

# Histostructure of the Locomotor Apparatus in the Three Deep-Water Species of Lanternfishes (Myctophidae): *Myctophum punctatum*, *Notoscopelus kroyeri*, and *Lampanyctus macdonaldi*

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**Abstract**—The morphological and functional characteristics of the somatic musculature’s histological structure have been studied for three species of deep-sea fish from the Myctophidae family: spotted lanternfish *Myctophum punctatum*, lancet fish *Notoscopelus kroyeri*, and rakery beaconlamp *Lampanyctus macdonaldi*. The average diameter of fast-twitch and slow-twitch muscle fibers in all studied species is large, and this indicator is highest in rakery beaconlamp. All species are characterized by a craniocaudal gradient of a decrease in the size of white muscle fibers. The shape of the fibers, from angular polygonal (spotted lanternfish) to the oval (rakery beaconlamp) and round (lancet fish), is a distinctive feature from other species of bony fish. In spotted lanternfish, a group of fibers of very small diameter, which are presumably small, slow-twitch oxidizing fibers, was also noted between the white and red muscles. The red muscles in the studied fish are poorly identified, since they are poorly developed. The studied species have a well-developed connective tissue carcass of white muscles, which indicates a certain friability of fast-twitch muscles. Both the red and white muscles in lanternfishes are a place of intense deposition of lipid reserves. Apparently, the high lipid content in muscle tissue helps to reduce the specific gravity of fish and increase their buoyancy.

**Keywords:** lanternfishes Myctophidae, *Myctophum punctatum*, *Notoscopelus kroyeri*, *Lampanyctus macdonaldi*, muscle tissue, fiber diameter, slow-twitch muscle fibers, fast-twitch muscle fibers

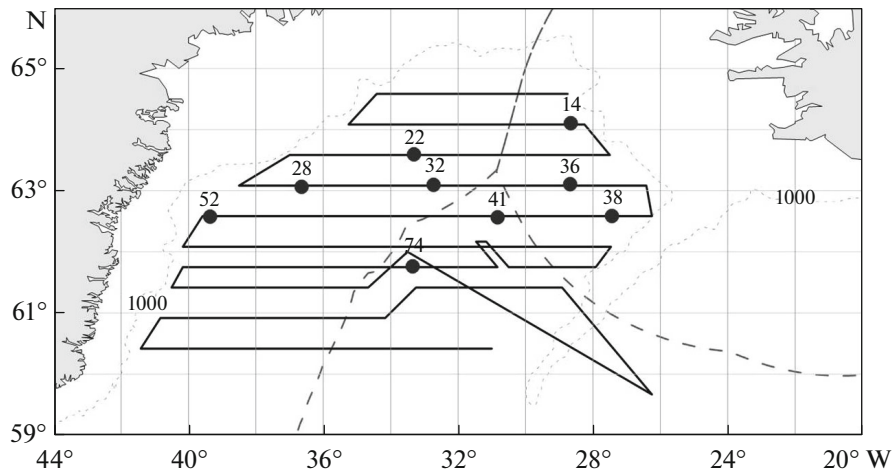
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## INTRODUCTION

Fish that live at great depths have specific properties that allow them to adapt to conditions of high pressure, absolute darkness, a peculiar food base, and other biotic and abiotic factors. Deep-sea fish are widespread and make up a significant part of the total fish biomass of the World Ocean (Gjøsaeter and Kawaguchi, 1980; Irigoien et al., 2014). They have long attracted the attention of specialists (Mead et al., 1964; Becker, 1983; Mauchline and Gordon, 1985, 1986; Haedrich and Merrett, 1988; Haedrich, 1996; Koslow, 1996; Merrett and Haedrich, 1997), and researchers have studied morphological features, growth processes, reproductive biology, metabolism, and nutritional characteristics of these fish (Mead et al., 1964; Mauchline and Gordon, 1985, 1986; Gauldie et al., 1991; Bergstad, 1995, 2013; Koslow, 1997; Drazen and Siebel, 2007). In recent years, the

issue of the influence of fisheries on the biological diversity of deep-sea ecosystems and stocks of deep-sea fish has attracted increasing attention (Koslow et al., 2000; Devine et al., 2006; Shank, 2010; Norse et al., 2012).

The family of lanternfishes (Myctophidae) is the most numerous among the bony fish by the number of species (33 genera and 248 species) (Fricke et al., 2019). These fish have a swimming bladder and are characterized by a rigid body. Many species make daily vertical migrations, which is associated with their feeding on the planktonic organisms. Owing to the high biomass of mesopelagic fish (lanternfishes dominate absolutely among them), which range from 0.9 to 2.0 billion t in the World Ocean (Gjøsaeter and Kawaguchi, 1980; Irigoien et al., 2014), they are of some interest for industrial fishing (Shust and Orlov, 2003), especially in conditions of a lack of locally produced food for rapidly developing aquaculture.



