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Research Article

Effect of Crossbreeding on Fecundity, Growth Performance, and Heterosis of Black Tilapia, Red Tilapia, and Mozambique Tilapia Reared in Earthen Ponds in West Java, Indonesia

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Abstract

Increased tilapia production is challenged by genetic decline. Hybridization efforts for performance improvement through a selection of the best parent and strain pairs are a promising option. The objective of this study was to evaluate the crossing of black tilapia, red tilapia, and Mozambique tilapia against the performance of fecundity, growth, and survival and estimate the value of heterosis. The experimental design used a completely randomized design with 3 replications while the treatments were different tilapia strains. The rearing activities were carried out in earthen ponds for 150 days with a stocking density of 10 fish/m2. The parameters observed included egg fecundity, growth, survival, and the value of heterosis. The results showed that the fecundity and growth values of crossbred black tilapia were significantly higher than others ($p<0.05$). The highest survival rate was shown by crossing pure strains of red tilapia. The hybrid of Mozambique tilapia and black tilapia (♀ MJ x ♂ NW) showed the highest mid-parent heterosis value on growth characters but produced negative heterosis on characters, fecundity, biomass, and survival. Overall, the crossbred of black tilapia (♀BS x ♂ NW) performed better than the inbred strains, with positive mid-parent heterosis in all characters measured. These results indicate that crossbreeding has the potential to be used as a candidate for cultivation and performance improvement through selection, although there were depressions, and the superiority of the crosses was not prominent.

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1. Introduction

Nila tilapia (*Oreochromis niloticus*) is a species that grows and reproduces quickly and is tolerant of various environmental conditions, making tilapia one of the fish species with the highest increase in production volume (El-Sayed, 2020a). Tilapia is a freshwater fishery commodity that has economic value (Subekti *et al.,* 2016). Tilapia production is predominantly driven by Asia, with Indonesia being the second-largest producer globally, after China, contributing 1,356,654 tons in 2022, including 262,917 tons from West Java (MMAF, 2022). These figures reflect Indonesia's increasing focus on tilapia farming, despite challenges such as market fluctuations and environmental sustainability concerns. While *O. niloticus* is economically significant, other species such as *O. aureus, O. spilurus, and O. mossambicus* are also cultivated globally. This diversification is partly due to the environmental challenges posed by large-scale O. niloticus farming, which has raised sustainability concerns (Yamasaki *et al*., 2022).

According to Gjedrem and Baranski (2009), and Todesco *et al.* (2016), and Lu *et al.* (2022) the improvement of cultivation characteristics can be achieved through hybridization methods, particularly diallel crossing, to form a synthetic base population with diverse genetics for breeding programs. Long-distance hybridization has different subgenomes and produces more genetic variation in the offspring, supplying more germplasm to cultivate new varieties (Liu, 2010; Zhong *et al*., 2019; Bartie *et al*., 2020; Liang *et al*., 2023), while hybridization of two closely related species can be a useful method to improve the viability of triploid hybrids (Jiang *et al*., 2022). While hybridization can improve genetic diversity and offer benefits such as better growth rates and stress tolerance, it is important to consider potential risks, including genetic erosion, environmental disruptions, and ethical concerns related to genetically modified organisms (GMOs) (Radona *et al*., 2016; Jiang *et al*., 2021; Xiao *et al*., 2022).

Some previous research reports related to diallel crossing in tilapia include reciprocal crosses of four populations of tilapia (O.niloticus) increasing genetic variation and producing higher growth and fillets than their parents (Neira *et al*., 2016). Similarly, reports on three tilapia strains showed high growth performance (Workakegn, 2019). According to Mbiru and Mchele (2015) and Mtaki *et al.* (2022), hybridization of *O. niloticus* and *O. urolepis* hornorum increased growth and produced male offspring. Zhou *et al.* (2019); and Robisalmi *et al.* (2020) reported that crossing black tilapia (*O. niloticus*, ♀) with blue tilapia (*O. aureus*, ♂) showed growth performance compared to its parents and produced 85% male offspring (Zak *et al*., 2014). Then, in red tilapia, hybridisation between red tilapia strains produced pure red color without black spots and increased male sex ratio (Lu *et al*., 2022). Sarker *et al.* (2023) reported that crosses between female tilapia (*O. niloticus*) and male (*O. mossambicus*) showed lower growth in freshwater ponds than in their reciprocals.

The phenotypic appearance expressed in the offspring is known as the phenomenon of hybrid vigor where the measurement result is called heterosis, which is also due to non-additive genetic effects. However, the value of heterosis is uncertain, depending on the parents, if the parents are not related to the cross, the offspring tend to display better performance (Falconer and Mackay, 1996; Hallauer *et al*., 2010; Zhong *et al*., 2019). The selection of strains used as parents in a cross can also play a role in determining heterosis, by improving the performance of the strains and thus increasing the specific capacity of the hybrids (Wang *et al*., 2006). In addition, the environment has the potential to alter genetic expression and exert influence on additive and nonadditive genetic components (Crespel *et al*., 2012). The results of studies of by Thoa *et al.* (2016) that employed diallel crossing on four strains of tilapia (*O. niloticus*) showed no heterosis effect. A similar report on diallel crossing in red tilapia found no difference in performance with the elders and resulted in low heterosis (Pongthana *et al,* 2010). Similarly, backcrossing activities on Red-Stirling and Chitralada red tilapia strains produced better growth and color but low heterosis values (Lago *et al*., 2017).

Bradbeer *et al.* (2019) stated that the basic processes governing the various stages of hybridization between Oreochromis strains and species remain unclear. This is because hybridization can have the adverse effect of contaminating genes within populations of native species. This process has the potential to genetically damage or integrate the original genetic constitution so that no native species is truly ‘pure’ (Huxel, 1999). In addition, with the genotype and environment (GxE) interaction, strains that have been genetically modified through selective breeding in favorable environments may not be as effective in less favorable environments (Khaw *et al.,* 2016; Omasaki *et al.,* 2016). The development and cultivation of hybridized fish has faced the problem of increasing mortality rates caused by disease and decreased growth rates and there has been a decline in production (Koolboon *et al*., 2014).

In West Java, research on genetic improvement of black tilapia through hybridization has been conducted and the results show that hybridization can improve growth. However, in its development, broodstock mismanagement caused a decline in growth and reproductive performance of tilapia. The cause of this situation is the use of unqualified broodstock, both in terms of quality and quantity during spawning so the possibility of inbreeding is high (Nugroho *et al.,* 2014; Rasidi *et al.,* 2015). In addition to black tilapia, other tilapia strains have been widely cultivated and have a very good reputation and track record among freshwater fish farmers, including red tilapia and Mozambique tilapia, but there is little research information on breeding programs through hybridization. To meet the program to increase national tilapia production, superior parents are needed in reproductive characteristics and quality tilapia seeds with high growth. Therefore, it is necessary to conduct improvement research by crossbreeding several tilapia strains and selecting the best parent and strain pairs.

This study aimed to evaluate the effect of crossbreeding of black tilapia (*O.niloticus*), red tilapia (*Oreochromis* spp.) and Mozambique tilapia (*O. mossambicus*) on fecundity, growth performance and heterosis. In addition, heterosis is estimated based on the average parent value (mid-parent heterosis) and one of the parents with the best value (high-parent heterosis).

