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# Lipid Profile of the Muscle Tissue of Some Mesopelagic Fish Species of the Families Stomiidae and Myctophidae from Different Depths of the Irminger Sea, North Atlantic

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**Abstract**—For the first time the qualitative and quantitative lipid profile (total lipids and polar and nonpolar lipids) of the muscle tissue of six mesopelagic fish species, which are representatives of two deep-sea families widespread in the World Ocean: Stomiidae and Myctophidae were studied. It was found the species specificity of lipid accumulation for the studied fishes, which indicates differences in the mechanisms of compensatory responses. Triacylglycerols are the main form of lipid storage in the studied species. However, an accumulation of cholesterol esters and waxes (lipid characteristic of vertical migrants) has also been recorded in *Borostomias antarcticus*. The revealed distinctive features of Myctophidae and Stomiatidae, related to the accumulation of cholesterol and variations in the content of different phospholipid fractions, indicate that the fishes of these families use different mechanisms for regulating and maintaining the physicochemical state (permeability and fluidity) of biological membranes under conditions of change in a set of environmental factors (temperature, salinity, hydrostatic pressure, and specific photoperiod) with increase in the habitat depth.

**Keywords:** lipids, phospholipids, mesopelagic fishes, Myctophidae, Stomiidae, North Atlantic
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## INTRODUCTION

Mesopelagic fishes living at depths of 200–1000 m are exposed to a set of extreme abiotic and biotic environmental factors, such as low temperatures, high hydrostatic pressure, specific photoperiod, and low food supply. Most of these fish species make vertical migrations to the epipelagic zone at night and return back to the depth at daytime by traveling hundreds of meters under conditions of a strong compression and temperature changes (Catul et al., 2011). Deep-sea organisms have successfully adapted to such habitat conditions, including the development of a considerable set of compensatory mechanisms of biochemical reactions, in which lipids and their components play a special role (Tocher et al., 2000; Arts and Kohler, 2009; Shillito et al., 2020). Lipids are multifunctional substances and considered as sufficiently labile biochemical molecules that are involved in many compensatory reactions of the body to maintain the homeostasis of metabolic processes (Kreps, 1981; Sidorov, 1983; Tocher et al., 2000; Hochachka and Somero, 2002; Arts and Kohler, 2009; Nemova et al., 2014; Murzina et al., 2020). For instance, it is known that high levels and variations of cholesterol esters (Sterol esters (cholesterol esters)), triacylglycerols (TAGs), and waxes form and maintain proper buoyancy in vertically migrating animal species (Neighbors, 1988; Phleger et al., 1999; Voronin et al., 2022). The fluidity of membrane phospholipids (PLs) is strongly influenced by temperature and hydrostatic pressure, with which the homeoviscosity of the bilipid layer is correlated (Macdonald, 2021; Winnikoff et al., 2021). At the same time, the strategies of the organism for adapting to living conditions are species-specific and form a variety of metabolic pathways that depend on factors such as direct or indirect (with metamorphoses) life cycle, diet, position in the trophic chain, and daily vertical migrations.

The study of the lipid profile of mesopelagic fish species as species among the most diverse and widespread marine organisms of the World Ocean is of great interest both for fundamental science and for biotechnology, if we consider these species as potential sources of biologically active substances (Catul et al.,

**Table 1.** Data on the studied mesopelagic fish species captured in the Irminger Sea, North Atlantic

| Species | Fish number, ind. | Collection period (date) | Station no. | Habitat (catch) depth, m |
|---|---|---|---|---|
| *Stomias boa* | 13 | July 6–July 29, 2018 | 120, 83, 84, 94, and 55 | 375, 400, 650, and 700 |
| *Malacosteus niger* | 14 | July 2–July 19, 2018 | 120, 83, 74, 84, 14, and 67 | 375, 400, 650, and 700 |
| *Notoscoplus kroyeri* | 17 | June 21–July 2, 2018 | 43, 29, 52, 66, 41, and 55 | 250, 325, 375, 400, and 700 |
| *Chauliodus sloani* | 16 | June 17–July 2, 2018 | 43, 66, 41, 14, 36, 38, and 55 | 250, 375, 400, and 700 |
| *Borostomias antarcticus* | 17 | June 23–July 12, 2018 | 83, 70, 74, 84, 94, and 38 | 400, 650, and 700 |
| *Symbolophorus veranyi* | 10 | July 10, 2018 | 120 | 375 |

2011; Irigoien et al., 2014; Eduardo et al., 2020). According to the latest estimates, the total biomass of all fish species in the mesopelagic zone ranges from 2.0 to 19.5 Gt, which equates to 100 times the annual catch of all existing fisheries in the world (Hidalgo and Browman, 2019). Previously, we studied the entire lipid spectrum (lipidome) of five mesopelagic fish species of five families, which are widespread in the Irminger Sea (North Atlantic) and differ from each other in life cycles, trophic relationships, habitat depths, and the presence (or absence) of daily migrations (Voronin et al., 2021, 2022; Murzina et al., 2022). The objects of our research were members of two of the most common fish families in the mesopelagic zone: myctophids (Myctophidae), which account for no less than 20% of oceanic ichthyofauna, and stomiatids (Stomiidae), one of the main predators of the mesopelagic zone of the World Ocean (*Biogeography*..., 1982; Eduardo et al., 2020).

The aim of our research is to study the lipid profile of the muscle tissue of members of Myctophidae (*Notoscopelus kroyeri* and *Symbolophorus verany*) and Stomiidae (*Chauliodus sloani*, *Stomias boa*, *Malacosteus niger*, and *Borostomias antarcticus*), which live in the North Atlantic in the depth range of 0–3071, 0–2308, 200–4700, 0–3527, 890–1450, and 0–3527 m, respectively (Porteiro et al., 2017; Orlov and Tokranov, 2019).

