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Original Article

Interannual variability in Antarctic krill (*Euphausia superba*) density at South Georgia, Southern Ocean: 1997–2013

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Antarctic krill (*Euphausia superba*) are a key species in Southern Ocean ecosystems, maintaining very large numbers of predators, and fluctuations in their abundance can affect the overall structure and functioning of the ecosystems. The interannual variability in the abundance and biomass of krill was examined using a 17-year time-series of acoustic observations undertaken in the Western Core Box (WCB) survey area to the northwest of South Georgia, Southern Ocean. Krill targets were identified in acoustic data using a multifrequency identification window and converted to krill density using the Stochastic Distorted-Wave Born Approximation target strength model. Krill density ranged over several orders of magnitude (0–10 000 g m^{-2}) and its distribution was highly skewed with many zero observations. Within each survey, the mean krill density was significantly correlated with the top 7% of the maximum krill densities observed. Hence, only the densest krill swarms detected in any one year drove the mean krill density estimates for the WCB in that year. WCB krill density (μ, mean density for the area) showed several years (1997/1998, 2001–2003, 2005–2007) of high values ($\mu > 30$ g m^{-2}) interspersed with years (1999/2000, 2004, 2009/2010) of low density ($\mu < 30$ g m^{-2}). This pattern showed three different periods, with fluctuations every 4–5 years. Cross correlation analyses of variability in krill density with current and lagged indices of ocean (sea surface temperature, SST and *El Niño*/Southern Oscillation) and atmospheric variability (Southern Annular Mode) found the highest correlation between krill density and winter SST (August SST) from the preceding year. A quadratic regression ($r^2 = 0.42$, $p < 0.05$) provides a potentially valuable index for forecasting change in this ecosystem.

Keywords: acoustic survey, Antarctic krill, ecosystem management, target identification, target strength, time-series.

Introduction

Antarctic krill (*Euphausia superba*), hereafter krill, is a key species in the Antarctic marine foodweb as a result of its large biomass (Atkinson *et al.*, 2009) and important role in the Antarctic foodweb as prey to fish, squid, penguins, other seabirds, and marine mammals including seals and whales (Croxall *et al.*, 1999). Krill is also thought to be an important influence on ocean biogeochemistry (Tovar-Sanchez *et al.*, 2007) and thus oceanic carbon cycles. Since the late 1970s, krill has been the target of an international fishery (Nicol *et al.*, 2011), managed within an ecosystem-based framework that is regulated in accordance with rules agreed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR).

Krill have a circumpolar habitat, constrained to the north by the Antarctic Polar Front (APF) and to the south by the continent (Atkinson *et al.*, 2009). This habitat is undergoing rapid environmental change such as loss of sea ice (Stammerjohn *et al.*, 2008), increasing sea temperatures (Turner *et al.*, 2005; Whitehouse *et al.*, 2008) and ocean acidification (Orr *et al.*, 2005); with recent changes and impacts summarized by Flores *et al.* (2012). At the same time, there have been recent developments in harvesting technology and products derived from krill that have further focused interest in exploiting this resource (Nicol *et al.*, 2011). This combined pressure has raised concern regarding the future sustainability of krill harvesting under the cumulative pressure of climate change and increasing fisheries (Schiermeier, 2010; Flores *et al.*, 2012).

The most recent estimate of post-larval krill biomass for the whole Southern Ocean was 379 MT (Atkinson *et al.*, 2009), with >50% of this biomass contained within the Atlantic sector. Atkinson *et al.* (2004) showed a decrease in krill abundance in the Southwest Atlantic sector of the Southern Ocean coincident with a decline in winter sea ice coverage. Trivelpiece *et al.* (2011) have more recently identified declines in krill-eating penguin populations on the Antarctic Peninsula, linking these with declines in krill abundance. Such changes highlight the importance of quantifying interannual variability in krill density within the Atlantic sector of the Southern Ocean (Reiss *et al.*, 2008; Reid *et al.*, 2010), particularly as these pressures are expected to increase over the coming decades.

Potentially, the most suitable places to monitor biological responses to climate change are where many species are highly thermally sensitive, usually at the margins of their biogeographic ranges (Hogg *et al.*, 2011). For krill, such a location exists at South Georgia where sea temperatures are towards the upper limit of the thermal range of krill (Flores *et al.*, 2012). This archipelago is a large, isolated land and continental shelf area in the Atlantic sector of the Southern Ocean (Figure 1). The island is located ~1800 km to the east of the South American continental shelf and around 300 km south of the Polar Front (PF). The region is dominated by the Antarctic Circumpolar Current (ACC), which transports nutrients and organisms, particularly krill, from the Antarctic Peninsula across the Scotia Sea to the South Georgia region (Murphy *et al.*, 2007a). The pelagic ecosystem at South Georgia is extremely productive and intense phytoplankton blooms support a rich foodweb (Atkinson *et al.*, 2001) that includes zooplankton, large densities of krill, and vertebrate predators (such as penguins, seals, and whales).

The population of krill at South Georgia are near or at their northerly limit and do not appear to comprise a self-sustaining population (Marr, 1962; Mackintosh, 1972), but instead probably arrive at the island in the prevailing flow of the ACC (Hofmann *et al.*, 1998; Murphy *et al.*, 1998; Thorpe *et al.*, 2007). Variability in krill abundance at South Georgia has been related to differences in the amount of krill that becomes entrained within the ACC flow at sites upstream of South Georgia (Murphy *et al.*, 1998; Brierley *et al.*, 1999), or to levels of spatial and temporal variability in the transport mechanism itself (Thorpe *et al.*, 2002; Trathan *et al.*, 2003; Reid *et al.*, 2010).

Interannual fluctuations in krill abundance at South Georgia were first noted during the whaling period in the early part of the twentieth century (Kemp and Bennet, 1932). There appear 2–3 years in each decade where the abundance of krill at South Georgia is low, the predator foraging and breeding performance is reduced, and the krill fishery reports reduced catch levels and rates (Fedoulov *et al.*, 1996; Brierley *et al.*, 1997; Murphy *et al.*, 1998). This variability is likely to result from local atmospheric and cryospheric change, the influence of upstream waters, and the role of coupled modes of climate variability such as the *El Niño*/Southern Oscillation (ENSO) and the Southern Annular mode (SAM; Trathan and Murphy, 2002; Meredith *et al.*, 2005; Murphy