2. Materials and Methods

2.1 Materials

This study was conducted at the Research Institute for Fish Breeding for seven months. The parents used were superior tilapia strains from several districts in West Java, namely black tilapia strain BEST from Bogor district, black tilapia Nirwana from Purwakarta district, red tilapia NIFI (National Inland Fisheries Institute) from Subang district, and Mozambique tilapia from Indramayu district. The four tilapias were crossed to produce 16 crosses consisting of four pure strain crosses and 11 hybrid crosses, but in this study, only four pure strain crosses and seven hybrid population crosses were successfully spawned. The test fingerlings used were the result of 60 days of rearing with a length of 5-6 cm and a weight of 3-5g. Body weight sampling tool using scales with Ohaus CL2000, USA 2019. The number of fry used for each crossing population was 750 fish (3 replicates), with a total of 8250 fish. The crossing scheme of tilapia is presented in Table 1.

2.1.1 Ethical approval

This study does not require ethical approval because it does not use experimental animals.

2.2 Methods

2.2.1 Spawning and rearing larvae

Spawning was carried out naturally in concrete ponds measuring 5 x5 x1 m^3 with a ratio of male and female broodstocks of 1: 3 (10 male and 30 female), each cross referring to Robisalmi *et al.* (2020). Egg harvesting activities were carried out on day 10, and hatched for five days in incubation tanks. Larval rearing was carried out for 60 days using a 2x2x1.5 m^3 happa placed in an earthen pond with stocking density between homogeneous populations of 500 fish/happa. Feeding was done ad libitum with a frequency of three times a day (08.00 am; 00.30 pm; and 04.30 pm). Water quality parameters such as dissolved oxygen 4.1-4.9 mgL^{-1}, temperature 28.6-29.1ºC, pH 7.59-7.81 and ammonia 0.05-0.2 mgL^{-1} were uniform. The rearing was done in the same earthen pond for all treatments (El-Sayed, 2020b).

Table 1. Diallel crossing scheme (punnet diagram) of four tilapia strains.

♀ ♂	BEST (BS)	Nirwana (NW)	Red NIFI (RN)	Mozambique (MJ)
BEST (BS)	**BS x BS**	BS x NW	BS x RN	-
Nirwana (NW)	NW x BS	**NW x NW**	NW x RN	NW x MJ
Red NIFI (RN)	RN x BS	RN x NW	**RN x RN**	-
Mozambique (MJ)	-	MJ x NW	-	**MJ x MJ**

2.2.2 Grow out

The grow-out activities of 11 crossbred tilapia populations were carried out in an earthen pond that was blocked by a net measuring 5x5 m^2 with a water depth of 0.8 -1m. The method used was experimental with a completely randomised design (CRD) consisting of 11 treatments (crossbred tilapia populations) with three replications. The stocking density of fish per treatment replicate was the same at 250 fish. Fish rearing was carried out for 150 days with commercial feed with 30-32% protein as much as 5% of biomass. The frequency of feeding was done at 08.00 am and 04.00 pm (two times a day).

2.3 Data Collected

Growth sampling activities on length and weight characters were carried out every 30 days during the 150-day rearing period. At the end of the rearing period, the fish were harvested, and the parameters of growth, survival, and fish biomass were measured. Parameters observed were egg fecundity, absolute growth, growth rate, feed conversion ratio, survival, and harvest biomass. Length and width measurements were made using a crossbar, body thickness measurements using a caliper, and weight measurements using digital oh haus scales. Then, to assess the phenotypic appearance of the pups, heterosis (mid -parent and high-parent) was calculated. Valentin *et al*. (2015) determined the relative fecundity rate by dividing the total number of eggs produced by the weight of the females. The total number of eggs was calculated by adding all the eggs retrieved by each female broodstock.

2.4 Analysis Data

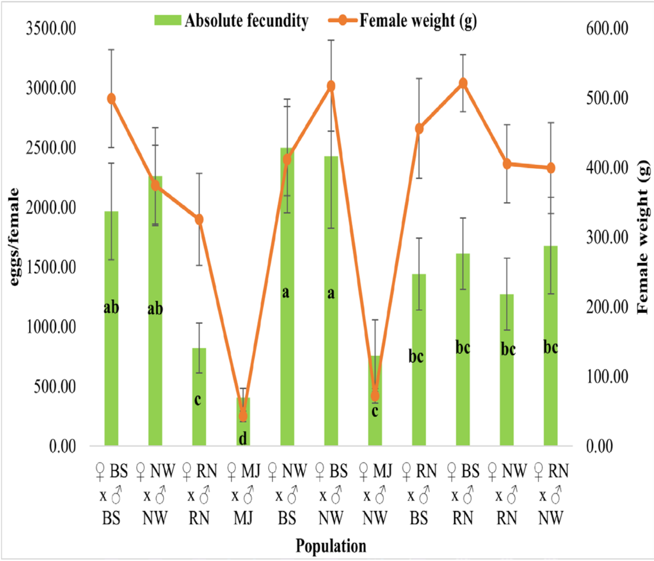
The data were initially checked for normality and variance homogeneity using the Kolmogorov-Smirnov and Levene's tests, respectively. One-way analysis of variance (ANOVA) was used to determine differences in parameters measured across treatments. Where there were significant differences between treatment means, post-hoc analysis was performed using the Duncan Multiple Range Test with IBM Statistical Package for the Social Sciences Statistics 22, and MS Excel was used to create the graphs. The calculation formulas used included, fecundity absolute and relative fecundity and were assessed using methodologies described by Coward and Bromage (2000). Absolute growth weight was calculated using the Ricker formula 1979. The weight-specific growth rate (SGR, $\%bw^{-1}$) was calculated as follows (NRC, 1983). Feed amount, biomass, and fish survival at the end of rearing were calculated based on the formula (Goddard, 1996). Hybrid performance relative to its parents can be expressed in two ways. Intermediate parental heterosis is the performance of a hybrid compared to the average performance of its parents. High parent heterosis is the comparison of hybrid performance to the performance of the best elders in the cross. Heterosis is usually expressed as a percentage and computed following Cruz and Ibarra (1997) and Fehr (1991).

3. Results and Discussion

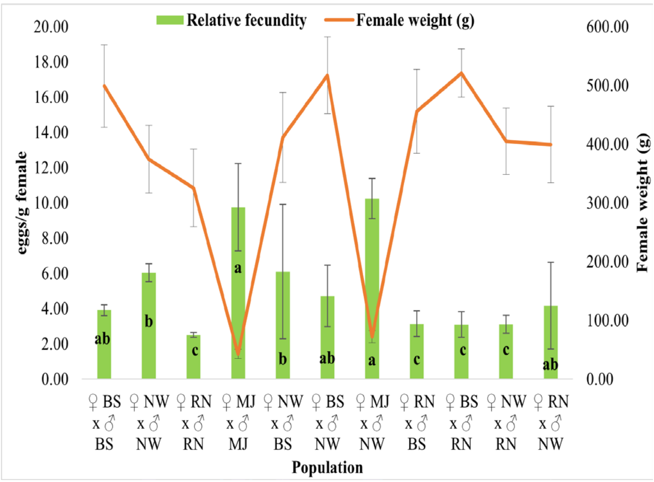
3.1 Results

3.1.1 Fecundity and growth performance

Spawning results from 11 crossbred populations of tilapia showed that fish with large parent body weights did not always produce high fecundity (Figure 1). Statistical analysis on absolute fecundity and relative fecundity parameters showed significantly different values ($P<0.05$). The highest absolute fecundity value was obtained by the hybrid population ♀NW x ♂BS (2500 grains) with a mean brood weight of 517 g followed by the crossbred ♀BS x NW♂ (2426 grains) with a body weight of 411 g; this value was significantly higher than the other populations ($P<0.05$), but not different from the other populations ($P<0.05$).0.05 nor significantly different from ♀BS x BS♂ and ♀NW x NW♂ parents ($P>0.05$). Furthermore, for relative fecundity, the highest value was shown by the hybrid population ♀MJxNW♂ (10.24 eggs/g female), which was significantly different from the other populations ($P<0.05$) but not different from the pure strain population ♀MJxMJ♂ ($P>0.05$).



