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Oceanographic variability and changes in Antarctic krill (*Euphausia superba*) abundance at South Georgia

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ABSTRACT

Oceanographic data collected to the north of South Georgia were examined for three consecutive summers (1996/97, 1997/98, 1998/99). The results show the existence of a shelf break front during each period. The most reliable means of defining the front was the potential density anomaly at the near-surface potential temperature minimum. In each year, off-shelf waters were separated from on-shelf waters by water with a potential density anomaly between 27.22 and 27.29 kg m^{-3}. During 1997/98, the near-surface potential temperature minimum was much colder and much shallower than in other years and was consistent with waters originating from much further south than South Georgia; these differences were further evident at a single deep off-shelf station. The oceanographic changes during 1997/98 were consistent with a mesoscale or large-scale movement of the southern Antarctic Circumpolar Current front. Acoustically determined densities of Antarctic krill, *Euphausia superba*, at South Georgia showed consistent patterns between years. Densities were substantially higher over the shelf compared with off-shelf, with the highest densities at the shelf edge; densities were also higher to the east of the island. During 1997/98, acoustic densities of krill were substantially higher than in other years. The coincidence of the elevated acoustic density and the cooler oceanographic conditions was explored. When data from all years were combined and analysed by Generalized Additive Model, an inverse relationship between acoustic density and temperature was apparent. Historical data were also examined and it was noted that the only other occurrence of such a high estimate of krill density at South Georgia, was when oceanographic conditions were also colder.

Key words: acoustic density, Antarctic Circumpolar Current, Antarctic krill, *Euphausia superba*, inter-annual variability, oceanography, Scotia Sea, South Georgia, southern Antarctic Circumpolar Current boundary, southern Antarctic Circumpolar Current front, Southern Ocean

INTRODUCTION

Variability in the distribution and abundance of Antarctic krill (*Euphausia superba* Dana) close to the sub-Antarctic island of South Georgia has been well documented (Heywood *et al.*, 1985; Priddle *et al.*, 1988; Brierley *et al.*, 1997, 1999a). However, the detailed mechanisms that drive this natural variability are not well understood. Determining the causes that underlie the variability is important for at least two reasons. First, a variety of marine predators at South Georgia are dependent upon krill, and variability in their breeding success is linked to levels of prey abundance (Croxall *et al.*, 1988). Secondly, the commercial fishery for krill at South Georgia (Everson and Goss, 1991; Murphy *et al.*, 1997; Trathan *et al.*, 1998) potentially competes with these predators. Management objectives in the Southern Ocean attempt to minimize this potential overlap between natural predators and the commercial fishery (Anon., 1992) and, as such, require a detailed understanding of the factors that drive variability in the krill stock.

Efforts to understand the mechanisms driving natural variability stretch back as far as the early part of the last century when the Discovery Expeditions were initiated in association with the shore-based whaling industry at South Georgia. Early analyses indicated that substantial levels of biological variability were linked with changes in mean temperature (Harmer,

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1931; Kemp and Bennett, 1932). Later, Mackintosh (1972) reviewed the available data and suggested that krill abundance was linked with cold and warm periods, which in turn were linked with variability in the extent and concentration of regional sea-ice and oceanography. Since then, other authors have emphasized that a large proportion of biological variability is probably driven by key variables in the physical environment (e.g. Maslennikov and Solyankin, 1988; Priddle *et al.*, 1988; Fedoulov *et al.*, 1996), in particular by variability in the southern portion of the Antarctic Circumpolar Current (ACC) (cf. Hofmann *et al.*, 1998; Tynan, 1998; Nicol *et al.*, 2000).

Krill at South Georgia are not thought to comprise a self sustaining population (Marr, 1962; Mackintosh, 1972; Everson, 1977), but are thought to arrive at the island in the prevailing flow of the ACC. Krill are generally considered to be a planktonic species with a distribution that is dependent upon the large-scale circulation of the south Atlantic (e.g. Murphy *et al.*, 1998). Variability in krill abundance at South Georgia is therefore thought to be related to differences in the amount of krill that becomes entrained within the ACC flow at sites upstream of South Georgia (e.g. Murphy *et al.*, 1998; Brierley *et al.*, 1999a), or to levels of spatial and temporal variability in the transport mechanism itself (the ACC), rather than to differences in food levels.

The movement of krill from the Antarctic Peninsula to South Georgia, has been modelled by Hofmann *et al.* (1998). Their study showed that wind-induced surface water movement (Ekman drift) potentially concentrates animals in the high-speed frontal regions of the ACC (see also Naganobu *et al.*, 1999). Hofmann *et al.* (1998) concluded that the high-speed fronts of the ACC were the primary mechanism for transporting krill to South Georgia. Variability in the location of these fronts (cf. Ikeda *et al.*, 1989) is likely to have important implications for krill. Movement of the fronts will potentially affect marine ecosystems both locally and downstream. The magnitude of any ecological impact will depend upon a number of factors including how much the front moves, how quickly it returns to its former position, and the time of year at which the movement occurs. Ecosystems could be buffered against some of these changes, with only the most extreme levels of physical variability being reflected through to biological processes. For example, centrally placed predators (cf. Tynan, 1998) feeding near to fronts may respond to changes in the front by relocating. However, if changes are extreme, foraging locations may become too far removed from the colony location.

