Growth performance and microstructure in the muscle fiber of red tilapia (*Oreochromis* spp.) under different cycles of fasting and refeeding

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Abstract. Fasting is a widely recommended feed management in aquaculture. Growth in fish is closely related to the muscles, through hyperplasia and hypertrophy. This study aims to evaluate the growth performance and muscle fiber of red tilapia, *Oreochromis* spp., in various cycles of fasting and refeeding. The activity was carried out at the Research Institute for Fish Breeding. The research method was experimental, with 5 treatments (each one with 4 replications), namely: (1) control (90 days of feeding), (2) 7 days of fasting and 83 days of refeeding, (3) 14 days of fasting and 76 days of refeeding, (4) 21 days of fasting and 69 days of refeeding, and (5) 28 days of fasting and 62 days of refeeding. Maintenance was carried out for 90 days. The results showed a decrease in the growth, along with the increase of the fasting period, but also a trend of accelerated growth after the refeeding period, with overcompensatory growth in the 7 days fasting treatment (S7). This study showed that the red tilapia fasting for 7 days and refeeding for 83 days had the highest muscle fiber frequency in the diameter class D>50 μm. All treatments showed the distribution of muscle fibers in a mosaic pattern, characterized by different fiber diameters. These results indicated hyperplasia and hypertrophy. Therefore, the protocol for the S7 treatment is effective for increasing the productivity of the red tilapia aquaculture.

Key Words: compensatory growth, muscle fibers, hyperplasia and hypertrophy, red tilapia.

Introduction. Currently, the focus of research is on the efforts to improve the growth performance of tilapia through both conventional and modern breeding programs. However, it is known that there is a simpler and more practical method that can be applied in the management of tilapia, namely the feed management. This strategy is carried out by developing various feeding methods based on reducing the feed input to avoid water quality problems and labor costs. The commercial feed is combined with alternative feed in a controlled manner, through body weight-based feeding or cycles of fasting and refeeding (Blanquet & Oliva-Teles 2010; Cuvin-Aralar 2012).

Feed restriction through fasting is a widely recommended feed management strategy in aquaculture, due to its positive effect on the fish growth performance, namely increasing the body size and thickness of fish meat at harvest, which is called compensatory growth. This phenomenon is described as a growth increase resulting from the proper refeeding process, after a period of feed restriction or fasting. The compensatory growth is accelerated in response to the feeding restriction, providing evidence that animals can "evaluate" the achieved growth and adjust for higher growth rates (Broekhuizen et al 1994). Several factors that influence compensatory growth are the duration of the lack of feed (nutrition), the developmental stage at the beginning of the lack of feed and the age, sex and conditions of the digestive tract (Ryan 1990). Fasting and refeeding have variable effects on the compensatory growth of tilapia, depending on the rearing phase and feeding time restrictions (Wang et al 2009; Breves et al 2014).

Several studies reported the effect of fasting on the growth performance, with various results. Pacu fish (*Piaractus mesopotamicus*), given dietary restrictions for a long time, was able to show an increased growth after being fed again (Takahashi et al 2011). Mullet fish (*Mugil chepalus*) fasted for 30 days had the same growth performance (weight gain, specific growth rate and final weight) as fish fed continuously (Akbary & Jahanbakhshi 2016). The results of the research of Xu et al (2019) on goldfish reported that goldfish fasted for 14 days, followed by 14 days of feeding, had a lower feed efficiency and the same weight gain as fish fed for 28 days. From the results of the research on tilapia, it was reported that the short-term fasting period of 2 days, followed by refeeding for 4 days, with a maintenance period of 60 days, resulted in a growth (weight gain and specific growth rate) that was not different from the control fish sample (Gabriel et al 2017). However, it is different from the report of Moustofa & El-Kader (2017) concerning the monosex black tilapia which, after 4-15 days of fasting and 30 days of refeeding, experienced a negative effect on their growth performance.

Growth is closely related to the muscles because muscle tissue covers 40-75% of the total body mass (Carani et al 2008). The muscle is one of the most important tissues, which is greatly affected by fasting and refeeding. There are genetic changes caused by the process of fasting and refeeding, resulting in differences in the growth rates and changes in the muscle tissue (Hornick et al 2000). Among the various muscle types, white muscle tissue represents more than 90% of the muscle tissue in most teleostean fish; therefore, changes in the fish body weight mainly occur due to changes in the muscle growth (Alami-Durante et al 2010). Muscle tissue growth in fish involves a combination of enlargement of muscle fibers (hypertrophy) and addition of new muscle fibers (hyperplasia), which will affect the bodyweight of the fish at the end of rearing (Rowlerson & Vegetti 2001; Johnston et al 2011; Zhu et al 2014). After 5 days of fasting 15 days of refeeding, tilapia showed significant hypertrophy and hyperplasia, with a total muscle frequency of more than 40% and a muscle diameter ranging from 20-30 μm (Nebo et al 2013).

Based on some of the studies above, it was noticed that fasting has a different effect on the fish growth performance. Overall, these findings provide insight into the beneficial role of implementing aquaculture management by fasting and refeeding for the fish growth, depending on the protocol used. Therefore, it is necessary to carry out further research on the red tilapia, *Oreochromis* spp., by modifying the existing protocols, while applying the method of fasting and refeeding. This study aims to evaluate the growth performance, morphological structure and morphometry of the red tilapia muscle fiber, during various cycles of fasting and refeeding.