(A)



(B)

Figure 1. Variations of mean absolute (a) and relative fecundity (b) of pure strain and crossbred tilapia populations.

Based on Table 2, the tilapia crossbred ♀BS x ♂NW showed the highest absolute length growth (15.90±0.37) cm and absolute weight growth (201.23±3.99g) and was statistically significantly different (P<0.05) compared to other crosses but not significantly different (P>0.05) with the pure strain population ♀NW x ♂NW (196.58±9.32 g) and crossbred RN x ♂NW (189.87±1.70 g) (P>0.05) for absolute weight growth characters. Overall, the coefficient of variation (CV) of crossbred populations of tilapia reared in earthen ponds on weight characters was greater than the CV of length characters (Table 2). The highest CV value was shown by the pure strain population ♀MJ x ♂MJ of 10.66±1.61% in length and 30.87±5.90% in weight characters, and the cross ♀MJ x ♂NW of 10.57±2.03% (length) and 36.36±5.61% (weight), statistically both crosses had CV values of length and weight that were significantly different from other crosses (P<0.05). The lowest CV value was shown by ♀NW x ♂RN cross for length characters (5.05±2.38%) and ♀RN x ♂RN pure strain cross for weight characters at 9.59±5.10%. population (37518 g), ♀BS x ♂NW cross (38461 g), ♀BS x ♂RN cross (38337 g) and ♀NW x ♂RN cross (37176 g). The biomass of the pure *O. mossambicus* cross was consistently the lowest at 3822 g. In line with the biomass, similar results were shown by the ♀RN x ♂RN pure strain crossbred which had the highest feed intake value of 2.24±0.32 g Fish d^{-1-1}, although not significantly different from the ♀BS x ♂BS, ♀BS x ♂NW ♀BS x ♂RN ♀NW x ♂RN populations, the lowest was shown by the pure strain ♀MJ x ♂MJ population at 11916.37g. Biomass and feed intake values are comparable to other parameters, namely Condition Factor (CF), wich is one of the growth indicators that describe the resilience and welfare of fish during maintenance in groundwater ponds. The highest CF value was produced in the cross of pure strain of black tilapia Nirwana (2.12±0.06) and red tilapia (2.10±0.03), but this value was not significantly different (P>0.05) with the cross of pure strain ♀BS x ♂BS, cross of ♀NW x ♂BS and ♀BS x ♂NW. The lowest CF value was shown by the pure tilapia population of 1.64 ± 0.11.

Table 2. Mean length, weight, absolute growth, and coefficient of variation of 11 crossbred populations of tilapia reared for 150 days in earthen ponds.

Population	Parameter							
	Initial Length (cm)	Initial Weight (g)	Final Length (cm)	Final Weight (g)	Length Gain (cm)	Weight Gain (g)	Coefficient of variation of Length (%)	Coefficient of variation of Weight (%)
♀BS x ♂BS	5.67±0.41	3.21±0.85	20.68±0.34	179.46±5.34	15.02±0.62^{bc}	176.25±5.93^{c}	6.06±0.29^{b}	14.07±1.22^{bc}
♀NW x ♂NW	6.17±0.13	3.69±0.14	20.92±0.60	200.27±9.38	14.76±0.48^{bc}	196.58±9.32^{ab}	5.52±1.36^{b}	13.68±1.51^{bc}
♀RN x ♂RN	6.26±0.29	4.11±0.41	20.63±0.38	182.49±10.81	14.37±0.63^{cd}	178.39±11.21^{c}	5.81±2.68^{b}	9.59±5.10^{c}
♀MJ x ♂MJ	5.61±0.1	2.69±0.09	12.99±0.36	36.29±4.89	7.39±0.31^{e}	33.60±4.82^{e}	10.66±1.61^{a}	30.87±5.90^{a}
♀NW x ♂BS	6.48±0.27	4.38±0.59	20.71±0.1	183.53±8.38	14.24±0.28^{cd}	179.16±8.00^{c}	6.12±2.17^{b}	17.96±5.38^{b}
♀BS x ♂NW	5.93±0.34	3.28±0.51	21.83±0.29	204.5±3.68	15.90±0.37^{a}	201.23±3.99^{a}	7.65±0.51^{ab}	14.37±3.42^{bc}
♀MJ x ♂NW	6.29±0.21	4.38±0.54	20.03±0.38	157.31±17.19	13.75±0.58^{d}	152.93±17.72^{d}	10.57±2.03^{a}	36.36±5.61^{a}
♀RN x ♂BS	5.88±0.11	3.25±0.24	21.23±0.88	178.29±11.75	15.34±0.66^{b}	174.74±9.57^{c}	5.94±1.77^{b}	14.8±3.09^{bc}
♀BS x ♂RN	6.65±0.45	4.74±0.86	21.55±0.11	189.49±6.52	14.91±0.34b^{c}	184.76±5.74^{c}	7.65±0.51^{ab}	14.37±3.42^{bc}
♀NW x ♂RN	6.44±0.69	4.41±1.09	21.16±0.14	189.18±5.58	14.73±0.67^{bc}	184.77±6.56^{bc}	5.05±2.38^{b}	17.91±3.79^{b}
♀RN x ♂NW	6.18±0.13	3.82±0.27	21.68±0.46	193.68±1.87	15.51±0.58^{b}	189.87±1.70^{abc}	5.35±1.20^{b}	15.95±2.91^{bc}

Different superscripts in the same column indicate significant differences (P<0.05) by Duncan's multiple tests (n=3). Values shown are mean and standard deviation

At the end of the 150-day rearing period, there was an increase in biomass, reflecting an increase in aquaculture productivity accompanied by an increase in the amount of feed consumed from the beginning to the end. Observations showed that the values of biomass, feed intake, and condition factor between most crossbred populations of tilapia were significantly different (P<0.05) (Table 3). The highest biomass value was shown by the ♀RN x ♂RN pure strain population at 38906 g, but this value was not statistically different (P>0.05) compared to the ♀BS x ♂BS pure strain

