Quest Journals
Journal of Research in Environmental and Earth Sciences
Volume 5 ~ Issue 2 (2019) pp: 50-63
ISSN(Online) :2321-3795 ISSN (Print):2321-3809
www.questjournals.org

Research Paper

Response of Progeny from reciprocal crosses of feral and domesticated *Clarias gariepinus* to hypoxic water

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ABSTRACT: Pure line and reciprocal crossbreeds of feral (F) African catfish (*Clarias gariepinus*) x domesticated (D) African catfish were compared for tolerance of hypoxia <1.0mg/l-1. Genotype–regime effects ($p< 0.05$) was observed for tail fin beat rate under hypoxic conditions. No differences ($p>0.05$) were observed for opercular beat rate in response to hypoxia. Progenies sired by feral African catfish had higher TBR (47.00 beats/min, 40.75 beats/min, 43.82 beats/min and 50.51 beats/min for the crosses ♀F×♂F, ♀D×♂D, ♀F×♂D and ♀D×♂F respectively) than those sired by domesticated African catfish. Crosses had no significant effect on the haematological indices of the progenies but the dissolved oxygen regime significantly affected ($p<0.05$) haematology such that values increased in response to hypoxia. Within population variability in haematological indices in response to hypoxia indicates that the cross ♀F×♂D shows a more consistent response of haemoglobin to hypoxia and the cross ♀F×♂D elicits a more consistent response of MCV to hypoxia while consistency in WBC under hypoxic conditions exist for the reciprocal crosses ♀F×♂D and ♀D×♂F. Origin of broodstock therefore affects swimming fitness under hypoxia but not haematological response.
KEYWORDS: catfish, crosses, hypoxia, response, variability

I. INTRODUCTION

The environment in which fish are cultured is defined by its water quality, a term that encompasses the physical, biological and chemical properties of the water with consequences for welfare, growth and reproduction of the aquatic organisms under culture. Profitable aquaculture is hinged on low expenditure on provision of optimal water quality in the aquaculture environment [1] while also considering the carbon footprint of aeration in ponds [2, 3]. The welfare of the organism in the culture medium as it relates to health and growth is determined in part by water quality with other factors such as feed and the genotype of the organism contributing as well. The quality of water in any culture environment is an important consideration when high density aquaculture is being contemplated [4]. The aquaculture environment is a complex system with the interplay of biotic and abiotic factors [5]. Several water quality parameters are responsible for creating a conducive environment in the culture system but dissolved oxygen is the most critical [6] since it requires constant monitoring to ensure adequacy in the aquaculture environment [7]. The reason behind the importance of dissolved oxygen lies in the fact that oxygen is first needed to carry out metabolism in the fish before production of waste products that create the other critical water quality parameters like ammonia and nitrite.

Within the feral environment, Clarias inhabit shallow areas and marginal swamps that are subject to fluctuations in dissolved oxygen [8]. Hypoxic conditions are sometimes created due to changes temperature [9] as well as human interference [10]. The solubility of oxygen in water is affected by water temperature [11] and since water is viscous and higher in density than air, aquatic organisms are laden with a high metabolic cost for oxygen uptake through the gills [12]. This notwithstanding, clariid catfishes have accessory breathing apparatus that allows them to utilize atmospheric oxygen by gulping air [13]. Moreover, domestication has been shown to have effects on fitness of aquaculture organisms [14] as well as welfare [15]. Air breathing has been shown to be directly related to increased hypoxic conditions in cultured *Clarias gariepinus* [16].

The consequences of exposure to either acute or chronic hypoxia include alteration of homeostasis [17], stress response and health challenges [18]. Evolutionary tendencies have led to development of strategies by fish to overcome these consequences through adaptation of their physiological and biochemical processes to target homeostatic adjustments for survival [19]. The status of fish health can be determined using haematological indices [20]. Several factors can modulate blood parameters in fish including the species,

aquatic environment, immune status and feeding adequacy, stage of sexual maturity and age [21]. The adequacy of haematological indices as a measure of response to stress lies in the fact that these parameters are pliable to changes in the environment. According to Sheikh and Ahmed [22], the overall quality of water, level of salinity, water temperature and dissolved oxygen saturation all influence blood parameters.

Hypoxic conditions can be rare in lotic environments and when dry season occurs, the fish move to deeper areas. In lenthic water such as the aquaculture pond, *Clarias gariepinus* are exposed to hypoxic water that is caused by algal blooms with no escape route. Hence, there could be some genetic-environment adaptation in the domesticated strains as against the feral strain. The main objective of this study was to evaluate the effect of the pure line and cross breeding of feral and domesticated strains on behavioural and haematological indices of *Clarias gariepinus*.

II. MATERIALS AND METHODS

Production of Progeny

Feral broodstock (F) were obtained from the fish landing site at Wadata and transported to Korex aquatic Farms Makurdi for acclimatization. A total of 10 feral broodstock comprising 5 males and 5 females were obtained. These were acclimatized for two weeks before being induced to breed artificially. The domesticated broodstock (D) were those within the fish farm with age >1 year.

Crossing of the feral and domesticated broodstock was done using one male and one female per cross (Table 1).

Table 1. The Punnett's square for the crosses

♀	♂	
	F	D
F	FF	FD
D	DF	DD

The female feral broodstock had average weight of 441.5±9.5g while the feral male broodstock weighed 401.5±3.5g on average. Mean weight of the domesticated female broodstock was 710.0±56.0g while that of the domesticated male broodstock was 593.5±11.5g. These were selected using standard criteria as described by de Graaf and Janssen [23].

Induced breeding was carried out using standard procedures as described by Haylor [24] and Haylor and Mollah [25] with the use of Ovaprim as hormone to stimulate final ova maturation and ovulation. Fry produced from each cross were nursed and transferred to four different earthen ponds for grow-out. The grow-out phase lasted for 4 months with fish being fed commercial artificial diets (Vital Feed®) *ad libitum***.**

Exposure to Hypoxia

A total of 60 samples of progeny from the crosses were randomly selected from the ponds (15 samples per cross) and transported in a well aerated plastic container for each cross to the Hatchery Unit of Department of Fisheries and Aquaculture, University of Agriculture Makurdi where they were acclimatized for 14 days in four different concrete tanks. During the acclimation period the fish were fed at 5% of their body weight and the water was renewed after every 3 days.

The experimental set up for hypoxia exposure comprised five plastic aquaria (55cm × 39.5cm × 29cm) with a capacity of 63,002.5cm^3 (63 litres) equipped with lids. The experiment was conducted in two batches: first hypoxia trials and next normoxia trials. Each tank was stocked with four (4) fish with a fish from each cross (tagged) being represented in each tank. Upon completion of the first trial, all fish were evacuated and new samples were selected for the next trial.

Hypoxic water was prepared using the boiling method as described by Butler, Schoonen [26]. Aliquots of water were boiled for 30 minutes in a large aluminium pot at atmospheric pressure using a charcoal stove. The boiled water was transferred to the plastic aquaria upon boiling and the tanks were covered immediately. A volume of 50L of deoxygenated water was added to each tank and covered with the lids. The water was allowed to cool in the tanks overnight with the lids tightly in place.

Normoxic water was obtained by adding dechlorinated tap water (50L) into each of the tanks after the hypoxic trials were over. The water was aerated using an aquarium air pump (Hailea Model ACO-318) for 30 minutes prior to introduction of fish.

For each of the trials, five fish were selected in each case with mean weights as presented in Table 2. The fish were tagged using coloured zip lock tags with a colour for each cross. Fish were introduced into each tank and all determinations concluded before the next tank was used.

