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Lipids and Fatty Acids in Some Mesopelagic Fish Species: General Characteristics and Peculiarities of Adaptive Response to Deep-Water Habitat

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Abstract: The lipid and fatty acid composition of muscles of mesopelagic fish species *Lampanyctus macdonaldi*, *Bathylagus euryops*, *Serrivomer beanii*, *Scopelogadus beanii* in the Irminger Sea at deep range were studied. The contents of the total lipids (TLs), total phospholipids (PLs), monoacylglycerols (MAGs), diacylglycerols (DAGs), triacylglycerols (TAGs), cholesterol (Chol), Chol esters, non-esterified fatty acids (NEFAs), and wax esters were determined by HPTLC; the PL classes were determined by HPLC; and fatty acids (FAs) were determined using GC. It was found significant differences in lipid profile of the studied fishes: Chol esters and waxes were dominant in *L. macdonaldii* and *S. beanii*, fish species with diel vertical migrations (DVM), while TAGs were prevalent in *B. euryops* and *Sc. Beanii*—non-migratory species. It was revealed the species-specific differences in FAs profiles of the studied fish. Along with this, it was detected the similarity of FAs in fish, which is associated with food sources. A comparative analysis of lipids and FAs among *L. macdonaldi* and *S. beanii* collected in the Irminger Sea and *L. alatus* and *S. beanii* collected in the Tropic Seamount revealed similar biochemical strategies for the accumulation of certain lipids characterized the mesopelagic inhabit despite latitude differences of the area of study.

Keywords: lipids; fatty acids; mesopelagic fish; mesopelagic zone; North Atlantic

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1. Introduction

The tremendous expanses and profound depths of the World Ocean contain enormous amounts of biological resources, including aquatic organisms. Although resources are mainly harvested in the relatively well studied upper 200-m epipelagic layer of the ocean [1–6], the most promising biotope in terms of biodiversity, biomass, and bioproductivity is the underlying mesopelagic layer (200–1000 m) [7–9]. Meanwhile, known data regarding the biology, ecology, trophic relationships between mesopelagic organisms, their distribution and the compensatory mechanisms of adaptation to the extreme environmental conditions is meager, especially for northern latitudes as compared to tropical and southern latitudes [3–6,10].

The special focus on the study of mesopelagic organisms is due to their high biological productivity, ecological significance and the unique bioactive substances the organisms contain, which can potentially be used in the biotech industry [3]. Their ecological role consists, first of all, in the crucially important redistribution of organic matter (carbon cycle) from the highly productive epipelagic zone towards the meso-, bathy-, and abyssopelagic zones through daily vertical migrations in many fish species [11–14]. Some papers [15,16]

discuss also the fundamental role of mesopelagic micronekton in maintaining the balance in matter and energy cycles under climate change. Furthermore, many mesopelagic species are important food items for commercial fishes such as the walleye pollock *Gadus chalcogrammus* or redfish *Sebastes mentella* [17–19].

Key metabolic components contributing significantly to the adaptation of aquatic organisms to extreme environmental conditions and to carbon cycling between oceanic layers are lipids and their fatty acids [20–22]. Differences in the habitat affiliations, life cycles, development patterns, intraspecies structure and dietary specializations of mesopelagic organisms can induce variations in the quantitative and qualitative parameters of the lipid metabolism which, in turn, cause differentiation in the adaptive response of the fishes [23,24]. Mesopelagic fishes in Arctic seas ecosystems have been reported to contain a sophisticated set of high-saturation fatty acids and are therefore promising as feedstock for manufacturing valuable bioactive products which promote the adaptation capacity of people living in polar and circumpolar regions [25–27]. According to latest data, it is the 'marine' lipids enriched in certain monounsaturated fatty acids that contribute to the known beneficial biological effects of "omega-3" FAs on human health [28]. This knowledge has triggered active studies of the biochemical composition of poorly studied deep pelagic fish species as potential sources of unique bioactive compounds [29].

The aim of this study was to investigate the lipid and fatty acid composition of four mesopelagic fish species belonged to 4 families abundant in mesopelagic zone: *S. beanii* (Serrivomeridae), *L. macdonaldi* (Myctophidae), *B. euryops* (Bathylagidae), *Sc. beanii* (Melamphaidae), sampled from the Irminger Sea (North Atlantic) at depths from 250 to 700 m. The studied fishes distinguished to each other by the presence or absence of vertical migrations in the life cycle. All four considered species in the North Atlantic are quite abundant and in some areas, for example, in the waters of the Mid-Atlantic Ridge, they are among the top ten dominant fishes in terms of biomass and abundance at depths over 750 m [30]. There are no absolute estimates of their abundance in the Irminger Sea, but according to their catch rates [31], it can be concluded that in this area they also dominate among meso- and bathypelagic fishes. Nevertheless, intensive fishing at the main depths of their habitat is practically not conducted, and due to the large size of the mesh in trawls using in beaked redfish *Sebastes mentella* fishery [32], they constitute an occasional and insignificant bycatch, which does not affect their populations significantly.

In addition, in the present paper we compared the lipid composition and usage of lipids in *S. beanii* and *L. alatus* sampled at the Tropic Seamount (North Atlantic) to examine the role of lipids in mesopelagic life focusing the attention on latitude differences of the studied areas on the one hand and the unity of deep-water environment from the other.

2. Materials and Methods

2.1. Sampling

Sampling of muscle tissue from mesopelagic fish—*Lampanyctus macdonaldi*, *Bathylagus euryops*, *Serrivomer beanii*, *Scopelogadus beanii*—was carried out during the surveys carried out in the Irminger Sea survey (59°60′–64°60′ N 26°20′–41°50′ W) in summer (June and July) onboard of R/V "Atlantida". Biological material of all the four species was sampled by trawling at 250-, 375-, 650-, and 700-m depths (except for *Sc. beanii*, which occurred only at 375 and 700 m depth) in the NEAFC regulatory area, in Greenland and Iceland exclusive economic zones (Figure 1). A 78.7/416 mid-water trawl (2492–02 design) was used, with the rope and net parts made of modern light-weight materials, with mesh sizes of 68 mm in the wings and 16 mm in the cod end. Sampling methods were according to the Manual for the International Deep Pelagic Ecosystem Survey in the Irminger Sea and Adjacent Waters developed and approved by the Working Group on International Deep Pelagic Ecosystem Surveys (WGIDEEPS) [33]. The total number of fish species collected for analysis was: *L. macdonaldi*—n = 16, *Sc. beanii*—n = 10, *S. beanii*—n = 16, *B. euryops*—n = 15.

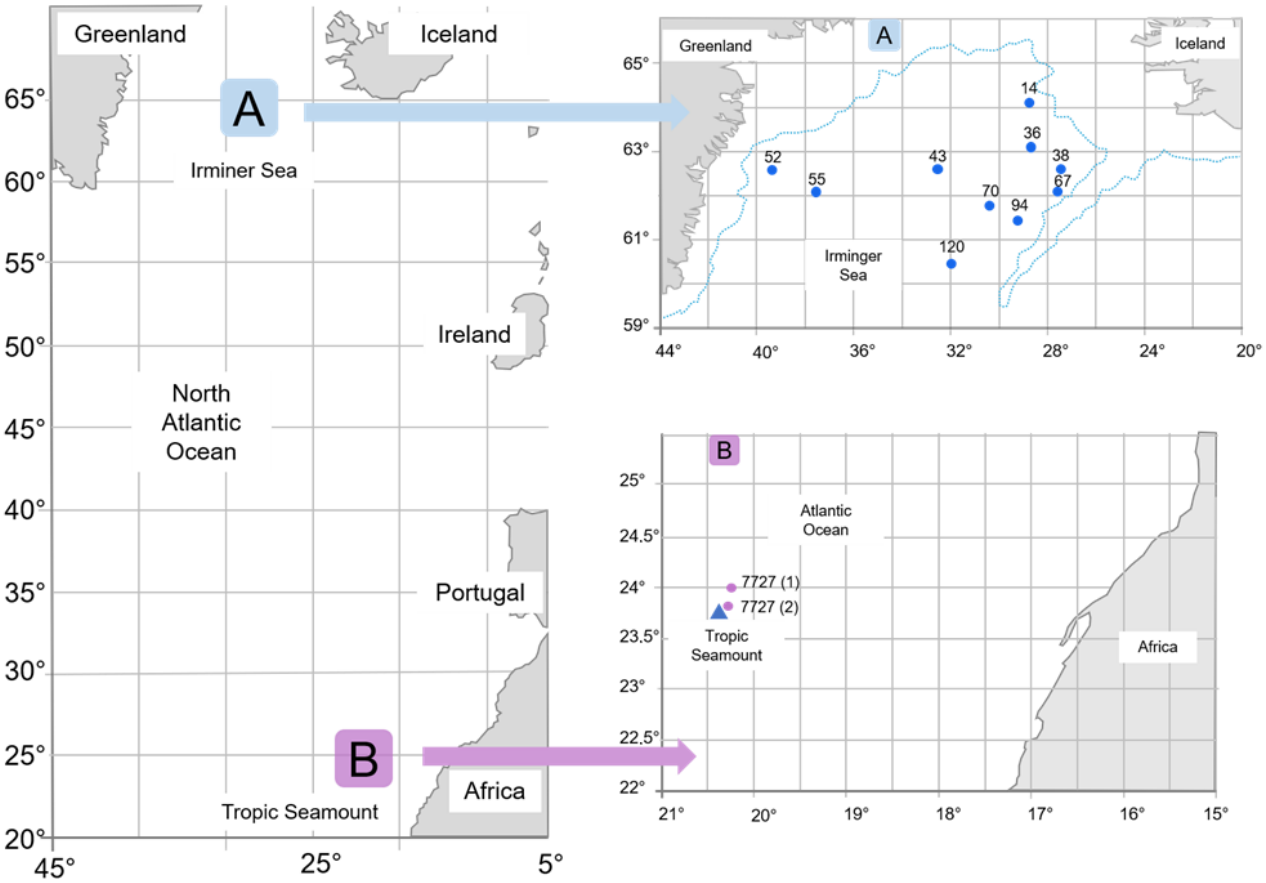

Figure 1. Schematic map of the collection sites of the mesopelagic fish (**A**) in the Irminger Sea (*Bathylagus euryops*, *Lampanyctus macdonaldi*, *Scopelogadus beanii*, *Serrivomer beanii*) and (**B**) in the Tropic Seamount area (*Lampanyctus alatus*, *Serrivomer beanii*).

The captured fish were identified to species level using the recommended guide [34]. The subset for lipid biochemical analysis was taken so that the capture coordinates coincided, and the horizontal distribution represented the total catch of the given species the most comprehensively. Sampling in the Irminger Sea was performed under the Agreement on Cooperation between the Federal Fisheries Agency and the Russian Academy of Sciences and pursuant to the Joint Research Program of the said parties.

Muscle tissue samples from mesopelagic fish—*S. beanii* and *L. alatus*—were collected in the Tropic Seamount area (24°03.2′–23°55.2′ N 020°39.9′–020°41.3′ W) in December 2021 during research under the "Program for multidisciplinary field research of the Southern Ocean ecosystem (Atlantic sector of the Antarctic) in 2021–2026" onboard R/V "Akademik Mstislav Keldysh". Trawling was carried out using Isaacs–Kidd mid-water trawl in the Samyshev–Aseev modification (IKMT-SAM, length 25 m, knotless 5 mm mesh net, cod end with Capron no. 15 insert, mouth area 6 m^2). Fish was sampled at depth range—0–588 m and 0–1440 m. Species identification was made using a guide [35]. The total number of fish species collected for analysis was: *L. alatus*—n = 11, *S. beanii*—n = 5.