The results showed that the specific growth rate and daily growth of tilapia reared in groundwater ponds had values that were not significantly different (P>0.05) in some populations but significantly different from the crossbred population of ♀MJ x ♂MJ and ♀MJ x ♂ NW (Figure 3). Tilapia SGR values ranged from 2.5-2.77 %bwday^{-1}, and DGR values ranged from 0.23-1.35 (gday^{-1}). The highest SGR was shown by the cross ♀BS x ♂ NW with a value 37.54 % higher than the pure tilapia population and 14.80 % higher than the cross ♀MJ x ♂ NW. Similarly, for the DGR parameter, the highest value was shown by the cross ♀MJ x ♂ NW, which was 82.96% higher than the pure strain population of tilapia and 24.44% higher than the cross ♀MJ x ♂ NW. Feed conversion ratio is an important parameter that describes how much feed is required for weight gain of growing fish and indicates the efficiency of aquaculture production (Hasan and Soto, 2017). The results showed that FCR and PER in 11 tilapia crosses had results that were not significantly different (P>0.05) between populations, but significantly different from the tilapia pure strain population (P>0.05). FCR values in this study ranged from 1.98-2.90, with the lowest value found in the cross ♀ NW x ♂ RN and the highest FCR value in the pure tilapia population. The PER values were found to range from 1.16-1.71, with the highest PER value in the ♀ NW x ♂ RN cross and the lowest PER value in the pure tilapia population. Tilapia populations that have low FCR values indicate that feed is well-utilized for growth.

The survival rate in this study appears to vary, where there are significant differences in some crossbred tilapia reared for 150 days (P<0.05) (Figure 5). This difference was due to the genetic factors of the broodstock used that differed between populations although there were environmental influences due to weather changes during rearing from rainy to dry season. In addition, mortality can be caused by handling factors, but according to field data this factor isnot significant because there were not many fish that experienced death after growth sampling was carried out. Based on Figure 5, the highest survival value was shown by pure red tilapia ♀RN x ♂RN at 85.47%, followed by pure black tilapia ♀BS x BS ♂ at 85.47%, but both were not significantly different (P>0.05) from crosses ♀ BS x ♂ RN and ♀ NW x ♂ RN. The highest mortality values were shown by the cross ♀ MJ x ♂ NW at 42.95% and the pure strain cross ♀ MJ x MJ ♂ at 49.60%, both of which were significantly different from the other crosses (P<0.05). The results of the study of the proportion of male and female ratios of each cross showed significant differences between crosses (P < 0.05) (Figure 6). The highest male ratio and the lowest female ratio of the total fish obtained at harvest at the end of rearing were 65.51% (males) and 34.66% (females), as shown by the cross ♀ BS x ♂ RN. In comparison, the lowest male ratio of 28.57% and the highest female ratio of 71.26% at harvest was produced by the cross ♀ NW x ♂ RN.

3.1.2 Heterosis

Mid-parent Heterosis

Based on the results of mid-parent heterosis analysis presented in Table 4, only the cross ♀ BS x ♂ NW has positive heterosis values for all measured characters compared to other crosses. Heterosis values on fecundity characters showed that the highest fecundity was produced by the cross ♀ NW x ♂ BS (18.80%), followed by ♀ BS x ♂ RN (18.18%) and ♀ BS x ♂ NW (17.11%), and ♀ RN x ♂ BS (3.45%), while the lowest and even negative mid-parent heterosis values

Table 3. Mean biomass, feed intake and condition factor of 11 crossbred tilapia populations reared for 150 days. in earthen ponds.

Population	Parameter				
	Initial Biomass (g)	Final Biomass (g)	Biomass gain (g)	Feed Intake (gFish d)$^{-1-1}$	Condition Factor
♀BS x ♂BS	802.3±210.18	38320.63±733.90	37518.34±850.44^{a}	2.03±0.12^{abc}	2.03±0.04^{ab}
♀NW x ♂NW	920.32±33.50	31326.47±2476.73	30406.16±2480.88^{bc}	1.75±0.16^{c}	2.12±0.06^{a}
♀RN x ♂RN	1025.11±100.09	39931.55±2711.56	38906.45±2762.90^{a}	2.24±0.32^{a}	2.10±0.03^{a}
♀MJ x ♂MJ	671.70±20.96	4493.92±723.710	3822.23±702.83^{f}	0.32±0.03^{e}	1.64±0.11^{e}
♀NW x ♂BS	1093.03±146.32	34173.09±3062.65	33080.07±3026.96^{b}	2.00±0.14^{abc}	2.06±0.06^{ab}
♀BS x ♂NW	818.96±127.07	39280.48±2179.36	38461.52±2234.40^{a}	2.17±0.09^{ab}	2.04±0.07^{ab}
♀MJ x ♂NW	1094.88±133.5	16969.74±3027.79	15874.86±3159.51e	1.08±0.07^{d}	1.88±0.08^{d}
♀RN x ♂BS	812.19±57.71	22574.57±1600.77	21762.38±1600.72^{d}	1.26±0.14^{d}	1.89±0.11^{d}
♀BS x ♂RN	1183.49±213.28	39521.12±3356.38	38337.63±3155.07^{a}	2.12±0.46^{abc}	1.91±0.04^{d}
♀NW x ♂RN	1101.29±270.55	38277.29±2596.04	37176.01±2821.85^{a}	1.96±0.15^{abc}	2.00±0.05^{abc}
♀RN x ♂NW	952.82±65.48	28924.30±1296.44	27971.49±1313.78^{c}	1.80±0.13^{bc}	1.94±0.06^{cd}

Different superscripts in the same column indicate significant differences (P<0.05) by Duncan's multiple tests (n=3). Values shown are mean and standard deviation.

were shown by crosses ♀ MJ x ♂ NW (-45.63) and ♀ NW x ♂ RN (-17.95%). The mid-parent heterosis value on length characters showed positive results in each cross ranging from 1.87-18.22%, with the cross ♀ MJ x ♂ NW having the highest mid-parent heterosis value (18.22%). The negative result was shown by the cross ♀ NW x ♂ BS at -0.44%. Positive heterosis values were also seen in weight characters produced by the cross ♀ MJ x ♂ NW with the highest heterosis value of 33.65%, followed by ♀ BS x ♂ NW (7.81%), ♀ RN x ♂ NW (4.79%) and ♀ BS x ♂ RN (3.84%), while the other crosses produced negative values with the lowest value in the cross ♀ NW x ♂ BS (-3.26%). Then, the cross ♀ MJ x ♂ NW showed similar results on height and thickness characters with the highest heterosis values of 23.63% (body thickness) and 18.29% (body height) and the lowest values were found in the cross ♀ NW x ♂ RN at -1.13% and -3.32%, respectively. In the biomass character, the positive mid-parent heterosis value was shown by the cross ♀ BS x ♂ NW at 13.39%, followed by ♀ NW x ♂ RN (7.29%) and♀ BS x ♂ RN (0.59%), while the heterosis value in the survival character was known that the cross♀ NW x ♂ RN had the highest value of 7.77% followed by ♀ BS x ♂ NW 3.78%, and ♀ NW x ♂ BS 0.54% while the other crosses produced negative values with the lowest heterosis in ♀ RN x ♂ BS of -42.84% (biomass) and -41.02% (survival).

