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ORIGINAL RESEARCH

Structural environmental enrichment improves Nile tilapia flesh quality

João Favero Neto . Bruno Lala . Carolina Santos . Roberto de Oliveira Roça . Rogério de Oliveira . Caroline Marques Maia . Percilia Cardoso Giaquinto

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Abstract Environmental enrichment is a reliable and useful tool for improving fish welfare in farms. Structural enrichment is widely studied and applied to fish, with positive effects also on the zootechnical parameters of fish farming. In our study, we examined whether artificial shelters and water hyacinth - structural enrichments - improve the quality of tilapia fillets. Tilapia juveniles (n = 480) underwent three independent treatments over 100 days: artificial water hyacinth enrichment, shelter enrichment, and control (no enrichment). After slaughtering, we evaluated physical-chemical indicators of meat quality. Whereas meat pH was not affected by the availability of enrichment, we found less lightness in terms of chroma b* of the flesh from tilapia raised with artificial water hyacinth and more flesh toughness in the texture of tilapia raised with shelter, indicating a higher-quality product. Regarding the fatty acid profile, differences were found when individually analyzed. All fatty acids that differed among treatments (C4:0, C23:0, C24:0, C16:1, and C24:1) exhibited better performance in groups reared with structural enrichment. In conclusion, improving Nile tilapia welfare with structural enrichment enhances its flesh quality. Thus, in addition to promoting the welfare of farmed fish, this enrichment may benefit both farmers and consumers.

Keywords Aquaculture . Fish farming . Fish fillet . Fish welfare, Meat quality, Oreochromis niloticus

Introduction

Aquaculture is a continuously expanding sector, accounting for approximately 82 million tons of fish production in 2018 (FAO 2022). This industry has been a leading sector over the last 50 years, growing at an average rate of 5.3% annually (FAO 2020), with a projected global growth estimate of 46.3% by 2030 (FAO 2020). In

João Favero Neto . Caroline Marques Maia (✉) . Percilia Cardoso Giaquinto
CAUNESP – Aquaculture Center of UNESP, São Paulo State University, Jaboticabal, SP 14884-900, Brazil
e-mail: carol@fishethogroup.net

Bruno Lala
Department of Veterinary Science, University Center UniFatecie, Paranavaí, Brazil

Bruno Lala . Carolina Santos . Roberto de Oliveira Roça
Department of Animal Breeding and Nutrition, UNESP, College of Veterinary Medicine and Animal Sciences, São Paulo State University, Botucatu, Brazil

Carolina Santos
School of Agriculture, UNESP, São Paulo State University, Botucatu, Brazil

Rogério de Oliveira
Department of Biodiversity and Biostatistics, Institute of Biosciences of Botucatu, São Paulo State University (UNESP), Botucatu, SP 18618-689, Brazil

Caroline Marques Maia
FishEthoGroup Association, Faro, Portugal

Caroline Marques Maia
Alianima organization, São Paulo, SP, Brazi

Percilia Cardoso Giaquinto
Department of Structural and Functional Biology, Institute of Biosciences of Botucatu, São Paulo State University (UNESP), Botucatu, SP 18618-689, Brazil

the light of increasing scientific evidence that fish are sentient beings and, therefore, capable of experiencing suffering (Brown 2015; Saraiva and Arechavala-Lopez 2019; Sneddon et al. 2003), the issue of animal welfare in aquaculture is becoming increasingly important, especially for species commonly farmed.

However, the physiological, behavioral, and psychological needs of captive fish have largely been ignored (Huntingford et al. 2006). In aquaculture, considering the various production phases, fish are inevitably subjected to acute and chronic stressors (Lefevre et al. 2016). To transform this scenario, environmental enrichment has been proposed and employed to enhance fish welfare in aquaculture. In production systems, environmental enrichment involves adding environmental stimuli to help fish cope with captivity and address their physiological, behavioral, and psychological needs (Arechavala-Lopez et al. 2021).

Structural or physical enrichment is the most recognized, widely used environmental enrichment strategy for fish, in laboratories as well as aquaculture facilities (Arechavala-Lopez et al. 2021). There is a growing interest in this form of enrichment, as evidenced by recent reviews on this subject (Jones et al. 2021; Näslund and Johnsson 2016; Zhang et al. 2023). Structural enrichment involves adding physical complexity to the environment through introduction of structures, objects, or another such modification (Poli 2009). In other words, this type of enrichment refers to modifying the environment by adding natural or artificial objects to provide comfort and behavioral fulfillment to animals (Zhang et al. 2019) introducing resources that may promote foraging, nesting, and shelter behaviours, for example.

