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Autumn food availability in Bransfield Strait for Antarctic krill *Euphausia superba* and the relationship between body size and fatty acid content

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ABSTRACT: Bransfield Strait is an important spawning, feeding and overwintering ground for Antarctic krill. Increases in both the biomass of krill and the ice-free extent of the strait make this area of great interest for krill fisheries. While krill are known to have access to food supplies beyond summer, lipid accumulation plays a pivotal role in their ability to survive the food-limited winter. Understanding the condition and dietary habits of krill during the pre-winter season is important for assessing how they respond to this period that is often characterized by short-lived phytoplankton blooms. For 5 consecutive autumns, from 2015 to 2019, krill obtained from the fishery in Bransfield Strait were used to assess their diet and to evaluate the roles of individual body condition and habitat features in shaping krill fatty acid profiles. Analysis of dietary fatty acids in krill indicated that they were generally in an active feeding condition in autumn, showing significant levels of essential fatty acids such as eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA). Fatty acid biomarkers displayed substantial inter-annual variation, with satellite data suggesting that sea surface temperature could be a potential factor contributing to this variation. Additionally, we observed strong correlations between krill body size and most of the fatty acid contents. There were positive correlations between size, EPA and DHA as well as negative correlations between size and a carnivorous diet. These findings suggest that krill exhibit differentiated feeding abilities and lipid retention based on their size.

KEY WORDS: Diet · Biomarker · Overwintering · Southern Ocean

1. INTRODUCTION

The climate in the Antarctic Peninsula area has undergone rapid change in the past 5 decades (Meredith & King 2005, Kerr et al. 2018a,b). Within the Antarctic Peninsula, Bransfield Strait is a semi-enclosed Antarctic sea (Masque et al. 2002) with complicated hydrography (see Fig. 1) and has been experiencing significant regional ecological challenges (Kerr et al. 2018a). Krill rely on Bransfield Strait during key life cycle events, including spawning, feeding and overwintering (Schmidt et al. 2014, Atkinson et al. 2019, Bernard et al. 2019, Warwick-Evans et al. 2022). During the winter months, noticeable surges in krill biomass indicate their active migration into the area (Reiss et al. 2017, Warwick-Evans et al. 2022). This

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poleward shift in distribution, with krill becoming more concentrated in Bransfield Strait and around the northern Antarctic Peninsula, signifies a response to changing environmental conditions (Veytia et al. 2021). The accessibility of Bransfield Strait has also increased through time, resulting in a commensurate increase in fishing activities in the region (Nicol et al. 2012, Reiss et al. 2017). Significant ecological challenges are expected, given the increasing climate pressure and changing climate regime, for which it is important to better understand krill's condition and its dietary status in the prewinter season since food availability is subject to rapid change, characterized by short-lived phytoplankton blooms.

Krill accumulate lipid reserves during summer while feeding on phytoplankton blooms, and these reserves form part of their winter survival strategy (Quetin & Ross 1991, Hagen et al. 1996, Bernard et al. 2019, 2022). Some phytoplankton fatty acids that are physiologically important, especially polyunsaturated fatty acids (PUFAs), cannot be synthesized by crustaceans de novo (Virtue et al. 1993, Dalsgaard et al. 2003, Kattner et al. 2007, Meyer 2012). Thus, dietary sources of PUFAs are critical for krill to obtain adequate nutrition. Fatty acid biomarkers can help describe krill diet and assess their physiological condition during autumn, and this information can be linked with ontogenetic morphology as well as environmental variables to describe relationships between krill feeding and their habitat (Hellessey et al. 2020, Walsh et al. 2020). Krill metabolize lipids throughout the winter, and it has been suggested that summer–autumn lipid reserves can provide metabolic energy for krill for about 5 mo (Virtue et al. 1993). A peak in lipid reserves in krill has been observed during April and May (Hagen et al. 2001, Hellessey et al. 2018). The quality and quantity of food available in autumn may have a significant impact on the metabolic state of krill in winter, yet compared to other seasons, the autumn krill diet has received little attention. The inaccessibility of scientific surveys during autumn likely contributed to this situation. However, in recent years, krill fishing vessels have operated almost year-round, which provides an opportunity to collect samples during autumn and to improve our understanding of krill biology and ecology in that season (Meyer et al. 2020).

We sampled autumn krill from the fishing fleet in Bransfield Strait for consecutive years and investigated their dietary sources. These data were then explored in relation to individual morphology and environmental variables (sea surface temperature [SST], chlorophyll *a* [chl *a*] and topography). This study aimed to (1) examine the dietary status of krill in Bransfield Strait in autumn and (2) evaluate the roles of krill condition and habitat features in structuring their fatty acid profiles.

2. MATERIALS AND METHODS

2.1. Sample collection

Krill were collected from trawlers (FV 'Long Teng', FV 'Fu Rong Hai') that operated in Bransfield Strait (Fig. 1) during autumn (April and May) from 2015 to 2019. Individual krill were stored in 5 ml plastic tubes and frozen at −20°C until they were returned to shore, where they were then transferred to a −80°C freezer at the Polar Marine Ecosystem Laboratory, Shanghai Ocean University. Individual adult krill were randomly chosen from the sample stock, with 30 specimens selected each year. Wet weight (WW, precision of ±0.01 g) and standard length (±0.01 mm) of each specimen were measured (Mauchline 1980), and sex was determined using the system of Makarov & Denys (1980). To remove the influence of stomach contents on the fatty acid profiles, only the muscle tissue of each individual was extracted and rinsed with Milli-Q water, freeze-dried

