Marine Biology (2026) 173:88
https://doi.org/10.1007/s00227-026-04816-7

ORIGINAL PAPER

Spatiotemporal variability in Antarctic krill (*Euphausia superba*) around South Georgia derived from Antarctic fur seal (*Arctocephalus gazella*) diets

J. Coleman[1] · P. Hollyman[1,2] · J. Ashburner[1] · M. Jessopp[3] · J. Forcada[1] · K. Owen[1] · I. J. Staniland[5] · C. M. Waluda[1] · M. A. Collins[1] · P. N. Trathan[1,4]

Received: 27 September 2025 / Accepted: 10 February 2026

Abstract

Despite its biological, biogeochemical, and economic importance, there is much about Antarctic krill (*Euphausia superba*) that remains poorly understood. This is especially true for its abundance, movement and retention in South Georgia waters, which is highly variable. Krill fluctuations exert bottom-up pressures on the entire ecosystem which are reflected in changes in breeding success and diet of dependent predators such as Antarctic fur seals (*Arctocephalus gazella*). This study investigates long-term datasets (2008–2021) documenting krill size distribution and abundance in Antarctic fur seal diet samples collected from two colonies that have geographically distinct and environmentally discrete foraging grounds. Krill length-frequency distributions generally followed a synchronous pattern across both sites with summer increases in length associated with growth, and winter decreases associated with senescence, mortality and possibly krill shrinkage, coupled with recruitment of smaller size classes. Bird Island seals, at the western end of the study region consistently took slightly larger krill (mean length 47.6 mm) than those at Maiviken (mean length 45.8 mm) in the east, possibly a result of continued krill growth during advection between the two areas, or differences in local oceanography. Krill cohorts visibly developed across years with large-scale recruitment of smaller krill occurring every 4–5 years. An anomalous period between 2017 and 2020 occurred when synchrony between the two sites broke down and later re-established, likely reflecting contrasting environmental conditions during this period. This study highlights the importance of having multiple spatially separated long-term monitoring sites, particularly in an ecological system recognised to be highly variable and experiencing significant changes.

Keywords Antarctic fur seal · Diet · Krill · South Georgia

Introduction

Antarctic krill (*Euphausia superba* Dana, 1852; hereafter referred to as krill), is a keystone species in the Southern Ocean (Mackintosh 1974) as well as being an integral component in biogeochemical cycles (Priddle et al. 2003; Cavan et al. 2019). It has a circumpolar, yet asymmetrical, distribution around the Antarctic continent, with more than 50% of the krill population found within the southwest Atlantic sector (Murphy et al. 2007a, b; Atkinson et al. 2019). South Georgia is a subantarctic island that lies within this hotspot for krill. The waters around South Georgia are highly productive (Atkinson et al. 2001; Whitehouse et al. 2008a, b), resulting in an island renowned for its abundant wildlife

---

Responsible Editor: E. Kozak.

✉ J. Coleman
jamiecoleman0303@gmail.com

[1] British Antarctic Survey, NERC, Madingley Road, Cambridge, UK

[2] School of Ocean Sciences, Bangor University, Askew Street, Menai Bridge, LL57 5AB, Bangor, UK

[3] School of Biological, Earth & Environmental Sciences, University College Cork, Cork, Ireland

[4] Ocean and Earth Science, University of Southampton, National Oceanography Centre Southampton, European Way, Southampton, UK

[5] International Whaling Commission, Vision Park, Histon, Cambridge, UK

populations (Atkinson et al. 2001; Murphy et al. 2007a, b; Coleman et al. 2024).

Although krill reproduction does occur at South Georgia (Tarling et al. 2007), those found in the waters around the island are not part of a localised self-sustaining population, but are reliant on recruitment from the Antarctic Peninsula and the Scotia Sea (Murphy et al. 1998; Matano et al. 2020; Ichii et al. 2023) via the Antarctic Circumpolar Current (ACC) (Trathan et al. 1997; Murphy et al. 2007a, b). By the time the krill are advected to South Georgia, they are generally already more than two years of age (Murphy et al. 2007a, b). The recruitment of krill into South Georgia waters is dependent on many large-scale, dynamic factors, including Antarctic winter sea ice extent and polar currents, making it highly variable (Brierley et al. 1999; Veytia et al. 2021). On a more local scale, krill's distribution and availability to predators around South Georgia is patchy and can be affected by various environmental factors including chlorophyll concentration, sea surface temperature, salinity and mixed layer depth (Trathan et al. 2003).

As an important prey species, fluctuations in krill stocks have bottom-up effects on consumers, impacting population dynamics (Croxall et al. 1999; Trathan and Hill 2016; Pallin et al. 2023), especially for species tied to land by their breeding cycle. For this reason, studying krill predators is an effective method of monitoring changes in the local krill-based ecosystem (Reid and Croxall 2001). One of the most abundant consumers of krill at South Georgia are Antarctic fur seals (*Arctocephalus gazella* Peters, 1875; hereafter fur seals) (Reid and Arnould 1996; Boyd et al. 2002; Forcada et al. 2023). This species was hunted to commercial extinction in the eighteenth and nineteenth centuries (Basberg and Headland 2012). Following a ban on sealing, the species recovered to pre-sealing numbers by the end of the twentieth century (Staniland et al. 2011; Hoffman et al. 2022) to a point where more than 95% of the world's breeding population used South Georgia (Forcada and Staniland 2009; Forcada et al. 2023). However, since 2009 the population has been in decline (Forcada et al. 2023).

During summer months (November–April) female fur seals spend 3–4 months alternating between nursing their pups on land and making foraging trips of up to seven days (Doidge et al. 1986). Once pups are weaned, females are no longer tied to land, however many remain in waters close to South Georgia, associating with the northern shelf break (Jones et al. 2020; Bamford et al. 2021). After mating, adult males generally disperse south associating more closely with the Antarctic continent and the ice edge (Boyd et al. 1998), although many non-breeding males and juvenile seals also remain around South Georgia in the winter (Duck 1990).

In addition to its biological importance (Trathan and Hill 2016; Juáres et al. 2021), krill is the subject of the largest fishery in the Southern Ocean (Nicol and Foster 2016; Trathan et al. 2024). Recognizing the importance of krill, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) was established by international convention and first met in 1982 to manage Southern Ocean fisheries (Kock et al. 2000). Despite the development of international cooperative resource management, the Southern Ocean still presents important scientific gaps in knowledge and understanding. Recent developments in fishing technology have allowed krill catches to increase (Trathan et al. 2021; Trathan 2023), in some cases to more than 800 metric tonnes per day per vessel (Nicol et al. 2012). The Southern Ocean is also witnessing recoveries of whales and fish species previously overexploited (Zerbini et al. 2019; Calderan et al. 2020; Hollyman et al. 2021), which will have further impacts on ecosystem trophic interactions as well as on krill dynamics (Hoffman et al. 2022). Most significantly, South Georgia (Whitehouse et al. 2008a, b; Nel et al. 2023) and the Antarctic Peninsula have experienced rapid warming over the past half a century (Meredith and King 2005; Constable et al. 2014) which is likely to affect krill dynamics in the region.

The CCAMLR Ecosystem Monitoring Program (CEMP) monitors changes in the key life-history parameters of selected dependent higher trophic-level species, including Antarctic fur seals, to better understand physical and biological variability in the Southern Ocean ecosystem (Agnew 1997; Kock et al. 2000). At South Georgia, monitoring work contributing to CEMP is carried out at Bird Island to the northwest of South Georgia and Maiviken situated on the Thatcher Peninsula on the main island (Fig. 1B). Inferring seal diet from scat contents found on land is a commonly used method for ecosystem monitoring and in seal biology more generally. Around South Georgia, krill is the most important prey item of fur seals (Reid 1995; Waluda et al. 2010). The size of krill carapaces found in scats is representative of those consumed by fur seals (Reid and Arnould 1996; Staniland 2005) and of the available population in South Georgia waters (Croxall et al. 1999; Reid et al. 1999, 2004a). This makes scat analysis a good candidate for low-cost, long-term monitoring of changes in population structure of krill, provided knowledge exists on where fur seals are foraging. Reid et al. (1999) used krill length frequency data from scats, collected at Bird Island, to look at interannual differences in krill throughout seven summers showing it was possible to identify the growth of krill between years and identify potential krill recruitment events in 1991 and 1994, represented by pulses of small, more numerous krill.