Numerous studies on structural enrichment in fish have demonstrated its positive effects, through addition of stones, hiding places, sticks, hanging ropes, and varied natural or artificial substrates. Benefits include reduced aggression (Favero Neto and Giaquinto 2020; Näslund and Johnsson 2016), stress reduction – along with improved post-exposure recovery from a stressful event (Cogliati et al. 2019; Favero Neto and Giaquinto 2020), decreased injury (Arechavala-Lopez et al. 2019), and minimized anxiety responses (Lopes et al. 2018).

The positive effects of structural enrichment are not limited to fish welfare but extend to the zootechnical parameters of fish farming. For instance, structural enrichment helps reduce aggressive behaviors leading to lower stress levels and energy expenditure (Favero Neto and Giaquinto 2020; Näslund and Johnsson 2016). These aggressive behaviors cause a metabolic imbalance, reducing glycogen and glucose reserves in muscles, which affects anaerobic glycolysis, and lactic acid production (Digre et al. 2010; Erikson et al. 2011; Subbaiah et al. 2015). Furthermore, they may also affect oxidative stress and lipid oxidation (Huang and Ahn 2019). Such changes may negatively impact the sensory, functional, and nutritional characteristics of the fillet (Huang and Ahn 2019; Østbye et al. 2018).

The decline in fillet quality due to stress may have a significant economic impact, as consumers judge by appearances (De Oliveira et al. 2017). Qualities such as texture and color, for example, are key factors in the decision to buy or reject a product. Therefore, the structural enrichment not only concerns animal welfare, but indirectly improves meat quality (De Oliveira et al. 2017).

Despite evidence that improving fish welfare during production positively influences fish meat quality (Fernandes et al. 2024), to our knowledge, there is no research linking meat quality with structural enrichment in Nile tilapia (*Oreochromis niloticus*). This species is one of the main freshwater fish globally farmed for human consumption, with production expected to intensify in the coming years (FAO 2022). Thus, here we evaluated whether artificial shelters and water hyacinth – structural enrichments that are easy to adapt and implement – improve the quality of tilapia fillets.

Materials and methods

Ethical statement

The procedures used in this study adhered to ethical principles in animal research and received approval from the Ethics Committee on the Use of Animals at the State University of São Paulo (CEUA – FMVZ – UNESP - protocol number 0175/2018).

Animals and holding conditions

The study was conducted in the Aquaculture Sector at the Experimental Lageado Farm Campus of Veterinary Medicine and Animal Science at the State University of São Paulo (UNESP), Botucatu, Brazil. Juve-

nile male Nile tilapia (*Oreochromis niloticus*) from a sex-reversed GIFT population, from a local producer, were kept for 15 days for acclimatization in a four-thousand-liter tank. The water was continually refreshed and the fish were fed four times a day. For the experiment, the fish (mean weight: 29.54 ± 0.58 g) were kept in twelve 300 L aquariums connected to a recirculation system. This system included biological and ultraviolet filters. Water was pumped into a 3-meter-high reservoir, then distributed by gravity to the aquariums.

Temperature control (26 ± 2 °C) was ensured using a 2000-watt heater in the reservoir and a 300-watt heater in each aquarium. Continuous aeration was provided by an air stone in each aquarium, and a photoperiod of 12L:12D (6 am-6 pm) was maintained. Water temperature was measured twice daily at 8:00 am and 5:00 pm. Dissolved oxygen, pH, ammonia levels, and nitrites were monitored weekly, in accordance with acceptable ranges for fish farming (Piper et al. 1982) during the trial period: 8.0 ± 1.6 ppm, 7.0 ± 0.2, 0.37 ± 0.15 ppm, and 0.16 ± 0.12 ppm, respectively.

Experimental design

The experimental period lasted 100 days, whereby the animals attained a final average weight of 204 ± 8.38 g, representing the mean table size of Nile tilapia. A total of 480 male juveniles were equally distributed across three treatments as shown in Figure 1, each with four replications (resulting in 12 groups with 40 fish in each). In Treatment 1, environmental enrichment using artificial water hyacinth was implemented in the aquariums. In Treatment 2, enrichment using artificial shelter was implemented. The aquariums in the control group received no environmental enrichment. At the end of the experiment, the fish were harvested, slaughtered, filleted, and the fillet quality was assessed by analyses of meat pH, color, texture, and fatty acid profile.

