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Comparative Analysis of the Fatty Acid Profiles of Antarctic Krill (*Euphausia superba* Dana, 1850) in the Atlantic Sector of the Southern Ocean: Certain Fatty Acids Reflect the Oceanographic and Trophic Conditions of the Habitat

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Abstract: The present study is the attempt to combine oceanologic measurements and biochemical analysis, which is as possible to implement on board as in a laboratory with chosen certain statistics to reveal trophic conditions and the environment state in which Antarctic krill live in season in real time on site. The fatty acid constituents of total lipids in juvenile and mature Antarctic krill sampled from the Bransfield Strait (BS), the Antarctic Sound (AS), and waters at the eastern tip of the Antarctic Peninsula (AP) collected during the 87th cruise of the R/V *Akademik Mstislav Keldysh* in January–February 2022 were analyzed. The fatty acid (FA) profile in juvenile and mature Antarctic krill was studied by gas chromatography with a mass selective detector to identify the qualitative composition and a flame ionization detector to quantify the studied FAs. Using NMDS analysis (quantitative panel), great difference was found between krill from the BS compared to krill collected in the AS and the AP. The differences are reliable owing to the following 16 FAs, most of them trophic biomarkers of microphytoplankton, and suggest regional differences, mainly in abundance and ability of forage objects. CTD measurements discuss the abiotic factors (potential temperature, salinity, and chlorophyll "a"). Compensatory modifications of the composition of FA components in Antarctic krill inhabiting different water areas are a way of maintaining the species' viability under certain and variable habitat conditions.

Keywords: Antarctic krill; fatty acids; trophic biomarkers; ontogeny; biochemical adaptations; Antarctic

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1. Introduction

Only six of the eleven euphausiid species inhabiting the Southern Ocean are endemic to the Atlantic Polar Front zone: Antarctic krill *Euphausia superba*, as well as *E. triacantha*, *E. frigida*, *E. vallentini*, *E. crystallophias*, and *Thysanoessa macrura* [1,2]. Antarctic krill is the most ecologically significant member of the crustacean order Euphausiacea and a pivotal structural component of the Antarctic ecosystem—the considerations that underlie the "krill-centric" Antarctic ecosystem concept [1,3]. Krill is an important food item for fishes, including commercial ones, for shorebirds, and for marine mammals [1]. Another ecological

function of krill is substantial reallocation of organic matter (carbon cycle) from the highly productive and constructive epipelagic domain to the bathypelagic domain [1–5]. Active discussions have lately revolved around the fundamental role of euphausiids and principal species—*E. superba*—in the preservation of a balanced cycle of matter and energy in the occurrence of climate change. As we know, ecosystem stability is tied to the constancy of its structure, the balance of matter and energy [6]. Therefore, Antarctic krill perform an essential role in adjusting the flow of nutrients among trophic levels [7–9].

Krill is characterized by a unique chemical composition and high nutritional value [10–13] and also forms large aggregations accessible to commercial fishing gear, which makes it one of the prime targets of fishing in the Southern Ocean [14,15], especially in the highly productive and commercially developed Atlantic sector of the Antarctic.

The maximum abundance of commercially important *E. superba* was found in the Atlantic sector of the Antarctic; krill inhabit these areas in dense aggregations in mesoscale gyres near submarine rises and islands [16,17].

The overall stability of the ecosystem is based on ecological factors, especially abiotic ones, together with features of marine aquatic communities, such as their species diversity. Antarctic marine organisms, including *E. superba*, are noted for several common ecological and biological traits, especially for their growth rate, size, and weight parameters, as well as their lipid and energy metabolism levels. These traits as well as characteristics of these animals, their physiology, and their biochemical metabolism, have developed through the specific conditions of their habitats.

It is worth noting that lipids and their oxidation products are reliable indicators for analysis and observations, both retrospectively and in the current assessment of the efficiency and characteristics of carbon (as well as nitrogen) cycling in both the pelagic and benthic zones [18–21]. Moreover, for high- and low-latitude ecosystems, which are "lipid-dependent" in the sense that it is lipids that enable temperature adaptation of ectothermic animals, studies like the present one are significant. Such studies allow us to expand our understanding of the fundamental processes of biota adaptation in terms of understanding the mechanisms of compensatory cellular reactions. The rate of lipid metabolism and their FA constituents determine the ecological niche of organisms in aquatic ecosystems. This is ultimately related to the seasonal and annual dynamics of ecosystem processes and the biodiversity of a particular region. Aquatic animals of the Arctic and Antarctic are characterized by adaptations that contribute to the "synchronization" of specific biochemical pathways of metabolism with the seasonal functioning of the aquatic ecosystem, which is especially pronounced for marine ones [22].

We studied the fatty acid profile of total lipids in juvenile and mature Antarctic krill caught from the Bransfield Strait, Antarctic Sound, and waters at the eastern tip of the Antarctic Peninsula. The samples were collected during the 87th cruise of the R/V *Akademik Mstislav Keldysh* in January–February 2022. In the present paper, we discuss the fatty acid profiles of juveniles and mature specimens of krill with regard to certain fatty acids and their combinations as proper markers of the hydrobiological and trophic conditions of the habitat. The study is an attempt to combine biochemical analysis. Results on the lipid and fatty acids' qualitative and quantitative similarities and differences are associated and pointed towards environmental conditions. The importance of such an approach is defined by its usefulness in getting results on board during the cruise to reveal and discuss the trophic conditions and environment in which Antarctic krill live in season in real time and almost on site; thus, there is a discussion of association by trophic interactions in the aquatic organisms' state. It is worth noting that the main multidisciplinary concept of the cruise was presented by our scientific group in [23]; the main aim of the cruise and research was the assessment of the current state of natural complexes of the Atlantic sector of the Southern Ocean and their multiperiod variability (ecosystems, bioproductivity, hydrophysics, and hydro-and geochemistry). There have already been several papers published based on the obtained results of composition and distribution of plankton communities in the Antarctic sector of the Southern Ocean [24]. In the present research, certain findings from this paper

are used to refer to the forage base (biotic factor) of Antarctic krill in the studied area, and the next biological papers associated with the study are about studying the distribution and demography of Antarctic krill and salpas in the same season and study area [25].

2. Materials and Methods

2.1. Sampling

Research areas included the Bransfield Strait (BS), Station 7299 (62°30.9′ S; 58°08.0′ W–62°30.8′ S; 58°08.0′ W); the Antarctic Sound (AS), Station 7331 (night catch, 3–5 AM) and Station 7332 (day catch, 1–2 PM) (63°28.6′ S; 56°31.2′ W–63°30.0′ S; 56°27.7′ W); and the eastern tip of the Antarctic Peninsula (AP), Station 7336 (64°28.8′ S; 56°04.7′ W–64°27.9′ S; 56°02.8′ W). Krill samples were obtained using pelagic double square micronekton nets (DSN) (505 µm mesh, 1.0 m^2 inlet area) equipped with a pterygoid deepener weighing 24 kg (Hydrobios, Altenholz, Germany) [24]. Oblique tows were performed at 0–300 m (BS), 0–490 m (AS), and 0–210 m (AP) at an average speed of 1.5 knots. Only at Station 7331, the samples were obtained using the Isaak–Kidd mid-water trawl modified by Samyshev–Aseev (IKMT-SA), at a depth of 0–440 m. The biological analysis of the sampled krill was described in [25]. The oceanographic measurements in the studied areas were performed recently [23,24]. The General Oceanics GO1018 water sampler system equipped with an Idronaut Ocean Seven 320 plus CTD probe and 18 sampling Niskin bottles from 5 to 10 L capacity was used for measurements of thermohaline properties of the environment. The casts were performed from the sea surface almost to the ocean floor (usually 5 m above the bottom); the distance between the sampler and the seafloor was controlled by the Valeport VA500 altimeter and the Benthos pinger. Processing of CTD data was performed using the REDAS5 software (version 5.78). The accuracy of the temperature and salinity sensors were 0.001 °C and 0.001 mS/cm, respectively. Chlorophyll "a" fluorescence intensity measurements were performed using a Seapoint Chlorophyll Fluorometer mounted on the CTD probe.

