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Spatiotemporal variability in Antarctic krill (*Euphausia superba*) around South Georgia from Antarctic Fur Seal (*Arctocephalus gazella*) diets at two long term monitoring sites

Thesis presented by
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Masters in Zoology

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2022



Table of Contents

Declaration ***2***
Abstract ***3***
Introduction ***4***
Methods ***8***
Results ***13***
Discussion ***26***
Acknowledgements ***33***
References ***34***
Supplementary Material ***43***

Declaration

"This is to certify that the work I am submitting is my own and has not been submitted for another degree, either at University College Cork or elsewhere. All external references and sources are clearly acknowledged and identified within the contents. I have read and understood the regulations of University College Cork concerning plagiarism and intellectual property."

Abstract

Despite its biological, biogeochemical, and economic importance, there is much about Antarctic krill (*Euphausia superba* Dana, 1852) that is still poorly understood. This is especially true for its recruitment into South Georgia's waters, which is highly variable and difficult to predict. Krill fluctuations exert bottom-up pressures on the entire ecosystem which can be reflected in changes in the breeding success and diet of dependent higher predators, such as Antarctic fur seals - *Arctocephalus gazella* (Peters, 1875). This study compares two long-term datasets (2008-2021) of Antarctic fur seal diet from Bird Island and King Edward Point, South Georgia, to investigate year-round krill dynamics. Foraging tracks from breeding female fur seals demonstrated that seals from the two sites forage in distinct regions. 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 ongoing senescence, mortality and possibly krill shrinkage, coupled with recent recruits with smaller body lengths entering the population. Using a multivariate approach, mixed layer depth, sea surface temperature, chlorophyll *a*, and salinity together explained 43% of the dissimilarities in krill length-frequency distributions predated by fur seals between seasons. Bird Island seals took significantly larger krill than those at KEP, 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 sites broke down and later re-established. The beginning and end of this anomalous period appears to coincide with switches in the El Niño Southern-Oscillation, however more data are needed to formally test this link. This study highlights the importance of having multiple spatially separated long-term monitoring sites; this is particularly important in this ecological system as it can vary over a range of scales, including local scales, and it is also recognised to be experiencing significant changes.

Introduction

Antarctic krill (*Euphausia superba;* hereafter referred to as krill), is a keystone species that dominates food webs in the Southern Ocean (Marr, 1962; Mackintosh, 1974; Murphy *et al.*, 2016; Schmidt and Atkinson, 2016; Sylvester *et al.*, 2021) as well as being an integral component in biogeochemical cycles (Priddle *et al.*, 2003; EJ. Murphy *et al.*, 2007; Cavan *et al.*, 2019). It has a larger biomass than any wild chordate on this planet, weighing almost as much as the entire human population (Atkinson *et al.*, 2009; Bar-On *et al.*, 2018; Meyer *et al.*, 2020). 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 (Atkinson *et al.*, 2009, 2019). Here, its latitudinal range is also the greatest, with krill found as far north as the southern edge of the Polar Front (Murphy *et al.*, 2007). South Georgia is a subantarctic island that lies within this hotspot for krill on the Scotia Ridge within the flow of the Antarctic Circumpolar Current (ACC), south of the Antarctic Polar Front (Fig 1, Murphy and Reid, 2001; Trathan and Murphy, 2003; Young *et al.*, 2014). The waters around South Georgia are highly productive and rich in nutrients (Atkinson *et al.*, 2001; Whitehouse *et al.*, 2008), resulting in an island renowned for its wildlife populations (Atkinson *et al.*, 2001; Holm-Hansen *et al.*, 2004; Murphy *et al.*, 2007). Millions of animals exploit the plentiful foraging opportunities in this region (Boyd *et al.*, 2002).

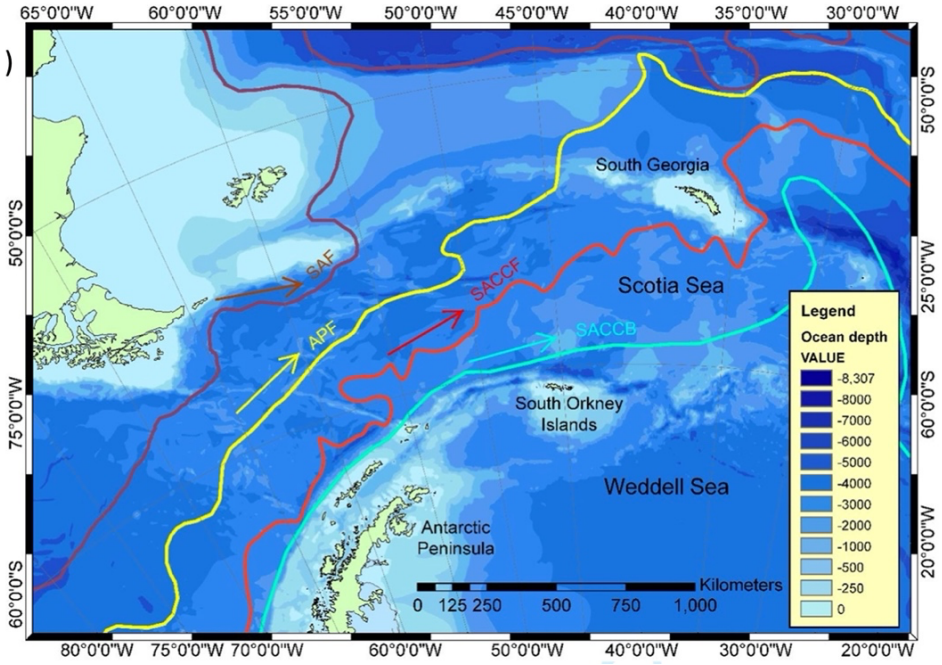


Figure 1. Location of South Georgia within the southwest Atlantic sector of the Southern Ocean in relation to the major fronts in the Antarctic Circumpolar Current (ACC): Sub Antarctic Front (SAF - brown); Antarctic Polar Front (APF-yellow); Southern Ocean ACC Front (SACCF - red); Southern ACC Boundary (SACCB - pale blue). Reproduced from Trathan *et al.*, (2022).

The krill found in the waters around South Georgia are not part of a localised self-sustaining population, and are reliant on recruitment from the Antarctic Peninsula (Everson, 1976; Ward *et al.*, 1990; Murphy *et al.*, 1998; Siegel and Watkins, 2016) via the ACC (Trathan *et al.*, 2003; Murphy *et al.*, 2007). By the time the krill is advected to South Georgia, it is already more than two years of age (Murphy *et al.*, 1998; Hofmann and Murphy, 2004; Murphy *et al.*, 2007). 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, which make it difficult to predict (Murphy *et al.*, 2007; Whitehouse *et al.*, 2008; Thorpe *et al.*, 2019; Veytia *et al.*, 2021). Although Antarctic sea ice does not generally extend as far north as South Georgia, it provides refuge and grazing habitat throughout the winter for juvenile krill prior to dispersal, and is therefore critical for survival of early life stages (Hofmann and Murphy, 2004; Piñones and Fedorov, 2016; Veytia *et al.*, 2021). Both sea ice and polar currents are known to vary naturally as well as with the El Niño Southern Oscillation (ENSO) and the Southern Annular Mode (SAM) (Trathan and Hill, 2016; Atkinson *et al.*, 2019). Recruitment of krill to South Georgia is therefore highly variable (Brierley *et al.*, 1999; Trathan *et al.*, 2003; Mori and Boyd, 2004; Saunders *et al.*, 2007; Veytia *et al.*, 2021). On a more local scale, krill's distribution and availability to predators around South Georgia is very patchy and can be affected by various environmental factors including chlorophyll concentration, sea surface temperature, salinity and mixed layer depth (Trathan *et al.*, 2003). Despite research into krill recruitment and distribution at South Georgia over much of the last century (e.g. Mackintosh 1974; Marr 1962; Atkinson *et al.*, 2019), aspects of this system and its variability are still poorly understood (Meyer *et al.*, 2020).

As an important prey species, fluctuations in krill stocks have bottom-up effects on consumers, impacting population dynamics (Croxall and Prince, 1987; Croxall *et al.*, 1999; Trathan and Hill, 2016), especially for species tied to land by their breeding cycle, often known as central place foragers (Orians and Pearson, 1979). One of the most abundant consumers of krill at South Georgia are Antarctic fur seals (*Arctocephalus gazella*, hereafter referred to as fur seals, Reid and Arnould, 1996; Boyd *et al.*, 2002), the only breeding otariid found in the Southern Ocean (Lowther, 2018). This species was hunted to commercial extinction between 1786 and 1820 (Basberg and Headland, 2012), with 1.2 million reported to have been killed on South Georgia alone (Weddell, 1825). Following a shift to whaling and a ban on sealing, Antarctic fur seals recovered to pre-sealing numbers

by the end of the 20th century (Staniland *et al.*, 2011; Foley and Lynch, 2020; Hoffman *et al.*, 2022), and 95% of the world's breeding population can now be found on South Georgia (Forcada and Staniland, 2009). During summer months (November-April) fur seals dominate South Georgia beaches. Females spend 3-4 months alternating between nursing their pups on land and making foraging trips of up to 7 days (Doidge *et al.*, 1986), usually within 100km of nursing beaches (Boyd *et al.*, 2002). Once pups are weaned, and females can disperse, only 30% of females winter in waters north of the Polar front (Jones et al., 2020). The rest remain in waters closer to South Georgia associating with the northern shelf break (Bamford et al., 2021). During this time adult males have dispersed South associating more closely with the Antarctic continent and the ice edge (Boyd et al., 1998). Throughout the year, the variability in success of South Georgia fur seals is largely linked to the availability of krill within their foraging area (Forcada *et al.*, 2005). For this reason, studying the biology of dependent predators can often be a simple, cost effective, method of monitoring changes in the krill-based ecosystem (Croxall and Prince, 1979; Reid and Croxall, 2001; Forcada *et al.*, 2005).

The Southern Ocean has a long history of overexploitation (Basberg and Headland, 2012; Zerbini *et al.*, 2019; Calderan *et al.*, 2020; Hollyman *et al.*, 2021). 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). Recognizing the importance of krill, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) was established to manage Southern Ocean fisheries in response to the rapid increase in krill fishery catches in the 1970s and early 1980s (Kock *et al.*, 2000). Despite the development of cooperative resource management in the Southern Ocean, this ecosystem is still the focus of important scientific concerns. Recent developments in fishing technology have allowed krill catches to increase (Trathan *et al.*, 2021), 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 (Calderan *et al.*, 2020; Hollyman *et al.*, 2021), which will have further impacts on krill dynamics (Hoffman *et al.*, 2022). Most significantly, South Georgia and the Antarctic Peninsula have experienced rapid warming over the past half a century (Meredith and King, 2005; Stammerjohn *et al.*, 2008; Constable *et al.*, 2014) which is likely to affect krill dynamics in the region.

As part of the management of the krill fishery, the CCAMLR Ecosystem Monitoring Programme (CEMP) was developed in 1987 (Agnew, 1997). This programme involves monitoring higher trophic-level species that are widely distributed and have a well-studied biology in order to better understand physical and biological variability in the Southern Ocean ecosystem (Agnew, 1997; Kock *et al.*, 2000). On South Georgia, CEMP is carried out on multiple species at Bird Island (BI) and King Edward Point (KEP), including Antarctic fur seals. The breeding performance and diet of Antarctic fur seals has been monitored at KEP since 2008, and at BI since before the CEMP programme began under the auspices of the British Antarctic Survey (BAS) monitoring programme. Inferring seal diet from scat contents found on land is a commonly used method for CEMP monitoring and in seal biology more generally. Squid beaks, feathers, fish bones, and otoliths can be recovered from scats and analysed to estimate prey importance (Reid *et al.*, 2006; Waluda *et al.*, 2010). Krill (Reid and Arnould, 1996; Casaux *et al.*, 2016), fish (Cherel *et al.*, 1997; Lea *et al.*, 2002; Reisinger *et al.*, 2018), squid (Lea *et al.*, 2002; Casaux *et al.*, 2003; Abreu *et al.*, 2019) and other prey items (Casaux *et al.*, 2016; Reisinger *et al.*, 2018) are of varying importance as diet varies across different Antarctic fur seal colonies across the Southern Ocean. However, around South Georgia, krill is the most important prey item (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, 2002; Staniland and Pond, 2005) and of the available population in South Georgia waters (Reid and Arnould, 1996; Croxall *et al.*, 1999; Reid *et al.*, 1999, 2004), making scat analysis a good candidate for low-cost and long-term monitoring of changes in the 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 BI, to look at interannual differences in krill throughout seven summers. They showed it was possible to identify the growth of krill between years and noted potential krill recruitment events in 1991 and 1994.

Fur seals from BI, at the northwest tip of South Georgia, despite showing niche partitioning through sex (Boyd *et al.*, 1998; Staniland and Robinson, 2008; Jones *et al.*, 2020) and age (Jones *et al.*, 2020), consistently forage to the northwest (Barlow *et al.*, 2002; Boyd *et al.*, 2002; Staniland and Boyd, 2003; Staniland *et al.*, 2004, 2011; Staniland and Robinson, 2008), where the local krill fishery occasionally operates (Trathan *et al.*, 2021). Summer tracking studies from other South Georgia sites have shown no foraging overlap with BI

fur seals (Boyd *et al.*, 2002; Staniland *et al.*, 2011). Those tracked from Stromness Bay, to the southeast, foraged perpendicular to the coast (Boyd *et al.*, 2002) towards the region currently targeted by the krill fishery in winter months (Trathan *et al.*, 2021). However, there are no published information on the foraging distribution or diet of fur seals from the CEMP monitoring site at KEP, nor whether the size distribution of krill differs between South Georgia CEMP monitoring sites. Therefore, the purpose of this research is to investigate the long-term dynamics of krill in the diet of fur seals at South Georgia. Specifically, I aim to:

1) Use previously unpublished tracking data to determine the foraging locations of Antarctic fur seals from KEP to compare against existing BI data and infer whether they are targeting the same waters and the same krill population.
2) Build on short-term summer studies by Reid *et al.* (1999) by investigating interannual patterns in krill length frequency at Bird Island over a longer period, and throughout the entire year.
3) Compare the intra and interannual length-frequency distributions of krill at Bird Island and King Edward Point to determine whether the krill population consumed by fur seals from these two sites are in synchrony.
4) Explore the environmental drivers of patterns or dissimilarities in krill length-frequency distributions at the two sites.