High-parent Heterosis

In addition to the value of mid-parent heterosis, this study also calculated the value of high-parent heterosis by comparing the phenotypic appearance of crosses against one of the best elders. In general, negative values in all measured characters were seen in the cross ♀ MJ x ♂ NW, compared to other crosses (Table 5). The calculation of high-parent heterosis on fecundity characters showed that only the crosses ♀ NW x ♂ BS (10.76%) and ♀ BS x ♂ NW (9.05%) showed positive results. The value of high-parent heterosis on length characters showed positive results in almost all crosses, ranging from 2.33-4.43%, with the highest value shown by the cross ♀ BS x ♂ NW and negative values were found in crosses ♀ MJ x ♂ NW (-4.20%) and ♀ NW x ♂ BS (-0.97%). In weight characters, positive values were obtained by crosses ♀ BS x ♂ NW (2.33%) and ♀ BS x ♂ RN (4.01%), while the other crosses produced negative values, with the lowest value in the cross ♀ MJ x ♂ NW (-21.13%). The same thing happened to the heterosis value of body thickness where the cross ♀ BS x ♂ RN (6.63%), while the lowest was in the cross ♀ MJ x ♂ NW (-6.74%). In height characters, the highest value was shown by the cross ♀ RN x ♂ BEST (4.85%) and the lowest in the cross ♀ MJ x ♂ NW (-16.30%). Furthermore, in the biomass character, only the cross ♀ BS x ♂ NW had a positive value (2.46%), while in the survival character, all crosses produced negative values, with the lowest value of -41.65% found in the cross ♀ RN x ♂ BEST.

3.2 Discussion

3.2.1 Fecundity and growth performance

Hybridisation is one of the fish breeding methods used to improve certain desired characteristics to increase aquaculture productivity. One of the conventional ways that is commonly done to improve certain economically valuable characteristics in animals or plants is to cross between different species. Qin *et al.* (2021) stated that crosses produce wide genetic variation and provide improvements in several characteristics. Xiao *et al.* (2022) stated that a basic population with extensive genetic resources is the basis for the development of sustainable cultivation because it will result in strong adaptability and a high level of resilience in a population. According to Joshi *et al.* (2018), hybridisation is effectively carried out to produce intermediate values of prominent parental characters, improve different pure breeds, introduce new

Table 4. Mid-parent heterosis of crossbred tilapia reared 150 days in earthen ponds.

Parameter	Mid-parent heterosis (%)						
	♀ NW x ♂ BS	♀ BS x ♂ NW	♀ MJ x ♂ NW	♀ RN x ♂ BEST	♀ BS x ♂ RN	♀ NW x ♂ RN	♀ RN x ♂ NW
Fecundity (eggs)	18.80	17.11	-45.63	3.45	18.17	-17.94	8.18
Total Length (cm)	-0.44	4.97	18.22	2.82	4.35	1.87	4.34
Body Weight (g)	-3.26	7.80	33.65	-1.19	4.76	-1.13	1.26
Width (cm)	-1.91	3.39	23.63	2.50	3.84	-3.31	4.79
Thickness (cm)	1.78	8.11	18.29	8.09	7.79	-0.50	2.68
Biomass (g)	-2.43	13.38	-6.10	-42.84	0.59	7.29	-19.30
Survival Rate (%)	0.54	3.78	-23.48	-41.02	-3.40	7.77	-20.43

genes, and obtain hybrid vigor. Then, the offspring of the hybrid population will show certain traits that are better or weaker than their parents (Xing *et al.,* 2022).

Several previous studies reported that fecundity in tilapia varied between 1544-2143 eggs (absolute fecundity) with a relative fecundity of 3.7-4.2 eggs/g (Almeida *et al*., 2013), then 50-2,600 grains per spawning with relative fecundity varying from 0.29 to 6.8 eggs/g (Mashaii *et al*., 2016), absolute fecundity 622-1191 grains and relative fecundity 3.6-10 eggs/g) (Sarmento *et al*., 2018), then Silva *et al.* (2020) reported that absolute fecundity in tilapia ranged from 2581-7084 grains and relative fecundity 2.2-4.9 eggs/g female. The fecundity in tilapia crosses ranged from 215-377 eggs, with relative fecundity ranging from 3.18-4.88 eggs/g (Nzohabonayo *et al*., 2021). The results in this study are in line with Russell *et al.* (2012) that tilapia is reported to mature early and have a smaller size than other tilapia, but show higher relative fecundity. Similarly, Silva *et al.* (2020) stated that non-inbred tilapia varieties produce less absolute fecundity but show higher relative fecundity than other genetic groups. Then Valentin *et al.* (2015) showed that fish that have lower weights show higher relative fecundity than tilapia with larger weights.

In this study, it is known that the number of fecundities of crossbred between tilapia species produces diverse values. The high absolute fecundity was only obtained in the reciprocal crossbred of black tilapia strain Nirwana with black tilapia strain BEST, this occurred because the cross was a crossbred between strains (intraspecific). The other crosses are included in interspecific crosses or between species. Wang and Li (2010), Hovick and Whitney (2014) and Kong *et al.* (2017) found that intra-specific mating can produce hybrids that are significantly more fertile than pure strain; due to potential genetic variation among different populations, hybrid results generally have higher spawning rates, hatching rates and viability. Meanwhile, Bradbeer *et al.* (2019) and Wang *et al.* (2019) reported that interspecific crosses tend to be detrimental for reproductive characters because they form less fertile lineages/viability, cause mortality in puppies, and do not produce hybrid vigour in offspring this may occur due to differences in the number of chromosomes or genomes of the parents (Zhang *et al*., 2014; Zhou *et al*., 2019; Cao *et al.,* 2021). According to Osure and Phelps (2006), spawning performance between tilapia strains is influenced by selection pressure during domestication, parent size, spawning time history and production patterns. In addition, fish reproductive performance is also strongly influenced by environmental factors such as the feed ration provided, the test environment, and broodstock-rearing methods (Thoa *et al*., 2017; Lal *et al*., 2021). In addition, the occurrence of spawning in tilapia is also influenced by the variability of fish behavior when interacting with their partners (Akian *et al*., 2017).

Table 5. High-parent heterosis of crossbred tilapia 150 days rearing in earthen ponds.

Parameter	High-parent heterosis (%)						
	♀ NW x ♂ BS	♀ BS x ♂ NW	♀ MJ x ♂ NW	♀ RN x ♂ BEST	♀ BS x ♂ RN	♀ NW x ♂ RN	♀ RN x ♂ NW
Fecundity (eggs)	10.76	9.05	-67.44	-26.72	-16.08	-44.15	-26.41
Total Length (cm)	-0.97	4.43	-4.20	2.70	4.22	2.33	3.69
Body Weight (g)	-8.25	2.33	-21.13	-1.84	4.01	-5.33	-3.13
Width (cm)	-2.07	2.23	-6.74	4.68	6.63	4.33	-0.40
Thickness (cm)	-5.50	0.39	-16.30	4.85	4.53	-4.85	-1.80
Biomass (g)	-11.87	2.46	-46.98	-43.69	-1.00	-4.45	-7.42
Survival Rate (%)	-12.99	-10.10	-40.69	-41.65	-4.46	-7.61	-4.33

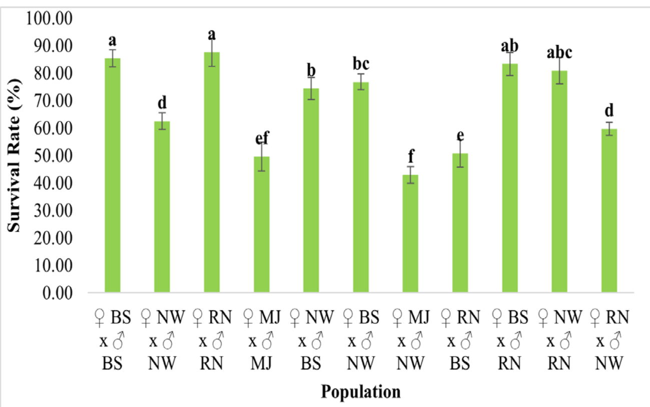


Figure 5. Survival Rate (SR) of 11 crossbred populations of tilapia reared for 150 days in earthen.