Procedures

During the experimental period, the fish were manually fed four times a day until satiation with extruded 4 mm feed pellets, formulated specifically for juvenile tilapia (Furuya 2010) (Table S1). The diet was isoproteic (29% protein) and isoenergetic (approximately 3000 kcal/kg). Artificial water hyacinth made of frayed nylon rope, mimicking the natural water hyacinth root, were fixed to a styrofoam structure to float, while artificial shelters were made of PVC pipes (10 cm in diameter and 20 cm in length).

At the end of the experimental period, 10 fish from each treatment were randomly selected, anesthetized with benzocaine (152 mg/l) (da Rocha et al. 2012) and slaughtered by sectioning the spinal cord (Freire and Gonçalves 2013). The skin of the fish was removed, and the animals were filleted. To avoid methodological errors, the procedures were performed by the same individual. The fillets were duly identified by the experimental group, and the right and left sides were standardized. Thereafter, they were packed individually

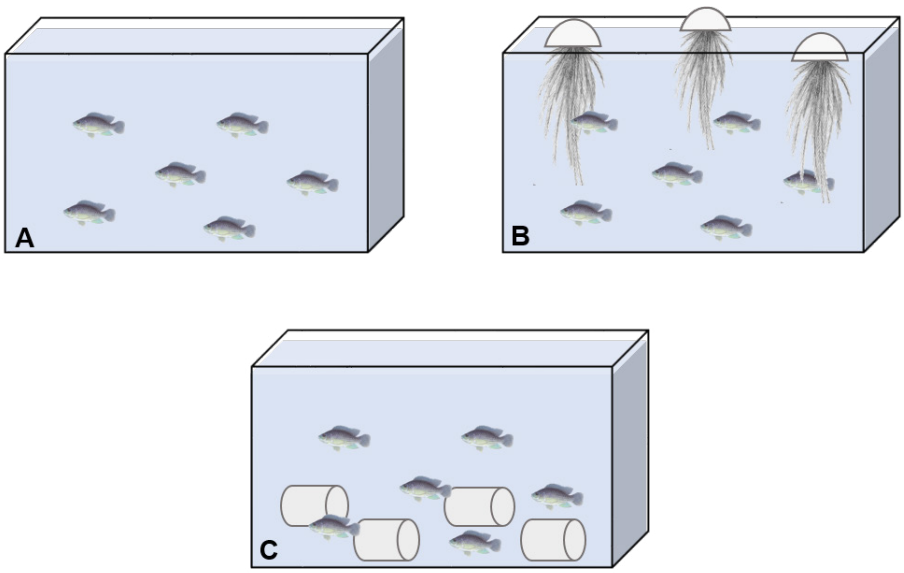

Fig. 1 Experimental design. (A) control, (B) treatment 1: artificial water hyacinth enrichment, and (C) treatment 2: shelter enrichment

in plastic film and stored in trays for cooling in a refrigerator at 4°C for 24 hours. For pH analysis, the left fillet was standardized. For the color, texture and fatty acid profile, the right-side fillet was standardized.

The pH was evaluated using a portable pH meter model HI-99163. For this purpose, 10 g of meat was ground with 40 mL of distilled water, and the pH of this solution measured. PH evaluation of the fillet was done twice: immediately after slaughter (0 h, initial) and after 24 h. The fillet color was assessed 24 h after storage with three different readings per sample. The following values of lightness (L*) were evaluated using a portable colorimeter (Chroma Meter CR-400) at a 90˚ angle: L* defines the lightness (L* = 0 black and L* = 100 white), chroma a* (red-green component), and chroma b* (blue-yellow component) (CIE 1977). The texture of the fillets was evaluated using a CT3-Brookfield texturometer (calibrated from pre-tests for the meat samples of the experiment). The deformation percentage was measured by compression at three different points (cranial, dorsal, and caudal), with a trigger load equal to 71 g, cylinder speed of 2 mm/s and a platform height of 20mm.