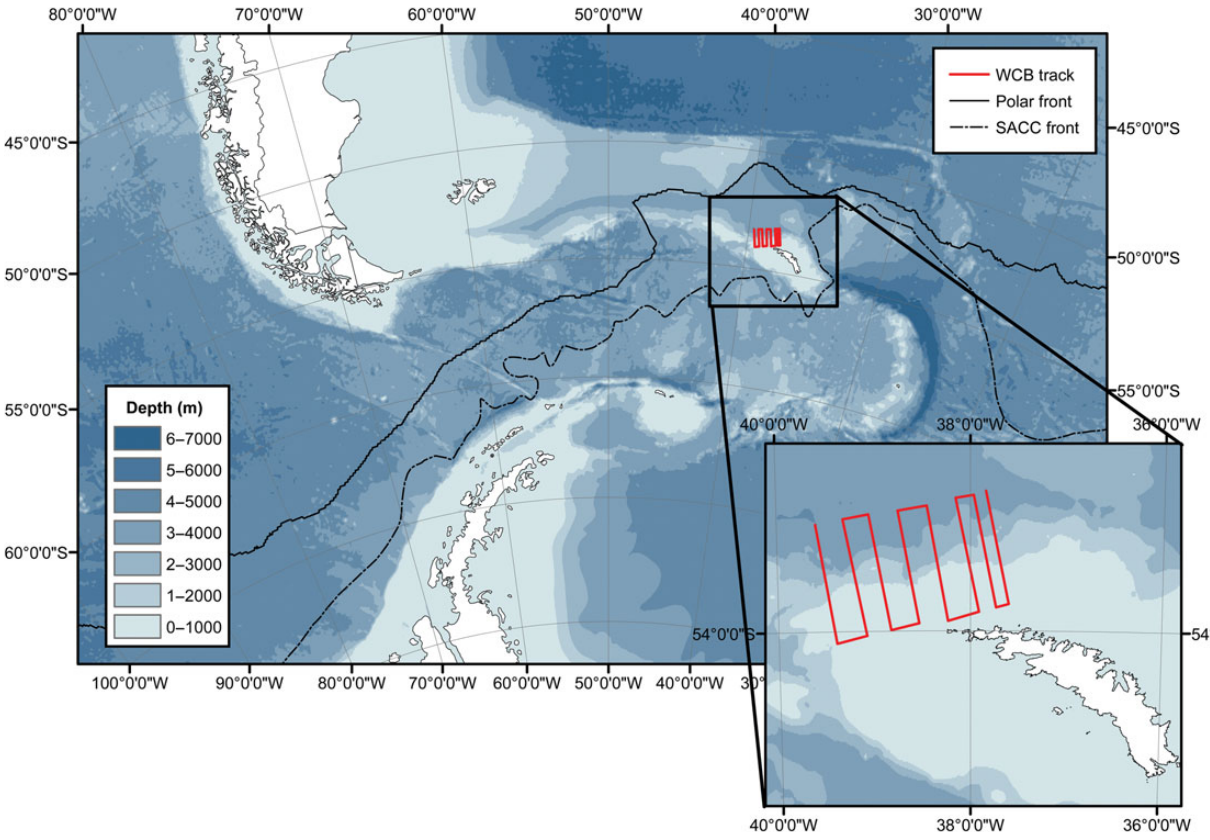

Figure 1. Current WCB acoustic transects. WCB as configured between 1996 and 2000 given in Brierley *et al.* (1999).

et al., 2007b; Whitehouse et al., 2008). The near surface waters of South Georgia are some of the fastest warming on the planet with a mean increase of ~0.9°C in January and ~2.3°C in August determined for the top 100 m of the water column over the last 80 years (Whitehouse et al., 2008). Such changes are almost certainly affecting krill populations.

Abundance and distribution data for ecological studies and for fisheries stock assessment of krill are largely undertaken using active acoustic techniques (Hewitt et al., 2004). The advantages of this approach are the rapid surveying of large areas at high vertical and horizontal resolution. However, acoustic methods provide an assessment of all acoustic backscatter in the echosounder beam. To generate a realistic estimate of krill density, the total acoustic energy has to be correctly partitioned into what is krill and consequently what is not using target identification techniques and then converted to krill density using the appropriate krill target strength estimates.

The relationship between krill target strength and krill density has been investigated since the 1980s with linear regressions (between target strength and krill length) being used to calculate pre-exploitation krill biomass (B_0) from the first international krill survey FIBEX (First International BIOMASS Experiment) in 1981 (Trathan et al., 1992). The most frequently used, and best supported of these regressions being that reported by Greene et al. (1991) and used in the CCAMLR 2000 survey (Hewitt et al., 2004). Subsequently, Demer and Conti (2003) refined an empirically validated physics-based model called the Stochastic Distorted-Wave Born Approximation (SDWBA), expanding on work by McGehee et al. (1998). A simplified version of the SDWBA, with fixed parameters for orientation and reflection coefficients, was adopted by CCAMLR for its estimation of B_0 in 2007 and revised in 2010 (CCAMLR, 2007, 2010).

Identification of acoustic targets as krill has also undergone significant development over the last three decades. Initially, visual examination of echograms by experts combined with targeted net samples was used to attribute scattering to different taxonomic groups. With the advent of the routine use of multifrequency echosounders, differences in scattering responses at different frequencies were implemented for identification of targets (Madureira et al., 1993; Korneliussen and Ona, 2003). The dB difference (ΔS_v) technique utilizes the difference in acoustic backscatter (dB re 1 m^{-1}) received from a target between two or more frequencies (e.g. $S_{v120-38}$). Net-validated krill targets have been shown to have a ΔS_v of between 2 and 12 dB using 120 and 38 kHz (Madureira et al., 1993: Watkins and Brierley, 2002). A modification of this objective two-frequency technique was then used as the standard method for attributing backscatter to krill in the CCAMLR 2000 survey (Hewitt et al., 2004). In 2007, CCAMLR adopted a theoretically based enhanced krill-identification algorithm. This used the range of krill lengths, found in the survey area, to tune three frequency (38, 120, 200 kHz) ΔS_v ranges to identify krill targets, which are in turn calculated using the SDWBA model (CCAMLR, 2007, 2010).

The British Antarctic Survey (BAS) has been estimating krill density to the northwest of South Georgia using acoustic surveys since 1981. Initially, these surveys were undertaken on an *ad hoc* basis (Brierley et al., 1999), but in 1997, they were formalized into a set of annually repeated transect lines in an area known as the Western Core Box (WCB, Figure 1; Brierley et al., 1997). Reanalysis of time-series data with increasingly refined techniques is worthwhile and yet time-consuming. Here we investigate the, now, longer time-series of krill density estimates using the latest CCAMLR-agreed method for krill biomass determination (CCAMLR, 2010). We also examine relationships between krill density at South Georgia and indices of climate variability, and compare with past interpretations of variability and change.