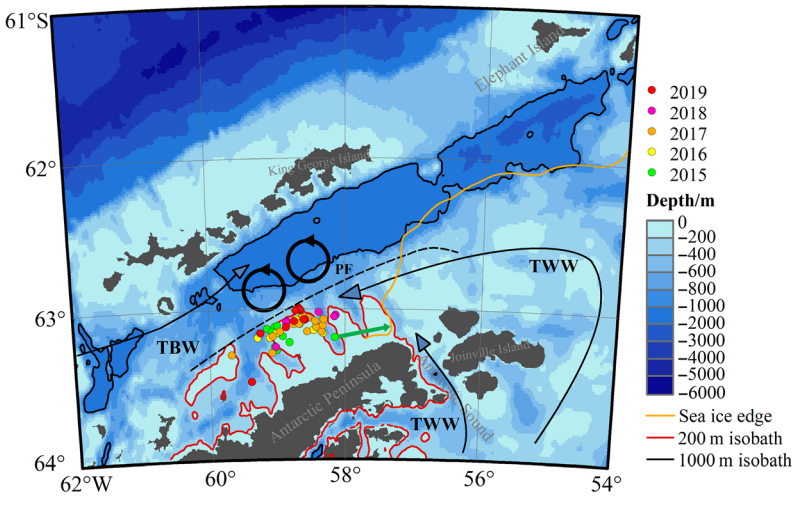

Fig. 1. Locations where krill were collected in Bransfield Strait each year. The peninsula front (PF, dashed line), 200 and 1000 m isobaths, bathymetry and average sea ice edge are shown

for 36 h and then ground to a powder. The powdered samples were stored in a moisture-proof cabinet until fatty acid analysis.

2.2. Fatty acid analysis

Total lipid was extracted according to the method of Folch et al. (1957), using chloroform–methanol (2:1 v:v) as a solvent. The muscle samples were extracted into chloroform–methanol for 24 h; then 4 ml of 0.9% NaCl solution was added and centrifuged for 1 min at 671 × *g* before standing for 2 h until phase separation. The lower phase was extracted and evaporated at room temperature under nitrogen gas flow. Methyl esterification occurred by adding a 28% potassium hydroxide–methanol solution and 14% boron fluoride methanol. Fatty acid methyl esters (FAMEs) were extracted with 2 ml hexane. FAMEs were analyzed using gas chromatography (7890B, Agilent Technologies)–mass spectrometry (Agilent 5977A), equipped with an SPTM-2560 column (60 m length, 0.25 mm inner diameter, 0.20 µm film thickness; Agilent Technologies).

2.3. Environmental data

Monthly averaged SST and chl *a*, used as a proxy for phytoplankton biomass, were calculated each year for the sampling locations; data were accessed by using the 'raadtools' package in R (Sumner 2015). For SST, the NOAA 1/4° Daily Optimum Interpolation Sea Surface Temperature from April to May over the 5 study years was used. For chl *a*, the MODIS Aqua level 3 standard mapped image (SMI) chl *a* data set with 4.6 km (at the equator) spatial resolution was used. To match the sampling location, the chl *a* data were recalculated by using a 9 km^2 box centred on each sampling location. Because of the minimal satellite data available for chl *a* in April and May, and because fatty acid indicators reflect long-term (weeks) lipid retention (Stübing et al. 2003), chl *a* data from March were used for this study to shed light on food availability. Monthly images of sea ice concentration (spatial resolution 25 km) were obtained from the National Snow and Ice Data Center (https://nsidc.org/data/G02202/versions/3). We also calculated the distance from the sampling location to the sea ice edge. For each monthly image, the ice edge was defined as the location where sea ice concentration was less than 15%, as determined by the ARTIST Sea Ice (ASI) algorithm (Spreen et al. 2008). To represent distance to the shelf area, the distances of the sampling location to the 200 m isobath were calculated using Matlab (MathWorks).

2.4. Statistical analysis

Due to the standard method used to extract the FAMEs in the laboratory, not all of the fatty acid components were resolved. From those that were detected, established fatty acid biomarkers were analysed to describe the diets of krill; namely, C15 isomer, C16:0, C16:1n7, C17 isomer, C18:0, C18:1n9, C20:1, C22:1, C18:2n6, C20:5n3 and C22:6n3 (Table 1). Principal components analysis (PCA) was used on the 11 marker fatty acids of individual krill to assess which of them contributed the most to diet over the 5 autumns. To lessen the impact of percentage differences, fatty acid data were log(x + 1) transformed (Pielou 1984). A Kruskal-Wallis test followed by a post hoc comparison was used to compare differences in SST and marker fatty acids between years; p-values were adjusted using the Benjamini-Hochberg method to avoid a Type I error; i.e. rejecting the null hypothesis when it should be accepted (Benjamini & Hochberg 1995).

Length–weight relationships (LWR) for each year were fitted using least-squares regression after natural log transformation. A *t*-test was used to test whether the regression coefficient, *b*, departed from empirical equations available in the literature. Condition factors (CFs) were calculated to investigate the body condition of krill during each autumn. After comparing the CFs obtained from multiple methods available, including Clark (1928), Htun-Han (1978) and Cone (1989), we found that CFs from the Clark (1928) method generated the best results when com-

Table 1. Main fatty acids used in this study and their application as biomarkers for dietary studies

Biomarker	Sources	Reference
C15+C17	Bacteria	Virtue et al. (1997)
PUFA/SFA	Carnivory	Cripps & Atkinson (2000)
20:1+22:1	Carnivory (Copepods)	Falk-Petersen et al. (2000)
16:1n7, EPA	Diatom	Dalsgaard et al. (2003), Stübing et al. (2003)
16:0, DHA	Dinoflagellate	Dalsgaard et al. (2003)
18:2n6	Flagellates	Volkman et al. (1989)

pared with LWRs. The equation of Clark (1928) is: $CF = 100aL^{b-3}$, where L is length (mm), a is the intercept coefficient and b is the slope coefficient which can be found from the LWR.

