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Compensatory growth of Nile tilapia fingerlings subjected to food restriction and re-feeding at low temperatures

Crescimento compensatório de alevinos de tilápia-do-Nilo submetidos à restrição alimentar e realimentação em temperaturas amenas

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ABSTRACT

This study aims to investigate the effect of different periods of fasting and re-feeding on compensatory responses in Nile tilapia fingerlings and the frequency of muscle fiber distribution. A total of 108 Nile tilapia fingerlings with initial weight of 1.64 ± 0.41 g and mean initial length of 3.60 ± 0.39 cm were used for 55 days. The fish were distributed in a water recirculation system in a completely randomized design with three treatments and four replications: Control - CO - (fish fed until apparent satiation throughout the experimental period); fasting 10 - J10 - (fish fed to apparent satiation for 15 days, followed by 10 days of fasting and re-feeding to satiation for 30 days); and fasting 15 - J15 - (fish fed to apparent satiation for 15 days, followed by 15 days of fasting and re-feeding to satiation for 25 days). Fish from the J15 treatment showed unsatisfactory results in terms of productive performance ($p<0.05$), such as lower final weight, apparent feed conversion, protein efficiency ratio, and survival, while fish from the J10 treatment achieved the same results as those animals kept in the CO treatment with the exception of the variables of relative weight gain and feed intake. Furthermore, food restriction directly influenced the growth of muscle fibers with a diameter smaller than 20 μm ($p<0.05$), and fish from the J15 treatment had the lowest frequency of fibers in this diameter class. Therefore, this study concludes that food restriction in short periods (10 days) and at low temperatures can present a compensatory growth, as they alter the process of hyperplasia and hypertrophy of muscle fibers without affecting the morphology of the fibers; however, 15 days of fasting under low temperatures do not compensate for growth and delays the hypertrophic growth of muscle fibers.

KEYWORDS: muscle fiber growth; feeding management; zootechnical performance of tilapia fingerlings; water temperature.

RESUMO

O objetivo do presente estudo é investigar o efeito de diferentes períodos de jejum alimentar e realimentação nas respostas compensatórias em alevinos de tilápias-do-Nilo, e a frequência de distribuição das fibras musculares. Foram utilizados 108 alevinos de tilápia-do-Nilo com peso inicial de 1,64±0,41 g e comprimento inicial médio de 3,60 ± 0,39 cm, durante um período de 55 dias. Os peixes foram distribuídos em um sistema de recirculação de água, em delineamento inteiramente casualizado com três tratamentos e quatro repetições: Controle - CO - (peixes alimentados até a saciedade aparente durante todo período experimental); jejum 10 - J10 - (peixes alimentados até a saciedade aparente por 15 dias, seguidos de 10 dias de jejum e realimentação até a saciedade por 30 dias); e jejum 15 - J15 - (peixes alimentados até a saciedade aparente por 15 dias, seguidos de 15 dias de jejum e realimentação até a saciedade por 25 dias). Os peixes do tratamento J15 apresentaram resultados insatisfatórios de desempenho produtivo ($p<0,05$), como menor peso final, conversão alimentar aparente, taxa de eficiência proteica e sobrevivência, enquanto os peixes do tratamento J10, atingiram os mesmos resultados daqueles animais mantidos no tratamento CO, com exceção das variáveis de ganho em peso relativo e do consumo de ração. A restrição alimentar influenciou diretamente no crescimento das fibras musculares com diâmetro menor que 20 μm ($p<0,05$), sendo que os peixes do tratamento J15 apresentaram a menor frequência de fibras nesta classe de diâmetro. Conclui-se que a restrição alimentar em curtos períodos (10 dias) e em temperaturas amenas podem apresentar um crescimento compensatório, alterando o processo de hiperplasia e hipertrofia das fibras musculares, sem afetar a morfologia das fibras, entretanto, 15 dias de jejum e sob temperaturas amenas não ocorre uma compensação no crescimento e atrasa o crescimento hipertrófico das fibras musculares.