Methods

Survey design and location

The present WCB survey area is a 133 by 80 km box located to the northwest of South Georgia (Figure 1), spanning the continental shelf break. The survey is made up of 8 acoustic transects (undertaken at a nominal speed of 10 knots), 25 XBT stations, 6 CTD stations, and Rectangular Midwater Trawl (RMT8) net sampling. It was designed as a stratified random survey, to calculate statistically valid variance estimates for the mean abundance values using established sampling theory (Jolly and Hampton, 1990; Brierley et al., 1997). Acoustic transects are run alternatively in on-shelf and off-shelf directions, with successive transects running west to east in the general alongshelf direction believed to be against the prevailing current (Trathan et al., 1997).

Although acoustically determined estimates of krill density around South Georgia are available from 1981 (Brierley et al., 1999), the first systematic grid survey of this area was undertaken in January 1994 (Brierley et al., 1997) and has been repeated each austral summer from January 1996. However, the first survey has not been included in our analyses because bad weather resulted in modification of four of the survey lines (Table 1). From 1996 to 2000, the survey area covered 100 by 80 km and consisted of ten acoustic transect lines. In the 2000/2001 season, the survey box was slightly enlarged to 133 km wide and eight transects. The mid-season acoustic survey (December–February) has been undertaken every year except 2008, where logistical constraints prevented the cruise from being undertaken.

Sampling of krill

When possible, an RMT8 (Roe and Shale, 1979) with a 4.5 mm mesh size and mouth opening of 8 m^2 was used to sample krill swarms within the WCB area. The total swept volume for each net catch was calculated and up to 100 krill were measured for total length

Table 1. Survey details.

	Dates of survey			
Cruise no.	Year	Day/month	Survey season	Legs done
JR17	1997	29 December–2 January	1997	10
JR28	1998	30 January–2 February	1998	10
JR38	1999	2–5 January	1999	10
JR45	2000	4–7 January	2000	8
JR57	2001	2–5 January	2001	8
JR70[a]	2002	24–27 January	2002	8
JR82	2003	13–16 February	2003	7
JR96	2004	8–16 January	2004	8
JR116	2005	6–10 January	2005	8
JR140	2006	29 December–1 January	2006	8
JR162	2006	25–28 December	2007	6
JR188	2009	31 December–3 January	2009	8
JR228	2009	20–23 December	2010	8
JR245	2010	26–30 December	2011	8
JR260	2012	2–5 January	2012	8
JR280	2012	2–5 December	2013	8

[a] No 200 kHz data for that cruise.

(TL), from the anterior edge of the eye to the tip of the telson and rounded down (Morris *et al.*, 1988).

Sea surface temperature, SAM index, and ENSO index

Sea surface temperature (SST, °C) data were obtained from the NOAA operational global analysis (Reynolds *et al.*, 2002; Smith *et al.*, 2007; available at http://rda.ucar.edu/datasets/ds277.0/data/oiv2/mnly/data). The monthly data at 1 × 1° resolution for the period January 1996–December 2013 were used. A single grid cell within the WCB region (53°30′S and 38°30′W) was selected to represent the region (see Trathan and Murphy, 2002). The *El Niño* 3.4 region temperature anomaly was used as a measure of ENSO strength in the tropical Pacific and was obtained from the National Center for Environmental prediction, NOAA/National Weather Service http://www.cpc.ncep.noaa.gov/data/indices/sstoi.indices. The SAM was used as a measure of atmospheric variability; data were obtained from http://www.nerc.bas.ac.uk/icd/gjma/sam.html. Monthly values were used (Marshall, 2003).

Acoustic data

Acoustic data were collected solely during daylight hours (at least 1 h after sunrise, and 1 h before sunset) to avoid the possibility of bias due to diurnal migration (Demer and Hewitt, 1995) or change in target orientation (Everson, 1982). Volume backscattering strength data (S_v; dB re 1 m^{-1}) were collected using a Simrad EK500 (38, 120, 200 kHz) from 1997 to 2002 and a Simrad EK60 (38, 120, 200 kHz) from 2003 to 2013. In this paper, austral summers correspond to split years and are referred to by the second year; for example, the Austral summer period of 1999/2000 is identified as year 2000. Standard-target echosounder calibrations (Foote *et al.*, 1987) were conducted annually during the mid-season survey on both instruments. Power settings were consistent within any one year, but varied between years reflecting then current recommendations (e.g. reducing power in higher frequency transducers to reduce non-linearity effects; Tichy *et al.*, 2003). The ping rate varied between 1.5 and 2.5 s, dependent on synchronization with other acoustic sounding instruments on the ship.

All acoustic data were processed using Myriax Echoview software (ver. 4.80): relevant values for the speed of sound and absorption coefficients were input (derived from the station CTD data taken during the survey); surface noise and false bottom echoes were identified and excluded from further analysis; likewise any interference spikes (using a 3 × 3 matrix convolution algorithm to identify and remove cells within single pings >30 dB different from surrounding cells); and time varied gain amplified background noise was subtracted (Watkins and Brierley, 1996). The ping by ping data were resampled to 5 m (vertical) by 500 m (horizontal) bins and imported into Matlab™ where all further analysis was undertaken.

Target identification and krill density estimation

The S_v at 120 kHz ($S_{v120\text{kHz}}$) were apportioned to krill or non-krill using a three-frequency variable window ΔS_v identification technique, and converted to wet-weight density (termed krill density) using the validated physics-based SDWBA *TS* model (CCAMLR, 2010). Krill swarm density was estimated by applying a −70 dB threshold value to the S_v at 120 kHz before the krill identification to quantify density from krill contained solely within krill aggregations. The −70 dB threshold was defined by Lawson *et al.* (2008) to reflect the minimum volume backscattering strength (krill density of 1.7 ind. m^{-3}) of an aggregation, based on the density of animals that corresponds to the maximum sensing distance over which a given krill can maintain some association with its nearest neighbour. Finally, the former accepted method for target identification (two-frequency fixed window $2 < S_{v120-38} < 12$) and *TS* model (Greene *et al.*, 1991) have been used to calculate krill density (Greene method) for comparison with previously published data.

The three-frequency method uses 120−38 kHz ($S_{v120-38}$) and 200−120 kHz ($S_{v200-120}$) variable windows where minimum and maximum ΔS_v values for the different annual size ranges of krill (identified from the net samples) were calculated using the SDWBA model, based on the distribution of 95% of the krill length frequencies estimated from a cumulative distribution function (with tails of 2.5% at each end of the distribution).

