Antarctic krill (Euphausia superba) are a key component of the Antarctic food web with considerable lipid reserves that are vital for their health and higher predator survival. Krill lipids are primarily derived from their diet of plankton, in particular diatoms and flagellates. Few attempts have been made to link the spatial and temporal variations in krill lipids to those in their food supply. Remotely-sensed environmental parameters provide large-scale information on the potential availability of krill food, although relating this to physiological and biochemical differences has only been performed on small scales and with limited samples. Our study utilized remotely-sensed data (chlorophyll a and sea surface temperature) coupled with krill lipid data obtained from 3 years of fishery-derived samples. We examined within and between year variation of trends in both the environment and krill biochemistry data. Chlorophyll a levels were positively related to krill lipid levels, particularly triacylglycerol. Plankton fatty acid biomarkers analysed in krill (such as n-3 polyunsaturated fatty acids) increased with decreasing sea surface temperature and increasing chlorophyll a levels. Our study demonstrates the utility of combining remote-sensing and biochemical data in examining biological and physiological relationships between Antarctic krill and the Southern Ocean environment.
part of the krill fatty acid profile, particularly in summer and autumn. EPA and DHA are also the n-3 LC-PUFA targeted by the krill fishing industry for application into nutraceutical products. The n-3 shorter chain PUFA, stearidonic acid (SDA, 18:4n-3), which is a flagellate marker, also plays a vital role in krill diet, although its precise function is not well understood.

Phytoplankton, such as diatoms and dinoflagellates, all naturally produce chlorophyll which can be remotely detected via satellites. Recent studies have shown that the colour of the ocean, due to shifts in the assemblage of these phytoplankton blooms, is changing with climate change. As these phytoplankton assemblages change, krill diet may also be altered as the climate changes. Phytoplankton biomarker levels will have more pronounced changes within krill diet as lower trophic level populations will shift more rapidly with climate change; thus, changes in phytoplankton blooms are a major cause of ecosystem level shifts (e.g. phytoplankton assemblage change) with climate change. Remotely-sensed SST data from satellites can also be collected over large geographic areas and long timeframes. Unfortunately, as of yet, there is no proxy for zooplankton, marine snow or bacterial assemblages that can be detected via satellite.

The krill fishery has been operating since the early 1970’s and in the mid-1990s the industry began to produce and sell krill oil as a nutraceutical due to its high levels of omega-3 containing oils. The krill fishery operates year-round in the South Atlantic Ocean (Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Area 48) and in particular near the West Antarctic Peninsula (WAP, CCAMLR Sub-Area 48.1), South Orkney Islands (SOI, CCAMLR Sub-Area 48.2) and South Georgia (SG, CCAMLR Sub-Area 48.3). Over the last few years the total catch has been approximately 300,000 tonnes of krill a year, and from a scientific research perspective the commercial harvest is a useful source of biological samples. Satellites collect environmental data such as SST, ocean colour, sea surface height, fluorescence, wind direction and wind speed. While satellite data must be calibrated and validated, it can fill in gaps of data collected in situ and provides wide-area coverage. Linking remotely sensed environmental data with analysis of krill samples collected by the krill fishery is a cost-effective approach to explore biological responses to environmental changes.

Our study uses three consecutive years of krill lipid data from fishery-derived samples collected throughout the South Atlantic Ocean. We simultaneously accessed satellite data to link krill signature biochemical data to environmental conditions seen at the location of krill collection. We hypothesise that changes in krill biochemistry, specifically their fatty acid dietary biomarkers, will track broad scale satellite-derived environmental data. Linking environmental drivers to krill diet will assist in ecosystem energy budget and food web models. By basing such models around environmental parameters, future environmental scenarios can be modelled, and krill diet and ecosystem responses will be more reliably predicted.

We aim to show if a link between the environment and krill diet exists by examining whether: (1) SST (°C) and chlorophyll a levels (Chl a, mg m⁻²) are correlated to total lipid (mg g⁻¹ krill dry weight) or phytoplankton fatty acid biomarkers (percentage (%) and mass (ug)) in a meaningful manner, (2) Chl a, total lipid and phytoplankton fatty acid biomarkers increase as SST decreases throughout summer and autumn, and the annual spring phytoplankton blooms and (3) larger shifts in SST and Chl a closer to the pole (currently an area in a state of flux) will drive larger shifts in krill biochemistry.

Results

Sea surface temperatures. During this study (Jan 2014 – Sep 2016) satellite-derived sea surface temperatures had the greatest variability in the South Orkney Islands (SOI), ranging from −1.28 to 1.93 °C (average 0.33 ± 0.86 °C), followed by South Georgia (SG) where temperatures ranged from −1.10 to 1.49 °C (average 0.49 ± 0.54 °C) and the West Antarctic Peninsula (WAP) which ranged from −1.28 to 0.94 °C (average −0.25 ± 0.78 °C). Temperatures decreased from summer into autumn in the WAP and SOI, and from the start of winter to spring in SG. However, in 2016, SST at WAP increased from summer into autumn and then decreased from early autumn onwards (Supplementary Fig. 1).

Chlorophyll a concentrations. The levels of Chl a varied depending on the location and the season (Supplementary Fig. 2). Values of more than 5.78 mg m⁻² of Chl a were observed in the SOI, and as low as 0.19 mg m⁻² in SG. Chl a increased in summer and decreased rapidly during the autumn of 2014 around the SOI. Chl a concentrations in other years were more consistent, although very few satellite measurements were recorded at SG due to the time of year, cloud cover, ice cover and suboptimal sun angle.