Exploratory plots (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m730p031_supp.pdf) showed that important fatty acid indicators such as eicosapentaenoic acid (EPA), docosahexaenoic acid (DHA) and C16 differed between the years and were influenced by krill size. To elucidate the potential biological and environmental drivers of fatty acid accumulation, 3 generalized additive models (GAMs) were applied to the data. The fatty acid data were consistent with a Gaussian distribution after natural log transformation. For the biological factors, we included sex, length and year as fixed terms in the model (bioGAM); for the environmental factors, we first included SST, chl *a*, distance to sea ice edge and distance to the 200 m isobath as the smooth terms and then added the sampling day of year and sampling location as smooth terms with random effects in the GAM model (CenvGAM). For a better correlation, we also applied a reduced GAM model (RenvGAM), with only SST, chl *a* and distance to the 200 m isobath included as environmental factors. Model implementations are listed in Table 2. GAM models were performed by using the packages 'lme4' and 'mgcv' (Wood 2011). All statistical analyses were done using R version 4.2.1 (R Core Team 2022).

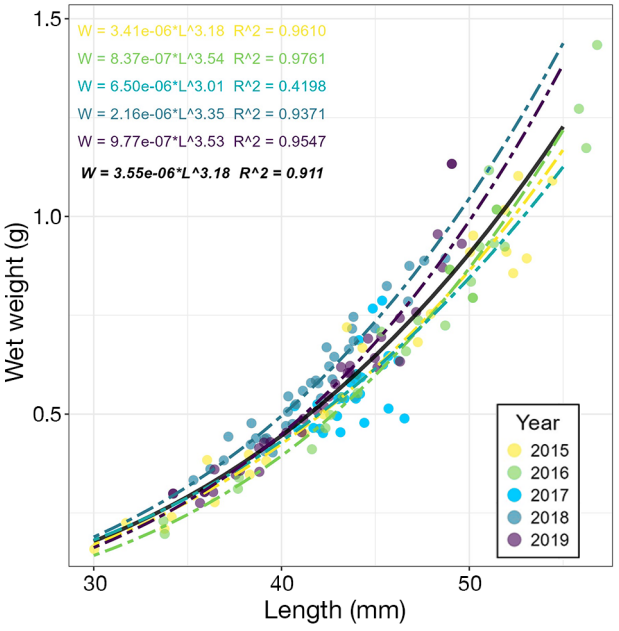

Fig. 2. Length–weight relationships of krill collected from Bransfield Strait in autumn, 2015–2019. Overall length–weight relationship for the whole sample is shown by the black line. Equations for each relationship are shown on the figure

3. RESULTS

3.1. LWR and CF

The LWRs autumn krill in Bransfield strait were fitted for all seasons combined (overall LWR) and each season (Fig. 2). At smaller sizes, the LWRs were quite consistent across the 5 seasons. LWRs for 2018 and 2019 indicated heavier krill at length than 2015–2017 for the larger krill in the length range. To assess the consistency of these findings, we compared the overall LWRs with those from a prior study on autumn krill conducted by Siegel (1992) in April of 1992 (equation: $W = 0.0018 \times L^{0.3436}$, WW units: mg). The results of the *t*-test revealed no statistically significant differences between the slope coefficients of the 2 regression equations ($t = -1.967$, $p = 1.949$). The CFs for each year are presented in Fig. 3. In terms of mean CFs, krill populations in 2018 and 2019 exhibited better health status, while the CFs for the other 3 years appeared similar to each other, suggesting that krill generally exhibited higher weight at length in 2018 and 2019 (Fig. 2). However, it is essential to highlight that CFs varied significantly with krill size. In 2015 and 2017, smaller krill showed better health conditions than larger krill, whereas in 2016 and 2019, CFs for smaller krill were poorer compared to other years. Furthermore, the length data of samples in 2017 exhibited a

Table 2. Variables of the generalized additive models (GAMs). Grey shading represents the model implementation used only as a trial; the other 2 models are analyzed in this study

GAM model	Type of variables	Terms
BioGAM	Fixed	Length, sex, year
CenvGAM	Fixed	Year
	Smoothed	SST, chl *a*
	Smoothed with random effect	Distance to sea ice edge, distance to 200 m isobath, locations, sampling day of year
RenvGAM	Smoothed	SST, chl *a*
	Smoothed with random effect	Distance to 200 m isobath

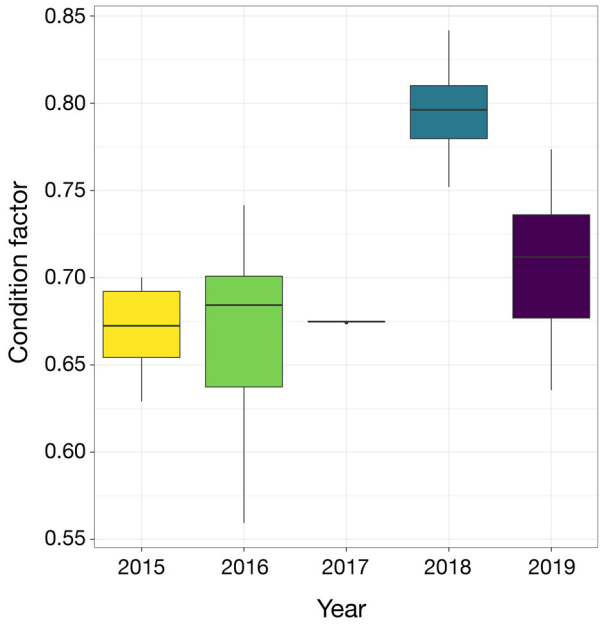

Fig. 3. Boxplot showing condition factors (CF) of krill collected during autumn in Bransfield Strait, 2015–2019. CF was calculated using the equation of Clark (1928), where $CF = 100aL^{b-3}$. Upper and lower box boundaries: interquartile range (IQR); bold line within the box: median; whiskers: 1.5 × IQR above/below box

notably tighter distribution, with a smaller standard deviation compared to other years.

