Seabird and seal responses to the physical environment and to spatio-temporal variation in the distribution and abundance of Antarctic krill at South Georgia, with implications for local fisheries management

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We used 22 years of seasonally and spatially consistent monitoring data to explore marine predator–prey numerical response relationships. Specifically, we tested whether indices of offspring performance (e.g. offspring mass near the time of their independence and/or growth rate) from three Antarctic krill-dependent predators, showed positive relationships with estimates of krill density, determined using fishery-independent acoustic surveys undertaken towards the middle of the predator breeding season. Results showed that indices of predator reproductive performance had little relationship with krill density. In most years, average krill densities were higher on-shelf than off-shelf, potentially providing ecological buffering for predators provisioning offspring. Interestingly, positive response relationships were evident between predator offspring mass and the spatial distribution of krill, measured using indices that represent levels of inequality (patchiness) in krill distribution. These relationships were strongest using indices that reflected the off-shelf krill spatial distribution. We found that krill density and predator offspring mass were also both negatively influenced by sea surface temperature and the Southern Annular Mode, indicating that the environment exerts strong control over ecosystem processes. Finally, we consider the relevance of our results to the ecological framework used by managers responsible for setting catch limits for the regional fishery for krill.

Keywords: Antarctic fur seals, Antarctic krill, ecological drivers, gentoo penguins, macaroni penguins, spatial and temporal variability.

Introduction

Determining numerical response relationships between marine predators and their prey is critical for understanding ecosystem function, operation and dynamics. It is especially important for the conservation and protection of dependent predators where their prey are also exploited commercially (Cury *et al.*, 2011; Sydeman *et al.*, 2017; 2021). Relatively few studies have explicitly examined the effects of prey distribution and abundance on predator processes using near-simultaneous data (Frederiksen *et al.*, 2006; Furness, 2007; Cury *et al.*, 2011; Erikstad *et al.*, 2013; Barbraud *et al.*, 2018; Pacoureau *et al.*, 2019).

One complicating factor is that forage species generally show high levels of recruitment variability, primarily driven by environmental variation rather than variation in internal population dynamics (see Cury *et al.*, 2014). Consequently, population levels can fluctuate by orders of magnitude between years, resulting in substantial variability in the distribution of resources, affecting availability to predators. In contrast, seabirds and marine mammals generally have high adult survival rates, low reproductive rates, and they often defer maturity for several years, so that predator population numbers generally vary by only a little between years. As such, air-breathing predator populations do not commonly track those of their prey, meaning that ecological mismatches or lags must occur (e.g. Furness and Camphuysen, 1997). Mismatches may

be through predator underutilization of prey, prey-switching (Furness, 2007), self-sacrifice of body condition, or alteration in breeding propensity and success (Hernandez *et al.*, 2015; Reed *et al.*, 2015), given individual parental capacity (e.g. differences in body condition, age, or experience). Furthermore, variation in offspring weight at independence, or overall breeding success, may vary with prey type or abundance (Kato *et al.*, 2001; Kadin *et al.*, 2012), plausibly again influenced by parental condition.

Another challenge is that seabirds and marine mammals generally show a high degree of flexibility in their foraging behaviour (both horizontally and vertically). As such, modelling predator–prey relationships at scales that matter to predators is challenging, as the life histories of most predators dictate that they must successfully forage across a range of spatial and temporal scales. For example, land-breeding marine predators, such as penguins and otariid seals, require adequate prey prior to breeding to build condition, throughout the breeding season for self-provisioning and for their offspring, and during the post-breeding period whilst parents recover and naïve offspring learn to fend for themselves. As such, penguins must find prey within close proximity of their colonies during brood (e.g. <65 km), but can explore more distant waters during incubation, crèche (e.g. >125 km), or after their offspring become independent (e.g. Warwick-Evans *et al.*, 2018; 2019). In contrast, lactating female otariid seals are a little less restricted

and can explore more distant waters (e.g. >125 km) for food just a few days after parturition (e.g. Staniland and Boyd, 2003). Almost certainly, this spatial-temporal patchwork of resource demand differs for different predator species, plausibly resulting in varying levels of intra- and inter-specific resource competition.

A further key difficulty is whether prey species are also highly mobile (as are most small pelagic fish), or move with ocean currents (as do micro-nekton or meso-zooplanktonic crustaceans). If so, a single snapshot in time may not adequately represent prey availability within the multi-dimensional foraging ambits of even central place foragers. Therefore, parameterizing models to reflect the dynamic prey field is still beyond most studies (but see Santora et al., 2014), especially for key forage species, such as lower-trophic level pelagic fish (e.g. anchovies or sardines) and euphausiid crustaceans (e.g. krill).

In addition to quantifying direct predator–prey numerical relationships, co-occurring and possibly confounding factors, especially ones attributed to climate variability or change, also need to be accounted for in models of predator–prey numerical responses. Such issues are now fundamental, as various studies have argued that prey availability is critical for predator productivity (e.g. Pichegru et al., 2012; Barbraud et al., 2018; Sherley et al., 2020; Sydeman et al., 2021).

With this level of species and ecosystem complexity, modelling predator–prey relationships at multiple scales to determine scale-dependencies in relationships is needed (Sydeman et al., 2017). However, data on prey distribution and abundance are generally only available at scales that reflect human activities, i.e. fisheries (e.g. Cury et al., 2011; Barbraud et al., 2018); this often also includes fishery independent surveys, as these are frequently designed around primary fisheries regions. Fisheries data are valuable, but may not reflect the actual needs of predators, or the scales of their foraging behaviour. Thus, predator–prey interactions, vital for a precautionary ecosystem approach to fisheries management and for species conservation, remain poorly characterized.

At Bird Island, South Georgia in the southwest Atlantic (Figure 1), our long-term study, ongoing since 1997, reflects (i) the reproductive output of land-based predators, and (ii) the availability of their primary prey, Antarctic krill *Euphausia superba* (hereafter, krill). Indices of reproductive output are available from a range of predators (Reid et al., 2005; Trathan et al., 2021), including for macaroni penguins (*Eudyptes chrysolophus*), gentoo penguins (*Pygoscelis papua*), and Antarctic fur seals (*Arctocephalus gazella*). Other predator species are also monitored at Bird Island (and elsewhere at South Georgia), but here we focus on these three diving species. These species are the most constrained in their foraging range during their summer breeding season (Trathan et al., 2006; Staniland et al., 2011; Ratcliffe et al., 2018), but all overlap to varying degrees with local, fishery independent, krill acoustic surveys (Fielding et al., 2014).

South Georgia is an oceanic island situated within the flow of the Antarctic Circumpolar Current (ACC; Figure 1). It experiences high levels of intra- and inter-annual variability in a range of ecosystem components, some of which are influenced by Southern Hemisphere teleconnections e.g. *El Niño* or the Southern Annular Mode (SAM) (Trathan and Murphy, 2003; Trathan et al., 2006; 2007; Murphy et al., 2007a; 2007b). Variation in physical ecosystem properties leads to biological variation, including variability in the abundance of krill
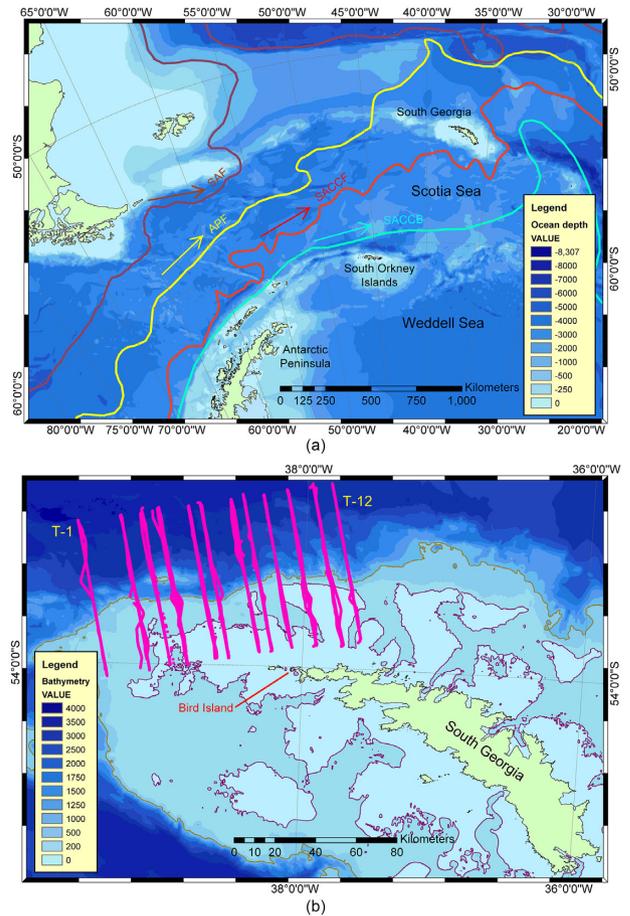
Figure 1. (a) The Scotia Sea showing the location and direction of flow for the major fronts in the Antarctic Circumpolar Current (ACC): Sub-Antarctic Front (SAF—brown); Antarctic Polar Front (APF—yellow); Southern ACC Front (SACCF—red); and Southern ACC Boundary (SACCB—pale blue). (b) The Western Core Box (WCB) showing transects from the different acoustic surveys between 1997 and 2020 (see Table 1); transects number from west (T-1) to east (T-12); Bird Island lies south of the WCB.