PALAVRAS-CHAVE: crescimento das fibras musculares; manejo alimentar; desempenho zootécnico de alevinos de tilápias; temperatura da água.

INTRODUCTION

In a natural environment, fish go through periods of food shortages because of several factors, such as climate change caused by the seasons, which can determine the success or failure of the farming. Knowledge on water quality is extremely important for pisciculture, and one of the main parameters for production is water temperature, which directly affects fish metabolism, oxygen consumption, growth, and survival (GODOY et al. 2021). Fish tolerance to temperature varies according to the species and stage of development. As fish are ectothermic, water temperature will determine body temperature; in cold water situations, the animal's organism also reduces its temperature and thus all physiological processes are compromised (LI et al. 2021).

Despite this situation, the animals manage to adapt and, after the critical period, they are able to resume their development through compensatory growth. This is possible given the heterogeneous nature of subsidies and foraging opportunities within and between habitats (ARMSTRONG & SCHINDLER 2011). Several studies indicate that fasting followed by re-feeding cycles can lead to improvements in the efficiency of feeding schedules in pisciculture and result in greater cost/benefit ratios (URBINATI et al. 2014). Thus, food deprivation has been adopted for a period of time as a technique that allows maintaining productivity with a lower expenditure on feed with a rapid growth phase after this deprivation.

Hyperphagia plays a key role in compensatory gain, as it allows the animal that has undergone a period of food restriction to regain the weight it should have had if it were fed continuously; therefore, compensatory gain is considered a response to hyperphagia (XIAO et al. 2012). According to SANTOS et al. (2018), short periods of food deprivation and subsequent re-feeding of fish is a strategy to promote compensatory growth, as it optimizes the supply and consumption of feed by animals, and it can be a human labor cost saving tool in this process. Recently, LUI et al. (2020) have concluded that juvenile tilapia subjected to a feed restriction of one day a week did not show any change in weight in relation to the animals that receive daily feed, although they do not recommend fasting as there was no economy in this process.

One of fish's most affected tissues during fasting and re-feeding cycles is the skeletal muscle, which corresponds to 60% of body mass (MAGNONI et al. 2013). In addition, the knowledge of the dynamics of muscle growth can provide a better understanding of the animal’s morphophysiology, with a view at the adoption of strategies to increase productivity (PEREIRA 2016). In fish, muscle growth occurs through the processes of hypertrophy, which is the increase in the size of the muscle fiber, and hyperplasia, which is characterized by the increase in the number of cells (MELO et al. 2016). A model organism for this research is the Nile tilapia (*Oreochromis niloticus*), because of its zootechnical performance characteristics, such as rapid growth, prolificacy, resistance to high and low temperatures, low concentrations of dissolved oxygen and high concentrations of ammonia in water, and resistance to disease and stress (EL-SAYED & FATTAH 2006, ZHU 2020).

Thus, this study seeks to investigate the effect of different periods of fasting and re-feeding on the compensatory responses in Nile tilapia (*Oreochromis niloticus*) fingerlings placed in an environment with low temperatures, as well as to verify the growth of skeletal muscle fibers during these fasting situations at low temperatures.

MATERIAL AND METHODS

The experiment was carried out at the Aquaculture Production Laboratory of the School of Agricultural Sciences of Federal University of Grande Dourados (UFGD), Brazil. A total of 108 sex-reversed Nile tilapia (*Oreochromis niloticus*) fingerlings were used with initial weight of 1.64 ± 0.41 g±sd and mean initial length of 3.60 ± 0.39 cm±sd, coming from a commercial fish farm located in Dourados, MS, Brazil. The animals were distributed in a completely randomized design containing three treatments and four replications, amounting to twelve 15-liter aquariums, coupled to a water recirculation system for an experimental period of 55 days. The aquarium water was kept at a low temperature because of the laboratory's water source and the period of the year (June) in which the experiment was carried out, in this way equipment to decrease the temperature was not required.