Table 2. Mean weights of progeny selected for the hypoxia trials (n = 10)

Cross	Mean	SE Mean	SD
FF	184.62	0.90	2.86
DD	183.50	0.50	1.58
FD	185.03	0.44	1.40
DF	187.16	0.20	0.63

SE = Standard Error; SD = Standard Deviation

Determination of behavioural pattern

The following parameters were monitored five (5) minutes after stocking the fish in each case (Hypoxic and normoxic). This was done as early as this to avoid excess stress and limit suffering of test organisms. The parameters which were monitored include: Opercular beat rate, per minute (OBR) and tail fin beat rate (per minute) (TBR). Opercular beat rate was monitored for each fish by four persons using a stop watch. Operculum movement is the number of times the target fish opens and closes its operculum within one minute. The number of tail swinging (Tail fin beat rate) within sixty seconds was also counted in the same manner using a stop watch.

Determination of Haematological Parameters

Blood samples were collected from the caudal vertebral vein/artery of the fish by venipuncture with sedation. Sedation was achieved using clove oil at 10 ppm. The lateral approach was employed in collection of blood. A needle was inserted close to the base of the caudal peduncle just below the lateral line and directed towards the ventral side of the vertebra and moved slightly while applying a negative pressure on the plunger. Once blood flow was established, the plunger was pulled up to enable suction of blood. The needle was pulled out and blood was immediately transferred into a K-2 EDTA blood tube and aspirated.

The blood cell automatic cell counter HeCo Vet C 9SEAC (Italy) was used to determine erythrocyte count (RBC), Haemoglobin concentration (Hb), Haematocrit value (Hct), Mean corpuscular volume (MCV) and White Blood Cell Count (WBC). Haematocrit was determined using the microhaematocrit method followed by automated reading. For haemoglobin, electrolyte lyses preceded the automated method. Mean corpuscular haemoglobin and mean corpuscular haemoglobin concentration were determined using mathematical relationships following Sink and Feldman [27].

Determination of Water Quality

Water quality parameters that were measured during the before and after the trials include temperature, pH and dissolved oxygen (DO). Water temperature and pH was determined using the Hanna Instruments HI98190 pH/ORP meter while dissolved oxygen was determined using the Hanna Instruments HI9147 portable dissolved oxygen meter.

Data Analysis

Data was analysed using R version 3.4.3 [28]. Descriptive statistics for water quality were obtained using Rmisc package in R [29] and reshape2 [30]. Differences in the behaviour across the treatments were determined using unpaired t-test in R while differences in haematological parameters were determined using one-way ANOVA in R via agricolae and emmeans packages [31, 32]. Mean separation was done using the Tukey HSD method implemented in multcomp package [33] and viewed using multcompView [34]. Graphical illustrations of water quality and behavioural pattern were done using the package ggplot2 [35].

III. RESULTS

Water Quality in the tanks used for the experiment was such that dissolved oxygen in both the normoxic and hypoxic trials reduced at the end of the trial compared to values at the start of the trials. However, all values were above $5mg.l^{-1}$ (Figure 1). In tanks with the hypoxic regime (Figure 2), dissolved oxygen levels decreased at the end of the experiment with values less than $1.0mg/l^{-1}$.

Water temperature in the tanks (Figure 3) was approximately uniform with values ranging from 27.35®C in tank 4 to 28.29®C in tank 1 for the normoxic regime while the hypoxic regime had temperatures ranging from 27.40®C in tank 4 to 28.22®C in tank 5. The pH in both regimes (Figure 4) indicates that values in the normoxic regime ranged from 7.16 (tank 5) to 7.75 (tank 3) while those in the hypoxic regime ranged from 7.13 (tank 3) to 7.90 (tank 1).