2.2. Fatty Acid Analysis

For biochemical analysis, the individual samples of the juveniles and mature specimens of krill were fixed at −80 °C in an Eppendorf CryoCube freezer (Eppendorf, Stevenage, UK) until delivery to the laboratory. In total, we analyzed 79 individual samples of juveniles (from 20 to 35 per location) and 84 samples of mature krill (from 24 to 35 per location).

The total lipids (TL) were extracted by the Folch method [26]. The fatty acid (FA) composition (% of total FAs) of total lipids in juvenile and mature Antarctic krill was studied by gas chromatography (GC) with a mass selective detector (MSD) used to identify the qualitative composition and a flame ionization detector (FID)—to quantify the studied FAs. The entire protocols are described in our previous papers [27,28]. Equipment of the Ecological Biochemistry Laboratory of the Institute of Biology KarRC RAS and Core Facility KarRC RAS was used in the present study.

2.3. Statistical Analysis

The obtained results were analyzed using the R programming language (v. 3.6.1.) in the RStudio integrated development environment with the following supplementary packages: readxl (v. 1.3.1), tidyverse (v. 1.3.0), and vegan (v. 2.5–7). Stage of development (juvenile or mature specimens) ordination in multidimensional space was performed by applying the non-metric multidimensional scaling (NMDS) algorithm to the studied parameters. The NMDS of the FAs composition was concerned only with physiologically valuable components accounting for more than 1% of total FAs [29]. The best metric of distances in the multidimensional attribute space was determined, and Spearman's method was applied for correlation analysis. The measure of divergence between the original and the modelled distance matrices was estimated by the stress index. For each biochemical parameter, the correlation with the NMDS ordination axes was calculated, and the statistical significance

of the coefficients was estimated based on the permutation test (at 999 permutations) [30]. On the ordination diagram obtained by the NMDS method, in order to assess the ecological optimum of individual developmental stages of *E. superba* using the empirical values of individual abiotic factors (temperature, salinity, oxygen, chlorophyll "a"), generalized additive models were fitted with drawing the isoline of a three-dimensional smoothing surface [31]. Significant differences were found using the multivariate Kruskal–Wallis test. A nonparametric Wilcoxon–Mann–Whitney rank sum test was used to identify pairwise differences [32]. Cluster analysis of development stage based on the FA composition was presented in the Euclidian space [30]. For correlation analysis, Spearman's method was applied [32].

3. Results

The biomass of the Antarctic krill among the surveyed areas differed (Figure 1).

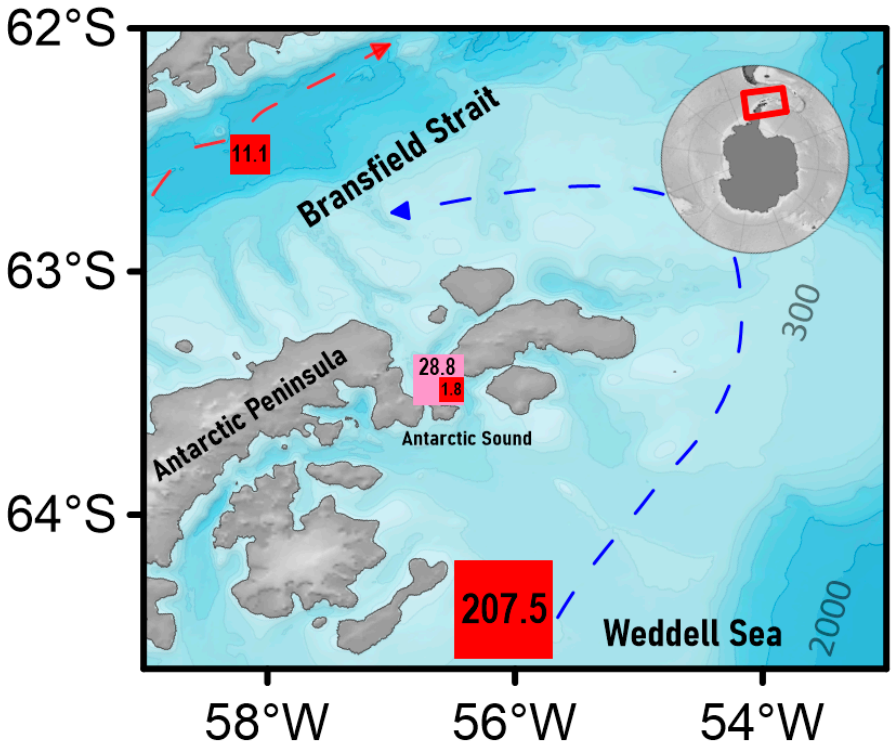

Figure 1. Map of *E. superba* collection and surveyed area with indication of biomass (the proportional size of squares as well as numerical biomass g/1000 m^3) and currents (by: [33,34]). Notes: The red line represents the Bransfield Current (BC), and the blue line represents the Antarctic Coastal Current (ACoC). Fishing gear: ■—IKMT-SA, ■—DSN.

In the BS, the Antarctic krill was collected at a single station located over the deepest point of the Central Basin. This area is strongly influenced by the Bransfield Current, which transports relatively warm waters from the west [35].

Based on CTD measurements, all three water masses are observed at the station in the strait (Figure 2).

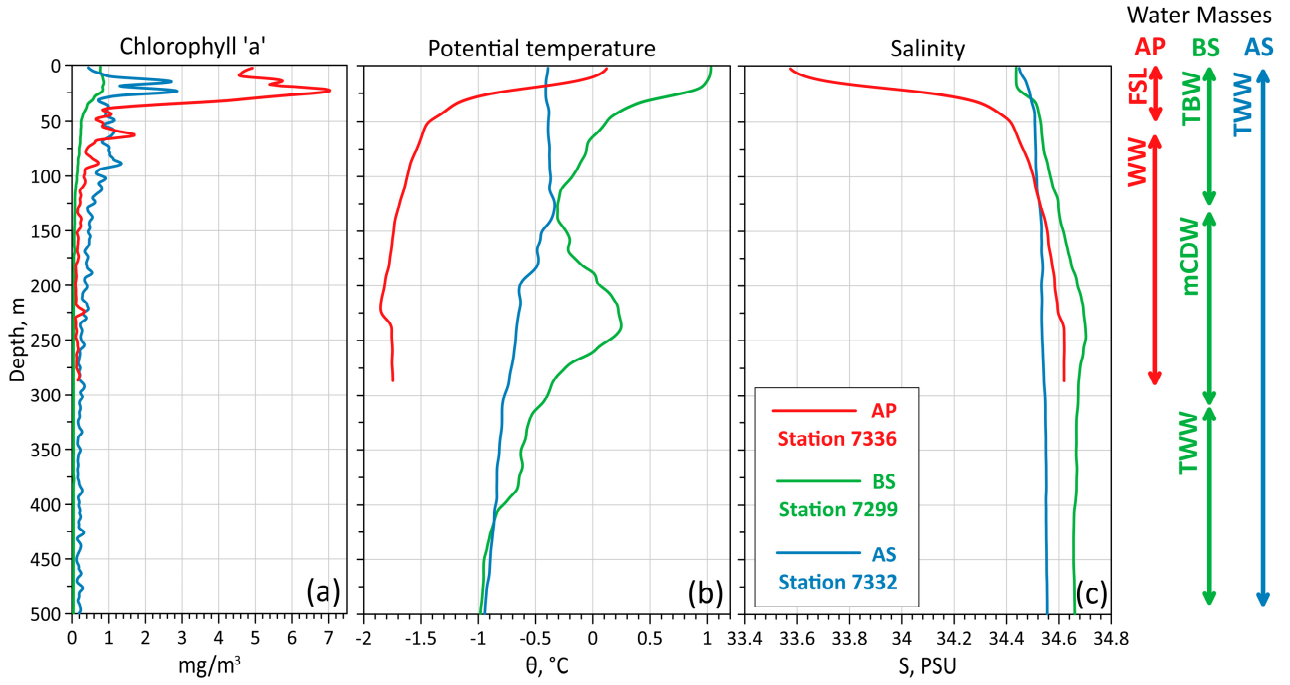

Figure 2. Chlorophyll "a" (**a**), potential temperature (**b**), and salinity (**c**) profiles measured in three studied regions: the Antarctic Peninsula (AP, red lines), Bransfield Strait (BS, green lines), and Antarctic Sound (AS, blue lines). The vertical limits of water masses are shown in the right panel. Abbreviations of water masses are as follows: WW—winter water of the Weddell Sea; FSL—freshened surface layer in the Weddell Sea; TBW—transitional zonal water with Bellingshausen Sea influence; TWW—transitional zonal water with Weddell Sea influence; mCDW—modified Circumpolar Deep Water.