The treatments were defined as: control (CO): fish fed until apparent satiation throughout the experimental period; Fasting 10 (J10): fish fed to apparent satiation for 15 days, followed by 10 days of fasting and re-feeding to apparent satiation for 30 days; and Fasting 15 (J15): fish fed to apparent satiation for 15 days, followed by 15 days of fasting and re-feeding to apparent satiation for 25 days.

Fingerlings were fed daily with commercial feed containing 45% crude protein and with a diameter of 1 mm. Water quality parameters such as dissolved oxygen (mg/L), pH, and electrical conductivity (µS/cm) were recorded weekly using portable digital potentiometers, while water temperature (°C) was measured daily (Table 1).

Table 1. Mean values of temperature (ºC), pH, dissolved oxygen (mg/L), and electric conductivity (µS/cm) of the water of Nile tilapia aquariums subjected to the treatments of Control, Fasting 10, and Fasting 15.

Parameters	Means
Temperature (°C)	17.7±2.22
pH	7.7±0.17
Dissolved Oxygen (mg/L)	6.72±0.19
Electric Conductivity (µS/cm)	84.4±5.64

At the end of the experiment, the fish were anesthetized with eugenol at a dose of 100 $mg.L^{-1}$ (DELBON & PAIVA 2012), counted and measured for performance assessments. The zootechnical performance of the fish was analyzed through feed consumption (FC): (total feed consumed during the experiment), feed efficiency, individual weight gain (WG): (final weight - initial weight), relative weight gain (%): [(final weight - initial weight)/initial weight]x100; total length (TL), specific growth rate (SGR): [(ln Final weight - ln Initial weight)/t]x100, where ln = Napierian logarithm and t = time in days, survival (S%): (final population/initial population)x100, and condition factor (CF): [(weight)/(total length^3)x100], feed conversion: (feed consumption/weight gain); feed efficiency (%): (weight gain/total consumption and feed)x100.

To assess muscle growth, two fish from each experimental unit were captured, which were induced under deep anesthesia until all reactions were lost (DELBON & PAIVA 2012). With the aid of a blade, a sample of the dorsal white muscle was removed, above the lateral line (NEU et al. 2016). The samples were fixed in 10% buffered formalin for 24 hours and processed for paraffin embedding. Semi-serial sections (6 µm) were obtained on a rotary microtome and submitted to hematoxylin-eosin staining. For morphometry, using an image analysis system, the smallest diameter of 200 muscle fibers per animal was determined and grouped into diameter classes (<20 µm, 20-50 µm, and >50 µm) to assess the contribution of hyperplasia and hypertrophy for muscle growth (ALMEIDA et al. 2008).

The results were submitted to Shapiro-Wilk and Levene's testing to verify normality and homogeneity. Given the assumptions, the parameters were analyzed by means of one factor analysis of variance and the Tukey test was applied when significant differences were detected ($p<0.05$) (ZAR 1999). For this end, the computer program Statistica 7.1 was used (STATSOFT 2005).

RESULTS

At the end of the 55-day experiment, less fish from the J15 treatment survived in relation to the fish from the CO and J10 treatment ($p<0.05$). For the CO and J10 treatments, survival was 62.5% and 57.2%, respectively (Figure 1). The values obtained for the mean water quality parameters are shown in Table 1; the temperature presented a value lower than that recommended as optimal for the development of the species.

The final weight of the fish subjected to 10 days of fasting did not differ significantly from those that were fed continuously ($p>0.05$). However, the treatment in which the fish fasted for 15 days differed significantly from the animals on continuous feeding ($p<0.05$), and the fish failed to compensate for growth after being re-fed, that is, they presented a partial compensatory growth. In this variable, the animals from treatments J10 and J15 did not obtain a significant difference (Table 2).