Fur seals from Bird Island consistently forage to the northwest (Barlow et al. 2002; Reid et al. 2006; Staniland et

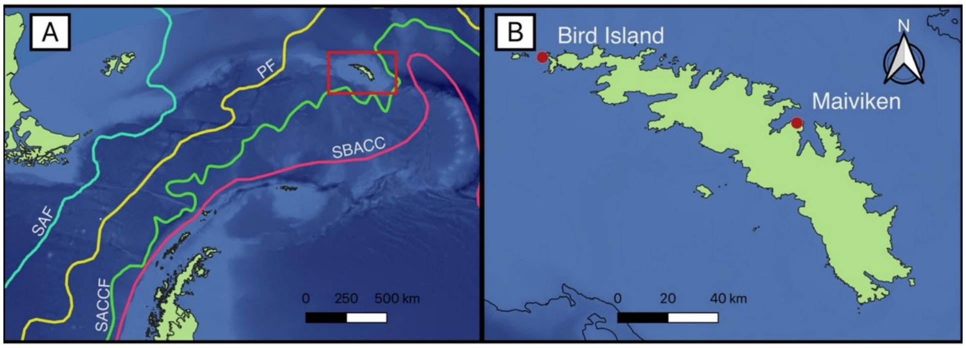

Fig. 1 (**A**) Location of South Georgia (red box) within the southwest Atlantic sector of the Southern Ocean in relation to the major fronts in the Antarctic Circumpolar Current (ACC): Sub Antarctic Front (SAF – light blue); Antarctic Polar Front (PF- yellow; Southern ACC Front (SACCF—green); Southern Boundary of ACC (SBACC—pink) (Orsi, AH., Harris 2019). **(1B**) Location of Maiviken and Bird Island study sites, South Georgia (British Antarctic Survey 2023)

al. 2011). Those tracked from Stromness Bay, to the southeast, foraged perpendicular to the coast (Boyd et al. 2002; Staniland et al. 2011) towards the region currently targeted by the krill fishery in winter months (Trathan et al. 2021). However, there are no published data on the foraging distribution or diet of fur seals from Maiviken, nor whether the size distribution of krill differs between sites. Therefore, the purpose of this study was to investigate the long-term dynamics of krill in the diet of fur seals at South Georgia at both Bird Island and Maiviken. Specifically, we set out to:

1) Use previously unpublished tracking data to identify the foraging distribution of Antarctic fur seals from Maiviken and determine whether they are targeting the same krill population as seals previously tracked from Bird Island;
2) Compare the intra- and inter- annual length-frequency distributions of krill collected from scats sampled at Bird Island and at Maiviken to examine synchronies in the krill population consumed by fur seals from these two sites; and
3) Explore the environmental drivers of patterns or dissimilarities in krill length-frequency distributions at the two sites.

Methods

Study location and field sampling

Antarctic fur seal scats were collected and processed from two fur seal breeding sites on South Georgia: Bird Island and Maiviken, between 2008 and 2021 (Fig. 1). At Bird Island, scats were collected in the vicinity of Freshwater Beach (54.011°S, 38.052°W), and at Maiviken scats were collected from King Edward Point (-54.280°S, 36.498°W) and Maiviken (-54.252°S, -36.501°W) on the Thatcher Peninsula. Ten scats per week were collected during summer months (October–March, inclusive) when seals are more abundant, and ten per fortnight were collected during winter months (April-September, inclusive). If present, ten carapaces were measured from each scat. Where 100 measurable carapaces were not present in the ten Bird Island scats, a further five scats were collected per sampling period. Scats collected during the summer were assumed to be from breeding females because males do not undertake regular foraging trips and females dominate the population ashore (Doidge et al. 1986). During winter, adult males move towards the Antarctic continent (Boyd et al. 1998; Dunn et al. 2025), and scats sampled will likely be from both immature animals and female fur seals (Bamford et al. 2021).

Scat processing and krill carapace measurements were carried out as reported by Reid et al. (1999). Krill total length (TL) was then calculated from the carapace length (Hill 1990). Fish otoliths and cephalopod beaks were identified to the lowest possible taxonomic level of classification according to Reid (1996) and Xavier and Cherel (2009) with the assistance of reference collections held by the British Antarctic Survey.

Telemetry

Summer tracking data from both locations were compared to establish whether seals from Bird Island and Maiviken were foraging in different locations. Thirty nursing females from Maiviken were equipped with Global Positional System (GPS) tags (either Sirtrack Fastloc Archival, 215 g or Wildlife Computers Mk 9, 50 g); 16 during the 2009/10 summer, and 14 during the 2010/11 summer. Tags had a 5-min recording interval. At Bird Island, 38 nursing females were fitted with satellite tags at Freshwater Beach and subsequently tracked. This included the deployment of six GPS tags during the summer of 2005/06 (Staniland et al. 2011), as well as 19 and 14 Platform Transformer Terminal (PTT) tags in the summers of 2007/08 and 2008/09, respectively (Staniland et al. 2020). Tracking data were not available for the entire duration of the study and therefore spatial inferences may not fully represent all years. However, tracks cover seasons of both high and low prey availability (Trathan et al. 2021), and therefore the core area used by tagged seals is considered representative of the foraging range of both Bird Island and Maiviken fur seals. Details of tag deployments are given in Online Resource 7.

Fur seals were captured for tag deployment and removal (4–16 days later) as described by Gentry and Holt (1982). Instruments were attached using cable ties to gauze that were glued to the animals fur centrally between the shoulder blades using epoxy resin (Boyd et al. 1998).

Data processing

Foraging data

GPS data were processed using R (R Core Team 2020). Obvious outlier points were removed using the "speedfilter" function in R's "trip" package (Sumner et al. 2009, 2011, 2021). GPS positions with insufficient satellites fixes (<4) or those associated with unrealistic swim speeds greater than 3 ms^{-1} were removed. PTT tag data were processed similarly, with points associated with swim speeds greater than 3 ms^{-1} removed. Tracks were plotted to distinguish if foraging habitat for animals from Bird Island and Maiviken were distinct. Bounding boxes rather than utilisation distributions or kernel densities were used to approximately define fur seal foraging areas and account for any interannual variability in foraging locations, given that tracking data were only available for a limited number of individual seals and years. The core foraging area for Bird Island was bounded in a box with the southwest vertex at 54.15°S, 40.00°W, and the northeast vertex at 53.40°S, 38.00°W, whilst that for Maiviken was bounded with vertices at 54.20°S, 36.60°W and 53.20°S, 35.40°W (Fig. 2).

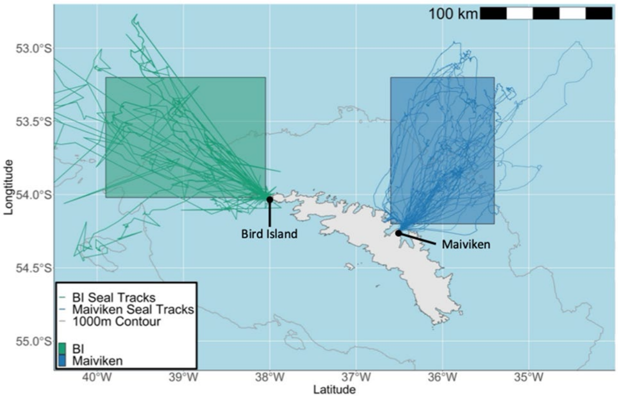

Fig. 2 Tracks of Antarctic fur seals from 2009/10 and 2010/11 seasons at Maiviken (blue) and 2005/06 (Staniland et al. 2011), 2007/08 and 2009/10 (Staniland et al. 2020) at Bird Island (green). Spatial polygons represent the regions for which environmental variables were cropped from Copernicus satellite data (https://marine.copernicus.eu)

Environmental data

The Copernicus Marine Environment Monitoring Service platform was used to obtain monthly, 0.25° resolution, sea surface temperature (Celsius), mixed layer depth (m) and salinity (practical salinity units) averages using the Global Ocean Physics Reanalysis dataset (Drevillon et al. 2021). This was repeated for chlorophyll *a* using the Ocean Global Biological Multiyear dataset (Perruche 2019). The monthly values were averaged over quarter (3 months) and season (6 months) and converted to raster files from October 2008 until June 2020. Rasters were cropped within the bounding boxes to give coarse regional environmental data (Fig. 4) relative to Bird Island and Maiviken foraging areas.

Krill length data

Krill length data for each site were binned into 2 mm (TL) size classes and aggregated at a range of temporal resolutions to explore differences in the size structure of the krill population selected by fur seals. This was done using a multivariate community analysis approach where each 2 mm size class represented a size cohort (or a nominal 'species') within the krill population such that differences in the proportions of size classes selected by fur seals contributed to the dissimilarity in diet between samples. Data were grouped by sampling site (Bird Island, Maiviken), by quarter (January-March, April-June, July–September, October-December) and by season (summer = October–March, winter = April-September), with multivariate analysis conducted using the Vegan Package (Oksanen et al. 2020) in R. Bray–Curtis dissimilarities were calculated using the "metaMDS" function and non-metric multidimensional scaling (nMDS) plots used to visualise Bray–Curtis dissimilarities between samples. The "adonis" function was used to perform a permutational analysis of variance (PERMANOVA) to test for differences in krill length frequency distributions between Bird Island and Maiviken.

The "ordisurf" function was used to overlay environmental variable gradients on nMDS plots to visualise relationships between diet and environmental variables. So that environmental variables could be compared they were all $\log_{10}$ transformed. Dissimilarities between samples based on Euclidean distance of environmental variables were calculated using the "vegdist" function. Relationships between krill length classes and environmental variables were then explored using the "bioenv" test across temporal scales of quarter and seasonal sampling periods. This method of exploratory data analysis has associated caveats since krill size bins are not independent. Therefore, while it is a highly effective method for visualizing anomalous multivariate differences against environmental gradients, we have not used the method for statistical analysis.

Results

Foraging

With the exception of one individual that did not leave Cumberland Bay, fur seals from Maiviken in both summers (2009/10 and 2010/11) headed north-east towards the 1000 m contour (and beyond) (Fig. 2). Seals from Bird Island foraged west and north-west towards (and beyond) the 1000 m depth contour (Fig. 2). Two fur seals ventured south-west of the bounding box, but most were encapsulated within the core foraging zones. Fur seals occasionally travel beyond their normal foraging areas especially in years with poor krill availability (Boyd et al. 1994), but Staniland (2002) suggested that differences in diets would not be reflected in scats collected on beaches due to the passage rates of fur seals and average swimming speeds needed to return to the colony from longer trips.

