Long-term effects of the larval photoperiod on the subsequent growth of shi drum *Umbrina cirrosa* L. specimens and the fillet texture at commercial size

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Abstract

Three groups of shi drum *Umbrina cirrosa* L. were reared with different photoperiod regimes: 24L, 12L:12D and 16L:8D (natural photoperiod) during the larval period and then all of them were transferred to a natural photoperiod. At 11.8 and 20 months of age, the body growth and the muscle parameters reached the highest values in the 24L and 12L:12D groups. The 16L:8D group showed the lowest growth. When comparing 24L with 12L:12D, the highest number of white fibres was found in the 24L group, whereas the greatest fibres size was reached in the 12L:12D group.

Commercial size (28-30 cm; 290-340 g) was reached at 20 months of age in the 24L and 12L:12D groups, but at 23 months in the 16L:8D group. When comparing the three groups at the commercial stage, the larval photoperiod effect was still observed, such that the highest fibres number was again found in the 24L group, whereas the greatest fibres size was reached in the 12L:12D group. The highest values of textural hardness were observed in the 16L:8D and 24L groups. A nutritional analysis was carried out in the 16L:8D group, which showed the following percentage values: 2.66, 21.2, 74.4, and 1.46 of fat, protein, moisture and ash, respectively.

Keywords: photoperiod; muscle cellularity; growth; texture.

Introduction

The growth of the skeletal muscle involves the recruitment of stem cells and subsequent hypertrophy of muscle fibres (Weatherley *et al*., 1988). The relative contribution of muscle fibre hypertrophy and hyperplasia to the total muscle growth varies according to endogenous and exogenous factors. Some of the most important external factors are temperature (Johnston, 1999; Johnston *et al.*, 1998; 2011; Ayala *et al.*, 2000a, 2001a,b, 2003; López Albors *et al.*, 2003; García de la Serrana *et al.*, 2012; Campos *et al.*, 2013a,b), the photoperiod (Johnston *et al*., 2003a, 2004), exercise training (Johnston and Moon, 1980), and diets (Weatherley *et al*., 1980; Fauconneau *et al*., 1997).

Photoperiod has been shown to affect sexual maturation, locomotor activity, smolting and growth in some species (Purchase *et al.*, 2000). Long and continuous photoperiods can stimulate feed efficiency and enhance the growth in different species, like Atlantic salmon *Salmo salar* L. (Johnston *et al*., 2003a, 2004), sea bream *Pagrus major* (Temminck and Schlegel, 1843) (Biswas *et al*., 2005) and Atlantic halibut *Hippoglossus hippoglossus* L. (Simensen *et al*., 2000). In cod *Gadus morhua* L., Nagasawa *et al*. (2012) found that the mean weight of juveniles reared under continuous light was 13% greater than those kept under a natural photoperiod for 120 days. These authors studied the molecular mechanisms of photic-induced plasticity of muscle growth and found changes in expression of the genes involved in epigenetic regulation. Other authors (Lazado *et al*., 2014) studied the myosin gene transcription in fast skeletal muscle of Atlantic cod and found that continuous light elevated mRNA levels of several myosins in muscle when compared to a natural photoperiod.

The shi drum *Umbrina cirrosa* L. is a member of the Sciaenidae family. This species is a good candidate for Mediterranean aquaculture because of its high growth rate, adaptability to culture conditions and high market price (Mylonas *et al*., 2004). In a previous work, Ayala *et al*. (2013) studied the larval growth of shi drum under different photoperiod regimes, finding a significant effect of light regime on muscle and body growth during the larval and early postlarval stages. However, it is unknown whether the larval photoperiod effect persists in more advanced life stages of this species, as found in salmon by Johnston *et al*. (2003a, 2004). These authors observed a long-term effect of the early photoperiod on the muscle cellularity of adult specimens of salmon. In commercial size specimens, the muscle fibre density was higher on salmon previously kept with continuous light resulting in firmer flesh (Johnston *et al*., 2004). Similarly, in cod, Imsland *et al*. (2007) found that short-term environmental manipulation during the early juvenile stage had a large impact on harvesting size of nearly 3 years later. In turbot *Scophthalmus maximus* L., Imsland *et al*. (2013) studied the long-term effect of

the photoperiod and found that long term rearing in continuous light reduced growth, whereas short term exposure to continuous light stimulated growth since the greatest final mean weights were reached in groups previously kept in short phases of 24L and then transferred to 16L:8D until harvest.