## MATERIALS AND METHODS

Muscle tissue samples of mesopelagic fishes were collected as part of research works in the Irminger Sea (North Atlantic, 59°60′–64°60′ N, 26°20′–41°50′ W) during the summer period (June–July) aboard the Atlantis research vessel (Panov et al., 2019; Pronina et al., 2021). Fish were caught by trawling at depths of 250, 325, 375, 400, 650, and 700 m in the Northeast Atlantic Fisheries Commission regulation area, Greenland fishing zone, and Icelandic Exclusive Economic Zone (Table 1). A mid-depth 78.7/416 m trawl (project 2492-02), the rope and net parts of which were made of modern lightweight materials, with a mesh size of 68 mm in the wings and 16 mm in the cod end were used. The trawl operation was monitored using a WESMAR TCS 785 hydroacoustic trawl control device (Western Marine Electronic, United States). Trawl operations were carried out using the methods described in the Guidelines for Performing the International Deep Sea Pelagic Ecosystem Survey (ICES, 2015). Species identification of fish from catches was carried out aboard using different identifiers (Kukuev et al., 1980; Dolgov, 2011; *Photo guide*..., 2019; Sutton et al., 2020).

Oceanological observations of water temperature, salinity, and hydrostatic pressure were carried out at trawling sites using a Sea Bird Electronics oceanological system (Sea-Bird Electronics, United States), including a CTD profiler (SBE-19plus V2 SEACAT-plus PROFILER SN 6376) with an SBE-33 control terminal.

Total lipids (TLs) were extracted from muscle tissue according to the Folch method (Folch et al., 1957) using a chloroform–methanol mixture (2 : 1 by volume). TLs were further separated using chromatographic methods: high-performance thin-layer chromatography for separating neutral (nonpolar) lipids and high-performance liquid chromatography for separating polar lipids (phospholipids). Lipids of individual classes (nonpolar and polar ones) were qualitatively identified according to the standards of the corresponding components (Sigma-Aldrich, United States), taking into account the correspondence of the values of the mobility index.

The content of neutral monoacylglycerols, diacylglycerols, TAGs, cholesterol (Chol), Sterol esters, free fatty acids, and total PLs remaining at the start was qualitatively and quantitatively determined using a CAMAG equipment system (Switzerland). TLs were fractioned on ultra-pure glass-based chromatographic plates (HPTLC Silicagel 60 $F_{254}$ Premium Purity (Merck, Germany)). The microquantity of a sample (2 μL) was applied using a Linomat 5 semi-automatic applicator (CAMAG, Switzerland) and TLs were separated into lipids of different classes using an ADC 2 automated chromatographic elution chamber (CAMAG, Switzerland) in a hexane–diethyl-ether–acetic-acid solvent system (32.0 : 8.0 : 0.8 by volume) (Olsen and Henderson, 1989). Lipid spots were stained in a sealed derivatizer (CAMAG, Switzerland) by spraying 2 mL of copper sulfate ($CuSO_4$) solution acidified with phosphoric acid ($H_3PO_4$) through a nozzle, followed by the development of stained spots by heating the plate to 160°C for 15 min. The content of lipid components was qualitatively and quantitatively determined in the chamber of a TLC Scanner 4 densitometer (CAMAG, Switzerland) in adsorption regime at a wavelength of 360 nm (Hellwig, 2005).

The content of individual phospholipid fractions (phosphatidylcholine (PC), phosphatidylethanolamine (PEA), phosphatidylserine (PS), phosphatidylinositol (PI), lysophosphatidylcholine (LysoPC), and sphingomyelin (SM)) was qualitatively and quantitatively determined using a Stayer liquid chromatograph (Aquilon, Russia)). Total PLs were fractioned on a 250 × 4 mm column filled with a Nucleosil 100-7 sorbent (Elsico, Russia) and using an acetonitrile–methanol–hexane–85%-phosphoric acid mixture (918.0 : 30.0 : 30.0 : 17.5 by volume) at a flow rate of 1 mL/min. The test PLs of individual classes were detected on a spectrophotometer by light absorption in the ultraviolet region of the spectrum at a wavelength of 206 nm (Arduini et al., 1996). To determine the change in the qualitative and quantitative phospholipid composition of the membrane of fish muscle tissue cells depending on the depth of fish catch, we calculated the ratio of the main choline PLs (chPLs) to amino-PLs (aPLs) by the formula: chPL/aPL = (PC + SM)/(PEA + PS).

The results were statistically processed using the R programming language (version 3.6.1.) in the RStudio development environment (https://www.posit.co) using additional packages: readxl (version 1.3.1), tidyverse (version 1.3.0), cowplot (version 1.1.1), and vegan (version 2.5–7). A descriptive statistics (arithmetic mean and its error) with the values grouped by catch depths was calculated for each studied species. The significance of differences in the levels of lipid and phospholipid components was estimated using the nonparametric Kruskal–Wallis test and the significance of differences between individual components was determined using the Wilcoxon–Mann–Whitney rank sum test. Correlation analysis ($r$) was performed according to Spearman and the correlation value was estimated using the Chaddock scale (Kabakov, 2016). The ordination of species in multidimensional space was performed using the algorithm of nonmetric multidimensional scaling for the studied features. The best distance metric in the multidimensional feature space was determined using the Spearman coefficient of correlation between the distance matrices. The measure of discrepancies between the initial and simulated distance matrices was estimated using the "stress" indicator (Shitikov and Mastitskii, 2017). The similarity between the studied species was estimated using the ANOSIM (R) algorithm and the percentage similarity was determined using a SIMPER statistical analysis. The influence of a set of external abiotic environmental factors (temperature and salinity) on the lipid profile of individuals of the studied species that were caught at certain depths was estimated using a canonical correspondence analysis (Shitikov and Mastitskii, 2017). The best distance metric was also determined using the Spearman coefficient.