Scat composition summary

In total, since October 2008, 9669 scats were collected: 5428 from Bird Island and 4211 from Maiviken. Antarctic krill was the most abundant prey species found in fur seal scats at both sites. Measurable krill carapaces were present in 3582 scats at Bird Island (65.63%), and 2523 at Maiviken (59.91%). At both sites, krill frequency of occurrence was greater during the summer (Bird Island = 79.07%, Maiviken = 71.56%) than during the winter (Bird Island = 43.30%, Maiviken = 36.76%), when fish made an increased contribution to the diet. Species composition of fish consumed varied between years and season with Nototheniidae spp. and Channichthyidae spp. most numerous (Online Resource 1).

Krill length

Krill length varied both inter- and intra- annually (Fig. 3 and Online Resource 2). Both sites exhibited a synchronous, cyclical pattern with a consistent decrease in median krill length in the third quarter (July- September) of the year and with the largest krill between the first and second quarters (Fig. 3). Summer medians were almost always higher than the subsequent winters (Online Resource 2). However, this was not the case in winter 2010, winter 2017 and winter 2019. Average krill length increased over the study period at both locations, but this was not significant.

While krill length from Bird Island and Maiviken follow the same pattern through most years, the relationship between the sites appeared to deviate for a period between 2017 and 2020. In the third quarter of 2017 (2017-3) mean (46.60 mm TL ± 4.58 st dev) and median (46.00 mm) krill size at Maiviken increased as Bird Island decreased (mean = 42.96 TL mm ± 4.26, median = 43.00 mm). This was followed by a rapid decrease in krill length at Maiviken at the beginning of 2018 and an increase at Bird Island. By the 4th quarter of 2018 Bird Island krill length had a mean of 52.54 mm ± 6.16 (median = 52.00 mm) which was much larger than krill at Maiviken (mean = 41.54 mm ± 6.16, median = 38.00 mm). From the third quarter of 2019 both sites returned to the synchronous pattern but did not return to the previous synchronicity until the third quarter of 2020

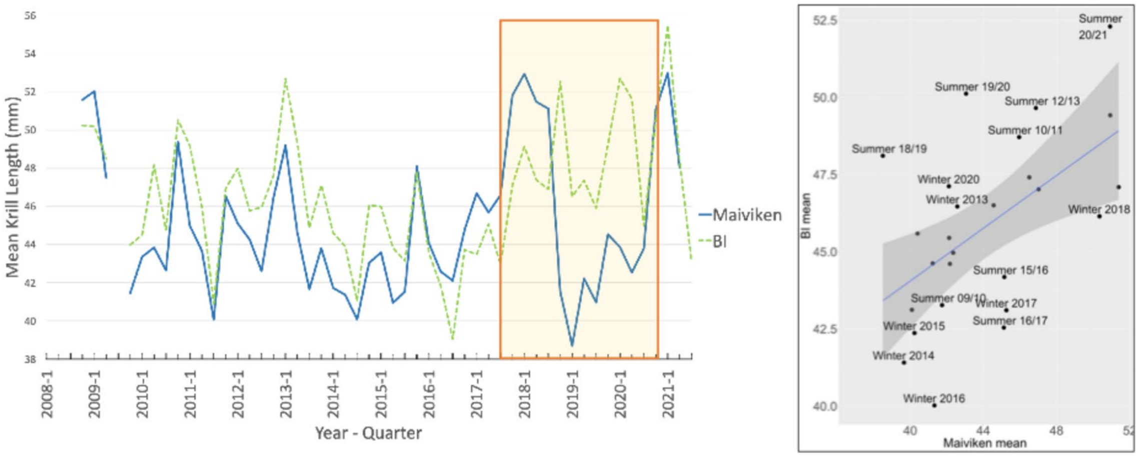

Fig. 3 Mean estimated length of krill from the carapaces found in fur seal scats per quarter of the year at Bird Island (BI; green dashed line) and Maiviken (blue continuous line). Orange box marks the period where the pattern of differences between the two sites breaks down. Right-hand plot shows the regression between mean seasonal krill size at both stations across the sampling period with outlier points labelled

(Fig. 3). With the exception of the first quarter of 2016 until the third quarter of 2018 and a brief period in 2008, average krill length at Bird Island was greater than that at Maiviken. The mean difference between sites in annual median length of summer krill size was 3.60 mm (95% CI: 3.33—3.89), when anomalous years are removed this was 2.63 mm (95%CI: 2.34—2.93) (Online Resource 3.) A regression of Bird Island mean krill length versus Maiviken mean length showed a significant relationship ($R^2 = 0.2799$, p-value = < 0.05) where greater residuals were mostly associated with the period between 2016 and 2020.

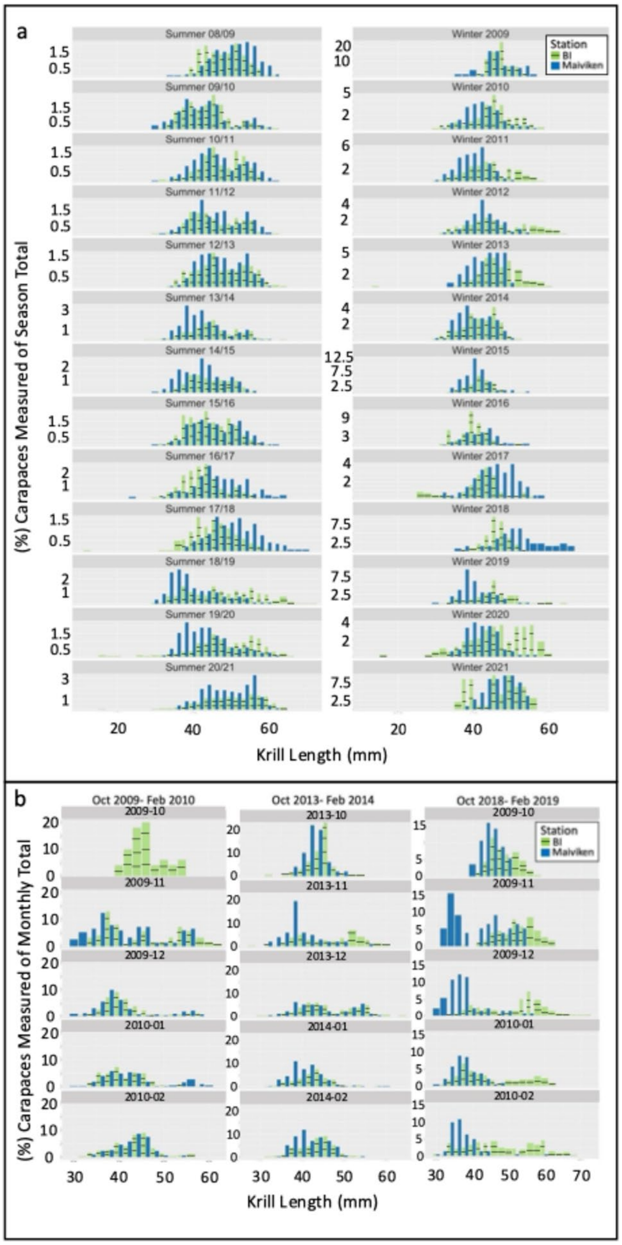

Fig. 4 **(a)** Summer (left) and Winter (right) length frequency distributions (expressed as a percentage of carapaces measured per site per season) of Antarctic krill taken from fur seal scats at Bird Island (BI; green with black stripes) and Maiviken (blue), South Georgia between 2008 and 2021 (**b**) Fluxes of smaller krill observed between the months of October and February in 2009, 2013 and 2018

Intra-annual variation

Monthly mean krill size was greater at Bird Island than Maiviken for all months of the year except July. A two-way ANOVA test with site and month as factors showed that this difference was significant (ANOVA, $F(1,144) = 27.640$, $P < 0.001$). Mean krill lengths were smaller during winter months than summer months with the minimum occurring in July at Bird Island and September at Maiviken. One way ANOVA tests with season as a factor showed this seasonal difference was significant at both Maiviken (ANOVA, $F(1,25) = 6.971 P < 0.001$) and Bird Island (P value < 0.001). In all years, increases in length were seen from January to the subsequent December, except for 2009 (mean decrease of 8.39 mm at Bird Island, 11.46 mm at Maiviken) and 2013 (decrease of 5.68 mm at Bird Island, 5.64 mm at Maiviken) at both sites and 2018 at Maiviken (decrease 15.78 mm). At Maiviken in 2016, there was also a small decrease in krill length (0.66 mm).

Length frequency distribution

Fur seals predominantly fed on krill ranging in length from 40–55 mm TL (Fig. 4a). Krill less than 30 mm were consumed but these were rare and largely restricted to Bird Island between 2017 and 2020. It was also rare that carapaces from krill greater than 60 mm TL were present. Length frequency histograms showed progression of size cohorts between years (Fig. 4a) with inclusion of smaller krill into the diet every 4–5 years. These shifts were most noticeable in summer 2009/10, 2013/14 and 2018/19 (Fig. 4a, b). At Bird Island and Maiviken these influxes of smaller krill occurred in November 2009 and 2013 (Fig. 4b). In 2018, the pattern became less clear, with smaller krill present from November at Maiviken and becoming dominant; at Bird Island, this was not the case (Fig. 4b). Appearances of much smaller krill at Bird Island, in winter 2017, summer 2019/20 and winter 2020, didn't result in a complete shift of krill sizes.