The relative weight gain parameter showed a significant difference between the three treatments ($p<0.05$). The CO treatment presented a greater total length, which differs from the J15 treatment ($p<0.05$), but there was no significant difference between CO and J10 ($p<0.05$). Feed consumption throughout the experiment was higher in the control treatment and significantly differed from the J10 and J15 treatments ($p<0.05$). The animals that were under a longer period of fasting (fasting for 15 days) had lower feed efficiency when compared to the CO and J10 treatments ($p<0.05$). As for the condition factor, there was no significant difference in any of the treatments ($p>0.05$).

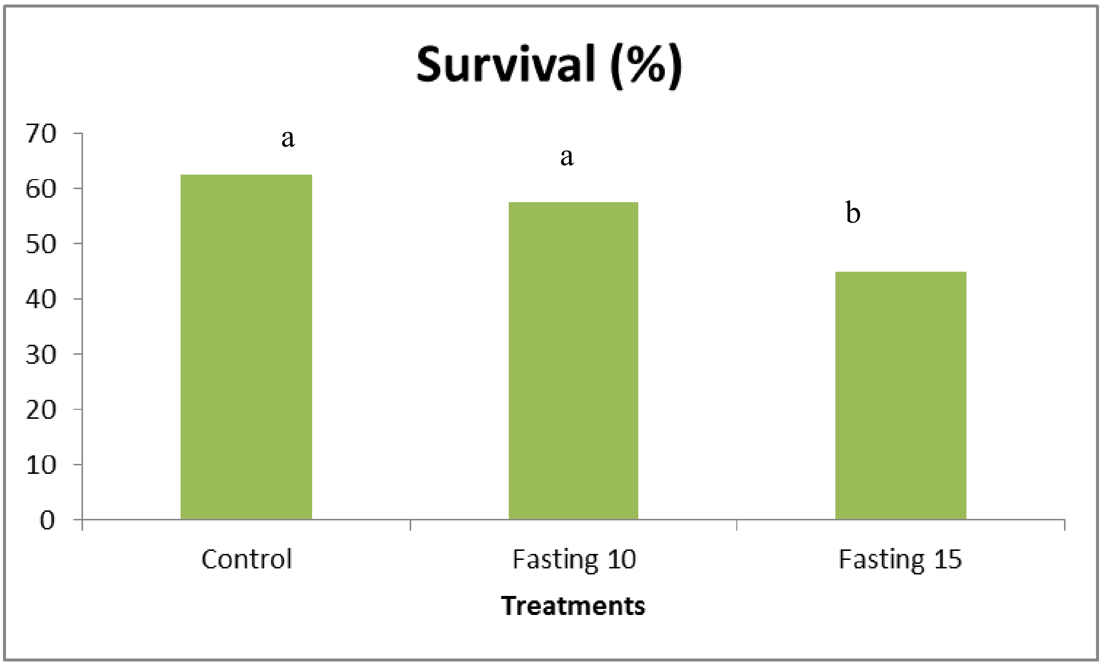

Figure 1. Survival of Nile tilapia (*O. niloticus*) subjected to food restriction and re-feeding. Control (CO): fish fed until apparent satiation throughout the experimental period; Fasting 10 (J10): fish fed to apparent satiation for 15 days, followed by 10 days of fasting and re-feeding to apparent satiation for 30 days; and Fasting 15 (J15): fish fed to apparent satiation for 15 days, followed by 15 days of fasting and re-feeding to apparent satiation for 25 days.

Table 2. Zootechnical performance parameters of Nile tilapia fingerlings subjected to different feeding managements.