3.2. Autumn diet

Based on fatty acid profiles, phytoplankton were the main contributor to the krill diets, as illustrated by the high proportions of fatty acids usually associated with herbivorous dietary sources (Tables 1 & 3), namely the diatom (16:1n7, EPA), flagellate (18:2n6) and dinoflagellate indicators (DHA). Furthermore, krill had consistent carnivorous and bacterial fatty acid profiles (20:1, 22:1n9 C15 + C17; Table 3) over the 5 yr. C16:0, EPA and DHA were the abundant fatty acids: the average C16:0 content ranged from 13 to 66 mg g^{-1}, EPA from 11 to 28 mg g^{-1} and DHA from 8 to 16 mg g^{-1} across 5 consecutive autumns (Table 3).

From the PCA (Fig. 4), the first 2 principal components (PCA1 and PCA2) explained 65.7% of the variance in fatty acid composition between the years (PC1, 41.7%; PC2, 24.0%). Over 75% of the variance was explained by the first 3 components. PC1 distinguished krill fatty acids in 2018, which had higher carnivorous-indicator loadings of 20:1 and 22:1n9. By contrast, krill fatty acids showed a high correlation with herbivore-dominant fatty acids in 2016 and 2017, but no differences between 2015 and 2016 or between 2016 and 2017.

3.3. Fatty acid and body size

The total quantity of fatty acids did not exhibit any significant correlation with CF ($p = 0.200$), body size ($p = 0.129$) or body weight ($p = 0.066$). However, visual examination of the data suggested that there were some relationships between most of the individual fatty acids and krill size, which was supported by the GAM results (Fig. 5). BioGAM revealed both positive and negative correlations between fatty acids and body size (Table 4), though the majority were negative. Phytoplankton fatty acid indicators, such as C16, C16:1n7, EPA and DHA, either exhibited no correlation or displayed only a slightly significant correlation with size (Fig. 5). Additionally, annual variations were observed across nearly all the fatty acids. Based on BioGAM, the factor sex contributed very little to the variability in fatty acid content.

3.4. Fatty acid and environmental factors

To explore which factors contributed to the annual variation in the fatty acid content of krill, the environmental data were incorporated into a GAM model, RenvGAM (Table 5). Of the environmental factors, SST and chl *a* exerted the strongest influence on the krill fatty acids. SST exhibited significant correlations with all the fatty acids in the GAM model; however, the relationships are complex (Fig. 6). Even though no consistent trend was observed in Fig. 6, we noted 2 types of patterns regarding the fatty acids: C16, C16:1n7, C18, C18:1n9, EPA and DHA showed a gradual fluctuation as the SST changed, while some fatty acids, e.g. C22:1n9, C20:1, C24:1n9, C18:3n6, C20:3n6 and C20:2, presented more irregular and dramatic variations at different SSTs with more extremes towards both ends of the temperature range. When the temperature was low, essential fatty acids (e.g. EPA, DHA, C16:0) remained low, while low-level fatty acids were at their higher extremes.

Correlations between chl *a* and fatty acids could not be explained, possibly due to the limited available satellite chl *a* data. Additional details regarding the predictions based on chl *a* can be found in Fig. S2. Other environmental factors were also considered in this study, including sampling location, distance to the sea ice edge, distance to the 200 m isobath and

Table 3. Mean ± SD mass (mg g^{-1} dry mass, precision of 0.01 mg) of each fatty acid, dietary fatty acid and ratios, from 2015 to 2019