In this study, variability in krill abundance was considered alongside high resolution oceanographic data in an attempt to determine whether differences in krill abundance at South Georgia, at a range of spatial scales, were related to differences in physical oceanographic conditions. Potential relationships were considered both within and between years. The study was focussed close to South Georgia and forms part of an extensive British Antarctic Survey programme aimed at understanding the regional krill-centred pelagic marine ecosystem.

METHODS

Data collection

The study was carried out during the Austral summers of 1996/97, 1997/98 and 1998/99 when the RRS James Clark Ross conducted combined oceanographic and biological cruises to the north of South Georgia (Table 1). Each year, two study areas (Fig. 1) were occupied over an 11-day period. These areas are referred to as the Western Core Box (WCB) and the Eastern Core Box (ECB). They form part of a long-term study designed to investigate levels of interannual biological and physical variability at South Georgia.

Each Core Box comprised ten 80 km transects running from off-shelf to on-shelf across the shelf break region (Fig. 1). Underway oceanographic and bioacoustic measurements were made simultaneously along each transect. The oceanographic data were collected using a Chelsea Instruments NvShuttle undulating oceanographic recorder (UOR) (Chelsea Technologies Group, West Molesley, UK). The acoustic data were collected using a Simrad EK500 scientific echo sounder (Simrad, Horten, Norway) operating at 38 and 120 kHz. Two transects were carried out each day at a nominal ship speed of 10 knots. During each night, two stations were sampled using a Neil Brown Mark III (Instrument Systems Inc., USA) (1996/97 and 1997/98) or a Sea-Bird 911-Plus (Sea-Bird Electronics Inc., Bellevue, WA, USA) (1998/99) conductivity-temperature-depth sensor (CTD); the stations were located 20 km from the ends of the second transect of each daily pair in either deep oceanic waters or shallow shelf waters (Fig. 1).

Table 1. Cruise dates.

	Western Core Box		Eastern Core Box	
Cruise	Start date	End date	Start date	End date
1996/97	29/12/1996	02/01/1997	23/12/1996	27/12/1996
1997/98	30/01/1998	03/02/1998	24/01/1998	28/01/1998
1998/99	02/01/1999	06/01/1999	27/12/1998	31/01/1998

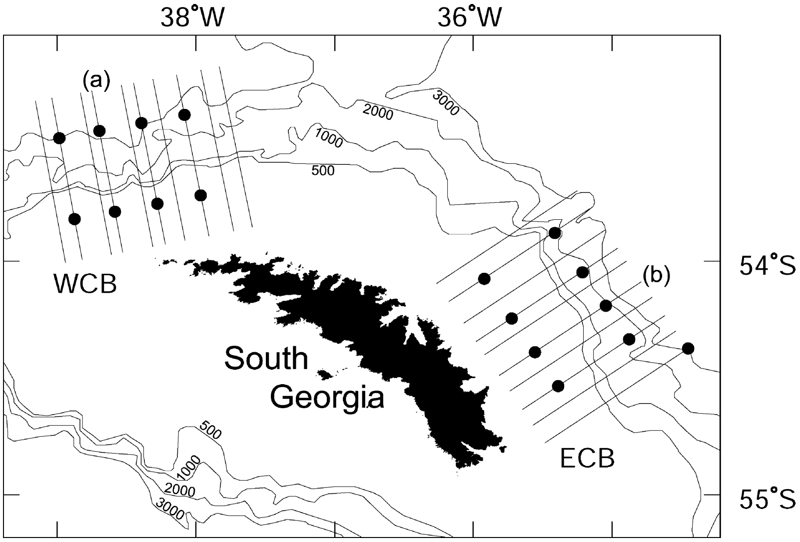


Figure 1. Plot of the South Georgia study area showing the Western Core Box and the Eastern Core Box. Undulating oceanographic recorder transects are shown as lines and conductivity-temperature-depth sensor stations as filled circles; transects referred to in Fig. 2 are indicated by (a) and (b). The 500, 1000, 2000 and 3000 m isobaths are shown.

Oceanographic data collection and processing

The UOR carried a suite of sensors to sample a variety of oceanographic variables including temperature, conductivity and pressure. The UOR trajectory was controlled so that it undulated between approximately 8 and 140 m except over the shelf where the maximum depth was restricted to avoid collision with the sea bed. The undulation frequency was nominally once every 6 min so that the UOR covered a complete cycle approximately every 1.85 km. The UOR sensors were calibrated under laboratory conditions prior to the start of each cruise and data were processed following the methods described in Brandon *et al.* (1999, 2000).

During the night stations, the CTD sampled the water column to a depth of 1000 m off-shelf and to near-bottom (approximately 250 m) over the shelf. The CTD data were calibrated using *in situ* salinity samples taken from a 12 bottle rosette, resulting in calibrated data that were accurate to better than 0.002 (1978 Practical Salinity scale). The CTD station data were used to adjust the salinity data collected by the UOR, giving an estimated accuracy for the UOR salinity data of approximately 0.007 (Brandon *et al.*, 1999).