In order to determine whether the early photoperiod influences the growth of shi drum in more advanced life stages, all the larval groups previously studied by us in this species (Ayala *et al*., 2013) were transferred to an ambient photoperiod after larval metamorphosis and kept in separate tanks until reaching commercial size. Also, textural values were analyzed at the end of the experiment (commercial size), to determine whether muscle cellularity influences the firmness of flesh in this species, as found in other species (Hatae *et al*., 1990; Hurling *et al*., 1996; Johnston *et al*., 2000a, 2004; Periago *et al*., 2005; Ayala *et al*., 2010). The results of this study may be of great interest to aquaculture since the manipulation of the photoperiod during the larval stage can not only accelerate growth during this early phase, but also to maintain these effects into the adult stages, leading to greater production at commercial size stages.

Material and Methods

This experiment was carried out with specimens of shi drum from a stock of spawners adapted to captivity at the Instituto Español de Oceanografía (Centro Oceanográfico de Murcia, Mazarrón, Spain). The rearing conditions of the specimens (eggs, larvae and postlarvae) were described in a previous study (Ayala *et al*., 2013). Briefly, 547,000 fertilized eggs were placed in one cylindrical, 1 m^3 capacity glass-fibre tank, with continuous light and å 21.5 ºC. Newly hatched larvae were divided into three groups. Each group was placed in two cylindrical, 0.5m^3 capacity glass-fibre larva cultivation tanks, with a density of 30 larvae/litre (15,000 larvae/tank). The three experimental groups were maintained under the following photoperiods from hatching until the end of the larval metamorphosis: 24-h light/0-h dark (24L) (continuous light); 16-h light/8-h dark (16L:8D) (natural light) and 12-h light/12-h dark (12L:12D). After the larval metamorphosis (July 2011), the specimens were transferred to a natural photoperiod (å16L:8D) into 2 m^3 capacity glass-fibre square tanks until the end of the experiment (20-23 months of age). At the beginning of the experiment the density of the fish was å 10 kg/m^3 in both the 24L and 12L:12D groups, but it was å 13.25 kg/m^3 in the 16L:8D group. In the subsequent stages the density was å 20 kg/m^3 in the 24L and 12L:12D groups, but it was å 30 kg/m^3 in the 16L:8D group. According to Collet (2007), the stocking density in the range of 10-50 kg/m^3 is optimal and results in similar growth in juveniles of this species. The fish were fed ñad libitumò. The composition of the feed was: 47 % protein, 20 % fat, 7.7 % ashes, 2.5 % cellulose, 1.4 % phosphorous. The trading company for the feed

was Skretting (Spain). The sampling points were carried out at 11.8 months of age (in June 2012), at 20 months (in January 2013, which coincided with the commercial size in the 24L and 12L:12D groups), and at 23 months in the 16L:8D group (commercial size in this experiment corresponded with the natural temperature of the sea, such that in June 2012 (first sampling point) it was increasing gradually from 21.5 to 26 ºC. In the subsequent sampling points, the temperature was å 14-15 ºC in January 2013 and ranged between 14.5 and 18 ºC in April 2013. Survival was å 100 % in all the tanks.

At each sampling point, 8-10 specimens from each light regime were randomly chosen, slaughtered by clove oil anesthesia and then delivered to the veterinary faculty of Murcia.

Quantitative analysis of body and muscle growth

Total body length and body weight were measured in all specimens. Also, the eviscerated body weight was measured at 20-23 months of age. After measuring these body parameters, the samples were cut transversely to the long body axis and whole body slices of 5 mm thickness were obtained. Then, whole cross muscle sections from each fish were photographed for measurement by a morphometric analysis system (Sygma-Scan Pro_5). Subsequently, these body slices were cut into smaller blocks and then snap frozen in 2-methylbutane over liquid nitrogen. Later, sections of 8 µm thickness were obtained from those frozen blocks in a cryostat (Leyca CM 1850) and stained with haematoxylin-eosin for morphometric studies.