For the fatty acid profile, total lipids in the fillet were extracted using the cold technique (Bligh and Dyer 1959) and for transesterification of the triacylglycerols, the samples were subjected to the Hartman and Lago technique (1973). The methyl esters were analyzed by an automatic gas chromatograph sampler (Trace GC Ultra, Thermo Scientific, USA) equipped with a 240 °C flame ionization detector and a fused silica capillary column (100 m long, 0.25 mm internal diameter and 0.20 μ m, Restek 2560). Identification of fatty acids was made based on the retention time of the standard (Sigma, FAME Mix, C4–C24) and the calculation of the peak areas determined by the Chromquest 5.0 Clarity Lite software, version 2.4.1.91. The quantification of these fatty acids in mg/g of lipids was performed in relation to the internal standard, methyl tricosanoate (Sigma).

Table S1 Diet formulations and nutritional composition (g/kg) of the feed provided to the fish in the environmental enrichment and control treatments.

Ingredients	
Soybean meal-45	43.50
Soy protein concentrate	10.00
Poultry flour	5.00
Ground corn	33.04
Soybean oil	0.50
Wheat middlings	2.00
DL-methionine	0.22
L-Threonine	0.36
L-Tryptophan	0.32
Dicalcium phosphated	2.01
Inert material (sand)	2.24
BHT [1]	0.02
Mineral vitamin mix [2]	0.60
Vitamin C	0.09
Salt	0.10
Total	100.00
Nutritional Composition	
Dry matter	86.23
Crude energy (kcal kg^{-1})	3762
Protein	31.86
Digestible energy (kcal kg^{-1})	3044
Digestible protein	29.75
Crude fiber	3.31
Ether extract	3.03
Calcium	0.81
Available phosphorus	0.53

[1]BHT: Butyl-Hydroxy-toluene (Antioxidant);
[2]Mineral vitamin mix (amount kg mix^{-1}): vitamin A (UI/kg) 9000, vitamin D3 (UI/kg) 2.500, vitamin E 300, vitamin K3 40, vitamin B1 60, vitamin B2 60, vitamin B6 60, vitamin B12 0.1, niacin 120.0, pantothenic acid 180, biotin 0.8, folic acid mg/kg 12, vitamin C 600, inositol 400, hill 850, selenium 0.8, chrome 0.5, iron 72, copper 24, zinc 50, manganese 30, iodine 1.2, cobalt 0.5.

Statistical analysis

The pH, color, texture and fatty acid profile variables of the fillets were independently compared across treatments using Generalized Linear Models (GLM), considering gamma distribution, which has considerable flexibility in adjusting asymmetric data. To identify statistically significant differences, pairwise comparisons were made using the Tukey-Kramer post-test. Differences were considered significant when the p-value of the statistical test was less than 5% ($p < 0.05$). Statistical analyzes were performed using the SAS tool (Statistical Analysis System), version SAS® 9.3.

Results

We found no statistical differences among the experimental groups considering fillet pH values, both immediately after slaughter (0 h; $p = 0.114$) and after 24 h storage ($p = 0.096$) (Table 1). Regarding flesh color, although no differences were found in the L* and a* characteristics of the tested treatments ($p = 0.133$ and $p = 0.159$, respectively), a significant reduction in lightness values was found for the artificial water hyacinth treatment compared to the control group, in terms of chroma b* ($p = 0.036$) (Table 2). Additionally, for fillet texture, toughness values also varied significantly among treatments. Specifically, tilapia fillets from the shelter treatment exhibited higher toughness values, indicating greater flesh firmness, compared to the control fillets ($p = 0.031$) (Figure 2).

Table 1 pH values of tilapia fillets for different types of treatments immediately after slaughter (0 h) and after 24 h storage

Treatments	0 h	24 h
Control	7.07 ± 0.07 [a]	6.49 ± 0.07 [a]
Artificial water hyacinth	7.02 ± 0.08 [a]	6.42 ± 0.09 [a]
Shelter	7.14 ± 0.19 [a]	6.50 ± 0.05 [a]

Mean pH values ± standard deviation. No statistical difference was found.