(Trathan et al., 2003; Murphy et al., 2007a; 2007b; Whitehouse et al., 2008; Fielding et al., 2014). As such, knowledge of predator–prey relationships is supported by an understanding of how physical processes drive prey abundance and distribution, that is, availability (c.f. Cury et al., 2008; Steel et al., 2012). At South Georgia, ecological understanding also includes knowledge about transport of krill from regions further south (Thorpe et al., 2004; Murphy et al., 2004a; 2004b), Whilst complementary knowledge about other ecological processes influencing predators and their prey is also accumulating (e.g. Forcada et al., 2005; 2008; Forcada and Hofmann, 2014), including the recovery of previously depleted populations of baleen whales (Zerbini et al., 2019; Baines et al., 2021) and their consumption of krill (e.g. Baines et al., 2022). Such changes in the guild of krill-eating predators may lead to changes in prey availability in certain habitats, which could have consequences for other species (c.f. Sladen, 1964; Laws, 1977).

In this study, we examine response relationships between annual indices of reproductive output for our three central place predator species, together with different metrics describing the availability of their primary prey, krill. The principal hypothesis tested is that indices of predator offspring

performance (e.g. offspring mass and/or growth rate) show positive relationships with krill density. Our krill acoustic surveys were located in the areas where our predator species preferentially forage in summer (Handley *et al.*, 2020), and where the fishery for krill has operated in winter (Trathan *et al.*, 2021); thus, our survey area includes parts of the ocean where krill are more predictable and/or more abundant. As our acoustic surveys span the shelf-break, this allowed us to investigate predator–prey interactions across the whole survey area, as well as spatial differences between on-shelf and off-shelf habitats. Thus, we further hypothesize that predator responses to krill are habitat specific, and that oceanographic conditions affect prey availability in different habitats. In addition, using environmental indices over the preceding winter period, we were able to explore how our monitoring data relate to previous lagged environmental states.

Our study not only provides information about the South Georgia ecosystem operation, but also provides insights into issues that fisheries managers should consider when implementing any decision rules to estimate sustainable catch limits for krill at local scales of management. Such insights are important, as krill fisheries are now concentrating effort (and catch) at increasingly small scales, often in coastal regions important to dependent predators (Trathan *et al.*, 2018; 2021; 2022; Warwick-Evans *et al.*, 2018; Watters *et al.*, 2020). More broadly, our study may also be relevant to the management of other forage species that vary at similar spatial and temporal scales (Sydeman *et al.*, 2021).

Material and methods

Study site

Our study location was the Sub-Antarctic island of South Georgia in the southwest Atlantic (Figure 1). South Georgia lies within the flow of the ACC (see above regarding the importance of the ACC), with the Antarctic Polar Front to the north and the Southern ACC Front to the south and east, although this latter front sometimes extends along the northern shelf-break (e.g. Orsi *et al.*, 1995; Thorpe *et al.*, 2004).

All acoustic data and predator monitoring data used in this study are available from the British Antarctic Survey's Polar Data Centre (see data availability statement below). We relate all data to the year in which the Austral summer ends, for example, the acoustic survey between 2006–12–25 and 2006–12–28 has a nominal year of 2007 (see Supplementary Table S1). Similarly, all predator indices relate to the year in which offspring reach independence, for example, the breeding season in the summer of 2006 and 2007 has a nominal year of 2007.

Acoustic survey data for Antarctic krill

Acoustic surveys targeting Antarctic krill within the Western Core Box (WCB; an area covering 132 km by 80 km) to the northwest of South Georgia (Figure 1b) have been described previously (Trathan *et al.*, 2003; Reid *et al.*, 2010; Fielding *et al.*, 2014). Here we extend the time series from 1997 to 2020, using only acoustic surveys that took place within a fixed time window (1 December to 16 February), given that known intra-annual variation in the timing of peak summer biomass can affect estimates of krill mean density at South Georgia (Saunders *et al.*, 2007; Reid *et al.*, 2010). The WCB

includes on-shelf and off-shelf areas sometimes used by predators foraging from Bird Island; Supplementary Table S1 gives the survey dates and research vessels used.

During each survey, acoustic data were collected along eight transects, although in some years not all transects could be completed (Table 1). The location of some transects changed after the first few years; therefore, for ease of reference we have uniquely labelled all transects (1–12). Acoustic data were depth integrated to 250 m (or to 2 m above the sea floor if shallower) with a horizontal average integration distance of 500 m. Any acoustic sampling intervals off-transect were removed as were sampling intervals with lengths greater than 1000 m (<0.5% removed in total). Krill density (g m^{-2}) was determined using the 3-frequency identification method (38, 120, and 200 kHz) and the Commission for the Conservation of Antarctic Marine Resources (CCAMLR) Target Strength model; see Fielding *et al.* (2014) for details. Our krill acoustic analyses use up-to-date methods endorsed by CCAMLR (Fielding *et al.*, 2016).

Krill, like many lower-trophic level species, are highly dynamic in their dispersion properties (distribution and abundance), occurring in loose, diffuse layers and dense, tightly packed swarms (Miller and Hampton, 1989; Brierley and Cox, 2015). Krill abundance is often represented by estimates of mean density (g m^{-2}) derived from acoustic surveys comprising pseudo-random parallel transects (e.g. Trathan *et al.*, 2003; Fielding *et al.*, 2014) following the approach of Jolly and Hampton (1990). This approach assumes transects are orthogonal to the major axis of krill distribution along the shelf-break, and the mean density on a given transect is considered to be an independent estimate of the mean density in the survey area. However, we took a different approach based on the observation that krill occur with spatial distributions that are highly skewed, with large parts of survey transects sampling little or no krill (e.g. Miller *et al.*, 1993). Further, single large krill swarms can significantly affect estimates of mean density (Fielding *et al.*, 2014) in a way that does not necessarily reflect the wider distribution of biomass. Therefore, we did not extrapolate density estimates to predefined strata, instead we based our characterization of krill on summaries of the individual integrated acoustic sampling intervals (each nominally 500 × 250 m) along all transects.

Patterns in species abundance and distributions (e.g. Greig-Smith, 1964; Lloyd, 1967) are key ecosystem considerations. Here we recognize that prey patchiness may be more important to predator feeding success than density averaged over a large area. Indeed, large prey patches may attract predators, which themselves act as cues for the arrival of other predators. Thus, the spatial arrangement of prey may be vital to aspects of ecosystem function. However, given the tendency of krill to form large swarms, strong serial correlation among density estimates along a single transect is expected and may raise estimates of variability in krill density on a survey compared with that estimated from transect means.

As such, to characterize the uneven distribution of krill, we considered a number of different metrics. Using the individual sampling intervals (see Table 1) we calculated the mean density (Density_Mean; g m^{-2}) and the standard deviation from all sampling intervals (Density_SD). We also derived the coefficient of variation for all sampling intervals (Density_CV; the ratio of the standard deviation to the mean), the median density (Density_Median; g m^{-2}), the quartile coefficient of dispersion (Density_QCD), which uses quantile information

Table 1. Cruises occupying the WCB between 1997 and 2020; (see Figure 1b).