Krill length-frequency distributions varied between season and year. The appearance of smaller krill at both sites in November 2009 resulted in a bimodal distribution which persisted at both sites throughout summer until the next occurrence of smaller krill in 2013 (Fig. 4a). The appearance of small krill in 2018 was supplemented by continued consumption of larger krill, resulting in a wider length distribution with a positive skew (Fig. 4a, b). There was a narrow spread in certain winters (noticeably 2009 and 2015), with fewer size classes representing a higher proportion of the season total. This was due to the low total numbers of carapaces measured in these seasons (Fig. 4a).

Multivariate analysis

Ordination analysis of seasons showed a large overlap in the length-frequency distributions of krill consumed by fur seals across seasons, although some clustering of winter samples was apparent (Fig. 5). There were obvious outliers suggesting some differences in the composition of krill lengths consumed by fur seals in particular seasons with most of these occurring between winter 2017 and summer 2020/21 from both sites. Summer 2017/18 until summer 2018/19 at Maiviken was separated from the main cluster but not grouped. At Bird Island the three consecutive summers between 2018 and 2021 were grouped with winter 2020. Winters of 2009 and 2017 were also isolated from other seasons. A PERMANOVA test using the "adonis" function was used to test for significant clustering of points within station/season combinations. This showed a significant overall difference between the two sites (PEMANOVA, F (1,90) = 5.29, P = 0.002). Additional PERMANOVAs showed significant differences between Maiviken and Bird Island during the winter (PEMANOVA, F (1,42) = 5.6396, P = 0.001) and summer (PEMANOVA, F (1,46) = 3.0943, P = 0.03). periods.

Summer and winter length frequency histograms were explored to assess the factors driving these differences (Online Resource 4). Maiviken fur seals took more krill smaller than the modal length, and Bird Island fur seals took more krill larger than the modal length for both stations (44 mm). The greatest differences observed in summer were within the 38–40 mm bin (8.27% of Maiviken krill, 4.51% of Bird Island krill) and 52–54 mm bin (6.93% of Maiviken, 9.64% of Bird Island). The greatest differences observed during winter were within the 38-40 mm bin (12.78% of Maiviken, 5.21% of Bird Island) and the 46–48 mm bin (11.49% of Maiviken, 19.42% of Bird Island).

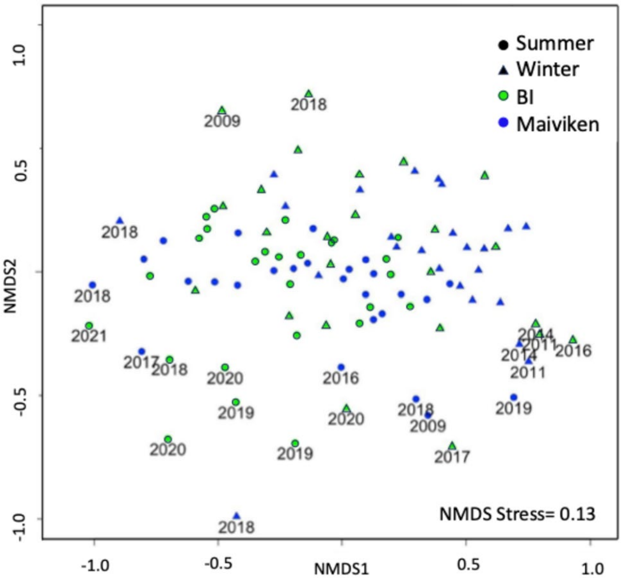

Fig. 5 nMDS ordination based on the composition of different krill sizes targeted by foraging fur seals at Bird Island (BI; green with black outline) and Maiviken (MV; blue) during winter and summer with outlying points labelled

Environmental Variables

Quarterly and seasonal means were extracted for all environmental variables. The correlation between dissimilarities in krill length-frequency and environmental variables was explored using the "bioenv" function. Mixed layer depth (MLD), sea surface temperature (SST), chlorophyll *a* (CHL) and salinity (SAL) together explained 43% of the dissimilarities in krill lengths preyed upon by fur seals between seasons. Using seasonal bins Maiviken winters were associated with cooler SST, lower CHL and deeper MLD than other seasons. High CHL concentrations and shallower MLDs split Bird Island 2018/19 and 2019/20 summers as well as Bird Island winter 2020 from the main clusters. There was a similar pattern with warmer SST with the addition of summer 2017/18 and winter 2018 at Maiviken (Fig. 6). Several outliers remained unexplained by environmental variables.

There were seasonal differences between environmental conditions at both sites (Table 1). SST and CHL were consistently greater at Bird Island, SAL remained constant between the two sites whilst MLD was greater in the third quarter at Maiviken and similar at all other times.

Discussion

This study used two spatially distinct, long-term diet datasets to compare krill consumed by foraging fur seals at two sites located approximately 100 km apart on South Georgia. Although tracking data were not available for all study years, the available data consistently showed that seals from the two colonies forage in regionally distinct locations, yet prey on similar sized krill which likely originated from the same metapopulation. The slightly larger krill (mean = 1.80 mm) observed at Bird Island were likely due to the advection time between sites (from east to west); allowing for growth, retention across the area, or small environmental differences. Despite the generally small differences in krill size, populations of krill at both locations followed a synchronous pattern with interannual progression of krill size before sporadic decreases, possibly associated with large scale influxes of smaller krill. Interestingly, this correlation broke down between 2017 and 2020. This could

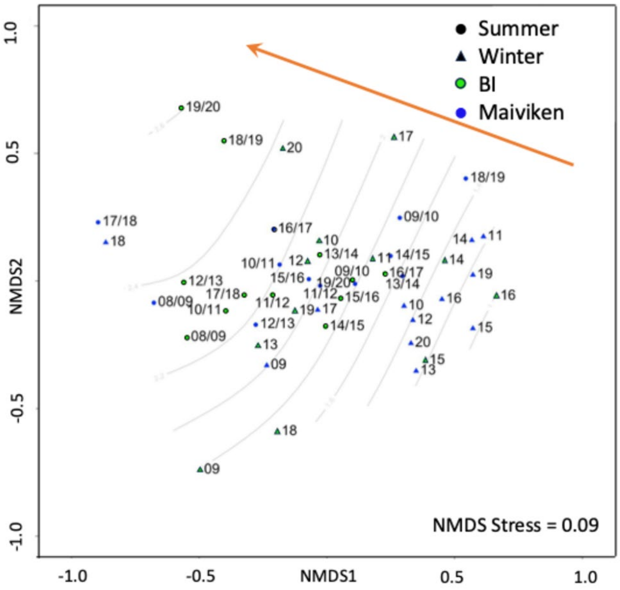

Fig. 6 nMDS ordination of dissimilarity in krill community lengths between seasons (Summer=October–March, Winter=April-September) at (BI; green with black outline) and (MV; blue) with sea surface temperature gradients and arrows showing increased SST

Table 1 Environmental means across Bird Island (BI) and Maiviken (MV) spatial polygons using Copernicus satellite data showing sea surface temperature (SST), mixed layer depth (MLD), salinity (SAL) and chlorophyll a (CHL *a*)

Variable	Site	Jan—Mar	Apr—Jun	Jul—Sep	Oct—Dec
SST (°C)	BI	**3.66**	2.28	0.55	1.55
	MV	**3.14**	1.81	0.19	1.13
MLD (m)	BI	30.22	62.58	**74.73**	39.47
	MV	29.88	63.93	**80.32**	38.24
SAL (psu)	BI	33.77	33.81	**33.85**	33.83
	MV	33.8	33.85	**33.91**	33.88
CHL *a* (mg.m^{-3})	BI	1.39	0.82	0.76	**1.64**
	MV	0.77	0.46	0.62	**1.36**

Highest seasonal value for each site is bold and lowest is underlined

be due to poor krill availability, an oceanographic change which led to differing foraging conditions, or other differences such as the vertical distribution of krill, as described by Ichii et al. (2020) and Bahlburg et al. (2023).

Cyclical recruitment

Periodic decreases in the size of krill every 3–5 years reflect similar patterns to those observed previously in fur seal and penguin diets at South Georgia (Reid et al. 1999) as well as in the diets of baleen whales (Mackintosh 1974). Reid et al. (1999), using an earlier subset of Bird Island data, suggested that increases in size over time reflect growth and development of cohorts, whilst decreases in mean krill length reflected recruitment pulses of new, younger, krill into the South Georgia system advected via the ACC (Trathan et al. 2022). In 1994 a reduction in krill length occurred in January/February at Bird Island (Croxall et al. 1999; Reid et al. 1999), whereas in our study, decreases in krill size occurred in November/December which corresponds with predicted transport times from the Antarctic Peninsula to South Georgia as sea ice recedes (Hofmann and Murphy 2004). This change in arrival time after the 2000s may be reflective of a different recruitment route of krill into South Georgia from the Scotia Sea rather than from further west in response to sea ice reduction (Ichii et al. 2023).