Captured adult fish was immediately put on freeze plate (−20 °C) and a piece of muscle was dissected by sterile scalpel. Muscle tissue for lipid analysis was biopsied from posteriodorsal region in each fish specimen. All procedures with fish were made in accordance with Declaration of Helsinki and the International Guiding Principles for Biomedical Research Involving Animals. The study was approved by the Ethics Committee of the Institute of Biology of the Karelian Research Centre of the Russian Academy of Sciences.

2.2. Lipid Extraction and Analysis

The total lipids (TL) from muscle tissue were extracted using the Folch methodchloroform-methanol (2:1, *v*/*v*) mixture [36]. In brief, until the analysis tissue was homogenated and fixed in choloform:methanol (2:1, *v*:*v*). Then the analyzed tissue sample was filtered, and the residue, retained on the paper filter, was rinsed with 30 mL of extractive mixture—choloform:methanol (2:1, *v*:*v*). To remove water-soluble impurities, 15 mL of the chloroform-methanol (2:1, *v*/*v*) and 3 mL of 0.74% aqueous potassium chloride solution were added to the extract in the separatory glass funnel (Schott Duran, Mainz, Germany) until the complete separation of organic phases. Lipids remained in the lower chloroform layer, whereas nonlipid substances moved to the upper aqueous methanol phase. Then the chloroform layer was withdrawn to evaporate under a vacuum on a rotary evaporator Hei-VAP Advantage HL/G3 (Heidolph, Schwabach, Germany), and dried in a vacuum over phosphoric anhydride to a constant weight. Total lipids were dissolved in chloroform/methanol in a glass tube with a Teflon-lined screw cap and stored at −20 °C until further processing.

2.2.1. Neutral Lipids Analysis

Qualitative and quantitative determination of individual lipid classes—total phospholipids (PL), monoacylglycerols (MAG), diacylglycerols (DAG), triacylglycerols (TAG), cholesterol esters (Chol esters), cholesterol (Chol), non-esterified fatty acids (NEFA) and wax esters was carried out using high-performance thin-layer chromatography (HPTLC). Fractionation of total lipids was carried out on ultrapure glass-based plates—HPTLC Silicagel 60 F_{254} Premium Purity (Merck, Darmstadt, Germany).The application of microvolumes of the sample was performed using a semi-automatic Linomat 5 applicator (CAMAG, Muttenz, Switzerland), and the separation of individual lipid classes was carried out using an ADC2 chromatographic chamber (CAMAG, Muttenz, Switzerland) in the solvent system hexane-diethyl ether-acetic acid (32:8:0.8, *v*/*v*) with used supersaturated zinc nitrate ($ZnNO_3$ * $6H_2O$) solution for maintaining humidity (47–49% humidity) [37]. Formation of visible individual lipid spots were stained in a solution of copper sulfate ($CuSO_4$) with orthophosphoric acid (H_3PO_4), followed by heating the plate to 160 °C for 15 min. Qualitative and quantitative determination of lipid components was carried out in the chamber of a TLC Scanner 4 densitometer (CAMAG, Muttenz, Switzerland) [38]. The identification of individual lipid classes was carried out according to the standards of the respective studied components (Sigma-Aldrich, Burlington, MA, USA), taking into account the correspondence of the Rf-values.

2.2.2. Polar Lipids Analysis

Qualitative and quantitative determination of individual phospholipid fractions—phosphatidylcholine (PC), phosphatidylethanolamine (PEA), phosphatidylserine (PS), phosphatidylinositol (PI), lysophosphatidylcholine (LysoPC) and sphingomyelin (SM) was performed by high-performance liquid chromatography (HPLC) and described in previously in Reference [2].

2.2.3. Fatty Acids Analysis

Qualitative and quantitative fatty acids (FAs) profile of the TL was analyzed by gas-liquid chromatography (GC) with flame-ionized detector (FID) and mass-detector (MS). FAMEs were separated on a GC with mono-quadrupole mass-selective detector "Maestro-αMS" (Saitegra, Moscow, Russia) for identification of FAs constituents. The separation of FAs was carried out for 120 min in isothermal configuration (200 °C) on a Zebron ZB-FFAP capillary column (Phenomenex, Torrance, CA, USA) using helium as a mobile phase. The SIM/SCAN mode: SIM mode for searching for FAs according to the analytical standards—Supelco 37, Bacterial Acid Methyl Ester (BAME) Mix and PUFA No.1 Marine source (all Sigma Aldrich, USA); SCAN mode was used for searching and identification unique FAs with scan parameters 50 to 400 *m*/*z*. The data were analyzed using "Maestro Analytic v.

1.025" software with NIST library. Next, after qualitative identification of FA with GC-MS, the quantitative determination was caried out using GC-FID. FAMEs were separated on a "Chromatek-Crystall-5000.2" gas chromatograph with a flame-ionization detector (FID) and an automatic liquid dispenser (Chromatek, Yoshkar-Ola, Russia). The separation of FAs was carried out for 120 min in isothermal configuration (200 °C) on a Zebron ZB-FFAP capillary column (Phenomenex, USA) using nitrogen as a mobile phase. Chromatek-Crystall-5000.2" software "Chromatek Analytic v. 3.0.298.1" (Chromatek, Yoshkar-Ola, Russia), the analytic procedure is described in Reference [2]. All GC parameters were identical between GC-MS and GC-FID except mobile phase (helium and nitrogen, respectively).

2.3. Statistical Analysis

The results were statistically processed using the R programing language (v. 3.6.1.) in the RStudio integrated development environment with supplementary packages: readxl (v. 1.3.1), tidyverse (v. 1.3.0), corrgram (v. 1.13), factoextra (v. 1.0.6), quantreg (v. 5.52), cowplot (v. 1.1.1), vegan (v. 2.5–7). To detect changes among the TL contents of the studied fishes, the models of median and quantile (for 10- and 90th percentile) linear regression were used. Species ordination in multidimensional space was performed by applying the non-metric multidimensional scaling (NMDS) algorithm to the investigated parameters. Multidimensional analysis of the fatty acid composition was applied only to major physiologically valuable components contributing more than 1% to total FA content [23]. The best metric of distances in the multidimensional attribute space was determined using Spearman's coefficient of correlation between distance matrices. The measure of divergence between the original and the modeled distance matrices was estimated by the Stress index [39]. Significant differences were assessed using the multivariate Kruskal-Wallis test. In cases where the Kruskal-Wallis test showed significant differences, a nonparametric Wilcoxon-Mann-Whitney rank sum test was used to identify pairwise differences. [40]. Differences between depth horizons regarding the fatty acid spectrum were estimated by the analysis of variance using distance matrices (ADONIS) in observation groups and randomized permutation test for correspondence analysis [39]. Differences between individual lipid parameters were deemed reliable when $p \leq 0.05$. The between groups/within group value variation ratio was estimated by the ANOSIM algorithm, and the percentage similarity between groups—by SIMPER analysis. Cluster analysis of depth horizons based on the fatty acid spectrum was performed in the Euclidian space [39]. Spearman's method was used for correlation analysis [40].

The study was carried out at the Laboratory of Ecological Biochemistry and using the equipment of the Core Facility of the Karelian Research Centre of the Russian Academy of Sciences.

3. Results

L. macdonaldi featured the highest content of total lipids (TLs) in muscles among the mesopelagic species in the study (Figure 2). This parameter varied within 25.22–46.28% dry weight (DW) in the 250–700 m depth range with an average of 36.79% DW throughout the surveyed depths. The lowest TL content (8.65% DW on average over the depth profile with variation from 3.12 to 21.35% DW among depth horizons) was detected in *S. beanii*. *B. euryops* and *Sc. beanii* exhibited similar depth-averaged muscle TL levels (16.71 and 19.74% DW, respectively) but the contents varied among horizons: in *B. euryops*—the TL content decreased while in *Sc. beanii*, the content was constant.: 375 m—22.32 and 19.74% DW, respectively; 700 m—17.18 and 19.73% DW, respectively.

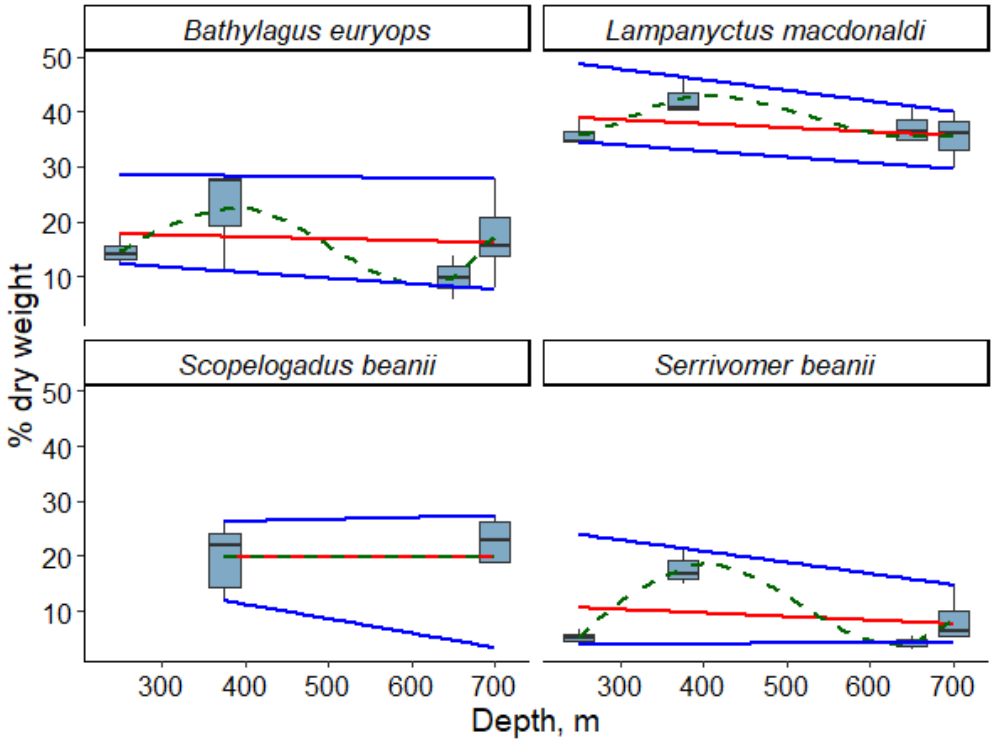

Figure 2. The change in total lipid content in muscles of mesopelagic fish species (*Bathylagus euryops*, *Lampanyctus macdonaldi*, *Scopelogadus beanii*, *Serrivomer beanii*) living at different depths in the Irminger Sea (North Atlantic). Note: red line—median linear regression, blue line—linear quantile regression (for the 10th and 90th percentiles), green line—smoothed regression.

We analyzed the dynamic of TLs in muscles of the studied mesopelagic fish species towards greater depths (Figure 2). Regression modeling revealed a downward trend in TL content depth-wise in *B. euryops* (R^2 = 0.01), *L. macdonaldi* (R^2 = 0.07), and *S. beanii* (R^2 = 0.05), whereas the TL content in *Sc. beanii* (R^2 < 0.001) remained stable at different depths apart from the decline in the 10th percentile. Furthermore, three species (excluding *Sc. beanii*) were characterized by elevation of muscular TL content at 375 m depth followed by a reduction at 650 m depth. The differences, however, were significant only in *S. beanii*. Due to the low coefficient of determination for all studied species, the linear regression models were used solely to determine the trend (increase or decrease) of depth-wise changes in the content of TL in muscles of fish.