The $S_{v120\text{kHz}}$ attributable to krill were integrated from 10 m below the surface to either a maximum of 250 or 2 m above the seabed, resulting in Nautical Area Scattering Coefficient (NASC; m^2 nautical mile^{-2}) values per 500 m along-track sampling unit. NASC were converted to krill density (g m^{-2}) and krill abundance (num. m^{-2}) as follows.

The krill length frequency probability density functions (pdfs) were used to derive weighted mean backscattering cross-sectional areas (σ) using one of the two different *TS* models: the empirically derived log-linear model (Greene model; Greene *et al.*, 1991), or the simplified version of the SDWBA (Conti and Demer, 2006), implemented with fixed values for krill speed of sound and density contrasts and a fixed krill orientation of −20° (mean) and 28° (standard deviation; hereafter $N[-20, 28]$) as adopted by CCAMLR (CCAMLR, 2010):

$$\sigma = 4\pi 10^{\mathrm{TS}/10} \quad (\mathrm{m}^2\ \mathrm{krill}^{-1}). \tag{1}$$

Likewise, they were also used to calculate weighted-mean wet masses per animal (W; g krill^{-1}) using the mass-to-length relationship calculated for the Scotia Sea in 2000 (Hewitt *et al.*, 2004):

$$W = 2.236 \times 10^{-6} \times \mathrm{TL}^{3.314} \quad (\mathrm{g\ wet\ mass\ krill}^{-1}). \tag{2}$$

Density (b, g wet mass m^{-2}) was calculated by multiplying the 120 kHz NASC attributed to krill by a weighted mean mass W divided by a weighted σ (Reiss *et al.*, 2008):

$$b = \mathrm{NASC} \times \big(\Sigma f_i \times W(\mathrm{TL}_i)/\Sigma f_i \times \sigma(\mathrm{TL}_i)/ \\ 1 \times 10^{-3}/1852^2\big) \quad (\mathrm{g\ wet\ mass\ m}^{-2}) \tag{3}$$

Survey krill density means (μ) and variances were derived according to Jolly and Hampton (1990). Finally, to examine trends in the 15-year series, a krill anomaly index (KIX) was calculated:

$$\mathrm{KIX} = x_j - \frac{\sum_{i=1}^{n} x_i}{n},$$

where x_i is the mean WCB krill density for year j in n years of the survey.

Results

Krill length

Net sampled krill from the mid-season period are only available from 1997 to 2006 and 2010 to 2013; samples from 2007 and 2009 were collected at other times within the same season (October 2006 and February 2009). The largest krill found in the WCB were

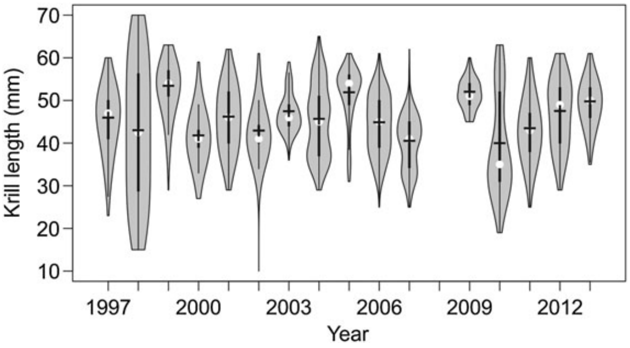

Figure 2. Krill length frequencies measured from RMT8 net samples for each year. The median values are white circles, and the mean values are black horizontal cross. The inter-quartile range is identified by the black bar.

Table 2. Identification ranges for different ΔS_v windows and acoustic estimates of krill density using the three-frequency identification window and SDWBA *TS* model, and fixed 2–12 dB window for $S_{v120-38}$ and the Greene *et al.* (1991) *TS* model.

	Identification window (dB)				SDWBA 3 freq		Greene 2 freq	
	$S_{v120-38}$		$S_{v200-120}$					
Survey season	Min	Max	Min	Max	Density ($g\ m^{-2}$)	*CV*	Density ($g\ m^{-2}$)	*CV*
1997	0.37	14.3	−5.3	3.9	31.66	26.05	19.69	20.05
1998	0.37	14.3	−5.3	3.9	38.85	27.95	21.25	22.09
1999	0.37	12.0	−5.3	1.4	9.69	19.79	14.86	20.61
2000	0.37	12.0	−5.3	1.4	2.74	35.46	10.39	29.05
2001	0.37	12.0	−5.3	1.4	36.74	27.48	33.36	31.78
2002	0.37	12.0	−5.3	1.4	137.03	30.06	64.70	31.27
2003	0.37	14.3	−5.3	3.9	84.59	57.90	36.56	56.12
2004	0.37	12.0	−5.3	1.4	26.12	9.75	10.75	15.45
2005	0.37	12.0	−5.3	1.4	89.42	60.58	30.75	48.08
2006	0.37	12.0	−5.3	1.4	119.11	44.91	49.98	43.49
2007	0.37	14.3	−5.3	3.9	61.12	26.20	26.36	28.76
2009	0.37	8.7	−5.3	1.4	28.83	11.77	14.68	6.78
2010	0.37	14.3	−5.3	3.9	15.05	26.02	4.10	22.64
2011	0.37	12.0	−5.3	1.4	59.00	46.58	28.52	45.54
2012	0.37	12.0	−5.3	1.4	90.11	46.16	31.96	42.86
2013	0.37	12.0	−5.3	1.4	61.76	39.09	22.80	37.40

The *CV* was calculated following Jolly and Hampton (1990).

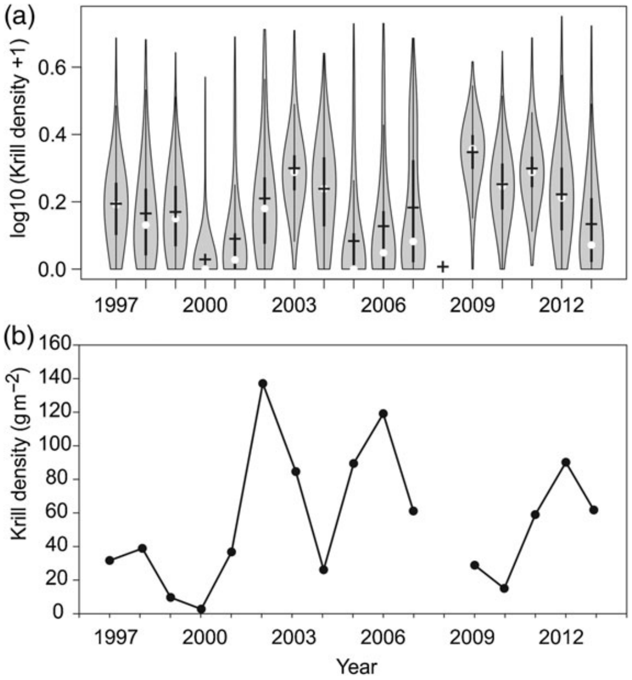

Figure 3. (a) Frequency distribution of log10(krill density+1) for each annual mid-season survey. The median (white circles), mean (black crosses), and inter-quartile range (black bar) is shown. (b) The mean WCB krill density from 1997 to 2013, calculated following Jolly and Hampton (1990).