Advection pathways to Maiviken and Bird Island

The mean, median and modal lengths of krill consumed by fur seals at Bird Island were consistently larger than those consumed at Maiviken, with the exception of the years 2016–2018, and during a brief period in 2008/09. An explanation for this larger krill size at Bird Island plausibly stems from the ecological connectivity of krill. The Southern ACC transports krill onto the shelf at South Georgia, primarily from the south, then to the east of the island, and then northwest past Maiviken, eventually arriving at Bird Island, with the flow finally heading north and westward (Young et al. 2014; Matano et al. 2020) via the Southern ACC Front (Trathan et al. 1997; Trathan and Murphy 2003; Murphy et al. 2007a, b). Given current speeds (4–8 cm s^{-1}) along the shelf reported by Matano et al. (2020) and krill growth rates (0.07 mm d^{-1}) reported by Arnold et *al.* (2004), over a distance of 175 km between Maiviken and Bird Island foraging areas, a krill growth of 1.75 mm to 3.5 mm TL could be anticipated during the estimated advection time (25–50 days). Allowing for growth, retention across the area, or environmental variation, the krill size differences observed here (~2.63 mm) could be attributed to growth during advection.

During the period 2017—2020 the synchronous, cyclical relationship between the two monitoring sites broke down, which suggests the circulation pattern transporting krill was in a different state, or fur seals were consuming krill from spatiotemporally distinct metapopulations. Anomalous seasons at both sites were characterised by environmental gradients, in particular for MLD, SST and CHL. However, there were no available environmental data presented here that fully explain the difference observed. Although large differences in krill length between sites did not occur until 2017, mean krill length at Maiviken first exceeded that at Bird Island in 2016. This coincided with the greatest MLD, lowest SST and lowest CHL for both sites during the study period. These local environmental changes could be signals of a larger mode of environmental variability which changed the state of the system. The El Niño Southern Oscillation (ENSO) and the Southern Annular Mode (SAM) are coupled climatic drivers which are known to indirectly influence krill advection to South Georgia (Trathan et al. 2006, 2022; Meredith et al. 2008). These factors are also known to influence SST around South Georgia, normally with a lag of 5–6 months (Meredith et al. 2008). To link these local changes to climatic drivers such as ENSO and/or SAM, testing against environmental lags over a longer timescale will require continued data collection at both sites to provide adequate statistical power. Other analyses to explore environmental perturbations at much broader geographic scales will also help, as perturbations have been reported in the years preceding the anomaly (2016/17, 2017/18 and 2018/19; e.g. Turner et al. 2020). Further work linking fur seal diet to broader scale drivers of environmental variability is now needed.

Interannual variation in sea surface temperatures close to our study sites, both on-shelf and off-shelf (Trathan et al. 2003), reflect variation in the strength and direction of flow in the ACC (Whitehouse et al. 2008a, b; Trathan et al. 2022). The main flow of the ACC bifurcates south of the island, providing different transport pathways for krill, with the main flow being anticyclonic around the east of the island and a less dominant cyclonic flow progresses around the west of the island (Trathan et al. 1997; Young et al. 2014; Matano et al. 2020). Consequently, depending upon large scale atmospheric and/or oceanographic forcing, there may be the potential for altered flow rates to the east or the west. Not only would this affect the delivery of krill to both Bird Island and Maiviken via differences in advection pathways, but also altered growth increments before arrival at the different monitoring sites as seen here. Understanding the oceanographic connectivity as the ACC arrives at South Georgia therefore remains critical to understanding krill delivery to predators (Trathan et al. 2022).

Implications of krill movement and recruitment

Summers prior to krill recruitment events were characterised by increased SST, which then decreased over time. However, at Bird Island, in summer 2018/19, SST remained high, suggesting that local oceanography was different, possibly as a result of an oceanographic/ atmospheric anomaly (see also Turner et al. 2020). Thus, although smaller krill appeared at both study sites in summer 2018/19, they did not become the dominant cohort in the diet at Bird Island, as happened at Maiviken. Larger krill might have remained available around Bird Island, resulting in fur seals preferentially selecting these over smaller krill in order to increase feeding efficiency (Descalzo et al. 2025). However, this season was associated with low pup numbers (Nagel et al. 2021) and low weaning weights at Bird Island (Trathan et al. 2021) with an increased proportion of fish in scats (Online Resource 1), which supports the theory that krill were in short supply as the observed influx of smaller krill was not retained at Bird Island. Additionally, Reid et al. (2004) showed at Bird Island in particular that krill in fur seal diet reflected that caught in adjacent waters by net.

Although fur seals usually take krill > 35 mm (Reid et al. 1999; Murphy and Reid 2001), they occasionally take some very small krill (< 30 mm), with noticeable occurrences throughout the asynchronous period. These influxes only occurred at Bird Island, which is generally lagged in relation to Maiviken (Young et al. 2014) suggesting these could be associated with a temporary change in the system which resulted in an alternative recruitment route. Although smaller krill may be associated with influxes of younger age groups into the system, there is little evidence of krill less than 2 + years old within the South Georgia system in summer, either from predator or scientific trawl data (Murphy et al. 1998; Hofmann and Murphy 2004; Murphy, Trathan, et al. 2007a, b). However, small krill have been described in the diet of mackerel icefish (*Champsocephalus gunnari*) (Main et al. 2009) and in trawls in winter (Ichii et al. 2023 Liszka et al. 2024), indicating that they are, at least occasionally, present in the local ecosystem.

Predator diets potentially reflect the species and life-history stages available in the local environment (Reid and Arnould 1996); as such, the abundance of a given prey item in the diet likely reflects its availability (or secondary consumption). Where preferred prey are unavailable, or in short supply, alternate prey may be taken. When influxes of small krill are detected in the diet, it presumably reflects broader drivers of ecosystem variability. To fully capture these events in the future, it would be valuable to have diet data from other predators that feed on krill, such as mackerel icefish who also are not limited to the surface waters and can sample krill at or near the seabed. Including mackerel icefish as an indicator or long term monitoring species as part of CEMP could help improve ecosystem monitoring (Everson 2002), as would regular plankton trawls over the South Georgia shelf in both summer and winter.

Increase in krill size – long term trend

The mean, mode and median size of krill taken by fur seals at Bird Island in our study were generally greater than those found during the 1991–1997 period (Reid et al. 1999), with an increasing (but not significant) trend observed at both sites until 2021. The increase in krill size compared to earlier studies could reflect a change in spatial population (e.g. Atkinson et al. 2019*)* or be reflective of a reduction of krill in the system (Forcada et al. 2023). Further, Ichii et al. (2023) have hypothesized that a regime shift has weakened the connection between the Antarctic Peninsula and South

Georgia, with the southern Scotia Sea now being the main driver of recruitment to South Georgia (Ichii et al. 2023). This may reflect altered connectivity, advection pathways and hence different growth rates.

Winter variability in diet

Winter krill sizes were generally smaller, with larger (55+mm TL) krill often completely absent, but with an increase in the fish dietary component at both sites (Online Resource 1), supporting previous winter diet studies (Reid 1995; Reid et al. 2006). Identifying the reasons for this observation are important and could reflect different processes. Firstly, in the winter, scats were derived from different demographic components of the fur seal population, with more immature seals and fewer adult females present. Alternatively, the observed seasonal differences could be due to different prey availability and distribution during the winter (Bahlburg et al. 2023). Depending upon circumstances, large krill, which are deeper in winter months (Ichii et al. 2020) may be beyond the reach of some fur seals. The biological and physical state of the Southern Ocean in winter is different to that of summer (Priddle et al. 1986; Constable et al. 2014), with cooler temperatures, greater MLD, lower CHL and differing current speeds. Another explanatory factor could be krill shrinking to cope with cooler, less productive conditions (Tarling et al. 2016). Using seasonal trawl data, a reduction in winter mean krill length around South Georgia was explained by shrinkage of female krill (Tarling et al. 2016). It is difficult to unambiguously explain these differences, especially given the small sample size of krill often available in winter scats. However it is likely that observed differences are a result of a combination of the above.

Conclusion and importance to fisheries management

South Georgia's predator populations remain critically dependent on episodic pulses of krill advected from the Weddell Sea and Antarctic Peninsula. These are interspersed with krill-poor periods likely driven by variability in the Antarctic Circumpolar Current (Murphy et al. 2007a, b; Reid et al. 1999). During these krill-poor periods, winter krill fishing has the potential to intensify resource depletion within predator foraging areas (Owen et al. 2024), reinforcing the need for spatially restricted and adaptive krill catch limits (Trathan et al. 2021). Given that fur seals and other higher predators return to breed in October–December, limited krill availability at this time could have direct consequences for maternal condition and reproductive success. Our results further highlight that recruitment events appear to occur every 3–5 years, with associated carryover effects between seasons and years (Trathan et al. 2021).

Additionally, seals from Bird Island are consuming prey from a modified prey field; krill along the north coast of South Georgia are likely to have been selectively predated (possibly very significantly) before reaching Bird Island (Trathan et al. 2012).This could be intensified as demersal fish and whale populations recover (Zerbini et al. 2019; Hollyman et al. 2021). Breakdowns between the two sites could also be explained by a change in the vertical distribution of krill in the north reducing their availability to fur seals who are restricted to foraging in the surface waters (<200 m). If predator depletion or environmental changes have reduced the availability of prey in these surface layers this may suggest that local predator populations are approaching carrying capacity. Given one of the objectives of the CCAMLR Convention is to maintain ecological relationships between harvested, dependent and related populations it is important to understand any changes in vertical and horizontal prey dynamics and include such predator diet data in future management procedures.