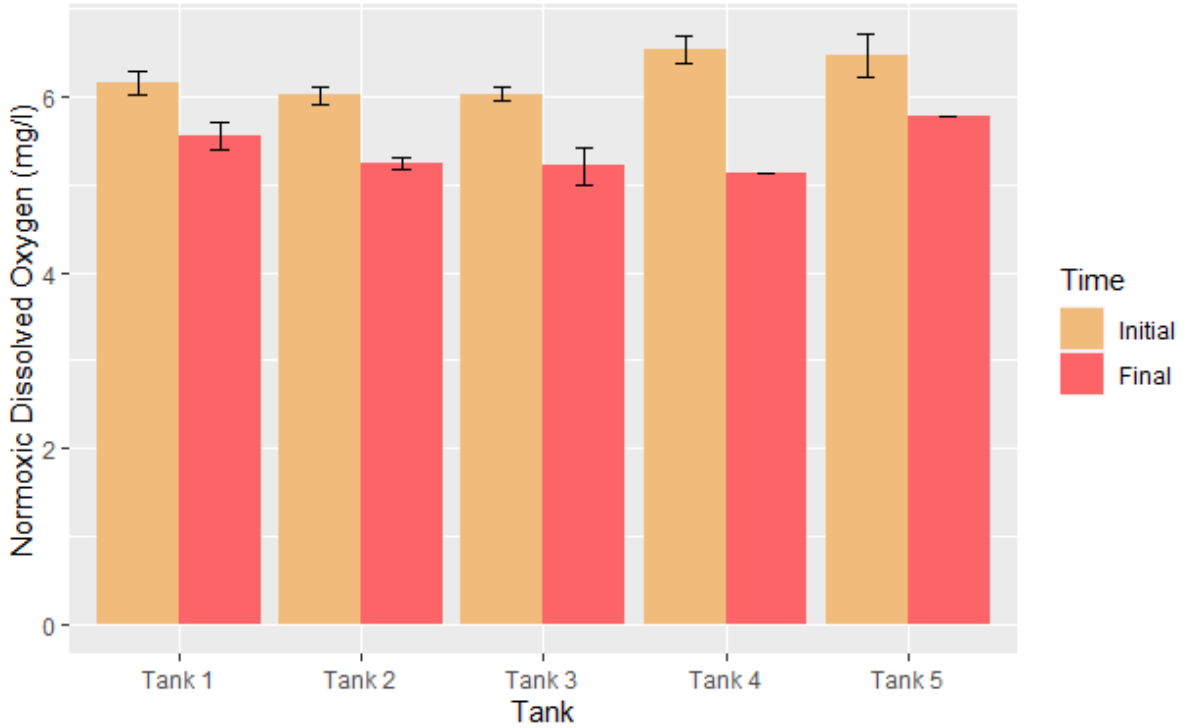

Figure 1. Dissolved oxygen in tanks with normoxic regime

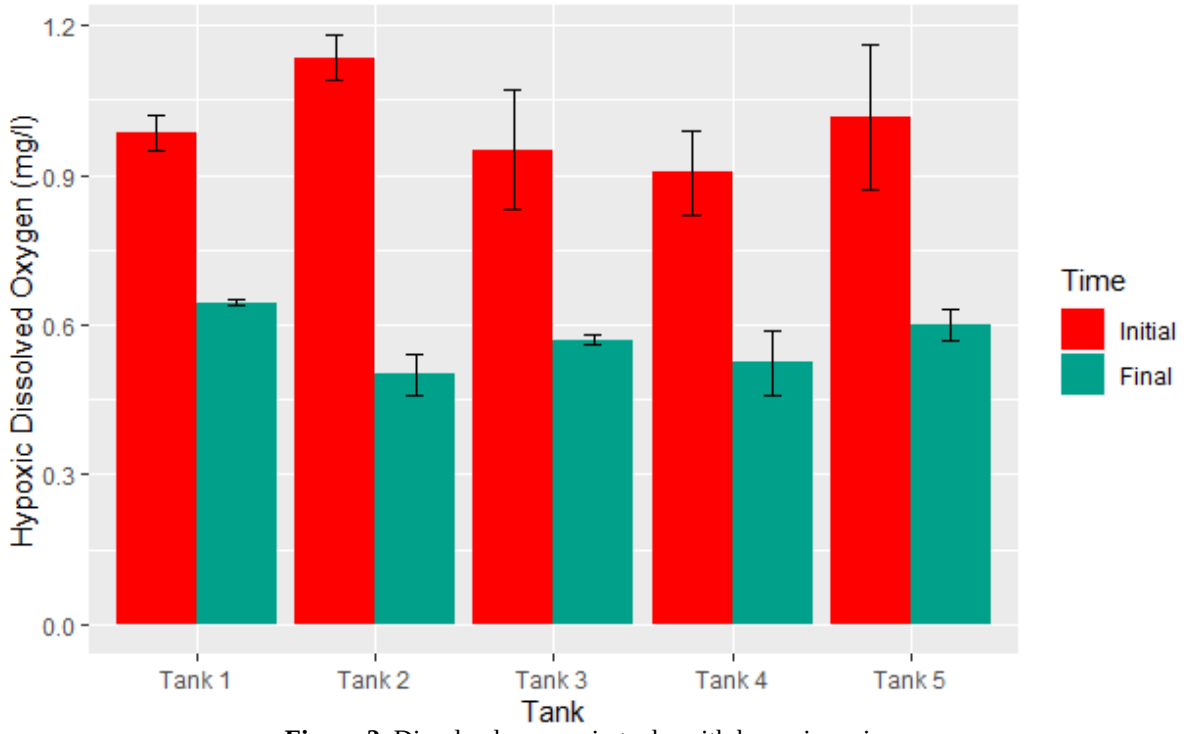

Figure 2. Dissolved oxygen in tanks with hypoxic regime

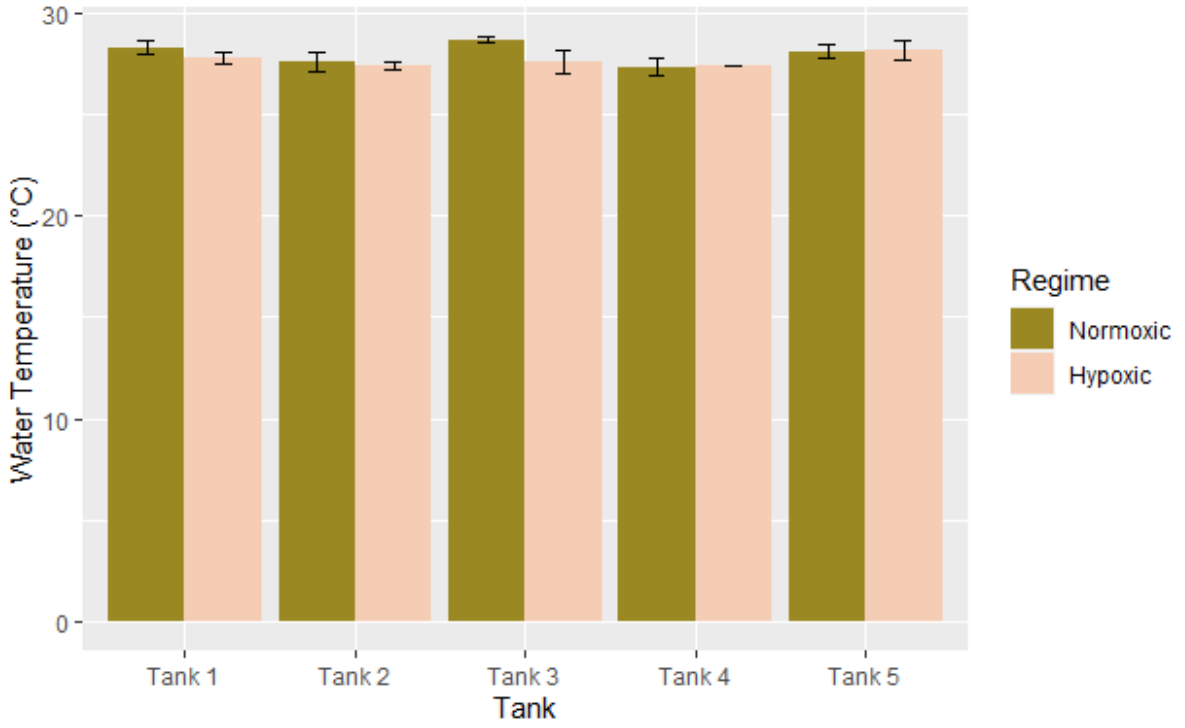

Figure 3. Water temperature in tanks with the normoxic and hypoxic regimes

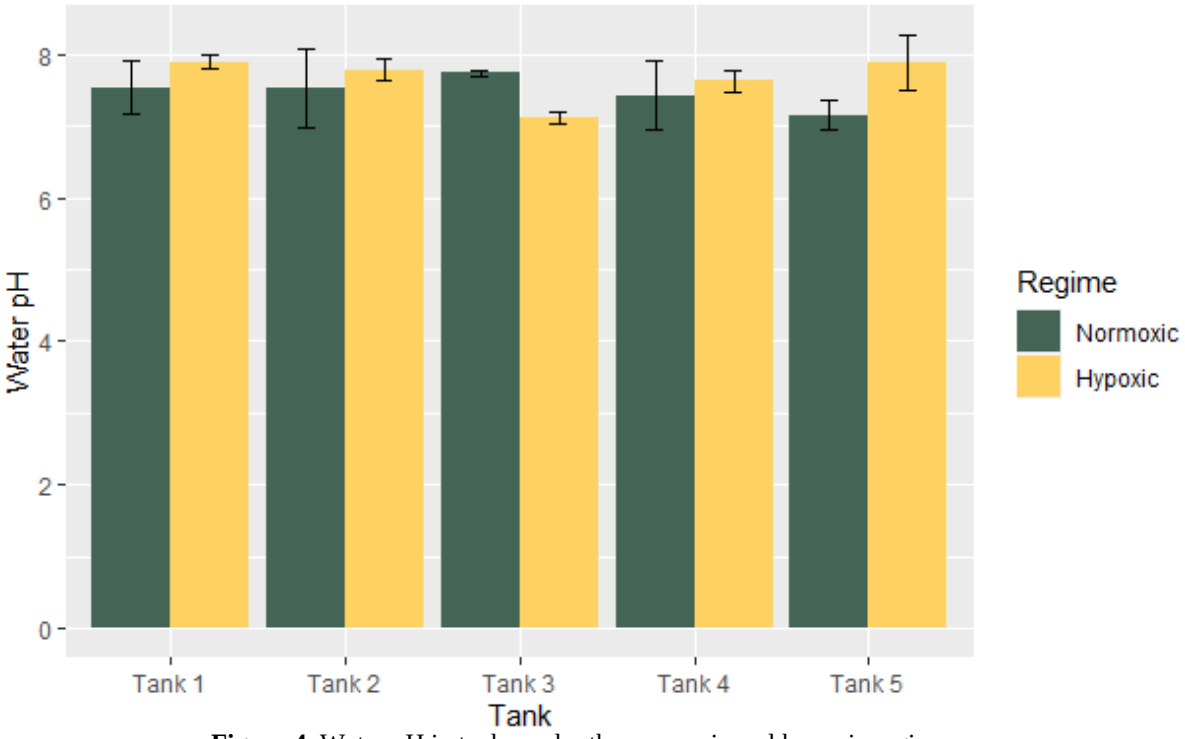

Figure 4. Water pH in tanks under the normoxic and hypoxic regimes

The behavioural pattern of the progeny from the various crosses under normoxic and hypoxic conditions (Figure 5-6) indicates a contrast between the normoxic and hypoxic regimes. Opercular beat rates (OBR) were significantly different ($p<0.05$) between the normoxic and hypoxic regimes in all treatments or crosses with values for the hypoxic regime being higher than the normoxic regime. Fish showed increased tendency to gulp air at the water surface under the hypoxic regime with increased swimming activity and subsequent lethargy prior to aeration.

