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Article

Reproductive Performance of the Three-Spotted Tilapia, *Oreochromis andersonii*, Founder Populations

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Abstract: Sustainable aquaculture in sub-Saharan Africa depends on the reliable supply of native Tilapia fingerlings, as reliance on exotic strains threatens biodiversity through hybridization and ecological competition. This study aimed to assess the reproductive performance of three founder populations of *Oreochromis andersonii* maintained in captivity for varying durations, to inform selective breeding and fingerling production strategies. A total of 513 fish from the NARDC population (over 10 years in captivity), Super Upper Zambezi (SUZ; 5 years), and Luangwa (LUA; 8 months) were reared in sex-segregated hapas under standardised conditions and later bred in intra-population pairs in smaller breeding hapas at a 2:1 female-to-male ratio. LUA fish had the lowest final body mass and condition factor, while NARDC and SUZ were similar and significantly higher. Although the gonadosomatic index varied across groups, pairwise differences between LUA and the other populations were not statistically significant. LUA exhibited the lowest relative fecundity and hatchability but had the highest percentage of females that spawned. These findings suggest that longer domestication periods improved body mass and hatchability, supporting NARDC and SUZ as suitable sources for immediate fingerling production. However, LUA's higher spawning participation highlights its potential role in maintaining reproductive traits and genetic diversity within selective breeding programs.

Keywords: Reproductive performance; Fecundity; Selective breeding; domestication; fecundity; Tilapia

Key Contribution: This study highlights the critical role of domestication time in shaping growth performance and reproductive success in *Oreochromis andersonii* broodstock. Newly introduced wild populations showed reduced body mass and hatchability but unexpectedly higher spawning participation, underscoring the complex trade-offs in early aquaculture adaptation.

1. Introduction

Globally, aquaculture is recognised as the fastest-growing industry, and Zambia has followed a similar trajectory. Over the past decade, the country has tripled its production, becoming the fifth-largest aquaculture producer by volume in Africa [**1**]. This growth is attributed to various

government and international agency interventions. Notably, in 2017, the government launched the Zambia Aquaculture Enterprise Development Project (ZAEDP) in partnership with the African Development Bank (AFDB), investing approximately 50 million USD [2].

A key objective of the project was to make fish farming profitable and sustainable nationwide by funding initiatives across the aquaculture value chain. It also aimed to reduce reliance on the exotic Nile tilapia (*Oreochromis niloticus*), which accounts for over 60% of Zambia's commercial aquaculture [3]. Most farms are in Southern Zambia, where its culture is legally permitted under the *Fisheries Act No. 22 of 2011* [4]. However, in other regions where the exotic species is prohibited (Eastern, Western, and Northern Zambia), farmers have resorted to illegally translocating or importing Nile tilapia, driven by a shortage of quality native fingerlings and the superior performance of the exotic species [5,6]. This illegal trade raises sustainability concerns, including the risk of Tilapia Lake Virus [7], and threatens native tilapia conservation through gene pool erosion mediated by hybridisation and ecological competition [8].

To address these challenges, the ZAEDP project launched a genetic improvement program (GIP) for the indigenous *Oreochromis andersonii*, receiving technical support from WorldFish, an organisation with decades of experience in developing genetically improved farmed tilapia (GIFT). The program, which ran from 2020 to 2023, aimed to develop a more resilient and productive strain of native tilapia. Following its completion, efforts continued under a new African Development Bank (AFDB) regional initiative, the Programme for Improving Fisheries Governance and Blue Economy Trade Corridors in the SADC Region (PROFISHBLUE), implemented by the Southern African Development Community (SADC) Secretariat. Similar initiatives are ongoing, with the shared goal of providing high-quality indigenous fingerlings to farmers. For example, the Zambia Aquaculture Program (ZAP), funded by the European Union, includes a genetic improvement component focusing on *Oreochromis macrochir*, another native tilapia species found in Zambia's northern and central regions [9].

These collective efforts have significantly contributed to the rapid expansion of Zambia's aquaculture industry, positioning it as one of the fastest-growing sectors in Africa. In 2022, Zambia was the second-highest contributor to the 2.2% increase in African aquaculture, following Ghana, with Tanzania and Rwanda in third and fourth place, respectively [10]. However, to sustain this growth, further research is needed on native tilapia species, particularly on their reproductive performance.