It was found that in the species caught in the area of the Tropic Seamount (*S. beanii* and *L. alatus*), the content of TL in muscle was significantly lower—5.15 and 6.87% of DW, respectively.

Figure 3 shows the distribution of the studied mesopelagic fish species in the multi-dimensional space of attributes (individual lipid classes) produced by the non-metric multidimensional scaling (NMDS) algorithm. ANOSIM detected reliable differences (R = 0.6851, $p < 0.05$) between the investigated species. SIMPER analysis revealed the average degree of general similarity between groups of species (45.0–71.4% similarity) generated by Chol esters, waxes, TAG, and PLs. *L. macdonaldi* demonstrated concentrated positioning on the vectors of waxes and Chol esters. The depth-averaged content of these lipids in muscles was 12.22 and 8.04% DW, respectively, while the content of the most common storage lipid—TAG—was 10.60% DW. *B. euryops*, *Sc. beanii*, *S. beanii* showed different vectors for TAGs and MAGs, which accounted for 6.87, 10.09, 3.21 and 0.33, 0.59, 0.42% DW, respectively. *B. euryops* and *Sc. beanii* exhibited similar (51.4% similarity) strategies of storing energetic lipids—with TAG dominance, whereas *S. beanii* stored equal shares of TAGs (3.21% DW) and Chol esters (3.54% DW). That said, *B. euryops* differed from *Sc. beanii*

in having a higher content of NEFAs in muscles—0.90 and 0.72% DW, respectively, while *Sc. beanii* stored more DAGs (0.85% DW) than *B. euryops* (0.62% DW).

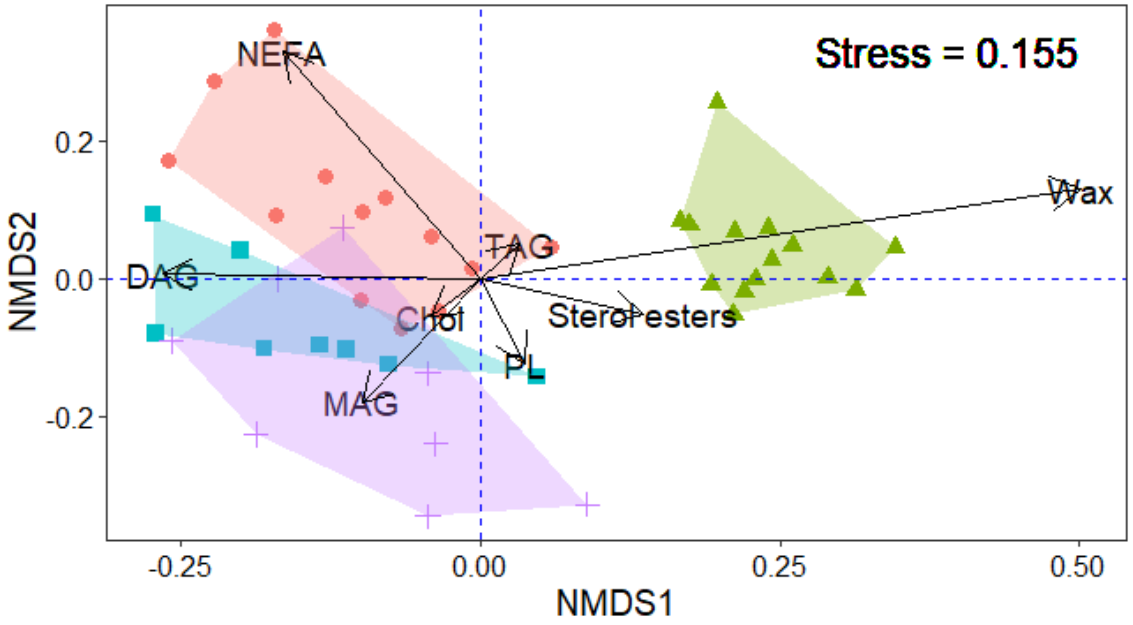

Figure 3. NMDS ordination of individual lipid classes in muscles of mesopelagic fish species (*Bathylagus euryops*, *Lampanyctus macdonaldi*, *Scopelogadus beanii*, *Serrivomer beanii*) living at different depths in the Irminger Sea (North Atlantic). Abbreviations: total phospholipids (PL), monoacylglycerols (MAG), diacylglycerols (DAG), triacylglycerols (TAG), cholesterol (Chol), non-esterified fatty acids (NEFA).

A smaller contribution to the distribution of the biochemical parameters in the mesopelagic species is made by structural lipids—total PLs and Chol. The content of these lipid classes in muscles of the investigated mesopelagic fish species across the Irminger Sea depths was 2.92 and 2.35% DW, respectively, in *L. macdonaldi*; 1.53 and 1.56% DW in *B. euryops*; 2.50 and 2.35% DW in *Sc. beanii*; 1.74 and 1.52% DW in *S. beanii*. It is noteworthy that the Chol/PL ratio, which represents biological membrane permeability or viscosity, showed minor variations, but unsignificant, among the species—0.81, 1.02, 0.94, and 0.87, respectively.

In *L. alatus* collected in the Tropic Seamount, the accumulation of lipids in form of Chol esters and waxes was the same as in relative species—*L. macdonaldi* in the Irminger Sea (Table 1). However, the content of these lipid classes in *L. alatus* was significantly lower (1.6 and 0.93% DW, respectively) compared to *L. macdonaldi*. Interesting, that there were no significant differences in the lipid classes composition and the content of certain lipids in *S. beanii* between those specimens collected in northern and southern latitudes: TAG—0.86% DW and Chol esters—1.39% DW.

Figure 4 maps depth-wise changes in individual lipid classes in each species (for visual convenience, the % DW contributions of each lipid class are in logarithmic form to bring the scale to the same magnitude). *B. euriops* captured from different depths showed significant variations in the Chol/PL ratio due to a reduction in PLs from 2.19 to 0.43% DW, and a gradual increase in NEFA content from 0.78 to 1.01% DW. *L. macdonaldi*, on the contrary, demonstrated a decline in NEFAs (from 1.47 to 0.52% DW) in muscles at "medium depths" with a simultaneous increase in DAGs (from 0.29 to 0.51% DW) and MAGs (from 0.32 to 0.49% DW). *Sc. beanii* increased wax storage from 0.98 to 1.82% DW depth-wise, while at the same time DAG and NEFA content declined gradually from 1.07 to 0.63 and from 1.03 to 0.42% DW, respectively. Contrarily, *S. beanii* maintained a stable level of waxes (0.75–1.07% DW) across depths, but the content of other lipid classes declined, with the most pronounced trend for MAGs (from 0.77 to 0.21% DW).

Table 1. The content of lipid classes (% dry weight) in muscle tissue of the studied mesopelagic fishes from Irminger Sea and Tropic Seamount.

Area	Irminger Sea	Tropic Seamount	Irminger Sea	Tropic Seamount
Fish species Lipid classes	*Lampanyctus macdonaldi*	*Lampanyctus alatus*	*Serrivomer beanii*	
PL	2.92 ± 0.14	0.77 ± 0.09 *	1.74 ± 0.36	0.64 ± 0.17 *
MAG	0.43 ± 0.02	0.12 ± 0.02 *	0.42 ± 0.12	0.15 ± 0.03 *
DAG	0.4 ± 0.03	0.28 ± 0.04 *	0.46 ± 0.12	0.3 ± 0.07
TAG	10.6 ± 0.44	1.76 ± 0.3 *	3.21 ± 0.78	0.86 ± 0.14
Chol	2.35 ± 0.08	1 ± 0.12 *	1.52 ± 0.25	0.86 ± 0.25
Chol esters	8.04 ± 0.36	1.6 ± 0.25 *	3.35 ± 0.55	1.39 ± 0.44
Waxes	12.22 ± 0.54	0.93 ± 0.15 *	1.11 ± 0.11	0.71 ± 0.26
NEFA	0.81 ± 0.13	0.4 ± 0.06 *	0.52 ± 0.1	0.25 ± 0.06 *

Note: Values are presented as M (means) ± SE (standard error). *—significantly different (Wilcoxon–Mann–Whitney test, $p \leq 0.05$) between species from the Irminger Sea and Tropic Seamount.

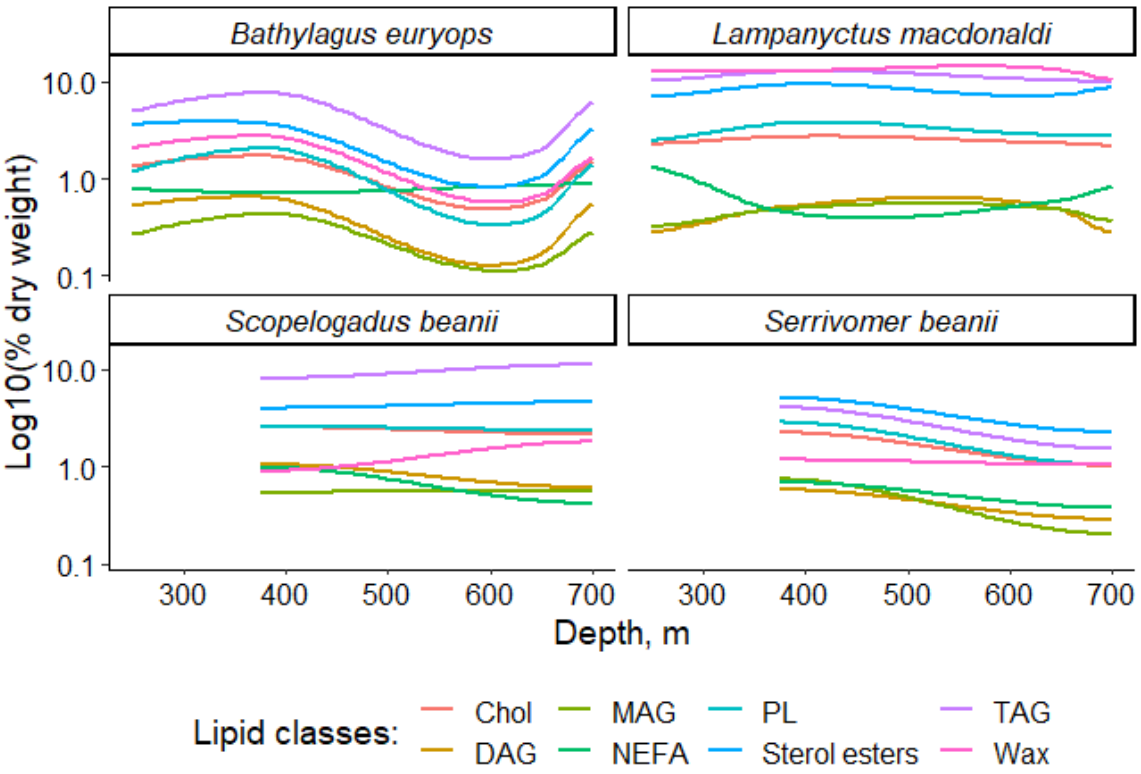

Figure 4. Patterns of change in individual lipid classes in muscles of mesopelagic fish species (*Bathylagus euryops*, *Lampanyctus macdonaldi*, *Scopelogadus beanii*, *Serrivomer beanii*) living at different depths in the Irminger Sea (North Atlantic). Note: abbreviations used as in Figure 3.