Fatty acid	2015 n = 24	2016 n = 24	2017 n = 28	2018 n = 35	2019 n = 35
C14:0	7.3 ± 2.67	8.67 ± 3.6	16.8 ± 7.73	8.6 ± 2.79	13.31 ± 4.76
C14:1n5	0 ± 0	0.04 ± 0.2	0.48 ± 0.16	0.55 ± 0.18	0.01 ± 0.03
C15:0	0.02 ± 0.05	0.01 ± 0.02	0.64 ± 0.2	0.41 ± 0.09	0.46 ± 0.11
C15:1n5	0.06 ± 0.03	0.07 ± 0.03	0.22 ± 0.19	0.39 ± 0.17	0.08 ± 0.04
C16:0	17.75 ± 5.37	23.12 ± 7.47	42.59 ± 17.56	22.02 ± 4.02	36.53 ± 9.96
C16:1n7	3.48 ± 1.33	5.07 ± 2.5	10.23 ± 6.67	4.73 ± 1.84	6.24 ± 2.91
C17:0	0.36 ± 0.22	0.32 ± 0.14	0.46 ± 0.23	0.43 ± 0.16	0.9 ± 0.34
C17:1n7	0.6 ± 0.53	0.45 ± 0.44	0.09 ± 0.18	1.15 ± 0.35	0.21 ± 0.14
C18:0	2.55 ± 1.37	2.75 ± 1.04	7.13 ± 5.18	2.92 ± 0.94	4.26 ± 2.22
C18:1n9t	0.78 ± 0.5	0.72 ± 0.36	0.57 ± 0.26	1.1 ± 0.47	0.37 ± 0.13
C18:1n9c	6.89 ± 2.03	9.37 ± 4.36	19.8 ± 8.62	8.52 ± 1.96	13.17 ± 5.15
C18:2n6t	1.92 ± 1.41	1.68 ± 0.96	1.09 ± 0.72	2.16 ± 0.95	0.87 ± 0.22
C18:2n6c	1.76 ± 0.7	1.56 ± 0.49	2.28 ± 0.59	1.95 ± 0.45	1.61 ± 0.49
C18:3n6	0.89 ± 0.54	0.79 ± 0.33	0.59 ± 0.25	1.32 ± 0.49	0.39 ± 0.11
C20:0	0.74 ± 0.48	0.65 ± 0.3	0.47 ± 0.22	1.53 ± 0.59	0.13 ± 0.04
C18:3n3	1.83 ± 0.9	1.3 ± 0.46	2.92 ± 2.06	1.72 ± 0.55	1.15 ± 0.57
C20:1	0.86 ± 0.36	0.99 ± 0.31	1.54 ± 0.72	1.68 ± 0.52	0.56 ± 0.23
C21:0	0.63 ± 0.41	0.55 ± 0.25	0.33 ± 0.17	1.46 ± 0.57	0 ± 0
C20:2	0.93 ± 0.6	0.82 ± 0.37	0.52 ± 0.24	1.68 ± 0.65	0.33 ± 0.12
C20:3n6	0.24 ± 0.15	0.23 ± 0.11	0.48 ± 0.24	1.69 ± 0.65	0.37 ± 0.13
C22:0	0.1 ± 0.06	0.09 ± 0.04	0.44 ± 0.21	0.49 ± 0.19	0 ± 0
C20:3n3	0 ± 0	0 ± 0	0.73 ± 0.34	1.86 ± 0.68	0.58 ± 0.23
C20:4n6	4.74 ± 3.08	4.16 ± 1.87	0.41 ± 0.19	1.42 ± 0.51	0.5 ± 0.15
C22:1n9	0.78 ± 0.36	0.87 ± 0.27	1.38 ± 0.67	1.93 ± 0.67	0.29 ± 0.21
C23:0	0.59 ± 0.39	0.52 ± 0.24	0.44 ± 0.23	1.87 ± 0.73	0 ± 0
C22:2n6	0.17 ± 0.52	0.13 ± 0.36	0.1 ± 0.19	9.04 ± 1.45	6.37 ± 1.21
C20:5n3	15.69 ± 6.65	20.71 ± 5.18	28.1 ± 13.33	11.06 ± 1.79	21.79 ± 5.03
C24:0	0.59 ± 0.39	0.59 ± 0.45	0.42 ± 0.22	2.05 ± 0.94	0 ± 0
C24:1n9	0.55 ± 0.35	0.53 ± 0.29	0.47 ± 0.18	2.25 ± 0.88	0.46 ± 0.16
C22:6n3	13.31 ± 4.58	14.76 ± 4.72	15.81 ± 5.9	8.39 ± 1.31	12.97 ± 3.24
SFA	30.62 ± 7.45	37.27 ± 11.02	69.72 ± 29.71	41.79 ± 6.81	55.57 ± 15.62
MUFA	14 ± 3.41	18.11 ± 6.7	34.78 ± 16.21	22.3 ± 3.96	21.4 ± 8.19
PUFA	41.47 ± 12.4	46.14 ± 8.53	53.04 ± 19.2	42.29 ± 5.79	46.94 ± 8.87

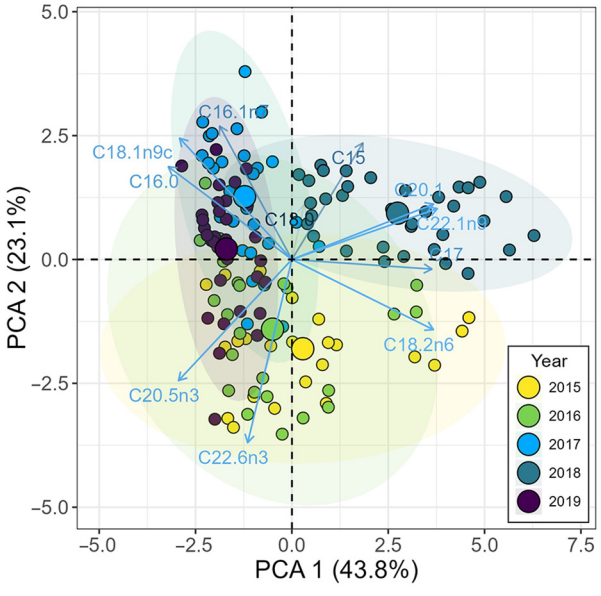

Fig. 4. Principal component analysis of percentage composition of fatty acids of krill collected in Bransfield Strait during autumn, 2015–2019

sampling date, none of which showed any correlations (Table S1).

4. DISCUSSION

4.1. Krill diet and body condition in the Bransfield Strait during autumn

The consistent aggregations of krill in Bransfield Strait during autumn indicate that the region provides an important habitat for krill in the prewinter season. On average, krill in this area exhibited higher weight at length compared to other areas during