A comprehensive understanding of reproductive performance is vital for maintaining a steady supply of high-quality fingerlings in sufficient quantities that meet market demand. In addition, assessing the reproductive traits of founder stocks for selective breeding programs is important in order to understand the reproductive strengths and weaknesses of each population being used. High fertility, proper spawning behaviour, and strong fry survival rates are essential traits in the founder stock. In this study, we evaluated the reproductive performance of three *Oreochromis andersonii* founder populations, a species considered the most suitable native tilapia for aquaculture in Zambia, as cited in Basiita *et al*. [5]. We hypothesised that differences in reproductive performance among the three populations would primarily be influenced by domestication time, whereas similarities would be as a result of uniform conditioning and management.

2. Materials and Methods

Three previously hydrogeographically isolated populations were used in this study: the National Aquaculture Research Development Centre (NARDC), which had been maintained at the station for over ten years; the Super Upper Zambezi (SUZ) population, collected from the wild and held at the research station for five years; and the Luangwa (LUA) population, collected from the wild eight months before the study began. The LUA and SUZ populations were approximately 1,080 kilometres apart, with the NARDC population located midway (Fig. 1).
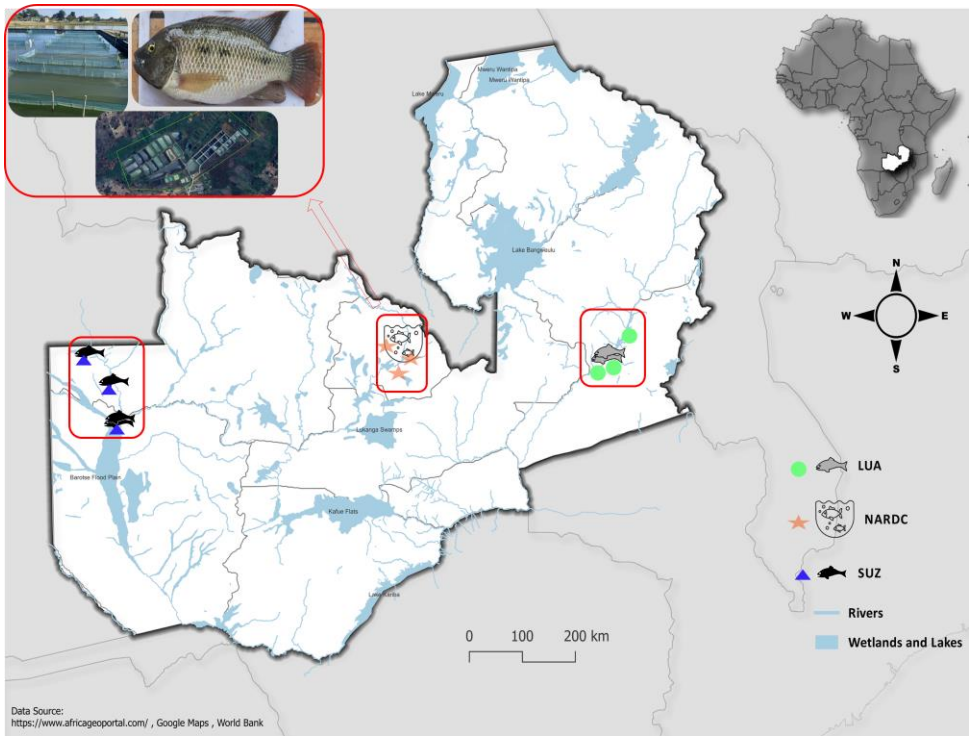
Figure 1. Map showing population origin geographic location: Zambia.

2.1. Experimental Design

A total of 513 fish (322 females and 191 males) were used in this study. Prior to conditioning, fish had an initial body mass ranging from 80-100 grams and were approximately three months old, except for the LUA population, whose exact age was unknown. LUA individuals were collected as immature fish and were unlikely to have previously spawned in the wild. The fish were tagged with passive integrated transponders (PIT), which assigned each fish a unique alphanumeric code. This was done to maintain track of individual broodstock in each population. Following tagging, the fish were placed in six hapas measuring 4m x 25m x 1.5m (width, length, and depth) based on population and sex.