The performed analysis of multidimensional non-metric scaling established the overlap of the studied fish species in the multidimensional feature space (Figure 5). The ANOSIM analysis revealed the similarity of the studied samples with a large overlap (R = 0.172, *p*-value = 0.007), as well as a relatively high similarity between species (65–85.8% similarity) when using the SIMPER analysis. The cumulative result of the conducted statistical tests indicates similar values of the content of PL classes in the muscle tissue of the studied fish species. The high variance of certain PL classes in the fish species however is evidence of some differentiation in the compensatory mechanisms used for re-arranging the physico-chemical state of biomembranes. Thus, *B. euryops* and *S. beanii* were shifted on the LysoPC vector—0.16 and 0.17% DW versus 0.14 and 0.13% DW in *L. macdonaldi* and *Sc. beanii*, respectively. *L. macdonaldi* and *S. beanii* demonstrated high similarity in the total set of PL classes (85.8%) but with a differentiation of value ordination between some

individuals within species groups on the PC, PS, PI, and SM vectors. The muscular levels of these PL classes were, respectively, 2.19, 0.05, 0.02, and 0.01% DW for *L. macdonaldi* and 1.95, 0.04, 0.03, and 0.003% DW for *Sc. beanii*. Statistically significant differences between these species were found only for PC and PS.

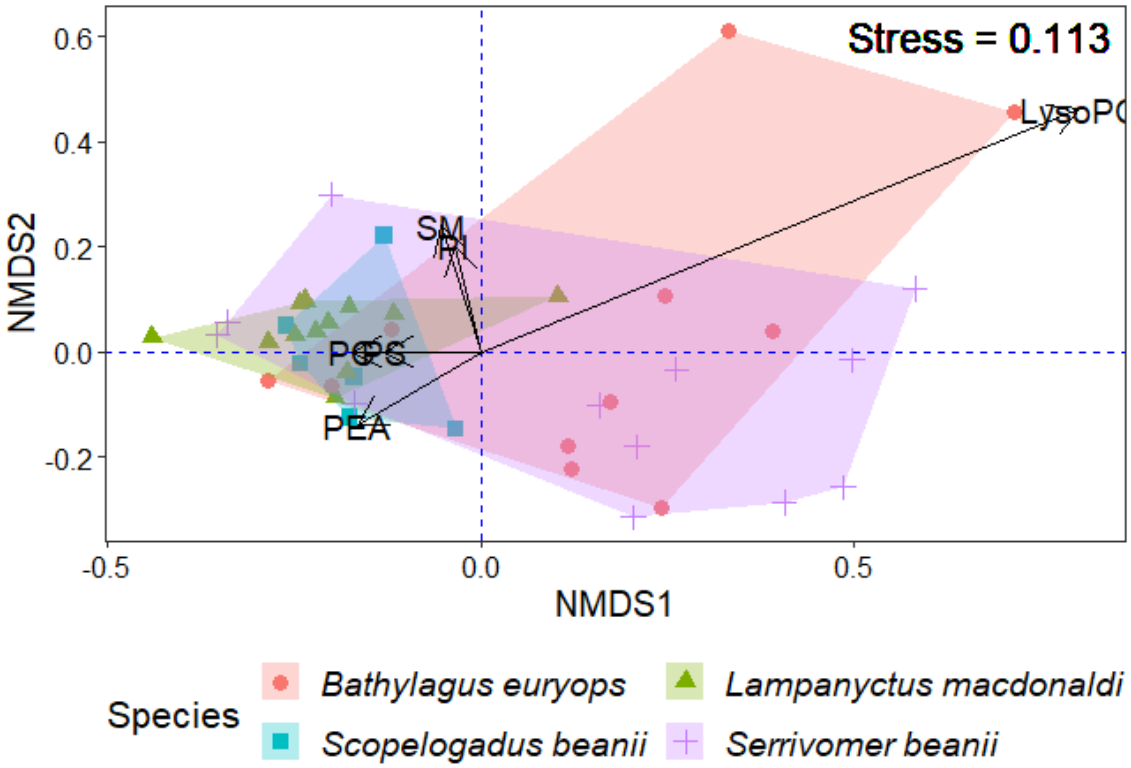

Figure 5. NMDS ordination of individual phospholipid classes in muscles of mesopelagic fish species (*Bathylagus euryops*, *Lampanyctus macdonaldi*, *Scopelogadus beanii*, *Serrivomer beanii*) living at different depths in the Irminger Sea (North Atlantic). Abbreviations: phosphatidylcholine (PC), phosphatidylethanolamine (PEA), phosphatidylserine (PS), phosphatidylinositol (PI) and lysophosphatidylcholine (LysoPC), sphingomyelin (SM).

A reliable change (decline) in PC content with depth was detected for *S. beanii* (from 2.36 to 0.78% DW), while *L. macdonaldi* showed a non-reliable upward trend for this phospholipid (from 1.84 to 2.04% DW) in muscles towards greater depths (Figure 6). Furthermore, *S. beanii* exhibited elevation of the LysoPC content with prevalence over PEA at depths from 375 to 650 m—from 0.25 and 0.21 to 0.41 and 0.20% DW, respectively. *B. euryops* showed a depth-wise rise in LysoPC content in muscles (0.01–0.23% DM), and an increase in PI content (0.001–0.022% DM) with a decline at 700 m depth (to 0.015% DM). *Sc. beanii*, on the other hand, demonstrated a synchronous decline in LysoPC (from 0.24 to 0.02% DW) and PI (from 0.03 to 0.02% DW) content in muscles depth-wise.

In the species collected in the area of Tropic Seamount, a relatively low content of total PL was found (0.64% DW in *S. beanii* and 0.77% in *L. alatus*) with PC dominance (0.42 and 0.53% DW, respectively). It was noted that the content of LysoPC in *S. beanii* was lower than in *L. alatus* (0.01 vs 0.05% DW), while in the "northern" species, the opposite was detected (Table 2).

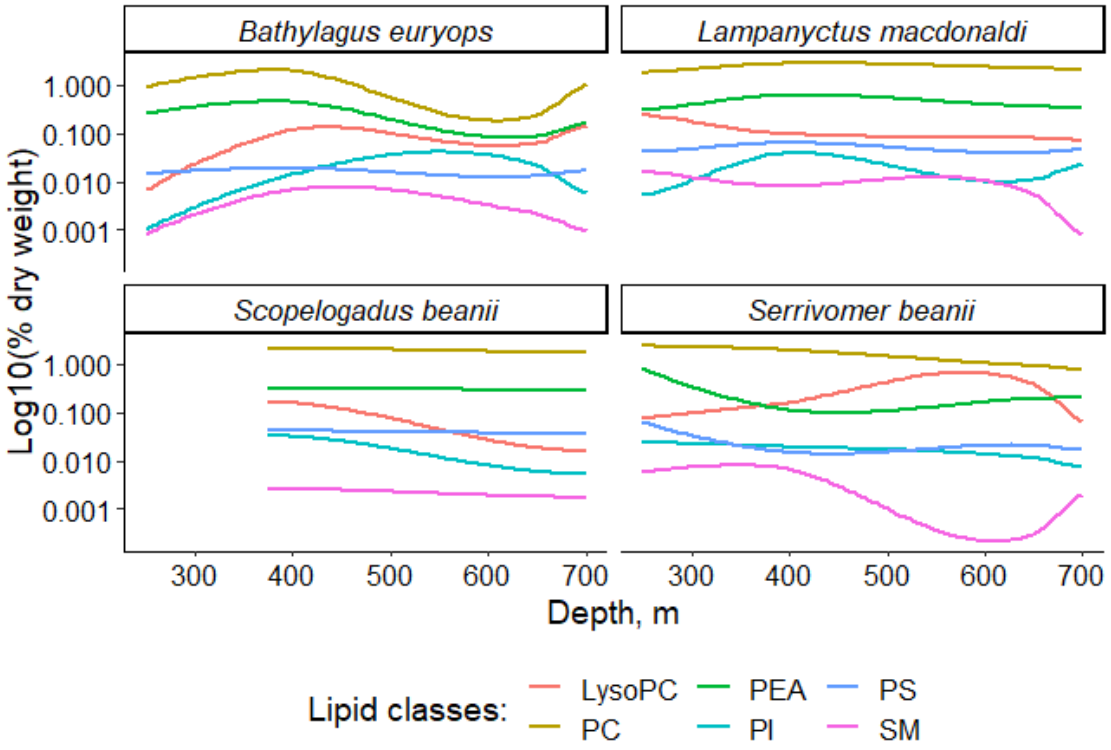

Figure 6. Patterns of change in individual phospholipid classes in muscles of mesopelagic fish species (*Bathylagus euryops*, *Lampanyctus macdonaldi*, *Scopelogadus beanii*, *Serrivomer beanii*) living at different depths in the Irminger Sea (North Atlantic). Note: abbreviations used as in Figure 5.

Table 2. The content of certain phospholipid fractions (% dry weight) in muscle tissue of mesopelagic fishes from Irminger Sea and Tropic Seamount.

Area	Irminger Sea	Tropic Seamount	Irminger Sea	Tropic Seamount
Fish species	*Lampanyctus macdonaldi*	*Lampanyctus alatus*	*Serrivomer beanii*	
PL fractions				
PC	2.19 ± 0.1	0.53 ± 0.07 *	1.28 ± 0.21	0.42 ± 0.09 *
PEA	0.39 ± 0.04	0.16 ± 0.02 *	0.32 ± 0.07	0.15 ± 0.05
PI	0.02 ± 0	0.01 ± 0	0.01 ± 0	0.02 ± 0.01
PS	0.05 ± 0	0.03 ± 0 *	0.03 ± 0.01	0.03 ± 0.01
LysoPC	0.14 ± 0.03	0.05 ± 0.03 *	0.17 ± 0.05	0.01 ± 0.01 *
SM	0.01 ± 0	0 ± 0 *	0 ± 0	0 ± 0

Note: Values are presented as M (means) ± SE (standard error). *—significantly different (Wilcoxon–Mann–Whitney test, $p \leq 0.05$) between species from the Irminger Sea and Tropic Seamount.

Figure 7 presents a comparative qualitative and quantitative muscle tissue fatty acid profile for the four mesopelagic fish species across the 250–700 m depth range. Analysis shows that the qualitative and quantitative composition and ratios of individual FAs differed between species, making the FA profiles of muscle tissue in the studied mesopelagic fish species-specific. Some FAs (chiefly minor ones) were present only in certain species (Figure 7). Reliable differences between species were corroborated by ANOSIM (R = 0.7483, *p*-value = 0.001). Still, species groups in the multidimensional attribute space (using the NMDS algorithm) were shaped similarly for individual lipid classes and for the fatty acid composition (Figures 3 and 8).