Fish were caught in the Irminger Sea under the Cooperation Agreement between the Federal Agency for Fisheries (Rosrybolovstvo) and the Russian Academy of Sciences (RAS) and as part of the Joint Scientific Research Program of the Federal Agency for Fishery and the Russian Academy of Sciences. Biochemical studies were carried out at the Laboratory of Ecological Biochemistry using the equipment of the Common Use Center of the Karelian Research Center, Russian Academy of Sciences.

## RESULTS

Among the studied mesopelagic fish species, *S. veranyi* was characterized by the highest content of TLs in the muscle tissue (37.13% dry weight) in comparison to *N. kroyeri* (the second studied species of the family Myctophaceae) was lower: 19.9% (Fig. 1). Three species of the family Stomiaceae (*S. boa*, *M. niger*, and *C. sloani*) did not differ from each other in the content of TLs in muscles (30.99, 29.21, and 27.63%, respectively); however, *B. antarcticus* had a significantly low content of TLs (16.10%). Correlation analysis did not reveal a significant dependence of TLs content on the habitat depth; however, a moderate direct ($r$ = 0.31) correlation dependence and an inverse ($r$ = –0.39) correlation dependence (according to the Chaddock scale) were established for two species: *C. sloani* and *B. antarcticus*, respectively. In *C. sloani*, the content of TLs in muscles increased at greater depths (700 m), while it decreased in *B. antarcticus*.

Statistical ANOSIM analysis on the quantitative content of lipids of different classes in the muscle tissue of the studied species revealed significant differences with overlap between the species ($R$ = 0.4637). Using multidimensional nonmetric scaling, it was found that *B. antarcticus* was characterized by a high accumulation of waxes (3.90% dry weight), while *S. veranyi* differed in the predominance of monoacylglycerols (3.70%) compared to the other species (0.16–0.65%) (Fig. 2). SIMPER analysis for the content of waxes and monoacylglycerols also showed a small similarity between these two fish species (19 and 28%, respectively). The other four species (*N. kroyeri*, *C. sloani*, *S. boa*, and *M. niger*) were characterized by the overlap of the values of the content of the studied lipids in the multidimensional feature space. The greatest similarity between these species was found in the content of TAGs and Sterol esters in muscle tissue (49–61 and 31–42% similarity, respectively), while general interspecific differences are expressed in the quantitative content of monoacylglycerols, diacylglycerols, and total PLs. It should be noted that the studied species of the family Myctophaceae (*N. kroyeri* and

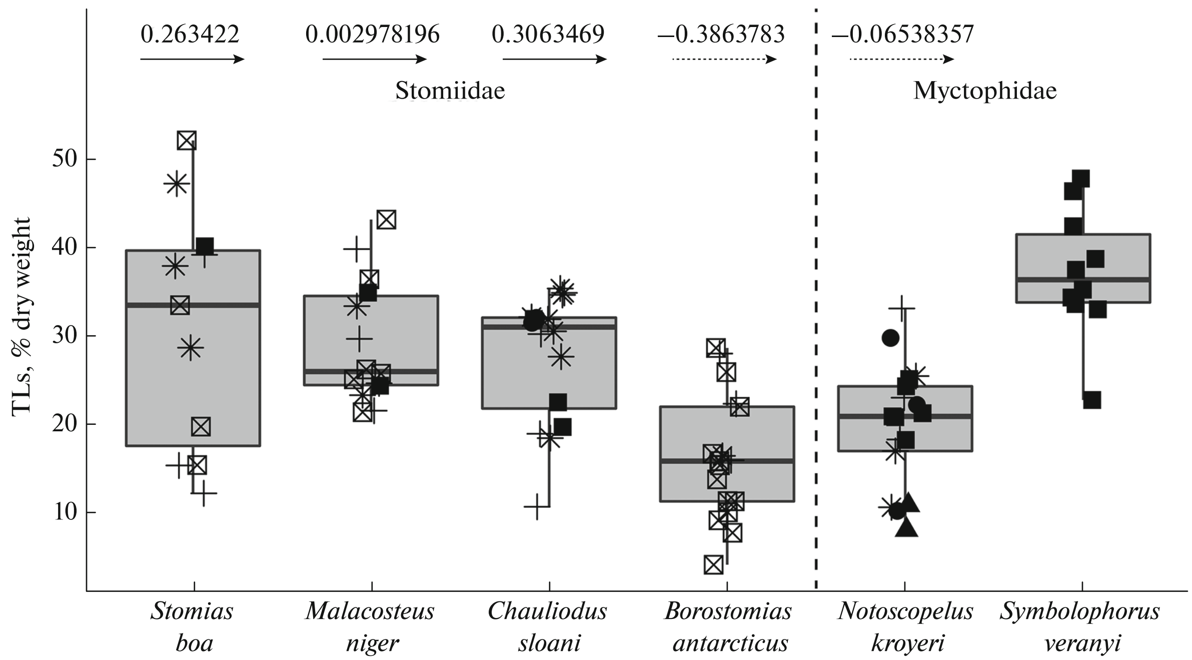


**Fig. 1.** Content of total lipids (TLs) in the muscle tissue of mesopelagic fish species of the families Stomiidae and Myctophidae living in the depth gradient of the Irminger Sea (North Atlantic). Each box describes the median (horizontal line inside the box), 1st and 3rd quartiles (lower and upper boundaries); whiskers indicate the minimum and maximum. The correlation (*r*) of the TL content with the depth is shown by arrows (the solid line means positive correlation and dotted line means negative correlation), with *r* values above them. Fishing depth, m: (●) 250, (▲) 325, (■) 375, (+) 400, (⊠) 650, (⋇) 700.