Methods

Study Location and Field Sampling

As part of the CEMP monitoring, Antarctic fur seal scats were collected and processed by seasonal Zoological Field Assistants from two fur seal breeding sites on South Georgia: Bird Island (BI) and King Edward Point (KEP), Cumberland Bay, between 2008 and 2021 (Fig 2). At Bird Island, scats were collected in the vicinity of Freshwater Beach (54.011°S, 38.052°W), and at KEP scats were collected between KEP (-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 scats per fortnight were collected during winter months (April-September, inclusive) when seals and therefore scats are less plentiful. If present, ten carapaces were measured from each scat. Where 100 measurable carapaces from krill were not present at BI, a further 5 scats were collected per sampling period. Scats collected

during the summer will mainly be from breeding females because males fast while holding territories and do not undertake regular foraging trips (Doidge *et al.*, 1986). During winter, adult males move towards the Antarctic continent (Boyd *et al.*, 1998), and sampled scats will be from both immature males and female fur seals.

Scats were collected using sterile plastic bags and processed promptly. When it was not possible to process samples immediately after collection, scats were frozen (-20°C). To process scats, they were mixed with warm water and gently broken down in the collection bag until solid material was able to sink. Floating material was decanted through a 1mm sieve, taking care not to pour off any larger solids. This process was repeated until solids could no longer be broken down further and were left in the bag. Solids were then removed into a sorting tray with water where they were cleaned, and fish otoliths and squid beaks removed for identification. Stored material was gently rinsed to remove any detritus before the remaining material was decanted from the sieve into another sorting tray. Warm water was added to separate the material further and isolate krill carapaces.

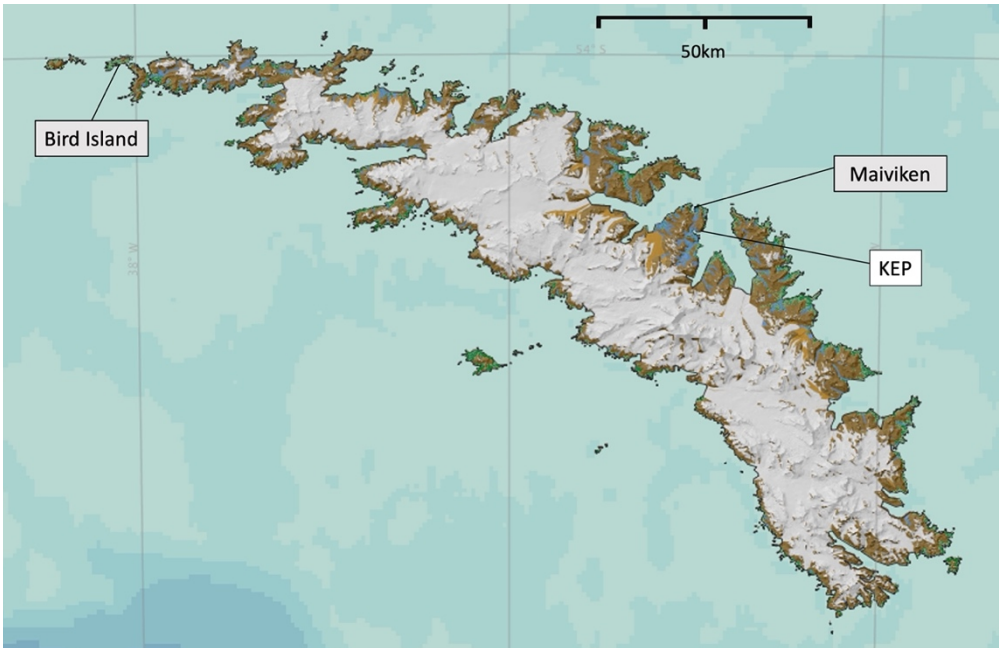


Figure 2. South Georgia and the location of Bird Island (BI), Maiviken and King Edward Point (KEP).

Where present, krill carapaces were identified and removed from the mixture before being processed immediately. Width and length of intact carapaces (Fig 3) were measured under a microscope at 10× magnification. Where scats were present, a sample of up to ten carapaces were measured per scat. Krill length was then calculated from the carapace length using the formula from Hill (1990):

Total Krill Length (mm) = (Total Carapace Length (mm) × 2.44) + 11.56

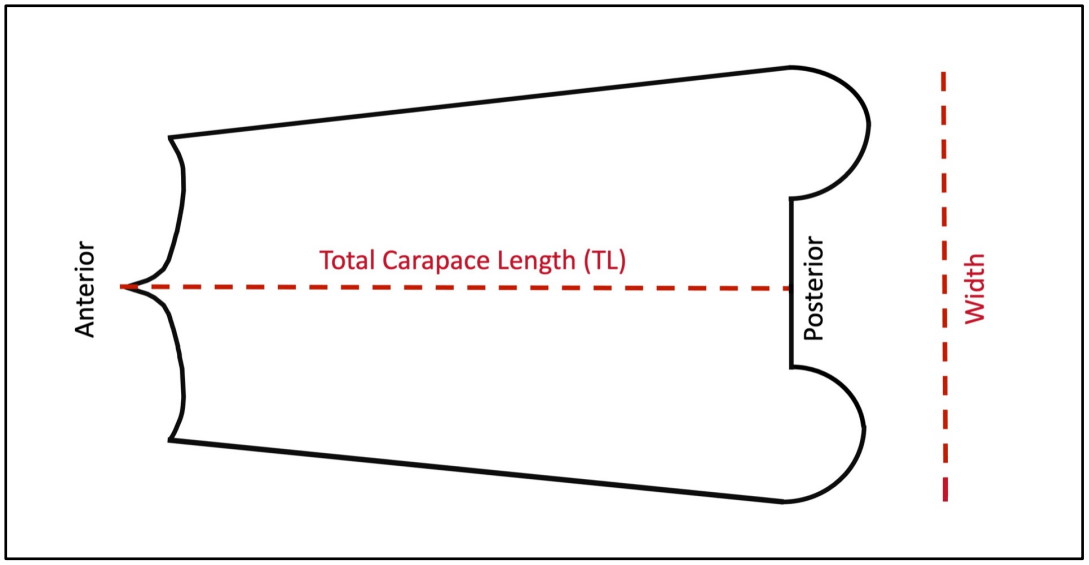


Figure 3. Diagram of a removed krill carapace with measurements necessary for calculating total krill length (mm).

Fish otoliths were also identified to the lowest possible taxonomic level of classification under a microscope according to Reid (1996). Cephalopods beaks were transported to Cambridge for identification by Jose C. Xavier (University of Coimbra)

Telemetry

Tracking data from both locations was compared to establish if BI and KEP fur seals were foraging in different locations. Thirty nursing females from KEP were equipped with GPS tags (Sirtrack Fastloc Archival, 215g) and tracked; 16 during the 2009/10 summer and 14 during the 2010/11 summer. Tags had a 5-minute recording interval and time depth recorders (TDRs) (Wildlife Computers Mk 9, 50g). KEP tracks from this study cover seasons of both high and low prey availability and therefore the core area used by tagged seals is considered representative of the foraging range of KEP fur seals. For BI, previous tracking studies (Barlow *et al.*, 2002; Boyd *et al.*, 2002; Staniland and Boyd, 2003; Staniland *et al.*, 2004, 2011; Staniland and Robinson, 2008) have shown high levels of consistency across years in foraging distribution (54.15°S, 40.00°W; 53.40°S, 38.00°W), and while fur seals do travel further in years with poor krill availability (Boyd *et al.*, 1994), Staniland (2002) suggested that these diets would not be reflected in scats collected on beaches due to the passage rates of fur seals and average swimming speeds to return to the colony. Representative tracks from six fur seals in the 2005/06 summer season published in Staniland *et al.*, (2011) were therefore used to illustrate this area.

For both locations, females with pups were selected after a visual inspection of health to ensure animals were representative of the breeding population and that there was a high probability of collecting representative data. Fur seals were caught using a noose pole and restrained on a stock board (Gentry and Holt, 1982). Instruments were attached using cable ties to gauze that was glued to the animals fur using epoxy resin centrally between the shoulder blades (Boyd *et al.*, 1998). Animal handling was restricted to less than 25 minutes. On return to the beach, animals were recaptured and restrained as above and the devices removed by cutting the cable ties and leaving the gauze to come off naturally during the annual moult. Tags remained on fur seals for 4 – 16 days. The joint University of Cambridge/ BAS Animal Welfare and Ethics Review Board approved all animal handling methodologies for fur seals.

Data Processing

Foraging Data

The telemetry data from BI and KEP 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). This makes calculations about the distance and speed that fur seals could conceivably swim between 5-minute sampling intervals. Positions with insufficient satellites fixes (<4) or those associated with swim speeds greater than 3 ms^{-1} and points were removed. Tracks were then plotted to distinguish if foraging habitat for animals from BI and KEP were distinct. Bounding boxes rather than utilisation distributions or kernel densities were used to approximately define fur seal foraging areas and account for interannual variability in foraging locations given that tracking data were only available for a limited number of fur seals and years. The core foraging area for Bird Island was 54.15°S, 40.00°W; 53.40°S, 38.00°W, whilst that for King Edward Point was 54.20°S, 36.60°W; 53.20°S, 35.40°W.

Environmental Data

The Copernicus Marine Environment Monitoring Service platform was used to obtain monthly, 0.25° horizontal 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) for the entire South Georgia maritime zone. This was repeated for chlorophyll *a* using the Ocean Global Biological Multiyear dataset (Perruche, 2019). The monthly values were then averaged over quarter and season and

converted to rasters from October 2008 until June 2020, after which data were not available. Rasters were cropped within the bounding boxes to give regional environmental data (Fig4) relative to BI and KEP foraging areas. BI bounding boxes were cropped using information from previous studies (Barlow *et al.*, 2002; Boyd *et al.*, 2002; Staniland and Boyd, 2003; Staniland *et al.*, 2004, 2011; Staniland and Robinson, 2008) whilst KEP tracking data presented here was assumed to be representative of fur seal foraging.

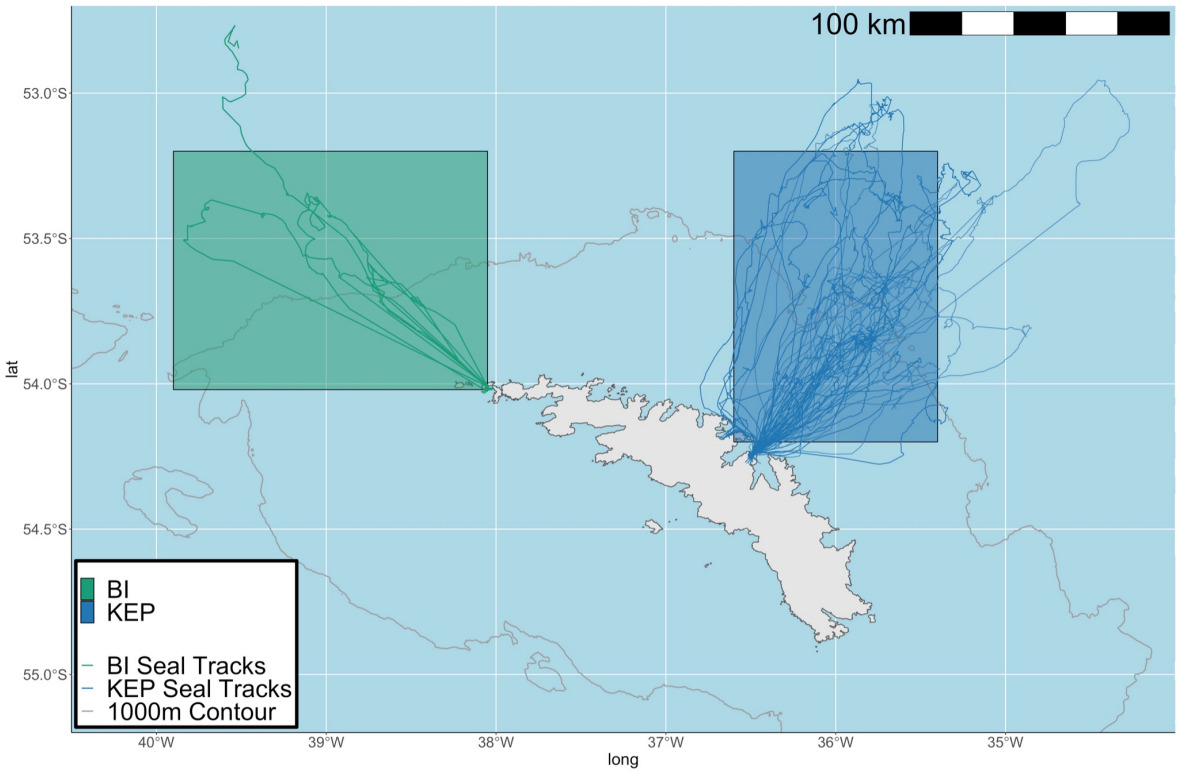


Figure 4. Tracks of Antarctic fur seals from 2009/2010 seasons at KEP (blue) and 2005 (Staniland *et al.*, 2011) at BI (green). Spatial polygons represent the regions for which environmental variables were downloaded from Copernicus satellite data (https://marine.copernicus.eu).

Krill Length Data

Krill length data for each site were binned into 2mm 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 instead of input data being the abundance of different species within the diet, 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 (BI, KEP), 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 frequency distributions between BI and KEP.

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 $\log_{10}$ 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.