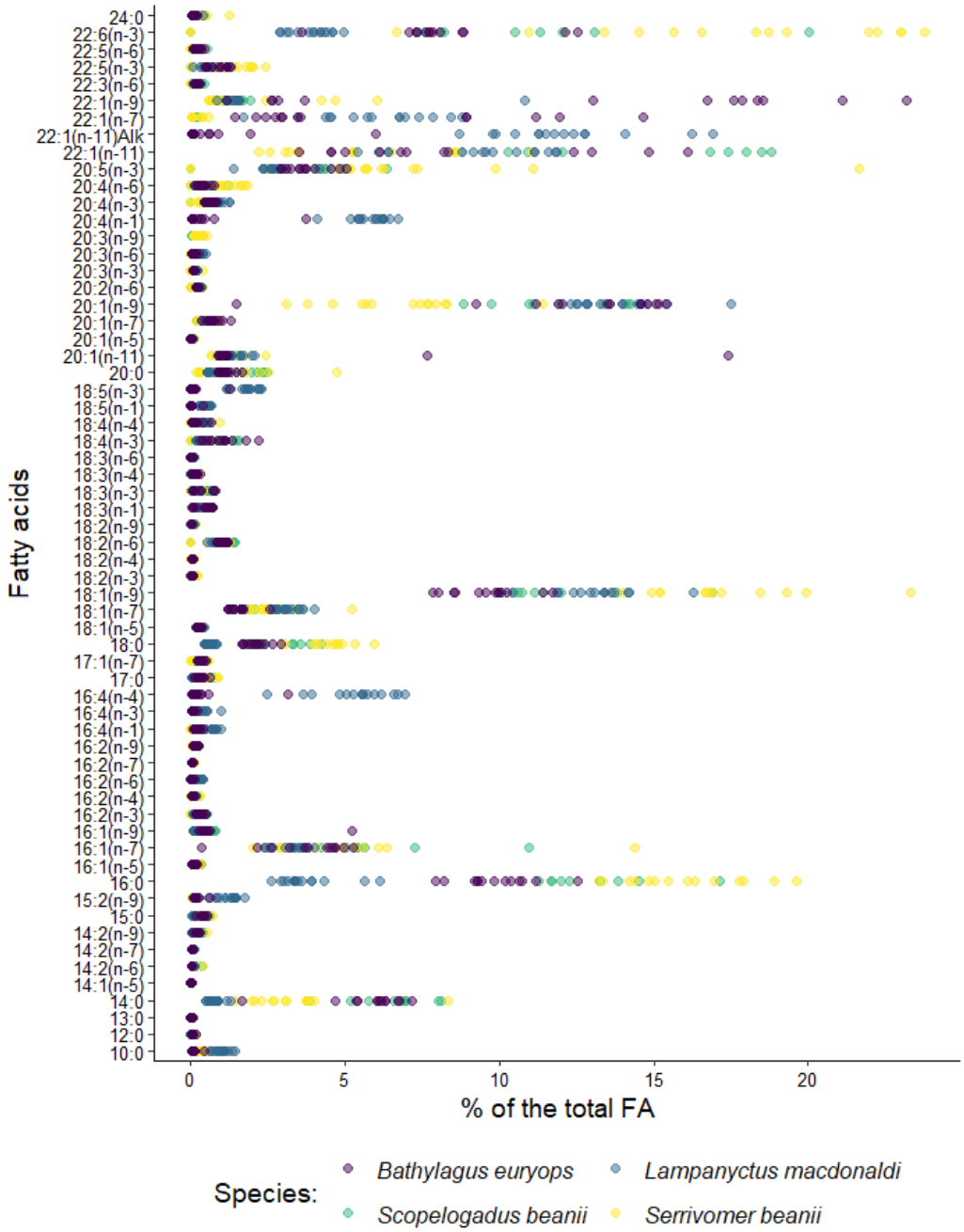

Figure 7. Fatty acids profile (% of the total FAs) of muscles of mesopelagic fish species (*Bathylagus euryops*, *Lampanyctus macdonaldi*, *Scopelogadus beanii*, *Serrivomer beanii*) living at different depths in the Irminger Sea (North Atlantic).

Monounsaturated fatty acids (MUFAs) dominated in all the species—51.58% of total FAs in *L. macdonaldi*; 58.50% of total FAs in *B. euryops*; 51.17% of total FAs in *Sc. beanii*; 41.28% of total FAs in *S. beanii* (Figure 9). A significant share in this FA group belonged to the oleic acid (OLE, 18:1(n-9)) (12.53, 9.37, 11.89, and 17.02% of total FAs, respectively) and fatty acids derived from copepods—20:1(n-9) (13.97, 12.78, 12.04, and 6.74% of total FAs, respectively) and 22:1(n-11) (7.59, 12.93, 14.62, and 5.49% of total FAs, respectively). *L. macdonaldi* was also noted for a high content of long-chain fatty alcohol derived from copepods 22:1(n-11)Alk (12.81% of total FAs), towards which the species is shifted in the multidimensional attribute space. *S. beanii* in the ordination plot is shifted towards detritus markers (18:1(n-7)—2.64% of total FAs; 16:1(n-7)—4.77% of total FAs), whereas *B. euryops* and *Sc. beanii*—towards copepod markers 20:1(n-9) and 22:1(n-11). Muscles of *L. macdonaldi*

and *B. euryops* contained also relatively high amounts of the 22:1(n-7) FA (7.50 and 11.12% of total FAs, respectively), while the share of this FA in *Sc. beanii* and *S. beanii* did not exceed 1% of total FAs.

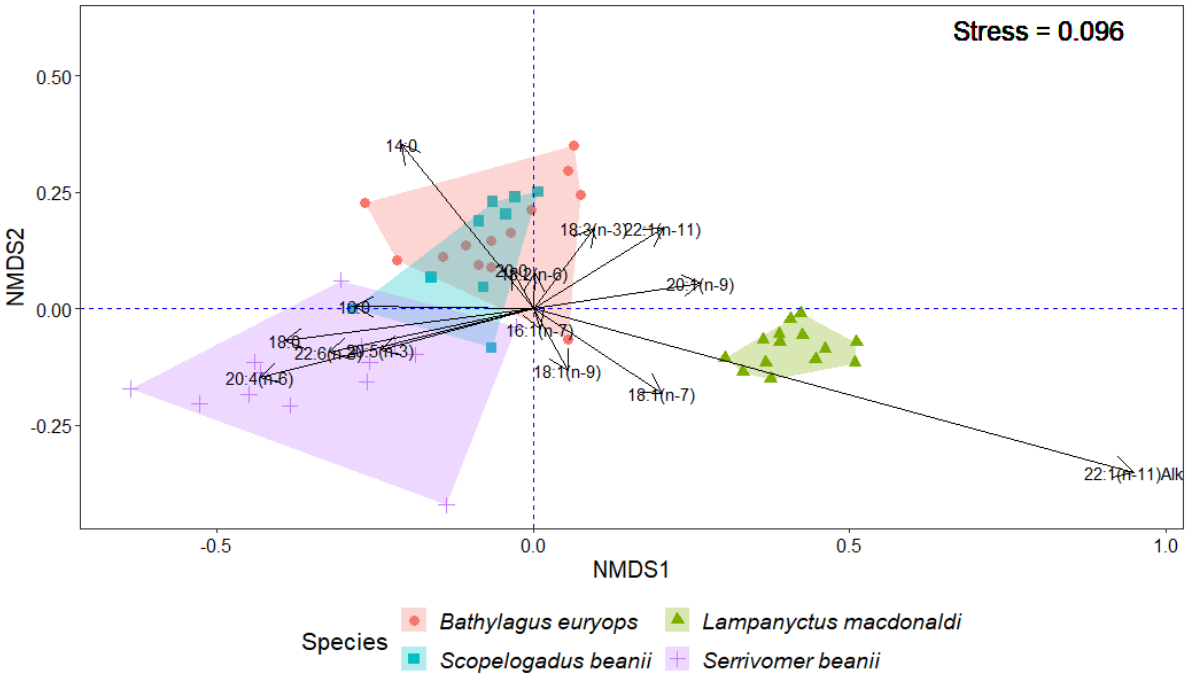

Figure 8. NMDS ordination of individual fatty acids in muscles of mesopelagic fish species (*Bathylagus euryops*, *Lampanyctus macdonaldi*, *Scopelogadus beanii*, *Serrivomer beanii*) living at different depths in the Irminger Sea (North Atlantic).

Polyunsaturated fatty acids (PUFAs) form the second largest FA group in terms of their quantity in muscles for three of the species—*L. macdonaldi*, *B. euryops* and *S. beanii* (28.27, 22.08, and 28.41% of total FAs, respectively). In *Sc. beanii* muscles, on the contrary, saturated fatty acids (SFAs) prevailed over PUFAs—25.58 vs. 20.76% of total FAs, respectively. The dominant family in the PUFA group was n-3 PUFAs but their quantities varied significantly among the species—10.89, 16.58, 16.91, and 24.68% of total FAs, respectively. As to another major PUFA family, n-6 PUFAs, its content varied very little (2.16, 2.20, 2.68, and 2.63% of total FAs, respectively). This combination leads to significant differences in the n-3/n-6 ratio between the species—5.07, 7.51, 5.64, and 8.06, respectively. The principal n-3 PUFAs proved to be the eicosahexaenoic acid (EPA, 20:5(n-3)) and docosahexaenoic acid (DHA, 22:6(n-3)) with muscular content of 2.46 and 4.12% of total FAs in *L. macdonaldi*, 3.97 and 8.62% of total FAs in *B. euryops*, 4.50 and 10.90% of total FAs in *Sc. beanii*, 7.44 and 17.71% of total FAs in *S. beanii*. Among n-6 PUFAs, analysis showed a relatively low content of the linoleic acid (LA, 18:2(n-6)) and arachidonic acid (AA, 20:4(n-6)) in *L. macdonaldi*—0.70 and 0.18% of total FAs, respectively. The levels of LA and AA in muscles of *B. euryops*, *Sc. beanii*, and *S. beanii* were 1.04 and 0.28; 1.21 and 0.62; 1.02 and 1.14% of total FAs, respectively. Concentrated positioning on the 22:6(n-3), 20:5(n-3), and 20:4(n-6) vectors in the ordination plot is seen for *S. beanii*. SIMPER analysis revealed high similarity in DHA content and, vice versa, low similarity in EPA content between *S. beanii* and other species: *L. macdonaldi*—80.6% and 27.4% similarity; *B. euryops*—82.8% and 23.8% similarity; *Sc. beanii*—62.2% and 23.8% similarity, respectively.