*S. veranyi*) had a maximum similarity (79%) in the content of Chol (2.28 and 6.77% dry weight, respectively) in the muscle tissue, while species of the family Stomiaceae had a similar level of similarity in the content of TAGs (*B. antarcticus*, 4.03; *C. sloani*, 11.70; *M. niger*, 13.37; and *S. boa*, 9.66% dry weight).

*B. antarcticus* had a negative correlation ($r = -0.58$) between the content of TAGs and an increase in habitat depth from 400 to 700 m. *S. boa* is oriented along the free fatty acid vector, which is confirmed by a significant correlation ($r = 0.51$) between the content of this lipid fraction and the depth. On the contrary, the amount of free fatty acids for another stomiatid species, *M. niger*, was inversely correlated ($r = -0.52$) with the depth of habitat; however, the content of waxes increased with depth ($r = 0.66$). The canonical correspondence analysis really revealed a decrease in the level of TAGs (from 6.70 to 4.31% dry weight) and levels of waxes (from 5.32 to 3.08%) and Sterol esters (from 5.16 to 4.15%) in *B. antarcticus* with increase in habitat depth (from 400 to 700 m), which was accompanied by changes in the water temperature and salinity (from 4.7 to 5.0°C and from 34.90 to 34.94‰, respectively) (Fig. 3). *A* similar trend was also observed for *M. niger*, while the other two species of the family Stomiaceae (*S. boa* and *C. sloani*) exhibited a high dispersion of the content of the studied lipids at different depths. It was shown that water temperature and salinity had a greater effect on the change in the content of free fatty acids in the muscles of species of the family Stomiaceae, while these abiotic factors influenced the TAGs fraction in a representative of the family Myctophaceae (*N. kroyeri*).

The ANOSIM statistical analysis for the quantitative content of PLs of different fractions in muscle tissue also revealed significant differences with overlap between the species ($R = 0.4044$). According to multivariate data analysis, it was found that the species *S. verany* individually differed from the other studied species in the multidimensional feature space, while the other five species overlapped with each other (Fig. 4). *S. veranyi* was characterized by a high content of PCs (4.67% dry weight) and a low content of PEAs (0.06% dry weight), while the content of these PLs in other studied species varied from 0.85 to 2.03 and from 0.17 to 0.43% dry weight, respectively. In combination with PCs, one should also note a relatively high content of LysoPC (0.55% dry weight) in *S. veranyi* compared to other species, for which this parameter was 0.02–0.32% dry weight. The SIMPER analysis showed that *S. veranyi* significantly differed in the PI content in the muscles (0.0006% dry weight). The similarity of all studied species in the phospholipid composition did not exceed 40%, with the highest percentage of similarity recorded for PC.

A higher interspecific heterogeneity in the content of polar PLs than that of nonpolar lipids was recorded with increase in habitat depth. Thus, the content of PI

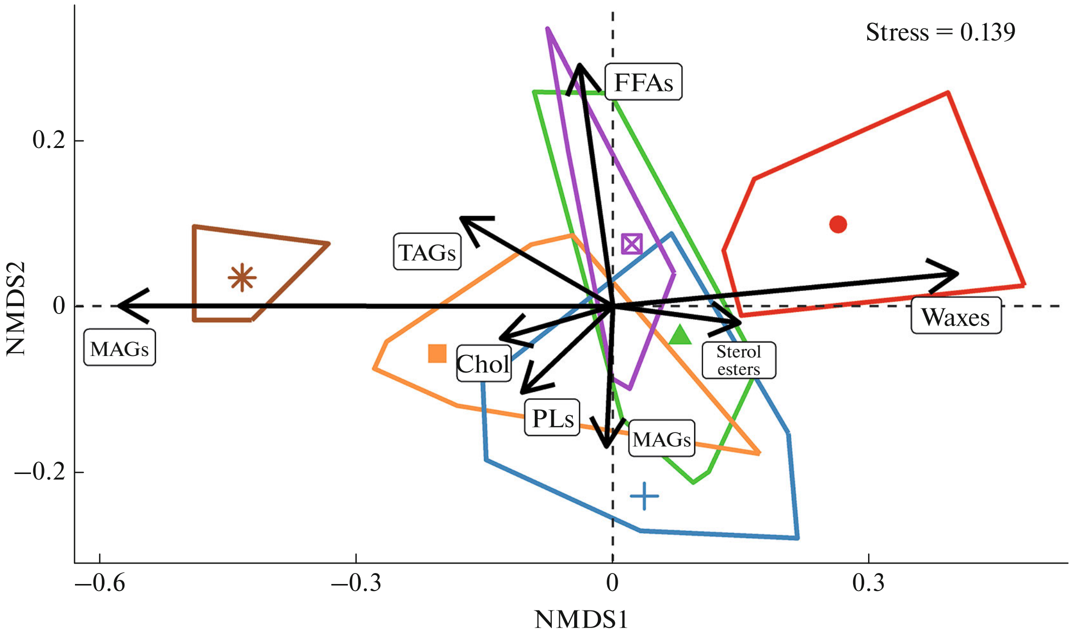


**Fig. 2.** Ordination of nonmetric multidimensional scaling (NMDS) of lipids of individual classes in the muscle tissue of mesopelagic fish species of the families Stomiidae and Myctophidae living in the depth gradient of the Irminger Sea (North Atlantic): MAGs, monoacylglycerols, DAGs, diacylglycerols, TAGs, triacylglycerols, Chol, cholesterol, Sterol esters, cholesterol esters, PLs, total phospholipids, FFAs, free fatty acids; fish species: Stomiidae: (●) *Borostomias antarcticus*, (▲) *Chauliodus sloani*, (■) *Malacosteus niger*, (⊠) *Stomias boa*; Myctophidae: (+) *Notoscopelus kroyeri*, (✳) *Symbolophorus verany*.

in *C. sloani* was significantly ($r = 0.58$) and that of PC and PS was moderately ($r$ = 0.49 and 0.46, respectively) correlated with increase in depth. At the same time, an increase in the content of PS was recorded at a depth of 375 m (up to 0.009% dry weight), where the water temperature and salinity increased to 6.05°C and 34.98‰, respectively (Fig. 5). On the contrary, another species of the family Stomiaceae, *S. boa*, had an inverse correlation ($r = -0.61$) of the content of PS with the depth and the content of this PL in this species increased at a depth of 400 m (up to 0.009% dry weight), where the water temperature and salinity decreased to 4.67°C and 34.90‰, respectively..

