



Summer distribution and demography of Antarctic krill *Euphausia superba* Dana, 1852 (Euphausiacea) at the South Orkney Islands, 2011–2015

**Krafft, Bjørn A.; Krag, Ludvig Ahm; Knutsen, Tor; Skaret, Georg; Jensen, Knut H. M.; Krakstad, Jens O.; Larsen, Stuart H.; Melle, Webjørn; Iversen, Svein A.; Godø, Olav R.**

*Published in:*  
Journal of Crustacean Biology

*Link to article, DOI:*  
[10.1093/jcbiol/ruy061](https://doi.org/10.1093/jcbiol/ruy061)

*Publication date:*  
2018

*Document Version*  
Publisher's PDF, also known as Version of record

[Link back to DTU Orbit](#)

*Citation (APA):*  
Krafft, B. A., Krag, L. A., Knutsen, T., Skaret, G., Jensen, K. H. M., Krakstad, J. O., Larsen, S. H., Melle, W., Iversen, S. A., & Godø, O. R. (2018). Summer distribution and demography of Antarctic krill *Euphausia superba* Dana, 1852 (Euphausiacea) at the South Orkney Islands, 2011–2015. *Journal of Crustacean Biology*, 38(6), 682-688. <https://doi.org/10.1093/jcbiol/ruy061>

---

#### General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.



The Crustacean Society

# Journal of Crustacean Biology

*Journal of Crustacean Biology* 38(6), 682–688, 2018. doi:10.1093/jcabi/ruy061

## Summer distribution and demography of Antarctic krill *Euphausia superba* Dana, 1850 (Euphausiacea) at the South Orkney Islands, 2011–2015

Bjørn A. Krafft<sup>1</sup>, Ludvig A. Krag<sup>2</sup>, Tor Knutsen<sup>1</sup>, Georg Skaret<sup>1</sup>, Knut H.M. Jensen<sup>3</sup>,  
Jens O. Krakstad<sup>1</sup>, Stuart H. Larsen<sup>1</sup>, Webjørn Melle<sup>1</sup>, Svein A. Iversen<sup>1</sup> and Olav R. Godø<sup>1</sup>

<sup>1</sup>Institute of Marine Research, Nordnesgaten 50, 5005 Bergen, Norway;

<sup>2</sup>Technical University of Denmark, National Institute of Aquatic Resources, Niels Juelsvej 30, DK-9850 Hirtshals, Denmark; and

<sup>3</sup>University of Bergen, Musèplassen 1, 5007 Bergen, Norway

Correspondence: B.A. Krafft; email: [bjorn.krafft@imr.no](mailto:bjorn.krafft@imr.no)

(Received 4 April 2018; accepted 21 June 2018)

### ABSTRACT

We carried out a survey of Antarctic krill (*Euphausia superba* Dana, 1850) from 2011 to 2015 to establish a long-term, time-series dataset of distribution, abundance, and demography for this species in the South Orkney Islands sector of the Southern Ocean. This species is abundant in this region and is subjected to high-intensity fishing, but previous assessments of density and population dynamics are few and outdated. Our data for Antarctic krill was collected from trawl stations along survey line transects covering the South Orkney plateau and shelf region during the summers of five consecutive years. We used concurrent data on hydrography, bathymetry, and proxies for algal biomass to describe potential spatial patterns of demography and abundance of *E. superba*. Comparative analysis of the demographic composition showed that 2012 differed from the other years by having a higher proportion of juveniles; otherwise a consistent pattern was found among years and within the study area. The highest biomass during the study period occurred along the northern shelf edge of the South Orkney Islands. Results of the linear mixed-effect model used to evaluate a diverse range of variables revealed that the only predictors for this hotspot were the short distance from land and great bottom depth. No clear differences in demographic composition for the study area were detected, which indicates that the area is highly dynamic and dominated by flux and advection of krill, both to, from, and within the area. Despite this finding, the results demonstrate that the shelf break on the northwest South Orkney Islands is predictable over time as a krill concentration and retention hotspot during the summer season.

**Key Words:** fisheries, maturity stage, Southern Ocean, time series, zooplankton

### THIRD INTERNATIONAL SYMPOSIUM ON KRILL

#### INTRODUCTION

The western South Atlantic sector of the Southern Ocean contains the highest concentrations of Antarctic krill (*Euphausia superba* Dana, 1850, hereafter krill) (Atkinson *et al.*, 2009). The krill fishery is regulated by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). During the last two decades, this fishery has been focused mainly in subareas 48.1 (Bransfield Strait and Elephant Island), 48.2 (South Orkney Islands), and 48.3

(off South Georgia Islands). It is difficult to describe and quantify how the population dynamics of the Antarctic krill change temporally and regionally, especially at somewhat larger spatial scales, because actual monitoring of the stock has been very limited in time and space. Nonetheless, the few existing small spatially scaled krill monitoring programmes provide valuable biomass and demography data (indices) that answer important questions about change in the krill stock. Monitoring of krill during the last two decades has been regularly performed by the U.S. Antarctic

Marine Living Resources Program in subarea 48.1 (Kinzey *et al.*, 2015) and the British Antarctic Survey in subarea 48.3 (Fielding *et al.*, 2014). Knowledge about the distribution and biology of the species in the South Orkney Islands, which has a high abundance of krill (Atkinson *et al.*, 2008) and is subjected to particularly high fishing activity (Nicol *et al.*, 2012), is fragmented and outdated.

Most fishing in subarea 48.2 occurs in a concentrated area over the shelf break northwest of the South Orkney Islands. The area includes two north-south oriented canyons, the Monroe and Coronation Troughs (Dickens *et al.*, 2014), which are described as hotspots for krill (Nicol *et al.*, 2012; Krafft *et al.*, 2015). The area is likely important for retention of krill that are advected along the shelf and slope region from areas further west and southwest or via deeper currents from the Weddell Sea region flowing east and turning north in a counter clockwise direction around the South Orkney plateau (Gordon *et al.*, 2001). The South Orkney plateau rises from abyssal depths to an average depth of approximately 300 m, with shallower parts closer to the islands. The shelf is defined as the area that is shallower than 1,000 m deep (Clarke & Johnston, 2003).