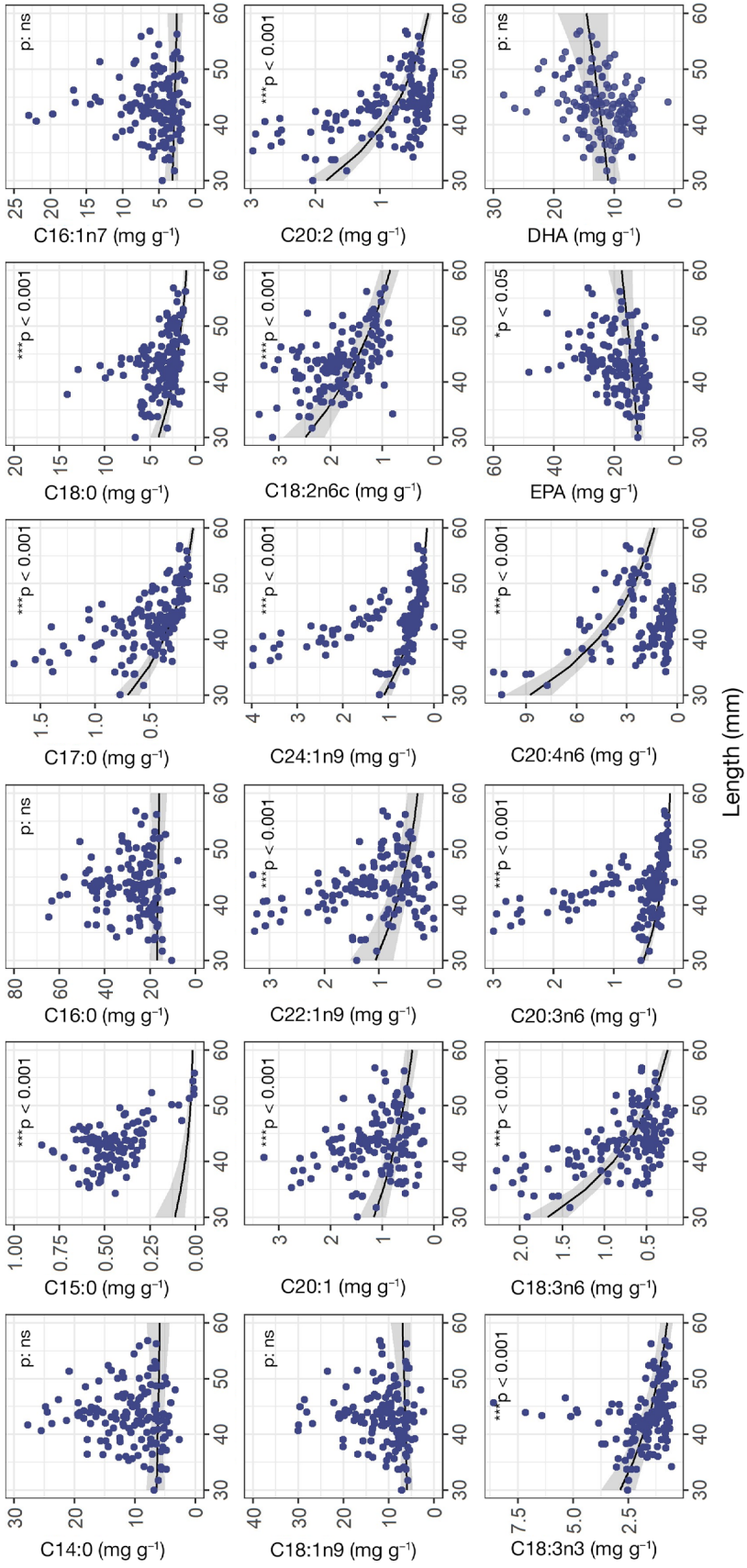

Fig. 5. Correlations between krill length and fatty acids based on BioGAM predictions

autumn, as determined from limited previous studies (Fig. S3) (Siegel 1992), which suggests that krill in the Bransfield Strait had body reserves that were as sufficient or better than krill from other areas. Krill in Bransfield Strait showed a high level of diatom and flagellate feeding, as reflected by the marker fatty acids EPA, 16:1n7, DHA and 18:2n6. Additionally, the presence of copepods and bacteria (potentially ingested as part of marine debris) in the krill diet was revealed by the fatty acid markers C20:1n9 + 22:1 and C15 + C17 isomers. In particular, the essential fatty acids EPA and DHA were recognizably higher than other seasons in the nearby areas (Ericson et al. 2018) and comparable to the krill in the area in autumn (Ericson et al. 2018), which suggests that krill were well-prepared for the coming winter season. EPA and DHA are known to be critical components needed to support krill growth, health and reproduction (Pond et al. 2005, Corsolini & Borghesi 2017). Lower concentrations of EPA and DHA could potentially lead to poorer health and have negative effects on the overwintering performance of krill. Conversely, higher amounts of EPA and DHA could benefit their overall wintering condition.

Despite the relatively good body condition of krill in Bransfield Strait during autumn, it is important to note that there were fluctuations between years, as shown by both LWFs and CFs. The highest LWR and CF were observed in 2018, and the krill in that year had a diet characterized by higher carnivory, as highlighted by the PCA, in which 2018 was separated from the other years along axis 1. Notably, in 2018, EPA and DHA content in krill were the lowest over the 5 study years. This supports the idea that a krill diet which is high in copepods does not favour the accumulation of EPA and DHA in krill tissues (Schmidt et al. 2014). However, it also emphasises the need for caution when using LWR and CF data to assess krill body reserves.