Table 2 Mean values (± SD) of lightness characteristics of tilapia fillet

Treatments	L*	a*	b*
Control	57.14 ± 2.32 [a]	12.09 ± 1.55 [a]	8.21 ± 1.13 [a]
Artificial water hyacinth	55.02 ± 1.34 [a]	12.26 ± 1.08 [a]	7.73 ± 0.65 [b]
Shelter	55.67 ± 1.60 [a]	13.16 ± 2.24 [a]	7.82 ± 0.81 [ab]

L* = the lightness (L* = 0 black and L* = 100 white), chroma a* = red-green component, and chroma b* = blue-yellow component (CIE 1977). Data are given as mean color values ± standard deviation. Different letters indicate a statistically significant difference among treatments ($p < 0.05$).

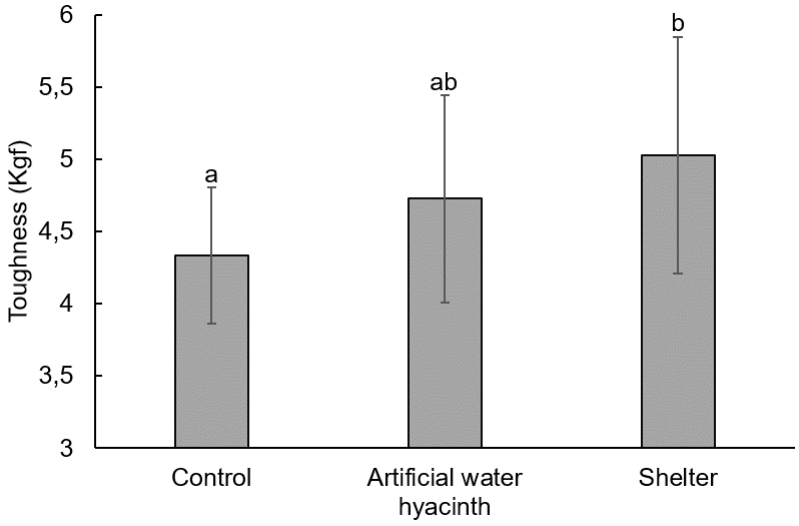

Fig. 2 Treatments affect fillet toughness. Mean values ± standard deviation are represented in the graph. Different letters indicate a statistically significant difference among treatments ($p < 0.05$).

Overall, there were no significant differences in the amount of fatty acids in the flesh ($p > 0.05$) among treatments (Tables 3, 4, and 5). Regarding the specific composition of saturated fatty acids in Nile tilapia muscle, only the amounts of butyric (C4:0), tricosanoic (C23:0), and lignoceric (C24:0) fatty acids differed among treatments (Table 3). The artificial water hyacinth treatment exhibited a higher quantity of C4:0 than both the shelter ($p = 0.011$) and control ($p = 0.044$) treatments, and a lower amount of C23:0 and C24:0 than the control treatment ($p = 0.001$). Furthermore, in the composition of monounsaturated fatty acids, only the amounts of palmitoleic acid (C16:1) and nervonic acid (C24:1) exhibited statistical differences among treatments (Table 4). For both fatty acids, the control group presented higher values than the shelter treatment ($p = 0.020$). No significant differences were found for polyunsaturated fatty acids (Table 5).

Discussion

In this study, we found that structurally enriching the environment of Nile tilapia production systems should not negatively affect the quality of the final product in terms of pH, coloration, texture, or fatty acid concentration. Conversely, our results indicate that the presence of water hyacinths and artificial shelters in the environment – simple and easily adapTable structural enrichments – should improve the coloration,

Table 3 Composition of saturated fatty acid profile (mg/100 g) of Nile tilapia muscle