Chl a varied the most around the SOI, ranging from 0.24 to 5.78 mg m⁻² (average 0.88 ± 0.85 mg m⁻²), followed by the WAP which ranged from 0.20 to 1.34 mg m⁻² (average 0.62 ± 0.30 mg m⁻²), and SG which ranged from 0.19 to 0.62 mg m⁻² (average 0.39 ± 0.11 mg m⁻²). SG had the smallest range of Chl a concentrations and the lowest average Chl a concentration. SOI had the biggest range of Chl a concentrations and the highest average Chl a concentration.
Geographic distribution. The geographic distribution of SST, Chl a and krill total lipid (mg g\(^{-1}\) dry weight, TLDW), for CCAMLR Sub-Areas 48.1, 48.2 and 48.3 can be seen in Figs. 1, 2 and 3. Higher SST and Chl a in the Bransfield Strait (W AP) reflect bathymetric and current features (Fig. 1) as well as the northern advection of water from the deep canyon to the south of the SOI49 (Fig. 2). These oceanographic features are known locations of higher SST and Chl a that occur within the SG and SOI areas. Krill TLDW is also higher in the Bransfield Strait (Fig. 1). To the northwest of SG, higher SST and lower Chl a values can be seen due to the faster flowing current originating off the slope of SG (Fig. 3).

Lipid and fatty acid general trends. Results describing the trends seen in krill TLDW, lipid classes and their fatty acids can be found in Ericson, et al.,7 and Hellessey, et al.,48. Briefly, krill TLDW and triacylglycerol (TAG) percentage (%) increased throughout summer to reach autumn highs in the WAP and SOI, whereas krill at SG had declining TLDW and TAG % throughout winter and spring. EPA and DHA (mg g\(^{-1}\) dry weight) followed the same seasonal trend as TLDW and TAG %. 16:1n-7c and SDA had variable quantities across all seasons, years and fishing locations. In summer, krill had high levels (% total fatty acids) of EPA, DHA and PUFA, but low 18:1n-9c/18:1n-7c ratios, indicating a more herbivorous diet.

Tracking fatty acid biomarkers using satellite derived environmental data. Clear seasonal trends can be seen in fatty acid biomarkers in krill throughout the fishing seasons, both in percentage composition and quantitative amounts (mass, ug). Most diatom-based markers in krill (such as EPA, 16:4n-1 and 16:1n-7c) increased in percentage throughout summer to reach autumn highs in the WAP and SOI, as did 16:0 percentages. In comparison, krill at SG had declining diatom-based markers and 16:0 percentages throughout winter and spring. Dinoflagellate markers in krill such as DHA and SDA showed similar trends to diatom markers in their percentages. Both diatom and flagellate markers in krill showed the opposite trend in their masses (low in summer and autumn, higher in winter/spring), but this could also be due to location of sampling (WAP/SOI in...
Figure 3. The geographic distribution of krill total lipid (mg g⁻¹ dry weight, TLDW), the chlorophyll a (Chl a) concentration (mg m⁻²) and the sea surface temperature (°C, SST) of Euphausia superba samples collected at South Georgia. Locations are points that krill were harvested by FV Saga Seas from June to September 2014–2016. Maps were produced using the RStudio (version 1.0.153© 2017) package ggmaps (Kahle and Wickham, http://journal.r-project.org/archive/2013-1/kahle-wickham.pdf). Map data© 2018 Google.

summer/autumn and SG in winter/spring). Table 1 provides the P-value for 1-way ANOVAs comparing models as well as the adjusted $r^2$ value and $\chi^2$ value for the associated model of best fit between the krill biochemical data (lipid and fatty acid content (mass) and composition (percentage)) and the environmental data (SST and Chl a) and their interaction terms from the South Atlantic region. Supplementary Tables 1–3 show these same relationships broken down into the smaller CCAMLR management sub-areas (SG, SOI and WAP, respectively).

Using environmental parameters as predictors of fatty acid biomarkers. The WAP had the most models that fit environmental factors with a significant relationship to the biomarkers in the krill found in that region (Supp. Table 3). The SG region had the next highest number of models that fit the biomarker/environment interaction relationship (Supp. Table 1). Both the overall South Atlantic area and the SOI had models that had less significant effects and correlations between the krill dietary biomarkers and the environment in those regions (Table 1 and Supp. Table 2). Based on these simple models, the best areas (due to their consistency and predictability in environmental factors) for use to examine krill dietary biomarkers are the WAP and SG, and the best environmental predictors for krill diet are SST, Chl a (8D 3 × 3) concentrations and the interaction of SST and Chl a (CCAMLR) concentrations (see Supplementary Materials).

The inter-relationships between environmental factors showed that TLDW increased as SST decreased in summer and autumn, but TLDW decreased as did SST in winter and spring. This was independent of Chl a levels, which were highest in the SOI in 2014, but the highest TLDW levels were in the WAP in 2016 (Fig. 4). The percentage of EPA increased after a decrease in Chl a levels (grazing effect), but generally followed the same yearly trends as Chl a. EPA was high then decreased in 2014, plateaued in 2015 and again started high and decreased throughout the summer and autumn of 2016 (Fig. 4).

In terms of the fit of models, no models had an adjusted $r^2$ value greater than 0.5 for the pooled data of the entire South Atlantic region (Table 1). The CCAMLR region data had multiple models with good fit, with many models exceeding an adjusted $r^2$ of 0.5. DHA percentage and 16:1n-7c mass fitted well with the interaction between SST and Chl a (8D 3 × 3) ($r^2 = 0.611$ and 0.551, respectively) in SG (Supp. Table 1). No fatty acids had an $r^2$ above 0.5 at the SOI (Supp. Table 2). DHA percentage was close to fitting with Chl a (8D 3 × 3), with an $r^2$ value of 0.498 at the WAP (Supp. Table 3). SST and Chl a (CCAMLR) fitted to PL and TAG percentages in the WAP ($r^2 = 0.564$ and 0.559, respectively). EPA percentage fitted well with an adjusted $r^2$ of 0.599 for its WAP model of SST and Chl a (CCAMLR).

