoody and Avise 2001; Fessehaye et al. 2006; Nelson 1995) since females prefer to mate with dominant males (Gonçalves-de-Freitas and Ferreira 2004). This would therefore impact the fertilization rates recorded during the breeding process. The successful

breeding behavior and fertilization of these populations could also be the result of a better adaptation to the breeding conditions prevailing in the tank.

The Nangbéto population displayed the lowest hatching rate. Since all the spawns were incubated under the same conditions and given the hatching rates of the different populations (Table 3), we can conclude that these results could be linked to the origins and the quality of the obtained eggs of the different populations. A genetic analysis of the populations (Fagbémi et al. 2021) showed that the Nangbéto population, which displayed poor reproductive performances, is genetically more distinct compared to the other populations collected in the three basins in general and in the Mono basin in particular. Overall, the variability in breeding performance noticed between different populations could be explained by respective origins and the good adaptive capacity to the breeding environment (Almeida et al. 2013) of Sohoumè, Togbadji, and Gobé populations. Also, the energy content (35% proteins and 6% lipids, crude energy = 17.4 MJ/kg) of the feed distributed to the breeders could be a factor that also affected the recorded breeding performance since it was reported by El-Sayed, Mansour, and Ezzat (2003) that the energy content of the feed in a certain proportion (up to 40% protein) could improve the breeding performances of the broodstocks.

Based on other studies that have focused on the selection of reproductively successful populations, only a few studies have estimated the genetic effects on reproductive traits, and from these studies, a moderate estimate of heritability of reproductive traits has emerged (Yoshida et al. 2017). Indeed, Yoshida et al. (2017) showed through their work that the heritability estimate for breeding traits such as spawning success, multiple spawning, and egg volume were 0.14, 0.16, and 0.08, respectively, and were moderate to low. Only a reproductive trait such as spawning frequency would have a high heritability (0.53) (Yoshida et al. 2017). Taking into account the results of the studies of Gall and Neira (2004), Charo-Karisa et al. (2007); Su, Liljedahl, and Gall (1997), Yoshida et al. (2017), it appears that the phenotypes of spawning and multiple spawning were not good indicators of the genetic merit of Nile tilapia females. Moderate estimates of heritability indicate high variation due to environmental effects. However, the estimated heritability of the spawning frequency

Parameters	Gbassa	Gobé	Nangbéto	Sohoumè	Togbadji
Mean gonadosomatic index (%)	-	-	-	-	+
Mean absolute fecundity (Eggs)	-	+	-	+	+
Mean relative fecundity (Eggs/g $\stackrel{\circ}{\rightarrow}$ )	-	+	-	-	+
Number of spawns per female (Spawns/Female)	-	+	-	+	+
Rate of multi-spawning female (%)	-	+	-	+	+
Mean fertilization rate (%)	+	+	-	+	+
Mean hatching rate (%)	+	+	-	+	+

(+) indicates the significant advantage of one or more populations compared to the others for the considered parameter; (-) indicates a significant disadvantage of one or more populations compared to the others for the considered parameter.

(0.53) could make this parameter a selection criterion (Yoshida et al. 2017). Thus, in the case of our study, the rearing conditions and the variable adaptation of the different populations tested to the rearing conditions would have had a considerable effect on the variability of recorded breeding performance. However, it should be noted that the identification of groups of females with the highest number of spawns could be a practical alternative to improve the reproductive performance of females by selecting only those specimens with a higher spawning frequency (Yoshida et al. 2017). Also, for the present study, consideration of the cumulative number of eggs collected over the period of the trials could guide the choice of the best performing populations (Hamzah et al. 2014).

In light of the results obtained during our study and taking into account the parameters that displayed significant differences between the different populations (Table 3), it appears that those of Togbadji (Mono basin), Gobé (Ouémé basin) and Sohoumè (Mono basin) taken in this rank order exhibit the best breeding performances. The genetic characterization of these populations carried out as a prelude to the present study showed a genetic differentiation between the Nangbéto population and all other populations (Fagbémi et al. 2021) which could be linked to the poor reproductive performance expressed by this population. This could explain the low reproductive performance expressed by this population. These low performances would be linked to the origins and the poor adaptation of this population to the rearing conditions. Also, the low mean weight of females in the Nangbéto population could explain the low mean absolute fecundity recorded since it is recognized that absolute fecundity increases with the weight of the female. It has also been reported that zootechnical performances such as growth and breeding within the same species could vary from one strain to another depending on the geographical origin (Khater 1986; Smitherman et al. 1988; Tave et al. 1990). However, the poor performances of this population could be improved by feeding a more suitable diet to the broodstock that also takes into account the source of the lipids supplied. Previous studies have shown that the reproductive performances of the broodstock was improved by taking into account the content and origin (animal or vegetal) of the lipids provided in the feed (El-Sayed, Mansour, and Ezzat 2005; Ng and Wang 2011; Santiago and Reyes 1993).

In conclusion, we noticed a variability between the breeding performances of the different populations tested according to their origin even within the same basin. Our study indicates that the populations of Togbadji, Gobé, and Sohoumè exhibit the best breeding performances with a benefit to the population of Togbadji (Table 3). However, a good selection could be made through the selection of the best individuals from

these populations.

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#### **Disclosure statement**

The authors declare that they have no conflict of interest.

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#### Data availability statement

All data generated or used during the study appear in the submitted article.

#### **Authors contributions**

Conceptualization: Charles Mélard, Carole Rougeot, Philippe Laleye Data curation: Mohammed N. A. Fagbémi, Razzak Oloukoule, Imaculé Baglo Funding acquisition: Charles Mélard, Carole Rougeot, Philippe Laleye. Investigation: Charles Mélard, Carole Rougeot, Philippe Laleye Methodology: Charles Mélard, Carole Rougeot, Mohammed N. A. Fagbémi Software: Mohammed N. A. Fagbémi Supervision: Charles Mélard, Carole Rougeot, Philippe Laleye, Djiman Lederoun Visualization: Mohammed N. A. Fagbémi, Djiman Lederoun Writing – original draft: Mohammed N. A. Fagbémi. Writing – review and editing: Charles Mélard, Carole Rougeot, Philippe Laleye, Djiman Lederoun, Mohammed N. A. Fagbémi

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