Results

Scat Composition Summary

In total, since October 2008, 9669 scats were collected: 5428 from BI and 4211 from KEP. Antarctic krill was the dominant prey species found in fur seal scats at both sites. Measurable krill were present in 3582 scats at BI (65.63%), and 2523 at KEP (59.91%). At both sites, krill frequency of occurrence was greater during the summer (BI = 79.07%, KEP = 71.56%) than during the winter (BI = 43.30%, KEP = 36.76%), when fish made an increased contribution to the diet. Species composition of fish consumed varied between years and season (Supplementary Material Fig 1). Measurements of 56,981 krill carapaces were made, 33,887 from BI and 23094 from KEP. In summer months, the average number of carapaces found and measured per scat was 7.56 ± 0.38 and 6.64 ± 0.43 (standard error) at BI and KEP, respectively. This is much more than in winter months, where an average of 3.97 ± 0.66 krill per scat were found and measured at BI and 3.19 ± 0.56 at KEP.

Krill Length

Krill length varied both inter- and intra-annually at both BI and KEP (Figs 4 and 5). Both stations 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 6). Summer medians were almost always higher than the subsequent winters (Fig 6). However, this was not the case in winter 2010, winter 2017 and winter 2019.

While krill length from BI and KEP follow the same pattern through most years, the relationship between the sites appeared to deviate for a period between 2017 and 2020. In the final quarter of 2017 (2017-4), mean (51.80 mm ± 5.48 st dev) and median (50 mm) krill size at KEP increased as BI decreased (mean= 47.09 mm ± 5.01, median =46 mm). This was followed by a rapid decrease in krill length at KEP at the beginning of 2018 and an increase at BI. By the 4th quarter of 2018 BI krill length had a mean of 52.54 mm ± 6.16 (median =52 mm) which was much larger than krill at KEP (mean =41.54 mm ± 6.16, median =38 mm). From the third quarter of 2019 both sites returned to the synchronous pattern but did not unite until the third quarter of 2020 (Fig 5). With the exception of the first quarter of 2016 until the third quarter of 2018, average krill length at BI was greater than that at KEP. A regression of BI mean versus KEP mean 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.

The quantile range of krill length at KEP remained consistent with a greater range during summers than during winters. This pattern was similar at BI except for summer 2018/19 and 2019/20, where there was an increase in the range. There was a larger quantile range at both stations in summer 2010/11 and 2011/12 (Fig 6).

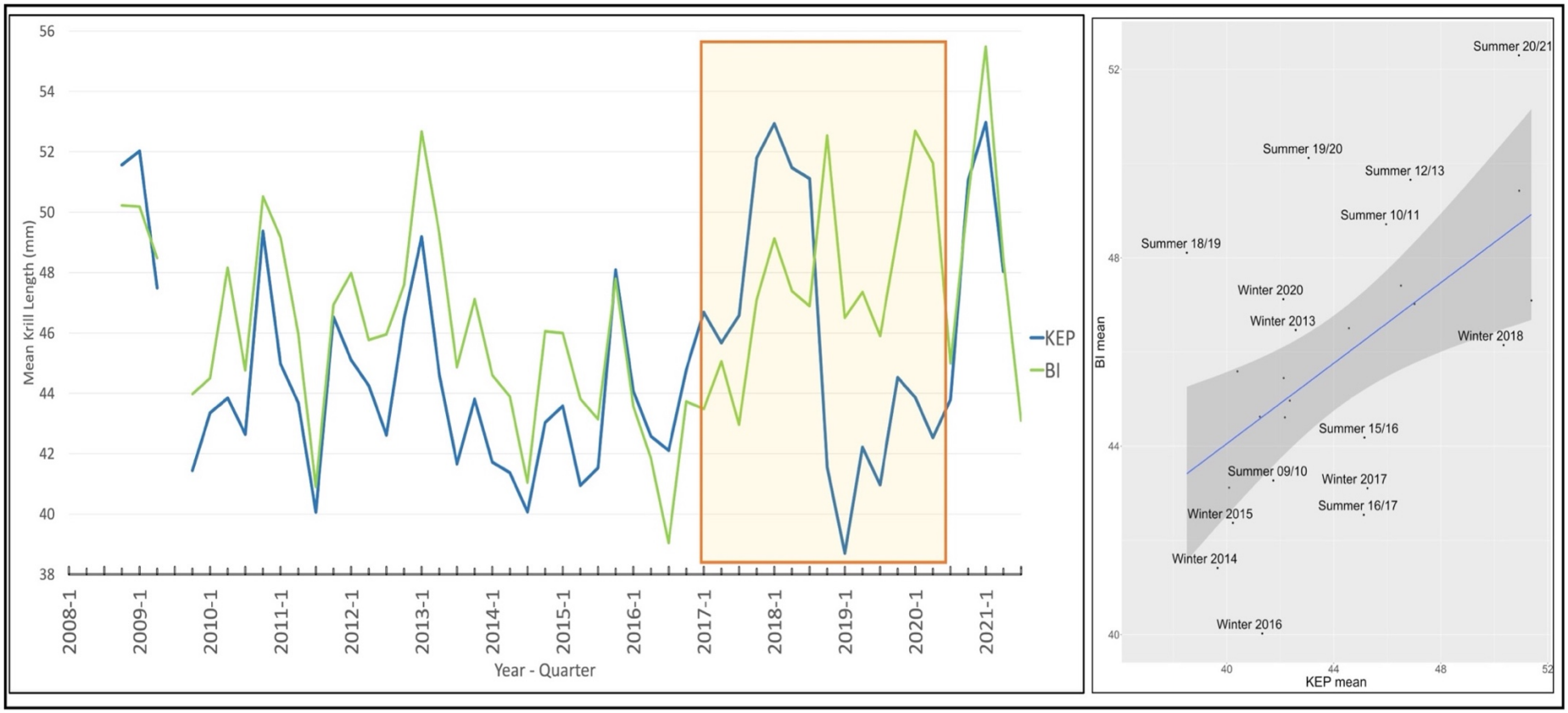


Figure 5. Mean length of krill carapaces found in fur seal scats per quarter of the year at Bird Island (BI; green) and King Edward Point (KEP; blue). Orange box marks the period where the pattern of differences between the two sites breaks down. Right-hand plot shows the regression between mean seasonal krill size at both stations across the sampling period with outlier points labelled.

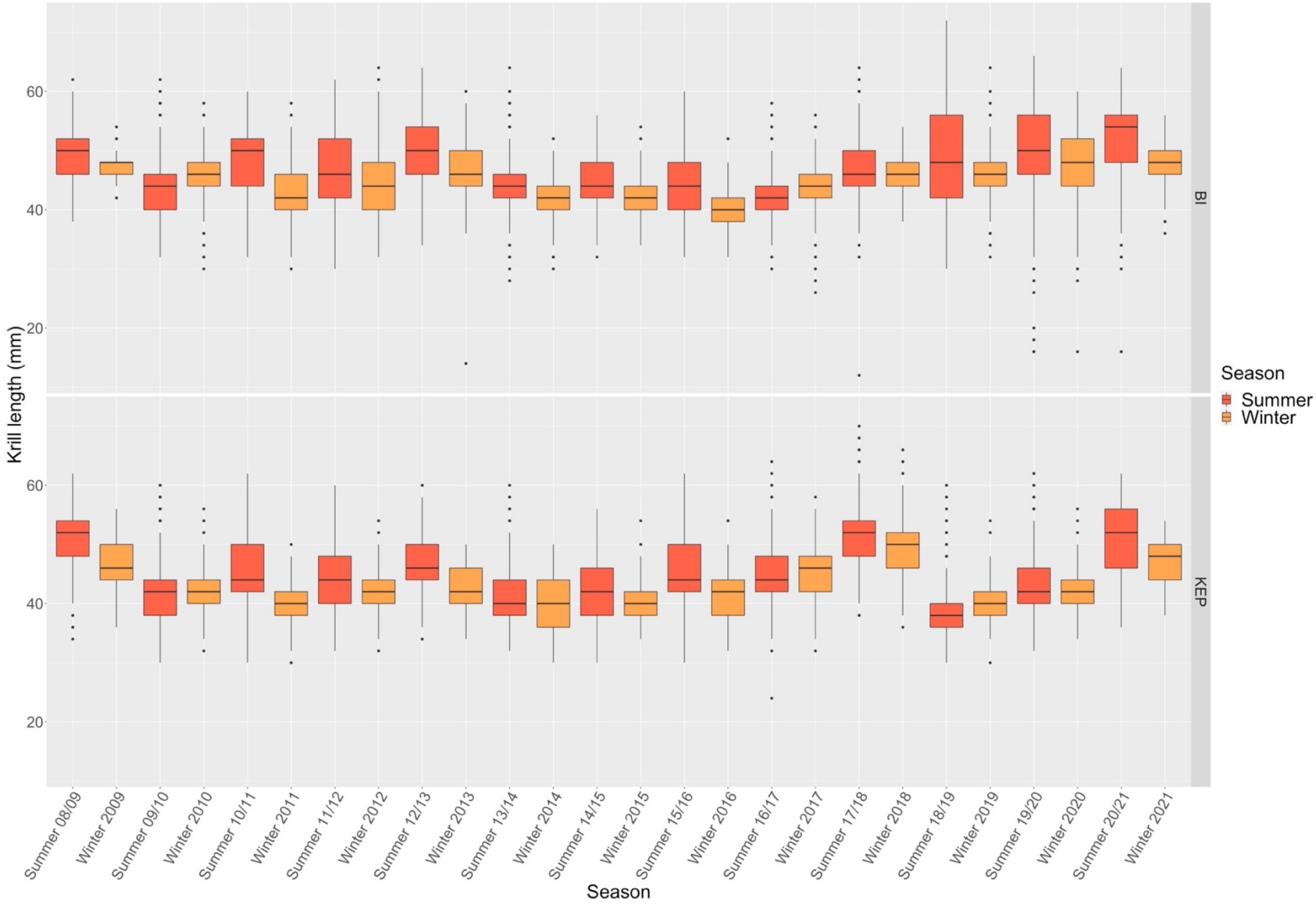


Figure 6. Boxplots of measured krill length between seasons at Bird Island (BI) and King Edward Point (KEP) from summer 2008/09 to winter 2021. Bars represent median, boxes the 25th and 75th percentile and whiskers the 1.5% interquartile range.

Intra-annual Variation

Monthly average krill size was greater at BI than KEP for all months except July (Fig 7). A two-way ANOVA test with station and month as factors showed that this difference was significant (P value <0.001). Krill lengths were smaller during winter months than summer months with the minimum occurring in July at BI and September at KEP. One way ANOVA tests with season as a factor showed this seasonal difference was significant at both KEP (P value <0.001) and BI (P value <0.001).. In all years, January lengths were less than the following December, except for 2009 (increase of 8.39 mm at BI, 11.46 mm at KEP) and 2013 (increase of 5.68 mm at BI, 5.64 mm at KEP) at both sites and 2018 at KEP (increase 15.78 mm). At KEP in 2016, there was also a small increase in krill length (0.66 mm).

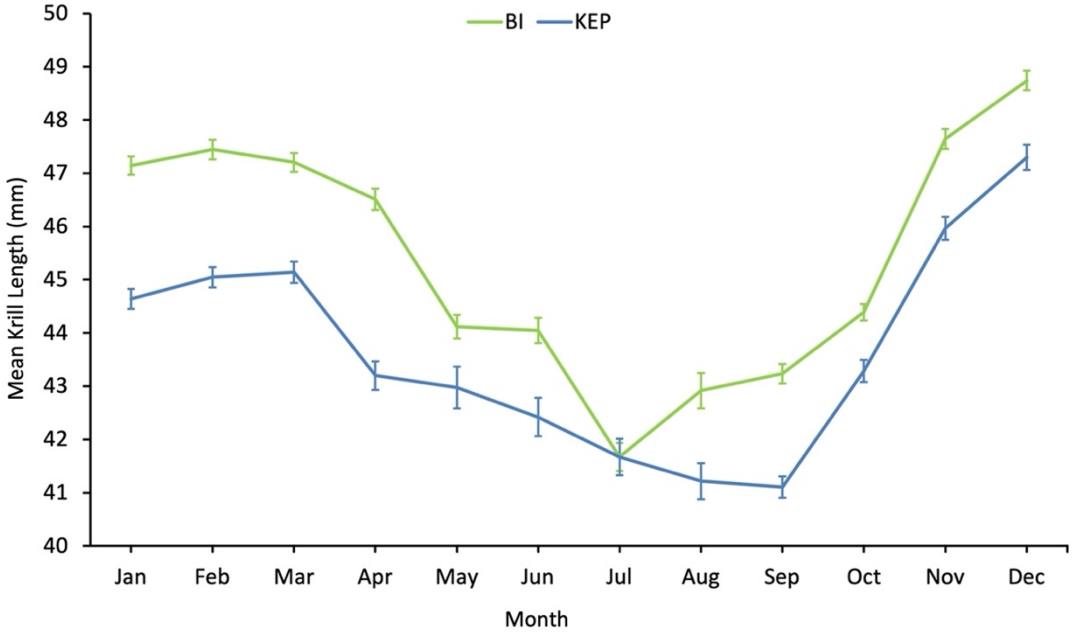


Figure 7. Mean monthly krill lengths with 95% confidence intervals, from scat data, at Bird Island (BI; green) and King Edward Point (KEP; blue) using all data from October 2008 until September 2021.

Length Frequency Distribution

Fur seals predominantly fed on krill ranging in length from 40-55 mm (Fig 8). Krill less than 30 mm were consumed but these were rare and largely restricted to BI between 2017 and 2020. It was also rare that krill greater than 60 mm were measured from scats. Length frequency histograms showed progression of size cohorts between years (Fig 8) 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 8, 9 & Supplementary Material Fig 2). At BI and KEP these influxes of smaller krill occurred in November 2009 and 2013 (Fig 9). In 2018, the pattern became less clear, with smaller krill present from November at KEP but not appearing at BI until December

(Fig 9). After the initial appearance, the smaller krill became the dominant cohort at KEP, whereas at BI it was less dominant until February. Appearances of much smaller krill (at BI in winter 2017, summer 2019/20 and winter 2020) didn't result in a complete shift of krill sizes and larger krill continued to appear in the diet for some time.