The current fisheries management protocol for the Antarctic region considers large-scale distribution and abundance information. Overall, 87% of the stock is found over deep oceanic water (Atkinson *et al.*, 2004). Smaller scale shelf and/or shelf break krill hotspots exist, and the current fishery mainly operates in these areas. These hotspots represent 13% of the total stock, and they are significant because they support key ecosystem functions, provide resilience for the stock, and are important areas for krill-dependent predators (Santora *et al.*, 2011). Hotspots may offer favourable food availability for krill as well as shelter from offshore currents, which may transfer krill to less productive areas (Hazen *et al.*, 2013). Other factors related to gregarious behaviour may be related to reproductive facilitation (Ritz, 2000), predator avoidance (Hamner *et al.*, 1983; O'Brien & Ritz; 1988, Evans *et al.*, 2007), or promote energetic advantages (Ritz, 2000; Ritz *et al.*, 2001). Although locations of high abundance areas are well known, the spatial distribution of krill can be quite variable and difficult to predict (Constable & Nicol, 2002).

During the 2010 meeting of the CCAMLR Working Group on Ecosystem Monitoring and Management, the Norwegian Antarctic krill fishing industry offered a commercial vessel to be used as research platform for an annual five-day scientific survey in the South Orkney region (Jensen *et al.*, 2010). A survey was designed according to the standards used in similar annual surveys undertaken in subareas 48.1 and 48.3 (SC-CAMLR, 2010).

The initial Norwegian scientific contribution in the South Orkney region was originally financed with a five-year perspective to establish systematic monitoring distribution, abundance, and population characteristics of Antarctic krill. The work presented here is the result of the first systematic surveys conducted from 2011 to 2015 in CCAMLR region 48.2. Although it was designed as an acoustic trawl survey, we explored only the trawl catch data for krill collected at stations along survey transect lines over the course of the times series. The main objectives of this part of a long-term study were to evaluate the survey design and performance to ensure further development and suitability for stock assessment and applicability to management decisions. Sexual maturation, sex ratio, and other population parameters, such as abundance and distribution, were used to describe potential relationships of these factors with bathymetry, hydrography, and proxies for algal biomass to evaluate the temporal predictability of the hotspot as krill concentration and retention areas.

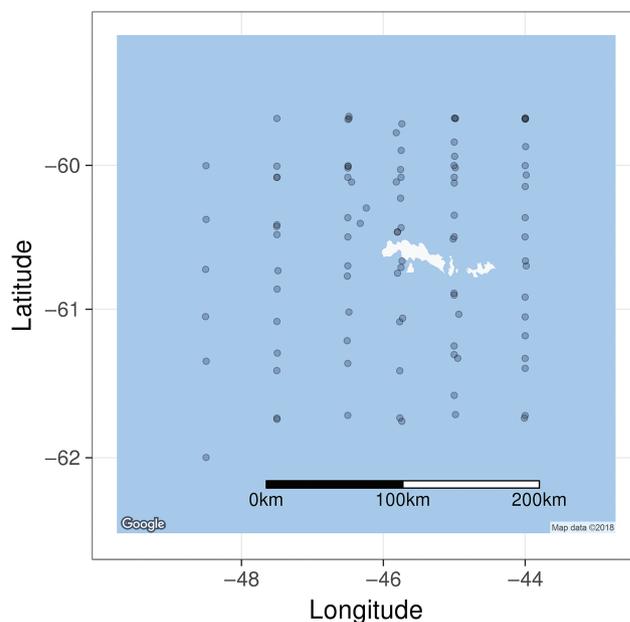
## MATERIALS AND METHODS

Data were collected during the summers of 2011 to 2015 (from 24 January to 12 February) in waters off the South Orkney

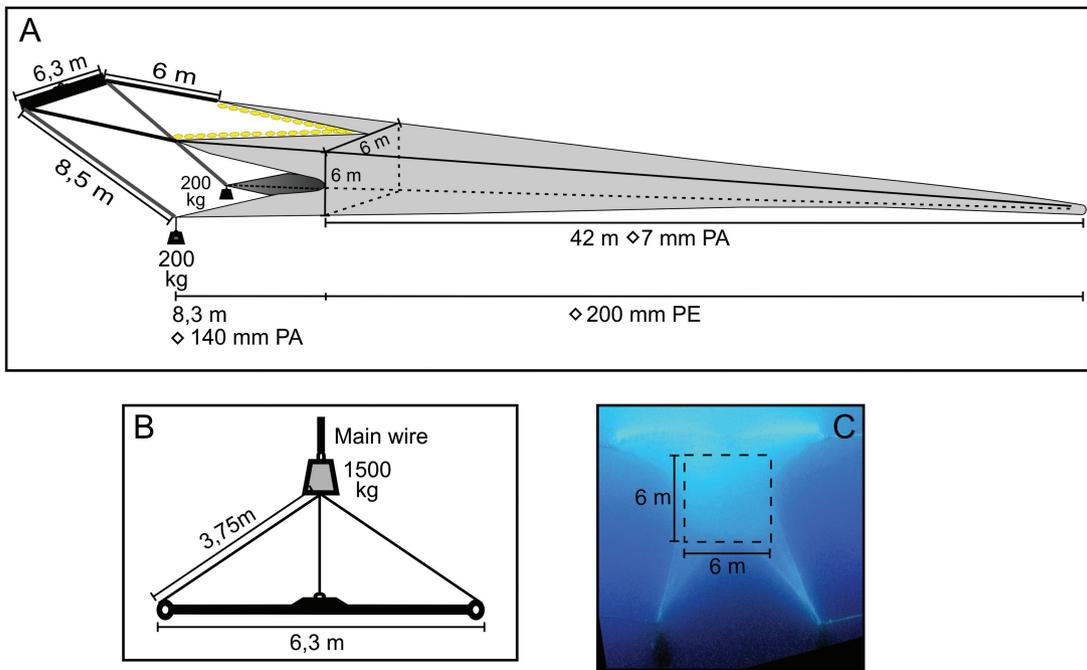
Islands. The research platforms employed were two commercial Norwegian ramp trawlers: FV *Saga Sea* (Aker Biomarine AS, Oslo, Norway) in 2011, 2013, and 2014, and FV *Jewel* (Rimfrost AS, Fosnavåg, Norway) in 2012 and 2015. The study area included the waters between 59°40'S and 62°00'S and from 44°00'W to 48°30'W. The survey design included trawl stations spaced 37.0–46.30 km (~20–25 nautical miles) apart along predetermined parallel north-south oriented transect lines (Fig. 1). Some parts of the study area could not always be covered due to drifting pack ice, which prevented ship operations, including trawling. This was particularly the case during the 2013 and 2015 surveys.