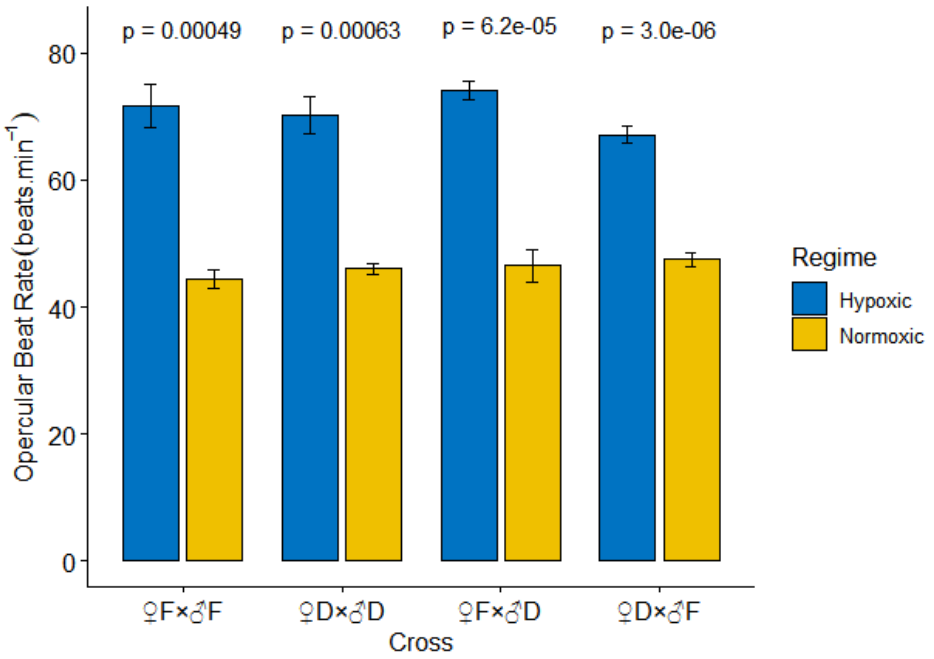

Figure 5. Opercular bet rate of *C. gariepinus* progeny under normoxic and hypoxic regimes

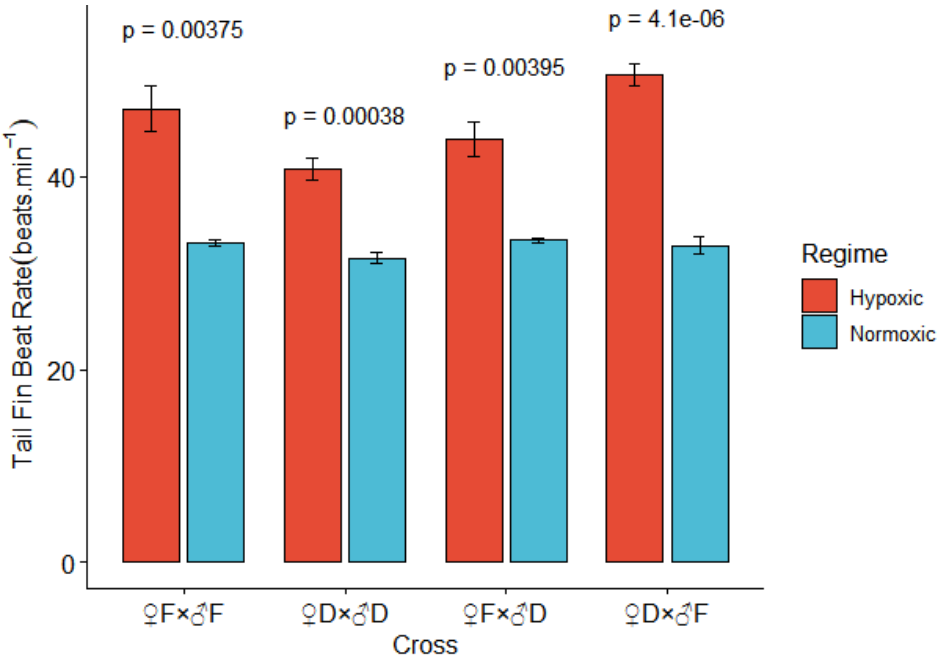

Figure 6. Tail fin bet rate of *C. gariepinus* progeny under normoxic and hypoxic reimes

The tail fin beat rate (TBR) was also significantly different ($p<0.05$) between the normoxic and hypoxic regimes with increased movement under the hypoxic regime compared to the normoxic regime (Figure 6). A comparison of the behavioural patterns for the crosses under the normoxic regime (Table 3) indicates that there was no significance difference ($p>0.05$) in both OBR and TBR for the progeny from the crosses. Under the hypoxic regime, (Table 3) there was no significant difference ($p>0.05$) between the progeny from the crosses for OBR but the TBR was significantly different ($p<0.05$) for the crosses tested.

Table 3. Behavioural pattern of progeny from reciprocal crosses of feral and domesticated *C. gariepinus* under normoxic and hypoxic regimes

Cross	♀F×♂F	♀D×♂D	♀F×♂D	♀D×♂F	p-value
			Normoxic regime		
OBR	44.34 ± 1.51	45.99 ± 0.95	46.53 ± 2.59	47.48 ± 1.14	0.618
TBR	33.10 ± 0.32	31.52 ± 0.54	33.37 ± 0.30	32.81 ± 0.87	0.131
			Hypoxic regime		
OBR	71.59 ± 3.41	70.3 ± 2.94	74.05 ± 1.51	67.14 ± 1.25	0.287
TBR	47.00 ± 2.35^{ab}	40.75 ± 1.12^{c}	43.82 ± 1.81^{bc}	50.51 ± 1.18^{a}	0.005

Means in the same row followed by different superscripts differ significantly ($p<0.05$)

The haematological indices of progeny from the crosses under normoxic conditions (Table 4) was not significantly different ($p>0.05$). Haemoglobin ranged from 11.49g.dl^{-1} in the cross ♀D×♂D to 13.00g.dl^{-1} for progeny of the cross ♀D×♂F. The values for mean corpuscular hemoglobin (MCH) that represents the average amount of hemoglobin in a blood cell ranged from 28.63pg in the cross ♀D×♂D to 33.61pg in progeny from the cross ♀F×♂D. The mean corpuscular hemoglobin concentration (MCHC), a measure of the average concentration of hemoglobin in a given volume of red blood cells was between 31.75g.dl^{-1} in progeny of the cross ♀D×♂D and 35.49g.dl^{-1} in progeny of the cross ♀D×♂F. The mean corpuscular volume (MCV), a measure of the average size of red blood cells ranged from 91.31fl for progeny from the cross ♀D×♂F to 98.78fl for progeny of the cross ♀F×♂D. Haematocrit, a measure of the percentage volume of red blood cells in the blood ranged from 35.70% in progeny from the cross ♀F×♂D to 36.64% in progeny from the cross ♀F×♂F. The number of erythrocytes or red blood cells (RBC) ranged from 3.62×10^{12}.l^{-1} in progeny from the cross ♀F×♂D to 4.08×10^{12}.l^{-1} in progeny from the cross ♀D×♂F. The number of leukocytes or white blood cells (WBC) ranged from 19.61×10^{9}.l^{-1} in the cross ♀F×♂F to 20.83×10^{9}.l^{-1} in the progeny from the cross ♀D×♂D.