Better fits were found, however, by using the SST and Chl a (8D 3 × 3) interaction in the model at the WAP (Supp. Table 3). TLDW, PL and TAG percentages fitted this interaction with adjusted $r^2$ values of 0.610, 0.655 and 0.568, respectively. EPA percentage ($r^2 = 0.689$), and EPA, DHA and 16:1n-7c masses ($r^2 = 0.615$, 0.892, 0.621) all fitted the SST and Chl a (8D 3 × 3) interaction at the WAP (Supp Table 3). Additionally, SDA mass correlated with SST and Chl a (8D 3 × 3) at the WAP ($r^2 = 0.560$; Supp. Table 3).

The best model fit of all of those tested was DHA mass at the WAP using the SST and Chl a (8D 3 × 3) interaction with an adjusted $r^2$ value of 0.892. This can be seen in Supplementary Fig. 3 which compares the slopes and fit of models from the different CCAMLR sub-areas to DHA mass against SST and Chl a (CCAMLR) and the 95% confidence interval around the model.

$\chi^2$ (chi-squared) values are shown for all models, whether they are for the pooled South Atlantic models (Table 1) or for the CCAMLR specific sub-areas (Supp. Tables 1–3).

Discussion

Krill lipid content and composition, specifically their fatty acid dietary biomarkers, correlate with changes in broad scale environmental data (SST and Chl a levels) derived from satellites. Krill eat, metabolise, and store lipids and fatty acids derived from their prey throughout the summer and early autumn when waters are warmer (higher SST) with more available food (diatoms and flagellates; higher Chl a)$^{2,40,48}$. In turn, they use these fatty
Table 1. *Euphausia superba* total lipid (mg g−1 dry weight, TLDW), and lipid class composition (phospholipid (PL) and triacylglycerol (TAG) percentage) and fatty acid (20:5n-3 (EPA), 22:6n-3 (DHA), and 18:4n-3 (SDA)) percentage composition (%) and mass (ug) per krill against sea surface temperature (SST), chlorophyll *a* (Chl *a*) and their interaction terms for all seasons and pooled locations across the South Atlantic sector. Chl *a* was measured at both an overall scale (overall) and an 8-day 3 km × 3 km (8D 3 × 3) pixel scale for the entire South Atlantic sector. Values given are for: P values (italics) and $r^2$ values (bold) for the model of best fit.
centages of fatty acids between years, seasons and locations so large scale Chl are more highly associated with the more specific and localised Chl a (8D 3) of krill (Euphausia superba) chlorophyll stomach and digestive gland weighing more from being full from chlorophyll rich items15,57,59. As TLDW natural Chl within the W AP but not from SOI). Many of the major essential krill fatty acid biomarkers were correlated to SST, from W AP will correlate with biomarkers from krill of krill in these regions. Therefore, the biomarkers will vary between regions naturally, but may still correlate with pixel used. Reasons for inconsistencies may be due to differences between regions as these vary with the local can provide a better prediction for either krill fatty acid percentages or masses, depending on the scale of Chl a fluctuations. Krill fatty acid masses can change dramatically (up to a 10 fold increase between summer and early winter), and hence Chl a (8D 3 3) data fluctuations are more apparent in localised areas, but not in the overall Chl a data. The interaction between SST and Chl a (overall) showed a significant relationship to EPA, SDA and 16:0 percentages, while EPA, DHA, and 16:1n-7c masses were more significantly related to the SST and Chl a (8D 3 3) interaction. Therefore, using different scales of Chl a in the SST and Chl a interaction within the models can provide a better prediction for either krill fatty acid percentages or masses, depending on the scale of Chl a pixel used. Reasons for inconsistencies may be due to differences between regions as these vary with the local environment in that area. These environmental differences will influence the primary production and hence diet of krill in these regions. Therefore, the biomarkers will vary between regions naturally, but may still correlate with the environmental data from that region (e.g. SST and Chl a from WAP will correlate with biomarkers from krill within the WAP but not from SOI). Many of the major essential krill fatty acid biomarkers were correlated to SST, Chl a and their interaction terms at varying scales.

Tukey tests revealed the interaction with TLDW was mainly driven by SST, and not Chl a, and that SST had a close relationship to TLDW in all locations. Because this relationship holds without the Chl a interaction term, it can be assumed that SST drives TLDW levels more than Chl a levels do. TLDW relates well to SST and Chl a (8D 3 3) interactions as it is scaled to the krill’s weight, which may be affected by both temperature64 and its stomach and digestive gland weighing more from being full from chlorophyll rich items15,57,59. As TLDW naturally increases throughout summer and autumn and decreases throughout winter and spring48, this would also coincidentally inversely follow the decrease of SST in summer and autumn, and decrease proportionally to SST in winter and spring. Therefore, the relationship between SST and TLDW may be coincidental due to the seasonal shift in how krill use their lipids aligning with seasonal shifts in SST. At the regional scale, TLDW was strongly related to Chl a (CCAMLR) levels in the SOI and WAP, although not in SG. This may be due to krill having a more herbivorous diet during summer and autumn when krill are harvested from the SOI and WAP and a more omnivorous diet during winter and spring whilst they are harvested at SG.

The interaction between SST and Chl a (CCAMLR) was significant for SG, however, and also the WAP, but not for the SOI. This may be due to larger SST shifts at the more extreme ends of the latitudinal scale at WAP and SG160. These locations would have the greatest extremes in environment, particularly for SST160, and as such any variations may explain why these locations show a strong relationship between TLDW and the environment. Similarly, at SG, Chl a (CCAMLR) was consistently low for all of winter and spring (when able to be recorded), whereas TLDW decreased dramatically during this period, so this may be giving false model fits for this area at this time of year. If readings of Chl a levels were possible throughout the winter season, a more closely related trend might be seen.