Before spawning, all crossbred populations were fed and maintained in the same environment, so variations in fecundity occurred due to genetic factors from different strains, indicating that the crossbred population is unlikely to experience inbreeding depression. Hernández-Gurrola *et al.* (2020) stated that a decrease in reproductive capacity occurs in populations that lose their genetic variability due to selection pressure and inbreeding. Yoshida *et al.* (2015) and Hamzah *et al.* (2016) stated that there is no significant relationship between genetics with body traits at harvest / or female body weight at mating and fecundity, where the size of females in different genetic groups does not affect reproductive traits. In addition, Trong *et al*. (2013) reported that the number of eggs produced by tilapia only represents a portion of the total number of eggs in the ovary.

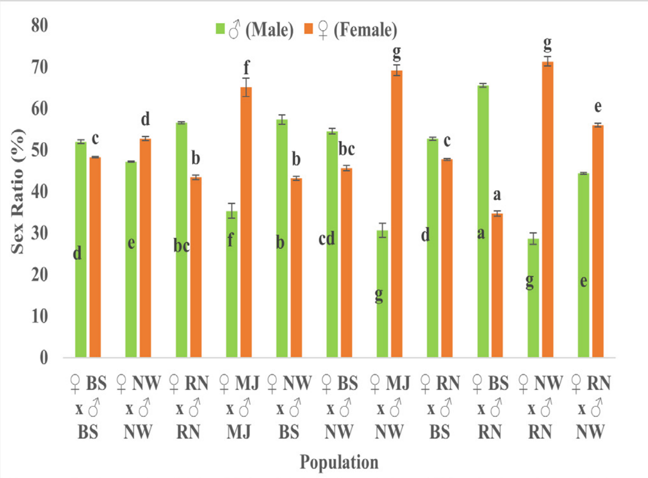


Figure 6. Proportion of male (♂) and female (♀) of 11 crossbred populations of tilapia reared for 150.

Growth is one of the parameters that is often measured to determine the success of a breeding program, in this case, hybridisation (Altinok *et al*., 2020). In addition, growth is also an important character that is the main goal in the hybridisation program (Chen *et al*., 2023). The results of 150 days of maintenance show that growth occurs well; this is indicated by the increase in the length and weight of fish every month. This increase indicates that all tilapia crosses have a good ability to compete for food and space. According to Trinh *et al.* (2021), as many as 80-90% of GIFT tilapia juveniles show a success rate in getting the feed given so that they have faster growth than other strains. According to a report by de Verdal *et al.* (2014), tilapia reared in extensive earthen ponds showed low growth due to a lack of fertilisation, resulting in low feed intake in the pond. Ridha (2012) stated in that the hybrid weight growth of tilapia from 180 days of breeding ranged from 203-223 g. Similarly, Robisalmi *et al.* (2020) reported that the crossing of female black tilapia with male blue tilapia reared for 120 days had the highest length and weight gain of 16.60 cm and 215.30 g. Zhou *et al.* (2019) reported that the crossbreeding of female black tilapia with male blue tilapia had the highest length and weight gain and that hybrid tilapia between *O. niloticus* and *O. aureus* reared for 120 days showed better absolute weight gain of 372.75 g and higher IGF1 hormone than both parents. The higher results reported by Novelo *et al.* (2021) in the crossbred population of tilapia reared 167 days resulted in a weight gain of 402-702 g.

The difference in length and weight growth between crosses in this study could be due to the different weights of the parents used between males and females. In addition, the strain of tilapia used and the direction of the cross between the use of male and female parents contributed to the performance of the pups. According to Tave *et al*. (1990) and Radona *et al.* (2016), the male and female parents used in the hybridisation program have a significant effect on the length and weight growth of the resulting pups. The variation in growth between crossing types indicates considerable genetic variation among fish strains, which is related to the proportion of genetic contribution from each strain and the direction of crossbreeding (Altinok *et al*., 2020). A low genetic distance value between two species indicates a closer relationship between them. On the other hand, the more distant the relationship, the greater the genetic distance value (Lind *et al.*, 2012; Saleky *et al.*, 2021). Genetic variation in a population illustrates biological information, adaptability to fluctuations, and environmental stress, and this is an indicator of conservation value, commercial value and long-term survival. The diversity of genetic variation can also be increased by crossing between populations of pure strains selected from selective breeding activities (Liang *et al*., 2023).

This study indicates that weight characters are more variable than length characters and can be interpreted as competition between individuals in the population to survive and obtain food, while low CV indicates low competition and good social interaction between individuals. In addition, differences in CV values between crossing populations may also be caused by the instability of traits derived from each pure strain that has different responses to the environment. Thodesen *et al.* (2011) reported that tilapia has a coefficient of variation on weight characters ranging from 17.90-37.70%. Khaw *et al.* (2016) reported that the CV value in tilapia was 12% for length characters and 36% for weight. Mengistu *et al.* (2020) reported CV on tilapia weight characters ranged from 19.40 -31.10%. Likewise, the report of Rossato *et al.* (2022) showed that the CV on the length character of tilapia was 11.67% and the weight character was 33.80%. De Donato *et al.* (2005) stated that the low level of coefficient of variation occurs due to inbreeding and genetic drift, but this can be improved by manipulating the rearing environment and applying selection for the next generation (Khaw *et al*., 2016; Sun, *et al*., 2022).

The high biomass value shown in the pure strain population of red tilapia was directly proportional to the feed intake value; this result indicates that the feed given can be consumed properly and put into energy to produce high biomass weight. Feed intake describes the amount of feed intake consumed at a given time. Abdel-Tawwab *et al.* (2010) stated that high feed consumption rates, nutrient utilisation, and digestibility of these nutrients lead to increased nutrient accumulation. This correlates with protein synthesis and lipid storage levels in muscle tissue and results in variations in growth rates. According to Herawati *et al.* (2019), high energy content in feed leads to reduced protein utilisation efficiency because excess energy can lead to decreased feed consumption and nutrient intake; conversely, if feed energy levels are insufficient, protein will be used for energy and not for tissue synthesis.