Under hypoxic conditions (Table 4), there was also no significant difference ($p>0.05$) in blood count values across the crosses. Haemoglobin concentration ranged from 16.18g.dl^{-1} in the cross ♀D×♂D to 16.93g.dl^{-1} for progeny of the cross ♀F×♂D. The values for mean corpuscular hemoglobin (MCH) ranged from 23.03pg in the cross ♀D×♂F to 26.63pg in progeny from the cross ♀F×♂D. The mean corpuscular hemoglobin concentration (MCHC) was between 37.97g.dl^{-1} in progeny of the cross ♀F×♂F and 40.27g.dl^{-1} in progeny of the cross ♀F×♂D. The mean corpuscular volume (MCV) ranged from 58.17fl for progeny from the cross ♀D×♂F to 66.02fl for progeny of the cross ♀F×♂D. Haematocrit ranged from 41.51% in progeny from the cross ♀D×♂F to 43.44% in progeny from the cross ♀F×♂F. The erythrocyte count ranged from 6.45×10^{12}.l^{-1} in progeny from the cross ♀F×♂D to 7.27×10^{12}.l^{-1} in progeny from the cross ♀D×♂F. The number of leukocytes ranged from 23.41×10^{9}.l^{-1} in the cross ♀D×♂F to 24.55×10^{9}.l^{-1} in the progeny from the cross ♀F×♂F.

A comparison of haemoglobin values between normoxic and hypoxic regimes (Figure 7) reveals a significant difference ($p<0.05$) between both regimes for progenies from all the crosses. There was more variability in values within the normoxic regime for the crosses ♀D×♂D, ♀F×♂D and ♀D×♂F while the variability under the hypoxic regime was large among progenies of the crosses ♀F×♂F, ♀D×♂D and ♀D×♂F.

There was also a significant difference ($p<0.05$) between MCH values at the normoxic and hypoxic regimes (Figure 8) for three crosses: ♀F×♂F, ♀F×♂D and ♀D×♂F with less variability in values at the normoxic and hypoxic regimes for the cross ♀F×♂D. Similarly, the MCHC values were significantly different ($p<0.05$) between the normoxic and hypoxic regimes for the crosses: ♀D×♂D, ♀F×♂D and ♀D×♂F while the cross ♀F×♂F did not exhibit a significant difference ($p>0.05$) in MCHC values (Figure 9).

There was a significant difference ($p<0.05$) between MCV values in the normoxic and hypoxic regimes. Values of MCV (Figure 10) was high in the normoxic regime for progeny from the cross ♀F×♂F and ♀D×♂D while variability was high in the normoxic regime for progeny of the cross ♀F×♂F and ♀D×♂F. Haematocrit variation was high in the normoxic regime for two crosses: ♀F×♂F and ♀F×♂D. Within the hypoxic regime, there was high variability of haematocrit (Figure 11) among progeny of three crosses: ♀D×♂D, ♀F×♂D and ♀D×♂F. On the whole, haematocrit values at the normoxic regime were significantly different ($p<0.05$) from the hypoxic regime for all crosses.

There was a significant difference ($p<0.05$) in RBC values between the normoxic and hypoxic regimes for all crosses (Figure 12). The pattern of variation was such that high variability was associated with the hypoxic regime with the crosses: ♀F×♂F, ♀D×♂D and ♀D×♂F with minimal variability within the normoxic regime.

The levels of WBC in blood of the progenies exposed to normoxic and hypoxic conditions (Figure 13) indicates that there is a significant difference ($p<0.05$) in values between the two regimes. Variability was high under the normoxic regime in the cross ♀F×♂F and ♀D×♂F while variability was high in the crosses ♀D×♂D and ♀D×♂F at the hypoxic regime.

Table 4. Haematological parameters of progeny from reciprocal crosses of feral and domesticated *C. gariepinus* under normoxic and hypoxic regimes

Cross	Haemoglobin (g.dl-1)	MCH (pg)	MCHC (g.dl-1)	MCV (fl)	Haematocrit (%)	RBC (×1012.l-1)	WBC (×109.l-1)
	Normoxic regime						
♀F×♂F	12.69 ± 0.38	33.22 ± 2.44	34.81 ± 1.70	96.28 ± 8.20	36.64 ± 1.05	3.89 ± 0.26	19.61 ± 0.51
♀D×♂D	11.49 ± 0.73	28.63 ± 1.98	31.75 ± 2.34	91.33 ± 7.55	36.32 ± 0.69	4.05 ± 0.24	20.83 ± 0.46
♀F×♂D	12.15 ± 0.45	33.61 ± 1.32	34.12 ± 1.60	98.78 ± 2.74	35.70 ± 0.85	3.62 ± 0.12	20.50 ± 0.40
♀D×♂F	13.00 ± 0.58	32.45 ± 2.78	35.49 ± 0.86	91.31 ± 7.35	36.55 ± 0.87	4.08 ± 0.26	20.71 ± 0.48
p-value	0.271	0.388	0.459	0.825	0.871	0.477	0.282
	Hypoxic regime						
♀F×♂F	16.49 ± 0.47	24.34 ± 1.85	37.97 ± 0.78	63.92 ± 3.87	43.44 ± 1.01	6.89 ± 0.41	24.55 ± 0.30
♀D×♂D	16.18 ± 0.45	23.73 ± 1.89	38.45 ± 1.42	61.64 ± 4.04	42.18 ± 1.07	6.96 ± 0.49	24.53 ± 0.44
♀F×♂D	16.93 ± 0.33	26.63 ± 1.62	40.27 ± 1.30	66.02 ± 2.88	42.13 ± 0.88	6.45 ± 0.41	24.13 ± 0.26
♀D×♂F	16.46 ± 0.48	23.03 ± 1.84	39.71 ± 1.33	58.17 ± 4.93	41.51 ± 1.10	7.27 ± 0.40	23.41 ± 0.30
p-value	0.682	0.538	0.533	0.562	0.601	0.608	0.092

No significant differences among means on the same column (p>0.05)