Material and Method

Research location and time. This activity was carried out at the tilapia commodity hatchery at the Research Institute for Fish Breeding during August-December 2020.

Growth. The test fish consisted of juvenile red tilapia, the second generation of family selection results in 2020. The fish had a length of 12.29±0.04 cm and a body weight of 35.59±0.17 g. The maintenance container for the study was a pool with 20 units (separated by walls), with a size of 2x1x1 m^3 filled with 1,700 dm^3 of water. Each tub unit is equipped with aeration and running water systems with a flow rate of 1 L $minute^{-1}$. The total number of fish used was 560 fish with a stocking density of 28 specimens, for each container. Before being given the treatment, the fish were acclimatized with feed at satiation, according to their biomass weight, with a frequency of 2 times a day (morning and evening), for 1 week. This study used a completely randomized design, with 5 treatments and 4 replications, consisting of fish fed continuously as control (K), 7 days of fasting and 83 days of refeeding (S7), 14 days of fasting and 76 days of refeeding (S14), 21 days of fasting and 69 days of refeeding (S21), 28 days of fasting and 62 days of refeeding (S28). The total maintenance time for each treatment was 90 days. During the maintenance, fish received commercial feed with a protein content of 30-32% and a frequency of 3 times a day, at satiation (08.00 am, 12.00 and 04.00 pm). To maintain the quality of the water, activities were carried out by piping and changing 60% of the water, every two days.

Growth sampling activity was carried out once a week. The parameters observed in this study included: the growth of absolute weight gain and specific growth rate (SGR) were calculated according to NRC (1977), feed conversion ratio was calculated by feed intake divided weight gain according to Goddard (1996). The growth of biomass is the difference between the initial biomass weight and the final biomass weight. The survival rate was calculated by number of fish at the end of the experiment divided by the number of fish at the beginning multiplied by 100. The number of samples observed each week, from each unit, was 15. Also, the biometric parameters were calculated, namely the condition factor and the hepatosomatic index were calculated according to (Jobling et al 1994). Biometric measurements were carried out to determine the fish condition factor (CF) at the beginning and at the end of the study, by measuring the total length and body weight of each specimen. Then the hepatosomatic index (HSI) was measured by weighing the fish liver, obtained by dissection. Below are some of the formulas used for the calculations:

$$W= Wt-W0$$

$$SGR= \frac{\mathrm{Ln}\,(Wt)-\ln(W0)}{t} x100$$

$$CF= \frac{W}{L^3} x100$$

$$HSI= \frac{Lw}{W} x100$$

Where:
Wt-the final body weight of fish (g);
W0-initial body weight (g);
t-the time duration of the experiment (days);
L-total length of fish (cm);
W-the body weight (g);
Lw-the liver weight of sample fish (g).

Muscle histology. The histological incision of the muscles was carried out in order to measure the diameter of the muscle fibers and the frequency of the muscle fibers. The sampling was carried out at the beginning of the maintenance at the end of the fasting periods (day 7, 14, 21 and 28) and after the refeeding periods. The number of fish specimens used for each histological sampling was 2 per replication. The muscle tissue was taken using a scalpel on the dorsal part of the fish (the white muscle), then the tissue was put into a bottle containing a 10% Neutral Buffered Formalin (NBF) fixative. The histological preparations were made by Hematoxylin-Eosin (HE) staining, in the Microbiology Laboratory of Research Institute for Fish Breeding. The results of the histological preparations were observed using a light microscope with a magnification power of 400x. Measurements were made by observing the smallest size of the muscle fibers' transverse sections, from 200 areas (Dubowitz et al 2013). Images were taken using a high-resolution camera (Q Color 3, Olympus, Melville, NY, USA), paired with a light microscope (Olympus BX45, Melville, NY, USA). The morphometric analysis were performed using an image analysis software, namely Image Pro Plus® 4.5 (Media Cybernetics, Silver Spring, MD, USA).

The parameters observed in this histological study were the diameter and the frequency of the muscle fibers, in order to determine the hyperplasia and hypertrophy conditions in the fish muscles. The method refers to Vegetti et al (1993), who categorize the muscle fibers into three different size classes, depending on their diameter, namely: <20, 20-50 and >50 µm in diameter. Then the frequency of fiber diameter was calculated in each class (<20, 20-50, and >50 µm), by including the standard deviation. Muscle fibers that have a diameter of <20 µm show a hyperplasia process and muscle fibers that exceed a diameter of 50 µm indicate a hypertrophic process (Weatherley et al 1988).

Statistical analysis. The data obtained were analyzed using a one-way analysis of variance (ANOVA) and followed by Duncan's Multiple Distance Test, if there were found differences. The significance of the differences was defined at $p<0.05$. These statistical analyses were performed using the SPSS 22 software.

Results

Growth performance. Based on the results of the study, it can be seen the pattern of red tilapia weight gain in various fasting and refeeding treatments (Figure 1). The fasting period causes red tilapia to experience a significant decrease in body weight gradually according to the time of fasting. However, after the refeeding period, the weight growth of fasting red tilapia has increased gradually until the end of the rearing period (90 days). In the 7-day fasting treatment (S7), the same weight growth pattern was observed as in the control treatment (fish fed continuously) at the 42nd day of rearing or the 35th day after refeeding. This indicates that compensatory growth has occurred, even during the rearing. At the end of the 90 days of maintenance, the length and weight growth under the S7 treatment were higher than in the control treatment. The treatments S14 and S21 only showed a partial growth and the treatment S28 refeeding could not produce a compensatory growth after a period of refeeding. Besides, the growth in these treatments was still lower than in the control treatment.