By combining diet and tracking data, this study demonstrates that fur seals from Maiviken and Bird Island exploit distinct foraging areas, whilst experiencing near-synchronous dietary conditions, even over distances of only 100–200 km. A temporary breakdown in this synchrony underlines the value of maintaining multiple, spatially separated monitoring sites to capture ecosystem variability that would otherwise be missed. Long-term diet datasets from different colonies therefore provide an essential early-warning system for detecting shifts in ecosystem state. Continued study of fur seal scats may look to incorporate genetic analysis allowing for scat data to be sexed (Schwarz et al. 2018) and alternative prey species to be identified (Drago et al. 2023) more accurately giving more context to help explain differences in size and changes during low krill periods.

More broadly, these findings underscore the urgency of understanding krill recruitment processes in a rapidly changing subpolar ecosystem. Declines in Antarctic fur seals have already been linked to krill availability (Forcada et al. 2023), and future recruitment will likely be further compromised by rising sea surface temperature (Atkinson et al. 2019; Chown and Brooks 2019), reduced sea ice in the Scotia Sea and the Antarctic Peninsula region (Meredith et al. 2019), ocean acidification (Constable et al. 2014; Meredith et al. 2019) and increased fishing (Chown and Brooks 2019). In this context, long-term, spatially resolved datasets such as those presented here are indispensable (Bestley et al. 2020). They not only advance ecological understanding of predator–prey dynamics but also provide the foundation for ecosystem-based fisheries management in the Southern Ocean.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-026-04816-7.

Acknowledgements We would like to thank all past and present zoological field assistants who helped with scat data collection as well as Sarah Robinson for the Bird Island tag data. Helen Peat who manages the science databases and Eugene Murphy, Rebecca Nagel, and Simeon Hill for insightful discussions and questioning throughout the writing process.

Author's contributions All authors contributed to the study conception and design. Iain Staniland, Jon Ashburner, Jamie Coleman and Kate Owens all took part in data collection. Claire Waluda managed and compiled the diet databases. Material preparation, and analysis were performed by Jamie Coleman. Project supervision was carried out by Mark Jessop, Martin Collins, Phil Hollyman and Phil Trathan. The first draft of the manuscript was written by Jamie Coleman and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding The authors have no relevant financial or non-financial interests to disclose. No funding was received for conducting this study.

Data availability The datasets generated and/or analysed during the current study are available from the UK Polar Data Centre (UKPDC) repository. Seal tracks are available at https://data.bas.ac.uk/full-record.php?id=GB/NERC/BAS/PDC/01220. Diet data accessed at https://data.bas.ac.uk/full-record.php?id=GB/NERC/BAS/PDC/01185 for Bird Island and https://data.bas.ac.uk/full-record.php?id=GB/NERC/BAS/PDC/01187 for King Edward Point.

Declarations

Conflicts of interest The authors declare there are no competing interests..

Ethics approval All sampling procedures used were regulated by the British Antarctic Survey Ethical Review Committee in collaboration with Cambridge University and the UK Home Office. Permission for this scientific study was given by the Government of South Georgia and the South Sandwich Island.

References

Agnew DJ (1997) Review the CCAMLR ecosystem monitoring programme. Antarct Sci 9(3):235–242

Atkinson A, Whitehouse MJ, Priddle J, Cripps GC, Ward P, Brandon MA (2001) South Georgia, Antarctica: a productive, cold water, pelagic ecosystem. Mar Ecol Prog Ser 216:279–308. https://doi.org/10.3354/meps216279

Atkinson A, Hill SL, Pakhomov EA, Siegel V, Reiss CS, Loeb VJ, Steinberg DK, Schmidt K, Tarling GA, Gerrish L, Sailley SF (2019) Krill (*Euphausia superba*) distribution contracts southward during rapid regional warming. Nat Clim Chang 9(2):142–147. https://doi.org/10.1038/s41558-018-0370-z

Bahlburg D, Hüppe L, Böhrer T, Thorpe SE, Murphy EJ, Berger U, Meyer B (2023) Plasticity and seasonality of the vertical migration behaviour of Antarctic krill using acoustic data from fishing vessels. R Soc Open Sci. https://doi.org/10.1098/rsos.230520

Bamford CCG, Warwick-Evans V, Staniland IJ, Jackson JA, Trathan PN (2021) Wintertime overlaps between female Antarctic fur seals (*Arctocephalus gazella*) and the krill fishery at South Georgia, South Atlantic. PLoS ONE 16(3):1–20. https://doi.org/10.1371/journal.pone.0248071

Barlow KE, Boyd IL, Croxall JP, Reid K, Staniland IJ, Brierley AS (2002) Are penguins and seals in competition for Antarctic krill at South Georgia? Mar Biol 140(2):205–213. https://doi.org/10.1007/s00227-001-0691-7

Basberg B, Headland RK (2012) The 19th century Antarctic sealing industry: sources, data and economic significance. Polar Rec 49(4):381–391. https://doi.org/10.1017/S0032247412000411

Bestley S et al (2020) Marine ecosystem assessment for the Southern Ocean: birds and marine mammals in a changing climate. Front Ecol Evol 8:338. https://doi.org/10.3389/fevo.2020.566936

Boyd IL, Arnould JPY, Barton T, Croxall JP (1994) Foraging behaviour of Antarctic fur seals during periods of contrasting prey abundance. J Anim Ecol 63(3):703. https://doi.org/10.2307/5235

Boyd IL, McCafferty DJ, Reid K, Taylor R, Walker TR (1998) Dispersal of male and female antarctic fur seals (*Arctocephalus gazella*). Can J Fish Aquat Sci 55(4):845–852. https://doi.org/10.1139/F97-314

Boyd IL, Staniland IJ, Martin AR (2002) Distribution of foraging by female Antarctic fur seals. Mar Ecol Prog Ser 242:285–294. https://doi.org/10.3354/meps242285

Brierley A, Watkins J, Goss C, Wilkinson M, Everson I (1999) Acoustic estimates of krill density at South Georgia, 1981 to 1998. CCAMLR Sci 6:47–57

British Antarctic Survey (2023) South Georgia GIS. Available at: https://www.sggis.gov.gs/home.

Calderan SV, Black A, Branch TA, Collins MA, Wood AG, Jackson JA, Kelly N, Miller BS, Leaper R, Lurcock S, Moore M, Olson PA, Širović A (2020) South Georgia blue whales five decades after the end of whaling. Endanger Species Res 43:359–373. https://doi.org/10.3354/esr01077

Cavan EL, Belcher A, Atkinson A, Hill SL, Kawaguchi S, McCormack S, Meyer B, Nicol S, Ratnarajah L, Schmidt K, Steinberg DK, Tarling GA, Boyd PW (2019) The importance of Antarctic krill in biogeochemical cycles. Nat Commun 10(1):1–13. https://doi.org/10.1038/s41467-019-12668-7

Chown SL, Brooks CM (2019) The state and future of Antarctic Environments in a Global Context. Annu Rev Environ Resour 44:1–30. https://doi.org/10.1146/annurev-environ-101718-033236

Coleman, J, Fenney, N, Trathan, PN, Fox, A, Fox, E, Bennison, A, Ireland, L, Collins, MA and Hollyman, PR (2024) A comparison of established and digital surface model (DSM)-based methods to determine population estimates and densities for king penguin colonies, using fixed-wing drone and satellite imagery, Remote

Sensing in Ecology and Conservation [Preprint]. https://doi.org/10.1002/rse2.424.

Constable AJ et al (2014) Climate change and Southern Ocean ecosystems I: how changes in physical habitats directly affect marine biota. Glob Change Biol 20(10):3004–3025. https://doi.org/10.1111/gcb.12623

Croxall JP, Reid K, Prince PA (1999) Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. Mar Ecol Prog Ser 177:115–131. https://doi.org/10.3354/meps177115

Descalzo M, Danieri GA, Harrington A, Negrete J (2025) The importance of krill in the diet of the Antarctic fur seal Arctocephalus gazella from Stranger Point (Isla 25 de Mayo/King George Island), South Shetland Islands. Polar Biol. https://doi.org/10.1007/s00300-025-03363

Doidge D, McCann T, Croxall J (1986) Attendance Behaviour of Antarctic Fur Seals. In: Gentry R, Kooyman G (eds) Fur Seals Maternal Strategies on Land and at Sea. Princeton University Press, pp 102–114

Drago M, Llorach C, Santa Cruz UO, Zenteno-Devaud L, Rebolledo L, Rita D, Gazo M, Cardona L (2023) Seasonal and interannual variability in the diet of young and subadult male Antarctic fur seals as revealed by stable C and N isotope ratios. Can J Fish Aquat Sci 80(1):69–84. https://doi.org/10.1139/cjfas-2022-0145

Drevillon, M., Fernandez, E. and Lellouche, J. (2021) Global ocean physics reanalysis. Copernicus Marine Environment Monitoring Service platform. https://doi.org/10.48670/moi-00021.

Duck C (1990) Annual variation in the timing of reproduction in Antarctic fur seals, *Arctocephufuus gazellu*, at Bird Island, South Georgia. J Zool 222(1):103–116. https://doi.org/10.1111/j.1469-7998.1990.tb04032.x

Dunn MJ, Waluda CM, Adlard S, Fox D, Lynnes AS, Morley TI, Forcada J (2025) Temporary absence of warming in the Northern Weddell Sea validates expected responses of Antarctic seals to sea ice change. Glob Change Biol. https://doi.org/10.1111/gcb.70290

Everson I (2002) Consideration of major issues in ecosystem monitoring and management. CCAMLR Sci 9:213–232

Forcada J, Staniland I (2009) Antarctic Fur Seal *Arctocephalus gazella*. In: Perrin WF, Wursig B, Thewissen JGM (eds) Encyclopedia of Marine Mammals, 2nd edn. Academic Press Elsevier

Forcada J, Hoffman JI, Gimenez O, Staniland IJ, Bucktrout P, Wood AG (2023) Ninety years of change, from commercial extinction to recovery, range expansion and decline for Antarctic fur seals at South Georgia. Glob Change Biol. https://doi.org/10.1111/gcb.16947

Gentry, RL and Holt, JR (1982) 'Equipment and Techniques for Handling Northern Fur Seals', *Report No. NMFS SSRF 758. U.S. Department of Commerce, NOAA, Seattle* [Preprint].