Table 4. Summary of p-values and adjusted R^2 values generated from the BioGAM model

Fatty acid	p	Adjusted R^2
C14:0	0.660	0.374
C15:0	1.06×10^{-6}	0.782
C16:0	0.659	0.537
C17:0	4.05×10^{-25}	0.792
C18:0	5.19×10^{-12}	0.604
C16:1n7	0.454	0.260
C18:1n9	0.426	0.444
C20:1	1.79×10^{-6}	0.624
C22:1n9	1.97×10^{-4}	0.646
C24:1n9	7.41×10^{-27}	0.887
C18:2n6	2.60×10^{-11}	0.400
C20:2	2.62×10^{-27}	0.869
C22:2n6	0.170	0.943
C18:3n3	2.07×10^{-7}	0.396
C18:3n6	8.71×10^{-27}	0.812
C20:3n3	2.99×10^{-16}	0.841
C20:3n6	4.89×10^{-26}	0.909
C20:4n6	1.02×10^{-24}	0.935
C20:5n3 (EPA)	0.016	0.588
C22:6n3 (DHA)	0.148	0.276

4.2. Role of body size in fatty acid accumulation

Krill size showed strong correlations with most of the fatty acids measured, although there was no consistent trend, and the correlations were either positive or negative depending on the fatty acid. Strong negative correlations were primarily observed for fatty acids which were detected at low levels, e.g. C15:0, C17:0, C22:1n9, C24:1n9 and C20:4n6. Less variability across the length range was observed when the individual fatty acid content was high, and these were most often positively correlated; e.g. C16:0, C16:1n7, C18:0, EPA and DHA.

A krill diet that is rich in diatoms typically promotes the accumulation of PUFAs, particularly EPA (Steinke et al. 2022). The slight positive correlation between EPA and body size in our study suggests that the feeding ability and fatty acid retention of krill improve as they grow. Larger krill have better grazing ability, when krill feed, although the filtering setae does not differ across size groups for postlarval krill and the krill feeding basket expands with increasing body length (Morris et al. 1988, Hofmann & Lascara 2000), which may contribute to the ability to amass this diatom indicator fatty acid. DHA, the second-highest PUFA, is often recognized as a flagellate biomarker and showed a less variable pattern correlated with body size. The above slightly significant correlation and non-correlation regression may suggest that EPA and DHA are prioritized for accumulation, regardless of the diet change. Some studies also suggest that DHA and EPA may not only come from the prey (Virtue et al. 1993, Schmidt et al. 2014, Ericson et al. 2019) but can also be synthesized and elongated from C18:3n3 and C18:2n6 (Sargent 1989, Bell et al. 2007), which are both negatively correlated with krill length. Bioconversion of EPA into DHA can be another possible reason (De Troch et al. 2012) contributing to the relatively stable concentration across all length classes.

C16:0, one of the most abundant fatty acids measured in krill during this study, did not show any correlation with body size, possibly due to its independence from food intake and its multiple functions in the krill body. C16:0 has been identified as the most consumed fatty acid as krill undergo development from eggs to larvae (Yoshida et al. 2011). Experiments have also shown a decrease in EPA and DHA levels after starvation, favouring the composition of C16:0 (Stübing et al. 2003). In the current study, another 16-carbon fatty acid, C16:1n7, also did not correlate significantly with krill length. C16:1n7 is a useful biomarker of diatom presence in the krill diet (Stübing et al. 2003). Given the variable content of C16:1n7 across

Table 5. Summary of p-values and adjusted R^2 values generated from the RenvGAM model. 200 iso: distance from sampling station to the 200 m isobath

Fatty acid	SST	Chl *a*	200 iso	R^2
C14:0	6.69×10^{-4}	0.181	0.554	0.211
C15:0	3.73×10^{-4}	0	0.521	0.724
C16:0	5.47×10^{-7}	3.87×10^{-4}	0.849	0.381
C17:0	7.13×10^{-5}	0	0.972	0.341
C18:0	2.05×10^{-7}	5.85×10^{-6}	0.036	0.392
C16:1n7	3.39×10^{-4}	0.246	0.551	0.200
C18:1n9	1.98×10^{-6}	0.037	0.936	0.305
C20:1	2.65×10^{-7}	0.085	0.138	0.358
C22:1n9	0	0.674	0.525	0.373
C24:1n9	8.56×10^{-7}	0.002	0.018	0.542
C18:2n6	0.006	0.021	0.698	0.191
C20:2	0	0.320	0.620	0.443
C22:2n6	0	0	0.459	0.950
C18:3n3	1.44×10^{-4}	0.304	0.014	0.216
C18:3n6	0	0.257	0.450	0.365
C20:3n3	2.47×10^{-4}	0.051	0.962	0.546
C20:3n6	0	0	0.004	0.614
C20:4n6	0	3.73×10^{-6}	0.456	0.496
C20:5n3 (EPA)	0	0.026	0.309	0.351
C22:6n3 (DHA)	5.8×10^{-4}	0.400	0.015	0.221