The standard survey trawl used was 42 m long, with a 36 m<sup>2</sup> mouth opening, constructed of 7 mm (stretched) diamond-shaped mesh from mouth to rear (Fig. 2). The trawl was towed using a 6 m wide steel beam with 200 kg weights at each lower wing tip and 1,500 kg attached to the beam to ensure fast deployment to depth and the best possible geometric stability of the trawl during sampling. A different trawl with a codend mesh of 11 mm was employed during the 2013 survey. Our standard trawl was lost at the Montevideo, Uruguay warehouse prior to departure, so we made a new trawl with the material we had available. A depth sensor (Marport™, Reykjavik, Iceland) attached to the headline transferred data to the wheelhouse to monitor trawl operations. At each station the trawl was lowered vertically from surface to ~200 m depth (or ~20 m above bottom if the water was < 200 m) and then hauled in at 3.7 km hr<sup>-2</sup> (~2.0 knots) including vessel and wire speed.

When landed on the trawl deck, the codend was opened and the catch was removed. The towing rig was then hung from a crane and flushed on deck to wash out any biological remains stuck in the net. The macrozooplankton and micronekton were sorted, identified to species or to the nearest taxonomic group, and weighed. Given the reasonably fast deployment of the trawl to maximum depth, very little water was filtered through the net on its descent. We considered each haul to start at maximum depth (a) and end when the trawl broke the sea surface upon recovery. The horizontal distance (b) was the distance the vessel moved between these two points. The oblique distance trawled, in meters ( $c = \sqrt{a^2 + b^2}$ ) and the associated water volume (m<sup>3</sup>) filtered were used to compute density and abundance of organisms caught by the trawl. The krill and associated organisms caught were converted to their weight equivalent (g m<sup>-2</sup>) using:



**Figure 1.** Survey trawl stations off the South Orkney Islands sampled during the summers of 2011–2015 (24 January to 12 February).



**Figure 2.** The standard trawl used during the 2011–2015 summer surveys off the South Orkney Islands with a 7 mm meshed inner net made of polyamide (PA), 140 mm meshed PA net in the mouth, and 200 mm meshed outer support net in polyethylene (PE) (A). Steel beam with rigging (B) and underwater image captured during towing showing the mouth opening (C).

$$\text{water filtered} = 36 \text{ m}^2 \times c$$

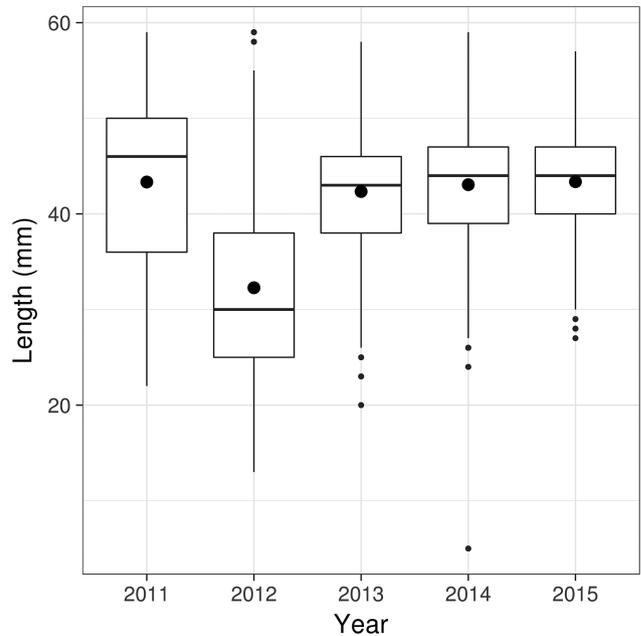
$$\text{weight (i)} = \text{weight (i)} / \text{water filtered} \times a$$

where i is the species or taxon being measured.

The entire catch of krill or a random subsample of a minimum of 100 individuals was used for length measurements. The measurement was taken from the anterior margin of the eye to the tip of telson, excluding the setae ( $\pm 1$  mm), according to Marr (1962). Sex and maturity stages were determined using the classification methods of Makarov & Denys (1981) and described in Krafft et al. (2010, 2015, 2016).

To obtain profiles of temperature ( $^{\circ}\text{C}$ ), salinity, and depth during the hauls, a CTD profiler (SAIV A/S, model SD208, Environmental Sensors and Systems, Bergen, Norway) was mounted on the trawl beam. An optional sensor measuring fluorescence (SAIV A/S, Environmental Sensors and Systems, Bergen, Norway) was employed during the surveys in 2012, 2013, and 2014. Data were recorded at 10 s intervals. Due to a malfunction in the storage unit, data were not recorded from the westernmost transect in 2014 or from the easternmost transect and northeastern part of the study area in 2015. Only data at depths  $\geq 1$  m were included in the analyses to allow time for the instrument to adjust to ambient water temperature and to avoid disturbances from turbid surface waters while deploying the trawl.

Measurements of the surface chlorophyll a concentration were also obtained from the moderate resolution imaging spectroradiometer satellite instrument (MODIS-AQUA, Washington, DC, USA; <https://www.nasa.gov/>). All available satellite passes (one or two per day) were used (courtesy of the Ocean Biology Processing group, NASA). The level 1A product was re-processed to level 3 quality but maintained at daily resolution rather than the 8-d binned product available from NASA. The MODIS chlorophyll a product had a resolution of  $1000 \times 1000$  m, and all available pixels were utilised to maintain this spatial resolution. This permitted us to match these



**Figure 3.** Size of Antarctic krill (*Euphausia superba*) sampled at the South Orkney Islands in 2011, 2012, 2013, and 2014. The boxes show the medians and quartiles, and the whiskers show the extremes within 1.5 times the interquartile range. The big black circles show raw means across all individuals.

data directly to the time periods sampled by the ship at the highest resolution possible. The amount of data available was limited over the study area due to the presence of clouds and sea ice.