Saturated fatty acid	Control	Artificial water hyacinth	Shelter
C4:0 *	0.03 ± 0.03 [a]	0.13 ± 0.21 [b]	0.02 ± 0.01 [a]
C6:0	0.04 ± 0.03 [a]	0.04 ± 0.04 [a]	0.09 ± 0.09 [a]
C8:0	0.03 ± 0.04 [a]	0.03 ± 0.03 [a]	0.02 ± 0.01 [a]
C10:0	0.02 ± 0.03 [a]	0.02 ± 0.02 [a]	0.01 ± 0.01 [a]
C11:0	0.02 ± 0.01 [a]	0.01 ± 0.01 [a]	0.04 ± 0.03 [a]
C12:0	0.05 ± 0.02 [a]	0.04 ± 0.02 [a]	0.08 ± 0.05 [a]
C13:0	0.02 ± 0.01 [a]	0.02 ± 0.02 [a]	0.04 ± 0.02 [a]
C14:0	2.46 ± 0.60 [a]	2.71 ± 0.54 [a]	2.41 ± 0.30 [a]
C15:0	0.11 ± 0.02 [a]	0.08 ± 0.04 [a]	0.13 ± 0.05 [a]
C16:0	24.62 ± 0.92 [a]	23.90 ± 0.90 [a]	23.66 ± 0.71 [a]
C17:0	0.07 ± 0.05 [a]	0.03 ± 0.02 [a]	0.22 ± 0.22 [a]
C18:0	4.91 ± 0.48 [a]	4.50 ± 0.34 [a]	5.62 ± 0.97 [a]
C20:0	0.12 ± 0.03 [a]	0.10 ± 0.06 [a]	0.10 ± 0.02 [a]
C21:0	0.02 ± 0.02 [a]	0.01 ± 0.01 [a]	0.04 ± 0.03 [a]
C22:0	0.04 ± 0.03 [a]	0.03 ±0.02 [a]	0.05 ± 0.04 [a]
C23:0 *	0.84 ± 0.39 [a]	0.04 ± 0.03 [b]	1.00 ± 0.22 [ab]
C24:0 *	0.32 ± 0.30 [a]	0.03 ± 0.03 [b]	0.22 ± 0.16 [ab]
Total	33.72 ± 5.97 [a]	31.77 ± 5.81 [a]	33.75 ± 5.76 [a]

Values are mean ± standard deviation. The asterisks indicate saturated fatty acids with statistical difference. Means with different letters indicate a statistically significant difference among treatments ($p < 0.05$).

Table 4 Composition of monounsaturated fatty acid profile (mg/100 g) of Nile tilapia muscle

Monounsaturated fatty acid	Control	Artificial water hyacinth	Shelter
C14:1	0.12 ± 0.04 [a]	0.12 ± 0.03 [a]	0.11 ± 0.02 [a]
C15:1	0.04 ± 0.03 [a]	0.02 ± 0.02 [a]	0.11 ± 0.09 [a]
C16:1 *	5.69 ± 0.87 [a]	5.49 ± 0.85 [ab]	4.37 ± 0.76 [b]
C17:1	0.08 ± 0.10 [a]	0.05 ± 0.09 [a]	0.05 ± 0.03 [a]
C18:1cis	29.65 ± 0.93 [a]	32.05 ± 1.68 [a]	30.56 ± 1.86 [a]
C18:1n9t	4.96 ± 0.65 [a]	5.09 ± 0.86 [a]	5.06 ± 0.66 [a]
C20:1	1.23 ± 0.20 [a]	1.49 ± 0.36 [a]	1.30 ± 0.09 [a]
C22:1	0.04 ± 0.04 [a]	0.02 ± 0.01 [a]	0.06 ± 0.03 [a]
C24:1 *	0.26 ± 0.34 [a]	0.06 ± 0.08 [ab]	0.04 ± 0.02 [b]
Total	42.06 ± 9.62 [a]	44.39 ± 10.41 [a]	41.65 ± 9.92 [a]

Values are mean ± standard deviation. The asterisks indicate monounsaturated fatty acids with statistical difference. Means with different letters indicate a statistically significant difference among treatments ($p < 0.05$).

texture, and even the nutritional quality of tilapia fillets. Thus, structural enrichment not only contributes to improved fish welfare, but also enhances the zootechnical parameters of the fillets.

Stress demands high aerobic energy to supply corporal maintenance mechanisms during activation, for adaptation and resistance to stressful conditions (Barton 2002). When fish experience stressful events, e.g., an increased amount and intensity of aggressive behavior, due to a sterile environment lacking adequate stimulation (Näslund and Johnsson 2016), such condition may lead to vigorous fight-or-flight swimming, increasing anaerobic glycolysis. This leads to lactic acid production and a consequent decline in muscle pH, accompanied by a faster onset of *rigor mortis* after slaughter (Digre et al. 2010; Erikson et al. 2011). However, we found no differences in pH values between enriched and sterile environment treatments (Table 1). A possible explanation for this is the development of an adaptive resistance response to chronic stress in fish (Raposo de Magalhães et al. 2020) during breeding.

It is worth mentioning here that the pH values obtained in this study, both immediately after slaughter and after 24 hours, fall within the range recommended by the Industrial and Sanitary Inspection of Animal Origin Products (Júnior and Oshiro 2017). This indicates that, although the tested environmental enrichments did not have positive effects on fillet pH, they did not adversely affect fillet quality in terms of pH.