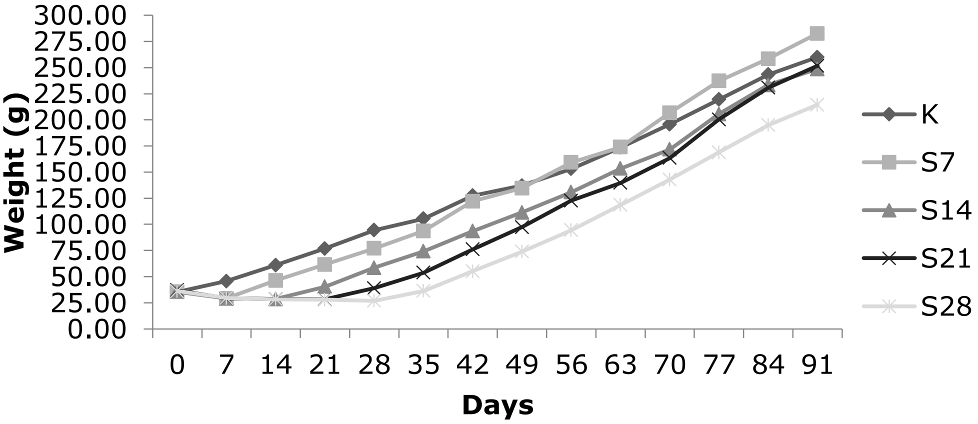

Figure 1. The growth pattern of red tilapia during maintenance.

Changes in the growth performance of red tilapia are presented in Table 1. After the fasting period, the lowest reduction in the body weight (17.64±1.81%) is shown in the treatment S7, while the highest weight loss (24.82±0.10%) was observed in the treatment S28, compared to the control. At the end of the experiment (90 days), the highest absolute weight growth was shown after 7 days of fasting and 83 days of refeeding (the S7 treatment), namely 10.22% higher compared to the control. Based on the data, it can be seen that in the S7 treatment the highest SGR reached 2.3% g day^{-1} and the lowest FCR value was of 1.29. These results indicate that red tilapia under the treatment S7 can utilize feed more efficiently for growth than under the control treatment and the other fasting treatments. The statistical results on the weight gain, SGR, biomass gain and feed consumption indicated that there was a significant difference between the S7 treatment and the other treatments ($P<0.05$), but the S7 treatment was not significantly different from the control ($P>0.05$). Related to the feed conversion ratio parameter, the S7 treatment was significantly different from the control ($P<0.05$), but not significantly different from the other treatments ($P>0.05$).

The highest value-added of biomass and total feed consumption was recorded for the S7 treatment and the lowest for the S28 treatment. The low value of the S28 treatment was due to a longer fasting period and to a shorter refeeding time, which prevented fish to take the time for the nutritional intake. Post-fasting, fish experienced an increased appetite, called hyperphagia. In the S7 treatment, the fish had a higher feed intake after 7 days of fasting, in sufficient quantity and time, so that the hyperphagia state lasted optimally. The results of the statistical survival rate test showed that the S14 treatment had a significantly different value ($P<0.05$) from the other treatments (Table 1). In this study, the value of the survival rate was classified as high, ranging from 95 to 100%, which indicated the fish resistance during the rearing. The amount of the fish body weight at the end of the rearing must be in line with the high survival rate, in order to achieve a maximum level of cultivation productivity. For all treatments, during the fasting period, there were no deaths in, but at the time of refeeding mortality occurred in the S7, S14 and S21 treatments. There were more deaths due to the handling factors, after the sampling activities, such as measuring the fish length and weight. As a result, some fish experienced stress after sampling, losing their appetite and starving to death.

Table 1

Growth performance of red tilapia under different cycles of fasting and refeeding

Parameters	*Treatments*				
	K	*S7*	*S14*	*S21*	*S28*
Initial weight (g)	35.7±1.3	35.5±1.4	35.8±1.5	35.4±1.5	35.6±1.4
Weight end of fasting (g)	-	29.5 ± 1.1^{a}	28.3 ± 1.2^{ab}	27.0 ± 1.4^{bc}	26.4 ± 0.8^{c}
Final weight (end of refeeding) (g)	259.9 ± 23.1^{ab}	282.5 ± 15.3^{a}	248.6 ± 15.4^{b}	251.7 ± 10.8^{b}	214.3 ± 9.1^{c}
Weight gain (g)	224.1 ± 24.1^{ab}	247.0 ± 15.3^{a}	10.6 ± 0.52^{b}	216.2 ± 10.2^{b}	178.7 ± 10.2^{c}
Survival (%)	100^{a}	98.2 ± 2.1^{ab}	95.54 ± 4^{b}	99.11 ± 2^{ab}	100^{a}
SGR (g day^{-1})	2.2 ± 0.10^{ab}	2.3 ± 0.08^{a}	2.2 ± 0.04^{b}	2.2 ± 0.05^{b}	2 ± 0.08^{c}
Biomass gain (g)	$5,747\pm530^{ab}$	$6,029\pm257^{a}$	$5,379\pm330^{bc}$	$5,489\pm148^{ab}$	$4,468\pm254^{c}$
Feed consumption (g)	$8,193\pm706^{a}$	$7,741\pm516^{a}$	$6,862\pm468^{b}$	$6,576\pm648^{bc}$	$5,950\pm274^{c}$
FCR	1.41 ± 0.02^{b}	1.26 ± 0.03^{a}	1.28 ± 0.02^{ab}	1.27 ± 0.03^{a}	1.32 ± 0.02^{ab}

Different superscripts in the same row indicate significant differences ($P<0.05$) by Duncan multiple tests (n=4). The values shown are the average value and standard deviation.