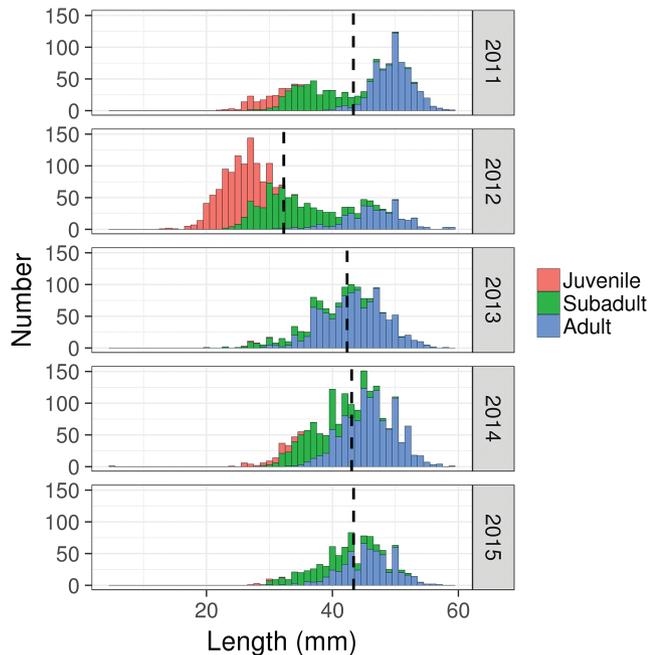
To extract bottom topography data, the vessel track positions were coupled to the elevation data from the bathymetric high-resolution-grid database (300 m) of the continental shelf

surrounding the South Orkney Islands northeast of the Antarctic Peninsula (Dickens *et al.*, 2014). The original data were downloaded from the Marine Geoscience Data System (<http://www.marine-geo.org/index.php>) as a gridded file in GEOTIFF format. It was imported to ArcGIS ([www.arcgis.com](http://www.arcgis.com)), converted from raster to ASCII, and then imported to Fledermaus (<http://www.qps.nl/display/fledermaus/main>), where it was converted to decimal latitude, longitude, and elevation (bottom depth) using

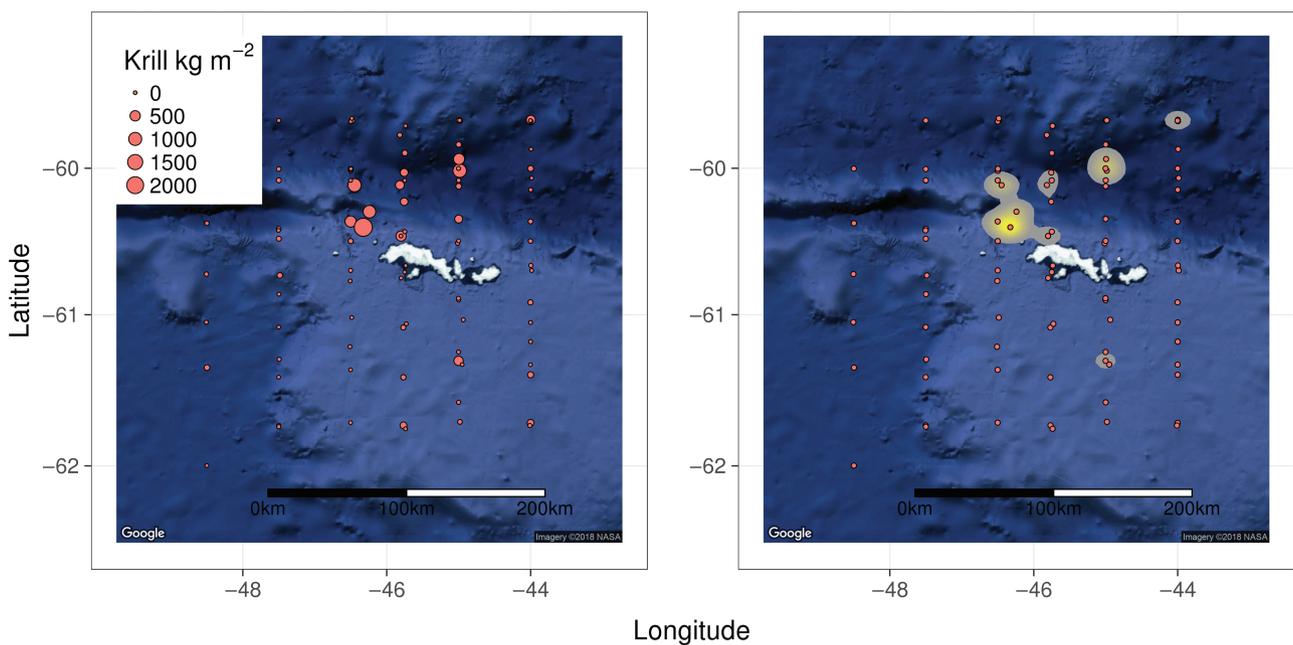
WGS84. Thereafter, a simple algorithm was developed to find the geographic position and associated bottom depth that most closely corresponded to individual station positions throughout the study period.

All statistics were performed, and data plotted, using R version 3.4.3 (R Development Core Team 2017; <http://www.r-project.org>). To look for cohort effects, krill length was compared between years causing a linear mixed effect model (LME) with krill length (mm) as the response variable and year as the categorical predictor. Sampling station was set as a random effect factor, with station names not replicated over years. Sample sizes for 2011, 2012, 2013, 2014, and 2015 were 1225, 1865, 1270, 1729, and 913 individuals, respectively. A Tukey honest significant difference (HSD) post hoc test was used to evaluate which years differed from each other with respect to krill length. A demographic plot (length frequencies for juveniles, subadults, and adults) for each year were generated to give an overview of dominant age classes for the different years.