70 mm TL observed in 1998, while the smallest krill measured was 10 mm TL observed in 2002 (Figure 2). The average mean length of krill from all nets sampled varied between years and ranged from 39 mm (2010) to 52 mm (1999), with no obvious trend in either the mean or median krill lengths over time. The individual krill lengths measured within any single year typically spanned a range of 32 mm, with only 2 years having particularly different ranges. In 1998, the krill lengths sampled ranged over 55 mm, and in 2009, the krill lengths sampled ranged 15 mm, both these years reflect krill sampled from just a single net, due to a lack of krill targets in the survey area in those years.

The largest mean krill lengths were observed in 1999, 2005, 2009, and 2013, constrained within a relatively small range of krill lengths. In each year following (i.e. 2000, 2006, and 2010), the mean krill length dropped by 7–12 mm and the range of krill length measures was wider. The large drops in mean length could indicate years of high recruitment of smaller krill (from the Scotia Sea) into the WCB region, while larger krill are perhaps more indicative of the growing local population.

Krill density

Sixteen mid-season annual acoustic surveys of krill were undertaken off the northwestern coast of South Georgia (Table 2) during a three-month window (December to February) over the period of 17 years 1997–2013. Krill density ranged from 0 (all surveys except 2011 where the minimum value was 0.06) to a maximum of 43 100 $g\ m^{-2}$ in 2012 (Figure 3a). The median values of krill density ranged from 0 to 17.9 $g\ m^{-2}$ and showed two periods of particularly low krill density (2000 and 2005) interspersed with periods where density was much higher (1997, 2003, and the highest in 2009). However, the observed interannual pattern of the median values of krill density did not match the variability observed in the maximum krill density values (Figure 3a). Where 5 years (1999, 2000, 2004, 2009, and 2010) had particularly low maximum krill density ($<1000\ g\ m^{-2}$) and 2002, 2003, 2005, 2006, and 2012 had particularly elevated maximum krill density ($>10\,000\ g\ m^{-2}$).

The mean WCB krill density estimates [calculated following Jolly and Hampton (1990)] for each year present a very different picture of interannual variability to the median, with a pattern more similar to the maximum krill density (Figure 3b). In fact, the mean WCB krill density was significantly correlated (Spearman's rank correlation $p < 0.05$, $n = 16$) with the krill density within the 93rd to 99th percentile of densities sampled, implying that 7% of the sampled distribution of highest krill densities determined the mean WCB krill density estimate.

Over the 16 years sampled, the mean WCB krill density ranged from 3 g m^{-2} in 2000 to 137 g m^{-2} in 2002 (Figure 3b, Table 2). There were three periods of low WCB krill density ($<$30 g m^{-2}): 1999/2000, 2004, and 2009/2010, and 1999, 2004, and 2009 also had lower *CV*s indicating either a small number of krill sparsely distributed or a small number of krill regularly distributed indicating low spatial variability between transect means. Separating these low krill density values were high mean WCB krill densities ($>$80 g m^{-2}), in particular 2002/2003, 2005/2006, and 2012. In each case, except in 2002, the high densities had high associated *CV*s, indicating large differences between the transect means which implies both high spatial variability and/or high krill densities (Figure 3a and b).

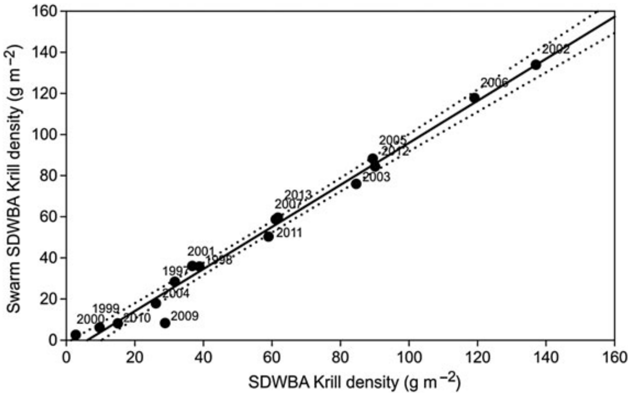

Figure 4. The relationship between the mean swarm krill density and mean krill density (distinguished using a −70 dB threshold on the 120 kHz data) estimated using the SDWBA *TS* model. A regression line (Swarm krill density = 1.02 SDWBA krill density −6.39, $r^2 = 0.99$) was fitted to the data (solid line) and is shown with associated 95% confidence intervals (dotted line).

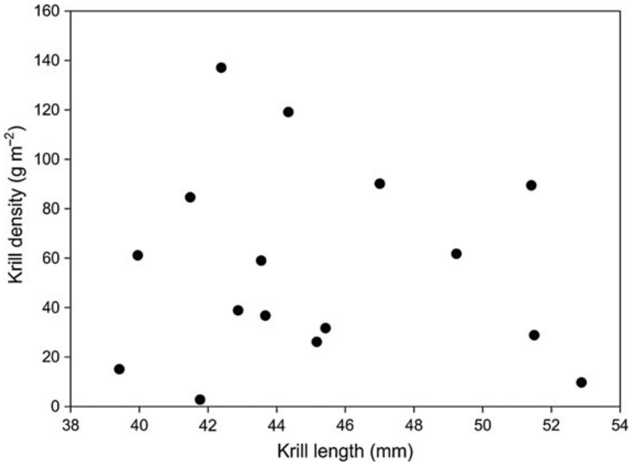

Figure 5. The relationship between the mean WCB krill density (g m^{-2}) and mean krill length (mm).

A comparison of WCB krill density and WCB krill swarm density (estimated by applying a −70 dB threshold to the 120 kHz data) showed them to be highly correlated with ∼98% of estimated mean krill density resulting from krill swarms (Figure 4). Only one outlier was evident, in 2009, where WCB krill swarm density was 8.2 g m^{-2} compared with a WCB krill density of 28.8 g m^{-2}; this suggests that ∼70% of the krill density of that year was not from swarming krill.

There was no obvious relationship between the mean WCB krill density and the mean (Figure 5) or median krill length.