**Fig. 1.** Sampling site map for studying the histology of lanternfishes (Myctophidae) in the Irminger Sea: (●) places and numbers of trawls, (—) traverses of the R/V *Atlantida*, (- -) boundaries of the EEZ, (···) isobaths.

The locomotor muscles of deep-sea fish, like most other species, include fast-twitch (white) and slow-twitch (red) fibers, providing various types of locomotor activity. The ratio of the muscles of these types in the representatives living at great depths varies significantly. The proportion of slow-twitch fibers ranges from 0 to 15% of the total muscle mass depending on the fish species divided into groups according to the principle of body rigidity and the presence of a swimming bladder (Blaxter et al., 1971). Moreover, the histological structural features (diameter, fiber density) in muscles of different morphofunctional types in deep-sea fish, judging by the available literature, have not been studied yet.

This study aims to reveal the relationship between the morphometric characteristics of somatic muscles and the growth and locomotor activity of three fish species belonging to the family of lanternfishes: spotted lanternfish *Myctophum punctatum*, lancet fish *Notoscopelus kroyeri*, and rakery beaconlamp *Lampanyctus macdonaldi*.

## MATERIALS AND METHODS

The material was collected during an international trawl-acoustic survey aimed at studying the deepwater redfish *Sebastes mentella* in June–July 2018 aboard the R/V *Atlantida* in the Irminger Sea (59°60′–64°60′ N, 26°20′–41°50′ W), in the area regulated by NEAFC (the Northeast Atlantic Fisheries Commission) and the exclusive economic zones (EEZ) of Greenland and Iceland (Fig. 1). Samples were taken from the catches of a 78.8/416-m deep-sea trawl (project no. 2492-02). During the survey, 121 trawlings were performed. In order to study the histology of lanternfishes, 16 individuals were selected from nine trawl catches performed at the depths of 375–700 m (Table 1). Species identification was carried out using taxonomic

keys (Becker, 1983; *Methodologicheskije materialy...*, 2006). The standard length (*SL*) and fish body weight were measured. Muscle samples were taken according to a single scheme for all fish: directly behind the head, in the middle part of the body under the dorsal fin, and in the region of the caudal peduncles (Fig. 2). Collected samples were stored in a 4% formaldehyde solution.

Gelatin histological sections, 15- $\mu$ m thick, were obtained on a freezing microtome and stained with Sudan III (Vecton, Russia) and Carazzi hematoxylin (Abris+, Russia). The diameter of white and red muscle fibers and their density were determined on the preparations (Appelt, 1959). The proportion of superficial lateral muscles in the region of the caudal peduncle was calculated by the application method (Avtandilov, 1973). The resulting material was processed statistically using Microsoft Office Excel software.

## RESULTS

Somatic muscles in all studied fish species include white (fast-twitch) and red (slow-twitch) fibers. As is observed for most of the other ecological groups of bony fish, the red muscles (*m. lateralis superficialis*) are located directly under the skin along the midline in the form of a portion of a triangular shape, protruding into the white muscles (*m. lateralis profundus*). The area occupied by slow-twitch fibers in the region of the caudal peduncle comprises  $2.6 \pm 0.48\%$  for spotted lanternfish,  $2.4 \pm 0.26\%$  for lancet fish, and  $3.9 \pm 0.28\%$  for rakery beaconlamp. Despite the small size of the studied fish species (spotted lanternfish, *SL* 6–9 cm; lancet fish, *SL* 13–17 cm; and rakery beaconlamp, *SL* 14–18 cm), the bulk of their skeletal muscles is formed by rather large fibers (Table 2).

**Table 1.** Information on the studied individuals of lanternfishes (Myctophidae)

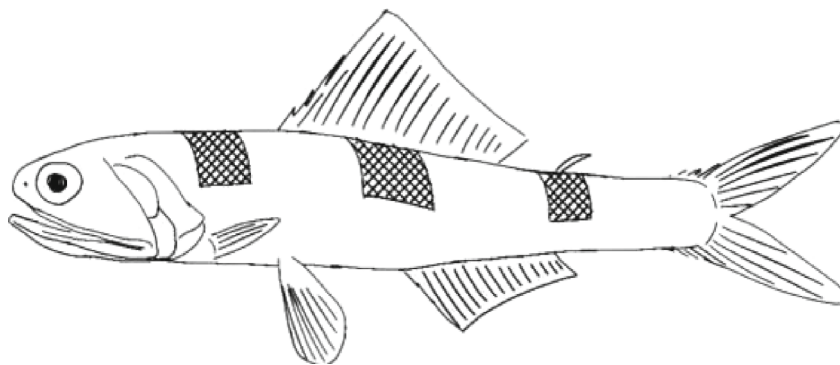
Species	Body length (SL), cm	Body weight, g	Date of catch	Trawl no.	Coordinates		Depth, m
					N	W	
<i>M. punctatum</i>	6.1	2.8	June 25, 2018	41	62°34'	30°50'	400
	8.8	5.6	June 25, 2018	41	62°34'	30°50'	400
	8.2	5.0	July 4, 2018	74	61°46'	33°20'	650
<i>N. kroyeri</i>	13.0	15.5	June 17, 2018	14	64°6'	28°39'	700
	13.6	17.5	June 21, 2018	28	63°4'	36°38'	700
	12.1	12.4	June 23, 2018	38	62°35'	27°27'	700
	13.9	18.8	June 25, 2018	41	62°34'	30°50'	400
	17.1	28.3	June 25, 2018	41	62°34'	30°50'	400
	13.6	17.6	June 28, 2018	52	62°35'	39°21'	375
	15.3	26.0	June 19, 2018	22	63°35'	33°18'	700
<i>L. macdonaldi</i>	15.3	26.0	June 21, 2018	28	63°4'	36°38'	700
	18.2	36.2	June 22, 2018	32	63°6'	32°44'	700
	14.3	22.2	June 23, 2018	36	63°6'	28°41'	700
	13.5	18.8	June 23, 2018	38	62°35'	27°27'	700
	16.6	31.0	June 28, 2018	52	62°35'	39°21'	375
	14.9	24.4	June 28, 2018	52	62°35'	39°21'	375