Figure 4. Multi Y axis plot of sea surface temperature (°C; black), total lipid dry weight (mg g−1; blue), chlorophyll a levels (mg m−2; green) and eicosapentaenoic acid (20:5n-3; EPA) percentage (%; yellow) for dates of krill (Euphausia superba) sample collection. Lines drawn for illustrative purposes to show general trends.
As TAG is a storage lipid in krill, it decreases from late summer through to the following late spring, when krill build stores for both reproduction and survival over winter. This peak in TAG also follows the peak in summer algal blooms (and thus peak Chl a) and is seen as a lag effect. This lag is due to both the time it takes for krill to metabolise TAG and the rate that krill convert fatty acids in algal TAG to their own PL stores. The PL percentages in krill tracked with Chl a (overall and 8D 3 × 3). PL has also been reported as a storage lipid in krill, and is known to be vital for the storage of essential n-3 LC-PUFA for reproduction and krill health. Interestingly, PL levels were not related to changes in SST, but tracked well with changes in Chl a, possibly due to the way that polar phytoplankton blooms can occur via a boom-bust cycle. Many types of algae in polar latitudes are high in PL and are also very green in colour, which could be one reason why krill PL are so closely related to Chl a levels. PL can be incorporated very quickly into krill tissue as krill predominantly store their lipids as PL. Therefore, there would be little lag between ingestion, metabolism and incorporation. Our data shows there is little to no lag seen between Chl a data and PL percentages.

The EPA:DHA ratio in krill was significantly related to Chl a (8D 3 × 3). A higher EPA:DHA ratio suggests that krill are consuming more diatoms than flagellates in their diet. This relationship could be due to diatom and flagellate blooms affecting the ocean colour readings (higher green values) from satellite more so than other factors. The green colour can be detected relatively easily in the ocean and ocean colour is changing far faster with the climate than was predicted by models. These changes in plankton community assemblages could also be changing faster than expected, which would be reflected in a changing EPA:DHA ratio. Krill potentially prefer a more diatom-based diet when blooms occur, even if flagellates are available in the water column. Such a dietary preference might skew the EPA:DHA ratio of krill, and could be related to the amount of Chl a being detected via remote sensing, whether at the 8D 3 × 3 or overall scale. The 16:1/16:0 ratio shows differences in plankton types being consumed by krill and was not associated with any Chl a or SST data over the whole South Atlantic, but did show differences at smaller CCAMLR region scales. This may be due to krill diet shifting with seasons at the same time as the krill fishery also shifts its fishing location at the end of autumn (from SOI or WAP) to the start of winter. The krill fishery operates at SG during winter and spring when algal populations are naturally lower in the water column, and most algae is bound in sea ice. Remote sensing during winter in polar regions is particularly hard for multiple reasons e.g. cloud cover, sea ice, and sun angle. These difficulties create gaps in the Chl a data available at SG, which may be falsely lowering these levels. Ground truthing the Chl a concentrations in SG throughout the winter season is one way of confirming this remote sampling data bias. Large-scale and long-term studies such as the Palmer Long-Term Ecosystem Research (LTER) program and the U.S. Antarctic Marine Living Resources (AMLR) program can ground truth their Chl a recordings by being present year round in a location to take water samples for Chl a analysis. Future technological advancements may also assist with such ground-truthing, including the use of deployed moorings that take water samples and record algal fluorescence year-round. Improving satellite algorithms for ocean colour data to be converted into Chl a concentrations in polar regions would significantly increase the number of data points available throughout winter. In turn, such enhanced data could then be better related to other factors, such as krill diet, with the remote sensed Chl a data being closer to the true Chl a levels present at that time of year.

Additionally, due to the occurrence of krill swarming, the spatial and temporal scales used may not be the tightest to fit krill dynamics as more than a single krill aggregation may be present in a 3 km × 3 km grid, and krill diet may vary greatly over an 8 Day period. However, total lipid content varies slowly, particularly in the whole animal, as does their fatty acid profile. So, large dietary differences in krill aren’t expected to be seen at this level over the period of 8 days or at a scale of 3 km × 3 km. If, however, this analysis was using the lipids and fatty acids of krill stomachs or digestive glands, then this may have a more significant impact as these would change greatly over the period of 8 days and would show variation within a 3 km × 3 km grid. This study used satellite-derived ocean colour and SST data in conjunction with fatty acid content and composition in krill diet at different times of year and in different locations. Cross-disciplinary work such as in this study is promising as it enables remote sensing and satellite oceanography specialists to better link with biological, physiological and ecological specialists. This collaboration may enable issues such as winter sampling of Chl a through satellites to be better understood, and solutions to issues such as sea ice and cloud cover to be resolved at a scale that is meaningful to the biology associated to that Chl a reading, whether primary producers or krill.

The relationship between SST, Chl a and krill lipid biochemistry presented here could be expanded to examine similar relationships in krill diet and krill lipid content and composition in other regions around Antarctica. The approach could also be used for other marine-based species both in the Antarctic and other polar areas where sampling is restricted.

**Methods**

**Krill sample collection and analysis.** Krill lipid and fatty acid data used for this analysis are published in Hellessey, et al. and Ericson, et al. Krill samples for which lipid and fatty acid data were derived were collected and analysed fortnightly from 3 adult male and 3 adult female krill, with samples collected by the fishing industry (FV Sega suez) in the South Atlantic Ocean (Area 48) (N = 391). Samples from January – May 2014 to 2016 from the WAP (Area 48.1) and SOI (Area 48.2), and June – September 2014 to 2016 from SG (Area 48.3) were used for this analysis. Boundaries and area size for the CCAMLR fishing sub-areas can be found at www.ccamlr.org. The mean body length (Standard length) of krill was 46.0 mm (±4.8) and the mean dry mass was 0.16 g (±0.05). The total lipid (mg g⁻¹ dry weight) of krill (TLDW) in each season of each year is given in Table 2.