Cruise	Year (nominal)	Transect (count)	Survey (km)	Interval (*n*)	Interval (0)	Density (g m-2)	Density (SD)	Density (CV)	Cruise (CV)
JR00017	1997	8	629.09	1298	0.21	56.07	394.69	7.04	0.64
JR00028	1998	8	635.41	1265	0.48	26.97	272.90	10.12	1.25
JR00038	1999	8	642.22	1299	0.09	67.69	591.38	8.74	0.74
AT00045	2000	8	560.25	1128	0.95	2.63	25.98	9.89	0.98
JR00057	2001	8	634.12	1270	0.81	29.43	288.26	9.80	0.84
JR00082	2003	8	428.53	859	0.10	82.15	622.82	7.58	1.84
JR00096	2004	7	475.87	954	0.32	22.72	115.59	5.09	0.29
JR00116	2005	8	601.92	1209	0.84	78.35	920.86	11.75	1.79
JR00140	2006	8	643.23	1289	0.75	112.00	893.16	7.97	1.32
JR00162	2007	6	479.06	961	0.60	57.10	312.04	5.46	0.69
JR00188	2009	8	638.62	1281	0.06	19.43	48.19	2.48	0.39
JR00228	2010	8	638.62	1275	0.12	13.86	97.34	7.02	0.80
JR00245	2011	8	623.78	1238	0.06	32.41	233.01	7.19	0.78
JR00260	2012	8	637.65	1277	0.36	87.02	1313.81	15.10	1.36
JR00280	2013	8	639.14	1280	0.64	52.41	582.58	11.12	1.03
JR00291	2014	8	642.14	1283	0.83	27.47	268.73	9.78	0.89
JR00304	2015	8	634.15	1104	0.65	21.90	196.13	8.96	0.67
JR15002	2016	8	642.47	1187	0.04	17.43	32.56	1.87	0.41
JR16003	2017	8	631.34	1206	0.48	18.32	71.95	3.93	0.58
JR17002	2018	8	629.38	1200	0.35	25.99	227.04	8.74	2.44
DY00098	2019	8	636.66	1338	0.23	21.28	171.68	8.07	0.74
JR19001	2020	8	628.24	1260	0.07	19.74	127.87	6.48	0.70

Interval (*n*) is the number of acoustic sampling intervals in the survey, while Interval (0) is the proportion with no krill recorded. Density (g m^{-2}) is the mean density for all sampling intervals. Cruise (CV) is the inter-transect coefficient of variation for all transects occupied in a given year (treating transects as sampling units). Density (SD) is the density standard deviation of all sampling intervals. Density (CV) is the density coefficient of variation for all sampling intervals.

Table 2. Pearson's Correlation coefficient for various derived indices based on acoustic surveys for krill (on-shelf and off-shelf combined) in the WCB between 1997 and 2020, (see Figure 1b).

	Interval (0)	Density g m^{-2}()	Density (SD)	Density (CV)	Density Median	Density (QCD)	Density (Gini)	Cruise (CV)
Interval (0)	1.00							
Density (g m^{-2})	0.12	1.00						
Density (SD)	0.20	0.90	1.00					
Density (CV)	0.49	0.40	0.68	1.00				
Density (Median)	-0.82	-0.12	-0.23	-0.59	1.00			
Density (QCD)	0.02	0.13	0.05	-0.06	-0.18	1.00		
Density (Gini)	0.68	0.37	0.46	0.76	-0.86	0.13	1.00	
Cruise (CV)	0.23	0.44	0.51	0.55	-0.34	-0.21	0.48	1.00

See Table 1 for column headings.

and is therefore less sensitive to outliers. We also calculated the Gini coefficient (Density_Gini), which is a measure of statistical dispersion, intended to represent inequality; a Gini coefficient of zero expresses perfect equality where all sample values are the same (low patchiness), whilst a Gini coefficient of one expresses maximal inequality among values (maximum patchiness). Finally, we also calculated the proportion of sampling intervals where no krill were detected (Reset_Zero). In addition, we estimated the mean density from the mean of each transect occupied (Cruise_Mean; g m^{-2}), the standard deviation of transect mean estimates (Cruise_SD) and the coefficient of variation across transects (Cruise_CV). With multiple krill indices from the WCB, we explored correlation coefficients between individual variables as a guide to possible collinearity (Table 2).

We calculated our krill indices for the full WCB survey area and separately for those sampling intervals and transects that occurred on-shelf (= <1000 m) and off-shelf (>1000 m), where the 1000 m isobath provides a near-contiguous division between on-shelf and off-shelf habitats. In total, this gave eight indices for krill for the full survey area (Figure 1b), eight for the on-shelf area, and eight for the off-shelf area.

Predator indices

All of our predator monitoring indices were collected at Bird Island, South Georgia (Figure 1b). The joint University of Cambridge and British Antarctic Survey Animal Ethics Committee approved all animal handling procedures relevant to the data used in this study.

Macaroni penguins

Macaroni penguin breeding phenology is consistent between years at Bird Island (Trathan *et al.*, 2021), so standard calendar dates are used for monitoring activities. Each year, arrival weights are collected as animals return to breed, with a minimum sample size of 50 male and 50 females. Nest counts are based on the number of occupied nests with eggs. Chick counts are based on nests with chicks. Breeding success is based on the number of chicks fledged per egg laid. Chick fledging weights are the average of a sample taken just prior to fledging with a minimum sample size of at least 100 birds in all years.

Gentoo penguins

Gentoo penguin breeding phenology varies between years at Bird Island (Trathan *et al.*, 2021), so standardized monitoring dates are determined by when particular events in breeding happen each year. Nest counts are based on all island counts one week after peak egg laying. Chick counts are based on when all eggs have hatched. Breeding success is based on the number of chicks fledged per egg laid. Chick fledging weights are the average of an all island sample taken just prior to fledging with a minimum sample size of 100 in most years, or 40 where fewer than 100 chicks fledge in a given year (e.g. in 2009).

Antarctic fur seals

Antarctic fur seal breeding phenology is determined each year from observations at the Bird Island special study beach (Doidge *et al.*, 1984); observations include the total cumulative number of pups born during the season, the number dying and the percentage mortality. Each year a random selection of pups are weighed at nearby Freshwater Bay, Bird Island, in

January, February, and March at standard intervals. On each occasion, >100 pups are weighed (male pups tend to be heavier, so samples include approximately equal sex ratios) with approximately half taken from the beach and half from the surrounding tussock.

Statistical analyses

We used R version 3.2.2 [2015–08–14; the R Foundation for Statistical Computing Platform: i386-w64-mingw32/i386 (32-bits)] and RStudio (version 1.0.136; RStudio, Inc.) to develop statistical analyses. We used ArcGIS (ESRI version 10.4.1) for all spatial analyses.

Acoustic indices for Antarctic krill—spatial, temporal, and environmental variation

To identify temporal and spatial differences, we used violinplots (R library *violplot*, version 0.3.5) to compare krill density within the WCB across years, including for each transect. We used analysis of variance to determine whether there were statistical differences. We used a Welch's *t*-test, assuming unequal variances, to compare average density on-shelf with that off-shelf.

Previous studies have suggested a relationship between bathymetric depth and krill density (e.g. Trathan *et al.*, 2003). Therefore, we used generalized additive models (GAM; R library *mgcv*, version 1.8–7) to characterize possible relationships with depth. We preferred GAMs (here and elsewhere in this study), as they do not assume *a priori* any specific form of relationship, and can be used to reveal and estimate non-linear effects of a given covariate on the dependent variable; GAMs are also flexible to implement. We therefore used a high-resolution bathymetric composition(Fretwell et al., 2009) as a covariate with depth values extracted at the location of each acoustic sampling interval in the WCB. To relate krill density to depth, we implemented GAMs with a spline smoother (*bs* = "*cr*") and either a negative binomial or Tweedie distribution (based on data distribution), with gamma = 1.4 to inflate the model degrees of freedom in the generalized cross-validation (GCV) or Un-biased Risk Estimator (UBRE)/Akaike information criterion (AIC) score by a constant multiplier (Wood, 2006). The absolute value of the GCV score is interpretable as an estimation of the lack of fit of the model. We implemented a separate GAM for each occupation of the WCB (one for each year), and one for all surveys combined.

We also characterized relationships between krill and other physical environmental indices as such relationships have been identified previously (Whitehouse *et al.*, 2008; Fielding *et al.*, 2014; Trathan *et al.*, 2021). For sea surface temperature (SST), we used monthly composite data (www.ncei.noaa.gov/erddap/; accessed 2021–12–03) with values extracted from cells close to the WCB (38°W to 40°W and 54°S to 55°S) and averaged over the nominal month of each occupation of the WCB. For sea surface height (SSH) we used monthly composite data from the Copernicus Global Ocean Physics Reanalysis dataset [variable "zos", sea_surface_height_above_geoid (m) available at resources.marine.copernicus.eu/product-download/GLOBAL_MULTIYEAR_PHY_001_030; accessed 2022–03–01] with values extracted for South Georgia and regions to the south (34°W to 40°W and 52°S to 58°S). SST and SSH can inform about fronts and habitat zones in the Scotia Sea (Venables *et al.*, 2012). Similarly, for the SAM (SAM; legacy.bas.ac.uk/met/gjma/sam.html; accessed 2021–12–03),

and for the *El Niño*-Southern Oscillation---Ocean Niño Index; (ONI; origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php; accessed 2021–12–03), we extracted values for the nominal month of each occupation of the WCB. SAM and *El Niño* can inform about larger scale oceanographic variability. We used SST, SSH, SAM, and ONI as a covariate in a series of GAMs relating each to our various derived indices of krill. We characterized relationships with each covariate separately, including the potential for lagged effects by extracting covariate values for all months in the calendar year prior to each occupation of the WCB. We did not explore lags at longer timescales as the WCB data are annual, and such relationships require data at a finer temporal resolution (e.g. Trathan and Murphy, 2003; Trathan *et al.*, 2006). GAMs were implemented with a spline smoother and a Gaussian distribution, and with gamma = 1.4. Where visual inspection of outputs suggested overfitting, the number of knots was restricted. We used the function *dredge* from R library *MuMIn* (version 1.43.17) to determine the best model fits, based on AICc and deviance explained; separate final models for each environmental covariate included the single best fitting month for each covariate. For the best fitting models, we explored the influence of survey date, by including a term to represent the deviance from the nominal WCB survey date; this never increased the deviance explained so was omitted thereafter.