Muscle growth was quantified by means of the morphometric analysis system cited above. The following parameters were measured: total cross-sectional area of the red and white muscles; number of white muscle fibres; size (area, minimum diameter and minor axis length) of white muscle fibres and muscle fibre density (number of white fibres/μm^2). The average size was estimated from å 500 fibres (± 10 SD) located at the intermediate and the apical sectors of the epaxial quadrant of the transversal section of the myotome.

Texture profile analysis (TPA)

TPA was measured at commercial size in all the fish within 24 hours after their collection. The samples were obtained from the dorsal musculature on the left side of each specimen using a texture analyzer (Brookfield QTS-25, CNS Farnell, Borehamwood, Hertfordshire, England) equipped with Texture Pro v. 2.1 software. The test conditions involved two consecutive cycles of 50% compression with 5 s between cycles. Measurements were taken with a flat-ended 20 mm diameter cylindrical probe. The crosshead moved at a constant speed of 50 mm/min. From the resulting forceï time curve, the following parameters were determined: hardness (N)

(maximum force required to compress the sample); cohesiveness (extent to which the sample could be deformed prior to rupture); springiness (cm) (ability of sample to recover its original form after the deforming force is removed); gumminess (N/cm^2) (the force needed to disintegrate a semisolid sample to a steady state of swallowing (hardness x cohesiveness); chewiness (N/cm) (the work needed to chew a solid sample to a steady state of swallowing (springiness x gumminess); adhesiveness (N/s) (work necessary to overcome the attractive forces between the surface of the food and the surface of the other materials with which the food comes in contact). All these parameters were calculated according to Bourne (1978). The measurements were done at room temperature (22ï 23 ºC) and samples were brought to temperature 30 min before the texture profiles analyses (TPA) were started.

Proximate composition

A nutritional analysis was carried out in the 16L:8D group. This group was reared under natural environmental conditions and represents fish usually found in the market. In subsequent studies, it will be necessary to study the nutritional composition in fish reared under different environmental conditions.

The flesh of dorsal and ventral fillets without skin and bones were homogenized after texture measurements in an Omni_Mixer (Omni International, Waterbury, CT) to obtain a homogenous sample. Samples were analyzed in triplicate for moisture, total fat, ash and total nitrogen content according to AOAC methods (1999). Total protein was calculated from Kjeldahl nitrogen analysis, using a 6.25 conversion factor.

Statistical Analysis

The statistical analysis was performed with SPSS 15.0 software. The mean and standard error of the mean (SEM) from each group of data were calculated. Data distribution was analyzed in each stage by the Shapiro-Wilk test for $P < 0.05$. Data showed a normal distribution ($P > 0.05$). Analysis of variance (ANOVA) was used to evaluate the effect of the photoperiod at each sampling point, for $P < 0.05$. Tukey´s test was used to compare means as post-hoc analysis.

Results

Muscle parameters and body growth

11.8-month-old specimens (356 days posthatching)

At this stage, the body growth was significantly greater in the 12L:12D and the 24L groups than in the 16L:8D group (Table 1).

In relation to the muscle parameters, the highest values of the transverse area of the white and red muscles were reached in the 24L group, followed by 12L:12D, whereas the 16L:8D group showed the lowest value (Tables 2, 3). However, these differences were only significant when comparing the 16L:8D group with the other groups.

The number of white muscle fibres showed similar results to those described for the transverse area of the myotome, such that it was higher in the 24L group, followed by the 12L:12D and the 16L:8D groups (Table 2; Fig. 1a,b). In the case of the muscle fibre density values, they were higher in the 16L:8D group, followed by the 24L and the 12L:12D groups. The white muscle fibres size was greater in the 12L:12D group, followed by the 24L group, whereas the 16L:8D group showed the lowest muscle fibres size.

20-month-old specimens (commercial size of the 24L and 12L:12D groups)

At this stage, the 24L and 12L:12D groups reached commercial size: å 28-30 cm total length, å 290-340 g total weight (Table 1). In contrast, the body growth and eviscerated body weight of the 16L:8D group was significantly lower than in the other groups.