**Satellite data extraction and analysis.** This study used ocean colour data from the NASA Moderate Resolution Imaging Spectroradiometer Aqua (MODIS-Aqua) L3 mapped data products (https://oceancolor.gsfc.
et al., and the modified algorithm in Johnson, May), winter (1 June to 31 August), and spring (1 September to 30 November).

Table 2. Average total lipid (mg g\(^{-1}\) dry weight, mean ± SD), length (mm) and weight (g) of Euphausia superba by sex, season and year. Seasons are defined as summer (1 December to 28 February), autumn (1 March to 31 May), winter (1 June to 31 August), and spring (1 September to 30 November).

|          | Total lipid content (mg g\(^{-1}\) dry weight) | Average length (mm) | Average dry weight (g) |
|----------|-----------------------------------------------|----------------------|------------------------|
|          | Males (N = 190)                              | Females (N = 201)    |                        |
| Summer 2014 | 148.9 ± 116.2                                | 148.0 ± 58.7         | 48.19 ± 0.21           |
| Autumn 2014 | 329.8 ± 68.3                                 | 268.6 ± 101.3        | 47.23 ± 0.17           |
| Winter 2014 | 210.6 ± 86.2                                 | 203.8 ± 66.4         | 42.04 ± 0.11           |
| Spring 2014 | 59.8 ± 12.7                                  | 114.8 ± 30.0         | 45.66 ± 0.14           |
| Summer 2015 | 168.1 ± 130.1                                | 166.7 ± 102.1        | 46.49 ± 0.17           |
| Autumn 2015 | 309.2 ± 60.8                                 | 303.8 ± 74.2         | 45.63 ± 0.14           |
| Winter 2015 | 234.1 ± 60.7                                 | 233.5 ± 64.3         | 48.42 ± 0.17           |
| Spring 2015 | 138.9 ± 17.2                                 | 131.3 ± 16.5         | 48.95 ± 0.20           |
| Summer 2016 | 271.8 ± 128.3                                | 217.2 ± 94.3         | 46.77 ± 0.19           |
| Autumn 2016 | 399.7 ± 51.8                                 | 361.3 ± 96.6         | 48.51 ± 0.21           |
| Winter 2016 | 209.0 ± 46.1                                 | 208.0 ± 57.2         | 44.01 ± 0.13           |
| Spring 2016 | 90.7 ± 26.6                                  | 120.1 ± 9.3          | 42.97 ± 0.13           |

Table 3. Decision table used for temporal and spatial fields for the red, green and blue wavelengths in Moderate Resolution Imaging Spectroradiometer (MODIS) to generate chlorophyll \(a\) data. The Commission for Conservation of Antarctic Marine Living Resources (CCAMLR) regions were defined as the West Antarctic Peninsula (W AP), the South Orkney Islands (SOI) and South Georgia (SG).

| Case | Temporal Averaging | Pixel averaging | Percentage (%) match |
|------|-------------------|----------------|----------------------|
| 1    | Daily             | 1 km × 1 km    | 4.18 (28)            |
| 2    | Daily             | 3 km × 3 km    | 7.01 (47)            |
| 3    | 8 Day             | 1 km × 1 km    | 21.64 (145)          |
| 4    | 8 Day             | 3 km × 3 km    | 27.91 (187)          |
| 5    | 8 Day             | Custom         | 46.26 (310)          |
|      |                   | CCAMLR         | 51.34 (344)          |
|      |                   | Regions        | 66.86 (448)          |

**Data and statistical analysis.** Statistical analysis was done in RStudio (version 1.0.153© 2017, packages nlme, ggplot2, ggmap, anytime, and reshape2). Multifactorial ANOVAs were performed using SST and Chl \(a\), as well as their interaction terms, as factors for the variables of total lipid content (mg g\(^{-1}\) dry weight), PL and
TAG percentage, individual fatty acid percentage and mass data for the fatty acids most associated with primary production (mostly diatom and flagellate markers), and the ratios of 16:1/16:0 and EPA:DHA. These were performed to examine diatom levels (higher EPA, higher 16:1) and to look at diatom or flagellate dominance in the diet (higher DHA, lower 16:1), for each location and season. Data were log or square root transformed when the assumptions of normality and homogeneity of variances were not met - Chl a is typically log distributed. Linear models were similarly produced using the same factors as for the multifactorial ANOVAs, including interaction terms, but sub-divided into summer/autumn and winter/spring models due to the large seasonal shift in SST arising from the change of harvesting location by the FV Saga Seas. Models were tested for fit using a standard regression table, where the adjusted $r^2$ value showed the fit of points to the confidence interval of the model. Models were additionally run through drop testing and Tukey post-hoc tests to ensure no compounding of results was occurring. Models of best fit had adjusted $r^2$ values $>0.5$, a $p$ value of $<0.05$ from the multifactorial ANOVAs and a $\chi^2$ value above 0.1. These models are shown within all tables throughout the Results and Supplementary Materials as greyed out.

Maps were produced within R using the maps and ggmap packages to see the geographic distribution of krill lipid content (mg g$^{-1}$ dry weight) as well as SST and Chl a.