Predator data—relationship with acoustic indices for Antarctic krill

Our predator indices reflect predator performance in different ways, each of which might change in response to prey availability; these include, *inter alia*: adult propensity to breed and adult arrival weight; counts of offspring at different times of the breeding season; offspring growth rates; offspring fledging or weaning mass; and offspring mortality. Each of these predator performance characteristics potentially responds to ecological events, including prey density, over differing time scales and with different lag periods (Hunt and Schneider, 1987; Murphy *et al.*, 1988). Consequently, some of our predator indices should reflect cumulative variability within the prey population over a number of days, or even over months, including over the preceding inter-breeding period. As such, we hypothesized that indices that reflect offspring performance, such as offspring growth, or offspring mass, should most closely relate to our simultaneous estimates of prey density (Boyd, 1999; Croxall *et al.*, 1999; Croll *et al.*, 2006). In contrast, other indices that reflect arrival weights, or nest initiation, are less likely to relate to krill biomass assessed nominally midway through the breeding season. In principle, all predator indices will to some degree reflect prey conditions over preceding months, and as such, some predator performance characteristics, such as breeding success or offspring fledging or weaning mass, are also likely to be highly correlated with other predator indices recorded earlier in the breeding season. Consequently, we also test the hypothesis that predator indices at time *n* are good predictors of subsequent predator indices at time *n + 1*, *n + 2* to time *n + z*.

To determine whether our predator indices related to instantaneous snapshots of the local prey population, we used Partial Least Squares Canonical Analysis (PLS-CA; R library *plsdepot*, version 0.1.17; Sanchez 2013) to explore fundamental relationships between predators and krill. PLS-CA regression is suitable when there is multi-collinearity among variables, as may be the case when derived variables originate

from the same data source, in our case, the WCB krill acoustic data, and where our predator indices are highly correlated. The blocks of variables in PLS-CA play a symmetric role (i.e. there are neither predictors nor responses). PLS-CA finds the directions of maximum covariance, allowing us to determine the most likely candidate variables to include in subsequent regression analyses comparing predator indices with our various indices of krill.

We used GAMs to further explore relationships between selected predator indices and the indices from the krill survey, implementing each predator index as a response variable, with a spline smoother and a Gaussian distribution, using gamma = 1.4. Where visual inspection of outputs suggested overfitting, the number of knots was limited. Given correlations between mean krill density and other derived krill indices (Table 2), predictors were included separately in model fits. We also included a term to account for variability in WCB survey date. Final models used a single covariate and none included the term for deviation in WCB survey date.

### Predator indices—environmental relationships

For selected predator indices, we used GAMs to characterize relationships between each predator index and selected environmental indices (SST, SSH, SAM, and ONI) for the nominal month of the WCB survey. We also looked for lagged effects by extracting environmental covariate values in the months prior. We explored each environmental index separately using GAMs with a spline smoother and a Gaussian distribution, with gamma = 1.4. We used the function *dredge* to determine the best model fits, based on AICc and deviance explained; final models included the single best fitting month for each covariate.

Results

Acoustic indices for Antarctic krill—spatial, temporal, and environmental variation

Over the duration of the study, there was strong inter-annual variability in the average density of Antarctic krill in the WCB (Figure 2a and b) as well as inter-transect differences (Figure 2c). However, given the high levels of variability observed, a two-way analysis of variance showed that differences were not significant between years at $p < 0.1$ (Year: $F = 3.073, df = 1, 170$; Transect: $F = 2.857, df = 1, 170$). Approximately 41.3% of acoustic intervals occurred on-shelf at depths <1000 m, while 58.7% occurred off-shelf. A Welch's t-test, assuming unequal variances, indicated that average density on-shelf was greater than that off-shelf ($t = 3.36, df = 21, p > 0.003$). There was no significant inter-annual linear trend in average krill density at $p < 0.1$, (AOV Survey: $F = 2.09, df = 21,1$; AOV off-shelf: $F = 0.23, df = 21,1$; AOV on-shelf: $F = 1.88, df = 21,1$). Assuming a nominal survey start date of January 1st, WCB survey date deviation showed no significant influence at $p < 0.1$, (AOV Survey: $F = 1.779, df = 1,20$; AOV off-shelf: $F = 0.003, df = 1,20$; AOV on-shelf: $F = 2.051, df = 1,20$).

Relationships between krill density and bathymetric depth varied between surveys. Most surveys (16 of 22; Figure 2b) had higher krill density on-shelf, and lower density off-shelf over deeper water. Some surveys (6 of 22; in 2000, 2001, 2006, 2007, 2016, and 2019, see Figure 2b) showed complex relationships, with either variable, or increasing krill density with
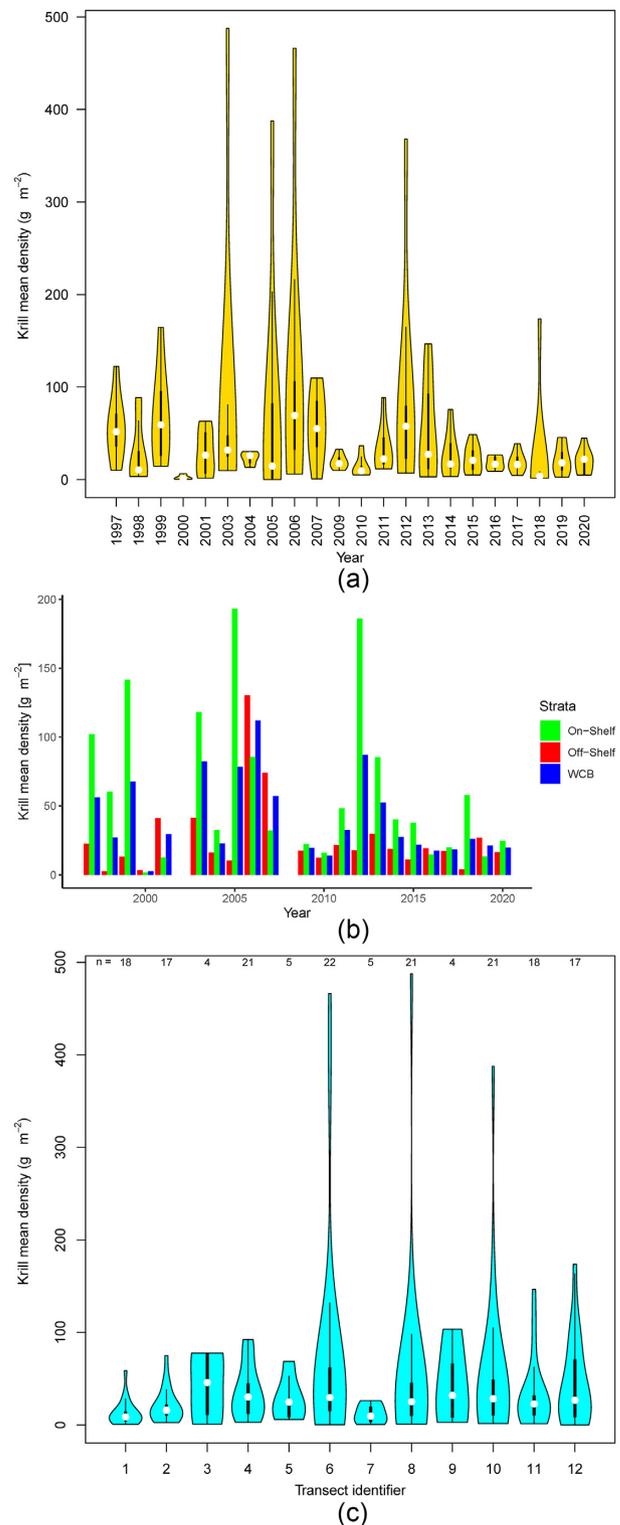
Figure 2. (a) Violin plots of krill density (g m^{-2}) from the WCB for each year (1997–2020). Plots show the distribution shape and summary statistics of the data, with the interquartile range (heavy bar), interquartile range × 1.5 (light bar), and median value (white circle). (b) Mean krill density (g m^{-2}) in the WCB for each year (1997–2020): on-shelf—green, off-shelf—red, and WCB—blue. (c) Violin plots of krill density (g m^{-2}) for each transect across all years (1997–2020). Plots show the distribution shape and summary statistics of the data, with the interquartile range (heavy bar), interquartile range × 1.5 (light bar), and median value (white circle). The number of occupations of each transect (n) is shown at the top. Transects number from west (T-1) to east (T-12), see Figure 1b.
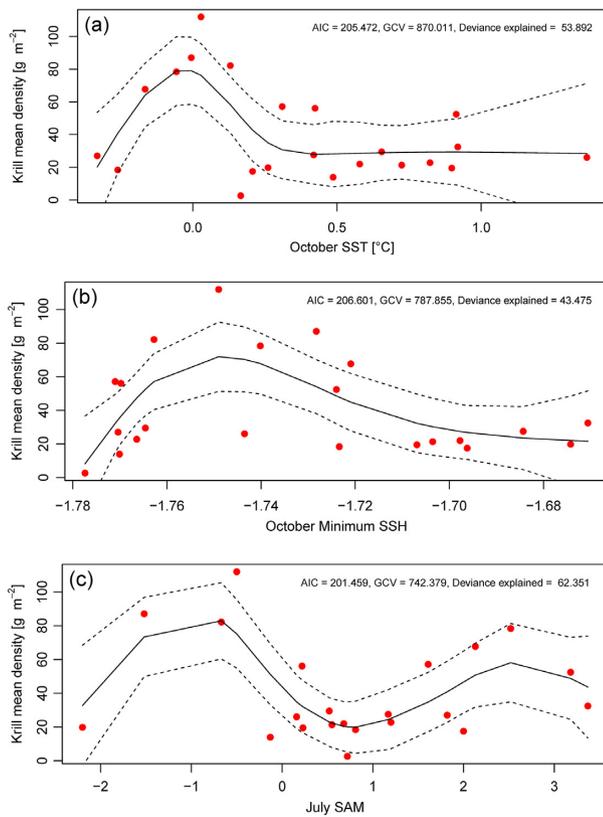
Figure 3. GAM for krill mean density (g m^{-2}; Density_Mean) against (a) SST (°C) in the preceding October; (b) minimum SSH in the preceding October; and (c) SAM in the preceding July. The function *dredge* was used to select the best model fit from all months, based on AICc and deviance explained. See also Supplementary Table 2.