Rakery beaconlamp has the largest white muscle fibers, regardless of their location in the body. There were no significant differences between spotted lanternfish and lancet fish in terms of the average value of this indicator. In all species, the craniocaudal gradient of a decrease in the size of white muscle fibers exhibits a similar tendency. Size variability is not high ( $CV = 18.6\text{--}26.8\%$ ), but the absolute values of the smallest and largest muscle fibers are significant ( $38.0\text{--}189.8\ \mu\text{m}$ ).

Sizes of slow-twitch fibers are significantly smaller than that of the fast-twitch ones. On average, the diameter of white fibers in spotted lanternfish is 2.9 times larger than that of the red fibers, 4.0 times in lancet fish, and 3.5 times in rakery beaconlamp. In spotted lanternfish, the diameter of slow-twitch fibers decreases in the caudal direction by 1.5 times, while it

does not change in lancet fish. Due to the loss of the body's red musculature in the rakery beaconlamp during the sampling, the diameter of its fibers is characterized by the samples taken from the caudal peduncle. In this area, the largest fibers are noted in the rakery beaconlamp. The largest slow fibers are observed in the cranial part of the muscles in a small-sized spotted lanternfish. The coefficient of variation in red muscles is higher than that in white ones ( $24.4\text{--}38.3\%$ ) (Table 2).

In spotted lanternfish, 80–100- $\mu\text{m}$  white muscle fibers form the modal class regardless of their topography (45–54%). In the middle of the body, such fibers comprise over 50%. The fraction of the largest fibers with a 140–160- $\mu\text{m}$  diameter in the cranial and caudal region is small, approximately 4%. The number of the