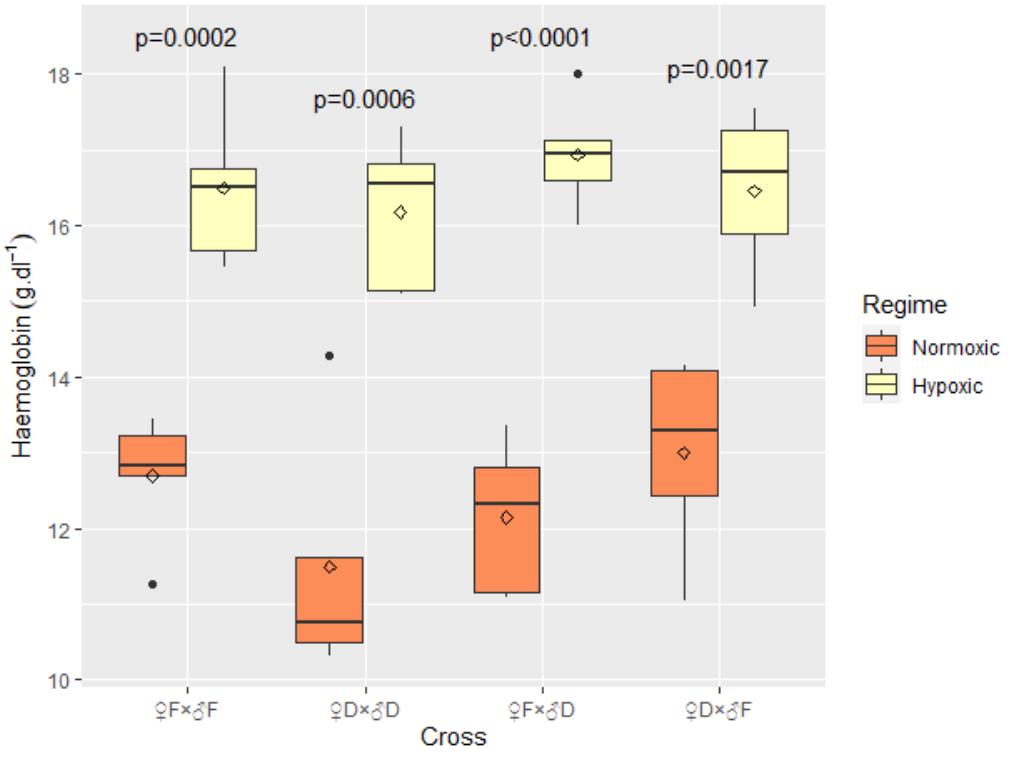

Figure 7. Comparison of haemoglobin in blood of progenies of crosses exposed to normoxic and hypoxic conditions

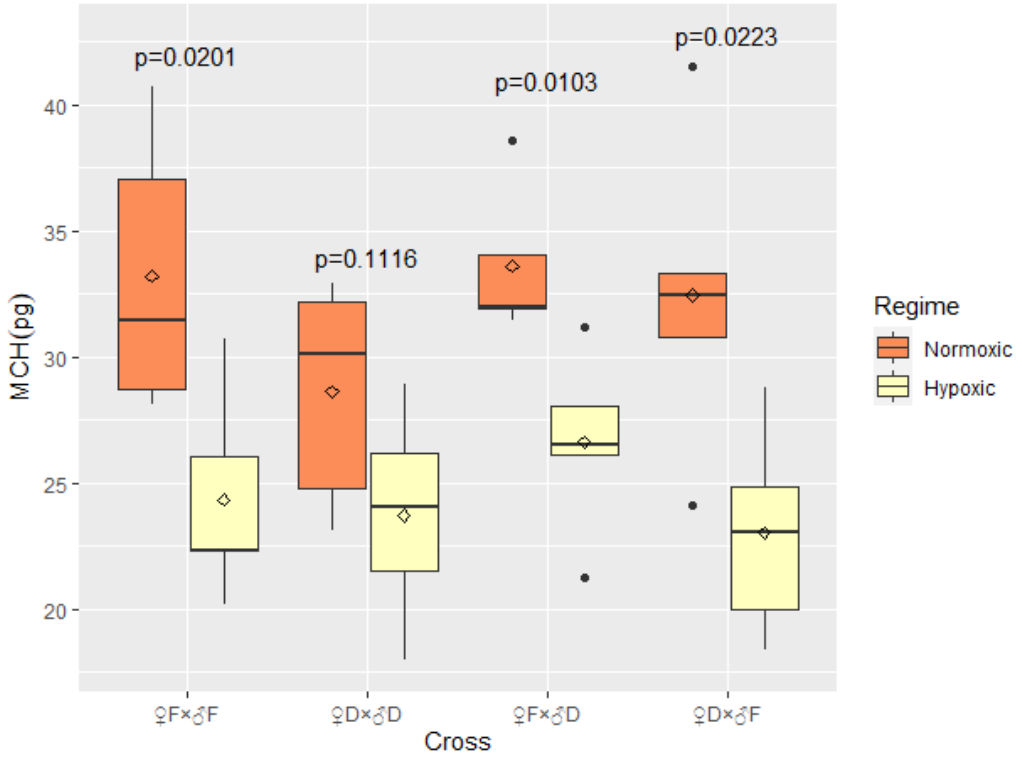

Figure 8. Comparison of MCH in blood of progenies of crosses exposed to normoxic and hypoxic conditions

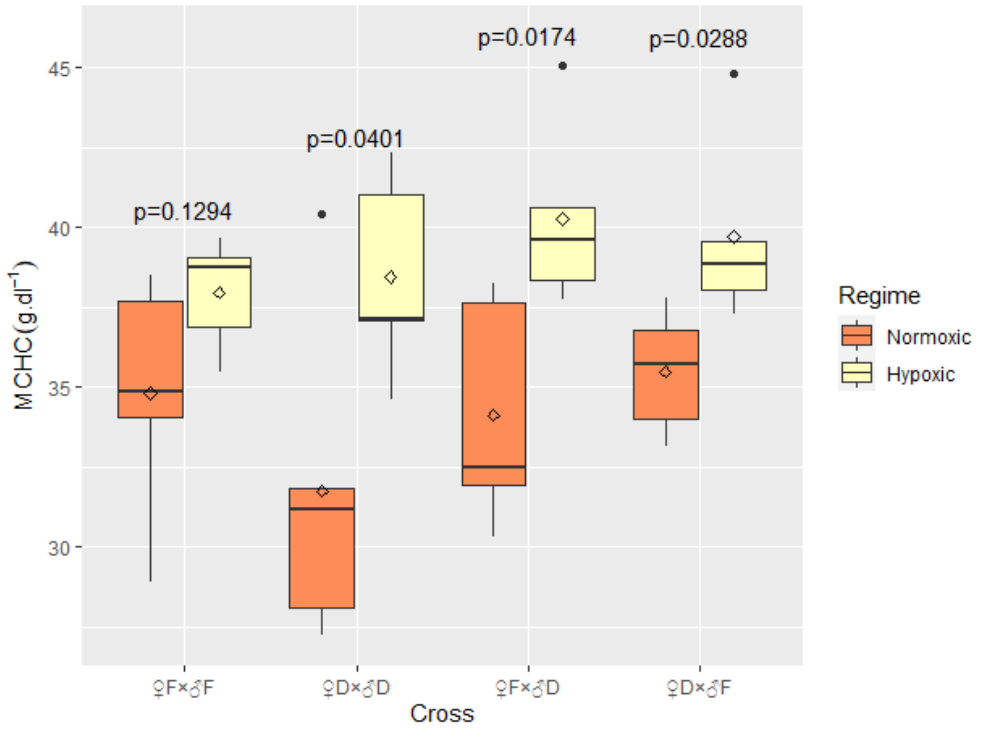

Figure 9. Comparison of MCHC in blood of progenies of crosses exposed to normoxic and hypoxic conditions