increasing water depth. The relationship for all surveys together showed a relationship with higher krill density on-shelf; binning depth (at 100 m intervals) to reduce levels of variability, showed that depth differences were highly significant (Supplementary Figure S1; AOV: $df = 1$, 26 459, $F = 26.19$, $p < 0.001$). GAMs using the Tweedie distribution explained greater levels of deviance than models with a negative binomial distribution, but levels of deviance explained remained low (<5% deviance explained).

Results from a series of GAMs exploring links between mean krill density and different environmental indices (SST, SSH, and SAM) are shown in Figure 3, Supplementary Table S2, and Supplementary Figure S2; models with ONI resulted in only limited levels of deviance explained. In all cases, results based on AICc and deviance explained reflect the best fitting models for each environmental index, using predictors from the best fitting month in the preceding calendar year. For local SST, the best fitting model was for October, explaining 50% of the variance; for SSH, the minimum SSH value in October provided the best fitting model, explaining 40% of the variance. For SAM, the best fitting model was for July, explaining 62% of the variance. The term for WCB survey date deviation was not significant.

## Predator data—relationship with acoustic indices for Antarctic krill

Our PLS-CA model reports the multidimensional direction in the krill indices space that explains the maximum

multidimensional variance direction in the predator indices space. The PLS-CA radar plots for each predator species (Figure 4) show that the derived krill variables most closely related to predator offspring fledging mass, or growth rate, were those variables that reflected variability in krill distribution, rather than overall krill abundance. This was the case for macaroni penguin fledging weight, gentoo penguin fledging weight and fur seal pup mass in March, with the Gini coefficient (Density_Gini; a measure of dispersion or inequality) and the coefficient of variation of all sampling intervals (Density_CV), showing the strongest correlations (Figure 4). In addition, the proportion of sampling intervals where no krill was detected (Reset_Zero) and the standard deviation of all sampling intervals (Density_SD) showed strong correlations with predator variables in some cases (Figure 4). The PLS-CA also revealed that the indices related to krill variability showed relationships with gentoo breeding success.

Each of the krill indices related to variability in distribution reflects the fact that krill are not evenly distributed but are concentrated in a subset of sampling intervals; thus, the greater the Gini index (or the greater the Density_CV, or the greater the proportion Reset_Zero), the greater the concentration of krill in some sampling intervals. As such, patchiness presumably makes an important contribution to feeding success for predators.

The PLS-CA scatter plot for each species (Figure 4) showed that each year of the study reflected differing ecological conditions; 1998, 2004, 2009, 2013, 2016, and 2018 were outliers, with 2009 and 2016 consistently extreme, with low ranking on the x-axis (t_1). The scatter plots also suggest that macaroni penguins experienced a more continuous spread of years, compared with either gentoo penguins or fur seals, which may be related to differences in diet (e.g. Waluda *et al.*, 2017).