**Fig. 2.** Scheme of histological sampling sites (▣) in fish of the family Myctophidae.

**Table 2.** Morphometric indicators of different types of muscles in the studied species of lanternfish (Myctophidae)

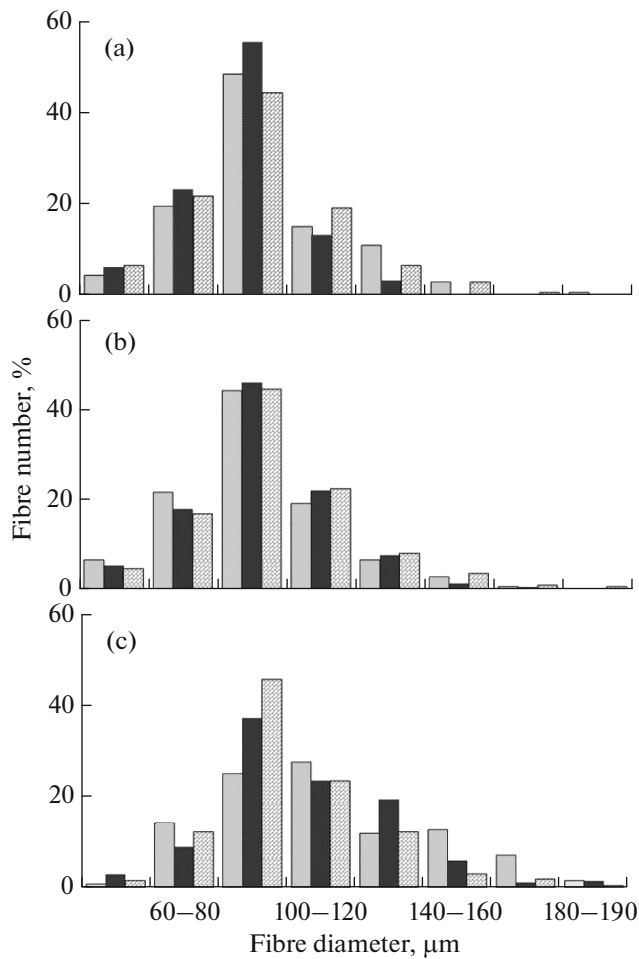
Localization of muscles	<i>M. punctatum</i>		<i>N. kroyeri</i>		<i>L. macdonaldi</i>	
	fiber diameter, $\mu$	CV, %	fiber diameter, $\mu$	CV, %	fiber diameter, $\mu$	CV, %
White muscles ( $n = 270$ )						
Behind the head	$94.0 \pm 1.34$ 49.5–181.5	23.3	$92.6 \pm 1.24$ 38.0–165.0	22.1	$111.4 \pm 1.82^*$ 49.5–184.8	26.8
Under the dorsal fin	$87.2 \pm 0.99$ 49.5–132.0	18.6	$95.7 \pm 1.36^*$ 46.2–189.8	23.4	$105.0 \pm 1.55^*$ 49.5–189.8	24.2
Caudal peduncle	$90.8 \pm 1.30$ 41.3–173.3	23.4	$90.4 \pm 1.21$ 49.5–148.5	21.9	$99.7 \pm 1.35^*$ 49.5–181.5	22.3
Average	$90.6 \pm 0.71$ 46.8–162.2	22.3	$92.9 \pm 0.74$ 45.6–167.8	22.6	$105.4 \pm 0.93^*$ 49.5–185.4	25.1
Red muscles ( $n = 60-180$ )						
Behind the head	$40.6 \pm 1.05$ 21.5–66.0	24.5	$22.8 \pm 0.69^*$ 9.9–34.7	28.8	–	–
Under the dorsal fin	$23.2 \pm 1.57$ 9.9–41.3	37.1	$23.1 \pm 0.89$ 8.3–49.5	36.6	–	–
Caudal peduncle	$27.4 \pm 0.75$ 8.3–52.8	37.0	$23.2 \pm 0.87^*$ 11.6–34.7	29.0	$29.7 \pm 0.87$ 9.9–49.5	28.0
Average	$30.9 \pm 0.68$ 24.0–53.4	38.3	$23.0 \pm 0.48$ 9.9–39.6	32.0	$29.7 \pm 0.87$ –	28.0

Numbers above the line are the average value and error of mean; below the line are the limits of variation of the indicator;  $n$  is the number of measured fibers; CV is the coefficient of variation; \* differences from spotted lanternfish are significant at  $p \leq 0.05$ .

smallest fibers increases in the caudal direction (Fig. 3a). For lancet fish, as well as for spotted lanternfish, fast-twitch fibers with a diameter of 80–100  $\mu\text{m}$  form a modal class (~45%). Individual fibers reach a size of more than 160  $\mu\text{m}$ . A group of fibers of 40–60  $\mu\text{m}$  (5–7%) is observed in all parts of the body, but in a larger amount, behind the head (Fig. 3b). In rakery beaconlamp, whose body is larger, the modal class of the head muscles falls into the range of 100–120  $\mu\text{m}$  (27%) and that under the dorsal fin and in the caudal peduncle is 80–100  $\mu\text{m}$  (37–45%). Fibers with a diameter of 180–190  $\mu\text{m}$  (up to 2%) were also noted. The fraction of small fibers (40–60  $\mu\text{m}$ ) in the rakery beaconlamp is much lower than that in the other species, comprising 1–3% (Fig. 3c).

In general, there is a regular (gradual) increase in the number and size of fibers in the white muscles in various parts of the body of the fish up to the values of the modal class and then a decrease in these parameters. Moreover, the proportion of relatively small fibers is negligible, and their diameter is not less than 40 microns. Therefore, the growth of white muscle tissue in the studied lanternfishes is performed to a greater extent by hypertrophy.

The modal classes of slow-twitch fibers of the red muscles differ in various parts of spotted lanternfish's body. The largest number of large fibers (40–60  $\mu\text{m}$ ) is found in the cranial part of the body (57%). In the middle part of the body, under the dorsal fin, the largest proportion of 10–20- $\mu\text{m}$  fibers (40%) was noted, while they are 20–30  $\mu\text{m}$  in the caudal peduncle (33%). Fibers with a diameter of 8–10  $\mu\text{m}$  are rarely found in the middle of the body and tail of fish (4%) (Fig. 4a). In the cranial area of the lancet fish, all size groups of muscle fibers are found except for the largest (40–60  $\mu\text{m}$ ). Most of them (~80%) have a diameter of 10–30  $\mu\text{m}$ . Under the dorsal fin, the modal class is formed by the fibers with a diameter of 10–20  $\mu\text{m}$  (42%), which can indicate hyperplasia processes, although they are possibly insignificant. Some small (8–10  $\mu\text{m}$ ; ~1.5%) and medium fibers (up to 6%) were noted in cranial muscle tissue samples (Fig. 4b). No fibers of this type were found in the caudal peduncle. In a rakery beaconlamp, the bulk of muscle fibers in the caudal region fall into the range between 20–30 and 30–40  $\mu\text{m}$  (74%). Small fibers account for 1.5% (Fig. 4c).