The studied sites were distinguished by water masses: FLS from 0 to 40 m and then WW at the AP location, TBW from 0 to 125 m, mCDW until 300 m, and finally TWW until 500 m, and only TWW at the AS. The potential temperature profiles were completely different at the studied locations. The maximum of chlorophyll "a" was detected at the AP from 0 to 50 m in comparison with other sites. The AP site was different in salinity profile vs. the BS and AS, which were almost equal.

The TL content in juvenile krill did not differ significantly between the BS and the AS, being 9.4% and 13.9% dry weight, respectively, but was reliably higher (24.5%) in juveniles from water at the eastern tip of the Antarctic Peninsula (Table 1). The TL content in mature krill differed significantly among the three surveyed areas: it was the lowest in krill from the BS (7.5%), the highest in krill from the waters of the AP (21.3%), and intermediate in krill from the AS (14.4%).

Among FA classes, SFA and PUFA due to (n-3) PUFA were dominant, and the contents "compete" between each other, in juveniles as in mature krill. It was found that the content of (n-3) PUFA was higher in both juveniles and mature *E. superba* collected from BS. The major FAs in the FA profile (in decreasing order) are 16:0, 20:5(n-3)—diatom main biomarker, 18:1(n-9), 22:6(n-3)—flagellate biomarker, 20:0, 16:1(n-7)—diatom biomarker, 18:4(n-3)—flagellate biomarker, 18:0, and 18:1(n-7).

The 20:5(n-3)/22:6(n-33) ratio associated with dominance of diatom vs. flagellates, the ratio more than 2 pointed on diatom-rich diet and less than 1.5—dinoflagellates: in the present study, the highest 20:5(n-3)/22:6(n-3) ratio was found in both juveniles and mature krill collected from the AS and from the AP (the ratio close to 2). In addition, the 16:1(n-7)/18:4(n-3) ratio had the same trend as 20:5(n-3)/22:6(n-3), both higher amounts suggesting that krill relied on diatoms in the AS and AP sites. The omnivority vs. herbivority index 18:1(n-9)/18:1(n-7) was significantly different in juveniles: higher in juveniles from the AP

and lower in juveniles from the BS, while in mature krill, no significant differences were found (Table 1).

Table 1. The content of the total lipids (% dry weight) and certain fatty acids (% of the sum of FAs) in juvenile and mature specimens of *Euphausia superba* collected in the BS, AS, and AP.

Developmental Stage	Juvenile			Mature		
Area	**AP**	**AS**	**BS**	**AP**	**AS**	**BS**
TL	24.47 ± 1.17	13.85 ± 1.68 a	9.4 ± 0.99 a	21.3 ± 0.66 *	14.43 ± 0.77 a	7.51 ± 0.32 a,b
12:0	0.12 ± 0	0.09 ± 0.01 a	0.08 ± 0.01 a	0.12 ± 0	0.07 ± 0 a	0.04 ± 0.01 a,b
14:0	9.84 ± 0.23	6.91 ± 0.36 a	8.75 ± 0.35 a,b	9.47 ± 0.14	7.56 ± 0.24 a	4.14 ± 0.24 a,b,*
15:0	0.18 ± 0.01	0.18 ± 0.01	0.32 ± 0.01 a,b	0.18 ± 0.01 *	0.16 ± 0	0.26 ± 0.01 a,b
16:0	21.51 ± 0.21	21.34 ± 0.45	22.57 ± 0.18 a,b	21.65 ± 0.1	22.26 ± 0.2 a	20.3 ± 0.21 a,b,*
18:0	3.22 ± 0.09	3.35 ± 0.1	2.22 ± 0.15 a,b	3.32 ± 0.13	2.42 ± 0.16 a,*	2.74 ± 0.17 a,b
19:0	0.04 ± 0.01	0.04 ± 0.01	0.1 ± 0.02 a,b	0.04 ± 0	0.04 ± 0.01 a	0.15 ± 0.02 a,b
20:0	6.68 ± 0.22	7.83 ± 0.75	1.68 ± 0.26 a,b	6.86 ± 0.18	3.09 ± 0.6 a,*	2.27 ± 0.15 a,b
23:0	0.05 ± 0	0.15 ± 0.04 a	0.98 ± 0.19 a,b	0.05 ± 0	0.24 ± 0.04 a	1.59 ± 0.23 a,b
24:0	1.25 ± 0.04	1.46 ± 0.14	0.32 ± 0.04 a,b	1.29 ± 0.03	0.57 ± 0.11 a,*	0.45 ± 0.03 a,b
cis16:1(n-7)	5.95 ± 0.17	6.73 ± 0.44	5.21 ± 0.29 a	6.31 ± 0.1 *	6.43 ± 0.16	3.59 ± 0.32 a,b,*
cis17:1(n-7)	0.7 ± 0.03	1.06 ± 0.05 a	0.73 ± 0.02 b	0.7 ± 0.02	0.74 ± 0.05 a,*	0.27 ± 0.05 a,b,*
cis18:1(n-9)	13.35 ± 0.16	10.92 ± 0.72 a	10.2 ± 0.75 a	13.34 ± 0.14	12.51 ± 0.24 a	9.24 ± 0.39 a,b,*
cis18:1(n-7)	4.53 ± 0.04	4.23 ± 0.32	5.91 ± 0.13 a,b	4.73 ± 0.04 *	5.82 ± 0.14 a,*	7.69 ± 0.19 a,b,*
cis20:1(n-9)	0.98 ± 0.03	0.66 ± 0.06 a	0.61 ± 0.07 a	1 ± 0.02	0.89 ± 0.04 a	0.56 ± 0.04 a,b
cis18:2(n-6)	1.39 ± 0.05	0.81 ± 0.1 a	1.83 ± 0.05 a,b	1.24 ± 0.04 *	0.95 ± 0.03 a	1.62 ± 0.05 a,b
cis18:3(n-6)	0.08 ± 0	0.06 ± 0.01 a	0.16 ± 0.01 a,b	0.08 ± 0	0.08 ± 0	0.07 ± 0.01 *
cis20:2(n-6)	0.05 ± 0	0.05 ± 0.01	0.18 ± 0.05 a,b	0.05 ± 0	0.11 ± 0.01 a	0.28 ± 0.06 a,b
cis20:4(n-6)	0.02 ± 0	0.04 ± 0.01 a	0.09 ± 0.02 a,b	0.02 ± 0	0.04 ± 0 a	0.13 ± 0.01 a,b
cis18:3(n-3)	0.72 ± 0.02	0.41 ± 0.05 a	1.19 ± 0.06 a,b	0.66 ± 0.02	0.53 ± 0.02 a	1 ± 0.06 a,b
cis18:4(n-3)	4.64 ± 0.28	2.34 ± 0.4 a	5.23 ± 0.14 b	3.77 ± 0.13 *	2.6 ± 0.12 a	2 ± 0.15 a,b,*
cis20:5(n-3)	15.41 ± 0.31	22.61 ± 0.58 a	18.35 ± 0.57 a,b	15.97 ± 0.22	22.22 ± 0.34 a	22.54 ± 0.46 a,*
cis22:5(n-3)	0.29 ± 0.01	0.42 ± 0.04 a	0.44 ± 0.04 a	0.29 ± 0.01	0.36 ± 0.01 a	0.62 ± 0.02 a,b,*
cis22:6(n-3)	8.31 ± 0.2	7.66 ± 0.76	12.11 ± 0.81 a,b	8.17 ± 0.18	9.75 ± 0.33 a	17.79 ± 0.58 a,b,*
SFA	43.34 ± 0.23	41.8 ± 0.58 a	37.49 ± 0.64 a,b	43.4 ± 0.22	36.72 ± 0.72 a,*	32.4 ± 0.54 a,b,*
MUFA	25.74 ± 0.32	23.8 ± 1.04	22.88 ± 1.04 a	26.33 ± 0.23 *	26.6 ± 0.47	21.52 ± 0.81 a,b
(n-3) PUFA	29.38 ± 0.37	33.44 ± 1.44 a	37.37 ± 1.42 a	28.87 ± 0.31	35.5 ± 0.63 a	43.96 ± 0.94 a,b,*
(n-6) PUFA	1.54 ± 0.05	0.96 ± 0.12 a	2.27 ± 0.02 a,b	1.39 ± 0.04 *	1.18 ± 0.04 a	2.11 ± 0.08 a,b
PUFA	30.92 ± 0.4	34.4 ± 1.56	39.63 ± 1.43 a	30.26 ± 0.33	36.68 ± 0.66 a	46.07 ± 0.95 a,b,*
18:1(n-9)/18:1(n-7)	3.07	2.58 a	1.73 a,b	2.82	2.15	1.20
20:5(n-3)/22:6(n-3)	1.85	2.95 a	1.51 a,b	1.95	2.28 a	1.27 a,b
16:1(n-7)/18:4(n-3)	1.28	2.87 a	0.99 a,b	1.70	2.47 a	1.8 a,b