The muscle parameters showed a similar tendency to those described in the previous stage. Thus, the transverse area of the white muscle and the number of white fibres were greater in the 24L group, followed by the 12L:12D group, showing the 16L:8D group to have the lowest value (Table 2; Fig. 1 c,d). The muscle fibre density was higher in the 16L:8D group, followed by 24L and 12L:12D ($P < 0.05$). The greatest white muscle fibres size was reached in the 12L:12D group, followed by 24L and 16L:8D. In relation to the transverse area of the red muscle, it was also smaller in the 16L:8D group than in the other groups, although the differences found in this parameter were not significant (Table 3).

When comparing the body and muscle growth reached in this stage in relation to the previous stage, we can observe that both body length and body weight increased significantly in the three photoperiod groups. Also, all the muscle parameters grew significantly in the three photoperiod groups, except the red muscle of the 24L group and the number of white fibres of the 12L:12D group, where the hyperplasia was not significant.

23-month-old specimens: commercial size in the 16L:8D group

At this stage, all the body parameters increased significantly in the 16L:8D group, reaching commercial size, with no significant differences with respect to the body values reached by the 24L and 12L:12D groups at 20 months of age (Table 1).

Muscle parameters of 23-month-old specimens of 16L:8D were compared with the muscle parameters of 20-month-old specimens of the 12L:12D and 24L groups in order to determine whether the muscle cellularity was similar among the three groups at commercial size. The results showed that the transverse area of the white muscle was greater in the 24L groups, followed by the 12L:12D and the 16L:8D groups, but these differences were not significant (Table 2). The number and the white muscle fibres density was also higher in the 24L group, followed by the 16L:8D group, showing the 12L:12D group to have the lowest values, although such differences were not significant either. In contrast, the white muscle fibres size was significantly greater in the 12L:12D group than in the other groups. When comparing the 24L with the 16L:8D group, the muscle fibres size did not show significant differences.

Textural and Nutritional parameters

Textural parameters were measured in all the groups at commercial size (20 months in the 24L and 12L:12D groups *versus* 23 months in the 16L:8D group). At this commercial stage, the textural values only showed significant differences for the hardness and adhesiveness parameters (Table 4). The hardness values were higher in the 16L:8D group, followed by 24L, showing the 12L:12D group to have the lowest values.

In order to determine whether the textural parameters were correlated with the muscle parameters, a correlation analysis was carried out between them, by attaching the data from the three photoperiod groups. This analysis showed a slight negative correlation among the muscle fibres size and most of the textural parameters (firmness, gumminess, adhesiveness, chewiness and springiness), but this correlation was not significant ($P > 0.05$). On the contrary, a positive correlation was found among the number and the density of the muscle fibres and most of the textural parameters, but this correlation was only significant when correlating the number of fibres with the gumminess and the cohesiveness parameters.

The nutritional analysis was carried out in the 16L:8D group (natural photoperiod). The results are shown in Table V, where they are compared with the results found in this species by other authors. Our values show a relatively low fat level (2.6%), corresponding to lean species belonging to the Sciaenidae family. Similarly, the rest of parameters (Table 5) are within the normal levels in sciaenids fish.

Discussion

Fish muscle is plastic in its response to environmental conditions: temperature, photoperiod, salinity, etc. Hence, the external factors influences the number and size of red and white muscle fibres (Johnston, 1999; Ayala *et al*., 2003; López-Albors *et al*., 2003; Johnston *et al*., 2000a,b, 2003a,b, 2004, 2011; Campos *et al*., 2013a). This influence can persist and produce long-term effects (Ayala *et al*., 2001a; Johnston *et al*., 1998, 2003a, 2004; Imsland *et al*., 2007; Steinbacher *et al*., 2011; García de la Serrana *et al*., 2012; Campos *et al*., 2013b).