Acoustic data collection and processing

The dual frequency acoustic data were collected and processed following the methods described in Brierley *et al.* (1997). These authors provide a full description so complete details are not repeated here. Acoustic calibrations followed Foote *et al.* (1987) and were carried out at Stromness Bay, South Georgia. Mean krill target strength (TS) was calculated for each Core Box using weighted mean krill length estimates (derived from net samples within each Core Box) in conjunction with the TS/mass relationship given in Brierley and Watkins (1996). Briefly, echo energy was summed vertically and averaged horizontally to yield mean volume backscattering strength (mvbs, dB). This was calculated for every 0.5 km integration interval along the transect and for each 2 m depth bin between 6 and 256 m. The difference in mvbs (Δmvbs) at 38 and 120 kHz was used to discriminate between different categories of acoustic target. A Δmvbs (120–38 kHz) of between 2 and 12 dB was used to discriminate Antarctic krill from other macro-zooplankton species and from nekton species (Madureira *et al.*, 1993; Brierley *et al.*, 1997).

The mean weight density of krill ($\mathrm{g\ m^{-3}}$) within each 2 m bin was derived from the 120 kHz echo signals classified as krill (on the basis of Δmvbs) by scaling with TS. Integration interval density values of krill were then calculated by averaging the 2 m depth bin values throughout the water column. The integration interval values along each transect were then averaged to give a mean transect density value. Transect density values were then weighted by transect length to give a weighted mean krill density and variance for a Core Box. A full statistical description of this methodology is given in Jolly and Hampton (1990).

At South Georgia, the continental shelf is relatively deep, mostly lying between 100 and 250 m; depths increase rapidly to over 3000 m beyond the shelf break. For each Core Box, transects were divided into two strata according to the depth of the sea bed; thus, off-shelf sections were defined as depths >500 m and on-shelf sections as depths <500 m. This depth was chosen as it was sufficiently deep to ensure that each survey transect was split into one continuous off-shelf section and one continuous on-shelf section. This depth also ensured that most transects were split into two nearly equal parts, giving off-shelf and on-shelf strata of almost equal area. Estimates of the mean weight density of krill for each off-shelf and each on-shelf strata were then derived, again using the method of Jolly and Hampton (1990).

Relationships between physical and acoustic data

Two types of analysis were carried out. The first considered the separate occupations of each Core Box and examined the relationships between the abundance of krill and a number of environmental parameters. The second examined larger scale temporal and spatial relationships and included data from both Core Boxes and from all years.

Fine-scale analyses

In order to examine relationships between krill density and the environment, physical data were averaged to the same spatial resolution as the acoustic data. The smallest scale used was that of the acoustic integration interval, that is 0.5 km; no comparisons were made at spatial scales less than this. To further simplify analyses, physical data were sub-sampled on the basis of depth; for the analyses described here, only data from the 30–35 m depth horizon were used. This depth range was selected as all UOR undulations extended to at least this depth; this depth was also above those regions where steep temperature and salinity gradients occurred, but near to where the main distribution of krill occurs (e.g. Godlewska and Klusek, 1987).

Relationships between the acoustic data and the physical data were explored using Generalized Additive Models (GAM) (McCullagh and Nelder, 1989) using the Splus 2000 (Mathworks, Natick, MA, USA) statistical package. The GAM is a regression method that relaxes the assumption of normality and linearity inherent in linear regression. It allows spline functions to be developed that are better predictors of the response data than are simple linear predictors; such functions are particularly useful where there are no *a priori* reasons to expect a linear response. The functions are estimated from the data using smoothing or local regression operations. A similar statistical approach has been used previously to explore relationships between acoustic and environmental data (Swartzman *et al*., 1994; Swartzman, 1997).

A variety of different error distributions are available in the Splus 2000 implementation of GAM. Based on the distribution of the individual mean krill density (g m^{-2}) values from the acoustic intervals (0.5 km) in each Core Box in each year, the gamma distribution was considered to be the most appropriate fit for the analyses reported here (cf. Miller and Hampton, 1989b). This was because the distribution of acoustic density values was heavily skewed, most values were below 20 g m^{-2}, but some were as high as 2000 g m^{-2}. In GAM, the dependent variable (in the analyses described here this was krill density) is modelled as the additive sum of splines generated from the proposed predictors. In these analyses, the physical predictors used were: distance along the shelf (km from the eastern margin of the Core Box), distance from the shelf break (km from the 500 m isobath), temperature (°C), salinity (1978 Practical Salinity scale), density anomaly (kg m^{-3}) and depth (m). The functions for each of the proposed predictor variables were estimated using a scatter plot smoother; in the analyses described here, a locally weighted regression smoothing function was used. For GAM models, the degrees of freedom for the overall fit is calculated from the equivalent number of parameters required for each of the individual predictors. For a locally weighted regression smoothing function, the parameters include the degree of the local polynomial to be used and the percentage of observations included in the neighbourhood; for our fine scale analyses a degree of 1 and a neighbourhood span of 0.25 were used.