Note: a—differences are significant ($p \leq 0.05$) between those from the AP within the developmental stage (juvenile or mature); b—differences are significant ($p \leq 0.05$) between those from the AS within the developmental stage (juvenile or mature); *—differences are significant ($p \leq 0{,}05$) between juveniles and mature specimens. MUFA—monounsaturated fatty acids, PUFA—polyunsaturated fatty acids, (n−3), (n−4), and (n−6) PUFA—main families of PUFA.

The multidimensional scaling method is used to analyze and visualize data using the location of points in a space of lower dimensionality than determined by the criteria for biochemical analysis. When analyzing the fatty acid profile, most often, either significant FAs accounted for as major components in an organism are considered or FAs whose content is more then 1–3% of the total FA, as has been shown in our studies [36] as in other papers [29]. The remaining acids (minor ones) are removed from the analysis. In the present study, we decided to take a different route to preserve the importance of the contribution of minor FAs to their input of the distinctive features of the studied groups of krill. Since the obtained data on the FA profile are essentially standardized (varying from 0 to 100% of the sum of the FAs), their further conversion can lead to data loss and error accumulation. Minor components in NMDS analysis do not make a significant contribution to ordination, whereas in this study, we describe the entire FA profile of krill and the differences between the studied groups. Therefore, we decided to divide qualitative and quantitative analysis into two separate algorithms. In the case of the "qualitative analysis" (Figure 3), the qualitative composition of each individual sample was used (FA content of each sample—individual krill) as obtained by gas chromatography, but was converted into a binary format, where 1 was taken for the presence of FA in the individual sample, and 0 for the absence of it. In the case of the "quantitative analysis" (Figure 4), the data obtained on the quantitative content of individual fatty acids by gas chromatography in their native

(and at the same time standardized) form were used. Thus, this allowed us to level out the quantitative factor when analyzing NMDS FAs and show the differences between groups in a qualitative sense, taking into account minor components, the concentration of which, although low, was determined to be significant.

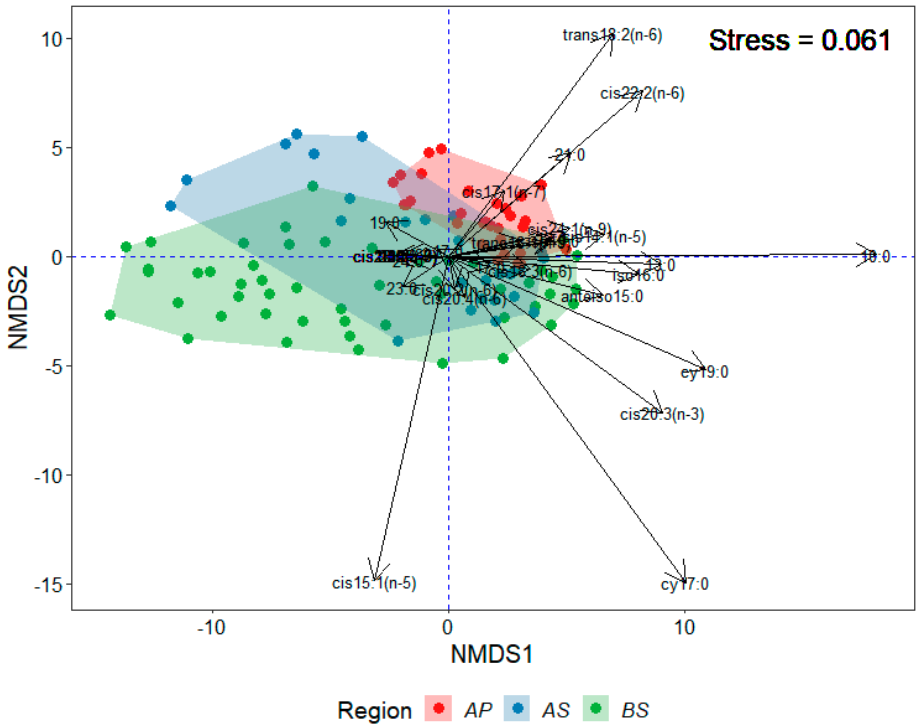

Figure 3. NMDS ordination of juvenile and mature Antarctic krill from the three surveyed areas (AP, AS, and BS) and of the axes of the fatty acids identified in them (by qualitative composition).

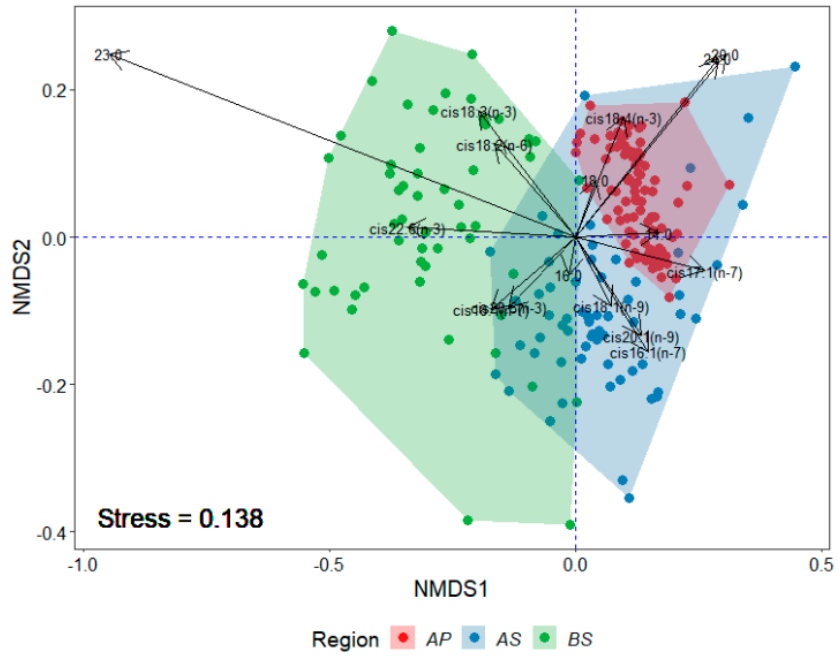

Figure 4. NMDS ordination of juvenile and mature Antarctic krill from the three surveyed areas (AP, AS, BS) and of the axes of the fatty acids identified in them (by quantitative composition).