2.2. Broodstock Nutrition and Management

All hapas were placed in one pond measuring 25 m x 40 m. To ensure the broodstock received a nutritionally complete diet, proximate analysis was conducted on the commercial feed to verify the manufacturer's declared nutritional composition. Proximate analyses were carried out at the Zambia Bureau of Standards (ZABS) laboratory, following the methods of the Association of Official Analytical Chemists (AOAC, 1990) [11] for parameters shown in Table 1. Based on the results, most nutrient levels were comparable and within the optimal ranges for tilapia broodstock [12,13], except for crude fat, where our lab analysis found a lower amount compared to literature recommendations for optimum tilapia broodstock diets [12]. To address this deficiency, squid oil was sprayed onto the feed pellets before feeding to raise the fat content. Squid oil has been shown to enhance reproductive performance and spawning success in various fish species, including tilapias [14,15,16].

Table 1. Commercial broodstock feed proximate analysis.

Nutrient	Manufacturer's Claim	Lab Analysis (Actual)
Crude Protein [%]	42	45 ± 0.001
Crude Fat [%]	12	8.61 ± 0.57
Carbohydrates [%]	Not provided	36 ± 0.03
Fiber [%]	3.0	3.49 ± 0.06
Ash (%)	6.8	7.79 ± 0.16
Moisture [%]	Not provided	8.61 ± 0.57

| Energy [kJ/g] | 2000 | 2062.71 ± 1.88 |

[1] Values are expressed as means ± standard deviation (SD). Gross energy is reported in kilojoules per gram (kJ/g). All analyses were conducted in triplicate and values are presented as mean ± standard deviation.

2.3. Water Quality Parameters

Water quality measurements were taken twice daily at 7 a.m. and 2 p.m. using an 86031 Multiple Parameters Water Tester (AZ Instrument Corp, Taichung, Taiwan). To ensure that the values were consistently within acceptable ranges for *Oreochromis andersonii* broodstock [17]. If any deviations were observed, appropriate mitigation measures were immediately implemented, such as aeration and introducing fresh water into the ponds. The mean water quality values over six months are presented in Table 2.

Table 2. Commercial broodstock feed proximate analysis.

Parameters	Mean value ± SD
Temperature [°C]	Temperature [°C]
Dissolved oxygen [mg/L]	Dissolved oxygen [mg/L]
pH	pH
Conductivity [μS/cm]	Conductivity [μS/cm]
Salinity [ppt]	Salinity [ppt]

[2] Values are presented as mean ± standard deviation.

2.4. Pairing for Breeding, Condition Factor and Batch Fecundity Estimation

After six months of broodstock conditioning, the fish were evaluated for spawning readiness. The mature fish were weighed (Wt), and their total length (L) was measured to calculate the condition factor (K) using the formula $K = 100 \times Wt/L^3$ [18].

The average body mass of broodstock selected for mating was 158.67 ± 0.096 g for females and 125.02 ± 0.067 g for males (Mean ± SD). Only females weighing more than 150g were used, as this threshold is considered optimal for reproductive performance in tilapia broodstock [19]. Females were paired with males of similar body mass at a 2:1 female-to-male ratio. The mating pairs were stocked in hapas measuring 2 m × 1 m × 1 m (width × length × depth). 40 pairs were set for LUA, 44 pairs for NARDC and 47 pairs for SUZ. The number of pairs set per population and the sex ratio were based on the number of mature fish per population at the time of pairing.

additionally, 40 fish per population were killed with an overdose of clove powder suspension, then the gonads were excised and weighed using an analytical balance (Mettler Toledo, Giessen, Germany) to calculate the gonadal somatic index (GSI), using the equation $GSI = (gonad\ weight/total\ body\ weight) * 100$ [20]. The ovaries were then placed in 10% formalin for preservation to later determine the batch fecundity by counting the number of hydrated oocytes as described by Hunter *et al.* [21].

2.5. Relative Fecundity, Percentage of Spawned Females, and Hatching Efficiency

Following pairing, females were inspected weekly for eggs over eight weeks. Eggs were gently removed by carefully opening the mouths of brooding females over a bowl. The eggs were then cleaned with a 10 ppt sodium chloride solution and counted. The egg counts were used to estimate the relative fecundity (number of eggs per gram of female). Additionally, the number of females that spawned was recorded to calculate the percentage of spawned females (*%SF*) using the equation *%SF = (total number of spawned females / total paired females) × 100*. During incubation, hatchery conditions were similar for all the populations. Eggs in the jars were regularly monitored, with dead eggs removed and their numbers recorded. At the end of the incubation period, the total number of hatched eggs was recorded to calculate the hatchability percentage(*H*) using the equation *H = (total hatched eggs / hatched + unhatched + dead eggs) × 100*.