At the end of the fasting period, the condition factor (CF) and the hepatosomatic index (HSI) decreased significantly ($P<0.05$) along with the fasting duration, compared to the controls (Figure 2). These results show that fasting time significantly affects the nutritional condition of the red tilapia body. At the end of the refeeding period, the value of the condition factor experienced an increasing trend in all fasting treatments, reaching the same value as the control treatment ($P>0.05$), which ranged from 1.96 to 1.99%. The treatment S7 showed the highest HSI value compared to the other treatments ($P<0.05$), at 9.89% higher than the control.

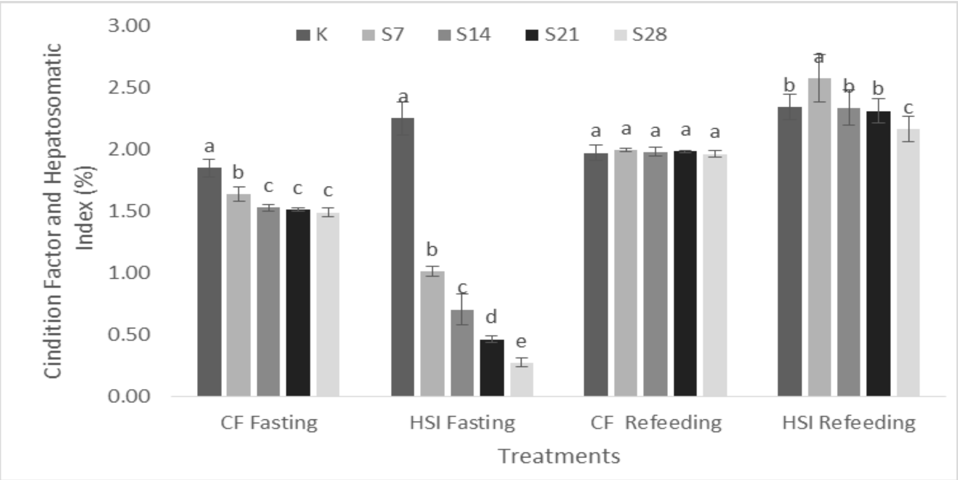

Figure 2. Condition factor (CF) and hepatosomatic index (HSI) of red tilapia fish after fasting and refeeding. Different superscripts in the CF and HSI indicate significant differences ($P<0.05$) by the Duncan multiple tests (n=4). The values shown are the means and the standard deviations.

Muscle fiber diameter. Based on the research results, it was concluded that fasting significantly affects the muscle red tilapia fish. The fasting treatment followed by refeeding affects the diameter of red tilapia muscle fibers as presented in the Table. 2. The results of muscle histology cross-sectional incisions at the end of the fasting and refeeding periods are presented in Figures 3 and 4. In this study, the red tilapia's muscle consists of round or polygonal muscle fibers separated by a soft connective tissue septum of the endomysium. Septa that are thicker than the connective tissue are known to separate the muscle fibers into fascicles and form the perimysium. The morphology of the satiated red tilapia's muscle fibers showed an increase in the recruitment of new muscle fibers with multinucleated cells with a peripheral nucleus. In the K treatment, a large number of muscle fibers with a central nucleus showed a pattern of mosaic hyperplasia. After the refeeding period, the red tilapia's muscle fiber morphology of showed a distinctive mosaic pattern with polygonal-shaped fibers. Small and large fibers were adjacent in all treatments.

In the present study, the largest muscle fibers diameter at the end of the fasting period was found in the treatment K (36.17 μm±0.72) and the smallest in the treatment S28 (26.26 μm±0.60). At the end of the refeeding period, the S7 treatment had the largest mean muscle fiber diameter (53.59 μm±0.42) and the lowest diameter value was found in the S28 treatment (42.85 μm±1.23). At the end of the fasting period, the muscle fiber diameter in all treatments was significantly smaller than in the treatment K. At the end of the refeeding period, the diameter in the S7 treatment was significantly larger ($P<0.05$) than in the other treatments but not significantly larger than in the treatment K ($P>0.05$). After fasting, the diameter of the muscle fibers showed a decreasing trend, while the density of the muscle fibers showed the opposite trend. After the refeeding period, the diameter of the muscle fibers increased, while the density decreased, in response to the fish's feeding.

Muscle fiber frequency. At the end of the fasting period, the statistical results showed a significant effect ($P<0.05$) of the treatments on the frequency of muscle fibers, with the highest values by diameter as follows: the S28 treatment dominated (20.50%) the $D<20$ μm class and the K treatment dominated (5.69%) the $D>50$ μm class. In all treatments, the frequency distribution of the muscle fiber diameter at the end of the refeeding period had a larger spread in the diameter class $D>50$ μm. Based on Table 3, the highest frequency distribution of muscle fibers in the diameter classes $D<20$ μm and 20 μm$<D<50$ μm was observed in the S28 treatment (2.44 and 66.94%, respectively). In diameter class $D>50$ μm, the highest frequency of the muscle fiber diameter was shown by the S7 treatment (57.13%) and the lowest by the S28 treatment (30.63%±1.25). The Duncan test results showed that in the diameter classes $10<D<20$ μm and $20<D<30$ μm, the muscle frequency in the S7 treatment was significantly lower than in the other treatments, but it did not differ from the treatment K. Likewise, in the diameter class $D>50$ μm, the muscle frequency in the S7 treatment was significantly higher than the treatments S14, S21 and S28, but not significantly different from the K treatment.