Broad-scale analyses

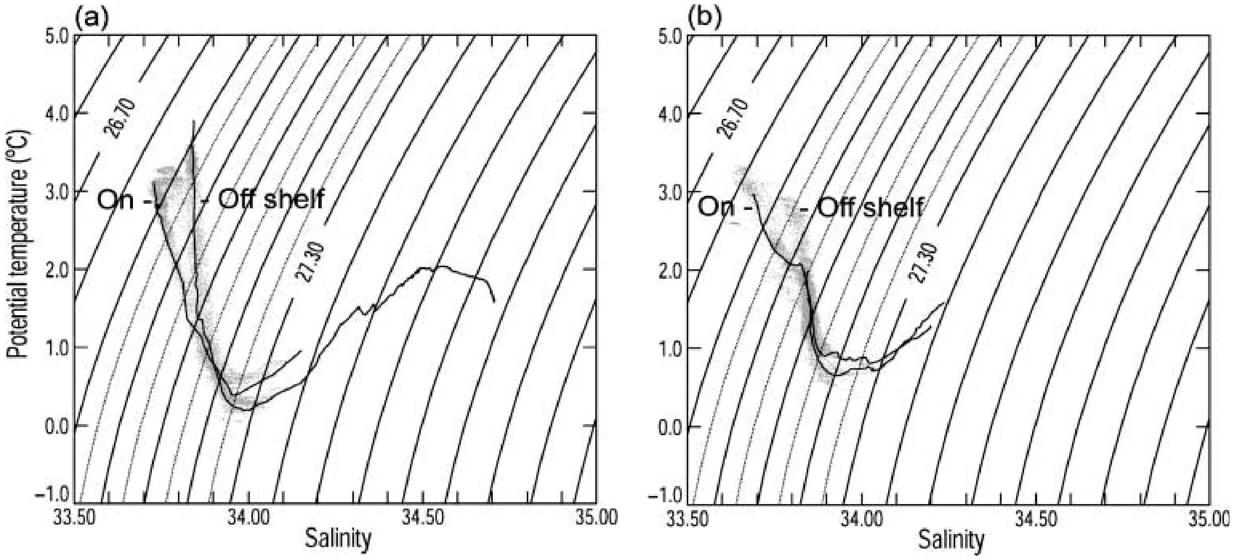
To relate the acoustic data to the physical data at a scale larger than the acoustic integration interval, data were again averaged to a comparable spatial resolution. The resolution used at this scale was that of the acoustic transect, that is, all data along a single transect were pooled to give a single estimate for that transect. Again, the physical data were sub-sampled on the basis of depth and only the 30–35 m depth horizon was used. For these GAM analyses, a gamma distribution was again considered to be the most appropriate fit. Similarly, the function for each of the proposed predictor variables was estimated using a locally weighted regression with a polynomial degree of 1 and a neighbourhood span of 0.25.

RESULTS

Physical data

Potential temperature (θ) and salinity plots for two of the UOR transects carried out during the 1996/97 survey are shown in Fig. 2. These transects

Figure 2. Potential temperature (°C) and salinity plots for selected undulating oceanographic recorder transects (see Fig. 1) (a) from the Western Core Box; and, (b) from the Eastern Core Box during 1996/97. Undulating oceanographic recorder data are shown by clouds of points, conductivity-temperature-depth sensor station data are shown as solid lines; density (sigma-*t*) anomaly surfaces (kg m^{-3}) are shown as curved contours.



demonstrate the relationship between the continuous UOR data and station-based CTD data. These figures also highlight the difference between the off-shelf and on-shelf waters, separated by a shelf break front (Brandon *et al.*, 1999, 2000). Increased variability in the surface waters and separation across the shelf break front was evident on both transects (Fig. 2). Separation across the front was best observed at the near-surface potential temperature minimum (θ minimum); that is, below the waters most recently influenced by seasonal warming and local effects. In general, the θ minimum was clearly defined off-shelf, but sometimes modified or eroded over the shelf. At the depth of the off-shelf θ minimum, the average temperature and salinity differed from that on-shelf, such that the potential density anomaly provided a means of separating waters across the front. This was most evident in the WCB where the 27.28 kg m^{-3} isopycnal separated off-shelf from on-shelf waters (Fig. 2).

Potential temperature and salinity plots for the CTD stations are shown in Fig. 3. These highlight the differences between the off-shelf and on-shelf waters; they also emphasize that the differences are more obvious in some years than in others. For example, the off-shelf and on-shelf description given by Brandon *et al.* (2000) was based on data from a year when the differences were very distinct (1996/97). Data from subsequent years (1997/98 and 1998/99) show that the magnitude of this difference varies between years.

From the CTD stations in the ECB, the following patterns were evident at the θ minimum. During 1996/97 the near-surface θ minimum was generally below 125 dbar off-shelf with a value of approximately 0.58°C; on-shelf it was slightly deeper (150 dbar) and slightly warmer (0.74°C). The density anomaly surface between 27.23 and 27.25 kg m^{-3} separated off-shelf from on-shelf waters. During 1997/98 the θ minimum was generally around 100 dbar off-shelf with a value of approximately −0.49°C; on-shelf it was slightly deeper (110 dbar) and warmer (−0.01°C). The density anomaly surface between 27.25 and 27.27 kg m^{-3} separated off-shelf from on-shelf waters. During 1998/99 the off-shelf θ minimum was deep, being below 140 dbar with a value of approximately 0.49°C; on-shelf it was still deeper (160 dbar) and warmer (0.84°C). The density anomaly surface between 27.22 and 27.26 kg m^{-3} separated waters across the front.