Our GAM analyses established which krill indices explained the greatest amount of variation for our selected response variables (macaroni penguin fledging weight, gentoo penguin fledging weight and fur seal pup mass in March; noting that offspring not reaching independence are not included). Krill density (Density_Mean), a measure regularly reported from krill acoustic surveys, showed little explanatory power for many of our predator indices (Supplementary Tables S3–S5). Similarly, the model term for WCB survey date had no explanatory power. The predictors that most commonly explained medium levels of deviance were those that reflected krill variability (patchiness), with the Gini coefficient (Density_Gini) frequently resulting in higher levels of deviance explained; this result is consistent with the output of our PLA-CA radar plot (Figure 4). In most years, there was a high value of the Gini coefficients and high values for the response variables (macaroni penguin fledging weight, gentoo penguin fledging weight and fur seal pup mass in March). However, a small number of years had low Gini coefficient values and low values for the response variable, which undoubtedly exert high influence in the models. The years with the lowest Gini coefficients were 2009 and 2016, with 2010 intermediate. The level of deviance explained by GAMs using the Gini coefficient varied depending upon which part of the WCB was used to develop krill indices (i.e. on-shelf or off-shelf, or on-shelf and off-shelf combined), though the patterns of deviance explained were similar across all three situations (Supplementary Tables S3–S5). The GAMs using the off-shelf Gini coefficient explained higher levels of deviance (Figure 5; Table 3) than did those for the full WCB survey
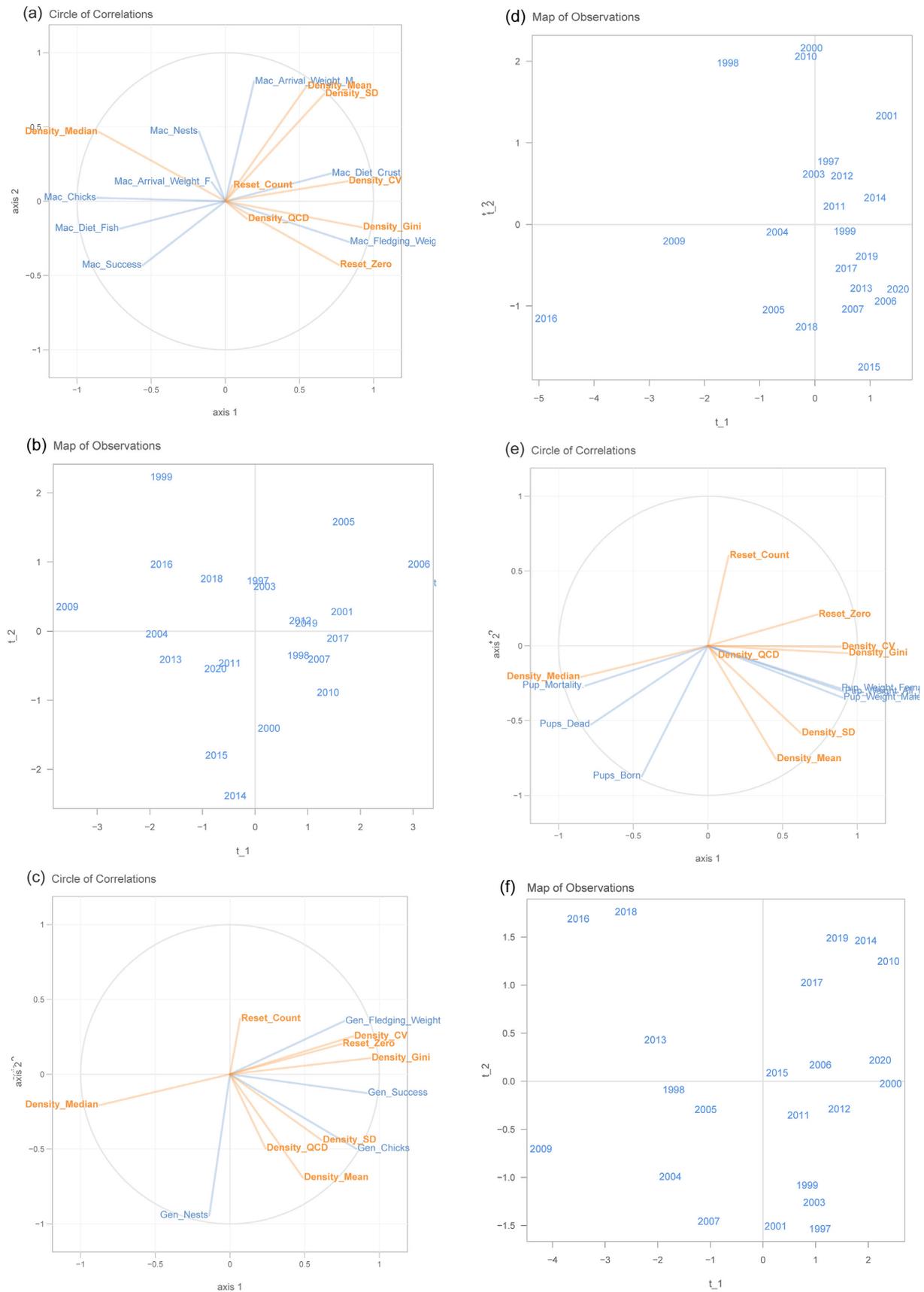
Figure 4. Partial Least Squares Canonical Analysis (PLS-CA) radar plots and scatter plots from separate analyses for macaroni penguin (a and b), gentoo penguin (c and d), and Antarctic fur seal (e and f) variables, each with krill monitoring variables for the WCB (combined on-shelf and off-shelf areas), across all years (1997–2020). In each radar plot, better-explained variables appear closer to the perimeter of the circle, where two variables are highly correlated, they appear near each other, where variables are negatively correlated they appear at opposite extremes, and uncorrelated variables appear orthogonal to each other. In the scatter plot, similar observations (years) appear close to each other.
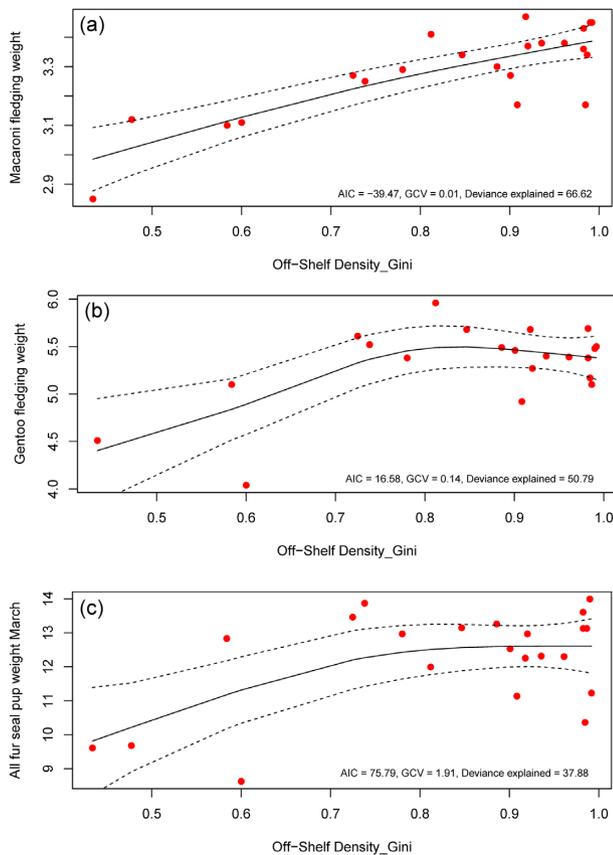
Figure 5. GAMs for offspring weight (kg) against the krill Gini coefficient (Density_Gini) calculated from off-shelf transects. (a) Macaroni penguin fledging weight; (b) gentoo penguin fledging weight; and (c) Antarctic fur seal pup weight in March. High Gini values imply more krill exists in fewer sampling intervals. See also Table 3.

area, or on-shelf indices. More restrictive analyses using only those years that varied by ±12 d of the nominal WCB survey start date ($n = 15$ years, see Supplementary Table S1) gave results comparable to those reported here.

GAM analyses using krill indices based on the krill density coefficient of variation (Density_CV), again, especially for off-shelf indices, also consistently explained high levels of deviation for macaroni penguin fledging weight, gentoo penguin fledging weight and fur seal pup mass in March (Figure 6; Table 4). This predictor had high explanatory power for all of the response variables associated with offspring mass. Similar to the Gini coefficient, this variable reflects patchiness, dispersion or inequality in the krill survey data. More restrictive analyses using only those years that varied by ±12 d of the nominal WCB survey start date ($n = 15$ years, see Supplementary Table S1) gave results comparable to those reported here.

GAMs using predictors based on predator status earlier in the year (Supplementary Tables S3–S5), e.g. the number of chicks, or the pup mass in months prior to March explained high levels of deviance for our response variables (macaroni penguin fledging weight, gentoo penguin fledging weight, and fur seal pup mass in March).

Predator indices—environmental relationships

Results from a series of GAMs exploring relationships between different predator indices and environmental indices

(e.g. local SST) provided high levels (>30%) of deviance explained (Supplementary Table S2). No significant relationships were evident with ONI, possibly because we only tested lag months in the preceding calendar year, whereas lags for predators with *El Niño* are reported to occur over longer time scales (Trathan *et al.*, 2006; 2007). In all cases, results reflect the best fitting models based on predictor indices from the months in the preceding calendar year, based on AICc and deviance explained. In general, local SST in the preceding October explained higher levels of deviance in predator indices than did SST in other months (Supplementary Table S2; Supplementary Figure S4). GAMs based on SAM had less predictive power for our predator indices, explaining much lower levels of deviance.

Discussion

We report results from one of the longest running, fishery independent assessments of predator and prey monitoring anywhere in the Antarctic, also one of the longest anywhere in the world ocean. Below, we explore results from the krill acoustic assessment, followed by plausible suggestions about how these results relate to local predators monitored at Bird Island. Finally, we explore various aspects of the dynamic operation of the South Georgia ecosystem, and implications for management of local fisheries that compete with predators for Antarctic krill.

Acoustic indices for Antarctic krill—spatial, temporal, and environmental variation

Our results (Figure 2a) support previous suggestions that high levels of inter-annual variability in krill density are characteristic of the South Georgia marine ecosystem (Brierley *et al.*, 1999; Trathan *et al.*, 2003; Fielding *et al.*, 2014). We found that krill density in most years was higher on-shelf than off-shelf (Figure 2b), supporting previous reports (Trathan *et al.*, 2003). Interestingly, the density of krill on-shelf does not covary with the density off-shelf (Figure 2b), indicating that there are different factors driving krill distribution and abundance on-shelf and off-shelf. As noted by Fielding *et al.* (2014), individual large swarms can lead to substantial differences in average density, and these in part, will contribute to on-shelf and off-shelf differences. However, more generally, it would now be interesting to determine whether on-shelf elevated krill density is also a result of accumulation through local production, concentration, or retention of krill arriving in the flow of the ACC, or even possibly as a result of differential mortality (e.g. consumption). At a smaller scale, some transects within the WCB also showed more predictable and higher levels of krill density than did others (Figure 2c); for example, transect 1 (Figure 1) consistently had a lower krill density than transect 11, though both were occupied on the same 18 occasions. As such, our results highlight that local variation in krill density occurs across a range of spatial scales and within short geographic distances, and that some of these differences are consistent across years (see also Hunt and Schneider, 1987; Murphy *et al.*, 1988; Trathan *et al.*, 2003). Areas that have high krill density, that are predictable across time, are likely to be focal areas for foraging krill-predators.