Table 2

The red tilapia's muscle fiber diameter (μm) at the end of the fasting period and at the end of the refeeding period

Treatment	*Mean muscle fiber diameter (μm)*	
	End of the fasting period	*End of refeeding period*
K	36.17 ± 0.72^{a}	52.66 ± 0.27^{a}
S7	31.42 ± 0.14^{b}	53.59 ± 0.42^{a}
S14	30.75 ± 0.29^{b}	47.50 ± 0.42^{b}
S21	27.46 ± 0.37^{c}	46.12 ± 0.46^{b}
S28	26.26 ± 0.60^{d}	42.85 ± 0.98^{c}

Different superscripts in the same column indicate significant differences ($P<0.05$) by Duncan multiple tests (n=4). The values shown are the average value and standard deviation.

Table 3

Frequency distribution of the red tilapia muscle fibers based on the diameter class (D<20 μm, 20<D<50 μm and D>50 μm) at the end of the fasting period and at the end of the refeeding period

Treatment	*Muscle fiber frequency (%)*					
	End of the fasting period			*End of the refeeding period*		
	D<20 μm	*20<D<50 μm*	*D>50 μm*	*D<20 μm*	*20<D<50 μm*	*D>50 μm*
K	7.50±1.29^{a}	86.81±1.89^{a}	5.69±1.07^{a}	0.00±0.00^{a}	43.56±0.72^{a}	56.56±0.88^{a}
S7	10.69±1.52^{b}	86.25±0.96^{a}	3.06±0.66^{b}	0.00±0.00^{a}	42.88±0.85^{a}	57.13±0.85^{a}
S14	13.31±1.07^{c}	85.94±0.97^{a}	0.75±0.20^{c}	0.50±0.41^{a}	58.25±0.65^{b}	41.25±0.96^{b}
S21	16.94±0.88^{d}	83.06±0.88^{b}	0.00±0.00^{c}	1.00±0.41^{b}	62.81±0.63^{c}	36.19±1.03^{c}
S28	20.50±0.41^{e}	79.50±0.41^{c}	0.00±0.00^{c}	2.44±0.43^{b}	66.94±1.56^{d}	30.63±1.25^{d}

Different superscripts in the same column indicate significant differences ($P<0.05$) by Duncan multiple tests (n=4). The values shown are the average value and standard deviation.

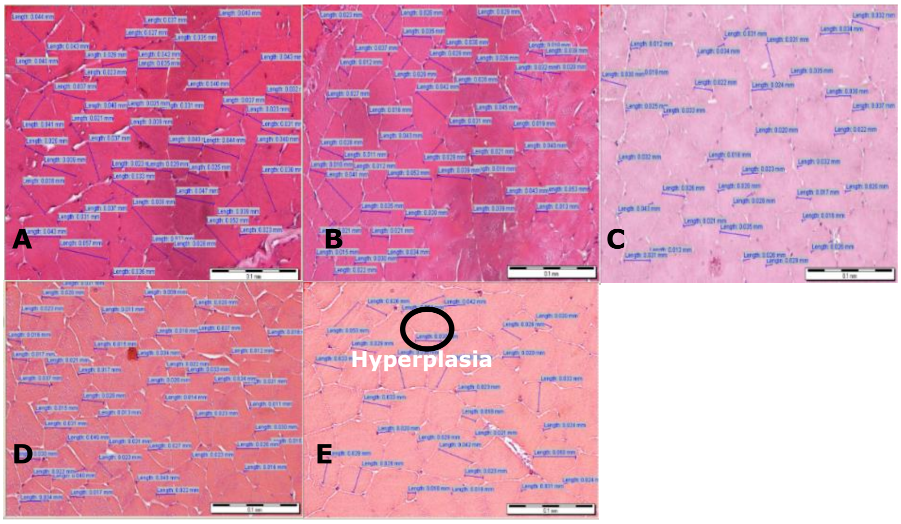

Figure 3. Histological cross-section of red tilapia muscle at the end of the fasting period (A (K), B (S7), C (S14), D (S21), E (S28)). Hematoxyline and Eosin stain (H&E); bar=0.1 mm.

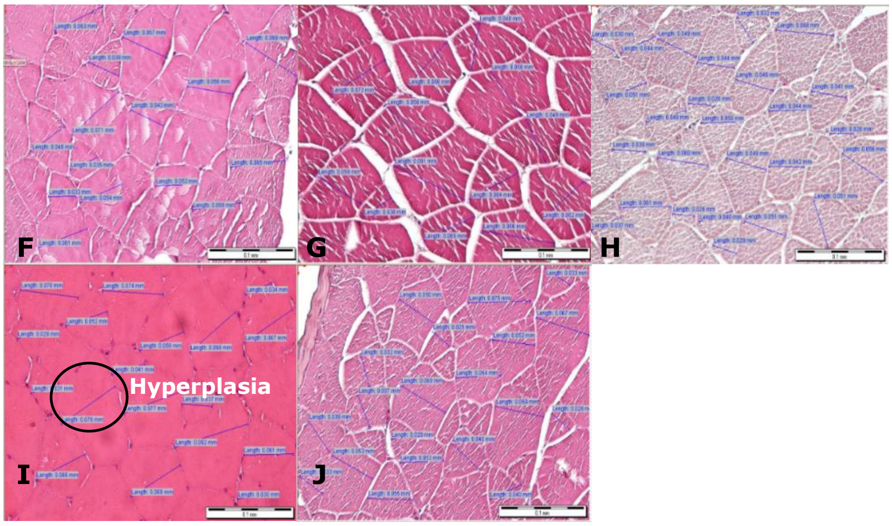

Figure 4. Histological cross-section of red tilapia muscle at the end of the refeeding period (F (K), G (S7), H (S14), I (S21), J (S28)). Hematoxyline and Eosin stain (H&E); bar=0.1 mm.