In *B. antarcticus*, *S. boa*, and *M. niger*, the amount of chPLs decreased and that of aPLs (mainly PC and PEA) increased with depth; the chPL/aPL ratio in these species was 4.30–5.53, 4.34–7.54, and 4.28–7.89, respectively. In *C. sloani* and *N. kroyeri*, the levels of PC and PEA remained unchanged throughout the depth range; however, the values of the chPL/aPL ratio varied from 3.58 to 3.98 and from 3.13 to 3.24, respectively. Also, an increase in the content of PS with increase in depth was recorded in these species. The above-described groups of fish species had similar changes in the amount of LysoPC in the muscle tissue: a decrease in its content in *B. antarcticus*, *S. boa*, and *M. niger* (by 0.08–0.22, 0.06–0.13, and 0.008–0.03% dry weight, respectively) with increase in depth and the preservation of its concentration in the depth range in *C. sloani* and *N. kroyeri* at the content of 0.01–0.02 and 0.01–0.11% dry weight, respectively.

## DISCUSSION

Mesopelagic fishes are among the most numerous and widespread hydrobionts in the World Ocean, which live in the depth range of 200–1000 m; however, their biology, ecology, trophism, and adaptive mechanisms (including biochemical ones) are poorly studied (Catul et al., 2011). The proportion of members of the families Myctophidae and Stomiidae is significant in oceanic ichthyofauna (*Biogeography*…, 1982; Olivar et al., 2017; Eduardo et al., 2020). Most of them make vertical migrations to the epipelagic zone at night in search of food (Kenaley, 2008; Olivar et al., 2012; Duhamel et al., 2014). Lipids as the most labile molecules are the main structural and energy components of the body, which are deposited in muscle tissue and involved in adaptive processes by forming compensatory responses to external environmental factors, as well as in the organic carbon cycle by transferring matter and energy between vertical water layers along the food chain (Ashjian et al., 2003; Petursdottir et al., 2008). The high content of TLs that we recorded in the muscle tissue of *S. veranyi* is a characteristic feature of fishes of the family Myctophidae (Lea et al., 2002). *S. veranyi* is characterized by more active feeding on fish items than that in species of the genus *Notoscopelus* (Podrazhanskaya, 1993), which may explain the

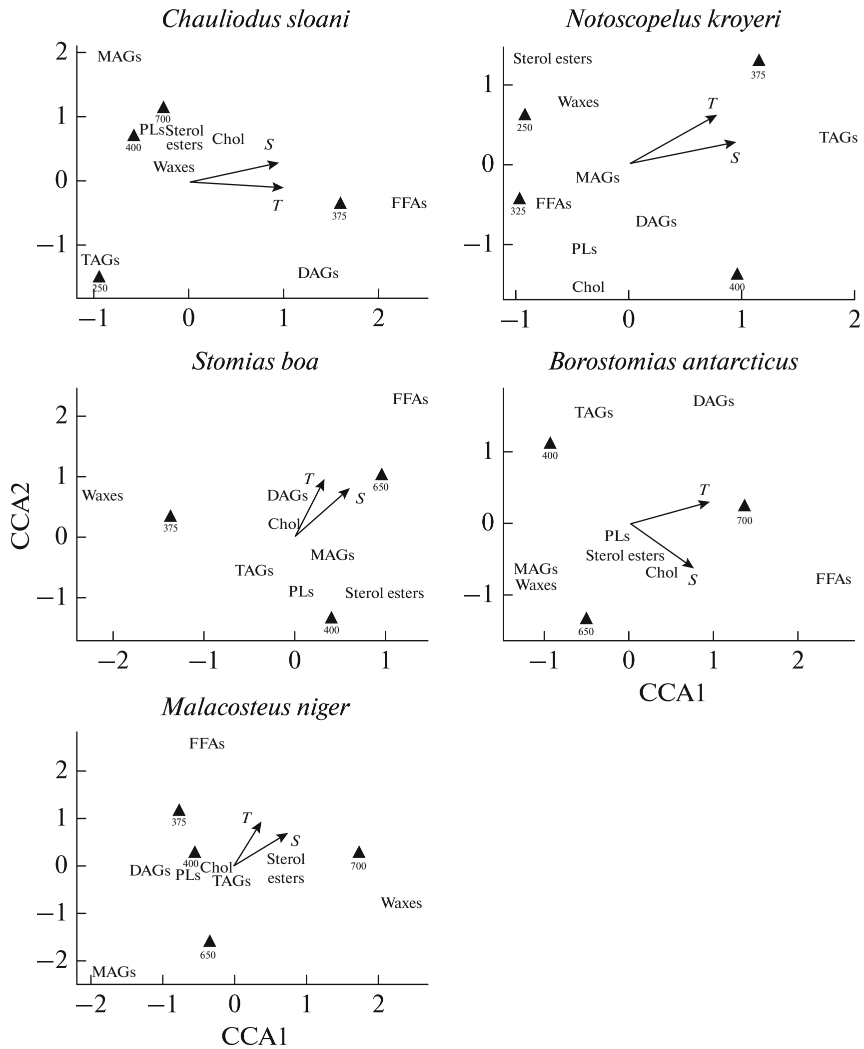


**Fig. 3.** Ordination of the canonical correspondence analysis (CCA) of the effect of temperature (*T*) and salinity (*S*) on the content of lipids of individual classes in the muscle tissue of mesopelagic fish species of the families Stomiidae and Myctophidae living in the depth gradient of the Irminger Sea (North Atlantic): (▲) fishing depth; depth values (m) are given under the triangles; see the designations in Fig. 2.