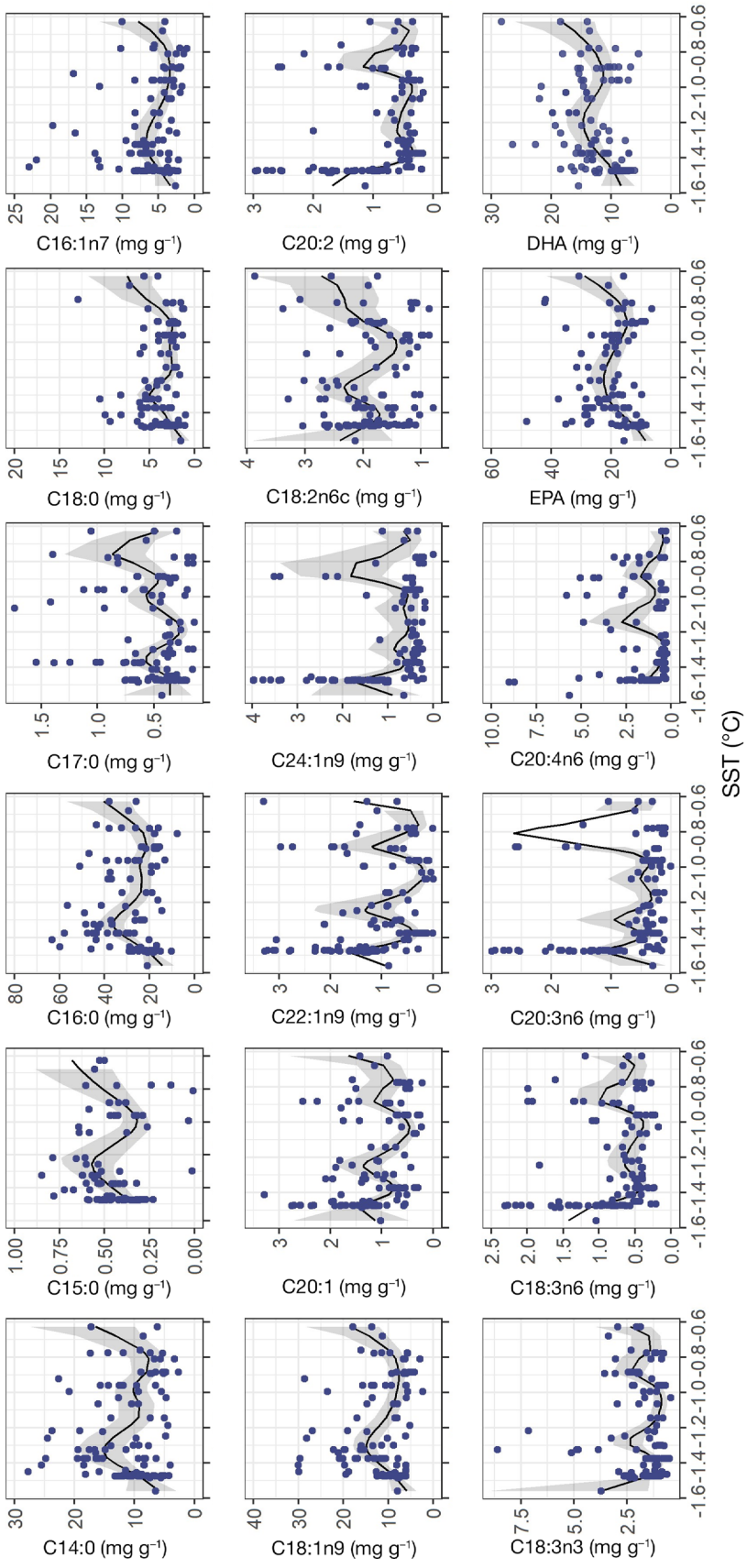

Fig. 6. Correlation between krill fatty acids and sea surface temperature (SST), based on RenvGAM predictions

all body sizes and its relatively high quantity, this suggests an accessible food source for the krill population.

C20:1 and C22:1n9 are often used as indicators of copepods in the diet. Both of these fatty acids showed a negative correlation with krill length, which differs from the findings of Schmidt et al. (2014) and Walsh et al. (2020). Similarly, C15 and C17 exhibited a similar trend to the copepod indicators. The low levels of copepod fatty acids and microbiota fatty acids may reflect the larger krill's ability to feed on phytoplankton. The contrasting patterns between EPA and copepods could further support the idea that a copepod-dominated diet may lead to reduced PUFA levels (Schmidt et al. 2014).

Other fatty acids, which were generally present in small amounts, consistently showed strong negative correlations with krill body size across the 5 yr autumn surveys. The clear contrast with the abundant fatty acids may suggest that the less critical fatty acids are under-accumulated in favour of essential fatty acids for overwintering. These essential fatty acids include not only the high-energy fatty acids (EPA, DHA) but also the low-cost fatty acids (C16:0, C18:0). The patterns observed in the present study, however, could provide further insights into the lipid accumulation strategy for overwintering strategies in wild krill. Correlations between size and lipid profiles have also been observed in other species, such as the Arctic copepod *Calanus finmarchicus* (Pepin et al. 2011) and perch (Góra et al. 2022). Additional research on how krill metabolise the fatty acids, and their bioconversion, is needed to fully understand the correlations between their body size and different fatty acids.

4.3. Potential environmental drivers

Similar to the correlation between body size and fatty acids, abundant fatty acids showed less variation corre-

sponding to SST. The accumulation of essential fatty acids appeared to be less sensitive to temperature change. The variation in low-level fatty acids corresponded to SST changes and likely resulted from the preferential accumulation of essential fatty acids (e.g. EPA, DHA, C16:0).

Chl *a* is an important indicator of phytoplankton biomass and has been shown to exert the most significant influence on dietary variations (Hellessey et al. 2020, Walsh et al. 2020). However, due to limited chl *a* data availability, this study cannot provide practical explanations for the correlation between the abundance of phytoplankton and krill diet. Because this study is based on samples collected from the fishery, the collection of environmental parameters was significantly restricted.

5. CONCLUSIONS

Krill in the Bransfield Strait during autumn were generally in good feeding condition, suggesting that the region could be considered an important foraging ground as well as an overwintering area, albeit with some variability between years. We hypothesize that krill size plays a significant role in energy dynamics. Therefore, when designing experiments related to nutrients or biochemical indicators, or when interpreting results, it is essential to evaluate the impact of size on the outcomes. This study combined fatty acid biomarkers with satellite environmental data, primarily SST, a useful approach given the relatively scarce *in situ* environmental data in the Southern Ocean. Most studies to date are based on short-term sampling due to the logistic complexity of scientific investigations, whereas environmental dynamics are a long-term and complex process. The use of long-term observations and samples from the krill fishery is encouraged, as this data source can provide good coverage over multiple years and across most seasons. The uninterrupted temporal sampling, concentrated working areas and guaranteed samples shows that fishing vessels have confirmed their role as effective sampling platforms. However, we also highlight the need for consistent collections of simultaneous environmental data if we are to use the fishery data to its fullest.

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