Ordination of juvenile and mature Antarctic krill from the three surveyed areas (AP, AS, BS) and of the axes of the fatty acids identified in them (by qualitative composition)

done by non-metric multidimensional scaling (NMDS) resulted in a fan-shaped orientation of the samples (Figure 3). Such orientation demonstrated a commonality of the FA qualitative composition with differences due to 23 individual FAs, chiefly minority ones, some of which are trophic markers of bacteria and microphytoplankton: 12:0, 13:0, 15:0, iso15:0, cis15:1(n-5), iso16:0, 17:0, iso17:0, cy17:0, 19:0, cy19:0, 21:0, 23:0, 24:0, cis14:1(n-5), cis17:1(n-7), trans18:1(n-9), cis24:1(n-9), cis18:3(n-6), cis20:2(n-6), cis20:4(n-6), cis22:2(n-6), cis20:3(n-3).

Ordination of juvenile and mature Antarctic krill from the three surveyed areas (AP, AS, and BS) and of the axes of the fatty acids identified in them (by quantitative composition) done by non-metric multidimensional scaling (NMDS) demonstrates a great difference between krill from the BS and krill collected in the AS and the AP (Figure 4). The differences of BS krill from those in the other two surveyed areas are reliable owing to the following 16 FAs: 14:0, 16:0, 18:0, 20:0, 23:0, 24:0, cis16:1(n-7), cis17:1(n-7), cis18:1(n-9), cis18:1(n-7), cis20:1(n-9), cis18:2(n-6), cis18:3(n-3), cis18:4(n-3), cis20:5(n-3), and cis22:6(n-3). Thus, it is possible to suggest the regional differences are mainly in abundance and ability of forage objects—phytoplankton for Antarctic krill the same for juveniles as for mature.

Thus, polyunsaturated fatty acids (PUFAs) dominated, due to (n-3) PUFAs, in juvenile krill, their content being reliably higher in individuals from the BS (39.6% and 37.3%); the PUFA content for specimens from the AP were 30.9% and 29.4%, and those for animals from the AS were 34.4% and 33.4%, respectively. The content of saturated fatty acids (SFAs) in immature krill varied among the three surveyed areas (BS—37.5%, AP—43.3%, and AS—41.8%), while the content of monounsaturated fatty acids (MUFAs) showed no significant differences between individuals from the AP and the AS (25.7% and 23.8%, respectively) but was reliably lower in juveniles from the BS (22.9%). The content of PUFAs, SFAs, and MUFAs in mature krill varied reliably among the three surveyed areas. The values for the BS, AP, and AS were, respectively, 46.1%, 30.3%, and 36.7% for PUFAs (predominantly (n-3) PUFAs); 32.4%, 43.4%, and 36.7% for SFAs; and 21.5%, 26.3%, and 26.6% for MUFAs.

4. Discussion

For aquatic organisms living in polar regions, their substantial accumulation of lipids, as well as how they are used, is essential for maintaining the vital functions and for the survival of aquatic organisms, e.g., krill, as the environmental conditions change over the year. Such adaptive behavior is of particular significance for aquatic organisms with a long life span, such as the Antarctic krill, which can live for up to 6 years [3].

The "commonality" of the quantitative FA composition of Antarctic krill from the AS and the AP as well as their "opposition" to krill from the BS appears to be due not so much to the genetically determined endogenous characteristics of their lipogenesis but to the complex interplay (compensatory responses) of their metabolism with the environment, namely the different oceanographic conditions, which, in turn, determine the composition and structure of plankton communities (foraging reserves). Thus, the BS was largely under the impact of three water masses: cold and saline transitional zonal water with Weddell Sea influence (TWW); relatively warm and fresh transitional zonal water with Bellingshausen Sea influence (TBW); and warm and saline-modified Circumpolar Deep Water (mCDW) [35,37]; these water masses propagate along the Antarctic Peninsula and the South Shetland Islands, forming cyclonic circulation in the central basin of the strait [38]. According to CTD measurements, all three water masses are observed at the station in the strait. The range of temperatures in the strait was −1.0 °C to 1.0 °C, which is within the optimal range for the growth and development of both juvenile and mature Antarctic krill [39]. Considering its abiotic and trophic conditions for krill larvae and juveniles, the BS area is regarded as a key wintering, spawning, and nursery area [40]. The deep-water part of the AS is powerfully influenced by Weddell Sea [24]. Waters in this strait are well mixed over the entire water column, probably due to the strong tidal currents and internal waves [41,42]. The temperature in this area was around −0.6 °C, reaching −0.9 °C at 500 m of depth, with notable salinity reduction in the surface water layer

due to ice melting. Waters in the AP were situated at the compact ice edge and featured above-zero temperatures at sea surface (0.1 °C), but the potential temperature at 200 m depth was −1.8 °C, and Chl "a" concentrations there were high (>2.4 mg m^{-3}). This cold water mass is called winter water (WW), and it is observed over the shelf areas near the Antarctic Peninsula [43]. Based on CTD measurements, it is located deeper than 50 m; in the upper ocean layer, a meaningful decrease in salinity (from 34.4 psu to 33.6 psu) was observed (Figure 2). This freshened surface layer is formed due to melting of sea ice. It was recently shown that this melted water leads to an increase in vertical stability, prevents vertical mixing, and provides conditions for the development of biological communities in the studied region of the Weddell Sea [44]. The melting of icebergs can also affect the thermohaline structure of the upper ocean layer and contribute to the observed increase in biological productivity [45].

The adaptations of marine organisms to temperature are most closely tied to the seasonal variation of metabolism; for poikilotherms, the temperature is the primary determinant of the rhythmicity of biological processes [46]. Being a stenotherm, Antarctic krill live in a narrow temperature range, from −1.8 °C to 5 °C [47]. Optimal temperatures, however, change through the ontogeny—krill aged 0+ stay near the surface, while older animals (aged 1+) are capable of vertical migrations, with water temperature and salinity changing with depth [7]. The compensation of temperature effects involves maintaining membrane fluidity, which is required for cell functioning, which influences the permeability and transport of ions/components, and activity of membrane enzymes. Many aspects of the role of some macromolecules, namely lipids and their FAs, in the compensation of temperature effects or temperature adaptations in Antarctic euphausiids, remain understudied. The greatest share of the FA profile of total lipids in Antarctic krill belongs to long-chain highly unsaturated fatty acids, which is evidence of their physiologically essential role in the aquatic organism [12,48,49].

The set of abiotic factors has a great effect on the trophic interactions facilitating the succession of development cycles in aquatic organisms. The distinction of the lipid composition and its FA constituents of aquatic organisms affects the metabolism of not only one organism but also other animals interconnected by trophic relations. Phytoplankton are the primary producers and the basis of food chains in aquatic ecosystems. The transfer and modification of matter and energy is carried out by the absorption of phytoplankton by herbivorous organisms, e.g., zooplankton, and by the transfer to higher trophic levels, which are represented by more highly organized animals e.g., fish and mammals. Not so much is known of the role of FAs in physiological processes in zooplankton, but the importance of the share of PUFAs in food items has been proven [50]. It has been shown that phytoplankton PUFAs can be metabolically modified by zooplankton and euphausiids into SFAs, MUFAs, and fatty alcohols accumulated in their bodies in the form of waxes, a long-term energy depot [51]. This modification satisfies the physiological needs of copepods to accumulate high-energy lipids and maintain the proper level of metabolism during the long winter period and the state of diapause [52,53].