2.6. Statistical Analysis

Statistical analyses were conducted using SPSS (version 23). Data normality was assessed with the Shapiro-Wilk test, and homogeneity of variance using Levene's test. All data (Body mass, Total Length, Condition Factor, Gonadal Somatic Index, Relative Fecundity, and Batch Fecundity) did not meet the assumption of normality; therefore, *Kruskal-Wallis* was used to test for statistical differences. *Dunn's* pairwise comparison with Bonferroni correction was performed for significant *Kruskal-Wallis* results to determine which mean was different. Visualisations were generated using the R package *ggplot2*. The *ggpubr* and *ggsignif* packages were used to annotate statistical significance and visualise pairwise comparisons on the box plots. Results were considered significant at *P ≤ 0.05.*

3. Results

3.1. Body Mass and Total Length of the Broodstock Before Pairing

The body mass and total length of broodstock from each population were measured after six months of conditioning and are presented in Table 3. The results showed that LUA had 40% significantly lower final body mass than NARDC and SUZ, whilst the total length did not differ significantly across populations.

Table 3. Commercial broodstock feed proximate analysis.

Parameter	LUA	NARDC	SUZ
Body mass [g]	182.400 ± 15.93a	341.250 ± 16.13b	334.000 ± 20.37b
Total Length [cm]	25.233 ± 0.4807a	27.347 ± 0.5189a	27.363 ± 0.93a

[3] Table 3 presents the mean final body mass (g) and the total length (cm) of Oreochromis andersonii broodstock from three populations (LUA, NARDC, and SUZ). with sample sizes of n = 40 for each population. Different superscript letters indicate significant difference (p ≤ 0.05). Values are presented as mean ± standard deviation.

3.2. Condition Factor and Gonadal Somatic Index of Broodstock Before Pairing

The Condition Factor was calculated to determine the physiological status or degree of nourishment of the broodstock after the six-month conditioning period, as well as the gonadal somatic index (GSI) to gauge the broodstock's maturity and spawning readiness, presented in Figure 2. The *Kruskal-Wallis* test detected significant differences (*P ≤ 0.05*) in Condition Factor between the populations. The LUA population was significantly lower compared to NARDC and SUZ, whilst NARDC and SUZ were not statistically significant (Fig. 2a). Similarly, GSI was also significant (*P=0.03*); however, further, *Dunn* post hoc pairwise comparison showed that LUA was not statistically different from NARDC and SUZ (Fig. 2b).
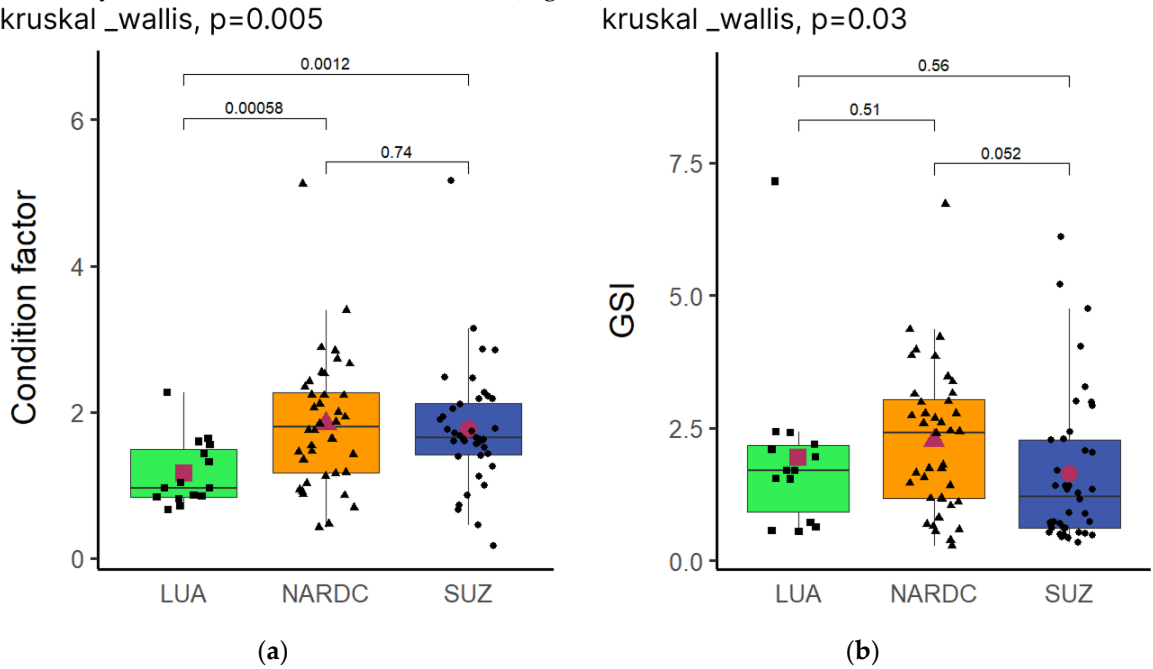