The distribution of krill length-frequencies 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 in 2013 (Fig 8). 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 8 & 9). There was a narrow spread in certain winters (noticeably 2009 and 2015) due to the low total numbers of carapaces measured in these seasons (Fig 9).

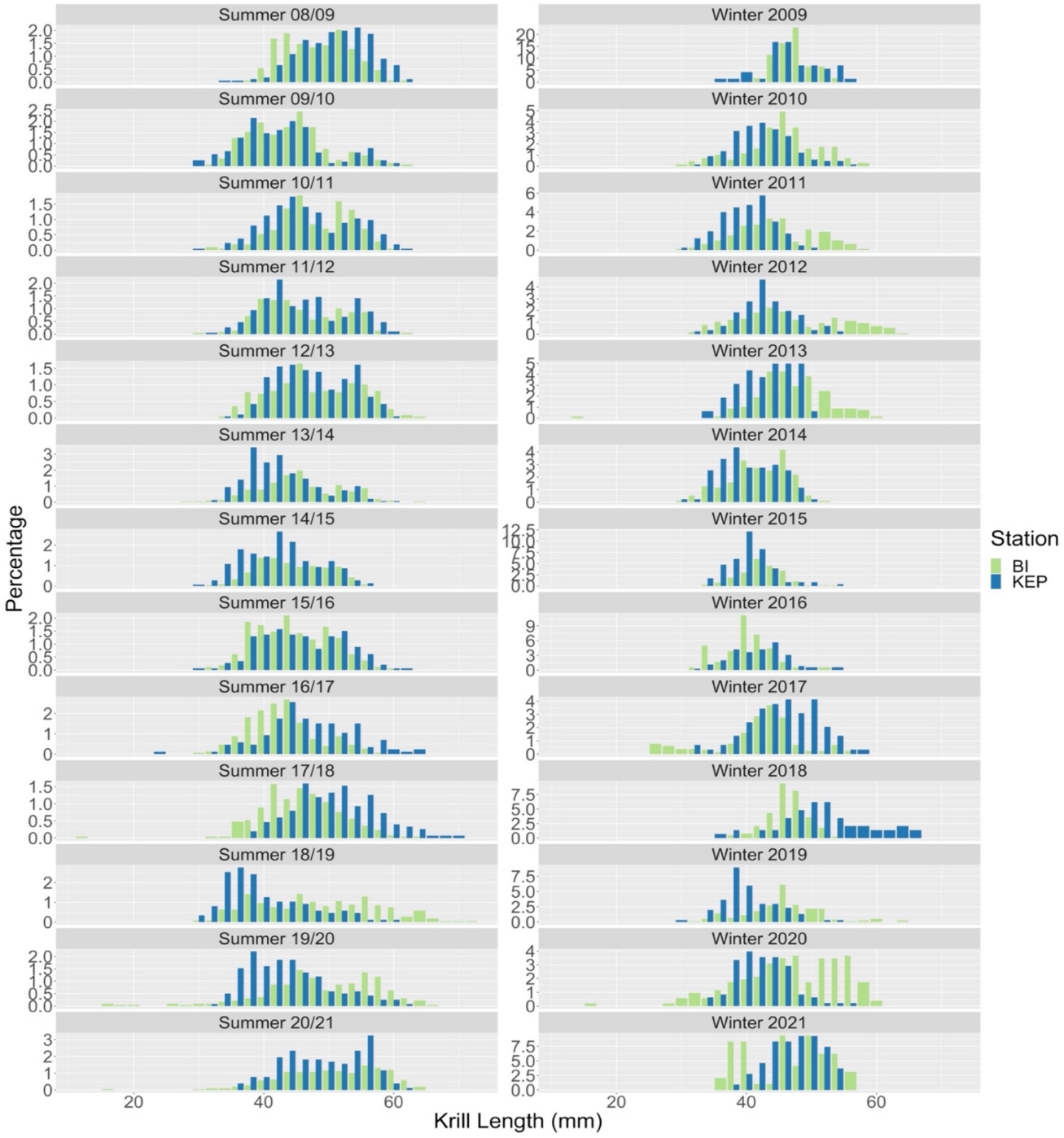


Figure 8. Summer (left) and Winter (right) length frequency distributions (expressed as a percentage of carapaces measured per site per season) of Antarctic krill taken from fur seal scats at Bird Island (BI; green) and King Edward Point (KEP; blue), South Georgia between 2008 and 2021.

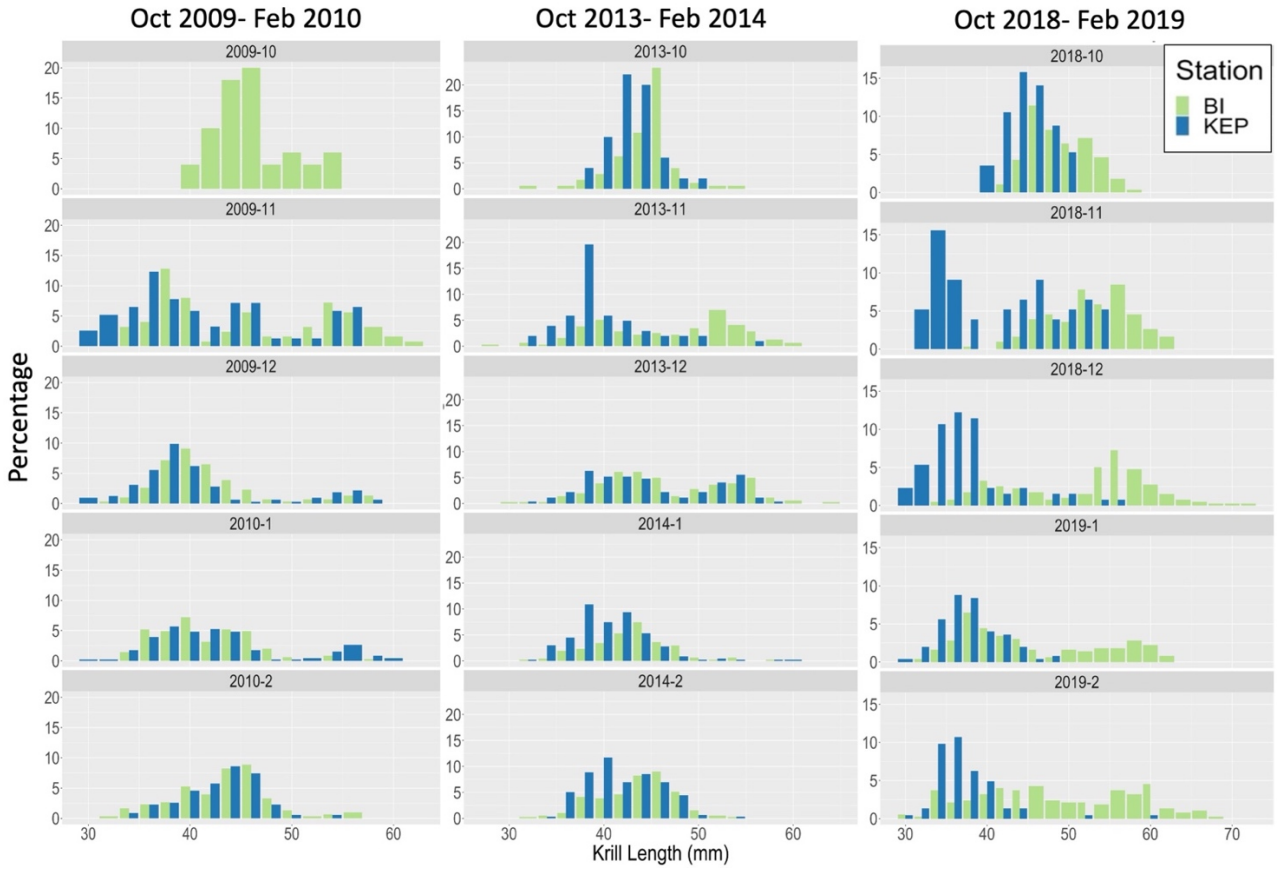


Figure 9. Length frequency distributions of Antarctic krill taken from fur seal scats at Bird Island (BI; green) and King Edward Point (KEP; blue) during fluxes of smaller krill observed between the months of October and February in 2009, 2013 and 2018.

Foraging

Tracking data from fur seals breeding at KEP were available for between one and three foraging trips per individual. With the exception of one individual that did not leave Cumberland Bay, fur seals from KEP in both summers (2009/10 and 2010/11) headed north-east towards the 1000m contour (and beyond). The geographic extent selected for KEP environmental data surrounds the core foraging areas based on available tracking data and previous studies.

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 10). There were obvious outliers suggesting some differences in the composition of krill lengths targeted consumed by fur seals in particular seasons. Most outliers occurred between winter 2017 and summer 2020/21 from both sites. There was a slight drop in the number of krill measured at KEP during this period but outliers were characterised by differences in krill lengths consumed between seasons. Summer 2017/18 until summer 2018/19 at KEP was separated from the main cluster but not grouped. At BI 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 (p value < 0.01). Additional PERMANOVAs showed significant differences between KEP and BI during the winter (p value = 0.01) and summer (p value = 0.01) periods.

Summer and winter length frequency histograms were explored to assess the driving factors behind these differences. Overall, they showed very similar distributions at KEP and BI (Fig 11), but KEP fur seals took more krill smaller than the modal length, and BI fur seals took more krill larger than the modal length (44mm). The greatest differences observed in summer were within the 38-40 mm bin (8.27% of KEP krill, 4.51% of BI krill) and 52-54 mm bin (6.93% of KEP, 9.64% of BI). The greatest differences observed during winter were within the 38-40mm bin (12.78% of KEP, 5.21% of BI) and the 46-48mm bin (11.49% of KEP, 19.42% of BI). During winter months, fur seals at BI consumed smaller krill (<30mm) not seen within the KEP fur seal diet although this represented less than 0.5% of their total diet. Similarly, KEP fur seals took a small amount of much larger krill (62+ mm) in winter months, but this represented less than 0.1% of their diet.

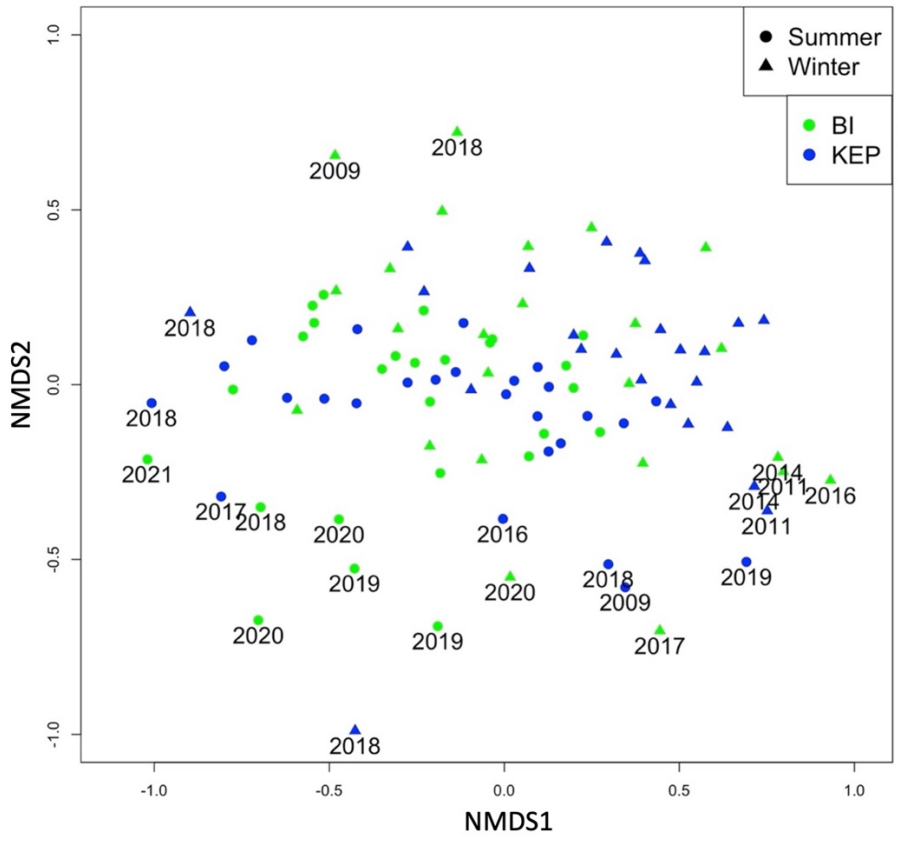


Figure 10. nMDS ordination based on the composition of different krill sizes targeted by foraging fur seals at Bird Island (BI; green) and King Edward Point (KEP; blue) during winter and summer with outlying points labelled.