Hill HJ (1990) A new method for the measurement of Antarctic krill *Euphausia superba* dana from predator food samples. Polar Biol 10(4):317–320. https://doi.org/10.1007/BF00238431

Hoffman JI, Chen RS, Vendrami DLJ, Paijmans AJ, Dasmahapatra KK, Forcada J (2022) Demographic reconstruction of Antarctic fur seals supports the Krill Surplus Hypothesis. Genes 13(3):541. https://doi.org/10.3390/genes13030541

Hofmann EE, Murphy EJ (2004) Advection, krill, and Antarctic marine ecosystems. Antarct Sci 16(4):487–499. https://doi.org/10.1017/S0954102004002275

Hollyman PR, Hill SL, Laptikhovsky VV, Belchier M, Gregory S, Clement A, Collins MA (2021) A long road to recovery: dynamics and ecology of the marbled rockcod (*Notothenia rossii*, family: Nototheniidae) at South Georgia, 50 years after overexploitation. ICES J Mar Sci 78(8):2745–2756. https://doi.org/10.1093/icesjms/fsab150

Ichii T, Mori Y, Mahapatra K, Trathan P, Okazaki M, Hayashi T, Okuda T (2020) Body length-dependent diel vertical migration of Antarctic krill in relation to food availability and predator avoidance in winter at South Georgia. Mar Ecol Prog Ser 654:53–66. https://doi.org/10.3354/meps13508

Ichii T, Igarashi H, Mori M, Mahapatra K, Nishikawa H, Okuda T (2023) Impact of the climate regime shift around 2000 on recruitment of Antarctic krill at the Antarctic Peninsula and South Georgia. Prog Oceanogr 213(March):103020. https://doi.org/10.1016/j.pocean.2023.103020

Jones KA, Ratcliffe N, Votier SC, Newton J, Forcada J, Dickens J, Stowasser G, Staniland IJ (2020) Intra-specific niche partitioning in Antarctic fur seals, *Arctocephalus gazella*. Sci Rep 10(1):1–15. https://doi.org/10.1038/s41598-020-59992-3

Juáres MA, Grech MG, Casaux R, Negrete J, Fógel J, Coria NR, Santos MM (2021) Size structure of Antarctic krill inferred from samples of Pygoscelid penguin diets and those collected by the commercial krill fishery. Mar Biol 168(3):1–12. https://doi.org/10.1007/s00227-021-03831-0

Kock, K-H, Agnew, DJ, Boyd, IL, Butterworth, DS, Croxall, JP, Mare, WKD. La, Everson, I., Mangel, M, Miller, DGM and Thomson, R (2000) Understanding CCAMLR's Approach to Management, (May), p. 57.

Mackintosh N (1974) Sizes of krill eaten by whales in the Antarctic. Cambridge University Press

Main CE, Collins MA, Mitchell R, Belchier M (2009) Identifying patterns in the diet of mackerel icefish (*Champsocephalus gunnari*) at South Georgia using bootstrapped confidence intervals of a dietary index. Polar Biol 32(4):569–581. https://doi.org/10.1007/s00300-008-0552-7

Matano RP, Combes V, Young EF, Meredith MP (2020) Modeling the impact of ocean circulation on chlorophyll blooms around South Georgia, Southern Ocean. J Geophys Res: Oceans 125(9):1–18. https://doi.org/10.1029/2020JC016391

Meredith MP, King JC (2005) Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. Geophys Res Lett 32(19):1–5. https://doi.org/10.1029/2005GL024042

Meredith MP, Murphy EJ, Hawker EJ, King JC, Wallace MI (2008) On the interannual variability of ocean temperatures around South Georgia, Southern Ocean: forcing by El Niño/Southern Oscillation and the Southern Annular Mode. Deep Sea Res Part II 55(18–19):2007–2022. https://doi.org/10.1016/J.DSR2.2008.05.020

Meredith, M, Sommerkorn, M, Cassotta, S, Derksen, C, Ekaykin, A, Hollowed, A, Kofinas, G, Mackintosh, A, Melbourne-Thomas, J, Muelbert, MMC, Ottersen, G, Pritchard, H and Schuur, EAG. (2019) 'Polar Regions.', in Pörtner, H-O, Roberts, DC, Masson-Delmotte, V, Zhai, P, Tignor, M, Poloczanska, E, Mintenbeck, K, Alegría, A, Nicolai, M, Okem, A, Petzold, J, Rama, B, and Weyer, N (eds) IPCC Special Report on the Ocean and Cryosphere in a Changing Climate.

Murphy E, Reid K (2001) Modelling Southern Ocean krill population dynamics: biological processes generating fluctuations in the South Georgia ecosystem. Mar Ecol Prog Ser 217:175–189. https://doi.org/10.3354/meps217175

Murphy E, Watkins JL, Reid K, Trathan PN, Everson I, Croxall JP, Priddle J, Brandon M, Brierley AS, Hofmann E (1998) Interannual variability of the South Georgia marine ecosystem: biological and physical sources of variation in the abundance of krill. Fish Oceanogr 7(3–4):381–390. https://doi.org/10.1046/j.1365-2419.1998.00081.x

Murphy E, Watkins J et al (2007a) Spatial and temporal operation of the Scotia Sea ecosystem: a review of large-scale links in a krill centred food web. Philos Trans R Soc Lond B Biol Sci 362(1477):113–148. https://doi.org/10.1098/rstb.2006.1957

Murphy E, Trathan PN, Watkins JL, Reid K, Meredith MP, Forcada J, Thorpe SE, Johnston NM, Rothery P (2007b) Climatically driven fluctuations in Southern Ocean ecosystems. Proc R Soc Lond B Biol Sci 274(1629):3057–3067. https://doi.org/10.1098/rspb.2007.1180

Nagel R, Stainfield C, Fox-Clarke C, Toscani C, Forcada J, Hoffman JI (2021) Evidence for an Allee effect in a declining fur seal population. Proc Royal Soc b: Biol Sci. https://doi.org/10.1098/rspb.2020.2882

Nel W, Hedding DW, Rudolph EM (2023) The sub-Antarctic islands are increasingly warming in the 21st century. Antarct Sci 35(2):124–126. https://doi.org/10.1017/S0954102023000056

Nicol S, Foster J (2016) 'The fishery for Antarctic krill: its current status and management regime.' In: Siegel V (ed) *Biology and ecology of Antarctic krill*. Advances in polar ecology. Springer, Cham, pp 387–421. https://doi.org/10.1007/978-3-319-29279-3_11

Nicol S, Foster J, Kawaguchi S (2012) The fishery for Antarctic krill - recent developments. Fish Fish 13(1):30–40. https://doi.org/10.1111/j.1467-2979.2011.00406.x

Oksanen, J, Blanchet, G, Friendly, M, Kindt, R, Legendre, P, McGlinn, D, Minchin, PR, O'Hara, R, Simpson, G, Solymos, P, Stevens, HH, Szoecs, E and Wagner, H (2020) 'vegan: Community Ecology Package'. R package version 2.5–7.

Orsi, AH., Harris, U. (2019) 'Fronts of the Antarctic Circumpolar Current - GIS data'. Australian Antarctic Data Centre. Available at: https://data.aad.gov.au/metadata/records/antarctic_circumpolar_current_fronts.

Owen KA, Goggins M, Black A, Ashburner J, Wilson A, Hollyman PR, Trathan PN, Waluda CM, Collins MA (2024) At-sea distribution of marine predators around South Georgia during austral winter, with implications for fisheries management. Polar Biol 47(7):663–679. https://doi.org/10.1007/s00300-024-03257-6

Pallin LJ, Kellar NM, Steel D, Botero-Acosta N, Baker CS, Conroy JA, Costa DP, Johnson CM, Johnston DW, Nichols RC, Nowacek DP, Read AJ, Savenko O, Schofield OM, Stammerjohn SE, Steinberg DK, Friedlaender AS (2023) A surplus no more? Variation in krill availability impacts reproductive rates of Antarctic baleen whales. Glob Change Biol 29(8):2108–2121. https://doi.org/10.1111/gcb.16559

Perruche, C. (2019) Ocean global biological multiyear dataset. Copernicus Marine Environment Monitoring Service. https://doi.org/10.48670/moi-00019.