Previous work has suggested that levels of krill abundance at South Georgia relate to environmental forcing, in particular to SSTs modulated by the effects of the SAM, or the

Table 3. Results from a series of GAMs for different predator response variables (macaroni penguin fledging weight, gentoo penguin fledging weight and fur seal pup mass in March) and predictor variables derived from the krill Gini coefficient from off-shelf transects from the WCB; (see Figure 1b).

Response	Predictor	AIC	GCV	Deviance	Pearson
Mac_Fledging_Weight	Off-Shelf_Density_Gini	-39.47	0.01	66.62	0.80
Gen_Fledging_Weight	Off-Shelf_Density_Gini	16.58	0.14	50.79	0.60
Pup_Weight_Male_March	Off-Shelf_Density_Gini	81.00	2.43	36.22	0.48
Pup_Weight_Female_March	Off-Shelf_Density_Gini	71.62	1.57	34.10	0.50
Pup_Weight_All_March	Off-Shelf_Density_Gini	75.79	1.91	37.88	0.51

Columns are Akaike information criterion (AIC), minimized generalized cross-validation score (GCV), Deviance explained, and Pearson's correlation coefficient. See Figure 5 and Supplementary Tables S3–S5.
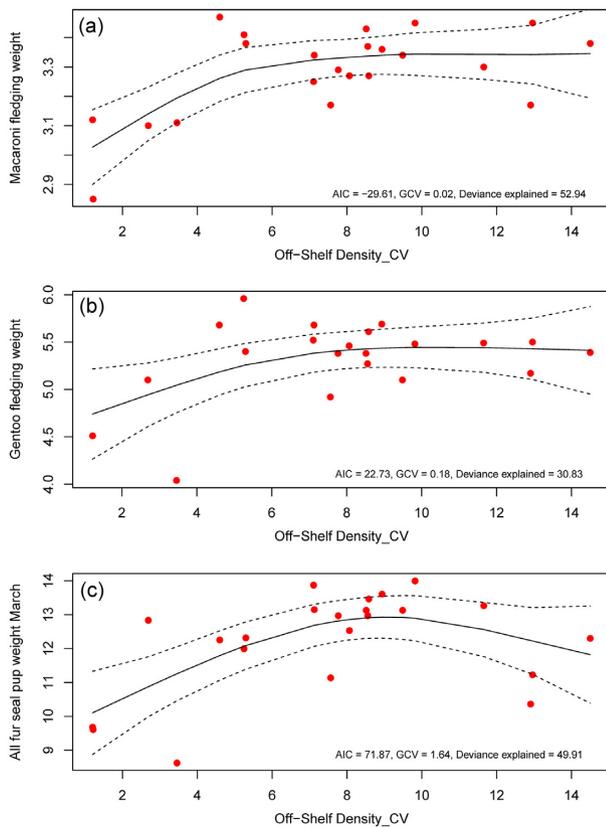
Figure 6. GAMs for offspring weight (kg) against the krill Density CV from off-shelf transects from the WCB. (a) Macaroni penguin fledging weight; (b) Gentoo penguin fledging weight; and (c) Antarctic fur seal pup weight in March. High values of Density_CV values imply greater variation in sampling intervals. See also Table 4.

El Niño-Southern Oscillation (ENSO) (Trathan et al., 2003; 2007; Murphy et al., 2007a; 2007b; Whitehouse et al., 2008; Fielding et al., 2014; 2021). Our results confirm the influence of both SST and SAM (Supplementary Table S2), with SST in the preceding October explaining high levels of deviation in krill density, and with SAM in the preceding July also having high influence. Cool SST, or negative SAM (when prevailing westerly winds shift further north), generally preceded surveys with high krill density (Figure 3; Supplementary Table S2), with the converse also apparent. SST variability is known to be spatially coherent at the regional scale, not just the local scale (Trathan and Murphy, 2003), emphasizing the potential for SST to reflect large scale patterns of krill biomass, probably also linked to krill movement or krill recruitment (Reid et al., 1999; Murphy et al., 2007b).

Models describing the flow of the ACC, show how zonal movements of the Southern ACC Front (SACCF) to the north of South Georgia can affect the transport of passive tracers representing krill into the region to the northwest of South Georgia (Thorpe et al., 2004; Murphy et al., 2004a), and these models have been supported by observations (Murphy et al., 2004b). Variability in the flow fields of the ACC also support the suggestion that alteration in the strength and the location of fronts may help explain variation in krill biomass at South Georgia (Thorpe et al., 2007). Such conditions also occur along the west Antarctic Peninsula where spatial-temporal variability in the delivery and distribution of ocean heat is related to ENSO (La Niña drives enhanced upwelling in this region) and SAM (+SAM drives a local response similar to that of La Niña) (Martinson et al., 2008).

It is plausible therefore, that relationships between krill density and SST, or SAM, are also moderated by similar environmental drivers affecting the location of the SACCF carrying krill to South Georgia, particularly where it impinges on the island's shelf (Supplementary Figure S5). Movement of fronts (e.g. the SACCF), both intra- and inter-annually, may alter spatial patterns of regional scale abundance and distribution of zooplankton, shifting krill closer to, or further away from, the South Georgia shelf. At South Georgia, such large-scale spatial variation may be evident as local-scale variation in density. Such a hypothesis requires further detailed study, beyond the current scope, as the small-scale footprint of the WCB does not fully encompass large-scale ocean variability. Importantly; however, SSH values more characteristic of the southern Scotia Sea show relationships with krill density in the WCB (Figure 3b; see also Supplementary Figure S2), consistent with spatial variation in ocean habitats. Moreover, other work also supports this hypothesis; for example, overall, 87% of the total krill stock exists over deep oceanic water (>2000 m; Atkinson et al., 2008), even though the large-scale distribution of krill is known to vary (Krafft et al., 2021). Indeed, Krafft et al. (2021) reported spatial differences across the Scotia Sea, but no decline in krill biomass since the previous such survey undertaken in 2000 (Trathan et al., 2001; Fielding et al., 2011). Krill standing stock in 2019 was estimated to be 62.6 million t (mean density of 30 g m^{-2}, with a sampling coefficient variation of 13%, over 2 million km^2), compared with an estimate in 2000 of 60.3 million t (29.2 g m^{-2}, CV 12.8%, over 2 million km^2), although methods and survey area differed. The highest mean krill densities in 2019 were at the South Orkney Islands (93.2 g m^{-2}) and the lowest at South Georgia (6.4 g m^{-2}). Comparison between both large-scale surveys indicates the existence of regional differences in krill density, distribution and biomass. Importantly, Krafft et al. (2021) concluded that it is currently not

Table 4. Results from a series of GAMs for different predator response variables (macaroni penguin fledging weight, gentoo penguin fledging weight and fur seal pup mass in March) and predictor variables derived from the krill Density CV from off-shelf transects from the WCB; columns as Table 3.

Response	Predictor	AIC	GCV	Deviance	Pearson
Mac_Fledging_Weight	Off-Shelf_Density_CV	-29.61	0.02	52.94	0.54
Gen_Fledging_Weight	Off-Shelf_Density_CV	22.73	0.18	30.83	0.48
Pup_Weight_Male_M	Off-Shelf_Density_CV	77.33	2.10	47.61	0.43
Pup_Weight_Female_M	Off-Shelf_Density_CV	69.24	1.45	43.24	0.34
Pup_Weight_All_M	Off-Shelf_Density_CV	71.87	1.64	49.91	0.39

See Figure 6 and Supplementary Tables S3–S5.

possible to assign any differences, or lack of differences, between the two survey datasets to longer term trends in the environment, krill stocks or fishing pressure. Further work is therefore now required to place the WCB within the larger context.

Predator data—relationship with acoustic indices for Antarctic krill

Although the spatial and temporal dynamics of krill arriving at South Georgia requires further study, what remains certain is that local scale variability in krill abundance is consistent with transport in the ACC (e.g. Figure 3b) and has important implications for predators. Pelagic predators, such as baleen whales, may be able to track large-scale spatial movements in biomass (Baines *et al.*, 2022), but land-based predators are constrained and are unlikely to have the capacity to respond; further, as more populations of baleen whale recover from historical exploitation, they may take a greater proportion of available krill than do land-based predators (c.f. Warwick-Evans *et al.*, 2022), with incrementally greater impacts on land-based predators. Such local scale variation in biomass therefore has important implication for ecosystem function and dynamics, ecosystem monitoring and ecosystem management.