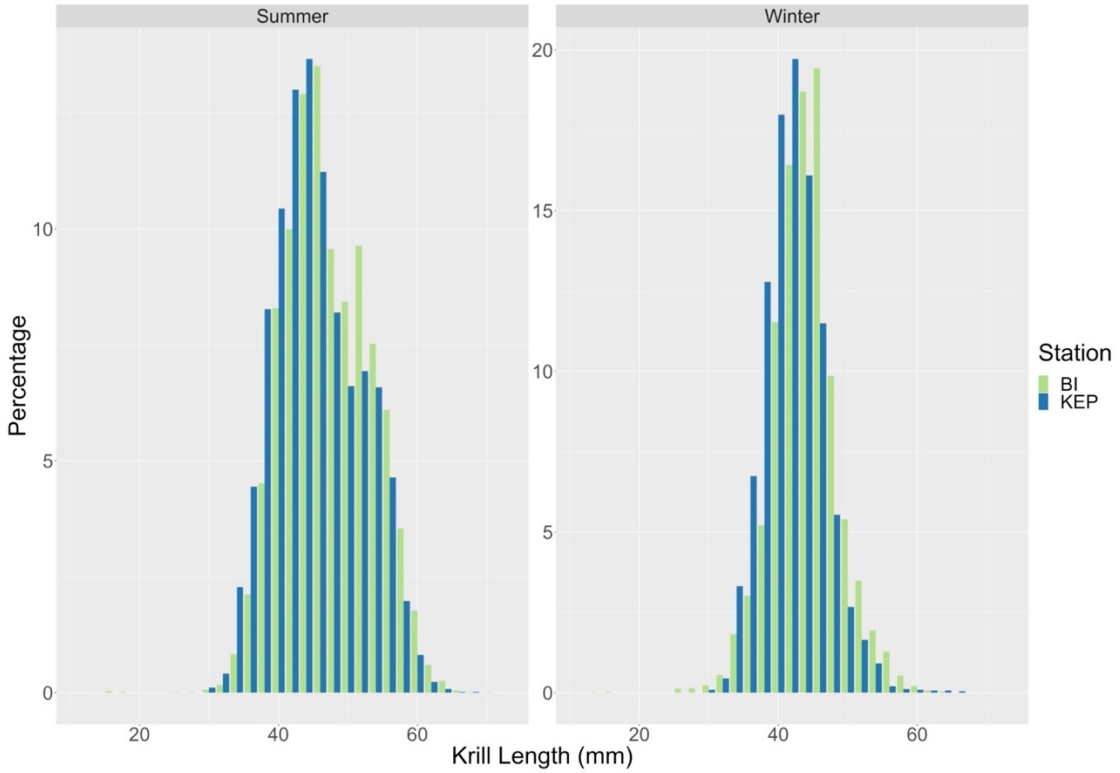


Figure 11. Length frequency histogram of Antarctic krill taken from fur seal scats at Bird Island (BI; green) and King Edward Point (KEP; blue), throughout all summers and all winters between October 2008 and October 2021.

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. Mixed layer depth explained 39% of the dissimilarities when quarterly periods of length data were used. When only summer data were used, SST was the greatest explanatory variable for dissimilarity (11.51%). SAL, SST and CHL together explained 17.56% of dissimilarities when only winter data was used.

When krill length frequency distributions were binned into quarterly periods and plotted on an nMDS ordination along with MLD (the environmental variable explaining most of the dissimilarity between samples, Fig 12) third quarter krill were associated with deeper MLD. The second quarter correlated with intermediate MLDs and 1st and 4th quarters were shallowest. Shallower MLD depths also isolated several outlier quarterly periods from the main clusters. Many of these were from the anomalous period between the first quarter of 2017 and the second quarter of 2020. Several outliers remained unexplained by environmental variables.

When krill length frequency distributions were binned into seasons and plotted on an nMDS ordination with the environmental gradients that best explained the dissimilarities between

samples, there were similar gradients associated with increased CHL and SST and reduced MLD (Fig 13 & Supplementary Material Fig 4). Most seasons were loosely clustered together within intermediate CHL, SST and MLD values. KEP winters were associated with cooler SST, lower CHL and deeper MLD than other seasons. High CHL concentrations and shallower MLDs split BI 2018/19 and 2019/20 summers as well as BI 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 KEP (Fig 13).

When length frequencies from summers only were analysed with a nMDS ordination (Supplementary Material Fig 6) there was one main cluster. Distances between the two sites during the same seasons were small, with the exception of KEP 17/18, 18/19 at both sites and BI 19/20. KEP 2017/18, BI 2018/19, BI 2019/20 were associated with comparatively higher levels of CHL and SST.

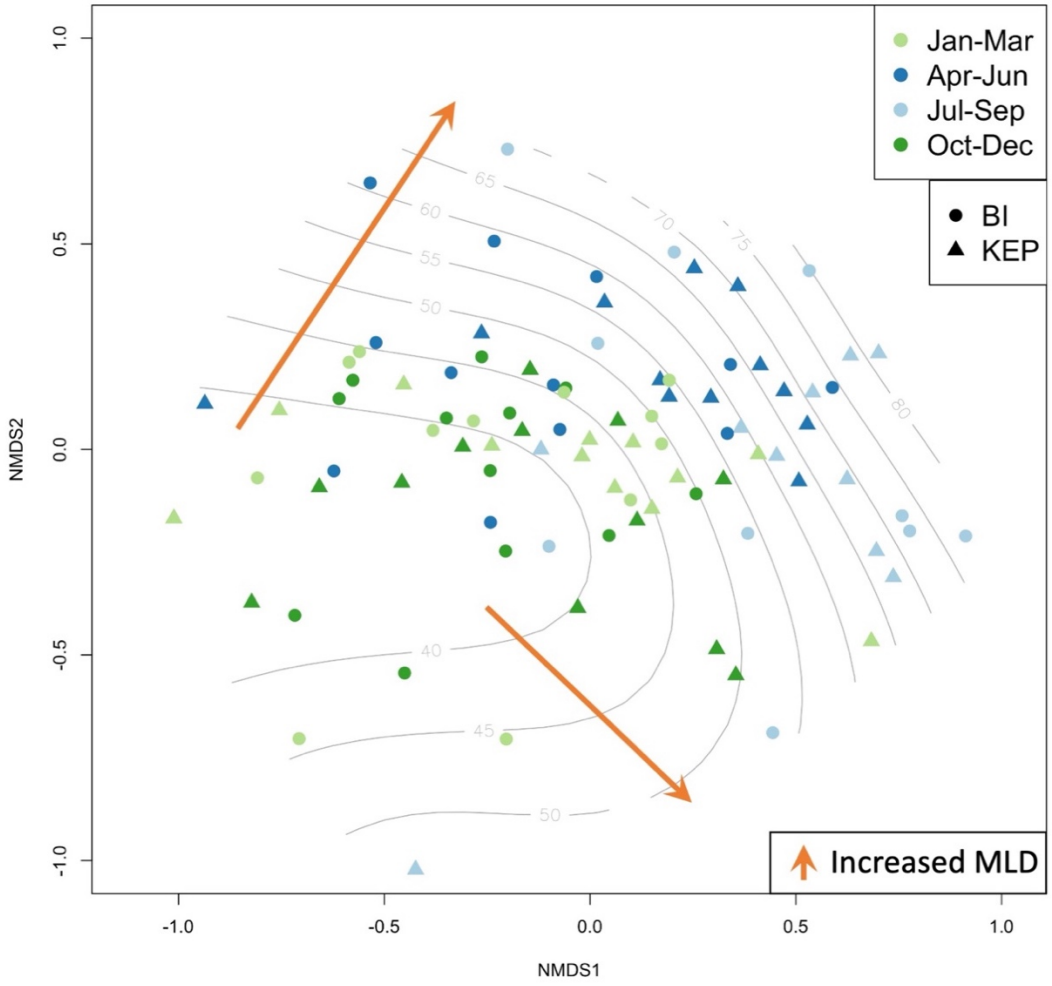


Figure 12. nMDS ordination of krill community lengths at (BI; green) and King Edward Point (KEP; blue) in quarterly periods from October 2008 (2008-3) until March 2020 (2020-1) (1=January-March, 2= April-Jun, 3=July-September, 4=October-December). Mixed layer depth gradients are plotted with arrows showing increased depths.

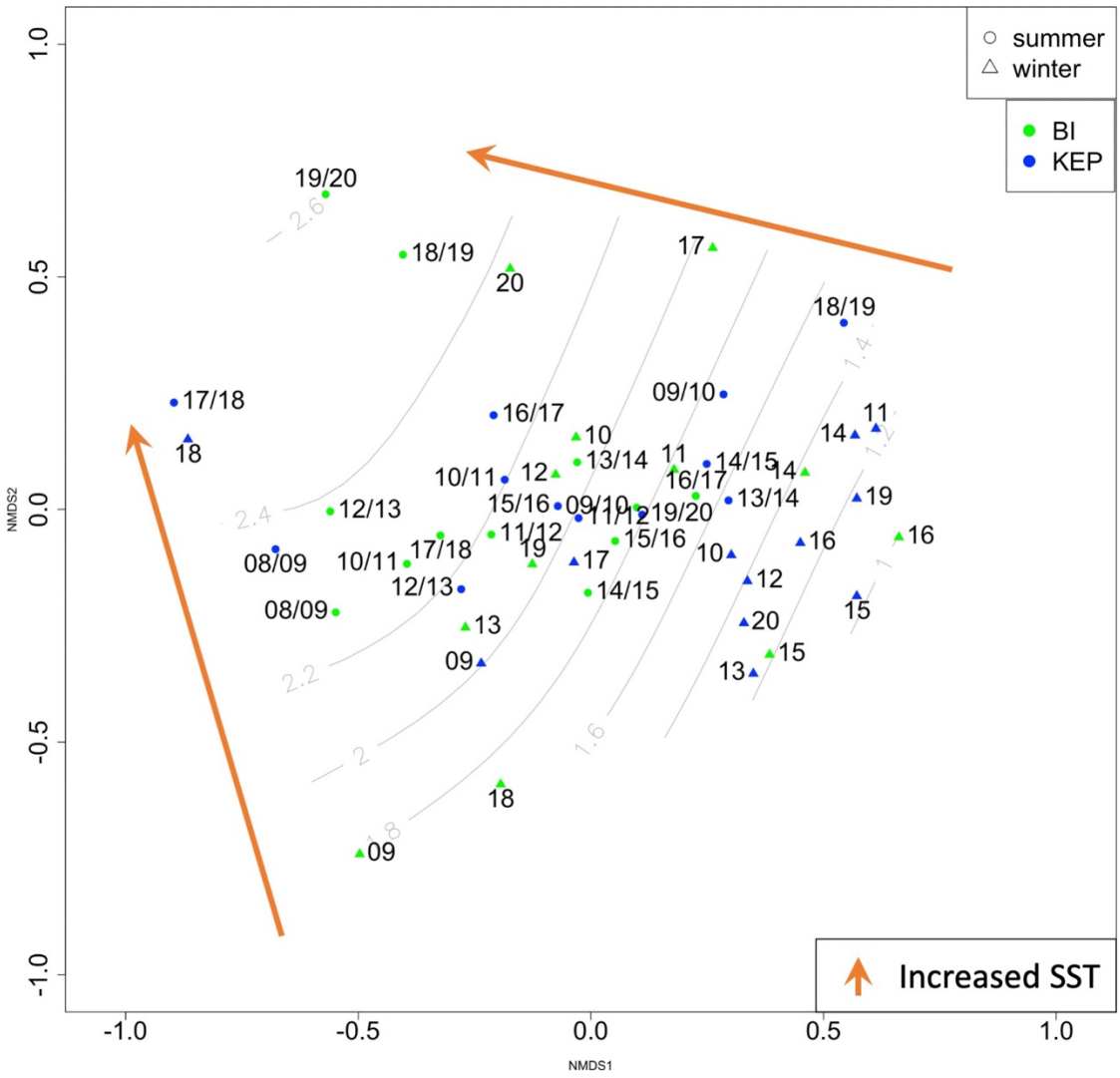


Figure 13. nMDS ordination of dissimilarity in krill community lengths between seasons (Summer = October-March, Winter = April-September) at (BI; green) and King Edward Point (KEP; blue) with sea surface temperature gradients and arrows showing increased SST.

When environmental variables alone were analysed on a nMDS plot there were 4 distinct clusters reflecting contrasting environmental conditions between sites and seasons; summer and winter clusters for BI; and summer and winter clusters for KEP (Fig 14). Winter 2016 at BI and winter 2020 at KEP were isolated from all other seasons, winter 2020 at BI falls within the summer cluster for KEP. There were seasonal differences between environmental conditions at both sites (Table 1). SST and CHL consistently greater at BI, SAL remained constant between the two sites whilst MLD was greater in the third quarter at KEP and similar at all other times.

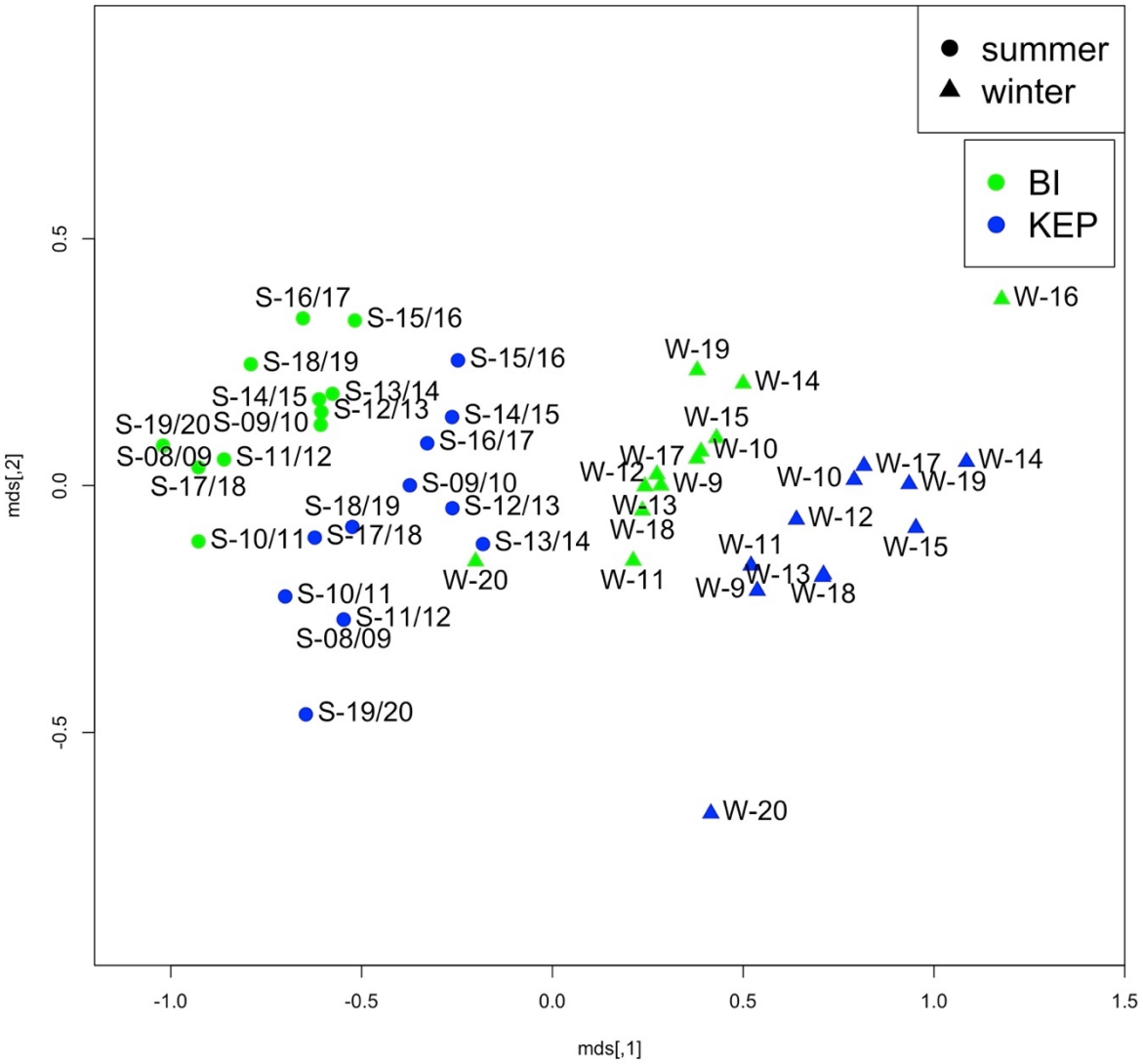


Figure 14. nMDS plot showing dissimilarities in chlorophyll *a*, mixed layer depth, salinity and sea surface temperature over time at Bird Island (BI; green) and King Edward Point (KEP; blue).