Priddle J, Heywood RB, Theriot E (1986) Some environmental factors influencing phytoplankton in the Southern Ocean around South Georgia. Polar Biol 5(2):65–79. https://doi.org/10.1007/BF00443379

Priddle J, Whitehouse MJ, Ward P, Shreeve RS, Brierley AS, Atkinson A, Watkins JL, Brandon MA, Cripps GC (2003) Biogeochemistry of a Southern Ocean plankton ecosystem: using natural variability in community composition to study the role of metazooplankton in carbon and nitrogen cycles. J Geophys Res Oceans 108(4):1–13. https://doi.org/10.1029/2000jc000425

R Core Team (2020) R: A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing

Reid K (1995) The diet of Antarctic fur seals (*Arctocephalus gazella* Peters 1875) during winter at South Georgia. Antarct Sci 7(3):241–249. https://doi.org/10.1017/S0954102095000344

Reid K (1996) A guide to the use of Otoliths in the study of predators at south. British Antarctic Survey

Reid K, Arnould JPY (1996) The diet of Antarctic fur seals *Arctocephalus gazella* during the breeding season at South Georgia. Polar Biol 16(2):105–114. https://doi.org/10.1007/BF02390431

Reid K, Croxall J (2001) Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. Proc R Soc Lond B Biol Sci 268(1465):377–384. https://doi.org/10.1098/rspb.2000.1371

Reid K, Watkins JL, Croxall JP, Murphy EJ (1999) Krill population dynamics at South Georgia 1991-1997, based on data from predators and nets. Mar Ecol Prog Ser 177:103–114. https://doi.org/10.3354/meps177103

Reid K, Jessopp MJ, Barrett MS, Kawaguchi S, Siegel V, Goebel ME (2004) Widening the net: spatio-temporal variability in the krill population structure across the Scotia Sea. Deep-Sea Res Part II Top Stud Oceanogr 51(12-13 SPEC.ISS.):1275–1287. https://doi.org/10.1016/j.dsr2.2004.06.014

Reid K, Davis D, Staniland IJ (2006) Spatial and temporal variability in the fish diet of Antarctic fur seal (*Arctocephalus gazella*) in the Atlantic sector of the Southern Ocean. Can J Zool 84(7):1025–1037. https://doi.org/10.1139/Z06-071

Schwarz D, Spitzer SM, Thomas AC, Kohnert CM, Keates TR, Acevedo-Gutiérrez A (2018) Large-scale molecular diet analysis in a generalist marine mammal reveals male preference for prey of conservation concern. Ecol Evol 8(19):9889–9905. https://doi.org/10.1002/ece3.4474

Staniland IJ (2002) Investigating the biases in the use of hard prey remains to identify diet composition using Antarctic fur seals (*Arctocephalus gazella*) in captive feeding trials. Mar Mamm Sci 18(1):223–243. https://doi.org/10.1111/j.1748-7692.2002.tb01030.x

Staniland IJ (2005) Sexual Segregation in Seals. In: Ruckstuhl K, Neuhaus P (eds) Sexual Segregation in Vertebrates. Cambridge University Press, pp 53–73

Staniland IJ, Morton A, Robinson SL, Malone D, Forcada J (2011) Foraging behaviour in two antarctic fur seal colonies with differing population recoveries. Mar Ecol Prog Ser 434:183–196. https://doi.org/10.3354/meps09201

Staniland, I, Waluda, C and Forcada, J (2020) 'Platform Transmitting Terminal (PTT) tracking of Antarctic Fur Seals at Bird Island, South Georgia, from 1995 - 2010 (Version 1.0) ', *UK Polar Data Centre, Natural Environment Research Council, UK Research & Innovation* [Preprint]. https://doi.org/10.5285/224003cc-8f77-4980-8cac-5574e179e4f8.

Sumner MD, Wotherspoon SJ, Hindell MA (2009) Bayesian estimation of animal movement from archival and satellite tags. PLoS ONE 4(10):7324. https://doi.org/10.1371/journal.pone.0007324

Sumner M, Wotherspoon S, Hindell M (2011) The Tag Location Problem. University of Tasmania

Sumner, M, Luque, S, Fischbach, A and Hengl, T (2021) Tools for the Analysis of Animal Track Data.

Tarling TA, Cuzin-Roudy J, Thorpe S, Shreeve R, Ward P, Murphy E (2007) No recruitment of Antarctic krill *Euphausia superba* in the South Georgia region: adult fecundity and the fate of larvae title. Mar Ecol Prog Ser 331:161–179. https://doi.org/10.3354/meps

Tarling GA, Hill S, Peat H, Fielding S, Reiss C, Atkinson A (2016) Growth and shrinkage in antarctic krill *Euphausia superba* is sex-dependent. Mar Ecol Prog Ser 547:61–78. https://doi.org/10.3354/meps11634

Trathan PN (2023) What is needed to implement a sustainable expansion of the Antarctic krill fishery in the Southern Ocean? Mar Policy 155(March):105770. https://doi.org/10.1016/j.marpol.2023.105770

Trathan PN, Hill SL (2016) The importance of krill predation in the Southern Ocean. In: Siegel V (ed) Biology and ecology of Antarctic krill. Springer International Publishing, Cham, pp 321–350. https://doi.org/10.1007/978-3-319-29279-3_9

Trathan PN, Murphy EJ (2003) Sea surface temperature anomalies near South Georgia: relationships with the Pacific El Niño regions. J Geophys Res Oceans 108(4):1–10. https://doi.org/10.1029/2000jc000299

Trathan P, Brandon M, Murphy E (1997) Characterisation of the Antarctic Polar Frontal Zone to the north of South Georgia in summer. J Geophys Res 102(C5):10483–10497

Trathan PN, Brierley AS, Brandon M, Bone DG, Goss C, Grant SA, Murphy EJ, Watkins JL (2003) Oceanographic variability and changes in Antarctic krill (*Euphausia superba*) abundance at South Georgia. Fish Oceanogr 12(6):569–583. https://doi.org/10.1046/j.1365-2419.2003.00268.x

Trathan PN, Murphy EJ, Forcada J, Croxall JP, Reid K, Thorpe SE, Camphuysen CJ (2006) Physical forcing in the southwest Atlantic: ecosystem control. In: Boyd IL, Wanless S, Camphuysen CJ (eds) Top predators in marine ecosystems: their role in monitoring and management. Cambridge University Press, pp 28–45. https://doi.org/10.1017/CBO9780511541964.004

Trathan PN, Ratcliffe N, Masden EA (2012) Ecological drivers of change at South Georgia: the krill surplus, or climate variability. Ecography 35(11):983–993. https://doi.org/10.1111/j.1600-0587.2012.07330.x

Trathan P, Fielding S, Hollyman PR, Murphy EJ, Warwick-Evans V, Collins MA (2021) Enhancing the ecosystem approach for the fishery for Antarctic krill within the complex, variable, and changing ecosystem at South Georgia. ICES J Mar Sci 78(6):2065–2081. https://doi.org/10.1093/ICESJMS/FSAB092

Trathan PN, Savoca MS, Friedlaender A, Baines M, Burkhardt E, Cheeseman T, Dalla Rosa L, Herr H, Secchi ER, Zerbini AN, Reisinger RR (2024) Integrating the needs of recovering populations of baleen whales into the revised management framework for the commercial fishery for Antarctic krill. Front Mar Sci 11(December):1–29. https://doi.org/10.3389/fmars.2024.1458042

Trathan, P, Fielding, S, Warwick-Evans, V, Freer, J and Perry, F (2022) ‘Marine predator responses to variability in the distribution and abundance of Antarctic krill at the sub-Antarctic island of South Georgia’, *ICES Journal of Marine Science*, (In Press).

Turner J, Guarino MV, Arnatt J, Jena B, Marshall GJ, Phillips T, Bajish CC, Clem K, Wang Z, Andersson T, Murphy EJ, Cavanagh R (2020) Recent decrease of summer sea ice in the Weddell Sea, Antarctica. Geophys Res Lett. https://doi.org/10.1029/2020GL087127

Veytia D, Bestley S, Kawaguchi S, Meiners KM, Murphy EJ, Fraser AD, Kusahara K, Kimura N, Corney S (2021) Overwinter sea-ice characteristics important for Antarctic krill recruitment in the southwest Atlantic. Ecol Indic 129(June):107934. https://doi.org/10.1016/j.ecolind.2021.107934

Waluda CM, Collins MA, Black AD, Staniland IJ, Trathan PN (2010) Linking predator and prey behaviour: contrasts between Antarctic fur seals and macaroni penguins at South Georgia. Mar Biol 157(1):99–112. https://doi.org/10.1007/s00227-009-1299-6

Whitehouse MJ, Korb RE, Atkinson A, Thorpe SE, Gordon M (2008a) Formation, transport and decay of an intense phytoplankton bloom within the High-Nutrient Low-Chlorophyll belt of the Southern Ocean. J Mar Syst 70(1–2):150–167. https://doi.org/10.1016/j.jmarsys.2007.05.003

Whitehouse MJ, Meredith MP, Rothery P, Atkinson A, Ward P, Korb RE (2008b) Rapid warming of the ocean around South Georgia, Southern Ocean, during the 20th century: forcings, characteristics and implications for lower trophic levels. Deep-Sea Res Part I Oceanogr Res Pap 55(10):1218–1228. https://doi.org/10.1016/j.dsr.2008.06.002

Xavier JC, Cherel Y (2009) Cephalopod beak guide for the southern Ocean. British Antarctic Survey, Cambridge, UK

Young EF, Thorpe SE, Banglawala N, Murphy EJ (2014) Variability in transport pathways on and around the South Georgia shelf, Southern Ocean: implications for recruitment and retention. J Geophys Res Oceans 119(1):241–252. https://doi.org/10.1002/2013JC009348

Zerbini AN, Adams G, Best J, Clapham PJ, Jackson JA, Punt AE (2019) Assessing the recovery of an Antarctic predator from historical exploitation. R Soc Open Sci. https://doi.org/10.1098/rsos.190368