(a)   (b)

Figure 2. Condition factor (a) and gonadosomatic index (GSI) (b) of *Oreochromis andersonii* broodstock from three populations (LUA, NARDC, and SUZ) after 6 months of conditioning. Sample sizes were n = 15 (LUA), 40 (NARDC), and 40 (SUZ). Brackets indicate pairwise comparisons between groups, with corresponding p-values shown above the brackets. The maroon-colored points in the middle of the boxplots represent the Mean.

3.3. Relative and Batch Fecundity

The *Kruskal-Wallis H* test showed significant differences in the relative fecundity of the three populations. Further, *Dunn post hoc* pairwis*e* comparison showed that LUA significantly differed from the NARDC and SUZ populations, whilst the NARDC and SUZ populations were not statistically different (Fig. 3a). Interestingly, there was no significant difference in the batch fecundity of the three populations (Fig. 3b).
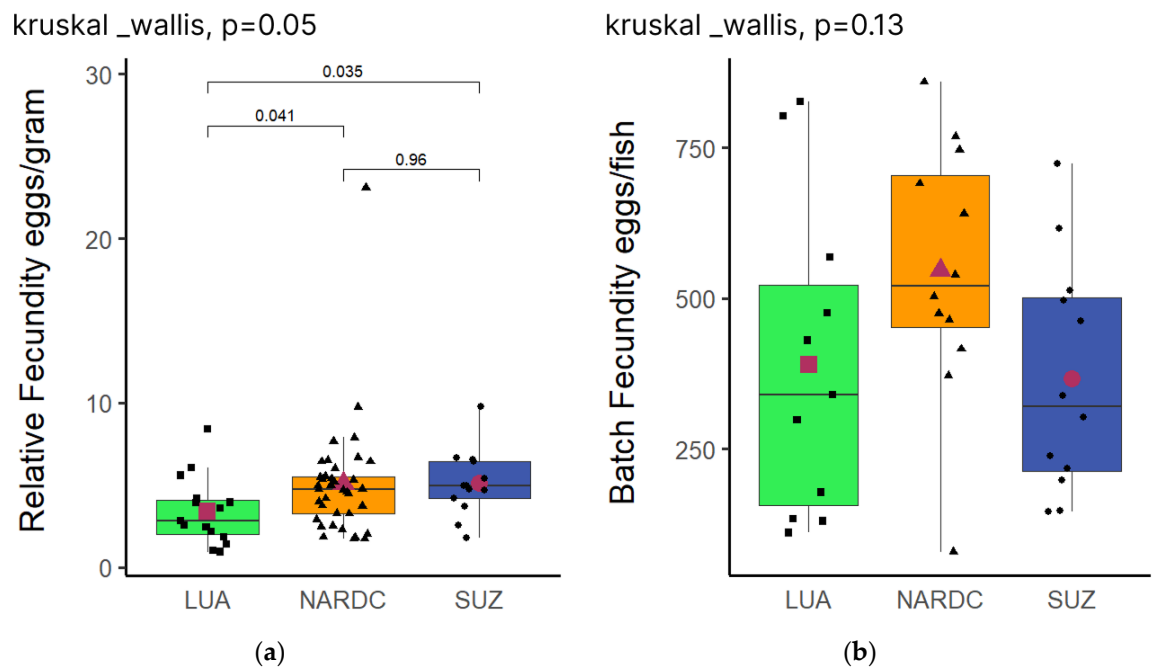

(**a**)   (**b**)

Figure 3. Relative fecundity (RF) (a) and batch fecundity (BF) (b) of *Oreochromis andersonii* broodstock from three populations (LUA, NARDC, and SUZ) after 6 months of conditioning. Sample sizes for RF were n = 15 (LUA), 37 (NARDC), and 13 (SUZ), and for BF were n = 11 (LUA), 12 (NARDC), and 12 (SUZ). Brackets indicate pairwise comparisons between groups, with corresponding p-values shown above the bracket. The maroon-colored points in the middle of the boxplots represent the Mean.