From the CTD stations in the WCB, the following patterns were evident. During 1996/97 the θ minimum was generally below 130 dbar off-shelf with a value of approximately 0.15°C; on-shelf it was slightly shallower (100 dbar) and slightly warmer (0.49°C). The density anomaly surface between 27.26 and 27.28 kg m^{-3} separated off-shelf from on-shelf waters. During 1997/98 the θ minimum was generally at 100 dbar off-shelf with a value of approximately −0.75°C; on-shelf it was at a similar depth, but was warmer (0.17°C). The density anomaly surface between 27.26 and 27.29 kg m^{-3} separated off-shelf and

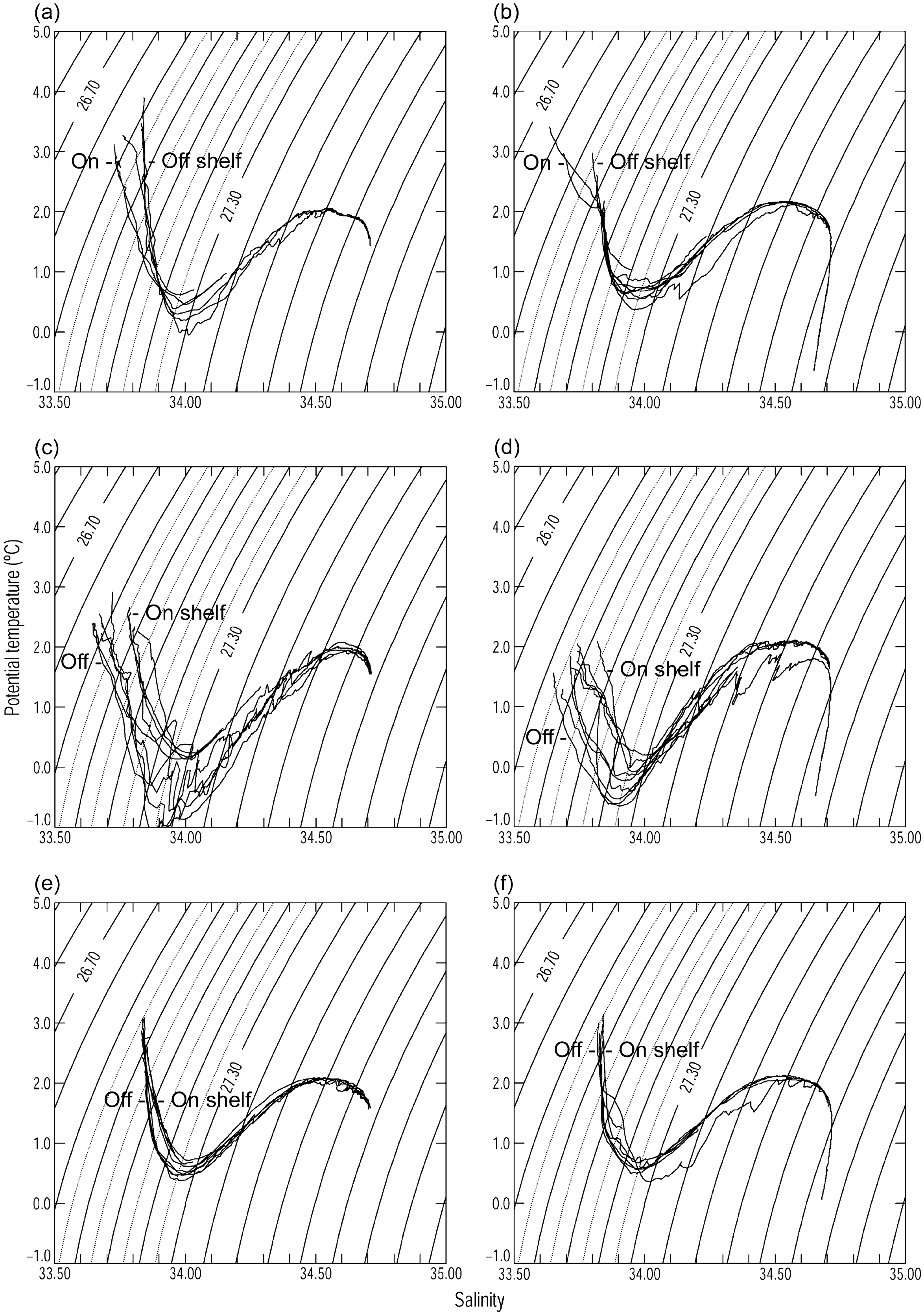

(a)
On -
- Off shelf
26.70
27.30
(b)
On -
- Off shelf
26.70
27.30
(c)
- On shelf
Off -
26.70
27.30
(d)
- On shelf
Off -
26.70
27.30
(e)
Off -
- On shelf
26.70
27.30
(f)
Off -
- On shelf
26.70
27.30
Potential temperature (°C)
5.0
4.0
3.0
2.0
1.0
0.0
–1.0
33.50
34.00
34.50
35.00
Salinity

Figure 3. Potential temperature (°C) and salinity plots for conductivity-temperature-depth sensor station data from (a) 1996/97 Western Core Box (WCB); (b) 1996/97 Eastern Core Box (ECB); (c) 1997/98 WCB; (d) 1997/98 ECB; (e) 1998/99 WCB; and (f) 1998/99 ECB. Density (sigma-*t*) anomaly surfaces (kg m^{-3}) are shown as curved contours.

on-shelf waters. During 1998/99 the off-shelf θ minimum was again deep, being below 140 dbar with a value of approximately 0.46°C; on-shelf it was at a similar depth and again warmer (0.68°C). The density anomaly surface between 27.26 and 27.27 kg m^{-3} separated off-shelf and on-shelf waters.