Discussion

Growth performance. Based on the research results, it was concluded that the growth pattern of the fasting red tilapia decreased at the end of the fasting period, but there was an increasing trend of growth after the refeeding period. This shows that during fasting, malnutrition occurred in red tilapia, which caused a decrease in the metabolic rate, but after the refeeding period the growth began to experience an upward trend, although only in the S7 treatment the growth was higher than in the control treatment (K), whereas in the other treatments, the growth at the end of maintenance was still lower than in the control. The low growth in the S14, S21 and S28 treatments was due to the short refeeding time, not sufficient for compensatory growth to occur. According to Zheng et al (2015), hunger reduces the metabolic capacity of the tissues and causes endogenous degradation of the energy sources (lipids, glycogen and protein) required for maintaining the physiological homeostasis of fish, which causes weight loss. Khotimah (2009) added that fish starving can cause energy use to be efficient due to a decreased metabolic rate, then when the refeeding process is carried out, there is a change in the pattern of the energy use for growth (derived from feed protein).

In this study, it was concluded that partial compensatory growth and even overcompensatory growth can be produced by the fasting treatment. Overcompensatory growth was produced by the S7 treatment, with a greater body weight value in red tilapia after 7 days of fasting, compared to fish fed continuously. As for the partial growth, it was observed in the S14 and S21 treatments, where the red tilapia weight could not reach the weight of the control fish, but showed a relatively fast growth rate. Laiz-carrión et al (2012) stated that compensatory growth is a phase of rapid growth, greater than normal or control growth, which occurs after a period of refeeding following a period of malnutrition. In the partial compensatory growth, the fish could not reach the same size as the control fish, but showed a relatively fast growth rate and had a better feed conversion, while overgrowth occurred when the animals experiencing restricted feed reached larger sizes for the same rearing period, compared to animals that are fed continuously (Jobling 1994; Ali et al 2003). Nicieza & Metcalfe (1997) stated that the effect of the nutrient deficiency on growth in length and weight can be substantially different (length growth increases but weight growth decreases). Therefore, the dynamics of growth recovery will also be different.

Several studies have shown that most fish species have a compensatory growth when fed normally after a period of starvation. Tian & Qin (2003) reported that snapper, after fasting for 1 week and refeeding for 8 weeks, showed a complete compensatory growth, whereas fasting for 2-3 weeks showed a partial compensatory growth. Likewise, the Persian sturgeon fish, after 1-3 weeks of fasting and 8 weeks of refeeding, showed a complete compensatory growth, as reported by Yarmohammadi et al (2015). As for black tilapia, it was reported that fasting for 5-10 days followed by feeding for 42 days resulted in partial compensatory growth (Nebo et al 2013). Gao et al (2015) stated that juvenile growth of tilapia, under a feed restriction (1-7 days) and maintained for a relatively long period (185 days), can match the growth of continuously fed fish, showing feed efficiency at the end of the maintenance period. Passinato et al (2015) confirmed that in adult fish (measuring 200 g) a feeding strategy to reduce feed costs would be 1 fasting day per week, which does not affect the growth performance, in terms of either compensatory rate or timing.

In this study, the phenomenon of compensatory growth is correlated with the absolute growth value and the specific growth rate. According to Ali et al (2003), Picha et al (2006) and Won & Borski (2013), the compensatory growth is usually characterized by hyperphagia, improved feed conversion ratio and high SGR. Jobling (1994) introduced several indicators of the occurrence of compensatory growth, including the high value of specific growth rates and bogy weight. this study concluded that tilapia, after 7 days, 14 days and 21 days of fasting, experienced a decrease in the body weight, but after refeeding they showed: (1) a higher weight growth rate and specific growth rate than the control, in the 7-day treatment, and (2) similar values as the controls, under the treatments with 14 and 21 days of fasting. The the SGR value during the refeeding suggested a recovery in terms of growth capacity and compensatory growth, in all treatments. This high growth value, especially in the 7-day fasting treatment, was followed by a lower feed conversion rate (FCR), compared to the control. This shows that in this treatment there was an improvement in the feed efficiency, where a smaller amount of feed was able to better increase the weight gain. This result is in line with Yarmohammadi et al (2015), who reported that Persian sturgeon, fasting for 1 week during the 8-week rearing period, had a weight gain value and specific growth rate of 75.84 g and 2.01, respectively, higher than the control. Nebo et al (2018) reported that black tilapia after 1 week of fasting and for 90 days of refeeding, had the same SGR value, but a lower weight gain than the controls. Likewise, Mozambique tilapia (*Oreochromis mossambicus)* showed a higher SGR after six weeks of refeeding, whereas at the eighth week of refeeding the SGR did not differ from the control. This result indicated that the compensatory growth was limited in the first six weeks of refeeding (Fox et al 2010).