Krill anomalies and environmental forcing

Many analyses have linked higher predator success indices with indicators of the physical environment variability at South Georgia. In particular, investigating links and lags between sea ice, SST, ENSO, and the SAM (Trathan and Murphy, 2002; Meredith *et al*., 2005; Trathan *et al*., 2007). In this paper, we examine the correlation (Pearson) between the mean WCB krill density and these previously examined climate indices (0–36 month lagged ENSO, 0–36 month lagged SAM, and 0–12 month lagged SST; Table 3). We observed no significant relationships between the mean krill density at South Georgia and the annual ENSO (or lagged ENSO) or the annual SAM index (or lagged SAM index) or sea ice extent (data not shown). The highest correlation ($p < 0.1$ after Bonferroni's correction) occurred between the mean krill density and the preceding August SSTs (Figure 6) with increasing temperature associated with decreasing krill density (quadratic regression, $r^2 = 0.42$, $p < 0.05$).

A krill anomaly index (KIX) was calculated to examine trends in krill density with time. Three eras were identified (Figure 7a): the first era from 1997 to 2001 was a period of less than average mean krill density associated with a period of warmer August SSTs; the second era from 2002 to 2007 appears to represent a period of greater than average krill densities and associated cooler August SSTs; finally, the last era covering 5 years (2008 to current) showed a switch from low to high densities within a shorter period and an associated change in SST. August and September SSTs within the WCB represent the coldest temperatures occurring throughout the year with the lowest variability (Figure 7b).

Table 3. Summary of Pearson's correlation probability (*p*) and factor (*f*) of SDWBA krill density and indices of SAM, ENSO, and SST for 0–12 month lagged data.

Lag (month)	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
SAM (*p*)	0.35	0.39	0.74	0.27	0.38	0.74	0.42	0.68	0.02	0.12	0.38	0.39	0.52
SAM (*f*)	−0.25	−0.23	0.09	−0.29	0.24	−0.09	−0.22	0.11	−0.58	0.41	−0.24	−0.23	−0.18
ENSO (*p*)	0.71	0.79	0.74	0.64	0.65	0.42	0.37	0.14	0.45	0.58	0.93	0.94	0.99
ENSO (*f*)	0.10	0.07	0.09	0.13	0.12	0.22	0.24	0.39	0.20	0.15	0.03	0.02	0.00
SST (*p*)	−0.68	0.88	0.36	0.03	0.02	**0.01**	0.57	0.48	0.22	0.24	0.40	0.66	0.37
SST (*f*)	0.11	−0.04	−0.25	−0.54	−0.57	**−0.64**	−0.16	−0.16	−0.33	−0.31	−0.23	−0.12	0.24

Factors significantly correlated with SDWBA krill density (at a level of $p < 0.1$, which is adjusted to $p < 0.0083$ using the sequential Bonferroni correction; Holm, 1979) are in bold.

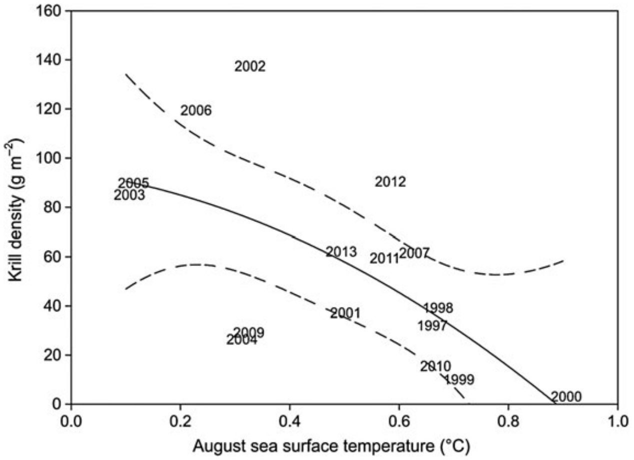

Figure 6. The relationship between the mean krill density (g m^{-2}) and the preceding August SST (°C). A quadratic regression line (Krill density = 94.38 – 30.01SST – 85.91SST^2, $r^2 = 0.42$, $p < 0.05$) was fitted to the data and is shown with associated 95% confidence intervals (dashed lines).

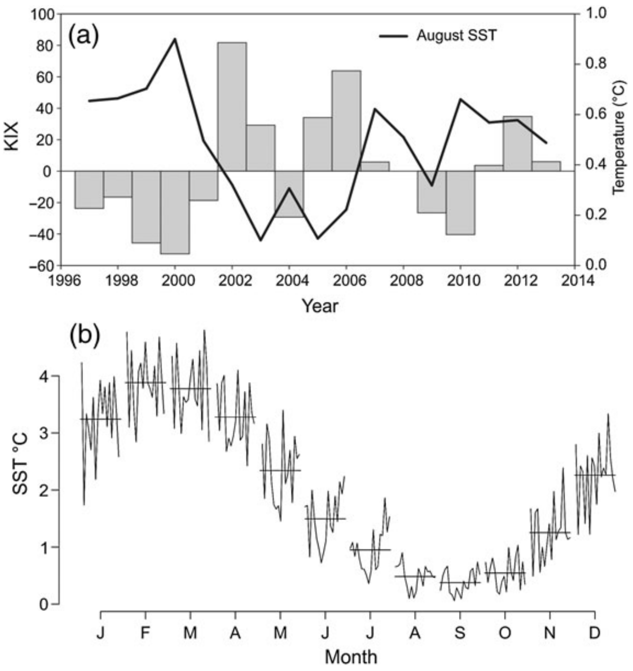

Figure 7. (a) Interannual variability in krill density anomaly index (KIX, grey bars) plotted with preceding August SST (black line). (b) Intra and interannual (1996–2013) variability in SST (from NOAA Reynolds *et al.*, 2002) for grid cell 37.5°W, 53.5°S plotted by month.

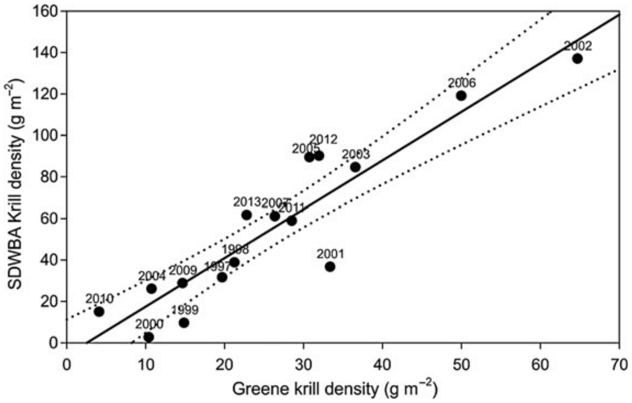

Figure 8. The relationship between the mean krill density estimated using "old" methods ($S_{v120-38\ \mathrm{dB}}$ 2–12 identification window and converted to krill density using the *TS* model in Greene *et al.*, 1991) and the mean krill density estimated using a three-frequency ($S_{v120-38}$ and $S_{v200-120}$) variable window and converted to krill density using the SDWBA *TS* model (CCAMLR, 2010). A regression line (SDWBA krill density = 2.35 Greene krill density − 5.96, $r^2 = 0.85$) was fitted to the data and is shown here with associated 95% confidence intervals (dotted lines).