Some general patterns were evident for both the ECB and the WCB. For example, off-shelf waters were generally cooler than on-shelf waters at the depth of the θ minimum (Table 2). Furthermore, at the θ minimum, temperatures were generally warmer in the ECB than in the WCB. However, these general patterns should be viewed in the context of surface modification. For example, the θ minimum for on-shelf waters was sometimes only weakly defined, with waters well mixed to the deepest levels. Also, above the θ minimum, seasonal surface warming and/or local surface modification sometimes led to cooler surface temperatures on-shelf, although at the depth of the θ minimum, on-shelf waters were always warmer. Also, surface temperature modification in the ECB was generally weaker than in the WCB, so that the ECB was generally cooler at the surface, although it was warmer at the θ minimum. Also evident from these results, was that the 1997/98 cruise was carried out during a much cooler but more variable period than were either the 1996/97 or 1998/99 cruises. Nevertheless, despite the considerable temperature differences between years, and between off-shelf and on-shelf waters, the density anomaly differences across the shelf break front were generally consistent. Thus, the shelf break front could generally be characterized by a density anomaly surface within the range 27.22–27.26 kg m^{-3} in the ECB and 27.26–27.29 kg m^{-3} in the WCB.

Also of note is the variability in potential temperature and salinity (Fig. 4) evident at the deep off-shelf CTD station located at the northeastern corner of the ECB (Fig. 1). This single station was sampled to near-bottom during each cruise. The depth of the θ minimum, and the temperature at the θ minimum differed between cruises (Table 3). Other water property indicators also varied, for example the temperature and salinity at the deep temperature maximum differed between cruises. During 1997/98, properties were consistent with the station lying south of the southern ACC front (SACCF) (Orsi *et al.*, 1995), either because of mesoscale intrusions, or of a large-scale movement in the front. In contrast, during 1996/97 and 1998/99, properties were consistent with the station lying north of the SACCF. During 1996/97, the deep temperature maximum, indicative of Circumpolar Deep Water (CDW), was sampled

Table 2. Mean water properties at the near-surface potential temperature minimum from conductivity-temperature-depth sensor stations occupied during 1996/97, 1997/98 and 1998/99.

	Western Core Box		Eastern Core Box	
Cruise	Off-shelf	On-shelf	Off-shelf	On-shelf
1996/97				
Number of stations	3	3	5	4
θ (°C)	0.148	0.489	0.582	0.742
Density (sigma-*t*) anomaly (kg m^{-3})	27.284	27.256	27.246	27.234
Depth (dbar)	133.7	99.7	125.0	153.8
1997/98				
Number of stations	4	4	5	4
θ (°C)	−0.749	0.168	−0.486	−0.010
Density (sigma-*t*) anomaly (kg m^{-3})	27.261	27.291	27.246	27.269
Depth (dbar)	97.8	96.0	98.6	111.0
1998/99				
Number of stations	4	4	4	3
θ (°C)	0.462	0.683	0.494	0.836
Density (sigma-*t*) anomaly (kg m^{-3})	27.266	27.261	27.262	27.217
Depth (dbar)	143.4	140.0	142.5	160.3

Figure 4. Potential temperature (°C) and salinity data from the deep off-shelf conductivity-temperature-depth sensor station located at the northeastern corner of the Eastern Core Box. Density (sigma-*t*) anomaly surfaces (kg m^{-3}) are shown as curved contours; (A) 1996/97, (B) 1997/98 and (C) 1998/99.

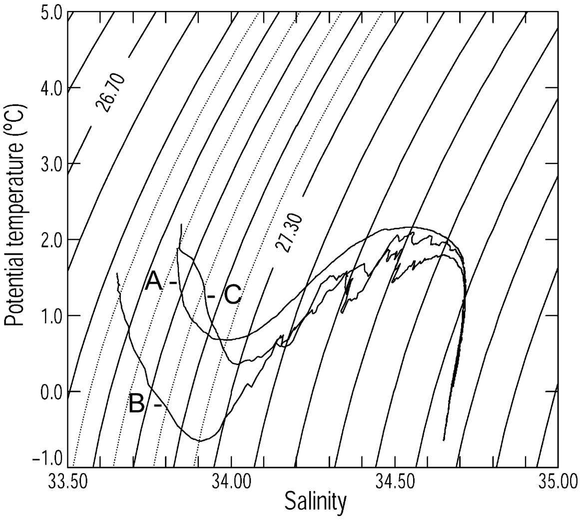


Table 3. Water property indicators from the deep conductivity-temperature-depth sensor station at the northeastern corner of the Eastern Core Box (see Fig. 1) occupied during 1996/97, 1997/98 and 1998/99.