The value of the condition factor in tilapia reared in earthen ponds shows a good range of values, indicating that during maintenance in earthen ponds, fish are in a healthy and prosperous condition (fulfilled nutritional intake). According to Robisalmi *et al.* (2021), the condition factor is an indicator of the physiological condition of the fish, where the low CF indicates that the fish lack nutrients. However, differences in condition factor values can also be caused by the proportion of males and females in each population and the amount of feed eaten. Silva *et al.* (2022) stated that each species and group of fish has a specific condition factor. The value in this study is in line with several previous research reports, namely, the condition factor of *O. spilurus* x *O. niloticus* ranges from 1.97-2.10 (Ridha, 2012), then in monosex and mixed-sex tilapia ranges from 1.73-1.97 (Githukia *et al*., 2015). Furthermore, the condition factor values of four GIFT tilapia cross combinations ranged from 2.13-2.49 (Novelo *et al*., 2021), and in three strains of *O. niloticus* tilapia reported at 1.94-2.05 (Abwao *et al*., 2023). Lower CF values indicate that the growth of fish in terms of length is relatively higher than the growth in weight, resulting in a more elongated body shape. Conversely, a higher CF value indicates that the fish experienced a greater increase in weight along with its length growth, resulting in a fatter body shape, which in turn increases its marketability (Githukia *et al*., 2015).

In this study, it was found that the effect of parents was more significant in the daily growth value of the cross than the specific growth. This result is in line with findings by Koolboon *et al.* (2014) that interspecific hybrid fish reared 175 days showed higher absolute growth values than specific growth; this is because hybrid performance depends on the combining power of each cross (Falconer and Mackay, 1996). Some previous research results (Ridha, 2012) reported that the SGR and DGR values in tilapia showed the daily growth value of *O. spilurus* x *O. niloticus* tilapia crosses ranged from 1.11 -1.22 (gday^{-1}) and the specific growth rate ranged from 2.26-2.30 %bwday^{1}, then the SGR value in mono sex and mixed-sex tilapia raised in soil ponds ranged from 1.47-1.83 (Githukia *et al*., 2015). Lower results were reported by Trinh *et al.* (2021) in that, the daily growth value of several tilapia strains reared for 230 days ranged from 0.20-0.51 gday^{-1}. Nugroho *et al.* (2014) stated that the genetic ability in fish populations resulting from short hybridisation programs would not be effective in increasing the productivity of the desired characteristics.

According to Gomelsky (2011) and Thongprajukaew *et al.* (2017), feed efficiency is indicated by a combination of increased appetite which occurs with effective feed utilization. Better feed utilization is also used for enzymatic digestion to produce high growth. The FCR and PER values in this study are still in line with several reports on tilapia including Novelo *et al.* (2021) who reported FCR values in four crosses of tilapia reared 167 days ranged from 1.46-1.57, F1 offspring of *O. spilurus* x GIFT *O. niloticus* crosses with FCR 1.42-1.45 (Ridha, 2012). The higher results in tilapia reared 180 days ranged from 2.55-2.58 (Abwao *et al*., 2023). Another report on the *O. mossambicus* × *O. aureus* cross had an FCR of 1.07 and PER of 3.06 (Correia *et al*., 2019). The cross of *O. niloticus* x *O. aureus* was reported to have FCR ranging from 1.05-1.14 (Poolsawat *et al*., 2022). The range of FCR and PER values of pure strains of tilapia (*O. niloticus*) in the rearing phase ranged from 2.29-2.79 (FCR) and 0.99 -1.53 (PER) (Abdel-Tawwab *et al*., 2010), then 1.41-1.62 (FCR) and 1.88-2.16 (PER) (El-Araby *et al*., 2020). FCR values in tilapia range from 1.25-1.153 with PER values ranging from 2.53-2.80. (Rapatsa and Moyo, 2017). As for red tilapia, it is known to range from 4.79-15.27 (Tuan Harith *et al*., 2022).

According to Thoa (2016), the survival rate is influenced by many factors, which include genetic and environmental aspects including water quality, weight and age of the female parent, different strains, and the effects of males and females. The survival rate in this study was lower than that reported by Mtaki *et al.* (2022) where the survival rate of *O. niloticus* (female) and *O. urolepis* (male) crosses resulted in 100% survival in various culture environments (freshwater, brackish and seawater). Likewise, the survival rate in four crosses of two tilapia strains, namely *O. shiranus* and *O. karongae*, has a high survival rate ranging from 97 to 98% (Snake *et al.* 2020). Likewise, Novelo *et al* (2021) produced high survival in tilapia crosses ranging from 99-100%. Khaw *et al.* (2016) stated that there is a negative correlation between survival and harvest biomass weight, where tilapia with higher SR tend to show low growth performance.

In addition to hybridisation activities to improve economically valuable traits such as growth, reproduction, and disease resistance, this program can also be used to generate genetic data in determining sex in tilapia. However, the results cannot be predicted because they are determined by various factors (Chen *et al*., 2018; Snake *et al*., 2020). According to Basavaraja and Raghavendra (2017), sex determination in tilapia is often not clear, where deviations in the mechanism of sex determination in tilapia can be caused by frequent interbreeding between species or strains that are influenced by the lack of purity of strains and the occurrence of natural sex reversal (genetic factors) and environmental factors such as high water temperature at the beginning of larval rearing which causes masculinization and feminization (Lozano *et al.,* 2014). The results of the sex ratio in this study are not much different from the report of Marengoni *et al.* (1998) which found that the crossing of three strains of tilapia showed a sex ratio ranging from 44% males: 56% females to 58% males: 37% female. However, higher results were stated by Snake *et al.* (2020) that interspecific crosses between male tilapia (*O. karongae*) and female tilapia (*O. shiranus*) produced 88% male pups, equivalent to tilapia treated with hormones to produce males. Likewise, Novelo *et al.* (2021) reported that the sex ratio of tilapia crosses ranged from 78-100% males. Meanwhile, 13 populations of red tilapia crosses showed male sex ratios ranging from 5-89% (Desprez *et al.,* 2006).

3.2.2 Heterosis

Heterosis value is a value that describes the change in measured characters in hybrids compared to their pure strains. Heterosis is a multifaceted biogenetic phenomenon that arises from the combination of various factors, which ultimately results in the performance of hybrid offspring (Yu *et al*., 2021). Quantification of hybrid vigour (heterosis) of crossbred populations is essential in relation to genetic improvement through hybridization programs. Two methodologies are used to assess the utility of heterosis: the mid parent and best parent methods. Mid parent heterosis calculates the difference in phenotypic appearance character values between the crossed population and the average of the two parents, while best parent heterosis calculates the difference between the crossed population and one of the best parents. Heterosis analysis is important because it can illustrate whether the phenotypic appearance of the crossed population has increased or decreased. Positive heterosis indicates that the crossed population outperforms its parents, and vice versa, where as positive heterosis value indicates that the crossed population outperforms its parents. Generally, the heterosis of hybrids is felt by F1 crosses that are characterized by superiority in various traits such as growth, development of environmental resistance, and disease resistance (Krasnovyd *et al*., 2020; Šimková *et al*., 2021).