differences in the accumulation of TLs in the muscles of the two studied representatives of Myctophaceae. The revealed differences in the content of TLs between the studied families and species are species-specific and determined by differences in the life cycles, the capability for vertical migrations, and the compensatory mechanisms of response to the combined effect of a set of environmental factors (hydrostatic pressure, temperature, salinity, trophism, etc.) (Phleger et al., 1999; Hochachka and Somero, 2002; Tocher, 2003; Perevozchikov, 2008; Petursdottir et al., 2008; Connan et al., 2010; Özdemir et al., 2019). Thus, ontogenetic variations were described for *C. sloani*, *S. boa*, and *B. antarcticus* during vertical migrations (vertical semimigrants): adult individuals migrate more actively in water during a day (Roe and Badcock, 1984; Klimpel et al., 2006; Eduardo et al., 2020). The biology of *M. niger* significantly differs from that of other studied members of the family Stomiaceae. According to the literature data (Stegeman et al., 2001; Sutton, 2005), the species does not make diurnal vertical migrations and feeds mainly on small crustaceans, although it has large jaw teeth. Both studied representatives of the family Myctophaceae are also vertical migrants; however, they differ in food specialization: *N. kroyeri* prefers crustaceans, while the food of *S. veranyi* contained small fish in addition to crustaceans of the genus *Themisto* (Hyperiidae) (Podrazhanskaya, 1993; Munschy et al., 2022).

A targeted fractional analysis of TLs showed that *B. antarcticus* accumulated a high content of waxes in the muscle tissue (compared to the other studied species). It is known that the concentration of waxes in the muscles of bony fishes is correlated with the habi-

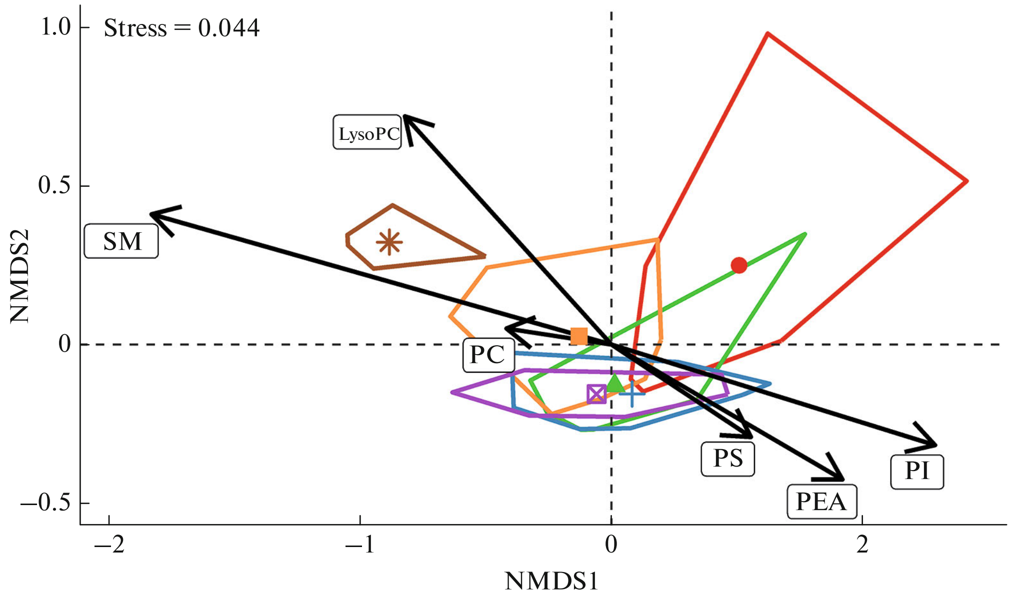


**Fig. 4.** Ordination of nonmetric multidimensional scaling (NMDS) of individual molecular species of phospholipids in the muscle tissue of mesopelagic fish species of the families Stomiidae and Myctophidae living in the depth gradient of the Irminger Sea (North Atlantic): PC, phosphatidylcholine; PEA, phosphatidylethanolamine; PI, phosphatidylinositol; PS, phosphatidylserine, LysoPC, lysophosphatidylcholine; SM, sphingomyelin; see the other designations in Fig. 2.

tat depth and associated with diurnal vertical migrations (Nevenzel, 1970). *B. antarcticus* probably uses compensatory mechanisms with this lipid, as well as with Sterol esters, which result from changes in the fluidity of the biological membrane of cells and are necessary to provide signaling and regulatory functions under conditions of change in abiotic environmental factors with depth (Neighbors, 1988; Phleger et al., 1999). In addition, there are mechanisms of wax splitting to "rapidly reacting" TAGs, the main consumable lipid fraction in fish (Gershanovich et al., 1991; Salvanes and Kristofersen, 2001). For other species, the predominance of reserve TAGs was recorded in the muscles. For predatory fishes, TAG molecules serve as the main and most beneficial form of energy storage owing to their rapid mobilization from adipocytes and as a result of the release of a high amount of energy (by 2.5 times higher than that during carbohydrate oxidation) (Lapin and Shatunovskii, 1981; Sweetman et al., 2014). Myctophid fishes are sometimes divided into two groups depending on the dominance of certain energy lipids in the muscles: fishes with a high content of TAGs and fishes rich in Sterols esters and waxes (Baby et al., 2014). In this study, it was revealed the dominance of TAGs in the studied fishes of the family Myctophidae; however, in our previous study (Voronin et al., 2022), Sterol esters and waxes prevailed in the muscles of the species *Lampanyctus macdonaldi*, which is most likely determined by differences in food items in the studied fish species. Moreover, different contents of monoacylglycerols and diacylglycerols (products of complete or partial TAG hydrolysis) may indicate different intensities of catabolism and anabolism processes in the body (Goutx et al., 2003). Monoacyl- and diacylglycerols are multifunctional molecules and involved in many physiological processes and cellular responses of the body as second messengers. The direction and rate of lipid metabolic reactions in different fish species are also discussed based on the content of monoacyl- and diacylglycerols and their variations in the tissues (Kol'man and Rem, 2009; Sandel et al., 2010).