The bulk of FA amounts is synthesized by phytoplankton algae and some heterotrophic bacteria. Macrozooplankton utilize unaltered PUFAs to perform the structural and storage functions in the organism. The FAs considered essential for zooplankton are 20:5(n-3) and 22:6(n-3). They are derived from the consumed phytoplankton, so a reduction in the transport of energy (in the form of these FAs) from primary producers to consumers may be a consequence of low FA content in phytoplankton. Tissues of juvenile and mature krill in our study contained high FA amounts of 16:1(n-7) and 20:5(n-3), which are diatom markers and point to the Antarctic krill's preferred food items. It is known that certain ratios of FAs allow for the discussion of trophic preferences and food items' ability (abundance) or their diversity in certain locations better than considering individual FAs and their content [48,54]. The 20:5(n-3)/22:6(n-33) ratio associated with the herbivore diet and domination of diatoms vs. flagellates is well used. The high ratios (more than two) indicate a prevalence of diatoms; in the present study, the diatom-rich diet is shown in

our study. This ratio in juveniles varied from 1.5 (BS) to 3 (AS) and in mature krill from 1.3 (BS) to 2.3 (AS). Another index of 18:1(n-7)/16:1(n-9) also supports this finding. The trophic markers of dinophytes have also been identified—18:4(n-3), 22:6(n-3)—but their signatures in krill organisms were less pronounced than the characteristics of diatoms. Based on the results provided by NMDS analysis, the quantitative one, it is important to note regional differences in the abundance (reflects on the content of trophic FAs in krill) and ability krill to consume phytoplankton. The most favorable for forage objects (and preferable ones—phytoplankton) was the AP, to which the AS was close, and the BS was distinguished by others and "stays" separately. According to the qualitative NMDS analysis, the "biodiversity" of food items was similar, which arises due to minor food sources like bacteria and zooplankton (due to 20:1(n-9)). Specifically, we did not find any trace of 22:1(n-11), which may indicate the majority of certain species of zooplankton since they are known to be distinguished by their ability to synthesize de novo these FAs, and thus the ratio of 20:1 to 22:1 FAs is considered species-specific [28,55–57].

5. Conclusions

This paper discusses the results of statistical processing (NMDS) of the lipids and fatty acids in juvenile and mature krill inhabiting three locations—the Bransfield Strait, the Antarctic Sound, and the waters at the eastern tip of the Antarctic Peninsula—in the austral summer of 2022 to reveal similarities and specific characteristics of the studied ecologically important species. The focus of the applied NMDS analysis was to preserve the importance of the contribution of minor FAs to the input of the distinctive patterns of the studied groups of krill. A commonality of the FA qualitative composition was found due to 23 individual FAs, chiefly minor ones, some of which are trophic markers of bacteria and microphytoplankton: 12:0, 13:0, 15:0, iso15:0, cis15:1(n-5), iso16:0, 17:0, iso17:0, cy17:0, 19:0, cy19:0, 21:0, 23:0, 24:0, cis14:1(n-5), cis17:1(n-7), trans18:1(n-9), cis24:1(n-9), cis18:3(n-6), cis20:2(n-6), cis20:4(n-6), cis22:2(n-6), and cis20:3(n-3). The quantitative composition demonstrates a great difference between krill from the BS and krill collected in the AS and the AP. These findings are supported by the oceanographic—potential temperature, salinity, and chlorophyll "a"—parameters measured and discussed in the paper. The differences between BS krill and those in the other two surveyed areas are reliable owing to the following 16 FAs: 14:0, 16:0, 18:0, 20:0, 23:0, 24:0, cis16:1(n-7), cis17:1(n-7), cis18:1(n-9), cis18:1(n-7), cis20:1(n-9), cis18:2(n-6), cis18:3(n-3), cis18:4(n-3), cis20:5(n-3), and cis22:6(n-3). It is possible to suggest that the regional differences in mainly abundance and ability of forage objects—phytoplankton, low content of FA in macrozooplankton—could be due to a less phytoplankton-dependent diet, for Antarctic krill as juvenile as mature. The "commonality" of the quantitative FA composition of Antarctic krill from the AS and the AP as well as their "opposition" to krill from the BS appear to be due to the complex interplay (compensatory responses) of their metabolism with the environment, namely the different oceanographic conditions, which, in turn, determine the composition and structure of plankton communities (foraging reserves). Thus, the BS was largely under the impact of three water masses: cold and saline transitional zonal water with Weddell Sea influence; relatively warm and fresh transitional zonal water with Bellingshausen Sea influence; and warm and saline-modified Circumpolar Deep Water (mCDW). The differences in environment reflect on the forage base of the studied locations—the biodiversity, abundance, and availability of the food items for small and large krill swarms and juveniles. The major FAs in the FA profile (in decreasing order) are 16:0, 20:5(n-3)—diatom main biomarker, 18:1(n-9), 22:6(n-3)—flagellate biomarker, 20:0, 16:1(n-7)—diatom biomarker, 18:4(n-3)—flagellate biomarker, 18:0, and 18:1(n-7). The 20:5(n-3)/22:6(n-33) ratio is associated with dominance of diatom vs. flagellates, the ratio of more than 2 pointed to a diatom-rich diet and less than 1.5 to dinoflagellates: in the present study, the highest 20:5(n-3)/22:6(n-3) ratio was found in both juveniles and mature krill collected from the AS and from the AP. In addition, the 16:1(n-7)/18:4(n-3) ratio had the same trend as 20:5(n-3)/22:6(n-3); both higher amounts suggest that krill relied on diatoms in the AS and AP sites. The omnivority vs. herbivority

index 18:1(n-9)/18:1(n-7) was significantly different in juveniles—higher in juveniles from the AP and lower from the BS—while in mature krill, no significant differences were found.

Compensatory modifications of the FA components in Antarctic krill inhabiting different water areas are a way of maintaining the species viability under certain and variable habitat conditions. Some of its physiological and biochemical features (high content of PUFAs and certain FAs as well as their assemblage and configuration) are the basis for the species' ecological role in the food chains of the Antarctic ecosystem and for its commercial significance (due to the high amount of physiologically important FAs—20:5(n-3), mainly, and 22:6(n-3)—and prominent content of the various MUFAs).

The applicability of the statistical processing, biochemical data, and oceanographic measurements were presented by us in our recent paper as well [58]. Both studies' results are useful for monitoring the state of Antarctic ecosystems and their economically and ecologically important species.

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References

1. Knox, G.A. *The biology of the Southern Ocean*; Cambridge University Press: New York, NY, USA, 1994; 444p.
2. Mayzaud, P.; Boutoute, M.; Alonzo, F. Lipid composition of the euphausiids *Euphausia vallentini* and *Thysanoessa macrura* during summer in the Southern Indian Ocean. *Antarct. Sci.* **2003**, *15*, 463–475. [CrossRef]
3. Johnston, N.M.; Murphy, E.J.; Atkinson, A.; Andrew, J.; Constable, A.J.; Cotté, C.; Cox, M.; Daly, K.L.; Driscoll, R.; Flores, H. at al. Status, Change and Futures of Zooplankton in the Southern Ocean. *Front. Ecol. Evol.* **2022**, *9*, 624692. [CrossRef]
4. Wiedenmann, J.; Cresswell, K.; Mangel, M. Tenperature-dependent growth of Antarctic krill: Predictions for a changing climate from a cohort model. *Mar. Ecol. Prog. Ser.* **2008**, *358*, 191–202. [CrossRef]
5. McBride, M.M.; Schram Stokke, O.; Renner, A.H.H.; Krafft, B.A.; Bergstad, O.A.; Biuw, M.; Lowther, A.D.; Stiansen, J.E. Antarctic krill *Euphausia superba*: Spatial distribution, abundance, and management of fisheries in a changing climate. *Mar. Ecol. Prog. Ser.* **2021**, *668*, 185–214. [CrossRef]
6. Yu, G.; Piao, S.; Zhang, Y.; Liu, L.; Peng, J.; Niu, S. Moving toward a new era of ecosystem science. *Geogr. Sustain.* **2021**, *2*, 151–162. [CrossRef]
7. Whitehouse, M.J.; Meredith, M.P.; Rothery, P.; Atkinson, A.; Ward, P.; Korb, R.E. Rapid warming of the ocean around South Georgia, Southern Ocean, during the 20th century: Forcing, characteristics and implications for lower trophic levels. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **2008**, *55*, 1218–1228. [CrossRef]
8. Schmidt, K.; Atkinson, A. Feeding and food processing in Antarctic krill (*Euphausia superba* Dana). In *Biology ad Ecology of Antarctic Krill*; Springer International Publishing: Cham, Switzerland, 2016; pp. 175–224.