In relating krill indices from the WCB to predator indices from nearby Bird Island, it is evident from our PLS-CA output (Figure 4), that there was no simple relationship between the two sets of monitoring indices. Each krill metric showed differing relationships with different predator species and different predator indices. That mean krill density (Density_Mean) had little relationship with many predator indices is interesting. Also of note is that the PLS-CA identified a small number of years that were ecologically distinct for each of the three predator species. Our GAM results provided further detail highlighting that mean krill density (Density_Mean) explained only small amounts of the deviance in predator monitoring indices (Supplementary Tables S3–S5), although we note that krill density was sufficient to support some predator reproduction in most years. GAMs using estimates of the median krill density (Density_Median) were generally better. However, GAMs that used indices related to krill spatial variability (patchiness) as predictors (e.g. Density_Gini, Density_CV; both reflecting spatial variation in krill density), explained much greater levels of deviance for our predator monitoring indices, with years of high(low) offspring mass occurring in years of high(low) krill spatial variability. In particular, the Gini coefficient (Density_Gini) explained some of the highest levels of deviation. Interestingly, each predator index was more related (higher deviance explained) to the off-shelf Gini coefficient (Figure 5, Table 3), rather than the on-shelf Gini coefficient or the wider WCB Gini coefficient. The off-shelf

Density_CV index also showed higher levels of deviance explained for our predator indices (Figure 6, Table 4).

Importantly, our GAMs also showed that there were substantial differences in how each predator species responded to the same krill variability indices. This is not surprising, as each predator species occupies a distinct niche and habitat, integrating prey availability across different time and space scales, with each predator species having different abilities to locate and capture prey, which may also be scale dependent (c.f. Mori and Boyd, 2004). The spatial distribution and structure of the prey field is therefore likely to be of importance, allowing a broad guild of krill predators to co-exist (Croxall *et al.*, 1985; Trathan and Hill, 2016), but each with differing levels of feeding success. Both Density_Gini and Density_CV capture aspects of krill distribution (patchiness) that appear to be important. Nevertheless, further work using swarm based analyses of krill (which also should include depth) will now be required.

The dynamics of how different predators interact with their prey, krill, is only at an early stage of understanding, particularly given different predator preferences for specific krill length classes (Hill *et al.*, 1996), and how this might then relate to krill distribution and abundance, or even to relationships with larger-scale processes such as recruitment. More detailed studies of how predators interact with their prey at local scales and how these might then relate to larger-scale physical ecosystem properties are now needed. Such studies may then help explain why our krill indices explain higher levels of deviance for offspring mass than for breeding success (Supplementary Tables S3 and S4), something that may also be related to parental quality, i.e. the number of offspring surviving to independence. Understanding such complexities is beyond the scope of the current study, but may help in explaining some of the observed differences between species; e.g. macaroni penguins and gentoo penguins (Supplementary Tables S3 and S4).

Spatial structure in the prey field (density, aggregation state, layer or swarm size, swarm separation, etc.) may relate to physical features such as bathymetry (e.g. Trathan *et al.*, 2003), or ocean currents (Murphy *et al.*, 2004a). Such structure may lead to predictable foraging habitats for predators (e.g. Bestley *et al.*, 2018; Warwick-Evans *et al.*, 2018; Harrison *et al.*, 2020). However, predators also have the potential to modify their own prey field as they feed; indeed, krill swarm structure may be a fundamental response for avoiding predation, whilst krill themselves continue to feed, mate and spawn (Tarling and Fielding, 2016). Thus, cumulative impacts of many predators could generate significant effects on local prey aggregation state, but are so far unquantified. With the recovery of Antarctic fur seal populations (Forcada *et al.*, 2005), and the ongoing recovery of humpback whale stocks (Zerbini *et al.*, 2019; Baines *et al.*, 2021), such effects may

accumulate. As such, if predators are a key driver of krill behaviour (Olson *et al*., 2016), it may be that land-based predators feeding in coastal or shelf waters generate different aggregation states of krill than do predators in the open ocean where predation risks will differ. Indeed, given that humpback whale abundance off-shelf now accounts for most whale biomass in the Scotia Sea (Baines *et al*., 2021; 2022), humpback whales could already be altering prey dynamics (and abundance) at regional scales. Moreover, such processes potentially provide mechanistic insight into long-standing debates surrounding the "krill surplus" hypotheses (Sladen, 1964; Laws, 1977).

Implications for ecosystem operation, and for management of local fisheries

Our results are relevant to the management of the international fishery for krill, under the control of the CCAMLR. We show that the status of a predator population recorded earlier in the breeding season may provide better explanatory power about its subsequent status, than does a single snapshot of prey resources determined from an acoustic krill survey (Supplementary Tables S3–S5). Thus, the recent past condition of a predator population is generally a good predictor of its future state.

Our results also highlight important concerns about food-web connections, ecosystem dynamics (e.g. Hill *et al*., 2006; Brasier *et al*., 2019) and management (e.g. Constable and de la Mare, 1996; Constable *et al*., 2000; Constable, 2001). Simply put, predator populations do not directly track prey populations, highlighting that ecological complexity has important implications for monitoring and management (e.g. Furness and Camphuysen, 1997). As outlined above, mismatches may be the result of a diverse range of factors. Some, or all of these, reflect life history traits that arise in response to variability in physical and biological environmental conditions (e.g. Forcada and Hoffman, 2014). However, our results also point to further levels of ecological complexity.

Krill density on-shelf is generally higher than that off-shelf (Figure 2b). However, over basin-wide scales, krill abundance off-shelf is greater than on-shelf, albeit with krill at lower density (Atkinson *et al*., 2008). Thus, off-shelf krill biomass potentially acts as a reservoir supplying on-shelf biomass (Supplementary Figure S5). This means that the rate of flow on-shelf is a key ecosystem process. Local krill on-shelf then potentially acts as a prey buffer for krill predators, including for penguins and fur seals. If higher krill density on-shelf buffers the amount of prey available to predators, direct linkages between local prey density and predator performance may be masked, or difficult to detect. Variation in the regional environment (e.g. SST, SSH, or SAM see Figure 3 and Supplementary Figure S2), particularly in how waters characteristic of the southern Scotia Sea influence South Georgia, probably also influence how prey becomes available to predators. Such a process could help explain why there is no obvious link, or functional relationship observed between krill density and predator performance. Finally, physical ecosystem variability probably drives variation in krill abundance, including known periodic recruitment processes in krill, and in the spatial and temporal structure of the prey field, which in turn, relates to predator productivity (Reid *et al*., 1999; Murphy *et al*., 2007a). In the future, as understanding increases, such

complexity might suitably be analyzed using Structural Equation Modelling (e.g. Westland, 2020).

The most important implication of our results is that CCAMLR should now consider factors other than simply krill distribution and abundance when setting catch limits. Knowledge about krill aggregation state and the consequences of krill movement in ocean currents (e.g. Trathan *et al*., 2022) remain sparse, yet such issues are important for sustainable management. Inappropriate management decision rules based on yield estimates of krill biomass, rather than spatial and temporal biomass distribution and rates of transport and cross shelf transfer, may have unintended consequence. For example, if krill biomass accumulates in on-shelf areas, this may be important over time scales reflecting months (i.e. carry-over effects, Trathan *et al*., 2021). If the on-shelf buffer of krill depletes more rapidly (with fishing) than it accumulates, this could compromise natural carry-over effects between months that are important to predators. Similarly, major ecological perturbations associated with physical properties (e.g. iceberg melt, Braakmann-Folgmann *et al*., 2022) could also affect the off-shelf reservoir of krill and subsequent on-shelf transfer. Such issues means CCAMLR must continue to develop improved ecosystem understanding as part of its precautionary management approach.

The ecosystem approach to fisheries management for coastal pelagic forage fish fisheries is under development globally, but remains challenged by the need for better understanding about how spatio-temporal variability in the distribution and abundance of prey species affects various predator population processes, including productivity. Here we have focused upon the Antarctic marine ecosystem, but similar issues of prey aggregation state (e.g. patchiness) and ecosystem complexity (e.g. differing habitats) could also affect other forage fish fisheries, such as those for sardine and anchovy (e.g. Sydeman *et al*., 2021).

Conflict of interest

There are no conflicts of interest with the publication of this article.

Supplementary Data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Funding

Data availability

The CEMP monitoring data from Bird Island underlying this article are available from the UKRI/BAS Polar Data Centre:

Macaroni penguin arrival weights—https://doi.org/gb69.

Macaroni penguin fledging weight—https://doi.org/gb7c.

Macaroni penguin breeding success—https://doi.org/gb7k.

Gentoo penguin nesting chronology—https://doi.org/gb78.

Gentoo penguin fledging weight—https://doi.org/gb7n.

Gentoo penguin breeding success—https://doi.org/gb7v.

Antarctic fur seal special study beach summary counts—https://doi.org/gb79.

Antarctic fur seal fur seal pup weight—https://doi.org/gb72.

The WCB acoustic survey data underlying this article are available from the UKRI/BAS Polar Data Centre:

Antarctic krill integrated acoustic survey data—https://doi.org/jd4h.

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