The results of the calculation of heterosis of tilapia reared for 150 days in this study are lower when compared with some reports of heterosis in tilapia, namely the high heterosis value on body weight characters reported by Marengoni *et al.* (1998) by 10% in the crossing of three strains of *O. niloticus* tilapia reared for 90 days. Then Ridha (2012) found that the F1 hybrid offspring of *O. spilurus* x *O. niloticus* reared 180 days showed heterosis value of body weight (17.40%), DGR (17.80%), SGR (6.5%) and Survival (3.2%). Furthermore, the crossing results of four tilapia strains showed the best heterosis value of 6.7% (body weight) and 6.8% (daily growth) and high heterosis in fillet characters ranging from 38-43% (Neira *et al*., 2016). Similarly, the cross between Red-Stirling and Chitralada red tilapia reared 190 days produced heterosis of body weight characters of 4.43% (Lago *et al.,* 2017). The results of the calculation of heterosis from negative to positive were reported by Thoa *et al.* (2016) that the value of heterosis in six crosses of tilapia resulting from 278 days of rearing showed positive and negative results ranging from -9.2% to 48.60%. The F1 offspring of diallel crosses of four strains of tilapia *O. shiranus* showed positive heterosis values of 180-day harvest weight characters ranging from 12.3%-17.0% (Maluwa and Gjerde, 2006a), but the F2 offspring showed that the average growth in the crossed population of tilapia *O. shiranus* was lower than the pure strain with average heterosis of -8.8% (Maluwa and Gjerde, 2006b). Bentsen *et al.* (1998) reported that body weight heterosis values in 56 tilapia crosses ranged from a low of -5.8% to a high of 14%. The value of heterosis in several other species is known to be shown in trout (*Salvelinus fontinalis*), which showed heterosis of body weight ranging from 4.9-23.8% (Crespel *et al*., 2012). Then a reciprocal cross between two strains of sturgeon fish produced low and intermediate heterosis values of 3% and 21% for growth characters and 14.51 and 73.48% for synthetic characters (Shivaramu *et al*., 2019). In nine catfish crossing populations, it is known that only the absolute weight growth character shows a high heterosis value with an average of 10.85%, while the SGR and survival characters show negative results (Koolboon *et al*., 2014). The negative heterosis results were reported for *Anabas testudineus* Bloch fish at -14.60%

(Piwpong *et al*., 2017).

The high value of mid-parent heterosis in the MJ♀ x NW♂ population is because the crossbred has a distant kinship and is produced from different species, namely *O. niloticus* and *O. mossambicus,* which allows the incorporation of complementary traits. According to Saleky *et al.* (2021) tilapia (*O. niloticus*) and Mozambique tilapia (*O. mossambicus*) strains in Indonesia have a high genetic distance, but morphologically, the two species have morphological similarities. Whitlock *et al.* (2000) found that hybridisation between genetically different populations has the potential to reduce drift and inbreeding and increase heterozygosity. When viewed from the high-parent value, the MJ♀ x NW♂ crossbred shows a negative value; this is because the inherited traits are more dominantly derived from Nirwana black tilapia, where Nirwana tilapia is the result of family selection and has advantages in freshwater on several characters such as growth, fecundity, disease resistance. The positive values of mid- and high-parent heterosis on all measured characters were shown by the cross of black tilapia ♀ BS x ♂ NW except on the survival character. According to Xu *et al.* (2015), one of the factors determining the success of the hybridisation program is the process of selecting the parents used, as well as the design of a good cross combination. The results of the calculation of mid-parent and high-parent heterosis on the characters measured in this study were because of differences in the genetic background of the crossed tilapia elders. This study showed that some hybrids were significantly greater than the parental progeny with positive heterosis. The better growth performance can be partly explained by differences in the genetic components of the parents. Some of the tilapia broodstock used in this study came from selected strains, which have been produced from selective breeding programs with fast-growth traits. When parental populations are continuously selected, hybrids will exhibit significant heterosis due to the accumulation of many different non-additive genetic variations. According to Ponzoni *et al.* (2011) and Delomas *et al.* (2019), in tilapia, the value of heterosis (*hybrid vigor*) in the enlargement phase will be achieved by crossing tilapia with distant relatives or also using selected strains. The results of crossing populations that have distant kinship show better heterosis values than inbreeding, which shows the fixation of damaging alleles (Söderquist *et al.*, 2020).

The performance of tilapia hybrids in this study showed diverse heterosis values, which were better, worse or the same performance as their parents. The diverse phenotypic performances of hybridised tilapia are in line with and confirm the theory that hybridisation results cannot be predicted in advance. This phenomenon occurs due to crossbreeding depression (Granier *et al*., 2011). According to Tave (1995) and Arifin *et al.* (2017), in hybridisation activities, dominant genetic diversity which is a combination of alleles will be exploited, accumulated and passed on to the next generation. Some factors that affect hybridisation between species include genetic structure, gamete compatibility, gene flow patterns from the parent species, and the crossing pattern used (Rahman *et al*., 2013). Heterosis is caused by a combination of many factors, including the hypothesis of dominance and overdominance (allelic interactions) and epistasis (nonallelic interactions) (Yu *et al*., 2021) besides that the amount of heterosis in crosses is influenced by the maternal effect (Bentsen, 1998), where genes involved in cytoplasmic organelles (mitochondria) can show a stronger contribution to some life traits (Šimková *et al*., 2021). In *et al.* (2017) stated that there are differences in the additive genetic value of certain characters due to differences in genetic background and selection history. In addition, differences in gene frequency between the two parents and gene interactions, to a certain extent, can determine the level of heterosis in crosses (Dai *et al*., 2014; Falconer and Mackay, 1996). Li *et al.* (2018) stated that differences in heterosis values are also influenced by the environment in which the cross-population is raised,and the characters measured because the environment has the capacity to affect additive and non-additive genetic components, which ultimately results in changes in phenotypic appearance (Yan *et al*., 2018). Similarly, Mbiru and Mchele (2015) and Moses *et al.* (2021) reported that the heterosis effect on growth performance of cultured tilapia varies widely among species and environments, so differences in species and environments affect the value of heterosis in tilapia growth characters.

Water quality parameters such as temperature, dissolved oxygen, pH, and ammonia were uniform because rearing was done in the same pond. Water parameters are within tolerable limits for good performance of freshwater fish rearing, especially tilapia (Boyd, 2015). Therefore, temperature, dissolved oxygen, pH, and ammonia may not significantly affect the various variables tested.

4. Conclusion

The results of crossbred between black tilapia, red tilapia and tilapia showed differences in growth, where crossbred of black tilapia produced the best growth and fecundity performance, while the highest survival value was produced by pure strains of red tilapia and black tilapia. Specifically, a hybrid of Mozambique tilapia x black tilapia showed the highest mid-parent heterosis value on growth traits but produced negative heterosis on fecundity, biomass, and survival traits. Hybridisation in this study was found to affect the fecundity, growth, and survival performance of tilapia.

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Authors' Contributions

All authors have contributed to the final manuscript. The contribution of each author is as follows, AR, NL, DA, BM; reared the fish, collected the data, performed growth analysis, drafted the manuscript. WP and DMM ; devised the main conceptual ideas, analyzed, and evaluated the final data, and did critical revisions of the manuscript. AR; performed designed the figures and tables, finalized the manuscript. All authors discussed the results and contributed to the final manuscript.

Conflict of Interest

The authors declare that they have no competing interests. All co-authors have seen and agreed with the contents of the manuscript.

Declaration of Artificial Intelligence (AI)

The author(s) affirm that no artificial intelligence (AI) tools, services, or technologies were employed in the creation, editing, or refinement of this manuscript. All content presented is the result of the independent intellectual efforts of the author(s), ensuring originality and integrity

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