Table 1. Environmental means across BI and KEP spatial polygons using Copernicus satellite data.

Variable	Site	Jan - Mar	Apr - Jun	Jul - Sep	Oct - Dec
SST (°C)	BI	3.66	2.28	0.55	1.55
	KEP	3.14	1.81	0.19	1.13
MLD (m)	BI	30.22	62.58	74.73	39.47
	KEP	29.88	63.93	80.32	38.24
SAL (psu)	BI	33.77	33.81	33.85	33.83
	KEP	33.80	33.85	33.91	33.88
CHL *a* ($mg.m^{-3}$)	BI	1.39	0.82	0.76	1.64
	KEP	0.77	0.46	0.62	1.36

Discussion

This study used two spatially distinct, long-term diet datasets to compare krill consumed by foraging Antarctic fur seals. The two colonies foraged in distinct locations, separated by approximately 100 km yet appear to be taking similar sized krill which likely originate from the same krill metapopulation. The slightly larger krill observed at BI were likely due to advection time between sites (east to west; Young *et al.*, 2014) allowing for growth, retention across the area or small environmental differences. Despite these small differences in krill size, populations of krill at the two locations followed a synchronous stochastic pattern with interannual progression of krill size before sporadic decreases, possibly associated with large scale influxes of younger krill. Interestingly, this correlation broke down between 2017 and 2020. This could be due to poor krill availability, an oceanographic change which segregated the krill populations, or differences in the vertical distribution or schooling behaviour of krill.

Krill length frequency data at both KEP and BI generally displayed cyclical intra-annual patterns with periodic decreases in the mode frequencies every 4-5 years. These reflect similar patterns to those observed previously in South Georgia fur seals and penguins (Reid *et al.*, 1999) as well as in the diets of baleen whales (Mackintosh, 1974). During the period 2017 - 2020 the synchronous, cyclical relationship between the sites broke down, with deviation in krill size between sites which suggests the circulation pattern transporting krill was in a different state, or fur seals were consuming krill from spatiotemporally distinct populations. Some anomalous seasons at both sites were isolated by environmental gradients, in particular MLD, SST and CHL. However, there were no outlying raw data that could explain this. Although large differences in krill length between sites did not occur until 2017, mean krill length at KEP first increased above BI in 2016. This coincided with the greatest MLD, lowest SST and lowest CHL for both sites during the survey period. These local environmental changes could be signals of a larger mode of environmental variability which has changed the state of the system. El Niño Southern Oscillation (ENSO) and the Southern Annular Mode (SAM) are coupled climatic drivers which are known to affect factors impacting krill advection to South Georgia (Meredith *et al.*, 2008). These factors are also known to impact South Georgia SST normally with a lag (Trathan and Murphy, 2003; Trathan *et al.*, 2006; Meredith *et al.*, 2008). In 2016, the strongest ENSO during the timespan of this study occurred (Fig 15), followed by another flip to La Niña in 2020 (National Oceanographic and Atmospheric Administration (NOAA), 2022). To link these local changes to climatic drivers such as ENSO and/or SAM testing against environmental lags over a much larger scale would be necessary. Moreover, environmental perturbations at much broader geographic scales have been reported in years preceding the anomaly (2016/17,

2017/18 and 2018/19; Turner et al., 2020), so further work linking fur seal diet to broader scale drivers of environmental variability are now certainly needed.

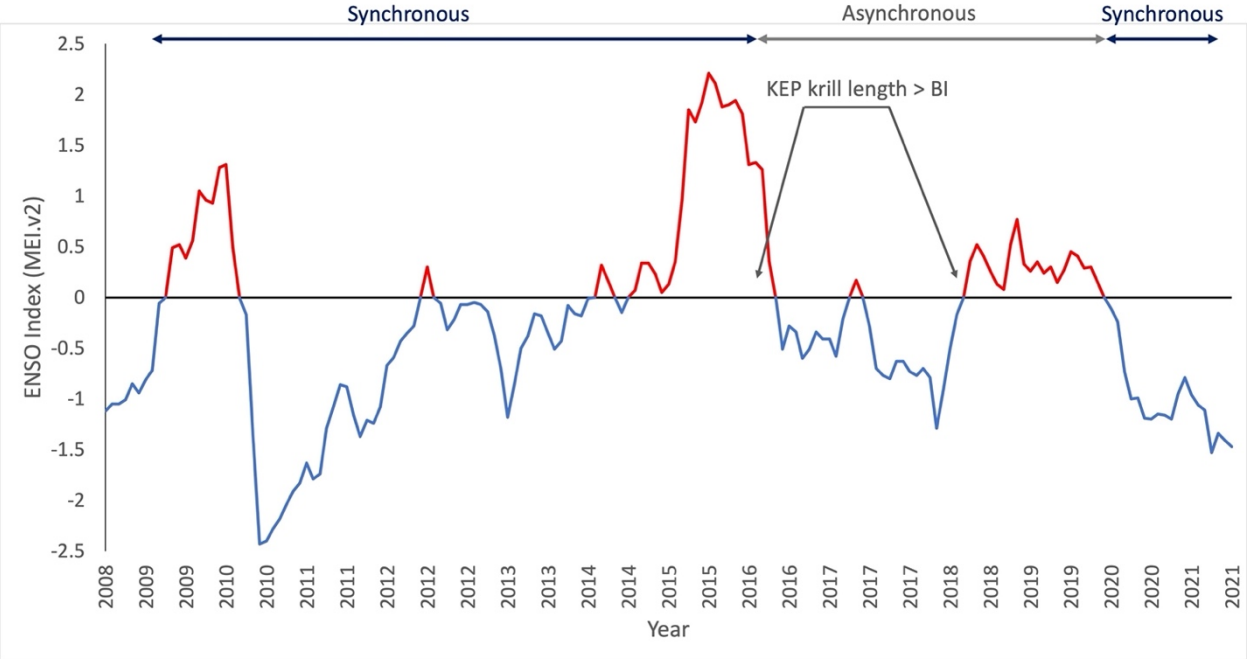


Figure 15. ENSO index reproduced from NOAA (2022) data with synchronous and asynchronous periods from this study labelled as well as the period where KEP krill mean length is greater than BI.

The length-frequency data showed that the modal length of krill increased from year to year at both sites before decreasing every 4-5 years, due to an influx of smaller krill. This is consistent with Reid et al. (1999) who suggested that increases in size over time reflect development of cohorts, whilst decreases in mean krill length reflected large recruitment pulses of new, younger, krill into the South Georgia system advected via the Antarctic Circumpolar Current (ACC). In 1994 a reduction in krill length occurred in January/February at BI (Croxall *et al.*, 1999; Reid *et al.*, 1999), whereas in this study decreases in krill size occurred in November/December which corresponds with predicted transport times from the Antarctic Peninsula to South Georgia (Hofmann and Murphy, 2004). From our results, influxes of smaller krill into the diet appeared to occur at similar times at both sites.

Pulses of krill recruitment will lead to periods of elevated krill biomass around South Georgia, with biomass likely to peak after a period of growth following the initial recruitment. However, prior to recruitment events, krill biomass may be low, leading to poor feeding conditions for predators (Reid *et al.*, 1999). Where recruitment events occur late in the breeding season, predators may have poor offspring productivity as seen in 1994 (Reid *et al.*, 1999). In summer 2018/19, although smaller krill appeared at both study sites, it did not become the dominant cohort in the diet at BI as it did at KEP. Larger krill may have remained abundant around BI,

resulting in fur seals preferentially selecting these over smaller krill. However, this season was associated with low pup numbers (Nagel *et al.*, 2021) and low weaning weights at BI (Trathan *et al.*, 2021), which supports a theory that krill was in short supply there, and this influx of smaller krill was not retained at BI. BI seals are consuming prey from a potentially modified prey field; krill predators along the northeast coast could have fed heavily (possibly very significantly) from krill supplies before they reach BI. Moreover, if fur seals (in combination with other predators) are consuming krill to the extent that the prey field has been altered significantly, it suggests that predator populations are approaching carrying capacity. Summers prior to krill recruitment events were characterised by increased SST, which then declined in subsequent years. However, at BI, in summer 2018/19, SST remained high, suggesting that local oceanography was somehow different, possibly as a result of an oceanographic/ atmospheric anomaly (see also Turner et al., 2020).

The mean, median and modal lengths of krill consumed by BI fur seals were consistently larger than at KEP with the exception of 2016-2018. Nevertheless, this general similarity in krill length-frequency is comparable to reported similarities described previously from historical fur seal diet data and trawl sample data (Watkins *et al.*, 1999; Mori and Boyd, 2004; Cox *et al.*, 2011). This suggests that both datasets are representative of the krill populations in the fur seal foraging areas. Multivariate plots of the Copernicus environmental data showed clear distinct groupings between each site and season demonstrating that the local oceanography is different between the two foraging sites. Krill is advected to South Georgia on the ACC around the south and then east of the island, possibly via the Southern ACC Front (Trathan *et al.*, 2003; Murphy *et al.*, 2007). Growth rates of krill whilst being advected between the two sites could explain some of the increases in krill size observed at BI (Melvin *et al.*, 2018). The cooler SST off Cumberland Bay may be indicative of stronger cooler flows that emanate from the Antarctic Peninsula carrying smaller krill. This, along with increased, year-round CHL at BI could allow for greater growth rates in summer and less shrinkage in the winter krill (Atkinson *et al.*, 2001). If differences between the two sites are the result of more optimal environmental conditions for growth at BI than KEP, then this relationship could be expected to change with increased warming and greater productivity predicted in the region (Meredith *et al.*, 2019). South Georgia's summer SST is towards the upper end of krill's thermal tolerance (Tarling et al 2020), and increases of temperature have been correlated with reduced krill in fisheries catch data (Fedoulov *et al.*, 1996) and diet data (Xavier *et al.*, 2017). Krill also have a bell-shaped curved response to CHL where too much or too little negatively affects biomass (Whitehouse *et al.*, 2009). Differences could also be a result of biases in prey selection by predators upstream (at

KEP). However, literature suggests fur seals and other land based predators favour larger krill sizes (Mackintosh, 1974; Hill *et al.*, 1996; Reid *et al.*, 1999).

Studies such as this rely on several assumptions including the accuracy of satellite-derived environmental data. There is evidence from *in situ* validation that Copernicus satellite data is robust and accurate (von Schuckmann *et al.*, 2017), but some discrepancies may occur. Here I used seasonal and spatial averages of satellite data to ensure environmental and krill data are averaged over comparable temporal scales and give greater confidence to the data. More year-round physical data should be collected around South Georgia to strengthen the value of satellite data.

The mean, mode and median size of krill taken by fur seals at BI, throughout this study were greater than during the 1991-1997 period reported by Reid *et al.*, (1999). Atkinson *et al.*, (2019) stated that along with declines in krill range and abundance throughout the Antarctic Peninsula region came an increase in the age structure of the population, with fewer younger individuals being recruited. This has resulted in less of a reduction in biomass than would be expected based on a stable age-structure (Atkinson *et al.*, 2019). The increase in krill size compared to earlier studies could reflect the change in size structure at the source of recruitment. However, these reductions in the krill population are not universally agreed upon (Cox *et al.*, 2018; Krafft *et al.*, 2021). Changes in productivity, and/or temperatures in the region could also explain this increase if they allowed for greater krill growth rates. One consideration when exploring interannual differences in this dataset is that the annual turnover of Zoological Field Assistants at BI and KEP could lead to small inconsistencies in measurements between years and locations. However, it is very unlikely that such discrepancies would explain systematic patterns or differences such as the ones described here. This could be tested by grouping krill length measurements into larger bins that would better encapsulate any smaller differences (e.g. 5 or 6mm bins)

In fur seal winter diets, krill sizes were smaller, with larger (55+mm) krill often completely absent, but with an increase in the fish dietary component observed at both sites. These are similar observations to previous winter diet studies (Reid, 1995; Reid *et al.*, 2006). While summer scats can be assumed to be representative of breeding females (Reid, 1995), this is not true in the winter months. During this time adult males have migrated south (Boyd *et al.*, 1998), but juvenile and immature (male and female) fur seals are more present on the beaches alongside adult females (Reid, 1995). If younger fur seals select smaller krill, this could potentially explain the differences in diet between winter months and summer months given fur seals are known to niche partition between sexes (Staniland *et al.*, 2010) and ages (Jones *et al.*, 2020). Alternatively,

seasonal differences could be due to different prey availability and distribution during the winter. The biological and physical state of the Southern Ocean in winter is different to that of summer (Heywood *et al.*, 1985; Priddle *et al.*, 1986; Constable *et al.*, 2014), with cooler temperatures, greater MLD, lower CHL and differing current speeds likely to be more favourable to some species. 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. It is likely that observed differences are a result of a combination of the above.