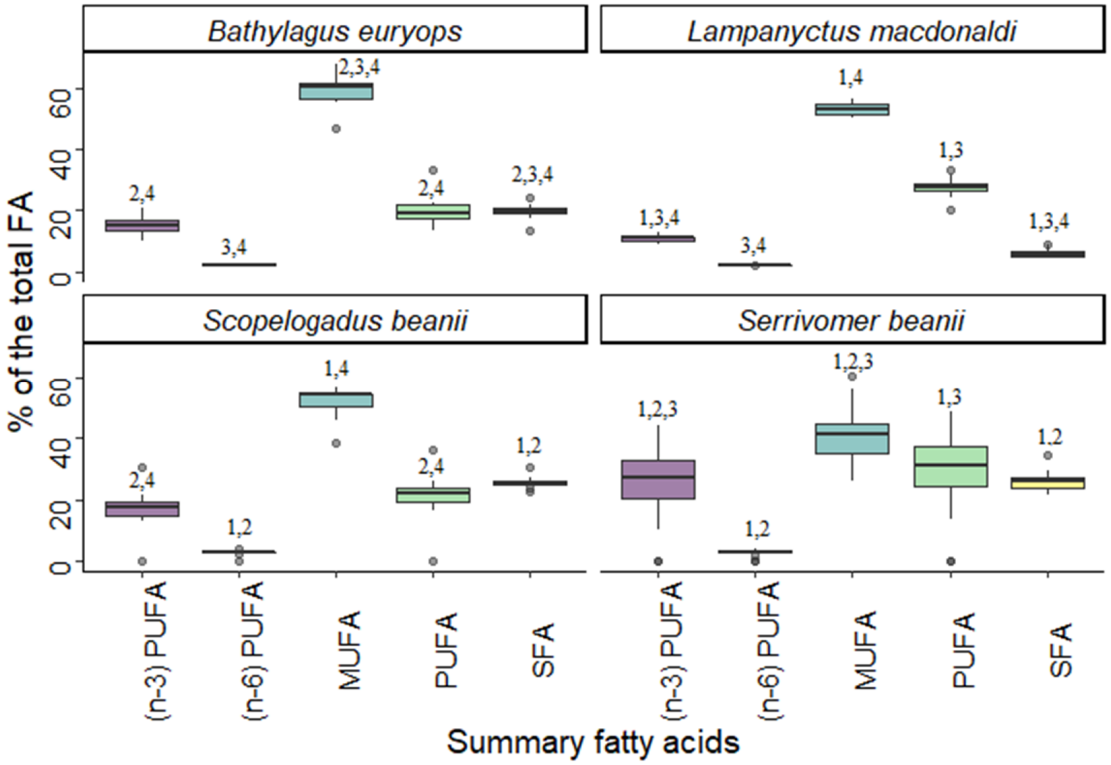

Figure 9. Certain FA classes (% of the total FAs) in muscles of mesopelagic fish species (*Bathylagus euryops*, *Lampanyctus macdonaldi*, *Scopelogadus beanii*, *Serrivomer beanii*) living at different depths in the Irminger Sea (North Atlantic). Abbreviations: saturated fatty acids (SFA), monounsaturated fatty acids (MUFA), polyunsaturated fatty acids (PUFA). Note: 1—significantly different (Wilcoxon–Mann–Whitney test, $p \leq 0.05$) between species and *B. euryops*, 2—significantly different (Wilcoxon–Mann–Whitney test, $p \leq 0.05$) between species and *L. macdonaldi*, 3—significantly different (Wilcoxon–Mann–Whitney test, $p \leq 0.05$) between species and *Sc. beanii*, 4—significantly different (Wilcoxon–Mann–Whitney test, $p \leq 0.05$) between species and *S. beanii*.

Muscles of *L. macdonaldi* showed a low SFA content (6.37% of total FAs) due to low content of individual SFAs (below 1% of total FAs) except for the palmitic acid (16:0), which contributed 3.80% of total FAs. SFA content in *B. euryops* was 17.67% of total FAs owing to the 14:0 and 16:0 FAs (5.25 and 8.76% of total FAs, respectively). The other two species, *Sc. beanii* and *S. beanii*, contained similar SFA content in muscles (25.58 and 25.91% of total FAs, respectively) but the quantities of individual FAs in the two species significantly differed—6.47 and 3.33% of total FAs for 14:0; 13.07 and 16.0% of total FAs for 16:0; 2.99 and 4.25% of total FAs for 18:0, respectively. In addition, *Sc. beanii* was shifted on the 14:0 FA vector in the ordination plot due to the prevalence of this acid in muscles.

Cluster analysis for the fatty acid spectrum detected vertical clustering in *Sc. beanii* (at 375 and 700 m depths) and *S. beanii* (by the 250–375 and 650–700 m depth horizons), while *L. macdonaldi* and *B. euryops* showed a "diffusion of depths" between clusters (Figure 10). Noteworthy are two distinct 4th order clusters in *S. beanii*, one of them encompassing the 650–700 m horizon, whereas the other one features a diffusion of 250 and 375 m depths into the cluster. Having applied ADONIS in observation groups and the randomized permutation test for correspondence analysis, we found reliable differences between the 375 and 700 m depths in *Sc. beanii*, and between the 650–700 and 250–375 m horizons in *S. beanii*. At greater depths, *Sc. beanii* experienced a rise in 20:1(n-9) and 22:1(n-11) from 10.96 and 12.10 to 13.40 and 17.77% of total FAs, respectively. At smaller depths (375 m), this species contained higher contents of DHA, 18:1(n-9), 16:0, and 16:1 (n-7) versus the 700 m depth—11.65 vs. 9.97, 12.53 vs. 10.59, 14.08 vs. 11.81, 6.57 vs. 5.00% of total FAs, respectively. *S. beanii*, on the contrary, showed an increase in DHA, EPA, AA, and

16:0 depth-wise—13.90–19.84, 5.02–8.78, 0.81–1.33, 15.83–16.09% of total FAs, respectively. At the same time, the content of 20:1(n-9), 22:1(n-11), and 16:1(n-7) in its muscles declined with depth—7.83–6.14, 6.35–5.02, 6.80–3.65% of total FAs, respectively.

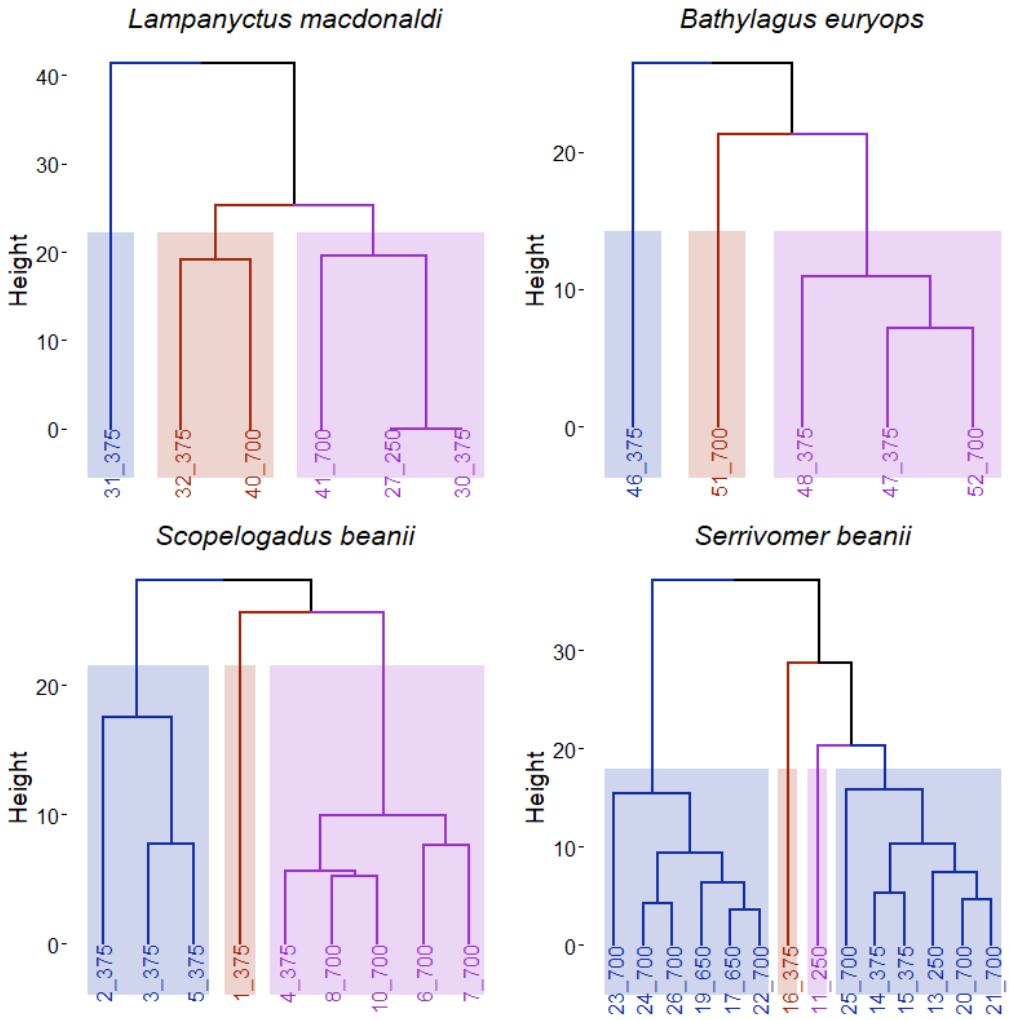

Figure 10. Cluster analysis of the muscle-tissue fatty acid composition in mesopelagic fish species (*Bathylagus euryops*, *Lampanyctus macdonaldi*, *Scopelogadus beanii*, *Serrivomer beanii*) living at different depths in the Irminger Sea (North Atlantic).

It was detected the absence of 22:1(n-11)Alk in *L. alatus* in comparison *L. macdonaldi*. The content of n-6PUFA was higher in fishes collected in the "southern" latitudes compared to the "northern" ones: 4.38 and 6.35% of total FAs in *S. beanii* and *L. alatus*, respectively (Table 3). The dominant FA among n-6 PUFA was AA—1.97 and 3.80% of total FAs, respectively. It is worth noting the higher content of n-3 PUFA in fishes collected in the area of Tropic Seamount (25.08 and 34.87% of total FAs, respectively), compared with individuals from the Irminger Sea (16.91 and 10.89% of total FAs in *S. beanii* and *L. macdonaldi*, respectively), due to DHA—17.61 and 25.66% of total FAs, respectively. In addition, the content of MUFAs was significantly low in fishes collected in the area of Tropic Seamount—*S. beanii* and *L. alatus* (35.25 and 26.74% of total FAs) in comparison to *S. beanii* and *L. macdonaldi* collected in the Irminger Sea (41.28 and 51.58% of total FAs, respectively). The low content of MUFAs was associated with low content of copepod FAs biomarkers—20:1 (n-9) (3.42 and 1.41% of total FAs, respectively) and 22:1 (n-11) (1.52 and 0.52% of total FAs). Notable that various n-4 and n-7 series PUFAs were detected in the studied deep-water fishes inhabiting as "northern" as "tropic" latitudes.

Table 3. Certain fatty acids (% of the total FA) in muscle tissue of mesopelagic fishes from Irminger Sea and Tropic Seamount.