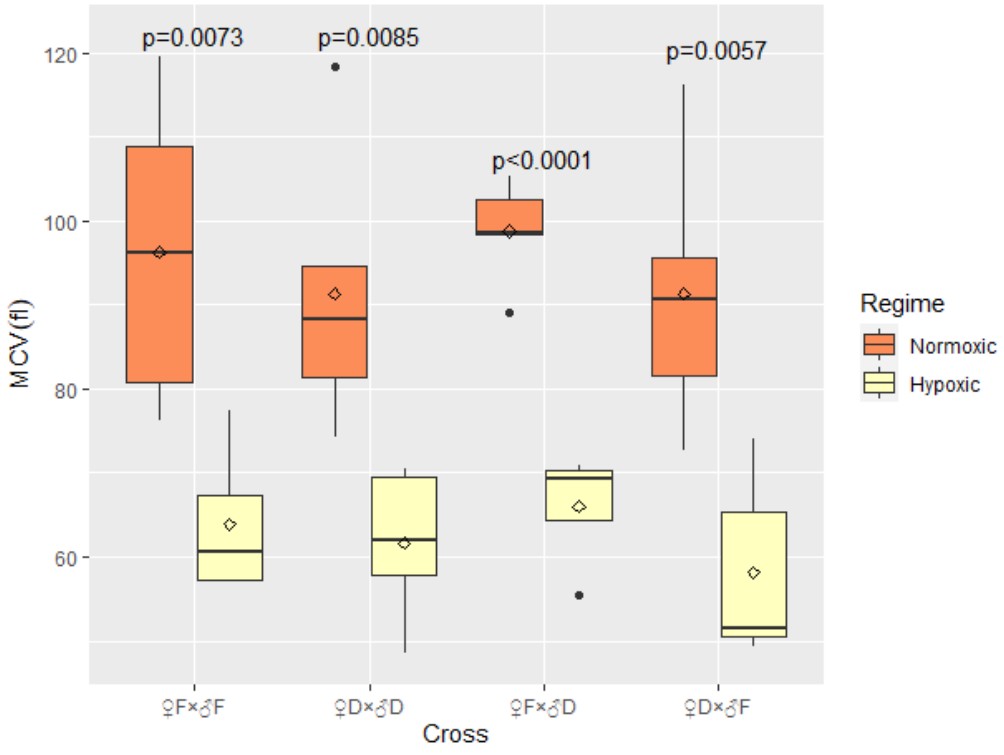

Figure 10. Comparison of MCV in blood of progenies of crosses exposed to normoxic and hypoxic conditions

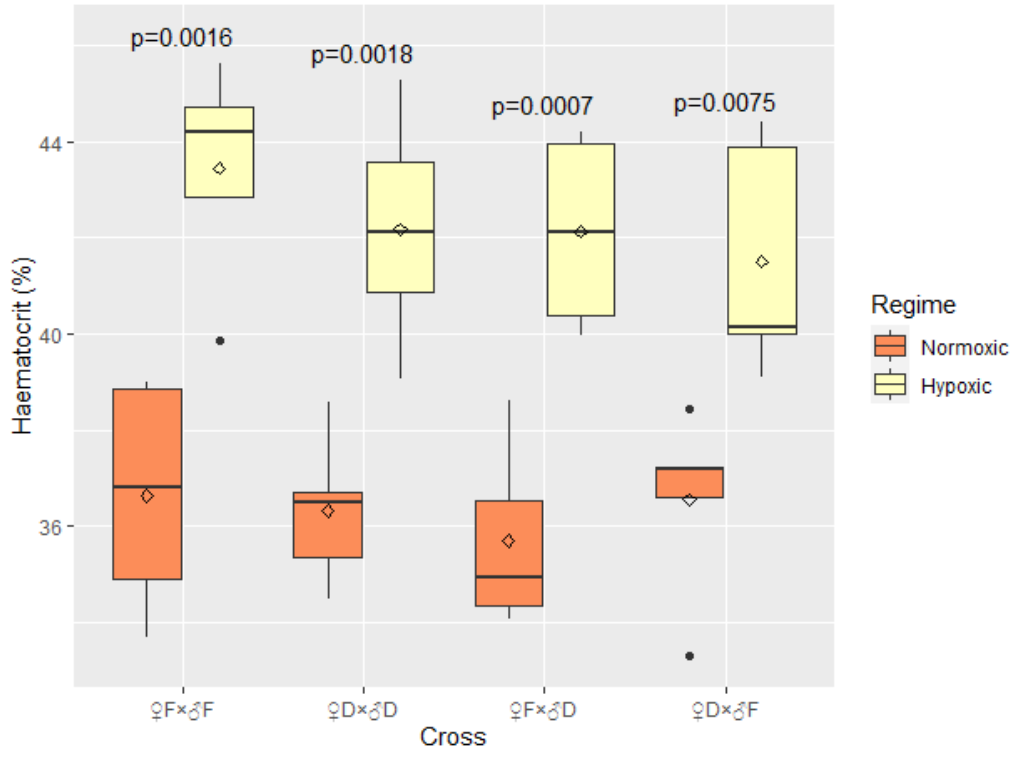

Figure 11. Comparison of haematocrit in blood of progenies of crosses exposed to normoxic and hypoxic conditions

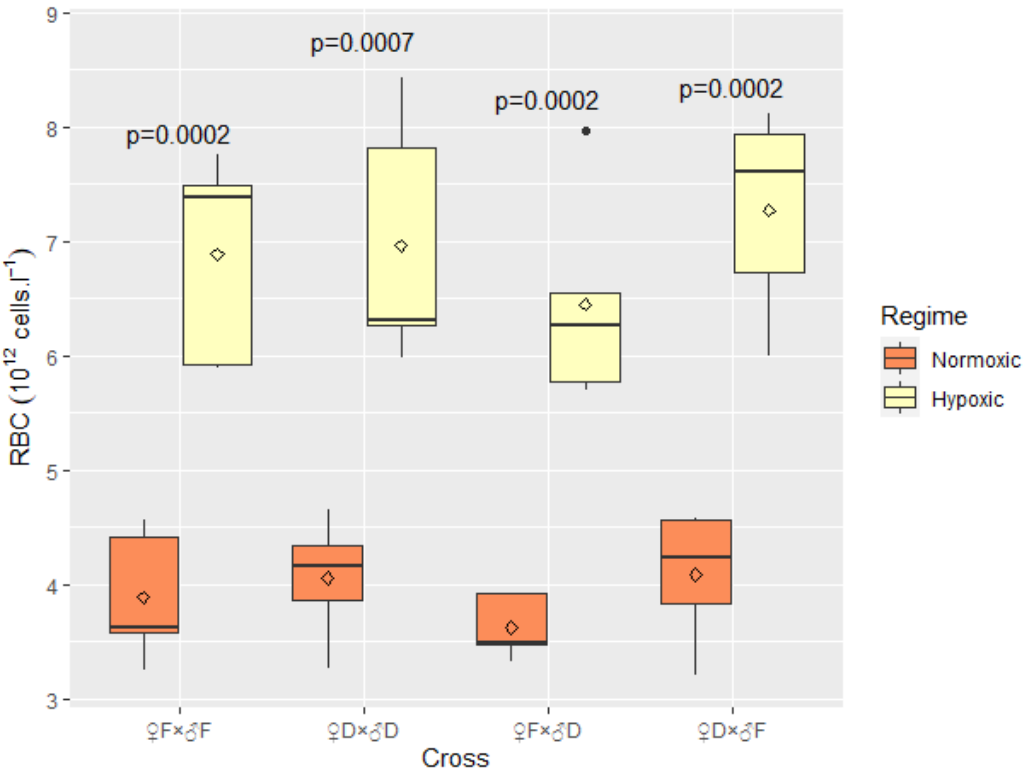

Figure 12. Comparison of RBC in blood of progenies of crosses exposed to normoxic and hypoxic conditions