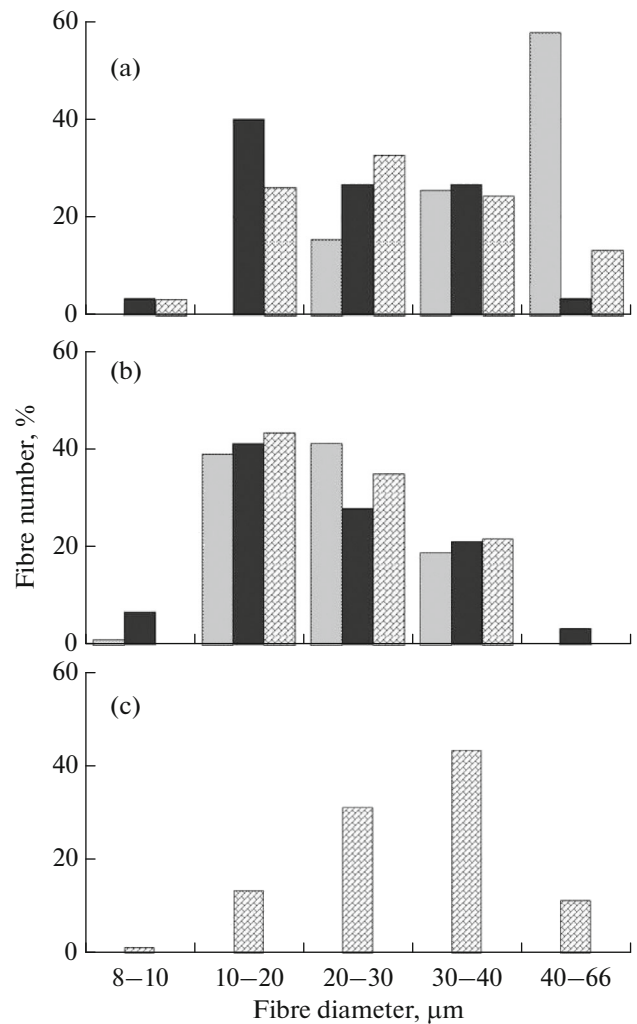


**Fig. 3.** Size composition of the fast-twitch fibers: (a) spotted lanternfish *Myctophum punctatum*, (b) lancet fish *Notoscopelus kroyeri*, (c) rakery beaconlamp *Lampanyctus macdonaldi*; (■) behind the head, (■) under the dorsal fins, (▨) caudal peduncle.

The number of fibers per unit area is one of the indicators determining the ratio of tissues in the muscles: muscle, adipose, and connective tissues. Since lipocytes are formed from fibroblasts and adventitious cells, one can suggest a complex of adipose and connective tissues. In spotted lanternfish and lancet fish, the density of white muscles is 72 and 74%, respectively. In rakery beaconlamp, the value of this indicator is significantly lower (64%).

In the red muscles, the fibers are most densely located in the rakery beaconlamp (73%), while more sparsely in the spotted lanternfish (67%) and the lancet fish (64%) (Fig. 5). The density of muscle fibers is associated with their shape and not just with the content of adipose and connective tissue.

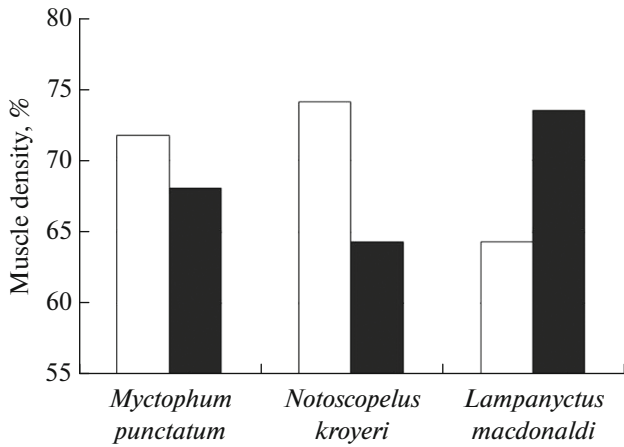
In a spotted lanternfish, glycolytic white fibers of a pronounced angular shape are located closer to the corium. Endomysium is formed by rather wide layers of loose connective tissue with relatively small fatty



**Fig. 4.** Size composition of the slow-twitch fibers: (a) spotted lanternfish *Myctophum punctatum*, (b) lancet fish *Notoscopelus kroyeri*, (c) rakery beaconlamp *Lampanyctus macdonaldi*; see Fig. 3 for designations.

inclusions. Lipocytes are large and filled with fat droplets but dispersed (Figs. 6a–6c). Significant accumulations of lipids were noted along the spinal column. Small fibers (>10 μm) make up a separate portion between the white and red fibers located directly under the skin (Fig. 6d). Fast-twitch fibers are round or oval in lancet fish. Lipid inclusions in the endomysium are more abundant in this species compared to spotted lanternfish. The endomysium is not very wide, sometimes filled with adipocytes, sometimes the borders between them are poorly distinguishable, and they look like conglomerates. Muscle fibers are tight (Fig. 7). Rakery beaconlamp has white fibers that are round or oval closer to the skin and somewhat angular closer to the spinal column. Significant accumulations of adipose tissue are observed. Endomysium is well developed, and individual lipocytes are not identified.