9. Hill, S.L.; Phillips, T.; Atkinson, A. Potential climate change effects on the habitat of Antarctic krill in the Weddel quadrant of the Sourthern Ocean. *PLoS ONE* **2013**, *8*, e72246. [CrossRef]
10. Ericson, J.A.; Hellessey, N.; Nichols, P.D.; Nicol, S.; Kawaguchi, S.; Hoem, N.; Virtue, P. New insights into the seasonal diet of Antarctic krill using triacylglycerol and phospholipid fatty acids, and sterol composition. *Polar Biol.* **2019**, *42*, 1985–1996. [CrossRef]
11. Yan, Y.; Lin, Y.; Zhang, L.; Gao, G.; Chen, S.; Chi, C.; Hu, S.; Sang, Y.; Chu, X.; Zhou, Q.; et al. Dietary supplementation with fermented antarctic krill shell improved the growth performance, digestive and antioxidant capability of *Macrobrachium nipponense*. *Aquac. Rep.* **2023**, *30*, 101587. [CrossRef]
12. Hellessey, N.; Johnson, R.; Ericson, J.A.; Nichols, P.D.; Kawaguchi, S.; Nicol, S.; Hoem, N.; Virtue, P. Antarctic Krill Lipid and Fatty acid Content Variability is Associated to Satellite Derived Chlorophyll a and Sea Surface Temperatures. *Sci. Rep.* **2020**, *10*, 6060. [CrossRef]
13. Gigliotti, J.C.; Davenport, M.P.; Beamer, S.K.; Tou, J.C.; Jaczynski, J. Extraction and characterization of lipids from Antarctic krill (*Euphausia superba*). *Food Chem.* **2011**, *125*, 1028–1036. [CrossRef]
14. Sologub, D.O. Modern Features of Distribution, Biology and Horizontal Migrations of Antarctic Krill (*Euphausia superba*) in the Atlantic Sector of Antarctica. Ph.D. Thesis, VNIRO Publ. House, Moscow, Russia, 2016; pp. 1–247.
15. Nicol, S.; Foster, J. The Fishery for Antarctic Krill: Its Current Status and Management Regime. In *Biology and Ecology of Antarctic Krill*; Springer: Cham, Switzerland, 2016; pp. 387–421.
16. Atkinson, A.; Siegel, V.; Pakhomov, E.A.; Rothery, P.; Loeb, V.; Ross, R.M.; Quetin, L.B.; Schmidt, K.; Fretwell, P.; Murphy, E.J.; et al. Oceanic Circumpolar Habitats of Antarctic Krill. *Mar. Ecol. Prog. Ser.* **2008**, *362*, 1–23. [CrossRef]
17. Siegel, V.; Watkins, J.L. Distribution, Biomass and Demography of Antarctic Krill, Euphausia superba. In *Biology and Ecology of Antarctic Krill*; Springer: Cham, Switzerland, 2016; pp. 21–100.
18. Marchand, D.; Marty, J.-C.; Miquel, J.-C.; Rontani, J.-F. Lipids and their oxidation products as biomarkers for carbon cycling in the northwestern Mediterranean Sea: Results from a sediment trap study. *Mar. Chem.* **2005**, *95*, 129–147. [CrossRef]
19. Rush, D.; Sinninghe Damsté, J.S. Lipids as paleomarkers to constrain the marine nitrogen cycle. *Environ. Microbiol.* **2017**, *19*, 2119–2132. [CrossRef] [PubMed]
20. Shilla, D.A. Sources and major biogeochemical pathways of organic matter in the mangrove system of Rufiji estuary. *Chem. Ecol.* **2019**, *35*, 524–536. [CrossRef]
21. Chen, X.; Dong, L.; Zhao, W.; Jian, H.; Wang, J.; Wang, F. The effects of metabolism and temperature on carbon isotope composition of lipids in marine bacterium *Shewanella piezotolerans* WP3. *Chem. Geol.* **2022**, *606*, 120963. [CrossRef]
22. Murzina, S.A. Role of Lipids and Their Fatty Acid Components in Ecological and Biochemical Adaptations of Fish of the Northern Seas. Ph.D. Thesis, IPEE RAS, Moscow, Russia, 2019; 376p.
23. Morozov, E.G.; Flint, M.V.; Orlov, A.M.; Frey, D.I.; Molodtsova, T.N.; Krechik, V.A.; Latushkin, A.A.; Salyuk, P.A.; Murzina, S.A.; Minin, K.V.; et al. Oceanographic and Ecosystem Studies in the Atlantic Sector of Antarctica (Cruise 87 of the Research Vessel Akademik Mstislav Keldysh). *Oceanology* **2022**, *62*, 721–723. [CrossRef]
24. Kasyan, V.V.; Bitiutskii, D.G.; Mishin, A.V.; Zuev, O.A.; Murzina, S.A.; Sapozhnikov, P.V.; Kalinina, O.Y.; Syomin, V.L.; Kolbasova, G.D.; Voronin, V.P.; et al. Composition and Distribution of Plankton Communities in the Atlantic Sector of the Southern Ocean. *Diversity* **2022**, *14*, 923. [CrossRef]
25. Bitiutskii, D.G.; Samyshev, E.Z.; Minkina, N.I.; Melnikov, V.V.; Chudinovskih, E.S.; Usachev, S.I.; Salyuk, P.A.; Serebrennikov, A.N.; Zuev, O.A.; Orlov, A.M. Distribution and demography of Antarctic krill and salps in the Atlantic sector of the Southern Ocean during austral summer 2021–2022. *Water* **2022**, *14*, 3812. [CrossRef]
26. Folch, J.; Lees, M.; Sloane Stanley, G.H. A simple method for the isolation and purification of total lipids from animal tissues. *J. Biol. Chem.* **1957**, *226*, 497–509. [CrossRef]
27. Pekkoeva, S.N.; Voronin, V.P.; Mishin, A.V.; Orlov, A.M.; Murzina, S.A. Living in the Extreme: Fatty Acid Profiles and Their Specificity in Certain Tissues of Dominant Antarctic Silverfish, *Pleuragramma antarcticum*, from the Antarctic Sound (Southern Ocean) Collected during the Austral Summer. *Diversity* **2022**, *14*, 817. [CrossRef]
28. Murzina, S.A.; Pekkoeva, S.N.; Kondakova, E.A.; Nefedova, Z.A.; Filippova, K.A.; Nemova, N.N.; Orlov, A.M.; Berge, J.; Falk-Petersen, S. Tiny but fatty: Lipids and fatty acids in the daubed shanny (*Leptoclinus maculatus*), a small fish in Svalbard waters. *Biomolecules* **2020**, *10*, 368. [CrossRef]
29. Petursdottir, H.; Gislason, A.; Falk-Petersen, S. Lipid classes and fatty acid composition of muscle, liver and skull oil in deep-sea redfish *Sebastes mentella* over the Reykjanes Ridge. *J. Fish Biol.* **2008**, *73*, 2485–2496. [CrossRef]
30. Shitikov, V.K.; Mastitsky, S.E. Classification, Regression, Data Mining Algorithms Using R. 2017. Available online: https://github.com/ranalytics/data-mining (accessed on 1 June 2023).
31. Wood, S.N. *Generalized Additive Models: An Introduction with R*; Hall/CRC and Chapman: Boca Raton, FL, USA, 2006; 410p.
32. Kabakoff, R. *R in Action: Data Analysis and Graphics with R*; Volkova, P.A., Translator; DMK Press: Moscow, Russia, 2014; p. 588.
33. Heywood, K.J.; Naveira Garabato, A.C.; Stevens, D.P.; Muench, R.D. On the fate of the Antarctic Slope Front and the origin of the Weddell Front. *J. Geophys. Res.* **2004**, *109*, C06021. [CrossRef]
34. Thompson, A.F.; Stewart, A.L.; Spence, P.; Heywood, K.J. The Antarctic Slope Current in a Changing Climate. *Rev. Geophys.* **2018**, *56*, 741–770. [CrossRef]