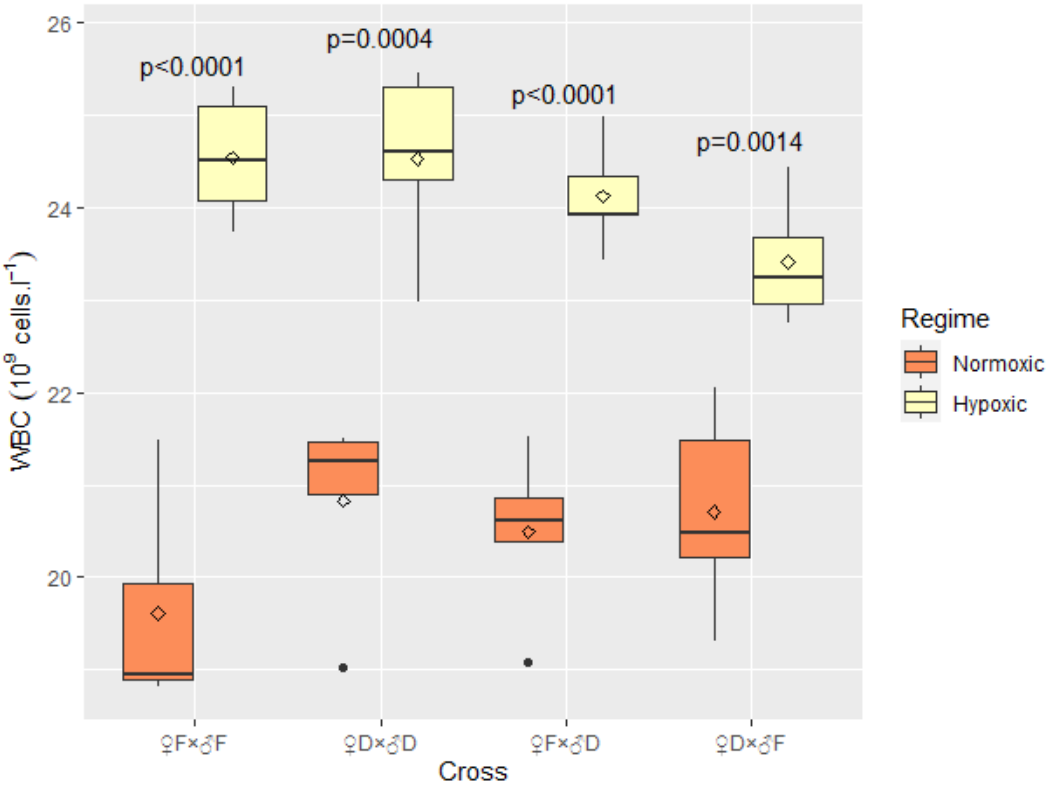

Figure 13. Comparison of WBC in blood of progenies of crosses exposed to normoxic and hypoxic conditions

IV. DISCUSSION

The entire gamut of physical, chemical and biological characteristics of water is what makes up water quality and this is important in aquaculture since the environment is controlled. Even though aquaculture systems are complicated, there are just a few water quality variables that are critical to fish growth and survival. The variable of great physiological importance is dissolved oxygen. The presence of hypoxia (DO levels <1–2 mg.l-1) aquaculture systems for even a few hours leads to fish stress with consequent adverse effect on fish growth and even mortality [36]. The behaviour of progenies from the various crosses as recorded in this study indicates that there is an effect of hypoxia on opercular activity since it increased under hypoxic conditions compared to normoxic conditions. There was no strain effect on the opercukar beat rate under both normoxic and hypoxic conditions. This implies that progeny responded in a similar manner to hypoxia by increasing opercular beat rate to compensate for deficiency in oxygen intake [37]. There was also an increase in tail fin beat rate (TBR) under the hypoxic regime. Tail fin movement was not affected by strain crossing under the normoxic regime but within the hypoxic regime, there was a genotype-regime interaction that resulted in a difference in tail fin activity among progeny of the crosses. It has been observed that active species increase swimming activity as a response to hypoxia [38]. In the present scenario, progenies from sires of feral origin displayed increased TBR compared to those from sires of domestic origin. Dam effects have been reported to be absent in a study to show tolerance of channel catfish and blue catfish hybrids to hypoxia [39].

Oxygen concentration is an important factor in blood chemistry and it is a determinant of respiratory success [40]. Fish can respond to hypoxia either by increasing gill surface area through the opening up of secondary lamellae of the gills [41, 42] or by increasing the concentration of red blood cells in order to increase oxygen carrying capacity of blood [43]. The progenies from crosses investigated in the current study responded in a similar manner with regards to their haematological variables under either normoxic or hypoxic dissolved oxygen regimes. The reason for this lies in the fact that the Afican catfish has a third coping strategy for hypoxia, its accessory breathing organ which enables the fish utilize atmospheric oxygen that can be acquired by jumping to gulp air [16]. There was a general increase in haematological indices for all crosses as a result of hypoxia.

The increase in haemoglobin (a protein that transports oxygen and gives blood its red tint) under the hypoxic regime indicates that there is a decrease in blood plasma level [44]. The increase in number of red blood cells under the hypoxic regime is characteristic of air breathing fish (Wells et al., 2005). Therefore, strain difference may not be expressed and offspring will generally inherit adaptive capability regardless of the point

of origin or even long domestication. Given these, values of mean corpuscular volume and mean corpuscular haemoglobin decreased under hypoxia indicating that with the increased production of haemoglobin, the available iron is not enough to cope and this creates a situation of microcytic anaemia. With the increase in haemoglobin, the mean corpuscular haemoglobin concentration also increased significantly in crosses that involved any domesticated parent. This indicates that adaptation is severely affected if genes are not purely from the feral or domesticated line. The haematocrit level which indicates the percentage volume of red blood cells increased under the hypoxic regime to compensate for oxygen deficiency. Studies have shown that haematocrit increases significantly within one hour of exposure to hypoxia [17, 45, 46]. As an additional strategy, the mean corpuscular volume (MCV) also increased in all crosses investigated. This is part of physiological response to enlarge oxygen carrying capacity of blood [47]. Increased levels of white blood cells as observed in this study is consistent with reports that show that WBC increase under hypoxic conditions [48].

Variability in the various haematological indices under the normoxic and hypoxic regimes indicates that there is some within population differences in adaptation to hypoxia. However, between population variation in blood count was identical for all the crosses. This indicates that genotypes that can tolerate hypoxia exist and can be isolated [39]. Strain and body size are two factors that contribute significantly to variation in tolerance of hypoxia in catfish [49]. The cross between the feral female and the domesticated male results in a more consistent response of haemoglobin to hypoxia than other crosses. The cross ♀F×♂D elicits a more consistent response of MCH and MCV to either normoxia or hypoxia than the other three crosses. Consistency in WBC under hypoxic conditions exist for the crosses ♀F×♂D and ♀D×♂F which are reciprocal crosses as opposed to the pure line crosses.

V. CONCLUSION

The genotype–environment effect was pronounced for swimming under hypoxia with the geographic origin of the African catfish sires playing a significant part. In the wild, African catfish would not be exposed to hypoxia as would domesticated catfish due to management and increased stocking density. This explains why they may not tolerate hypoxia compared to domesticated catfish. This also affected the crossbreeds between feral and domesticated African catfish. There was no significant strain effect on haematology of the African catfish in response to hypoxia. Variability in haemoglobin, MCV, MCHC and WBC were not high in some crosses. This implies that further studies are required to select for tolerance to hypoxia using these blood indices. The current study is the first attempt to show the effect of domestication on hypoxia tolerance of the African catfish.

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