**Fig. 5.** Density of muscle fibers of different morphofunctional types in the spotted lanternfish *Myctophum punctatum*, lancet fish *Notoscopelus kroyeri*, and rakery beacon-lamp *Lampanyctus macdonaldi*: (□) white muscles, (■) red muscles.

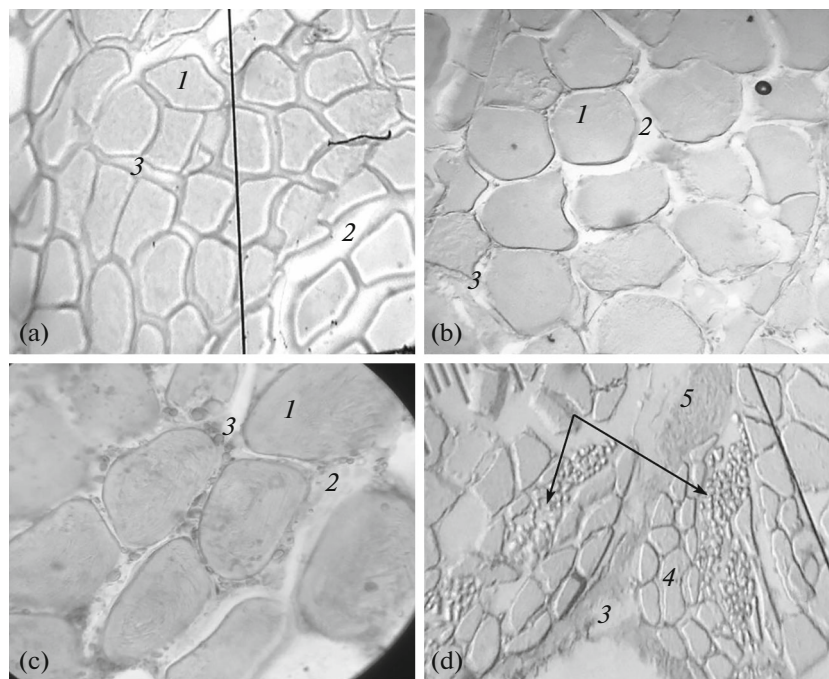
There is a lot of adipose tissue around the spinal column (Fig. 8).

Red fibers are significantly less in number than white fibers. Red fibers are difficult to identify because red muscle has a lot of adipose tissue. Oxidative fibers have a different shape, from round to somewhat angular.

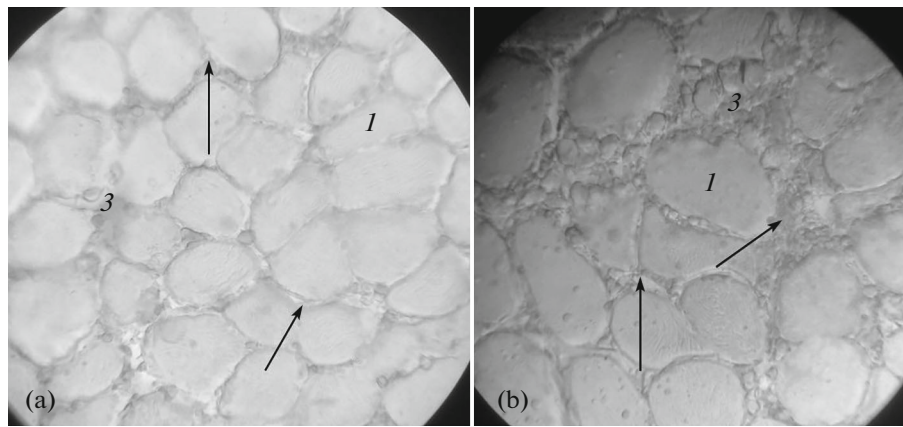
## DISCUSSION

The somatic muscles of the studied lanternfishes of the Myctophidae family include fibers of two morphofunctional types: fast-twitch and slow-twitch. The slow-twitch red fibers that form the superficial lateral muscles are significantly smaller than the fast-twitch white ones, regardless of their location in the fish's body. The proportion of red muscles is small and amounts to 2.4–3.6% of the area occupied by white muscles in the region of the caudal peduncle (Fig. 5). Previous studies on lanternfishes showed that their representatives, which have a swimming bladder and a rigid body, contain from 2 to 7% slow-twitch fibers (Blaxter et al., 1971). In general, a low number of deep-sea fish species have few red muscle fibers (Gordon, 1972). In roach *Rutilus rutilus*, bream *Abramis brama*, sibel *Pelecus cultratus*, and asp *Aspius aspius* (Cyprinidae), differing in swimming activity and classified as long-distance runners (stayers), which are quite sturdy fish with cruising locomotor abilities (Boddeke et al. 1959), the proportion of red muscles in the caudal peduncle is 10.3–15.8% (Panov, 1982a, 1982b).