The survey grid covered an area of  $\sim 250 \times 250$  km. This included, but was significantly larger than, the area where commercial vessels catch most krill. To investigate the uniqueness of the krill hotspot, we followed two main steps. First, we pooled samples for all years and performed a two-dimensional kernel density estimation (kde2d) using the `stat_density_2d` function from the `ggmap` library of R. For this to be possible, we first converted the catch in each sample ( $\text{g krill m}^{-2}$ ) into a pseudo-frequency, where the mass of krill was rounded off to the nearest whole number. From this analysis we created a map showing where kde2d defined krill hotspots. Samples from 2011 were not included in this analysis because no catch weights were recorded for this year. Second, the samples were divided into two groups: one was the samples within the hotspot areas defined by kde2d, and the second included the samples outside the hotspots. We then compared the two groups with respect to abiotic and biotic factors such as temperature, salinity, krill size, and proportion of females. For each of these variables, a Welch t-test was used to compare samples taken within and outside the hotspots.



**Figure 4.** Demography of *Euphausia superba* over different years of sampling around the South Orkney Islands.



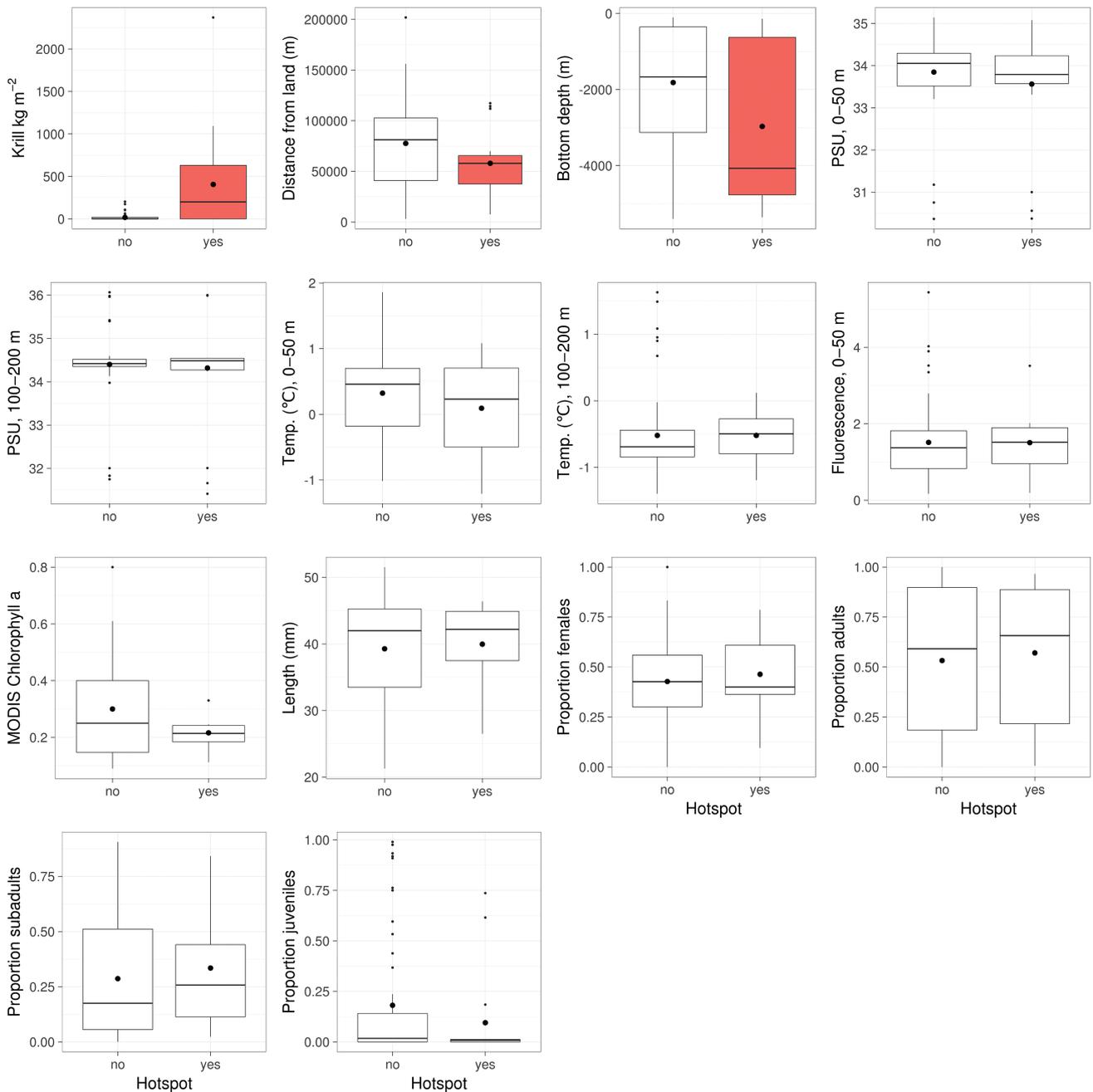
**Figure 5.** Location of stations around the South Orkney Islands during the 2011–2015 investigations. The left panel provides an overview of the abundance of *Euphausia superba* ( $\text{g m}^{-2}$ ) at all stations visited. The right panel shows hotspots of *Euphausia superba* (grey/yellow) defined by two-dimensional kernel density estimation. The areas with highest -probability density (yellow) are the areas with highest probability of catching krill. Samples outside the grey and yellow areas (i.e., outside hotspots), have a probability of catching krill that is close to zero during the times of sampling.

We created a demographic plot (length frequencies of juveniles, subadults, and adults) for each sampling date each year to search for potential differences in maturation over sampling dates. We also tested for a south-north difference in maturation, as an effect of advection time, by dividing the data in two at the mean latitude of all samples (i.e., at latitude = -60.52771°). Samples equal to or at the southern side of this border were categorised as southern, whereas the others were dubbed northern. These data were analysed with the same type of LME described above, but the categorical predictor was latitude (with the levels southern and northern as described above) rather than year.

RESULTS

The LME for length over years showed a statistically significant effect of year ( $F_{4,94} = 16.480, P < 0.001$ ; Figs 3–6, Supplementary material Fig S1). The Tukey HSD post hoc test revealed that 2012 was the only year that differed from the others. As seen from the demographic plots divided over years (Fig. 3, Supplementary material S1), 2012 differed most from the others by having a higher proportion of juveniles.