Cruise	Property indicator	Depth (dbar)	θ (°C)	Salinity
1996/97	θ min	115	0.677	33.982
	θ max	395	2.162	34.557
	S max	1237	1.447	34.716
1997/98	θ min	83	−0.647	33.908
	θ max	367	1.874	34.522
	S max	1319	1.251	34.714
1998/99	θ min	129	0.354	34.020
	θ max	355	2.097	34.554
	S max	1135	1.335	34.717

(Fig. 4). Below this, temperatures and salinities gradually decreased towards the character of Antarctic Bottom Water. During 1997/98 and 1998/99 substantial vertical variability was evident at the deep temperature maximum, consistent with interleaving of the main water types. During these cruises, the deep temperature maximum of CDW was eroded and less obvious; it was most deeply eroded during 1997/98, consistent with shoaling of CDW (cf. Orsi *et al.*, 1995).

Acoustic estimates of density

The general distribution and acoustic density of krill encountered during the cruises has been reported elsewhere (Brierley *et al.*, 1997, 1999b). In the present study, the density of krill has been further apportioned into four strata, off-shelf and on-shelf in the WCB, and off-shelf and on-shelf in the ECB. The average densities of krill calculated for these strata (Table 4) show that the density off-shelf was substantially lower than that on-shelf. This was true in both Core Boxes and in all years. The results also indicate that the density of krill in the WCB was generally lower than in the ECB; however, this was not always the case, as in 1998/99 they were approximately equal.

GAM analyses

The results from the GAM analyses from the individual Core Boxes and from the analyses combining Core Boxes across years highlighted issues relating to scale. The analyses at the scale of the acoustic integration interval of 0.5 km showed either a lack of any relationship between the dependent variable (krill) and the proposed predictor variables (temperature, salinity, density anomaly, depth, distance along the shelf and distance from the shelf break), or inconsistent relationships. In contrast, the analyses at the scale of the acoustic transect highlighted relationships at a larger scale than existed between Core Boxes and across years. These relationships are highlighted in the sections below.

Fine-scale analyses

The separate GAM analyses at the scale of the acoustic interval using data from individual Core Boxes (i.e. for the ECB and the WCB for each of the 3 years), produced results with little consistency; the response to the majority of the predictor variables showed little or no repeatable pattern between the separate analyses. Such a lack of consistency suggests that the included variables were either not important explanatory variables for predicting the mean weight density of krill, or that they reflected scales (0.5 km) where relationships include a highly stochastic element. The only clear patterns evident between Core Boxes and between years were for those GAMs where bathymetry was included as a predictor variable, in which case, results were always similar and were little altered by the other factors included in the analyses.

The results for the WCB showed very strong influences of bathymetry at depths <500 m. For GAMs using only bathymetry as a predictor variable, residual

Table 4. Acoustic density of Antarctic krill during 1996/97, 1997/98 and 1998/99. Estimates calculated for off-shelf portions of transects (depth > 500 m) are shown separately from those on-shelf (depth < 500 m).

	Western Core Box			Eastern Core Box		
Cruise	Off-shelf	On-shelf	Off/On together	Off-shelf	On-shelf	Off/On together
1996/97						
Distance (km)	485.67	298.99	784.66	408.37	392.03	800.39
Density (g m^{-2})	10.95	48.26	25.17	27.91	82.51	54.65
Variance	14.72	95.52	18.44	8.09	114.82	36.55
CV (%)	35.03	20.25	17.06	10.19	12.99	11.06
1997/98						
Distance (km)	478.92	314.98	793.81	402.38	396.10	798.48
Density (g m^{-2})	4.33	47.38	21.41	128.21	173.10	150.48
Variance	0.35	111.83	17.96	2195.30	1060.98	879.54
CV (%)	13.75	22.32	19.80	36.55	18.82	19.71
1998/99						
Distance (km)	485.71	312.23	797.92	404.88	395.59	800.47
Density (g m^{-2})	5.11	22.81	12.04	8.67	13.75	11.18
Variance	0.56	13.92	2.14	3.65	63.15	17.46
CV (%)	14.64	16.36	12.16	22.03	57.80	37.37

deviance was substantially reduced (between 17 and 47%) when compared with the null model (that is, the overall mean); the smoothed bathymetric term was always highly significant ($P < 0.001$). The residuals from these analyses showed no lack of fit and no significant correlation when compared against the predictor bathymetry ($r^2 < 0.01$; $P > 0.05$). The plots from these GAM models are shown in Fig. 5a,c,e, where the ordinates represent the relative importance of the predictor variable on the response variable. These figures show that in each Core Box in each year, the most marked positive relationship with bathymetry was over the shelf at depths of between 250 and 750 m.