Comparisons with previously reported studies that used the WCB krill acoustic data

Krill density estimated using the three-frequency ΔS_v identification technique and the SDWBA was significantly linearly correlated with krill density estimated using a 2–16 dB two-frequency identification technique and the Greene model of *TS* to biomass (Figure 8). This will allow previous estimates of krill density for the South Georgia region to be compared with these new updated values (e.g. Reid *et al.*, 2010, etc.). Krill density estimated using the three-frequency identification and SDWBA model were approximately twice the estimates using the Greene method (Table 2).

Discussion

The distribution of krill is described as patchy (Marr, 1962) and its behaviour commonly described as obligate swarming (Hamner *et al.*, 1989; Tarling *et al.*, 2009). The aggregation behaviour of krill will have a large influence on the distribution and advective fate (Zhou and Dorland, 2004), as well as affecting their susceptibility to krill-consuming higher predators (Mori and Boyd, 2004). The heterogeneous nature of krill distributions is evident in the large range of krill densities observed within the WCB surveys in this study. The densities exhibited an extremely skewed distribution, with many zero observations and abundance estimates linked to large densities constrained to small regions (relative to the surveyed area). This distribution is well recognized for krill (Murray, 1996) as well as common to many schooling fish, particularly North Atlantic herring (Petitgas, 1993). Within herring biomass surveys, the degree of coverage of these rare but large aggregations is considered the dominant contributor to the total uncertainty in ocean survey biomass estimates (Løland *et al.*, 2007). This suggests that, like herring biomass surveys, an adaptive design survey where the sampling intensity depends on the densities observed during the survey (Thompson and Seber, 1996; Harbitz *et al.*, 2009) will provide more confident estimates of krill biomass and distribution than the frequently used randomized parallel acoustic transects. However, in the context of an ecosystem time-series investigating change, using a formalized survey design permits year-to-year comparison in place of a formal stock assessment of a single species.

A comparison of total krill and krill swarm densities indicated that in all but one year, 98% of the mean krill density resulted from krill identified from swarms. This is consistent with the opinion that swarms are the basic unit of organization of krill (Watkins *et al.*, 1986). Cox *et al.* (2011) observed a factor of sevenfold difference in the number of swarms observed during the period of 1997–1999 in the WCB region, with the lowest number of swarms

(107) observed in 1999. Within this study, the maximum krill densities were similar in 1997 and 1998 and lower in 1999 (Figure 3c), and during those 3 years, the 1999 WCB krill density estimate was the lowest with a small *CV*. This suggests that years of low WCB krill density result from both fewer and less dense swarms. This is reinforced by the significant correlation between the mean WCB krill density and the top 7% of the maximum krill density values. Therefore, both krill-dependent predators and fisheries must see large differences in the availability of krill between years at South Georgia. To accommodate this, higher predators may have to forage for longer periods (Fraser and Hofmann, 2003), or prey switch (Croxall *et al.*, 1999). An alternative is to employ different life history strategies to buffer against prey fluctuations, such as high annual survivorship, protracted longevity, delayed sexual maturity, and a relatively low reproductive rate (Hunt *et al.*, 1996).

It is not clear in 2009, the 1 year where krill swarm densities were only 28% of the total krill estimate, whether krill were not swarming or organisms that do not form swarms were misidentified as krill. It is notable that 2009 also had other extreme observations of high surface and air temperatures, low foraging success in many krill-dependent predators, and low performance in the fishery for icefish (Hill *et al.*, 2009). This poor performance in higher predators and fishery is perhaps indicative of a lack of krill in surface waters and, therefore, suggests a misidentification of non-swarming organisms as krill. Net samples from the region in April 2009 caught large numbers of *Euphausia triacantha* and *Themisto gaudichaudii*, which are common in northern Scotia Sea waters, and few *E. superba* (Ward *et al.*, 2012). These organisms are slightly smaller than krill, but can form layers with dB differences similar to krill (Madureira *et al.*, 1993).

This paper presents a re-analysis of acoustically derived krill density from the WCB using the most up-to-date CCAMLR methods for target identification and target strength to krill density conversion (CCAMLR, 2010). In addition, estimates were also calculated using the dual-frequency (120–38) fixed identification window (2–12) and Greene model (Table 2) for reference and comparison with previously published densities for this region (Brierley *et al.*, 1999; Reid *et al.*, 2010). Discussions in this paper centre on the new estimates.

Krill density estimates for the WCB region ranged from 2.7 to 136.7 g m^{-2} and span net-derived krill densities for regions of rare occurrence (3.3 g m^{-2}) to exceeding estimates from areas with a regular occurrence of dense swarms (60.1 g m^{-2}), estimated from Russian krill surveys and fishing trawls (Voronina, 1988). They are of a similar order of magnitude to densities of 33.8 and between 32–64 g m^{-2} given for the South Georgia area, calculated from the reanalysis of the B0 CCAMLR 2000 acoustic survey (Fielding *et al.*, 2011) and historical net numerical densities (Atkinson *et al.*, 2004), respectively. The WCB krill density estimates show several years of moderate to high (>30 g m^{-2}) krill density interspersed with 1 or 2 years of low density (<30 g m^{-2}): 1999/2000, 2004, and 2009/2010. This pattern suggests major fluctuations occurred every 4/5 years, supporting previous indications of periodicity from a much shorter time-series (Brierley *et al.*, 1999).

We observed no significant trend, such as a decline, over the 16 years of krill density estimates, contrary to that reported by Atkinson *et al.* (2004) for the South Atlantic sector. However, the 4/5-year periodicity observed in these data is consistent with that presented for the last 6 years (1998–2004, Figure 3B in Atkinson *et al.*, 2004) by Atkinson *et al.* Assessments of krill density from net samples around the South Shetland Islands similarly do not show a decline in krill abundance (Trivelpiece *et al.*, 2011), although they did observe a decline in the recruitment strength. This suggests that krill variability observed at South Georgia could be representative of the wider South Atlantic krill stock. Further investigation is needed to standardize methodology and compare long-term krill density observations in the Southern Ocean.