The location of the most conspicuous hotspot, as defined by the kde2d estimation, was along the northern shelf edge off South Orkney Islands (Fig. 5). Based on the evaluated variables, the strongest predictors for a hotspot were distance from land and bottom depth. Hotspots were closer to land than samples taken outside the hotspots, and the mean bottom depth inside hotspots was deeper



**Figure 6.** Different abiotic and biotic measures outside and within the hotspot areas for *Euphausia superba*. Significant differences between the two types of locations are marked with different coloured boxes. Each plot is based on mean values from each station.

**Table 1.** Results from Welch t-tests using data based on mean values for each station.

Variables	t	df	P
Krill/m <sup>-2</sup>	3.080	20.044	0.006
Distance from land	2.221	39.629	0.032
Bottom depth	2.400	26.724	0.024
Salinity, 0–50 m	0.800	19.902	0.433
Salinity, 100–200 m	0.245	19.362	0.809
Temperature, 0–50 m	1.179	25.465	0.249
Temperature, 100–200 m	0.002	46.362	0.998
Fluorescence, 0–50 m	0.026	18.918	0.980
MODIS Chl. a	1.795	21.136	0.087
Length (mm) of krill	0.365	32.537	0.717
Proportion of female krill	0.673	31.859	0.506
Proportion of adult krill	0.375	26.251	0.711
Proportion of subadult krill	0.619	24.629	0.542
Proportion of juvenile krill	1.265	36.304	0.214

than that outside hotspots (Fig. 6, Table 1). There were no differences in means of the samples between areas outside and inside the hotspots for all other variables (Fig. 6, Table 1). No north-south gradient in size of the krill was found (LME,  $F_{1,97} = 1.647$ ,  $P = 0.203$ ; Supplementary material Fig. S2). No clear pattern of increased maturation level of the krill over the days of sampling within each year or over the years pooled was detected (Supplementary material Fig. S3). When the same data were visualised in a demographic plot, no clear differences in demographic composition between northern and southern samples were found (Supplementary material Fig. S3).

## DISCUSSION

The data from these surveys represent a snapshot in time taken during the same period of the krill annual cycle over five consecutive years (2011–2015) in the South Orkney Islands. The short summer at these latitudes is when the krill deposit their main fat stores (Quetin & Ross, 2001), and it coincides with their energy demanding reproduction (Siegel, 2012). The period also coincides with the lowest sea-ice cover of the season, which is essential for optimising the area covered by the research vessel. Except for the year 2012, a consistent pattern of demographic composition was found over the years in the sampled area. Further, there were no clear spatial effects on demographic composition of the krill. These results indicate that the study design, including the density and location of trawl stations, the trawl gear used, and the trawling method employed, produced apparently representative and robust results with respect to spatial and temporal demographic patterns and trends. The higher composition of juveniles in 2012 likely reflected natural oscillations in production, recruitment, or advection processes. Population parameters are dynamic and change over time. Data collected over an extended time period will likely support in-depth analysis of likely changes in the future population.

Based on the variables that were evaluated, the only predictors for the conspicuous hotspot along the northern shelf edge off South Orkney Islands were distance from land (short) and bottom depth (deep). Few studies have demonstrated a clear and consistent relationship between single environmental factors and krill density (e.g., temperature, salinity, oxygen concentration, nutrient levels, dissolved organic matter, seawater stability, frontal systems and latitude) (Witek *et al.*, 1981; Weber *et al.*, 1986). Hydrographical features are known to affect the distribution of krill on a broad range of scales (Nicol *et al.*, 2000). Siegel *et al.* (2013) found a weak correlation between the abundance of krill and chlorophyll *a* in the Antarctic Peninsula region. Trathan & Murphy (2003) described a fine-scaled relationship between krill density and their environment

based on analysis of active targeting by the krill fishery along the shelf break zones with the highest densities of krill in the Scotia Sea and Antarctic Peninsula. The upper circumpolar deep water (UCDW) interacts with the shelf break in the Antarctic Peninsula region, and where deep canyons intrude into the shelf, the UCDW transports krill through the canyons onto the shelf (Ashijan *et al.*, 2004; Lawson *et al.*, 2004). The UCDW also provides the deep troughs and canyons with nutrients, leading to increased total phytoplankton and diatom biomass (Kavanaugh *et al.*, 2015). This might modify krill behaviour (diel vertical migration, swarming and continuous swimming) and thereby impact krill distribution, resulting in retention and accumulation in such local areas. A deeper understanding of these bathymetrically complex habitats combined with the cyclonic circulation and eddies is important for describing mechanisms for retaining krill within such shelf habitats.

The area recognised as a krill hotspot in the South Orkney Islands sector is mainly associated with waters influenced by the Weddell Sea (Murphy *et al.*, 2004) south of the Antarctic Circumpolar Current (ACC), which strongly dominate the rest of the Scotia Sea (Orsi *et al.*, 1995). A pathway for deep outflow of Weddell Sea Deep Water with the Weddell Front is directed by the topography around the South Orkney Shelf (Gordon *et al.*, 2001) and contributes to the Weddell–Scotia Confluence and the transport of krill (Marr, 1962; Mackintosh, 1972; Thompson *et al.*, 2009). This outflow from the Weddell Sea is fundamental to the krill ecology of the Scotia Sea (Marr, 1962; Mackintosh, 1972; Murphy *et al.*, 2004). The scale of this northerly flow of Weddell Sea-influenced waters both to the east and west of the South Orkney Islands is likely to vary and thereby influence variability in krill densities along the edge of the northern shelf.

The South Orkney Islands are in the Southern Ocean region where some of the strongest signals of global climate change have occurred during the past decades (Forcada *et al.*, 2006; Stammerjohn *et al.*, 2012). Krill are stenothermal, cold-water animals that are especially vulnerable to minor changes in temperature during the early stages of development. The warming trend is likely to favour other macro- and mesozooplankton species that occupy the more northerly parts of the ACC (Whitehouse *et al.*, 2008). Recent studies suggest that the distribution of pelagic salps has shifted southward over the past century (Pakhomov *et al.*, 2002; Atkinson *et al.*, 2004). Increased focus on assessing the distribution of krill and other key ecosystem components as well as potential interspecific relationships should be emphasised in future studies. The area studied in this research program encompasses a fraction of the total distribution of krill. Data from this study combined with results of similar studies conducted in the South Shetland and South Georgia areas could form an integrated monitoring effort extending across the Scotia Sea and linking the three active fishing areas, thus providing better scientific data for use in fisheries management.

## SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Crustacean Biology* online.

S1 Figure. Demography of *Euphausia superba* over different years and dates of sampling.

S2 Figure. Length of *Euphausia superba* for samples taken in the northern or southern part of the study area.

S3 Figure. Demography of *Euphausia superba* in the northern and southern parts of the study area.

## ACKNOWLEDGEMENTS

This study was part of project KRILL, which was supported by the Norwegian Research Council (NFR grant 222798), the Norwegian Ministry of Foreign Affairs, and the Norwegian Institute of Marine Research (IMR). We extend our gratitude to Aker BioMarine AS,

Rimfrost AS, and the captains and crew of FV *Saga Sea* and FV *Jewel*. We thank Ronald Pedersen (IMR) for technical support on data sampling. We are also grateful for the constructive criticisms from two anonymous reviewers and the editors, which contributed to improve the manuscript.

## REFERENCES

- Ashijan, C.J., Rosenwaks, G.A., Wiebe, P.H., Davis, C.S., Gallager, S.M., Copley, N.J. Lawson, G.L. & Alatalo, P. 2004. Distribution of zooplankton on the continental shelf off Marquerite Bay, Antarctic Peninsula, during austral fall and winter, 2001. *Deep Sea Research Part II*, **51**: 2073–2998.
- Atkinson, A., Siegel, V., Pakhomov, E.A., Jessopp, M.J. & Loeb, V. 2009. A re-appraisal of the total biomass and annual production of Antarctic krill. *Deep Sea Research Part I*, **56**: 727–740.
- Atkinson, A., Siegel, V., Pakhomov, E. & Rothery, P. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature*, **7013**: 100–103.
- Atkinson, A., Siegel, V., Pakhomov, E.A., Rothery, P., Loeb, V., Ross, R.M., Quetin, L.B., Schmidt, K., Fretwell, P., Murphy, E.J., Tarling, G.A. & Fleming, A.H. 2008. Oceanic circumpolar habitats of Antarctic krill. *Marine Ecology Progress Series*, **362**: 1–23.
- Clarke, A. & Johnston, N.M. 2003. Antarctic marine benthic diversity. *Oceanography Marine Biology Annual Review*, **41**: 47–114.
- Constable, A.J. & Nicol, S. 2002. Defining smaller-scale management units to further develop the ecosystem approach in managing large-scale pelagic krill fisheries in Antarctica. *CCAMLR Science*, **9**: 117–131.
- Dana, J.D. 1850. Synopsis generum crustaceorum ordinis “Schizopoda.” *American Journal of Science and Arts*, ser. 2, **9**: 129–133.
- Dickens, W.A., Graham, A.G.C., Smith, J.A., Dowdeswell, J.A., Larter, R.D., Hillenbrand, C.D., Trathan, P.N., Arndt, J.E. & Kuhn, G. 2014. A new bathymetric compilation for the South Orkney Islands region, Antarctic Peninsula (49°–39°W to 64°–59°S): Insights into the glacial development of the continental shelf. *Geochemical Geophysics Geosystems*, **15**: 2494–2514.
- Evans, S.R., Finnie, M. & Manica, A. 2007. Shoaling preferences in decapod crustaceans. *Animal Behaviour*, **74**: 1691–1696.
- Fielding, S., Watkins, J., Trathan, P.N., Enderlein, P., Waluda, C.M., Stowasser, G., Tarling, G.A. & Murphy, E.J. 2014. Interannual variability in Antarctic krill (*Euphausia superba*) density at South Georgia, Southern Ocean: 1997–2013. *ICES Journal of Marine Science*, **9**: 2578–2588.
- Forcada, J., Trathan, P.N., Reid, K., Murphy, E.J. & Croxall, J.P. 2006. Contrasting population changes in sympatric penguin species in association with climate warming. *Global Change Biology*, **12**: 411–423.
- Gordon, A.L., Visbeck, M. & Huber, B. 2001. Export of Weddell Sea deep and bottom water. *Journal of Geophysical Research*, **106**: 9005–9017.
- Hamner, W.M., Hamner, P.P., Strand, S.W. & Gilmer, R.W. 1983. Behaviour of Antarctic krill, *Euphausia superba*: chemoreception, feeding, schooling, and molting. *Science*, **220**: 433–435.
- Hazen, E.L., Suryan, R.M., Santora, J.A., Bograd, S.J., Watanuki, Y. & Wilson, R.P. 2013. Scales and mechanisms of marine hotspot formation. *Marine Ecology Progress Series*, **487**: 177–183.
- Jensen, N., Nicoll, R. & Iversen, S.A. 2010. The importance of obtaining annual biomass information in CCAMLR Sub-area 48.2 to inform management of the krill fishery. *Working Group on Ecosystem Monitoring and Management, Commission for the Conservation of Antarctic Marine Living Resources*, 10/09, [<https://www.ccamlr.org/en/wg-emm-10/09>].
- Kavanaugh, M.T., Abdala, F.N., Ducklow, H., Glover, D., Fraser, W., Martinson, D., Stammerjohn, S., Schonfield, O. & Doney, S.C. 2015. Effects of continental shelf canyons on phytoplankton biomass and community composition along the western Antarctic Peninsula. *Marine Ecology Progress Series*, **524**: 11–26.
- Kinzey, D., Watters, G.M. & Reiss, C.S. 2015. Selectivity and two biomass measures in an age based assessment of Antarctic krill (*Euphausia superba*). *Fisheries Research*, **168**: 72–84.
- Krafft, B.A., Kvalsund, M., Søvik, G., Farestveit, E. & Agnalt, A.-L. 2016. Detection of growth zones in the eyestalk of the Antarctic krill *Euphausia superba* (Dana, 1852). *Journal of Crustacean Biology*, **36**: 267–273.
- Krafft, B.A., Melle, W., Knutsen, T., Bagoien, E., Broms, C., Ellertsen, B. & Siegel, V. 2010. Distribution and demography of Antarctic krill in the Southeast Atlantic sector of the Southern Ocean during the austral summer 2008. *Polar Biology*, **33**: 957–968.