Regarding fillet coloration, a significant feature for consumers, Nile tilapia should have a light, slightly pink color due to myoglobin, hemoglobin, and hemocyanin (Maia and Ogawa 1999). In this study, we found differences in chroma b* in fillet coloration; fillets from fish reared in a sterile environment exhibited more yellowing compared to those reared with artificial water hyacinth as enrichment (Table 2). Additionally, although fillets from fish previously raised in an environment with shelters did not differ in this respect from those raised in a sterile environment, they also did not differ from fillets of fish reared with artificial water hyacinth, indicating an intermediate condition. Indeed, there is evidence that different treatments or management techniques can result in differences in fillet coloration (Duarte et al. 2021).

Increased fillet yellowing from fish raised in a sterile environment may occur due to higher stress levels they experienced in an unenriched environment. Previous studies have shown that animals raised without environmental resources are more stressed, exhibiting less latency to initiate confrontation and a higher frequency and intensity of this behavior, mobilizing energy reserves for fight or flight (Favero Neto and Giaquinto 2020; Mendonça et al. 2010). Thus, stressful captive conditions can trigger metabolic changes in fish, which may be associated with pigment accumulation in the flesh, giving it a more yellowish hue.

Variation in coloration may be related to four main groups of pigments providing color to cells: melanin, carotenoids, pteridines, and purines (Maia and Ogawa 1999). These pigments participate in chemical and

Table 5 Composition of polyunsaturated fatty acid profile, omega 6 (ω6) and omega 3 (ω3) (mg/100 g) of Nile tilapia muscle

Polyunsaturated fatty acid	Control	Artificial water hyacinth	Shelter
ω6			
C18:2cis	0.32 ± 0.05 [a]	0.39 ± 0.10 [a]	0.36 ± 0.05 [a]
C18:2n6t	16.52 ± 1.09 [a]	16.62 ± 0.18 [a]	16.80 ± 0.80 [a]
C18:3n6	1.00 ± 0.14 [a]	0.85 ± 0.13 [a]	1.04 ± 0.09 [a]
C20:2	0.97 ± 0.06 [a]	0.98 ± 0.10 [a]	1.01 ± 0.18 [a]
C20:3n6	0.97 ± 0.24 [a]	0.91 ± 0.11 [a]	0.86 ± 0.17 [a]
C20:4n6	2.27 ± 0.45 [a]	1.89 ± 0.24 [a]	2.26 ± 0.63 [a]
C22:2	0.27 ± 0.18 [a]	0.26 ± 0.19 [a]	0.24 ± 0.15 [a]
Total	22.31 ± 5.92 [a]	21.91 ± 5.97 [a]	22.56 ± 6.02 [a]
ω3			
C18:3n3	0.76 ± 0.10 [a]	0.84 ± 0.18 [a]	0.76 ± 0.02 [a]
C20:3n3	0.12 ± 0.03 [a]	0.09 ± 0.06 [a]	0.12 ± 0.07 [a]
C20:5n3	0.06 ± 0.02 [a]	0.05 ± 0.04 [a]	0.04 ± 0.03 [a]
C22:6n3	0.98 ± 0.56 [a]	0.95 ± 0.25 [a]	1.13 ± 0.16 [a]
Total	1.92 ± 0.46 [a]	1.93 ± 0.48 [a]	2.04 ± 0.52 [a]
ω6 + ω3	24.23 ± 4.79 [a]	23.84 ± 4.82 [a]	24.60 ± 4.87 [a]

Values are mean ± standard deviation. No statistical difference was found.

biochemical reactions that alter the meat color, including redox potential, oxygen consumption reactions, metmyoglobin reductase activity, and susceptibility to lipid oxidation (Jiang et al. 2021; Sohn and Ohshima 2010). In the early stages of lipid oxidation, the formation of hydroperoxide occurs, a primary product of this reaction, which is not only present in fish but also in red meat animals (Sohn et al. 2005). Initially, it does not impart any flavor but can lead to the appearance of brown or yellowish coloration in fish tissue. Although the yellowish color does not affect fish meat quality, it may be unappealing to consumers, aesthetically (Truong et al. 2016), increasing the likelihood of rejection.