The studied species of Myctophidae and Stomiidae differed in the content of Chol, which is one of the most important lipid components of biomembranes. Its presence regulates morphological stability, as well as the permeability of membrane for dissolved substances (Kol'man and Rem, 2009). The revealed differentiation of the fish species may indicate evolutionarily determined mechanisms of the compensatory response and protection of the fish to the impact of abiotic environmental factors, in particular, the manifestation of an adequate adaptive response that regulates the morphological state of biological membranes during hydrostatic pressure change.

The established correlation dependences of changes in the content of the identified lipids in the muscle tissue of the fish in the depth gradient indicate the trend of adaptive responses to changing living conditions of the organism. Thus, a decrease in the TAGs content with increase in depth was recorded for *B. antarcticus*, which may indicate an increase in energy consumption (e.g., an increased motor activity), as well as the paucity of food supply at great depths (Scott

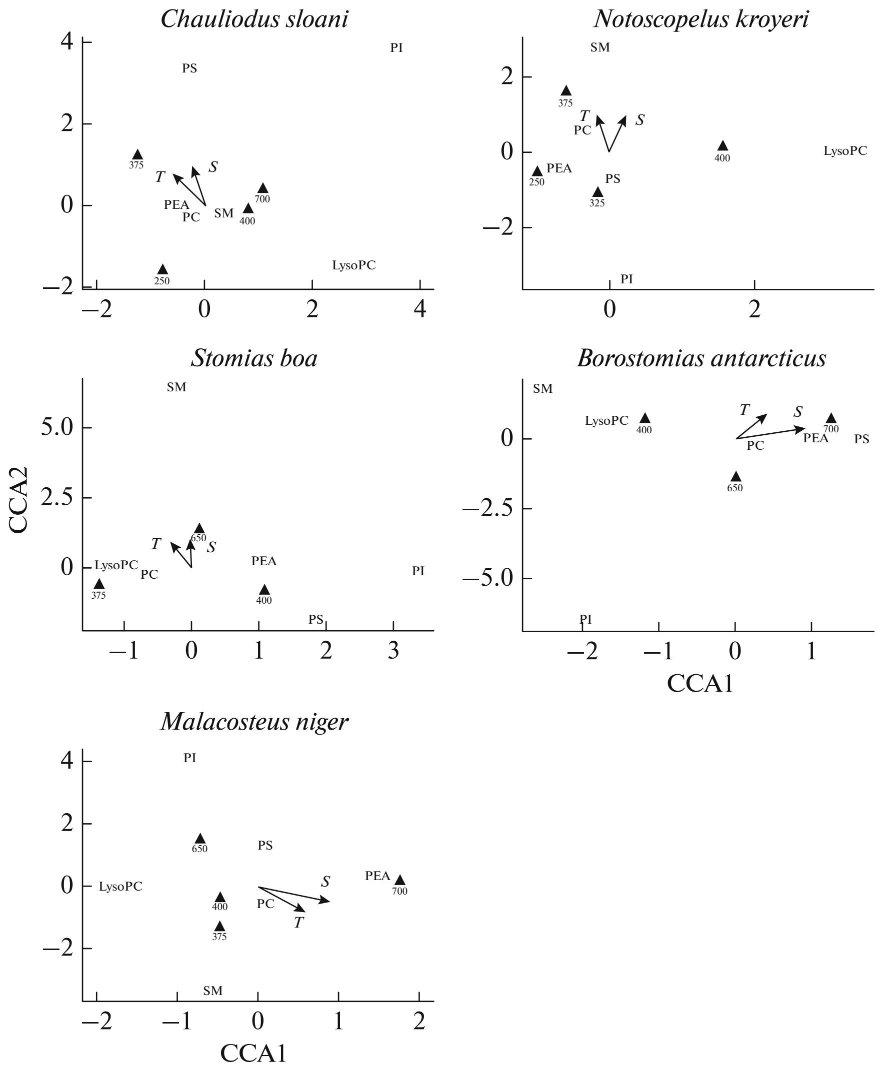


**Fig. 5.** Ordination of the canonical correspondence analysis (CCA) of the influence of temperature (*T*) and salinity (*S*) on the content of individual molecular species of phospholipids in the muscle tissue of mesopelagic fish species of the families Stomiidae and Myctophidae living in the depth gradient of the Irminger Sea (North Atlantic). See the designations in Figs. 3 and 4.

et al., 2002; Voronin et al., 2021). Variations in the content of free fatty acids and an accumulation of waxes in the muscles were recorded in nonmigratory *M. niger*, which is more characteristic of vertically migrating species (Neighbors, 1988; Phleger et al., 1999). The data of our research suggest diurnal vertical migrations in this species in the full or limited range of depths; however, there are very few data based on the results of studies using locking gears for this species (Stegeman et al., 2001; Suton, 2005). Variations in the content of free fatty acids in muscles in the depth range were also recorded in *S. boa*; however, as in *C. sloani*, a high dispersion of values was recorded for lipids of other classes in this species at different depths. This relative homogeneity of lipid content in the depth gradient may be determined by ontogenetic changes in the spatial distribution of these species and variations in their vertical migrations (Klimpel et al., 2006; Eduardo et al., 2020). Differences in the lipid composition were established between the studied fish species living at different depths with different combinations of environmental factors, such as temperature and salinity. It was shown that an increase in their values within the species tolerance was accompanied by the deposition of lipids in the form of TAGs in myctophid fishes, while it leads to a decrease in the content of free fatty acids in the muscles of Stomiidae.