35. Frey, D.I.; Krechik, V.A.; Morozov, E.G.; Drozd, I.D.; Gordey, A.S.; Latushkin, A.A.; Mekhova, O.S.; Mukhametianov, R.Z.; Murzina, S.A.; Ostroumova, S.A.; et al. Water Exchange between Deep Basins of the Bransfield Strait. *Water* **2022**, *14*, 3193. [CrossRef]
36. Voronin, V.P.; Nemova, N.N.; Ruokolainen, T.R.; Artemenkov, D.V.; Rolskii, A.Y.; Orlov, A.M.; Murzina, S.A. Into the Deep: New Data on the Lipid and Fatty Acid Profile of Redfish *Sebastes mentella* Inhabiting Different Depths in the Irminger Sea. *Biomolecules* **2021**, *11*, 704. [CrossRef] [PubMed]
37. Tokarczyk, R. Classification of water masses in the Bransfield Strait and Southern part of the Drake Passage using a method of statistical multidimensional analysis. *Pol. Polar Res.* **1987**, *8*, 333–336.
38. Frey, D.I.; Krechik, V.A.; Gordey, A.S.; Gladyshev, S.V.; Churin, D.A.; Drozd, I.D.; Osadchiev, A.A.; Kashin, S.V.; Morozov, E.G.; Smirnova, D.A. Austral summer circulation in the Bransfield Strait based on SADCP measurements and satellite altimetry. *Front. Mar. Sci.* **2023**, *10*, 1111541. [CrossRef]
39. Tarling, G.A.; Shreeve, R.S.; Hirst, A.G.; Atkinson, A.; Pond, D.W.; Murphy, E.J. Natural growth rates in Antarctic krill (*Euphausia superba*): I. Improving methodology and predicting intermolt period. *Limnol. Oceanogr.* **2006**, *51*, 959–972. [CrossRef]
40. Reiss, C.; Cossio, A.; Santora, J.A.; Dietrich, K.S.; Murray, A.; Greg Mitchell, B.; Walsh, J.; Weiss, E.L.; Gimpel, C.; Jones, C.D.; et al. Overwinter habitat selection by Antarctic krill under varying sea-ice conditions: Implications for top predators and fishery management. *Mar. Ecol. Prog. Ser.* **2017**, *568*, 1–16. [CrossRef]
41. Krek, A.V.; Krek, E.V.; Krechik, V.A. The Circulation and Mixing Zone in the Antarctic Sound in February 2020. In *Antarctic Peninsula Region of the Southern Ocean*; Morozov, E.G., Flint, M.V., Spiridonov, V.A., Eds.; Springer: Cham, Switzerland, 2021; Volume 6, pp. 83–100. [CrossRef]
42. Khimchenko, E.; Frey, D.; Morozov, E.G. Tidal internal waves in the Bransfield Strait, Antarctica. *Russ. J. Earth Sci.* **2020**, *20*, ES2006. [CrossRef]
43. Thompson, A.F.; Heywood, K.J. Frontal structure and transport in the northwestern Weddell Sea. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **2008**, *55*, 1229–1251. [CrossRef]
44. Izhitskiy, A.; Romanova, N.; Vorobieva, O.; Frey, D. Impact of Ice Melting on Oceanographic and Hydrobiological Characteristics of Surface Waters in the Powell Basin, Weddell Sea, in January–February 2020. *Oceanology* **2022**, *62*, 439–446. [CrossRef]
45. Morozov, E.G.; Krechik, V.; Frey, D.; Zamshin, V. Currents in the Western Part of the Weddell Sea and Drift of large Iceberg A68A. *Oceanology* **2021**, *61*, 589–601. [CrossRef]
46. Ozernyuk, N.D. Ontogenetic temperature adaptations of enzymes of poikilothermic animals. *Uspechi Sovrem. Biol.* **2004**, *124*, 534–541.
47. Ross, R.M.; Quetin, L.B.; Baker, K.S.; Vernet, M.; Smith, R.S. Growth limitation in young Euphausia superba under field conditions. *Limnol. Oceanogr.* **2000**, *45*, 31–43. [CrossRef]
48. Stübing, D.; Hagen, W.; Schmidt, K. On the use of lipid biomarkers in marine food web analyses: An experimental case study on the Antarctic krill, *Euphausia superba*. *Limnol. Oceanogr.* **2003**, *48*, 1685–1700. [CrossRef]
49. De Felice, A.; Manini, E.; Biagiotti, I.; Leonori, I. Bioenergetics of *Euphausia superba* and *Euphausia crystallorophias* in the Ross Sea. *Diversity* **2023**, *15*, 480. [CrossRef]
50. Smyntek, P.M.; Teece, M.A.; Schultz, K.L.; Storch, A.J. Taxonomic differences in the essential fatty acid composition groups of freshwater zooplankton relate to reproductive demands and generation time. *Freshw. Biol.* **2008**, *53*, 1768–1782. [CrossRef]
51. Sargent, J.R.; Henderson, J.R.; Tocher, D.R. The Lipids. In *Fish Nutrition*; Halver, J.E., Ed.; Academic Press: New York, NY, USA, 1989; pp. 154–218.
52. Lee, R.; Hagen, W.; Kattner, G. Lipid storage in marine zooplankton. *Mar. Ecol. Prog. Ser.* **2006**, *307*, 273–306. [CrossRef]
53. Kattner, G.; Hagen, W. Lipids in marine copepods: Latitudinal characteristics and perspective to global warming. In *Lipids in Aquatic Ecosystems*; Arts, M.T., Brett, M., Kainz, M.J., Eds.; Springer: New York, NY, USA, 2009; pp. 257–280.
54. Schmidt, K.; Atkinson, A.; Petzke, K.J.; Voss, M.; Pond, D.W. Protozoans as a food source for Antarctic krill, *Euphausia superba*: Complementary insights from stomach content, fatty acids, and stable isotopes. *Limnol. Oceanogr.* **2006**, *51*, 2409–2427. [CrossRef]
55. Dalsgaard, J.; John, M.S.; Kattner, G.; Müller-Navarra, D.; Hagen, W. Fatty acid trophic markers in the pelagic marine environment. *Adv. Mar. Biol.* **2003**, *46*, 225–340. [CrossRef] [PubMed]
56. Falk-Petersen, S.; Sargent, J.R.; Lønne, O.J.; Timofeev, S. Functional biodiversity of lipids in Antarctic zooplankton: *Calanoides acutus*, *Calanus propinquus*, *Thysanoessa macrura* and *Euphausia crystallorophias*. *Polar Biol.* **1999**, *21*, 37–47. [CrossRef]
57. Graeve, M.; Hagen, W.; Kattner, G. Herbivorous or omnivorous? On the significance of lipid compositions as trophic markers in Antarctic copepods. *Deep. Sea Res. Part I Oceanogr. Res. Pap.* **1994**, *41*, 915–924. [CrossRef]
58. Murzina, S.A.; Voronin, V.P.; Bitiutskii, D.G.; Orlov, A.M. Modeling of the Distribution and Relationship with Abiotic Environmental Factors of Juvenile and Adult Antarctic Krill *Euphausia superba* Based on Actual Hydrophysical Measurements. *Oceanology* **2023**, *63*, 568–573. [CrossRef]