3.4. Percentage of Spawned Females and Egg Hatchability

The percentage of *Oreochromis andersonii* broodstock that spawned from the total number of pairs set per population was calculated. The results showed that the LUA population had the highest rate of spawning females (Fig. 4a). In addition, the hatchability of the spawned eggs was also analysed. Conversely, the LUA population had the lowest hatchability percentage, while SUZ was highest, followed by NARDC (Fig. 4b).
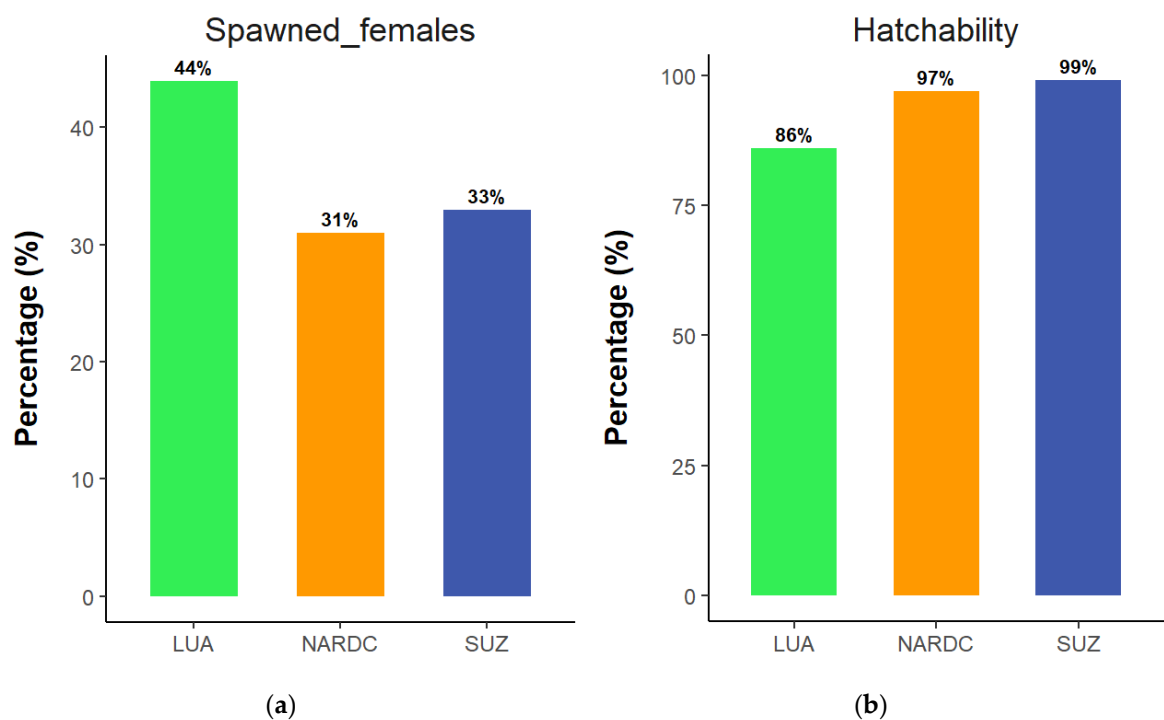
Figure 4. Percentage of spawned females (a) and hatchability (b) of *Oreochromis andersonii* broodstock from three populations (LUA, NARDC, and SUZ) after 6 months of conditioning. Sample sizes were *n* = 15 (LUA), 40 (NARDC), and 40 (SUZ).

4. Discussion

Several factors have been reported to influence tilapia's reproductive performance, with environmental conditions such as temperature, photoperiod, water quality, and nutrition being significant [22,13]. In this study, these conditions were similar across three populations of *Oreochromis andersonii* (LUA, NARDC, SUZ), and broodstock received a nutritionally complete diet. This ensures that any observed differences in reproductive performance among the populations can be attributed to domestication time, population origin, or genetic differences, while the lack of differences would be associated with uniform later-life conditioning. This study provides critical insights into the reproductive performance of *Oreochromis andersonii* in real aquaculture settings.