Variability in krill density around South Georgia is hypothesized to result from changing amounts of krill dispersed across the Scotia Sea from spawning sites around the Southern Scotia Arc and Antarctic Peninsula (Murphy *et al.*, 2007a, b). Changes in the magnitude of this dispersal have been linked to recruitment fluctuations at the spawning sites (Siegel and Loeb, 1995) and variation in ocean circulation and sea ice extent (Loeb *et al.*, 1997; Siegel *et al.*, 1998). Cold temperatures around South Georgia have been linked with high krill densities from fishery data (Fedoulov *et al.*, 1996). Here, we show a statistically significant relationship between winter SST in the WCB region and krill density, where increasing August water temperatures are associated with decreasing krill density. This relationship with winter, rather than summer, sea temperatures indicates that highest krill densities at South Georgia are more associated with hydrography and therefore recruitment into the population, rather than local summer temperatures or productivity. This is consistent with the current understanding of the controls on the local krill population at South Georgia of allochthonous recruitment into a local adult population (Murphy *et al.*, 2007a; Reid *et al.*, 2010).

SSTs at South Georgia are shown to be positively correlated with SSTs across the Scotia Sea to the Antarctic Peninsula, one of the key source regions for krill at South Georgia (Murphy *et al.*, 2007a), with between a 3- and 12-month lag (Figure 9 in Meredith *et al.*, 2008). Therefore, high krill densities in austral summer at South Georgia are linked to cold SSTs across the Scotia Sea within the ACC in the preceding austral summer. Cold SSTs south of the APF are linked to negative anomalies in SAM in the Atlantic sector (Meredith *et al.*, 2008), which are associated with the advection of sea ice further north and a resulting increase in sea ice coverage. Thus, high krill densities at South Georgia are linked with favourable (ice) krill nursery grounds from the preceding year. This association between nursery grounds, transport through a variable ACC [and therefore location of the Subantarctic Circumpolar Current Front (SACCF)], and the link to variation in atmospheric and oceanic circulation has been speculated previously (Whitehouse *et al.*, 1996; Trathan and Murphy, 2002; Murphy *et al.*, 2007a). It is these complex linkages from recruitment success, to delivery to South Georgia, in addition to high predation pressure that likely drive the unexplained variability between krill density and SST.

Variations in krill density at South Georgia have been associated with variation in ice cover further south, the position of the SACCF relative to the Island and therefore linked to variation in atmospheric and oceanic circulation processes (Fedoulov *et al.*, 1996; Trathan and Murphy, 2002; Murphy *et al.*, 2007a; Meredith *et al.*, 2008). The location of the SACCF around South Georgia is variable, and a more easterly location of the SACCF has been associated with warmer waters closer to South Georgia (Trathan *et al.*, 2000; Thorpe *et al.*, 2002). The potential role of the SACCF in dispersing and transporting krill as it crosses the central Scotia Sea and wraps around the east and north coast of South Georgia before retroflecting north has been highlighted in modelling studies (Hofmann *et al.*, 1998; Murphy *et al.*, 2007a). Changes in its position relative to the Island may affect the pathways of transport of krill into the region and processes by which krill become entrained onto the shelf (Trathan *et al.*, 2003; Young *et al.*, 2011). A more detailed understanding of the processes generating local temperature fluctuations and the local role of the SACCF in the ecosystem are required to the temporal variability in delivery of krill to South Georgia.

Understanding the oceanographic, krill and predator interactions that generate fluctuations in the ecosystem has been a long-term goal for research around South Georgia (Forcada *et al.*, 2005; Reid *et al.*, 2005; Murphy *et al.*, 2007a, b). Long-term trends in krill–predator success (breeding success of fur seals and gentoo penguins) indicate predator failures coinciding with warm austral summer SST years (Forcada *et al.*, 2005). Predator failure, identified by low fur seal pup production, was observed in 1998, 2000 (Forcada *et al.*, 2005), and 2009 (BAS, unpublished data). These coincide with years of relatively (1998; 2009) and extremely (2000) low krill density. In only 1 year (2004) is there a mismatch between krill densities (low) and predator performance (high). However, pup survival data (BAS, unpublished; Staniland, pers. comm.) shows a lower survival rate, indicative of poor food availability, during this year compared with 2003 and 2005. Seasonal surveys in 2004 observed high densities of krill in the WCB region, but only later in the year in April (Reid *et al.*, 2010). This mismatch in 2004 may have been caused by a short period of low krill density being anomalously recorded in the January survey (Brierley *et al.*, 2006), the complex oceanographic effects of a very large iceberg on the South Georgia shelf in January 2004 blocking advection, or the inherent complexity of trying to link krill density with predator success indicators that are controlled not just by density, but prey distribution, prey switching, and previous annual success (Reid *et al.*, 2005).

Understanding the links between climate-related changes in oceanographic conditions and the dynamics of pelagic species of zooplankton and fish and the consequent impacts in oceanic ecosystems is crucial for predicting the impacts of future climate variability and change. There is an increasing body of literature that discusses interannual variability in marine zooplankton in relation to climate (Perry *et al.*, 2004). Many of these have focused on the long time records contained with the CPR surveys and linked to “standard” climate indices such as the North Atlantic Oscillation (Planque and Reid, 1998), northern hemisphere temperature (Beaugrand *et al.*, 2002), and Pacific Decadal Oscillation (McGowan *et al.*, 2003). Less focus has been made on Southern Ocean populations, often related to the logistical complexity and cost of maintaining time-series in the Antarctic.

Long-term observations provide an important basis for developing the required understanding and generating mechanistic models of the processes that underpin the links in the ecosystem. Around South Georgia, the last decade has seen significant increases in our understanding of the complexity of the mechanisms involved in generating fluctuations in the local ecosystem (see reviews by Murphy *et al.*, 2007a, b). This study adds further support to the view that the fluctuations are linked to regional changes in krill recruitment, which in turn are associated with variation in oceanographic conditions. However, the study has also shown that the development of the time-series of detailed observational data of sufficient duration allow valuable indices to be developed, which have potentially high utility for monitoring ecosystems and for management. Around South Georgia, the relationship between changes in krill density and winter SST provides a useful focus for both prediction and further testing of understanding of the processes generating fluctuations in this ecosystem. This relationship may also provide valuable information for predicting higher predator success at South Georgia as well as fishery success for both the krill fishery and krill-dependant fish species such as mackerel icefish.

Finally, it is interesting to note the differences in the relationships between krill and SST reported here and those proposed by earlier studies. This highlights the fact that short time-series do not necessarily reveal the full complexity of environmental relationships, and that long time-series of data are needed to comprehend ecological complexity. Trathan and Murphy (2002) highlight the need for caution when exploring environmental variability driven by SST indices, noting that data may not be stationary over different time-scales. As the WCB krill density time-series increases in duration, further complexities may become apparent in our understanding of the factors driving variability in the abundance and distribution of krill.

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