Although Antarctic fur seals usually take krill greater than 35mm (Reid *et al.*, 1999; Murphy and Reid, 2001), there were occasionally some very small krill (less than 30mm) in the diet. These mostly occur at BI with three noticeable occurrences in: winter 2017, summer 19/20 and winter 2020. The fact that these influxes only occurred at BI, which possibly is lagged in relation to KEP (Young *et al.*, 2014) and are all within the asynchronous period suggests these could be associated with a temporary change in the system which resulted in an alternative recruitment route. If prey availability is reduced then it could be that fur seals resorted to feeding on less favourable cohorts. Smaller krill could 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 from predator and trawl data (Murphy *et al.*, 1998; Hofmann and Murphy, 2004; Murphy *et al.*, 2007). However, Main *et al.* (2009) found small krill in the diet of mackerel icefish (*Champsocephalus gunnari*) in South Georgia suggesting they are present. Another hypothesis is that these were not *E. superba*, which at this smaller size could be harder to differentiate. The reason for their appearance in the diet could be due to low abundance of alternative prey species, consumption as secondary prey of fish, or they were accidentally consumed with mouthfuls of larger krill within a swarm. Differences of interpretation of these very small krill influxes could have significant impacts on the state the system is assumed to be in when they occur. It is necessary to establish if smaller krill are always present in this system, the use of mackerel icefish as an indicator species may help answer this question (Everson, 2002).

Diet studies can tell us a lot about a species and the ecosystem they inhabit (Casaux *et al.*, 2016). This study focusses on the distribution of krill lengths in the diet of fur seals which have been shown previously to be representative of the wider krill population (Reid *et al.*, 1999). More frequent concurrent sampling of krill from diet and ship surveys would reinforce this assumption. Although krill is the most important prey species in fur seal diet at South Georgia, it remains difficult to estimate the relative abundance or availability of krill beyond a simple presence or absence. This is especially true at BI where an additional 5 scats were collected if

100 carapaces were not found in the first ten sampled scats, which may bias estimates of krill availability. Therefore, it would be useful to look at other components of the diet as a proxy for krill availability. For example, Reid *et al.*, (2006) indicated that when krill were less abundant, the myctophid *Protomyctophum choriodon* and the icefish *Champsocephalus gunnari* became more important in the diet possibly due their increased availability as a result of differing water temperatures or changes in fur seal behaviour. However, abundances of otoliths and squid beaks can also be biased as a result of different stomach retention and digestion rates (Staniland, 2002; Reid *et al.*, 2006; Jobling and Breiby, 2011; Casaux *et al.*, 2016) leading to underestimates and certain species to be missed completely (Casaux *et al.*, 2016). Additionally, identification of eroded otoliths can be difficult, especially within the notothenioid group. The use of genetic analysis on faecal material alongside osteological analysis would give greater confidence to estimates of hard parts made from the rest of the scat (Keszka *et al.*, 2020) allowing for more confident conclusions to be drawn. Additionally, genetic analysis of scats would allow for scat data to be sexed (Schwarz *et al.*, 2018), adding more value to the data, especially during winter months where both males and females are present.

Tracking data gives context to the diet data collected at CEMP monitoring sites. This study shows the foraging distribution of fur seals from KEP were distinct from BI fur seals (Barlow *et al.*, 2002; Boyd *et al.*, 2002; Staniland and Boyd, 2003; Staniland *et al.*, 2004, 2011; Staniland and Robinson, 2008). This study identified a breakdown in the dietary synchrony between KEP and BI, highlighting the importance of having multiple spatially separated monitoring sites. These allow us to understand how wider ecosystem processes may differentially affect regions, even at scales of 100-200km. The fact that KEP fur seals are foraging in the region intensively fished for krill can provide critical information for management of the South Georgia krill fishery. However, this fishery only operates during the winter months for which there are currently only limited fur seal tracking data available. During winter, fur seals are not tied to colonies and can range further. For this reason it is difficult to infer spatial overlap of diet samples from different sites with the winter krill fishery, although Bamford *et al.* (2021) showed high overlap of predicted winter foraging sites between fur seals and the krill fishery. South Georgia's krill population is not self-sustaining (Everson, 1976; Ward *et al.*, 1990; Siegel and Watkins, 2016) and relies on influxes from Antarctica on polar currents (Siegel and Watkins, 2016). Diet data provided here and in previous studies (Reid and Arnould, 1996; Reid *et al.*, 1999) suggests that important influxes of smaller krill from further south potentially recruit into the South Georgia system from November throughout summer and that influxes are not continuous and sometimes arrive later (Reid *et al.*, 1999). If this is true, when stocks are low between influxes, winter fishing has the potential to deplete the krill found within this foraging

area, suggesting catches should be spatially limited and controlled (Trathan et al., 2021). With fur seals returning to land in South Georgia in October and giving birth in November/December, this could have serious implications for prepartum condition and early breeding success. With greater understanding of this system, in particular krill recruitment events, it may be possible to consider predator diet data in fisheries management planning. Trathan *et al.*, (2021) showed carryover affects between seasons, where less krill in winter was carried over to subsequent summers and reflected in predator success. If recruitment events occur every 4-5 years as observed in this study, carryover effects between years would be expected where declines in krill biomass were seen as time progresses, and mortality increases, after recruitment events. This should be considered by fisheries managers to alleviate any competition that might occur between predators and the fishery as biomass declines.

There is an urgent need for a better understanding of this dynamic and rapidly changing subpolar ecosystem, especially with respect to the recruitment of krill, which lies at the heart of the biodiverse and abundant predator populations at South Georgia. There will likely be significant changes in coming years with krill influenced negatively by increases in sea surface temperature (Flores *et al.*, 2012; Piñones and Fedorov, 2016; 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 (Trivelpiece *et al.*, 2011; Chown and Brooks, 2019). The return of krill-feeding whales (Baines *et al.*, 2021) will also influence ecosystem dynamics with many arguing that through increased competition for krill, penguins and fur seals could lose out (Laws, 1977; Ainley *et al.*, 2010). An alternative train of thought is that through fertilising of the oceans, the increase in whales could allow for greater productivity and increases in krill (Nicol *et al.*, 2010; Savoca *et al.*, 2021). In such a rapidly changing dynamic system, long term datasets such as these are integral in identifying changes in ecosystem state (Bestley *et al.*, 2020). With better monitoring comes early identification of changes giving CCAMLR the ability to modify fishing activities and alleviate pressure on the ecosystem so ensuring sustainable management.

Acknowledgements

I would like to thank all past and present zoological field assistants and marine biologists from Bird Island and King Edward Point who helped with data collection and scat processing also to all the teams on station who tolerated the smells of scat sampling down the laboratory corridors. Many thanks to the management science staff at KEP and BI who supervise the ZFA projects and oversee the long-term monitoring programmes. Thank you to John Ashburner who carried out the 2009 and 2010 GPS deployments at Maiviken. Helen Peat who manages the science databases and repeatedly helped me with data retrieval, Eugene Murphy and Simeon Hill for insightful discussions and questioning throughout the writing process. A special thanks to Phil Hollyman and Rebecca Nagel who fielded endless stats and R based questions. A final thanks to my supervisors for your wisdom, patience and guidance throughout this challenging but enjoyable learning process.

Personal Contribution

Although much of the data collection was carried out by zoological field assistants and marine biologists at the two locations. I was responsible for collecting scats and processing samples at King Edward Point during October 2015-December 2016 and March 2021-December 2021. I also contributed to sample collection and processing during the summer of 2018/19 at Bird Island. For this thesis, I carried out all data analysis and writing.

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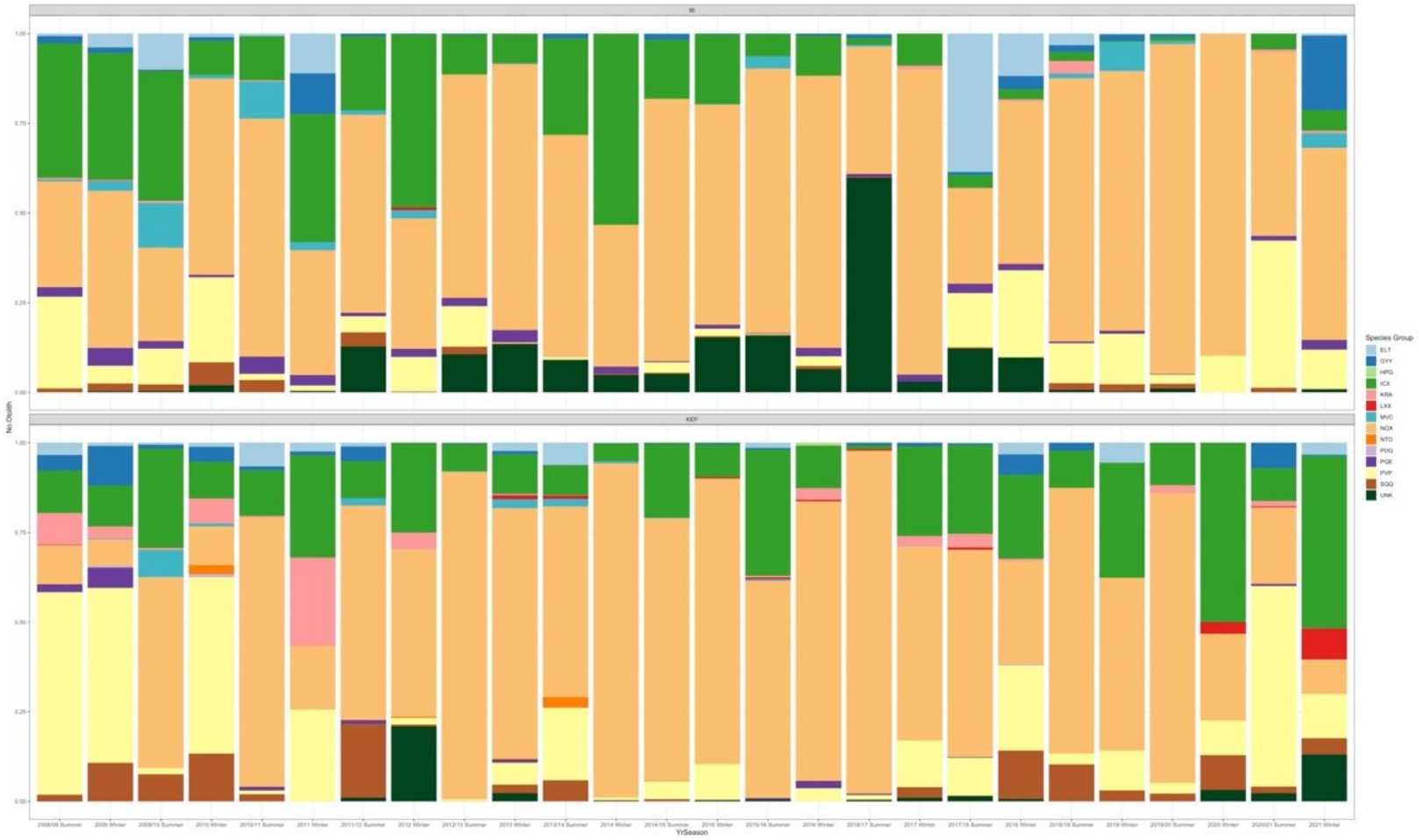
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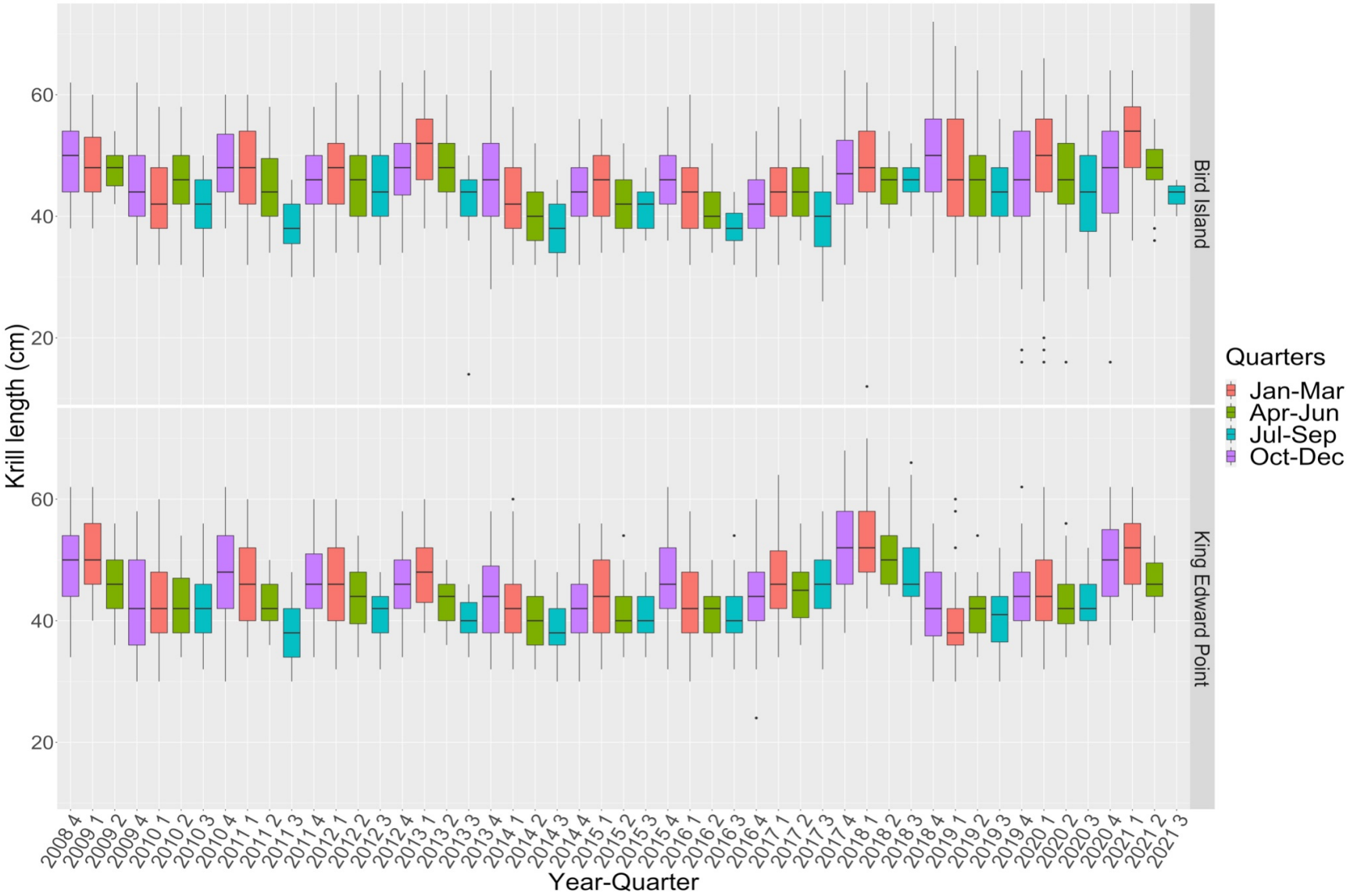
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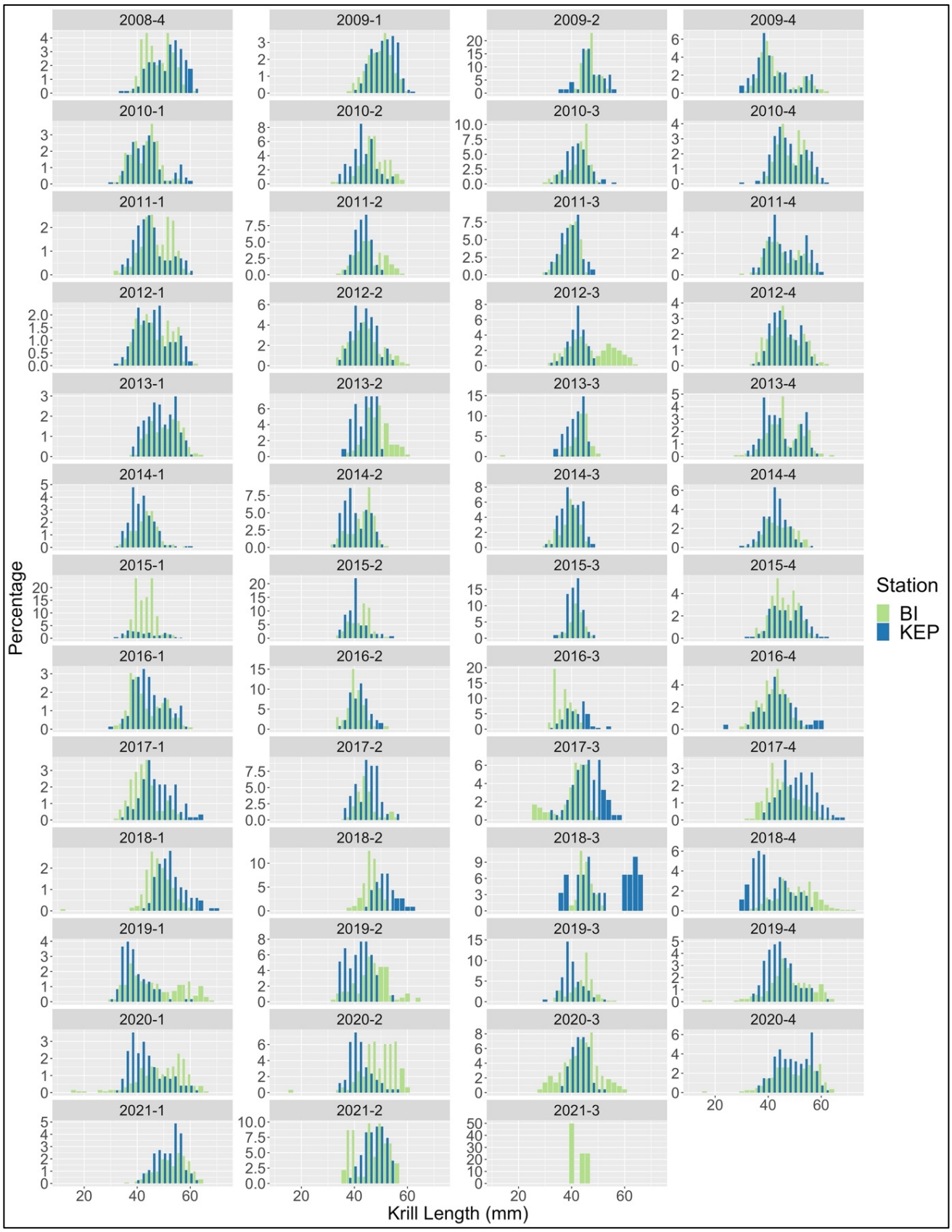
Supplementary Material