Variables	Treatments		
	Control	Fasting 10	Fasting 15
Final weight (g)	3.48 ± 0.74 a	2.65 ± 0.08 ab	2.29 ± 0.24 b
Final length (cm)	5.95 ± 0.42 a	5.46 ± 0.09 ab	5.26 ± 0.14 b
Total feed consumption (g)	14.61 ± 1.87 a	9.04 ± 2.59 b	6.20 ± 2.18 b
Weight gain (g)	1.84 ± 0.74 a	1.01 ± 0.08 ab	0.65 ± 0.24 b
Relative weight gain (%)	112 ± 0.38a	61 ± 0.03b	39 ± 0.13c
Specific growth rate (% day)	1.29 ± 0.38 a	0.84 ± 0.05 ab	0.58 ± 0.18 b
Feed conversion (%)	8.94 ± 2.89a	8.97 ± 2.36a	10.04 ± 3.26b
Feed Efficiency (%)	12.53 ± 4.33a	12.10 ± 3.77a	11.12 ± 3.67b
Condition factor	1.63 ± 0.06	1.62 ± 0.08	1.57 ± 0.05

Mean ± standard deviation. Values followed by different letters on the same line indicate significant differences at 5% probability by the Tukey test. Control (CO): fish fed until apparent satiation throughout the experimental period; Fasting 10 (J10): fish fed to apparent satiation for 15 days, followed by 10 days of fasting and re-feeding to apparent satiation for 30 days; and Fasting 15 (J15): fish fed to apparent satiation for 15 days, followed by 15 days of fasting and re-feeding to apparent satiation for 25 days.

Regarding the variable of the frequency distribution of muscle fibers in diameter classes (Figure 2), in the <20 µm class, there were significant differences between treatments ($p<0.05$), in which the lowest frequency was observed in the J15 group (1.22% compared to 2.34% for the CO and J10 treatments). Regarding fiber classes with diameters between 20 and 50 µm and above 50 µm, no differences were observed between groups ($p>0.05$) (Figure 2).

Regarding muscle morphology, in the CO, J10, and J15 treatments, normal tissue characteristics were observed with polygonal or rounded muscle fibers separated by a thin connective tissue septum: the endomysium. A mosaic growth pattern was observed, which was characterized by muscle fibers of different diameters (Figure 3).

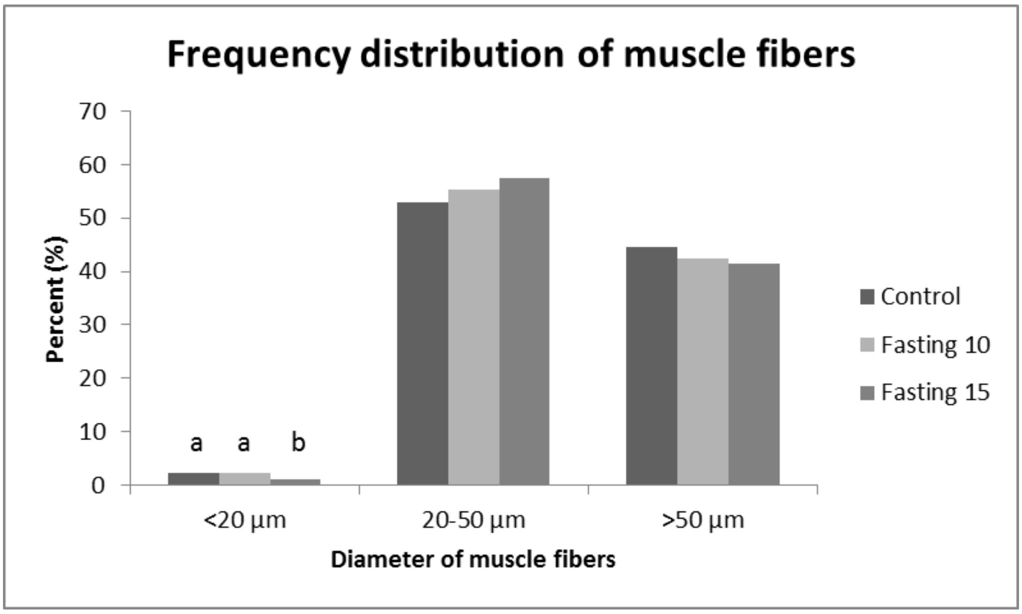

Figure 2. Frequency distribution (%) of muscle fibers in diameter classes (<20 µm, between 20 and 50 µm, and >50 µm) of fish subjected to different feeding strategies in the Control, Fasting 10, and Fasting 15 treatments.