The established low percentage of similarity (not more than 40%) in the composition of PLs between the studied species indicates the species-specificity of compensatory responses with PLs, which are aimed at maintaining the integrity of cell membranes under the influence of abiotic environmental factors, such as pressure, temperature, and salinity. Under normal conditions, the qualitative and quantitative content of PLs in animal tissues is characterized by a relative stability, and the change in the content of PLs of individual classes results from changes in environmental conditions (Hochachka and Somero, 2002; Kostetskii et al., 2013). In addition, the plasma membrane is characterized by a qualitative asymmetry in the content of PLs of different classes on the external and internal layers, on which PC and PEA are the dominant phospholipids, respectively (Daleke, 2003; Boldyrev et al., 2006). However, a significant predominance of PC and an extremely low content of PEA were recorded in the muscles of *S. veranyi*, which is a characteristic feature of cold-water fishes (Velanskii and Kostetskii, 2008). It should be emphasized that PC molecules can also be used as energy sources if the body requires them (Nemova et al., 2014). In this case, one of the products of PC hydrolysis is LysoPC, the content of which was also higher in *S. veranyi* than in other studied species. It is known that the accumulation of LysoPC increases the permeability of the cell membrane for ions, which may indicate a distinctive feature of this species in the strategy of reorganization of the physicochemical state of the biomembrane under the influence of environmental factors (Osadchaya et al., 2004; Berdichevets et al., 2010). This mechanism is presumably realized in the studied individuals of this species, which is indirectly confirmed by a significantly low (compared to other species) content of PI, a precursor of phosphoinositides, which increase the amount of intracellular $Ca^{2+}$ necessary for proper motor activity under conditions of high hydrostatic pressure (Kol'man and Rem, 2009; Sandel et al., 2010).

The species specificity of the qualitative and quantitative composition of PLs in individual fish classes at certain depths is determined by the choice of an adaptive strategy by the species to deep-sea habitat conditions to maintain the integrity of the biomembrane (Hochachka and Somero, 2002; Boldyrev et al., 2006; Macdonald, 2021). Thus, differences in the structural transformation of the cell membrane with increase in depth were recorded between two species that are relatively similar in the accumulation of neutral lipids, *C. sloani* and *S. boa*. An increase in the content of PC and PI in *C. sloani* makes it possible to increase the membrane permeability for additional entry of $Ca^{2+}$ ions into the cell (Kol'man and Rem, 2009). At the same time, the content of PS in these two species varied in different directions with increase in depth. It is known that minor PS can be indirectly (by regulating the activity of membrane-bound enzymes) involved in the formation of system units of muscle fiber (myotubes) during myoblast fusion, which is especially important for fish species with a predatory lifestyle (Verma et al., 2017). It should be noted that water temperature and salinity significantly influenced the concentration of PS in the skeletal muscles of *C. sloani* and *S. boa,* which indicates the involvement of PLs of this class in processes of membrane reorganization through ion permeability, as well as its excitability and transmission of transmembrane signals (Makarova and Golovko, 2001).

A topological asymmetry of PLs is observed in the spatial orientation of plasma membranes: PC and SM (chPLs) prevail on the external monolayer, while PEA and PS (aPLs) prevail on the internal monolayer (Kagan et al., 1984). The use of the chPL/aPL ratio made it possible to distinguish two isolated groups of the studied species, which differ in change in the quantitative content of individual PLs in the skeletal muscles. Thus, a decrease in PC content and an increase in PEA content with increase in depth was recorded for *B. antarcticus*, *S. boa*, and *M. niger*, which leads to a reorganization of the physicochemical state of the membrane and a change in the ratio of charges on the external and internal monolayers of the membrane (Sidorov, 1983). At the same time, a decrease in the concentration of LysoPC was observed as a compensatory response in these species, which leads to a decrease in the membrane permeability for ions (Berdichevets et al., 2010). The second group of the studied fish species (*C. sloani* and *N. kroyeri*) was characterized by the preservation of the chPL/aPL ratio, as well as by the preservation of the concentration of LysoPC, with variations at certain depths. In this way, *C. sloani* and *N. kroyeri* presumably maintain the homeostasis of the microenvironment within a cell, which is necessary for the normal functioning of membrane-bound enzyme systems (Boldyrev et al., 2006).

## CONCLUSIONS

The study of the lipid profile of the six fish species belonging to the two most common families, Myctophidae and Stomiidae, in the mesopelagic zone of the World Ocean made it possible to identify species-specific qualitative and quantitative differences in the accumulation of reserve and structural lipids in skeletal muscles, which indicate a number of features in the choice of mechanisms of body's compensatory responses during habitation under extreme environmental conditions. TAGs are the main form of energy storage in the studied species; at the same time, an accumulation of Sterol esters and waxes was also recorded in *B. antarcticus*, which is characteristic of vertically migrating fish species of lipid classes. The discovered differences between the species of the families Myctophaceae and Stomiaceae in the content of Chol in muscles are explained by different mechanisms of regulation of the morphological stability of the membrane and indicate the evolutionarily determined pattern of the compensatory response. The dynamics of changes in the amount of neutral lipids is typical for vertically migrating fish species; however, a relative homogeneity of the lipid profile was recorded in *C. sloani* and *S. boa* at certain depths, which is determined by the ontogenetic features of the spatial distribution. The change in the content of the studied PLs differs in the studied species and depends on the method of regulation of the permeability and microviscosity of the membrane under conditions of change in environmental factors (temperature, salinity, hydrostatic pressure, etc.) with depth.

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## 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.

## OPEN ACCESS



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