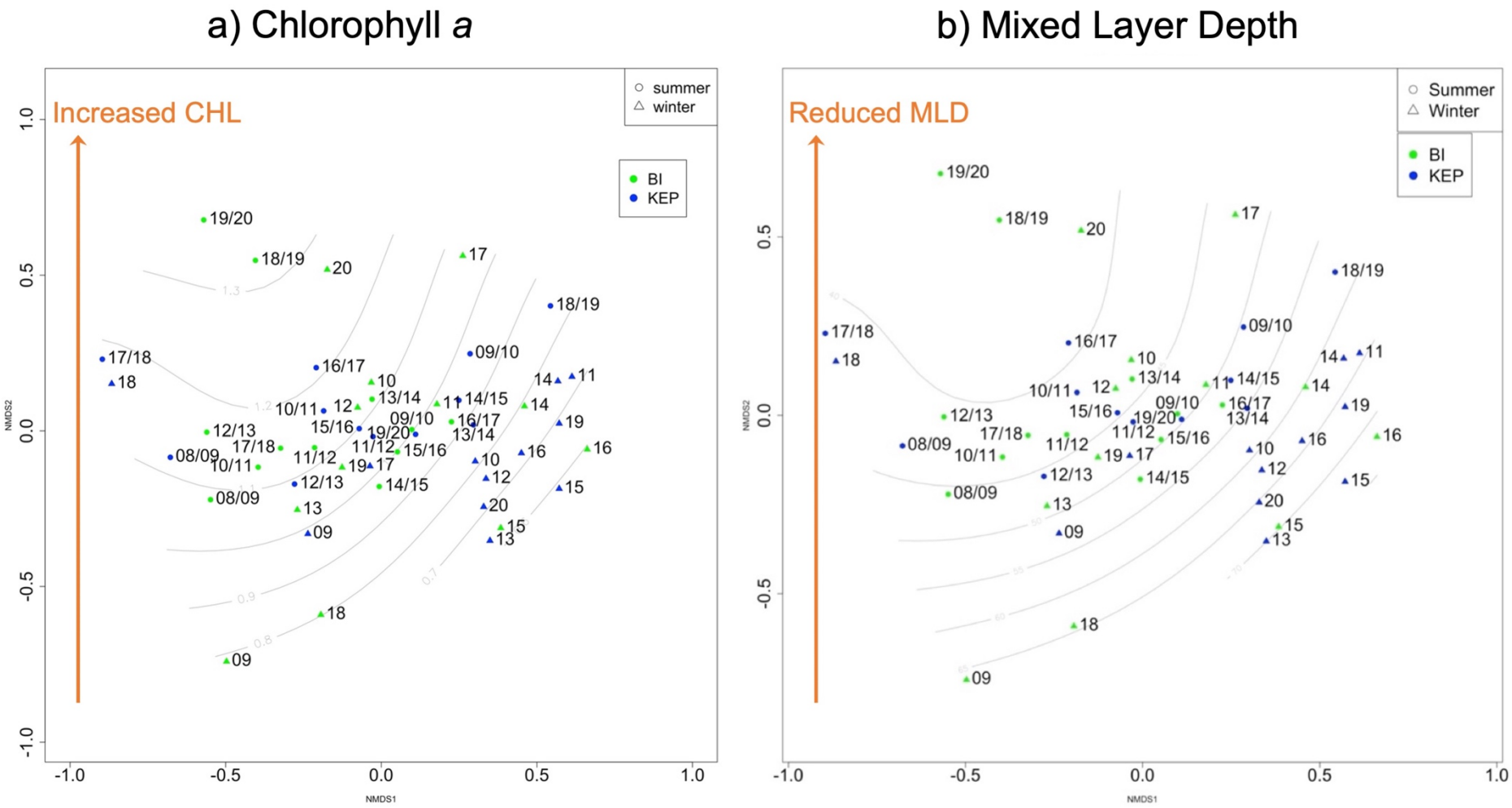
Supplementary Material Figure 1. The proportion of different fish groups in the diet of fur seals; *Electrona* species (ELT), *Gymnoscopelus* species (GYY), *Harpagifer georgianus* (HPG) Channichthyidae spp. (ICX), *Krefftichthys anderssoni* (KRA) Myctophidae spp. (LXX), *Muraenolepis* spp. (MVC) Notothenioidei spp. (NOX) *Notolepis coatsi* (NTO), *Paradiplospinus gracilis* (PDG), *Parachaenichthys georgianus* (PGE), *Protomyctophum* spp. (PVP), Teuthoidea spp. (SQQ), unknown species (UNK)



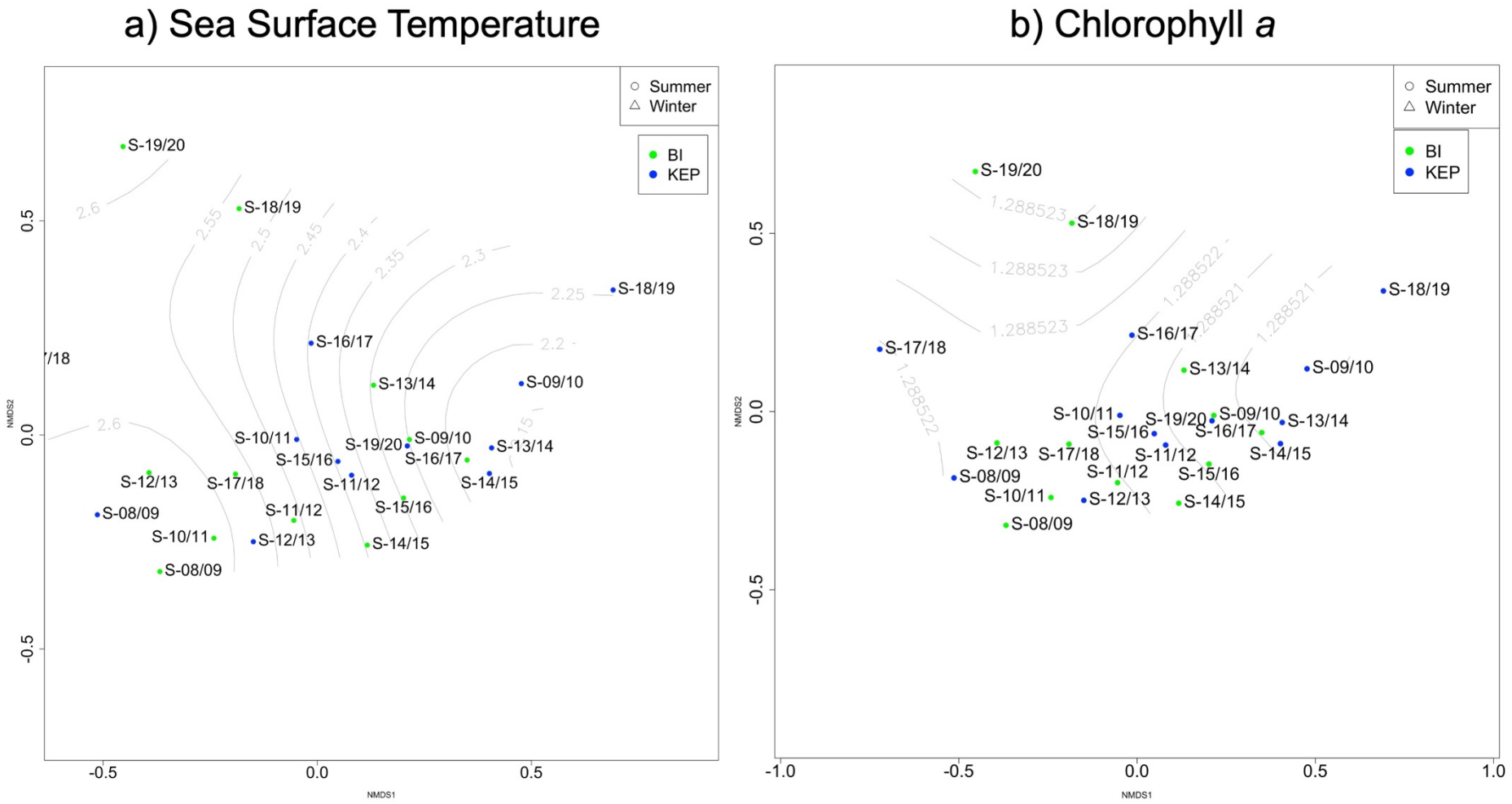
Supplementary Material Figure 2. Box plots expressing median changes in krill length over quarter year periods from 2008 to 2021 at Bird Island (top) and King Edward Point (bottom).



Supplementary Material Figure 3. Length frequency histograms of krill preyed on by Antarctic fur seals at (BI; green) and King Edward Point (KEP; blue) every 3 months from October 2008 to 2021.



Supplementary Material Figure 4. NMDS ordination of dissimilarity in krill community lengths between seasons (Summer = October-March, Winter = April-September) at (BI; green) and King Edward Point (KEP; blue) with a) chlorophyll *a* and b) mixed layer depth gradients.



Supplementary Material Figure 5. NMDS plot showing dissimilarities in krill length selected for by fur seals (BI; green) and King Edward Point (KEP; blue) with a) sea surface temperature and b) chlorophyll *a* gradients