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References

1. Hill, S., Murphy, E., Reid, K., Trathan, P. & Constable, A. Modelling Southern Ocean ecosystems: krill, the food-web, and the impacts of harvesting. Biological Reviews 81, 581–608 (2006).
2. Murphy, E. J. et al. Spatial and temporal operation of the Scotia Sea ecosystem: a review of large-scale links in a krill centred food web. Philosophical Transactions of the Royal Society B: Biological Sciences 362, 113–148, https://doi.org/10.1098/rstb.2006.1957 (2007).
3. Clarke, A. Lipid content and composition of Antarctic krill, Euphausia superba Dana. Journal of Crustacean Biology 4, 285–294 (1984).
4. Atkinson, A. et al. Feeding and energy budgets of Antarctic krill Euphausia superba at the onset of winter—II. Juveniles and adults. Limnology and Oceanography 47, 953–966 (2002).
5. Stübinger, 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. Limnology and Oceanography 48, 1685–1700 (2003).
6. Saunders, R. A. et al. Predatory impact of the myctophid fish community on zooplankton in the Scotia Sea (Southern Ocean). Marine Ecology Progress Series 541, 45–64, https://doi.org/10.3354/meps11527 (2015).
7. Ericson, J. A. et al. Seasonal and inter-annual variation in the Fatty Acid Content and Composition of Euphausia superba samples derived from the Scotia Sea fishery. Journal of Crustacean Biology 38, 662–672, https://doi.org/10.1093/jcbiol/ruy032 (2018).
8. Hagen, W., Van Vleet, E. & Kattner, G. Seasonal lipid storage as overwintering strategy of Antarctic krill. Marine Ecology Progress Series. Oldendorf 134, 85–89 (1996).
9. Ju, S.-J. & Harvey, H. R. Lipids as markers of nutritional condition and diet in the Antarctic krill Euphausia superba and Euphausia crystallorophias during austral winter. Deep Sea Research Part II: Topical Studies in Oceanography 51, 2199–2214 (2004).
10. Schmidt, K. & Atkinson, A. Feeding and food processing in Antarctic krill (Euphausia superba Dana). Biology and Ecology of Antarctic Krill, 175–224 (2016).
11. Passmore, A. et al. DNA as a dietary biomarker in Antarctic krill, Euphausia superba. Marine Biotechnology 8, 686–696 (2006).
12. Töbe, K., Meyer, B. & Fuentes, V. Detection of zooplankton items in the stomach and gut content of larval krill, Euphausia superba, using a molecular approach. Polar Biology 33, 407–414 (2010).
13. Bottino, N. The fatty acids of Antarctic phytoplankton and euphausiids. Fatty acid exchange among trophic levels of the Ross Sea. Marine Biology 27, 197–204 (1974).
14. Fricke, H., Gerecken, G., Schreiber, W. & Oehlenschlager, J. Lipid, sterol and fatty acid composition of Antarctic krill (Euphausia superba superba Dana). Lipids 19, 821–827 (1984).
15. Virtue, P., Nicol, S. & Nichols, P. Changes in the digestive gland of Euphausia superba during short-term starvation: lipid class, fatty acid and sterol content and composition. Marine Biology 117, 441–448 (1993).
16. Mayzaud, P. Spatial and life-cycle changes in lipid and fatty acid structural profiles of the Antarctic euphausiid Euphausia superba, in Antarctic Communities: Species, Structure and Survival Cambridge University Press (1997).
17. Kohlbach, D., Graeve, M., David, C., Lange, B. & Flores, H. Dynamics in diet sources of Antarctic krill species revealed by lipid and stable isotope analyses. (2015).
18. Schaafisma, F. L. et al. Spatio-temporal variability in the winter diet of larval and juvenile Antarctic krill, Euphausia superba, in ice-covered waters. Marine Ecology Progress Series 580, 101–115 (2017).
19. Ericson, J. A. et al. Adult Antarctic krill proves resilient in a simulated high CO2 ocean. Communications Biology 1, 190, https://doi.org/10.1038/s42003-018-0195-3 (2018).
20. Hellesley, N. et al. Regional variability of Antarctic krill (Euphausia superba) diet as determined using lipid, fatty acid and sterol composition. Polar Biology (in review) (2019).
21. Nichols, P. D., Palmisano, A. C., Smith, G. A. & White, D. C. Lipids of the Antarctic sea ice diatom Nitzschia cylindrus. Phytochemistry 25, 1649–1653 (1986).
22. Butler, W. E. Omega-3 Fatty Acids—Science, Efficacy, and Clinical Use in Cardiology. (2007).
23. Virtue, P. et al. Krill growth and condition in Western Indian Ocean sector of the Southern Ocean 30–80°E at austral summer 2006. Deep Sea Research Part II: Topical Studies in Oceanography 57, 948–955 (2010).
24. O’Brien, C., Virtue, P., Kawaguchi, S. & Nichols, P. Aspects of krill growth and condition during late winter–early spring off East Antarctica (110–130 E). Deep Sea Research Part II: Topical Studies in Oceanography 58, 1211–1221 (2011).
25. Yokida, T. Environmental influences on reproduction in Antarctic krill, Euphausia superba PhD Thesis, thesis, University of Tasmania, (2009).
26. Kolacowska, A., Kolakowski, E. & Szczypiński, M. Winter season krill (Euphausia superba D.) as a source of n-3 polyunsaturated fatty acids. Food/Nahrung 38, 128–134 (1994).
27. Nicol, S., Foster, J. & Kawaguchi, S. The fishery for Antarctic krill—recent developments. Fish and Fisheries 13, 30–40 (2012).
28. Hill, S. L. Prospects for a sustainable increase in the availability of long chain omega 3s: lessons from the Antarctic krill fishery. In Omega-3 Fatty Acids, 267–296 (Springer, 2013).
29. Schutt, E. The Global Omega-3 Market: A Look at the Numbers and the Consumer. Science of Omega-3: Balancing the Scales Omega-3 Centre Conference, Sydney, Australia (2016).
30. Moore, J. K. & Abbott, M. R. Surface chlorophyll concentrations in relation to the Antarctic Polar Front: seasonal and spatial patterns from satellite observations. *Journal of Marine Systems* 37, 69–86 (2002).

31. Johnson, R., Stratton, P. G., Wright, S. W., McNinn, A. & Meiners, K. M. Three improved satellite chlorophyll algorithms for the Southern Ocean. *Journal of Geophysical Research: Oceans* 118, 3769–3783 (2013).