Area	Irminger Sea	Tropic Seamount	Irminger Sea	Tropic Seamount
Fish species	*Lampanyctus macdonaldi*	*Lampanyctus alatus*	*Serrivomer beanii*	
Fatty acids				
14:0	0.78 ± 0.06	1.71 ± 0.12 *	3.33 ± 0.44	1.83 ± 0.34 *
15:0	0.08 ± 0.01	0.56 ± 0.03 *	0.43 ± 0.03	0.55 ± 0.12
16:0	3.74 ± 0.25	19 ± 0.32 *	16 ± 0.54	16.88 ± 3.48
17:0	0.04 ± 0	0.8 ± 0.05 *	0.51 ± 0.05	0.61 ± 0.14
18:0	0.6 ± 0.04	5.71 ± 0.25 *	4.25 ± 0.27	5.83 ± 1.72
20:0	0.68 ± 0.04	1.58 ± 0.19 *	1.17 ± 0.35	1.19 ± 0.34
24:0	0.08 ± 0.03	0.77 ± 0.08 *	0.23 ± 0.09	0.21 ± 0.08
16:1 (n-9)	0.1 ± 0.01	0.46 ± 0.02 *	0.42 ± 0.02	0.38 ± 0.08
16:1 (n-7)	3.2 ± 0.13	3.07 ± 0.32	4.77 ± 0.83	4.32 ± 0.6
17:1 (n-7)	0.27 ± 0.01	0.78 ± 0.04 *	0.19 ± 0.07	0.75 ± 0.13 *
18:1 (n-9)	13.16 ± 0.34	17.67 ± 0.81 *	17.02 ± 0.69	18.61 ± 1.8
18:1 (n-7)	3.12 ± 0.1	2.07 ± 0.12 *	2.64 ± 0.23	2.61 ± 0.25
18:1 (n-5)	0.31 ± 0.02	0.11 ± 0.01 *	0.3 ± 0.01	0.19 ± 0.05 *
20:1 (n-11)	1.44 ± 0.08	0.17 ± 0.02 *	1.19 ± 0.12	0.41 ± 0.18 *
20:1 (n-9)	13.82 ± 0.36	1.41 ± 0.13 *	6.74 ± 0.58	3.42 ± 2.23
22:1 (n-11)	9.27 ± 0.57	0.52 ± 0.17 *	5.49 ± 0.74	1.52 ± 1.15 *
22:1 (n-9)	1.96 ± 0.63	0.1 ± 0.01 *	1.77 ± 0.49	2.26 ± 2.14
22:1 (n-7)	5.88 ± 0.5	0.09 ± 0 *	0.15 ± 0.05	0.4 ± 0.32
10:0	0.99 ± 0.06	0.52 ± 0.13 *	0.24 ± 0.04	0.36 ± 0.27
18:2 (n-6)	0.78 ± 0.03	0.91 ± 0.04 *	1.02 ± 0.05	1 ± 0.11
18:3 (n-6)	0.05 ± 0.01	0.07 ± 0.03	0.04 ± 0	0.02 ± 0
20:2 (n-6)	0.29 ± 0.01	0.23 ± 0.01 *	0.21 ± 0.02	0.16 ± 0.03
20:3 (n-6)	0.35 ± 0.01	0.18 ± 0.01 *	0.12 ± 0.01	0.22 ± 0.03 *
20:4 (n-6)	0.19 ± 0.01	3.8 ± 1.74 *	1.14 ± 0.12	1.97 ± 0.55
22:5 (n-6)	0.08 ± 0.01	1.09 ± 0.08 *	0.23 ± 0.02	0.78 ± 0.19 *
16:4 (n-4)	5.32 ± 0.32	0.32 ± 0.03 *	-	-
18:2 (n-4)	0.04 ± 0	0.12 ± 0.01 *	0.06 ± 0.01	1.27 ± 1.17 *
18:3 (n-4)	0.07 ± 0.01	0.07 ± 0.02	0.13 ± 0.01	0.09 ± 0.02 *
18:4 (n-4)	0.29 ± 0.06	0.02 ± 0 *	0.18 ± 0.08	0.04 ± 0.01
16:2 (n-3)	0.1 ± 0.01	0.38 ± 0.02 *	0.2 ± 0.02	1.62 ± 1.25 *
16:4 (n-3)	0.32 ± 0.06	0.03 ± 0 *	-	-
18:2 (n-3)	0.04 ± 0	0.18 ± 0.01 *	0.14 ± 0.01	0.19 ± 0.03
18:3 (n-3)	0.18 ± 0.02	0.46 ± 0.04 *	0.18 ± 0.03	0.22 ± 0.03
18:5 (n-3)	1.8 ± 0.09	0.01 ± 0 *	-	-
20:4 (n-3)	0.8 ± 0.07	0.68 ± 0.08	0.42 ± 0.03	0.66 ± 0.07 *
20:5 (n-3)	2.68 ± 0.15	6.11 ± 0.29 *	7.44 ± 1.23	4.82 ± 0.8
22:5 (n-3)	0.48 ± 0.04	0.81 ± 0.03 *	1.39 ± 0.17	1.02 ± 0.23
22:6 (n-3)	3.9 ± 0.17	25.66 ± 1.62 *	17.71 ± 1.36	17.61 ± 4.47
22:1 (n-11)Alk	12.12 ± 0.58	-	-	-
SFA	5.99 ± 0.35	30.13 ± 0.56 *	25.91 ± 0.93	27.11 ± 5.68
MUFA	53.19 ± 0.51	26.74 ± 0.97 *	41.28 ± 2.52	35.25 ± 4.6 *
SCFA	1 ± 0.06	0.61 ± 0.13 *	0.33 ± 0.04	0.47 ± 0.25
(n-9) PUFA	1.44 ± 0.09	0.28 ± 0.02 *	0.59 ± 0.04	0.34 ± 0.09 *
(n-7) PUFA	0.04 ± 0	0.11 ± 0.01 *	0.13 ± 0.01	0.1 ± 0.01 *
(n-6) PUFA	2.24 ± 0.05	6.35 ± 1.67 *	3 ± 0.14	4.38 ± 0.65
(n-4) PUFA	5.86 ± 0.32	0.71 ± 0.04 *	0.5 ± 0.1	0.41 ± 0.05
(n-3) PUFA	10.75 ± 0.34	34.87 ± 1.75 *	28.2 ± 2.28	25.08 ± 5.65
PUFA	27.69 ± 0.82	42.52 ± 1 *	32.47 ± 2.37	31.47 ± 5.29

Note: Values are presented as M (means) ± SE (standard error). *—significantly different (Wilcoxon–Mann–Whitney test, $p \leq 0.05$) between species from the Irminger Sea and Tropic Seamount.

4. Discussion

Mesopelagic fish inhabit the twilight zone of the World Ocean in the 200–1000 m depth range, which constitutes some 20% of the total ocean [41]. According to the latest estimates, the total fish biomass in the mesopelagic zone may be 2 to 19.5 gigatons, i.e., approximately 100 times the total annual global harvest [9,42]. Mesopelagic fish play an important part in the processes of carbon and energy transformation and cycling between oceanic layers [43–45], being simultaneously predators for zooplankton [46,47] and food for larger fish [48], birds [49], and marine mammals [50–52]. Lipids are the principal structural and energetic components of marine organisms, primarily deposited in muscles and liver, part of which is then passed on along the food chain [24,53].

The high TL content that we found in *L. macdonaldi* muscles is characteristic of lanternfishes [54]. The species-specific patterns of TL accumulation and variations in muscles at different depths in *L. macdonaldi*, *B. euryops*, *Sc. beanii*, and *S. beanii* are associated with their different life cycles, ability to perform daily vertical migrations, and with adaptations to abiotic factors (temperature, salinity, specific photoperiod, pressure, etc.) at high depths [24,55–67]. To wit, *S. beanii* is known to have a complex life cycle with metamorphoses [67], species of the genus *Lampanyctus* can perform daily vertical migrations (although the genus has non-migrating members, too—*L. regalis*), and *B. euryops* was found to migrate towards deeper water horizons with age [13,68,69]. A significant effect on the processes of lipid storage, transfer, and transformation is produced also by the dietary specializations of fishes [70,71]. The depth-related differences in TL accumulation detected in our study possibly point to differences in the diets and foraging rates, as well as to an overall reduction in food availability at high depths [24,72–75].

The principal mechanisms for biochemical adaptation of fish to a wide set of extreme yet stable abiotic factors and to severe food shortage at high depths is alteration of the array and ratios of neutral and polar lipids in organs and tissues [10,76]. We observed the deposition of wax esters to dominate over storage TAGs and Chol esters in *L. macdonaldi* muscles, which serves the task of supplying the organism with energy during periods of food shortage and maintaining adequate buoyancy during vertical migrations of the fish in the water column [13,55,58,62]. High concentrations of waxes in the muscle tissue of bony fishes are known to correlate with the mesopelagic environment and be associated with daily vertical migrations [77]. The mechanisms involving waxes and Chol esters are targeted at alteration of cell membrane fluidity and implementation of the signaling and regulatory functions in response to depth-related changes in abiotic factors [58,62]. There are also mechanisms for decomposition of wax esters to "fast-responding" TAGs, which enable the organism's quick response to energy losses to vertical migrations [56,78]. *S. beanii* demonstrated a qualitatively similar strategy of lipid storage but quantitatively the content of Chol esters, TAGs, and waxes was much lower. Accumulation of high Chol esters and wax ester concentrations in muscles as well as depth-related variations of the NEFA content in the tissue (as demonstrated in our study) are characteristic features of vertically migrating fish species [58,62]. Vice versa, the prevalence of storage TAGs over Chol esters and waxes found in muscles of *B. euryops* and *Sc. beanii* appears to be the most beneficial form of energy storage for organisms living at greater depths, since these two species belong also to the bathypelagic category (living at depths down to 3237 and 2500 m, respectively) [69,79,80]. The dominance of neutral TAGs over other storage lipids in a tissue is associated with the accumulation of energetically valuable states as a "strategic reserve", considering the molecule's high energy capacity (2.5 times higher energy release than from carbohydrates) and prompt mobilization from adipocytes [20]. That said, we observed a rise in the content of waxes in *Sc. beanii* at greater depths, which may indicate certain flexibility in the use of molecular forms of energy storage.

The observed variations in MAG and DAG content in muscles of the studied species shape/are shaped by the differences in the rates of catabolism and anabolism of the stored lipid molecules, which can be related to the crucial distribution of foods among the horizons or indicate how much these lipid classes are involved as secondary messengers in

the organism's responses. The revealed changes in the content of MAGs and DAGs in the muscle tissue of the studied species indicate differences in the intensity of the processes of catabolism and anabolism. These variations may be associated with an extremely significant distribution of food at the studied depths, and also indicate the intensity of the participation of lipids as secondary messengers in compensatory responses of aquatic organisms. To wit, DAG molecule is involved in the regulation of protein kinase C activity for the organism's locomotion under high hydrostatic pressure [81,82].

L. macdonaldi, *Sc. beanii*, and *S. beanii* have been found to maintain cell membrane integrity at different depths by adjusting the Chol to PL ratio in membranes. In *B. euryops*, however, it was found a reduction in Chol/PL ratio with depth due a significant decline in the content of PLs (from 2.19 to 0.43% DW) and Chol (from 2.19 to 0.60% DW). It is known that Chol content in the organism depends on the habitat conditions and on the diet since not all organisms can synthesize sterols de novo [65,83–86]. Cholesterol involvement in the PL bilayer regulates membrane fluidity and permeability and maintain its integrity to secure adequate functioning of membrane-bound enzymes and ion channels as response to fluctuations of abiotic environmental factors [63,87,88].

Total PL content in tissues is normally constant, so the differences and variations in the qualitative and quantitative composition of individual PL classes in marine organisms are caused by changes in the ambient conditions (temperature, pressure, salinity, etc.) [57,63,89,90]. In the present research it was detected differences in the content of some PL classes, especially PC and PS, between the migrating *L. macdonaldi* and the non-migrating *Sc. beanii*. Normally, plasma membrane features a qualitative asymmetry of the content of PL classes on the membrane outer (PC and SM) and inner (PEA and PS) layers [91,92]. The minor compound PS is also known to participate in regulating membrane microviscosity by altering ion permeability, membrane excitability, and transmission of exterior signals into the cell [93]. The distinctions between *L. macdonaldi* and *Sc. beanii* may indicate differences in their strategies of rearranging the physico-chemical state of biomembranes in response to changes in the environment, in particular to the abrupt change in pressure for the migrating species, to maintain the interior microenvironment homeostasis. Another mechanism for regulating membrane permeability to ions is LysoPC build-up, which we observed in *S. beanii* and *B. euryops* at greater depths. It is a known fact that LysoPC build-up in tissue cells makes membranes more permeable to ions and the products of its degradation—NEFAs, glycerophosphoric acid esters, and choline—are utilized in the synthesis of bioactive compounds (e.g., hormones or neuromediators), which are then used to provide for intensive muscular activity and coordination of actions [94–96]. The variations we observed in the minor PI at some depth horizons simultaneously with changes in DAG content in *Sc. beanii* and *B. euryops* muscles possibly suggest that these lipids are involved in regulating the activity of the enzymatic systems responsible for the transport of Ca^{2+} ions through cell membranes [81,82].