In this study, the red tilapia experienced an appetite increase (hyperphagic) after each period of fasting. The duration of hyperphagia varied from a few days to several weeks, depending on the length of the fasting period. Hyperphagia promotes rapid growth in the presence of the compensatory growth phenomenon, as shown in the S7, S14, and S21 treatments. The fasting red tilapia can maintain hyperphagia two to three times longer than the duration of the fasting period (Abdel-Tawwab et al 2006). A similar behavior was reported on the hybrid sunfish (Hayward et al 1997), yellow perch (Hayward & Wang 2001), barramundi (Tian & Qin 2004) and juvenile rainbow trout (Nikki et al 2004). According to Jobling & Johansen (1999) and Yengkokpam et al (2013), fasting and refeeding fish will determine an increased appetite (hyperphagia). Hyperphagia contributes to the recovery of the energy deficits caused by the fasting period and results in an increased growth performance. The survival rate on juvenile red tilapia ranged between 95-100%, at the end of the experiment, which indicated the resistance of tilapia. The survival rate on juvenile red tilapia with weight (35 g) was not affected by the fasting for up to four weeks, ranging from 95-100%, at the end of the experiment, which indicated the resistance of tilapia. This result is in line with the report of Moustofa & El Kader (2017) on the monosex tilapia seeds (3.5 g) which were fasted for 4-15 days, but showed a survival rate ranging from 70 to 100%. Nebo et al (2018) reported that black tilapia (30.2 g), after up to 3 weeks of fasting, showed high survival rates, ranging from 79 to 84%. Likewise, in several other species it was reported that fasting did not affect the survival, such as in the red snapper, which after 32 days of fasting followed by 28 days of refeeding, showed a survival value of 96% (Lee et al 2016). *Mugil cephalus* fish are known to have a 100% survival rate after a fasting period of 30 days (Akbary & Jahanbakhshi 2016).

The value of the condition factor and the hepatosmatic index in this study increased after the refeeding period. These results indicate that after refeeding there is no restriction process in the protein synthesis. Therefore, the fish liver size increases because its nutritional needs are met. Relative changes in the condition factor and liver weight are major indicators of the physiological condition and weight loss caused by the lack of feed. This is probably the result of energy utilization for the basal metabolism, where energy needs are met by the liver glycogen reserves, followed by the use of the protein contained in fish muscles. The hepatosomatic index is considered a morphological index that is sensitive to the nutritional patterns. Caruso et al (2014) stated that fasting causes a decrease in the overall level of digestive enzymes, the most affected enzymes by the dietary deficiencies including: proteases, trypsin, chymotrypsin and carboxypeptidase A, amylase, and carboxypeptidase B. These enzymes are then increased after refeeding. Xu et al (2019) stated that the liver is an important energy storage organ. When food is not available, the substances stored in the liver of the fish are consumed first and the hepatosomatic index decreases.

According to Goede & Barton (1990) and Richter (2007), a simple measure of the level of energy reserves is known as the condition factor (CF). CF is also a quantitative parameter of the state of nutritional adequacy of fish because of its effects on growth, reproduction and survival. Caruso et al (2012) stated that low HSI values can be associated with nutritional problems because the fish liver size is relatively correlated with the nutritional status. The significant decrease of the HSI value in the fasting treatment shows the importance of the presence of liver fat reserves during the fasting period in tilapia. The results in this study are in line with the report by Sakyi et al (2020), stating that black tilapia, after 3-21 days of fasting, has lower values of the condition factor and HSI than the control, decreasing with the length of the fasting period and ranging from 1.14 to 1.54 and from 1.11 to 2.12, respectively. However, after a refeeding period of 21 days, the value was not significantly different of the control treatment. Gabriel et al (2018) also reported a decrease in CF and HSI values in tilapia fish: after 2 days of fasting and 2-4 days of periodical refeeding during the 60-day rearing period, the CF and HIS values were lower than in the controls, ranging from 1.76 to 1.83. Likewise, tilapia fed once a day had lower CF and HSI values than fish fed 2 to 4 times a day (Thongprajukaew et al 2017). As for other species, such as the mullet fish, it was reported a decrease in the CF values and HSI, ranging from 0.41 to 0.55 and from 0.80 to 0.92, after fasting 10, 20 and 30 days (Akbary & Jahanbakhshi 2016). After 14 days of fasting, goldfish experienced a decrease in CF and HSI values, but after 14 days of refeeding it showed insignificant differences, compared to the controls, at the end of the maintenance (Xu et al 2019).

Muscle fiber. In this study, the white muscle fibers of red tilapia show different diameters, being covered by a connective tissue layer, the endomysium, where capillaries and nerves can be found, and the perimysium which is the connective tissue sheath that holds the fibers in the fascicles together, to potentiate the muscle action. The presence of nucleated cells indicates the process of cell differentiation. These cells will migrate to the newly generated myoblasts, where they will be aligned and combined to produce new muscle fibers. According to Rescan (2019), the development of adipose tissue is a long-term process, occurring in the myosepta and perimysium of the fish, a connective tissue present in the adult fish muscles. The study of changes in muscle diameter has a particular role to play in understanding the fish growth and development processes. Muscle mass, indicated by the size of the muscle diameter, has a high correlation to the economic value of fish farming. According to Johnston et al (2011), the growth rate of fish is directly dependent on the accumulation of skeletal muscle mass which amounts to more than half of the total body weight and mainly contains protein. Skeletal muscle is one of the main sites for maintaining the energy homeostasis of organisms, other than the liver and heart. The high metabolic capacity of the skeletal muscle is driven by a broad requirement for ATP and is required to generate force and movement. The processes which constitute the main mechanisms in the muscle energy metabolism are the glycolysis and oxidative metabolism (requiring oxygen) (Mukund & Subramaniam 2020).