4.1. Pre-Spawning Condition of Broodstock

There were notable differences in the broodstock's body mass after six months of conditioning among the populations (Table 3). The LUA population exhibited the lowest final body mass, being 40% lower in comparison to both NARDC and SUZ. We anticipated that the LUA population would attain a comparable final body mass to that of the other populations, given that their initial body mass before conditioning was within a similar range. Furthermore, if the LUA population had been pre-stunted before their inclusion in this study, due to factors such as limited food availability, predation, and competition in the wild, it was still expected that they would achieve final body mass similar to NARDC and SUZ through the process of compensatory growth. Compensatory growth is defined as a phenomenon where previously deprived fish, upon receiving an ample supply of high-quality feed, demonstrate exponential growth to attain their respective age-weight [**23**]. The lack of compensatory growth in the LUA population may be attributed to their shorter duration of domestication, which implies that they were still in the process of acclimatising to the aquaculture environment. In contrast, NARDC and SUZ had already been acclimatised to the aquaculture environment for over 10 and 5 generations, respectively. The LUA population was introduced to aquaculture only 8 months before the study; therefore, the first generation in the aquaculture environment. Acclimatisation to aquaculture involves confinement, adaptation to formulated feeds, and adjustment to human husbandry practices [**24**]. All these elements can significantly affect the feeding efficiency of newly

introduced fish, in turn impacting their weight gain and ultimately their condition factor (K), which serves as a quantitative measure for evaluating the relative level of nourishment [25]. Notably, the LUA population also displayed the lowest condition factor (*K = 1.2*) in comparison to NARDC and SUZ (*both K ~1.8*) (Fig. 2a). These results show that domestication time has a clear impact on the condition factor and consequently the body mass gain of *Oreochromis andersonii*. In the present study, the population with the longest domestication time (NARDC) had the best condition factor and achieved the greatest final body mass.

The *Kruskal-Wallis* test revealed significant differences in the gonadal somatic index (GSI) among the three populations. However, post hoc *Dunn* pairwise comparisons showed no significant differences between LUA versus NARDC or SUZ (Fig. 2b). The gonadosomatic index (GSI) reflects the proportion of energy allocated to gonadal development relative to somatic growth, serving as an indicator of reproductive investment [26]. GSI is a valuable measure for comparing reproductive maturity, as it accounts for body size differences by expressing gonad weight relative to an individual's total body weight. This result indicates that the LUA population invested energy in reproduction as efficiently as the NARDC and SUZ populations, despite being new to the aquaculture environment and likely disadvantaged during the early conditioning periods due to possible acclimation adjustments.

4.2. Relative and Batch Fecundity

Our results revealed borderline significant differences in the relative fecundity of the three populations (*P = 0.05*). *Dunn* pairwise comparison showed that LUA had significantly lower relative fecundity (*P ≤ 0.05*) than NARDC and SUZ (Fig. 3a). These findings align with Mohamed *et al*. [27], who similarly reported reduced relative fecundity in *Oreochromis mossambicus* with decreasing broodstock size. In our study, LUA broodstock were approximately 40% smaller than those of NARDC and SUZ (Table 3). However, our results are contrary to those of Elsherbeny [28], who found higher relative fecundity in smaller *Oreochromis niloticus* broodstock. This discrepancy may be explained by domestication history: unlike our study, Elsherbeny [28] examined fish from a single, equally domesticated population, all similarly acclimatised to aquaculture conditions. In our study, the LUA population may have needed time earlier on to acclimate to aquaculture conditions, hence the observed lower relative fecundity. The NARDC and SUZ populations that were acclimated to the aquaculture environment exhibited no significant difference (*p = 0.96*) in their relative fecundity.

No significant differences were observed in the batch fecundity among the populations (Fig. 3b). Previous studies suggest that batch fecundity is influenced primarily by geographic and environmental factors [29,30]. In this study, all populations experienced similar conditions and underwent a six-month conditioning period, likely neutralising pre-existing differences between populations. Schofield *et al.* [31] similarly reported no significant differences in batch fecundity in *Oreochromis niloticus* across different salinity treatments. While their study focused on environmental stress, their results suggest that batch fecundity may be a relatively stable trait. Therefore, it is conceivable that in the present study, where conditions were kept uniform, with only population origin and domestication time as variables, batch fecundity would also not be significantly different across populations.