The species-specific qualitative and quantitative features of the muscle tissue FA profile (including minor components) we have detected in the studied mesopelagic fishes are indicative of the species' distinctive characteristics related to their different dietary specializations, life cycles, mechanisms and strategies for biochemical adaptation to the habitat conditions [23,24,64,97]. There are some reports [54,98] that among mesopelagic fishes MUFA accumulation in the organism is a distinctive feature of lanternfishes mainly related to their diet. In our study, however, MUFAs prevailed in all the four families. *L. macdonaldi*, *B. euryops*, and *Sc. beanii* contained high levels of the FAs that are biomarkers of Calanus copepods (20:1(n-9) and 22:1(n-11))—the main food item for planktivorous consumers [24,72,73,99]. Feeding on zooplankton in *L. macdonaldi* is also corroborated by the muscular accumulation of waxes and the long-chain alcohol 22:1(n-11)Alk, which are abundant in Calanus copepods [100,101]. The presence of calanoid-derived FAs detected in *B. euryops* and *Sc. beanii* corroborates previously published results of studies on the food items consumed by these species as indicated by stomach content composition [69,80]. Noteworthy is the depth-wise rise in the content of the 20:1(n-9) and 22:1(n-11) FAs and increase in the 22:1/20:1 ratio (1.22–1.47) in *Sc. beanii*, forming two distinct horizons for

the life of this species. This may indicate that the prevalent food item for individuals of this species living at greater depths—700 m and more—is the deep-water *Calanus hyperboreus* [72,73]. *S. beanii* muscles contained comparatively high amounts of OLE, 18:1(n-7), and 16:1(n-7) FAs, which are plentiful in Arctic hyperiid amphipods *Themisto* sp. foraging on mesozooplankton [102].

Equally important among MUFAs is OLE, which is one of the key FAs in lipid metabolism. High OLE content was detected in all the four species, especially in *S. beanii*. At the same time, *S. beanii*, as well as *B. euryops* and *Sc. beanii* had a relatively high lipid metabolism index (16:0/18:1 (n-9) = 0.97, 0.94, and 1.11, respectively), whereas this index in *L. macdonaldi* was comparatively low (0.30). It is likely that *L. macdonaldi* uses alternative sources to replenish its energy as a variant of the organism's adaptive response [103].

High content of essential PUFAs of the omega-3 family (namely DHA and EPA) in habitats with low temperatures and high hydrostatic pressure is one of the main compensatory mechanisms through which organisms respond to changes in the environment [21,104,105]. As has been demonstrated previously, DHA and EPA content in fish muscles are altered to regulate membrane viscosity and the functional activity of membrane-bound enzymes to meet locomotion demands [2,104,106]. Our study detected direct correlation of EPA and DHA with growing depth for migrating species and, vice versa, inverse correlation for non-migrating species. This divergence may indicate differences in the rate of the organism's compensatory response to changes in hydrostatic pressure in migrating and non-migrating species. Interestingly, the vertically migrating *L. macdonaldi* had the lowest DHA and EPA levels among the fishes studied. It is known from the literature [23,107] and our previous studies [72,108] that these FAs are actively involved in the rearrangement of the membrane physico-chemical state in vertically migrating species. *L. macdonaldi* probably uses another strategy in its compensatory response to changes in environmental conditions during vertical migrations. The low percentage similarity between *S. beanii* and other mesopelagic fishes in the study may be due to a greater exogenous supply of EPA since this acid, together with some MUFAs, is plentiful in Arctic hyperiid amphipods [102]. Similar build-up of EPA and DHA towards greater depths has been described in our previous studies on beaked redfish [75].

The consistently low content of n-6 PUFAs in the studied species is evidence that individual FAs of this family make a minor contribution to the organism's adaptations. Hence, the physico-chemical state of biomembranes in these mesopelagic fishes is primarily regulated by adjusting FAs of the n-3 family, which results in a significant alteration of the n-3/n-6 ratio in the organism. It is known that n-3 and n-6 PUFAs shape the inner structure of biomembranes and form the optimal conditions for adequate functioning of integral proteins [108]. Noteworthy is the prevalence of LA over AA in *S. beanii*, possibly arising from more active synthesis of PI and eicosanoids [109–111]. In addition, low AA content may point to the absence of echinoderms, foraminifera, and seaweeds in fish diets [112–115].

The 14:0, 16:0, and 18:0 FAs are principal acids in animal organisms, being synthesizable de novo, and are precursors of physiologically valuable FAs with unsaturated bonds [78]. The comparatively high content of palmitic acid (16:0) detected in *Sc. beanii* and *S. beanii* may indicate active synthesis inside the organism as well as trophic connection with krill [116], while 14:0 FA content in *Sc. beanii* points to plankton as part of the species' diet [117]. Furthermore, the prevalence of SFAs over PUFAs in this species is most likely a result of its predominant foraging on salps in summer and fall [118].

Considering the unique lipid and fatty acid composition of the mesopelagic fishes studied, they qualify as potential objects for biotechnology, aquaculture, and food industry. Recent studies [119] reviewing existed knowledge about negative effects of wax esters on animals (mainly their digest ability) due to absence of any recommendations on the dose of these lipids and focused on the statement that consumption of moderate amounts by mammals exert beneficial health effects due to long chain MUFA (namely cetoleic FA—22:1(n-11) and gondonic FA—20:1(n-9) derived from zooplankton diet) and monounsaturated long-

chain fatty alcohols (namely docosenol 22:1(n-11) and eicosenol 20:1(n-9) derived from zooplankton diet). In our study, *L. macdonaldi* could be considered as an object for tests and assays of searching research on efficacy of wax esters on health due to their high content in muscles of these fish. Living at low ambient temperatures, high-latitude deep pelagic organisms specifically feature a prevalence of n-3 series of PUFA, which are more valuable for humans, over n-6 FAs [120]. In the present study, we indicated high content of essential and physiologically important for human health EPA and DHA. Notable that the content of docosapentaenoic FA, 22:5(n-3), known together with EPA and DHA as neuroprotective agent [121], was also significant in the studied fishes especially in *B. euryos* both "northern" and "tropical" latitudes. Moreover, some biological effects of PUFAs beneficial for humans arise from interactions with MUFAs—the combined effects of several FAs components and unique composition discussed. Recent studies have demonstrated positive health effects of a combination of EPA, DHA, long-chain MUFAs, and fatty alcohols in waxes [119]. In our study, *Sc. beanii* and *B. euryops* performered high content of cetoleic 22:1(n-11) FA that are known as n-3 PUFA catalyst [122]. Long-chain n-3 PUFAs are also known to have anti-atherosclerotic effect and to reduce inflammatory and allergic reactions; they are effectively used in the clinical practice of treating cardiovascular diseases and neurodegenerative disorders [28,123,124]. According to latest studies, products of the synthesis of a highly active compound (N-docosahexaenoyl ethanolamine) from DHA enhance neuron recovery after traumatic brain injuries [125]. It was found that *B. euryops* and *L. macdonaldi* have 18:5(n-3) FA known as precursor to eicosanoids, this FA undergoes peroxidation without the formation of secondary products—ketodiens [126]. Lipid and phospholipid classes rich in unsaturated fatty acids possess membrane repairing and hepatoprotective properties [127]. Lipid extracts are being considered as potential analogs of antimicrobial peptides since substances of lipid nature possess antimicrobial activity and the degree of the effect depends on the array and ratios of lipids and fatty acid components in the extract [128–130].

The strategy of lipid composition and usage of lipids among fish species collected in the Irminger sea (*S. beanii* and *L. macdonaldi*) and in the area of Tropic Seamount (*S. beanii* and *L. alatus*) was revealed. However, it is known that biotic and biotic environmental factors have a significant impact on the quality and quantity of the composition of lipids and their fatty acid components [13,24,55–66]. Thus, differences were revealed in the accumulation of FAs in the muscle of the "northern" and "southern" individuals, which may be due to external environment. In particular, a higher content of n-6 PUFAs in the "southern" fishes inhabiting waters with a higher ambient temperature led to such compensatory reaction as a control to the degree of unsaturation of lipids of biomembranes [21,120]. It is well known that aquatic organisms, mainly pelagic, from the tropic waters are characterized by the dominance or absolute prevalence of n-6 PUFAs. At the same time, a higher content of n-3 PUFAs was also found in individuals from the area of Tropic Seamount due to DHA, which may be associated with the mesopelagic lifestyle and inhabiting depth water horizons with stable cold temperature [131]. In our study, a significant prevalence of MUFAs in fishes from "cold" waters was found, however, it is associated with an increase in the concentration of FAs markers of calanoid copepods (20:1(n-9) and 22:1(n-11)). The content of MUFAs in fishes from the Tropic Seamount was lower. It should also be noted that *L. alatus* lacked the fatty alcohols 22:1(n-11)Alk characteristic of copepods of the genus Calanus, which may indicate dietary differences between the two species of *Lampanyctus* caught in different latitudes.

5. Conclusions

Indeed, lipids are maintained adaptive response of the organisms to the deep-water living. The study on the profile of lipids and fatty acids in the muscle of mesopelagic fish of the Irminger Sea performed significant differences in the accumulation of TL associated with differences in life cycles, the main peculiarity is the presence of daily vertical migrations, as well as compensatory reaction of the organism to the environmental factors in depth-vise gradient. The prevalence of TAGs was found in the muscles of non-migratory

(without DVM) *B. euryops* and *Sc. beanii*, whereas in species that perform DVM—*L. macdonaldi* and *S. beanii*, the contents of Chol esters and waxes were high. It was revealed general and unified deep-vise fluctuations in PL fractions in muscles of the studied fishes in the Irminger Sea and in the Tropic Seamount. Such PL reorganizations leads to maintain physicochemical state of the biomembrane under the influence of external environmental factors (temperature, depth) and ensures the maintenance of homeostasis of the internal microenvironment, which is especially characteristic of species capable to vertically migrations over long distances during a day. The dominance of MUFAs in muscle was detected, mainly due to trophic-derived FAs of the genus Calanus—20:1(n-9) and 22:1(n-11), as well as high content of the 18:1(n-9). It is known that one of the adaptive features to deep-water habitat is the accumulation of 18:1 FA. Notable, *L. macdonaldi* had a high content of long-chain alcohol—22:1(n-11)Alk. Among PUFAs, the dominance of the n-3 PUFAs was revealed due to the physiologically significant 20:5(n-3) and 22:6(n-3). A comparative analysis between *L. macdonaldi* and *S. beanii* from the Irminger Sea and *L. alatus* and *S. beanii* from the Tropic Seamount found similar biochemical strategies for the accumulation of lipid classes despite the latitudinal differences in the study areas.

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