Nile tilapia meat typically has a firm texture, along with a fibrous and succulent appearance (Picard et al. 2012). In our study, fish reared in an environment enriched with shelters resulted in firmer fillets than those in a sterile environment without structural enrichment (Figure 2). Furthermore, even though the fillet of fish raised in an environment with artificial water hyacinth did not differ in texture from that of fish in a sterile environment, it was also similar to the fillet of fish from an environment enriched with shelters, indicating an intermediate condition.

Meat softening occurs due to the degradation and denaturation of fish muscle proteins by endogenous and microbial proteases (Subbaiah et al. 2015). *Post-mortem* changes lead to weakening and fragmentation of muscle fibers, loss of muscle cell integrity, affectingmeat texture (Listrat et al. 2016). While these processes are natural, they can be accelerated based on the previous physiological conditions of the fish. Stress caused by improper handling and high stocking densities reduces texture properties and fillet quality (Wu et al. 2018). Studies in Nile tilapia, and other fish species, have demonstrated increased stress in fish raised in unenriched environments (Favero Neto and Giaquinto 2020; Mendonça et al. 2010). Thus, the enrichments used in our study – especially shelters – likely reduced fish stress responses, minimizing fillet softening.

Regarding fatty acids, we found no differences in total values for fillets from enriched or unenriched environments, whether considering saturated, monounsaturated or polyunsaturated fatty acids (Tables 3, 4, and 5). However, when analyzed separately, we obtained some better responses associated with the use of structural enrichments. In the saturated fatty acid group, C4:0 (butyric acid) showed a higher value in the fillets of fish raised with artificial water hyacinth as enrichment (Table 3). Although there are no specific studies with fish, we know that C4:0 is linked to e varied human health benefits. This fatty acid is associated with appetite reduction, promotion of energy expenditure and fat oxidation by activating brown adipose tissue, as well as reduction of insulin resistance, improving dyslipidemia and antioxidant properties (Fluitman et al. 2018; Li et al. 2018).

Saturated fatty acids C23:0 (tricosanoic acid) and C24:0 (lignoceric acid) showed lower values in the artificial water hyacinth treatment compared to fish in an unenriched environment (Table 3). These fatty acids typically appear in low amounts in products and play a role in energy synthesis. Thus, the higher concentration of these acids in fish meat may indicate a higher energy demand, possibly associated with stress levels in an unenriched environment. In fact, a recent study found that environmental and nutritional stressors in tilapia are commonly related to an increase in the concentration of this fatty acid in meat (Lala et al. 2020).

Regarding monounsaturated fatty acids, we found a higher value for C16:1 (palmitoleic acid) in fillets of fish raised in an unenriched environment compared to those of fish reared in environments with shelters (Table 4). This fatty acid has a dual role in human health and diseases. While some studies associate high levels of C16:1 in tissues and plasma with higher risks of dyslipidemia, obesity, and insulin resistance (Okada et al. 2005; Stefan et al. 2010), others associate this fatty acid in the diet with reduced risks of diabetes, inflammation, and cardiovascular disease (Guillocheau et al. 2019; Hu et al. 2019).

Additionally, fillets of fish in a sterile environment showed a higher quantity of the monounsaturated fatty acid C24:1 (nervonic acid) compared to those raised in an environment with shelters (Table 4). The proportion of this fatty acid in serum lipids is associated with serum levels of plasmalogens (Yamazaki et al. 2014), which aid the functioning of brain cell membranes and are responsible for synaptic, cognitive, memory, and intelligence functions (Lewkowicz et al. 2019; Song et al. 2022). C24:1 plays an important role in signal transduction (Straccia et al. 2012). A possible explanation is that tilapia kept in an unenriched environment may need faster physiological responses and greater adaptability to the environment due to increased stress, frequent and intense confrontations, and a constant state of alertness, reflecting in the higher amount of C24:1. Further research is needed to address this issue.

Conclusions

In conclusion, our findings indicate that structural enrichment with artificial water hyacinths and artificial shelters has a positive impact on important zootechnical parameters related to the quality of tilapia fillet, with benefits for producers and consumers. Considering previous studies that demonstrated the benefits of this type of enrichment for the physical, behavioral, and psychological welfare of cultivated fish, it is vital to encourage the application of structural enrichment in commercial tilapia production.

Competing interests The authors declare that they have no competing interests.

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