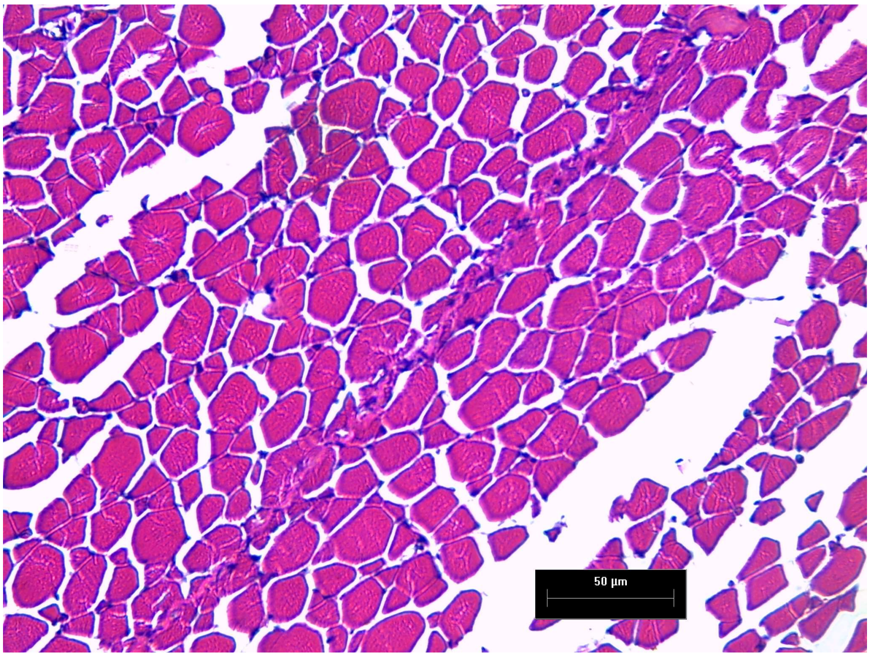

Figure 3. Photomicrograph of white striated skeletal muscle of a Nile tilapia fingerling. Image at 40X.

During periods of food restriction, tilapia from the J10 and J15 treatments did not show morphological changes in muscle fibers compared to fish from the Control treatment.

DISCUSSION

The parameters of water quality, pH, dissolved oxygen, and electrical conductivity assessed in this study showed adequate values for the species (BOYD 2015). However, the water temperature remained below the recommended values for the species' growth, which is between 27° and 30 ºC (NIVELLE et al. 2019). In our study, the mean water temperature in the experimental units was below 18 °C; under conditions below this value, the growth of tilapia fingerlings is compromised because their appetite is reduced (GOMES et al. 2019) in addition to suppressing their immune system. This fact may have interfered with the survival rate of the fish, in particular the animals submitted to the J15 treatment, which underwent a longer period of food restriction and, together with the low water temperature, further reduced the consumption of the diet, possibly affecting physiological processes, such as the metabolism of nutrients, thus leading to a higher level of stress and, consequently, reducing immunity, which, associated with the time of food restriction, did not allow these animals to meet their nutritional needs to obtain good development, as well as for their maintenance, in this way promoting protein catabolism. METCALFE & MONAGHAN (2001) state that nutritional deficiencies arising from long periods of food restriction in early stages of development can compromise the ability of organisms to recover when adequate food levels are restored, and this is directly related to the results of this study. In this initial phase, 15 days of fasting in low temperatures cause losses in the group and no body weight recovery.