The presence of underdeveloped red muscles does not exclude the possibility of classifying the objects of our study as stayers with low swimming activity. A similar pattern is observed in freshwater Chinese sleeper *Percottus glenii* (Eleotridae), which has low mobility. By his locomotion qualities, he is rather an ambus-



**Fig. 6.** Musculature of spotted lanternfish *Myctophum punctatum*: (a) near the corium, (b) near the spinal column, (c) in the lateral part of the section, (d) superficial lateral muscle; 1—fast-twitch white fibers; 2—endomysium; 3—lipocytes; 4—large slow-twitch red fibers; 5—vagus nerve; (→) a layer of small red fibers. Magnification 150×.



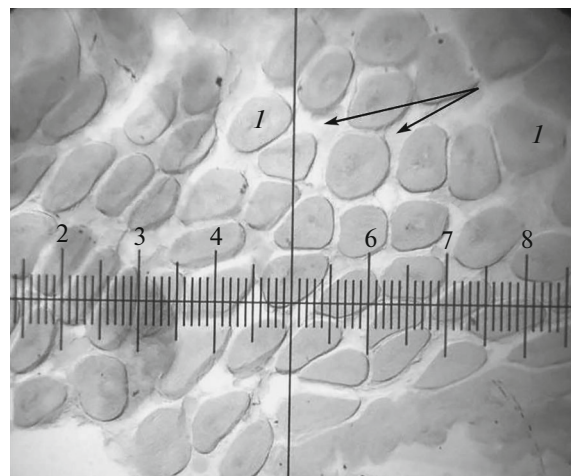
**Fig. 7.** White muscles of the lancet fish *Notoscopelus kroyeri* in the (a) dorsal and (b) lateral parts of the section: (→) endomysium; see Fig. 6 for the other designations. Magnification 150×.

cader. The proportion of superficial lateral muscle in its caudal peduncle is 3.2% (Panov and Smirnov, 1996). In the bluntnose minnow *Pimephales notatus*, which prefers the search type of locomotion before intensive swimming in usual calm conditions, the proportion of slow-twitch fibers at the level of the anal fin is 3.2–3.8% of the transverse section of the caudal peduncle (Weatherley and Bresania, 1982).

In deep-sea fish, a low protein content is observed, which is associated with the lack of the need for quick swimming at a considerable depth as a result of a decrease in visual interaction between a predator and its prey (Childress et al., 1990). In bathypelagic fish species, the protein content is 4–7% lower compared to the coastal fish species (Denton and Marchall, 1958). Despite the relatively well-developed muscle system of the fish according to technological analysis, when muscles with skin make up from 52.6% of the body weight of the rakery beaconlamp to 62.2% of the lancet fish (Bykov et al., 1990), the number of enzymes associated with aerobic and anaerobic metabolism of mesopelagic fish are generally lowered. This is especially true for lactate dehydrogenase and pyruvate kinase associated with energy metabolism in white glycolytic muscle fibers (Sullivan and Somero, 1980). It is assumed that the reduced metabolic rate in the muscles of deep-sea fish is the result of their significant decrease in swimming activity (Somero and Childress, 1980). At the same time, up to 54% of the total protein of white muscles in deep-sea fish falls on the sarcoplasmic or myogenic fraction (Slebenaller and Yancey, 1984). In active pelagic species, chub mackerel *Scomber japonicus*, and Japanese pilchard *Sardinops melanostictus*, 38–40% of proteins are accounted for by the soluble sarcoplasmic proteins. The insoluble fraction is part of the contractile myofibrillar and connective tissue proteins (Hashimoto et al., 1979). The total share of these fractions decreases with a decrease in the total amount of protein (Slebenaller and Yancey, 1984).

Respiratory rate decreases rapidly with increasing habitat depth of mesopelagic fish, which is also true for lanternfishes. A decrease in oxygen consumption per muscle mass unit implies a change in muscle metabolism in deep-sea fish due to the quantitative and qualitative composition of the enzymes involved in this process (Torres et al., 1979).