32. Zeng, C., Xu, H. & Fischer, A. M. Chlorophyll-a estimation around the Antarctica peninsula using satellite algorithms: hints from field water leaving reflectance. *Sensors* 16, 2075 (2016).

33. Deppeler, S. L. & Davidson, A. T. Southern Ocean phytoplankton in a changing climate. *Frontiers in Marine Science* 4, 40 (2017).

34. Dutkiewicz, S. et al. Ocean colour signature of climate change. *Nature communications* 10, 578 (2019).

35. Hancock, A. M. et al. Ocean acidification changes the structure of an Antarctic coastal protistan community. *Biogeosciences* 15, 2393–2410 (2018).

36. Fraser, W. R. & Hofmann, E. E. A predator's perspective on causal links between climate change, physical forcing and ecosystem response. *Marine Ecology Progress Series* 265, 1–15 (2003).

37. Schofield, O. et al. How do polar marine ecosystems respond to rapid climate change? *Science* 328, 1520–1523 (2010).

38. Behrenfeld, M. J. et al. Annual bloom–bust cycles of polar phytoplankton biomass revealed by space-based lidar. *Nature Geoscience* 10, 118 (2017).

39. Montes-Hugo, M. et al. Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic Peninsula. *Science* 323, 1470–1473 (2009).

40. Garibotti, I. A., Vernet, M. & Ferrario, M. E. Annual recurrent phytoplanktonic assemblages during summer in the seasonal ice zone west of the Antarctic Peninsula (Southern Ocean). *Deep Sea Research Part I: Oceanographic Research Papers* 52, 1823–1841 (2005).

41. Moline, M. A., Prezelin, B. B. & Schofield, O. Palmer LTER: Stable interannual successional patterns of phytoplankton communities in the coastal waters off Palmer Station, Antarctica. *Antarctic Journal of the United States* 32, 151 (1997).

42. Helbling, E. W., Villafañe, V. E. & Holm-Hansen, O. Variability of phytoplankton distribution and primary production around Elephant Island, Antarctica, during 1990–1993. *Polar Biology* 15, 233–246 (1995).

43. El-Sayed, S. & Weber, L. Spatial and temporal variations in phytoplankton biomass and primary productivity in the Southwest Atlantic and the Scotia Sea. *Polar Biology* 1, 83–90 (1982).

44. Arrigo, K. R., van Dijken, G. L. & Bushinsky, S. Primary production in the Southern Ocean, 1997–2006. *Journal of Geophysical Research: Oceans* 113, https://doi.org/10.1029/2007JC004551 (2008).

45. Whitehouse, M. J. et al. Rapid warming of the ocean around South Georgia, Southern Ocean, during the 20th century: Forcings, characteristics and implications for lower trophic levels. *Deep Sea Research Part I: Oceanographic Research Papers* 55, 1218–1228, https://doi.org/10.1016/j.dsr.2008.06.002 (2008).

46. Tarling, G. A. et al. Growth and shrinkage in Antarctic krill *Euphausia superba* is sex-dependent. *Marine Ecology Progress Series* 547, 61–78 (2016).

47. Nicol, S. & Foster, J. The Fishery for Antarctic Krill: Its Current Status and Management Regime. *Biology and Ecology of Antarctic Krill*, 387–421 (2016).

48. Hellesy, N. et al. Seasonal and Interannual variation in the lipid content and composition of *Euphausia superba* Dana, 1850 (Euphausiacea) samples derived from the Scotia Sea fishery. *Journal of Crustacean Biology* 38, 673–681, https://doi.org/10.1093/jcbiol/ruy053 (2018).

49. Korb, R. E., Whitehouse, M. J., Thorpe, S. E. & Gordon, M. Primary production across the Scotia Sea in relation to the physico-chemical environment. *Journal of Marine Systems* 57, 231–249 (2005).

50. Kawaguchi, S. Reproduction and larval development in Antarctic krill (*Euphausia superba*). *Biology and Ecology of Antarctic Krill Springer, 225–246 (2016).

51. Schmidt, K., Atkinson, A., Pond, D. W. & Ireland, L. C. Feeding and overwintering of Antarctic krill across its major habitats: The role of sea ice cover, water depth, and phytoplankton abundance. *Limnology and Oceanography* 59, 17–36 (2014).

52. Schmidt, K., Atkinson, A., Venables, H. J. & Pond, D. W. Early spawning of Antarctic krill in the Scotia Sea is fuelled by “superfluous” feeding on non-ice associated phytoplankton blooms. *Deep Sea Research Part II: Topical Studies in Oceanography* 59–60, 159–172, https://doi.org/10.1016/j.dsr2.2011.05.002 (2012).

53. Kohlbach, D. et al. Dependency of Antarctic zooplankton species on ice algae-produced carbon suggests a sea ice-driven pelagic ecosystem during winter. *Global change biology* 24, 4667–4681 (2018).

54. Kohlbach, D. et al. Ice Algae-Produced Carbon Is Critical for Overwintering of Antarctic Krill *Euphausia superba*. *Frontiers in Marine Science* 4, https://doi.org/10.3389/fmars.2017.00310 (2017).

55. Meyers, B. et al. The winter pack-ice zone provides a sheltered but food-poor habitat for larval Antarctic krill. *Nature Ecology & Evolution* 1, 1853 (2017).

56. Mayzaud, P., Albessard, E. & Cuzin-Roudy, J. Changes in lipid composition of the Antarctic krill *Euphausia superba* in the Indian sector of the Antarctic Ocean: influence of geographical location, sexual maturity stage and distribution among organs. *Marine Ecology Progress Series* 173, 149–162 (1998).