The final weight and total length obtained after 55 days of experiment revealed that the J15 treatment presented a lower value than the control treatment, which supports the study of WANG et al. (2000) who have observed that, when carrying out research with Nile tilapia juveniles in the phase of greater development, food deprivation for three days each week can be very severe, thus limiting the fish capacity for compensatory gain and/or loss of weight. The same responses have been found in our study, as the animals that were submitted to prolonged fasting could not achieve the similar performance as those that were fed continuously.

However, the CO and J10 treatment did not differ significantly in the parameters of final weight, final length, weight gain, and feed efficiency ratio, as that there was growth compensation by the fish submitted to food restriction. According to BLAKE & CHAN (2006), after starvation stress, most fish can show compensatory growth and eventually reach normal growth status after sufficient re-feeding time. These results corroborate the data obtained in the study with food restriction of grass carps, which, when induced to periods of food restriction of 14 days followed by 14 days of re-feeding, were able to have complete compensatory gain when compared to animals fed 28 days continuously (XU et al. 2019). In our study, it is possible to verify that the animals submitted to the J10 treatment resumed their growth, showing no differences from the other treatments, however the low water temperature does not allow the speed of protein deposition to be similar to the animals that consume daily, and this it is more evident in animals that were submitted to 15 days of fasting, because with the low temperature the animal's metabolism is reduced and prevents it from converting food into muscle, and thus its growth is impaired.

In the parameter of feed conversion and feed efficiency, our study showed that the group of fish submitted to the J15 treatment obtained the worst values in relation to the other treatments, which demonstrates that the period of prolonged fasting combined with low temperature reduced the metabolism and affected not only the metabolic expenditure for maintenance but also the use of nutrients in the animal organism, in this way not allowing the achievement of a good performance; thus, its applicability is inefficient as the main purpose of this feeding technique is to reduce the costs with feed. The J10 and CO treatments did not differ significantly in feed conversion and efficiency parameters, which indicates that growth occurs after re-feeding from the increase in food intake and the activity of digestive enzymes, thus promoting compensatory gain (CARUSO et al. 2014).

In addition to knowing the impact of food restriction on zootechnical performance characteristics, it is important to understand the real impact on the morphology and muscle growth of fish, since muscle tissue, in addition to representing most of the animal’s body mass, is also an important source of animal protein in the human diet (XU et al. 2019). Previous reports have shown that fasting significantly reduces the size of white muscle fibers, which suggests that white muscle is the main target in this condition (FAUCONNEAU et al. 1995).

In our study, the frequency distribution of muscle fibers was significantly altered according to the food treatment adopted. A smaller number of fibers was observed in the class of diameters smaller than 20 μm for the J15 treatment. This class characterizes the presence of fibers newly formed by the hyperplasia process, which will, later, increase in volume by the hypertrophy mechanism (ROWLERSON & VEGGETTI 2001). Our results suggest that the lower frequency of fibers in this diameter class in the J15 treatment is related to the greater difficulty of the fish in returning to normal muscle growth because of the delay in the muscle hypertrophy process.

Regarding the frequency of fiber distribution in the diameter class between 20 and 50 μm, there was no significant difference between the treatments studied. Such results reinforce the data obtained by KUNIYOSHI et al. (2019) who, when analyzing prolonged fasting followed by re-feeding in pacus, have found non-significant results in the variable of 20 and 50 μm diameter class, noting the beginning of differentiation and hypertrophy during this period.

Food restriction did not change the morphological characteristics of muscle fibers in any of the treatments, similarly to what has been verified by NEBO et al. (2013), in which the analyzed tilapia showed preserved muscle morphology and a mosaic muscle growth pattern, as we have found in our study.

CONCLUSION

The tilapia fingerlings subjected to short periods of fasting (10-day fasting), in low temperatures presented a compensatory growth; however, the 15-day fasting associated with low water temperature is not interesting in this stage of development because, in addition to the performance being compromised, there is a delay in the hypertrophic growth of skeletal muscle fibers.

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