In this study, it was found that there were changes in the morphology and morphometry of the red tilapia muscle fibers when fasting and after refeeding. Like other vertebrates, satellite cells (muscle stem cells) in tilapia are located on the periphery of muscle fibers and connective tissue, where they migrate to fuse and form new fibers (Yin et al 2013). The presence of multiple nuclei in the connective tissue indicates a process of differentiation and/or proliferation for the growth or maintenance of muscle tissue. Skeletal muscle depends on the regeneration, which maintains the homeostasis and repair injuries. This process involves the recruitment of tissue stem cells, the muscle progenitor cells and the subsequent proliferative response of the newly generated myoblasts (Stern et al 2009).

The results of the study, in all treatments, showed that the distribution of muscle fibers formed a mosaic pattern characterized by different fiber diameters, an indication of the degree of new fiber formation. According to Fernandez et al (2000), the presence of large and small fiber diameters in white muscle is called a mosaic appearance. Carani et al (2008) reported a greater percentage of fiber in adult tilapia, with a larger fiber diameter (>32 μm) than in juveniles. Then rainbow trout was reported to have white muscle which increases faster than in brown trout and in brook trout, at the same weight, with a diameter of 31-40 µm (30.55%) and 41-50 µm (22.15%), respectively (Karahmet et al 2014).

De Mello et al (2016) stated that there are differences in the distribution of different fibers in the freshwater pomfret, between small fish and large fish as well as male and female fish. Buck et al (2017) noticed that in the tilapia culture period there was a gradual recruitment of new muscle fibers with a smaller diameter (<20 µm) and an enlargement of muscle fibers with a diameter of >50 µm. Fasting red tilapia (7 days to 28 days) presented a lower frequency increase in muscle diameter (size D<20 µm) than the control treatment. This indicates the occurrence of hyperplasia of the muscle fibers due to the fasting treatment, which is characterized by the presence of small and round fibers. The high frequency of muscles with a diameter of D<20 µm indicates an active hyperplasia growth mechanism and the presence of muscle fibers with a diameter greater than 30 µm indicates the beginning of differentiation and the occurrence of the hypertrophy process (Rowlerson & Veggeti 2001). This result differs different from the observations of Seiliez et al (2012), concerning the small size of the muscle fiber diameter, which illustrates the presence of muscle proteolysis due to the protein degradation in juvenile trout that undergo fasting for 14 days. According to Johnston et al (2011), changes in fish muscle fibers are influenced by several factors, namely temperature, swimming activity and availability of food. As for the larval stage, the dynamics between the hyperplasia and hypertrophy processes are a biological marker for the developmental phase towards the juvenile and adult stages (Vo et al 2016).

Mosaic hyperplasia occurs in large-growing fish, such as tilapia, and the production of new fibers is found throughout the myotome. This results in a mosaic pattern with different fiber diameters, as seen in the histological incisions of red tilapia muscle. Mosaic hyperplasia causes a large increase in the frequency of muscle fibers during the juvenile phase of growth. In hyperplasia, the fusion between satellite cells results in the formation of new myotubes on the surface of the existing fibers, which will further differentiate into muscle fibers (Johnston et al 2011). Yamashiro et al (2016) reported that tilapia larvae receiving enriched feed with 1.39% Phenylalanine showed the highest hyperplasia process in the muscle fibers with a diameter <20 µm by 80%.

The hypertrophy process is seen to occur more after the completion of the refeeding process. This is indicated by the increasing muscle fiber frequency in the dimension class >50 µm, together with a decreasing frequency in the 20-50 µm diameter class. This change in the distribution of fibers in red tilapia was present in all treatments, as an evidence of a hypertrophic muscle growth. However, there was still a frequency of the muscle fibers of a diameter <20 µm, indicating that the recruitment process for new muscle fibers was still ongoing during the period from the beginning to the end of maintenance. According to Johnston (2011), during the muscle growth in the hypertrophy process, the muscle fibers expand and absorb the satellite cell nucleus to maintain a relatively constant ratio between the cell nucleus and the cytoplasm. In the process of hypertrophic growth, satellite cells activate the fusion with existing muscle fibers by increasing the number of myonuclei and the synthesis of myofibrils, which causes an increase in the diameter or surface area of the muscle fibers. Then hypertrophy is also characterized by an expansion of the area of the muscle fibers, with an increase in muscle protein synthesis (Rowlerson & Vegetti 2001).

Conclusions. This study showed that fasting has a negative effect on the growth and biometric value of red tilapia, but under a treatment of 7 to 21 days of fasting, after the refeeding period, it demonstrated a phenomenon of partial and complete compensatory growth. After 7 days of fasting, red tilapia had a better growth performance and feed efficiency than the control and the other fasting treatments. The effect of fasting and refeeding significantly affects the morphology and morphometry of red tilapia fish. Red tilapia at the end of the fasting period had a diameter of the muscle fibers that showed hyperplasia and at the end of the refeeding period they showed a hypertrophy phase. Red tilapia fasting for 7 days and refeeding for 83 days showed the highest mean diameter and frequency of muscle fibers. Therefore, the protocol for the S7 treatment is effective and can be applied for increasing the productivity of the red tilapia aquaculture.

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