57. Alonsoz, F., Virtue, P., Nicol, S. & Nichols, P. D. Lipids as trophic markers in Antarctic krill. II. Lipid composition of the body and digestive gland of *Euphausia superba* in controlled conditions. *Marine Ecology Progress Series* 296, 65–79 (2005).

58. Virtue, P. et al. Condition of larval (farcilia VI) and one year old juvenile *Euphausia superba* during the winter–spring transition in East Antarctica. *Deep Sea Research Part II: Topical Studies in Oceanography* 131, 182–188 (2016).

59. Morris, D. J., Eversen, I., Ricketts, C. & Ward, P. Feeding of krill around South Georgia. II. Relations between feeding activity, environment and vertical distribution. *Marine Ecology Progress Series* 20, 203–206 (1984).

60. Hagen, W., Kattner, G., Terbrüggen, A. & Van Vleet, E. S. Lipid metabolism of the Antarctic krill *Euphausia superba* and its ecological implications. *Marine Biology* 95, 90–104, https://doi.org/10.1007/s00227-0005-0527 (2001).

61. Mayzaud, P., Albessard, E., Virtue, P. & Boutoule, M. Environmental constraints on the lipid composition and metabolism of euphausiids: the case of *Euphausia superba* and *Meganyctiphanes norvegica*. *Canadian Journal of Fisheries and Aquatic Sciences* 57, 91–103 (2000).

62. Huntley, M. E., Nordhausen, W. & Lopez, M. D. Elemental composition, metabolic activity and growth of Antarctic krill *Euphausia superba* during winter. *Marine Ecology Progress Series* 23, 39–40 (1994).

63. Ericson, J. & et al. New insights into the seasonal diet of Antarctic krill using triacylglycerol and phospholipid fatty acids, and sterol composition. *Polar Biology* 42, 1985–1996 (2019).

64. Atkinson, A. et al. Natural growth rates in Antarctic krill (*Euphausia superba*): II. Predictive models based on food, temperature, body length, sex, and maturity stage. *Limnology and Oceanography* 51, 973–987 (2006).

65. Rayner, N. A. Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. *Journal of Geophysical Research* 108, https://doi.org/10.1029/2002JD002670 (2003).

66. Varpe, O., Jorgensen, C., Tarling, G. A. & Fiksen, Ø. Early is better: seasonal egg fitness and timing of reproduction in a zooplankton life-history model. *Oslo* 116, 1331–1342, https://doi.org/10.1111/1399-0995.15893 (2007).

67. Ross, R. & Quetin, L. Reproduction in euphausiids. in *Krill*. Springer, 150–181 (2000).

68. Yoshida, T., Virtue, P., Kawaguchi, S. & Nichols, P. D. Factors determining the hatching success of Antarctic krill *Euphausia superba* embryo: lipid and fatty acid composition. *Marine biology* 158, 2313–2325 (2011).
69. Nichols, P. D., Palmisano, A. C., Volkman, J. K., Smith, G. A. & White, D. C. Occurrence of an isoprenoid C25 diunsaturated alkene and high neutral lipid content in Antarctic sea-ice diatom communities. *Journal of Phycology* 24, 90–96 (1988).

70. Skerratt, J., Nichols, P., McMeekin, T. & Burton, H. Seasonal and inter-annual changes in planktonic biomass and community structure in eastern Antarctica using signature lipids. *Marine Chemistry* 51, 93–113 (1995).

71. Kahru, M., Lee, Z. & Mitchell, B. G. Contemporaneous disequilibrium of bio-optical properties in the Southern Ocean. *Geophysical Research Letters* 44, 2835–2842, https://doi.org/10.1002/2016GL072453 (2017).

72. IOCCG. Ocean Colour Remote Sensing In Polar Seas. Babin, M., Arrigo, K., Bélanger, S. & Forget, M-H. (eds). *IOCCG Report Series*, No. 16. (2015).

73. Smith, R. C. *et al.* The Palmer LTER: A long-term ecological research program at Palmer Station, Antarctica. *Oceanography* 8 (1995).

74. Holm-Hansen, O., Amos, A. E., Villafañe, V. & Helbling, E. W. *In situ* evidence for a nutrient limitation of phytoplankton growth in pelagic Antarctic waters. *Antarctic Science* 6, 315–324 (1994).

75. Phleger, C. F., Nelson, M. M., Mooney, B. D. & Nichols, P. D. Interannual and between species comparison of the lipids, fatty acids and sterols of Antarctic krill from the US AMLR Elephant Island survey area. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology* 131, 733–747 (2002).

76. Kirkwood, J. M. *A guide to the Euphausiacea of the Southern Ocean*. (Information Services Section, Antarctic Division, Dept. of Science and Technology, 1982).

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**Author contributions**

N. Hellessey conceived of the project, performed lab work and analysis and wrote the manuscript. R.J. collected all environmental data and transformed this into chlorophyll *a* data using Johnson *et al.* (2013) algorithm. J.A.E. assisted with lab work. P.D.N. assisted with study conception, lab work and analysis. N. Hoem provided samples from Aker BioMarine and provided partial funding of the project. S.K. and S.N. assisted with drafting and revising the manuscript. P.V. conceived of the project and procured the funding as well as assisting in the lab. All authors reviewed the manuscript.

**Competing interests**

The authors declare the following competing interests: Steve Nicol has been employed to provide scientific advice to the Association of Responsible Krill Fishing companies and Nils Hoem works for Aker BioMarine as their Chief Scientist. Lipid data contained in this paper will be available through the Scientific Committee for Antarctic Research (SCAR) Southern Ocean Diet and Energetics Database (https://data.aad.gov.au/trophic/). Satellite data used throughout the paper is freely available currently to download at (https://oceancolor.gsfc.nasa.gov/data/aqua/) and (https://data.nodc.noaa.gov/ghrsst/L4/).

**Additional information**

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