In the present study, the 11.8-month-old specimens maintained with continuous light during the larval period (24L group) showed the highest values of both the hyperplasia and the transverse area of the myotome, followed by the 12L:12D group, showing the 16L:8D (natural photoperiod) to have the lowest values of these parameters. These results are similar to those found in previous studies of the larval and early postlarval phases of these experimental groups (Ayala *et al*., 2013), and show that the larval photoperiod effect persists in more advanced age stages of this species.

The results also showed that the continuous light photoperiod promoted hyperplasia, which coincides with previous results in this species (Ayala *et al*., 2013) and in salmon (Johnston *et al*., 2003a, 2004). In this latter species, Johnston *et al*. (2003a, 2004) maintained salmons with 24L and natural photoperiods for a short time and later both experimental groups were transferred to a natural photoperiod. Four months after transferring the salmons to a natural photoperiod, Johnston *et al*. (2003a) found the highest hyperplasia values in the 24L group. Similarly, two weeks after transferring the salmons to a natural photoperiod, Johnston *et al*. (2004) observed that the number of fast muscle fibres and the hypertrophy was higher at 24L, with the effect more marked on the number than on the size of the fibres.

In the present study, the hypertrophy was higher in the 12L:12D than in the other groups, which shows that the shorter photoperiod promotes this muscle parameter, as found previously in larva and postlarval stages of this species (Ayala *et al*., 2013).

Body growth (length and weight) at 11.8 months was similar between the 24L and 12L:12D groups of the present study, which differs from the results found in the early phase (Ayala *et al*., 2013), where the 24L group showed significantly more growth than the other groups. The greater growth of the 12L:12D group in the present study compared to that of the previous experiment shows a compensatory growth in the advanced stages of this group in comparison with the early stages. In contrast, the 16L:8D group did not reach the size of the other groups. In salmon, the body weight was also higher in the 24L group than in the natural photoperiod group

four months and two weeks after transferring the salmons to natural photoperiod (Johnston *et al*., 2003b, 2004, respectively). In two groups of cod reared at 24L and at a natural photoperiod for 120 days, Nagasawa *et al*. (2012) observed that the muscle growth of the 24L group was greater not only at 120 days, but also two months after the two groups were transferred to a natural photoperiod (at 180 days). These authors studied the molecular mechanisms of photic-induced plasticity of muscle growth. According to their results, the lasting effects of the photoperiod indicated an epigenetic transcriptional memory that could be due to chromatin remodelling that occurred during the first four months in response to photoperiod changes (Nagasawa *et al*., 2012).

Commercial size (å 28-30 cm, å 290-340 g) was reached at 20 months in the 24L and 12L:12D specimens, whereas the 16L:8D group reached this commercial size stage three months later (at 23 months of age). The results found at commercial size differ from those found in the salmon study (Johnston *et al*., 2004). These authors observed that the natural photoperiod group of salmon grew faster than the 24L group from 6-9 months after seawater transfer until harvest (commercial size), such that both groups reached commercial size at the same age. Also, the mean weights were similar at the end of the trial in both groups of salmon. In cod, Imsland *et al*. (2007) found that the juveniles reared under continuous light during the initial three month period and then transferred to sea pens resulted in 1-9% larger size at harvesting compared to fish reared at a stimulated natural photoperiod.

When comparing the muscle cellularity of the three groups at commercial size (20 months in 24L and 12L:12D groups *versus* 23 months in 16L:8D group) we observed that the hyperplasia and the muscle fibres density was greater in the 24L group, whereas the 12L:12D group showed the highest hypertrophy values. These results are similar to those found in the previous stages of the present and the preceding works on shi drum (Ayala *et al*., 2013), showing a long-term effect of the larval photoperiod on muscle cellularity in subsequent life stages. Similarly, Johnston *et al*. (2004) observed a persistent effect of early light regime on muscle cellularity in commercial size salmon, such that the size distribution of fibres differed between the different light regimes groups, showing the 24L group to have the highest fibre density. In turbot, Imsland *et al*. (2013) studied the long-term effect of photoperiod manipulation for 46 months and found that the short-term exposure to 24L stimulated growth, whereas the long-term rearing at 24L reduced growth. Thus, at harvest, the greatest mean weights were reached in the group previously kept to short-term exposure at 24L and then transferred to 16L:8D until harvest.