- Krafft, B.A., Skaret, G. & Knutsen, T. 2015. An Antarctic krill (*Euphausia superba*) hotspot - population characteristics, abundance and vertical structure explored from a krill fishing vessel. *Polar Biology*, **38**: 1687–1700.
- Lawson, G.L., Wiebe, P.H., Ashijan, C.J., Gallager, S.M., Davis, C.S. & Warren, J.D. 2004. Acoustically inferred zooplankton distribution in relation to hydrography west of the Antarctic Peninsula. *Deep Sea Research Part II*, **51**: 2041–2072.
- Mackintosh, N.A. 1972. Life cycle of Antarctic krill in relation to ice and water conditions. *Discovery Reports*, **36**: 1–94.
- Makarov, R.R. & Denys, C.J.I. 1981. *Stages of sexual maturity of Euphausia superba*. Biomass Handbook no. 11. The Scientific Committee on Antarctic Research, Cambridge, UK.
- Marr, J. 1962. The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). *Discovery Reports*, vol. **32**. National Institute of Oceanography, Cambridge University Press, Cambridge, UK.
- Murphy, E.J., Thorpe, S.E., Watkins, J.L. & Hewitt, R. 2004. Modeling the krill transport pathways in the Scotia Sea: Spatial and environmental connections generating the seasonal distribution of krill. *Deep Sea Research Part II*, **51**: 1435–1456.
- Nicol, S., Foster, J. & Kawaguchi, S. 2012. The fishery for Antarctic krill - recent developments. *Fish and Fisheries*, **13**: 30–40.
- Nicol, S., Pauly, T., Bindoff, N.L., Wright, S., Thiele, D., Hosie, G.W., Strutton, P.G. & Woehler, E. 2000. Ocean circulation off east Antarctica affects ecosystem structure and sea-ice extent. *Nature*, **406**: 504–507.
- O’Brien, D.P. & Ritz, D.A. 1988. The escape responses of gregarious mysids (Crustacea: Mysidacea): towards a general classification of escape responses in aggregated Crustacea. *Journal of Experimental Marine Biology and Ecology*, **116**: 257–272.
- Orsi, A.H., Whitworth, T., III & Nowlin, W.D. 1995. On the meridional extent and fronts of the Antarctic circumpolar current. *Deep Sea Research Part I*, **42**: 641–673.
- Pakhomov E.A., Froneman, P.W. & Perissinotto, R. 2002. Salp/krill interactions in the Southern Ocean: spatial segregation and implications for the carbon flux. *Deep Sea Research*, **49**: 1881–1907.
- Quetin, L.B., & Ross, R.M. 2001. Environmental variability and its impact on the reproductive cycle of Antarctic krill. *American Zoology*, **41**: 74–89.
- Ritz, D.A. 2000. Is social aggregation in aquatic crustaceans a strategy to conserve energy? *Canadian Journal of Fisheries and Aquatic Sciences*, **57**: 59–67.
- Ritz, D.A., Foster, E.G. & Swadling, K.M. 2001. Benefits of swarming: mysids in larger swarms save energy. *Journal of Marine Biological Association of the United Kingdom*, **81**: 543–544.
- Santora, J.A., Sydeman, W.J., Schroeder, I.D., Wells, B.K. & Field, J.C. 2011. Meso-scale structure and oceanographic determinants of krill hotspots in the California Current: implications for trophic transfer and conservation. *Progress in Oceanography*, **91**: 397–409.
- Scientific Committee, Commission for the Conservation of Antarctic Marine Living Resources (SG-CAMLR). 2010. *Report of the fifth meeting of the subgroup on acoustic survey and analysis method. Cambridge, UK, 1 to 4 June 2010*. Report of the Twenty-ninth Meeting of the Scientific Committee (SC-CAMLR-XXIX/6). CCAMLR, Hobart, Australia.
- Siegel, V. 2012. Krill stocks in high latitudes of the Antarctic Lazarev Sea: seasonal and interannual variation in distribution, abundance and demography. *Polar Biology*, **35**: 1151–1177.
- Siegel, V., Reiss, C.S., Dietrich, K.S., Haraldsson, M. & Rohardt, G. 2013. Distribution and abundance of Antarctic krill (*Euphausia superba*) along the Antarctic Peninsula. *Deep Sea Research Part I*, **77**: 63–74.
- Stammerjohn, S.E., Massom, R., Rind, D. & Martinson, D. 2012. Regions of rapid sea ice change: an inter-hemispheric seasonal comparison. *Geophysical Research Letters*, **39**: L06501 [doi: 10.1029/2012GL050874].
- Thompson, A.F., Heywood, K.J., Thorpe, S.E., Renner, A.H.H. & Trasvinã, A. 2009. Surface circulation at the tip of the Antarctic Peninsula from drifters. *Journal of Physical Oceanography*, **39**: 3–26.
- Trathan, P.N. & Murphy, E.J. 2003. Sea surface temperature anomalies near South Georgia: relationships with the Pacific El Niño regions. *Journal of Geophysical Research*, **108**: 1–10.
- Weber, L.H., El-Sayed, S.Z. & Hampton, I. 1986. The variance spectra of phytoplankton, krill and water temperature in the Antarctic Ocean south of Africa. *Deep Sea Research*, **33**: 1327–1343.
- Whitehouse, M.J., Meredith, M.P., Rothery, P., Atkinson, A., Ward, P. & Korb, R.E. 2008. Rapid warming of the ocean around South Georgia, Southern Ocean, during the 20<sup>th</sup> century: forcings, characteristics and implications for lower trophic levels. *Deep Sea Research Part I*, **55**: 1218–1228.
- Witek, Z., Kalinowski, J., Grelowski, A. & Wolnomiejski, N. 1981. Studies of aggregations of krill (*Euphausia superba*). *Meeresforschung*, **28**: 228–243.