Mesopelagic fish species grow slowly and reach a small size, live long enough, mature early, and spawn several times during their life (Childress et al., 1980). Groups of fish living at different depths store lipids for life to an unequal extent. Taking into account our data, a significant amount of lipids in the form of separate groups of lipocytes and their conglomerates accumulates in the muscles of the studied lanternfish species. Moreover, it is difficult to identify the specific features of the accumulation of fat reserves on the basis of histological structures. It was shown earlier that bathipe-



**Fig. 8.** White muscles of rakery beaconlamp *Lampanyctus macdonaldi*: (→) fat accumulations; see Fig. 6 for the other designations. Magnification 150×.

lagic fish store less energy substances than mesopelagic migrating species, i.e., the calorie content of the body of the latter is slightly higher. Both of these groups accumulate much more energy than epipelagic species (Childress et al., 1980). For fish migrating vertically, large lipid reserves are necessary not only to regulate the volume of the swim bladder but also to increase the rate of metabolic processes in the warmer water of the epipelagic zone (Moku et al., 2000).

The data obtained indicate that the growth of the studied lanternfish species takes place due to hypertrophy of fast-twitch fibers that differ in their shape: round, oval, or angular. Most of them have a diameter exceeding 80  $\mu\text{m}$ , which is typical for slow-growing fish. The diameter of the largest fibers reaches virtually 190  $\mu\text{m}$  (lancet fish, rakery beaconlamp). Even larger fibers (>500  $\mu\text{m}$ ) were found in Nototheniidae, which use labriiform locomotion by pectoral fins. In adult yellowbelly rockcod *Notothenia neglecta*, hyperplasia is actually absent in the muscles, and their growth is performed due to hypotrophy. Muscle hyperplasia ceases when the fish leads a demersal lifestyle (Davison and MacDonald, 1985; Battram and Johnston, 1991). In fish that are fast-growing and reach significant size, the growth of the muscle mass occurs due to hyperplasia, i.e., by increasing the number of small fibers (Weatherley and Gill, 1981). The diameter of red fibers is on average less than white ones. The size exceeds 10  $\mu\text{m}$  in most of them (>90%), and some of them are quite large. In the fast-growing European bass *Dicentrarchus labrax* FL 5–13 cm, the average size of white fibers ranges from 30 to 44  $\mu\text{m}$ , and the average diameter of fast-twitch fibers is approximately 60  $\mu\text{m}$  in muskellunge *Esox masquinongy*, reaching significant size (FL 70 cm) (Weatherley et al., 1988; Viggetti et al., 1990).

Especially large transverse sizes of muscle fibers are characteristic of marine fish. In Chinese sleeper, growing slowly and not reaching large size (its average weight is 3.1 g of a fish of comparable size), the muscle fibers are significantly less on average than that of lanternfishes. White fibers of Chinese sleeper have a diameter of 33.4–36.8  $\mu\text{m}$ , while red fibers are 16.9–18.3  $\mu\text{m}$ . Some fast-twitch fibers reach a diameter of 70  $\mu\text{m}$ . Fibers with a diameter of <10  $\mu\text{m}$  are observed in the surface layer of red muscles (up to 50%) (Panov and Smirnov, 1996). In the common bully *Gobiomorphus cotidianus* (Eleotridae), a New Zealand endemic that reaches a maximum TL of 15 cm (Froese and Pauly, 2019), the diameter of individual glycolytic muscle fibers reaches 130  $\mu\text{m}$  (Davison, 1983).

## CONCLUSIONS

The somatic musculature of the fish belonging to the Myctophidae family is built on the principle inherent in many marine and freshwater species of bony fish. It consists of fast-twitch white fibers, which make up the bulk of the muscles, and red muscles (slow-

twitch oxidizing fibers), which locate superficially. The latter are poorly developed in lanternfishes and in a number of other species (Nototheniidae, Eleotridae, Cyprinidae) that are characterized by low swimming activity.

The studied species of deep-sea fish are small in size and grow slowly, which is due to reduced enzymatic activity and a low content of total protein and its fractions in white muscles. In addition to these factors, the growth of lanternfishes is determined by the processes of hypertrophy of fast-twitch muscle fibers, whose size significantly exceeds that in fast-growing species of bony fish reaching a large body size.

The structure of white muscles in lanternfishes is similar to that in other species of bony fish. Their peculiarity is the shape of the fibers: from angular polygonal (spotted lanternfish) to oval (rakery beaconlamp) and round (lancet fish). A spotted lanternfish has a group of very small fibers in the area bordering the white muscles. It is not yet possible to identify them, but, apparently, these are small, slow-twitch oxidizing fibers. A similar structure was noted in Nototheniidae in the region of superficial lateral muscles (Davison and MacDonald, 1985). In the connective tissue carcass, endomysium, a large amount of adipose tissue accumulates both in the form of individual distinguishable lipocytes and their accumulations. This indicates a well-developed loose connective tissue and a certain friability of muscle fibers in lanternfishes. Red muscles are also a place of intense deposition of lipid reserves. Apparently, the high lipid content in muscle tissue helps to reduce the specific gravity of fish and increase their buoyancy (Becker, 1983).

## COMPLIANCE WITH ETHICAL STANDARDS

*Conflict of interests.* The authors declare that they have no conflicts of interest.

*Statement on the welfare of animals.* All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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