In relation to the textural parameters, most groups showed a positive correlation with muscle fibres density, although this correlation was hardly ever significant. Johnston *et al*. (2004) found similar results, such

that the highest fibre density of the 24L group was accompanied by firmer flesh. This correlation between muscle fibre density and flesh firmness has also been observed in other fish species (Hatae *et al*., 1984, 1990; Hurling *et al*., 1996; Periago *et al*., 2005). These results show that the early photoperiod effects observed in the larval phase of shi drum (Ayala *et al*., 2013) persist in subsequent life stages and influences the characteristics of the flesh, in particular the texture. In turbot, Imsland *et al.* (2013) found that photoperiod had only a minor effect on textural and flesh quality. However, these authors found a tendency towards higher texture shear force and hardness in the 24L group.

In relation to nutritional composition, studies of shi drum are scarce. In our study, the fat levels were relatively low, similar to those found in other sciaenids, like the meagre *Argyrosomus regius* (Asso, 1801) (Piccolo *et al*., 2006). The protein levels in the shi drum in our study were also similar to those found in meagre by the cited authors. Our results also agree with those obtained by Segato *et al.* (2007) from the dorsal fillet, with the exception of the fat content, which was higher in our samples from both the dorsal and ventral fillets. This could be due to the fact that the lipid content of farmed fish flesh is significantly higher in ventral than in dorsal fillets, as demonstrated by Testi *et al.* (2006). From a nutritional point of view, we have considered that the proximal composition analysis in a homogenized portion of the whole flesh, including both dorsal and ventral areas as an edible portion of fish, gives better information about the total composition than the commonly used dorsal area.

On the other hand, our results showed a higher content of moisture and protein and lower total fat and ash content than those obtained by Segato *et al*. (2006) and Zafer *et al.* (2012) for whole-body of shi drum. These results may be explained because the total fat in our study did not include viscera, like the liver which has a high fat content. Furthermore, we used fillets without skin and bones, so the ash content is lower than in the case of whole-body samples. However, other factors, like diet, can also influence the differences found among the cited works. Alasalvar *et al.* (2002) and Orban *et al*. (2002) described that farmed fish show higher fat and lower moisture than wild specimens, due to high dietary fat level in the feed and reduced activity, whereas protein is considered to be a stable component of the fish body in respect to diet and feeding level depending mainly on fish weight (Shearer, 1994). Also, the chemical composition can vary depending on age, size, sex environment and season (Silva and Chamul, 2000).

Since the nutritional analysis was only carried out in the 16L:8D group, it is not possible to know whether the photoperiod regime influenced these quality parameters in the other groups or no. Further studies

would be necessary to determinate if this environmental factor influences in the physicochemical composition of this species.

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Table 1. Mean values (± SEM) of the total length and the body weight. Different superscripts indicate significant differences ($P < 0.05$) among light regimes within each stage.

Sampling point	Photoperiod regime	Total body length (cm)	Total body weight (g)	Eviscerated weight body (g)
11.8 months	16L:8D	16^{a} (0.65)	53.12^{a} (6.94)	
	24L	22.15^{b} (1)	142.35^{b} (18.56)	
	12L:12D	23.3^{b} (1.124)	156.47^{b} (24.07)	
0 months (commercial size in 24L and 12L:12D specimens)	16L:8D	21.84^{a} (0.78)	150^{a} (25.92)	132.5^{a} (22.81)
	24L	30.75^{b} (0.79)	343.75^{b} (29.74)	325.69^{b} (27.34)
	12L:12D	28.69^{b} (0.91)	291.61^{b} (32.54)	260.63^{b} (28.76)
23 months (commercial size in 16L:8D specimens)	16L:8D	28.69 (0.38)	306.62 (6.03)	276.88 (6.87)

Table 2. Mean values (± SEM) of the white muscle of shi drum. Different superscripts indicate significant differences ($P < 0.05$) among light regimes within each sampling point. White fibres density: white muscle fibres density (number of fibres/μm^2) $x10^5$