4.3. Percentage of Spawned Females and Hatchability

Regarding the percentage of spawned females, the results indicated that the LUA population had the highest percentage of spawned females (Fig. 4a). These findings could be attributed to two factors. Firstly, broodstock sizes. Previous studies have shown that larger females have a slightly reduced ability to spawn [32]. The NARDC and SUZ populations were 40% larger compared to LUA. Secondly, the longer use of these two populations (NARDC and SUZ) at the aquaculture station could have resulted in reduced reproductive performance over time. In long-term hatchery stocks, this can occur unintentionally. Typically, fish that perform well are selected as broodstock for the next generation, often based on traits such as growth and survival. However, some studies have reported that these traits may be negatively correlated with reproductive success in species like tilapia and rainbow trout [32,33]. Furthermore, several factors can influence the participation of tilapia females

in spawning, including temperature, photoperiod, nutrition, and management [**34,35**]**.** In the present study, these factors were similar across the populations, which may indicate that the observed differences in spawning participation could be a result of domestication time. In this case, domestication time is inversely related to spawning participation, implying that newly introduced fish in aquaculture from the wild may spawn more readily compared to long-term hatchery populations. This is possibly linked to the reproductive strategy of fishes, including tilapia, to synchronise spawning with periods of food abundance to maximise offspring survival [**36**]. Given that the LUA population had been recently introduced to aquaculture, the sudden increase in the availability of feed may have functioned as a cue to prioritise spawning. This strategy may be more active in newly captive fishes than in long-term hatchery populations that have been captive for several generations and are already accustomed to abundance and continuous feeding in aquaculture systems.

The SUZ population had the highest hatchability rate (99%). In comparison, the LUA population had the lowest (86%) (Fig. 4b). These findings align with Osure & Phelps [**37**], who reported that recently introduced Nile tilapia populations to aquaculture environments had lower hatch rates and survival to the swim-up stage compared to strains that had been domesticated for 20-30 years. These results highlight the influence of domestication on hatchability and fry survival, with longer domestication periods generally leading to improved offspring hatchability due to better adaptation to aquaculture conditions [**37**]. The eggs from the LUA population represented the first generation (F1) in the aquaculture environment. Unlike the SUZ and NARDC populations, which had been reared in aquaculture for multiple generations, F1 fish undergo significant phenotypic changes and face natural selection pressures as they adapt to new conditions [**38**]. These phenotypic changes can increase vulnerability to environmental stressors, often leading to higher mortality rates and lower hatchability [**39**].

4.4. Fingerling Supply and Selective Breeding Programs

The local aquaculture industry faces the pressing challenge of an insufficient supply of native *Oreochromis andersonii* fingerlings. The findings of this study offer two practical solutions to address this issue. Firstly, in the short term, fingerling supply can be improved by leveraging the higher fecundity, better condition factor, and superior weight gain performance observed in the SUZ and NARDC populations. These two populations can be utilised and crossbred to provide a reliable and enhanced supply of fingerlings to farmers in Zambia.

Secondly, for a long-term solution, the results present promising opportunities for improving fingerling quality through selective breeding. Each of the three studied populations exhibited distinct strengths that can be harnessed. Selectively breeding these populations could lead to developing a superior strain that combines these desirable traits. Moreover, the observed differences in reproductive performance among the populations suggest underlying genetic variation [**40**], further supporting their potential in selective breeding programs. However, this study also highlights important trade-offs that hatcheries and selective breeding programs must consider. While introducing wild stock into breeding programs is essential to enhance and maintain genetic diversity in the long term [**41,42**], it may lead to reduced short-term production efficiency. As observed in the present study, wild populations may exhibit lower performance compared to long-term aquaculture populations before they acclimatise to the aquaculture environment. Therefore, careful planning is required to balance the immediate demands of fingerling production with the long-term goals of genetic sustainability.

5. Conclusions

Our results support the hypothesis that domestication time significantly influences differences in reproductive traits among *Oreochromis andersonii* populations, as reflected by differences in body mass, hatchability, and female participation in spawning despite similar management. In contrast, the relative similarity observed in gonadal somatic index and fecundity across populations suggests that uniform later-life conditioning may mitigate domestication effects, population origin or underlying genetic differences in these traits. Our results offer promising solutions for addressing

the immediate demand for high-quality native tilapia fingerlings. The NARDC and SUZ populations demonstrated superior fecundity and hatchability, making them well-suited for use to meet the immediate local industry's fingerling demand. However, the LUA population, more recently from the wild, exhibited higher spawning efficiency, presenting an opportunity to enhance genetic diversity in long-term breeding programs.

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