Sampling point	Photoperiod regime	Transverse area of the White muscle (mm^2)	White muscle fibres minor axis length (μm)	Number of white muscle fibres	White fibres density
11.8 months	16L:8D	281.16^{a} (31.66)	45.91^{a} (1.29)	112542.36^{a} (9458.39)	39.3^{a} (0.18)
	24L	566.44^{b} (44.49)	50.18^{ab} (1.28)	181046.77^{b} (10213.72)	31.8^{b} (0.11)
	12L:12D	543.98^{b} (56.19)	53.55^{b} (2.27)	167566.27^{ab} (23661.5)	30^{b} (0.19)
20 months (commercial size in 24L and 12L:12D specimens)	16L:8D	570.38^{a} (61.49)	51.5^{a} (1.33)	171519.94^{a} (15197.75)	27.22^{a} (1.91)
	24L	995.42^{b} (63.98)	55.78^{b} (0.63)	248389.63^{b} (16589.3)	25.1^{a} (1.38)
	12L:12D	920.44^{b} (95.78)	61.23^{c} (0.74)	209467.42^{ab} (21948.98)	21.6^{a} (1.25)
23 months (commercial size in 16L:8D specimens)	16L:8D	875.36 (30.77)	56.89 (0.48)	212079.45 (14140.07)	24.52 (2.06)

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436 **Table 3.** Mean values (± SEM) of the red muscle of shi drum. Different superscripts indicate significant differences ($P <$

437 0.05) among light regimes for each sampling point.

Sampling point	Photoperiod regime	Transverse area of the red muscle (mm^2)
11.8 months	16L:8D	10.39^{a} (0.98)
	24L	35.40^{b} (3.98)
	12L:12D	23.91^{b} (4.42)
20 months (commercial size in 24L and 12L:12D specimens)	16L:8D	25.51^{a} (7.37)
	24L	36.94^{a} (2.99)
	12L:12D	37.77^{a} (2.47)
23 months (commercial size in 16L:8D specimens)	16L:8D	41.82 (3.72)

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Table 4. Mean values (± SEM) of the textural values at commercial size (20-23 months). Different superscripts indicate significant differences ($P < 0.05$) among light regimes.

Photoperiod regime	Hardness (N)	Gumminess (N)	Adhesiveness (N/s)	Cohesiveness (ratio)	Chewiness (N/mm)	Springiness (mm)
16L:8D	22.93^{a} (3.4)	8.25^{a} (0.9)	-0.55^{a} (0.1)	0.38^{a} (0.02)	25.28^{a} (3.6)	2.97^{a} (0.1)
24L	17.34^{ab} (2.9)	7.47^{a} (0.8)	-0.24^{b} (0.03)	0.47^{a} (0.04)	19.8^{a} (3.3)	2.61^{a} (0.3)
12L:12D	11.52^{b} (1.5)	5.72^{a} (1.0)	-0.43^{ab} (0.05)	0.48^{a} (0.05)	15.3^{a} (3.4)	2.52^{a} (0.2)

447 **Table 5.** Mean values (± SEM) of the nutritional parameters from the 16L:8D group of the present study. Our results are

448 compared with the results found in shi drum by Segato et al. (2006, 2007) (mean values ± SD) and Zafer et al. (2012).

	16L:8D group (dorsal and ventral fillet)	Dorsal fillet (Segato et al., 2007)	Whole-body (Segato el al., 2006)	Whole -body (Zafer et al., 2012)
Moisture (%)	74.41 (0.44)	76.4 (0.2)	63.6 (0.5)	72
Protein (%)	21.24 (0.14)	21.5 (0.2)	18.9 (0.1)	18
Total fat (%)	2.66 (0.53)	0.5 (0.1)	13.5 (0.5)	4.3
Ash (%)	1.46 (0.06)	1.4 (0.1)	4.8 (0.1)	4.0

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Fig. 1. Transverse white muscle sections of 11.8 months old specimens (**a,b**) and commercial size specimens (**c,d**) from the 24L (**a,d**), 16L:8D (**b**) and 12L:12D (**c**) groups. Bars **a**: 100 µm; **b,d**: 66.66 µm; **c**: 50 µm; *W* white muscle fibres; *nW* new white muscle fibres.