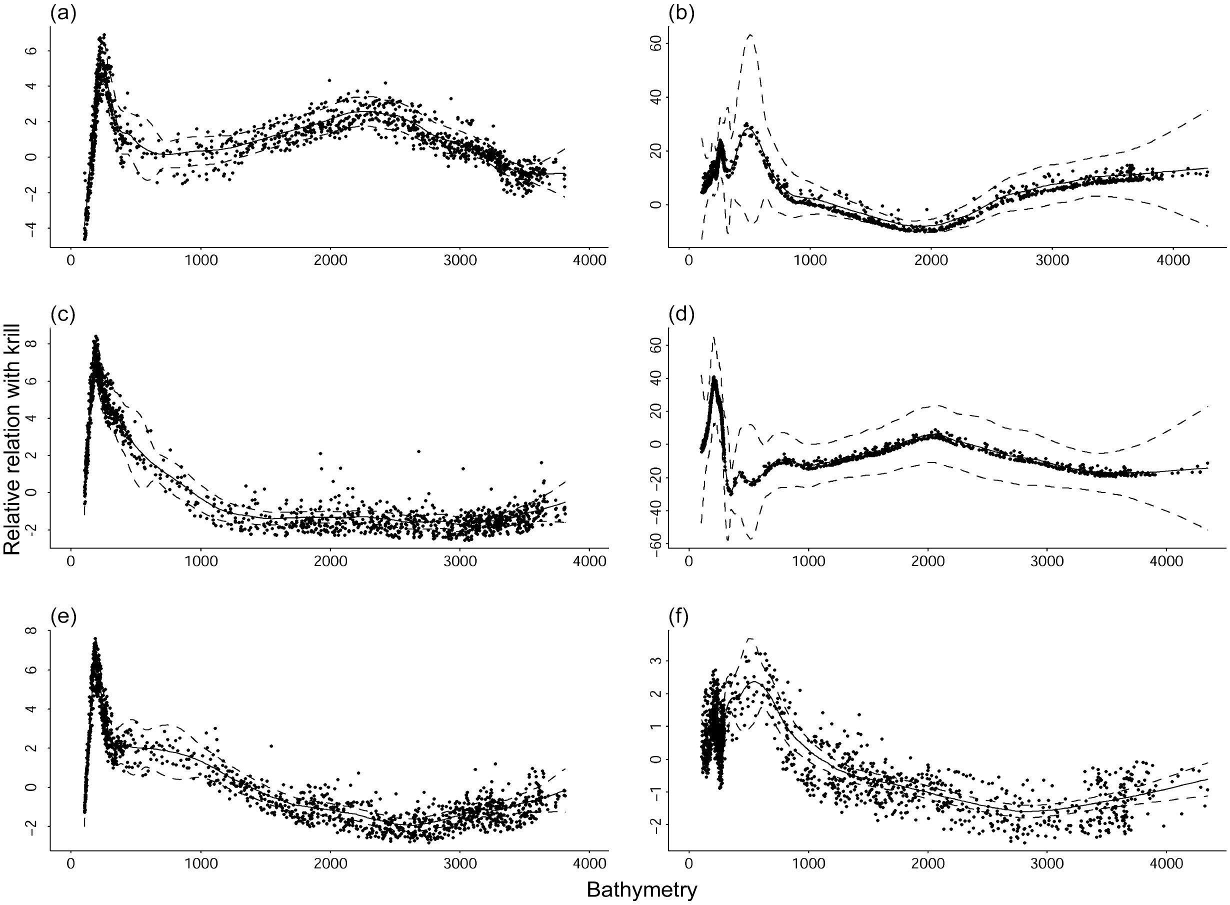
The results from the ECB were a little more variable but, nevertheless, still consistent. For the GAMs using only bathymetry as a predictor variable, residual deviance was reduced (between 6 and 23%) when compared with the null model, but not as much as for the WCB; however, the smoothed bathymetric term was always highly significant ($P < 0.001$). For each analysis the residuals showed no correlation when compared against the predictor bathymetry ($r^2 < 0.01$; $P > 0.05$). The plots from these GAM models are shown in Fig. 5b,d,f. The figures again show that the mean weight density of krill is significantly influenced by bathymetry. The plots in Fig. 5b,d indicate wider confidence intervals than those in Fig. 5a,c,e,f. This is possibly a consequence of the elevated biomass found in the ECB during 1996/97 and 1997/98. Identical GAM analyses using a subset of the krill density data with values constrained to be less than the 90% quantile generated similar results but with much reduced confidence intervals; this suggests that very extreme values are difficult to model.

Broad-scale analyses

Output from the GAM analysis based on data from both Core Boxes and from all years is shown in Fig. 6a. This plot shows that the mean weight density of krill, at the scale of the individual transect, can be modelled using temperature; the residual deviance was reduced (58%) when compared with the null model and the terms were highly significant ($P < 0.001$). For this analysis the residuals showed no significant correlation when compared against the predictor temperature ($r^2 < 0.02$; $P > 0.05$). The GAM (Fig. 6a) indicates that temperatures within the range 1.50–2.25°C have a near-linear relationship with the mean weight density of krill, with low temperatures associated with high levels of krill and high temperatures associated with lower levels of krill. Above 2.25°C the analysis shows that temperature has little or no relationship with the mean weight density of krill.

Given the strong influence of bathymetry upon the mean weight density of krill (Fig. 5), GAM analyses combining the Core Boxes were also carried out for off-shelf transect locations (depths >500 m) as well as for on-shelf transect locations (depths <500 m). The results from these separate analyses (Fig. 6b,c) showed essentially the same picture; that is, high levels of krill were associated with low temperatures, whilst low levels of krill were associated with high temperatures.

Figure 5. Generalized Additive Models for estimating the mean weight density (g m^{-2}) of krill from bottom depth (m) as a predictor. The ordinate represents the relative importance of the predictor on the response variable. The points show the partial deviance residuals for each acoustic interval; the predicted model is shown by the solid line and the 95% confidence intervals by the dashed lines. Models for (a) 1996/97 Western Core Box (WCB); (b) 1996/97 Eastern Core Box (ECB); (c) 1997/98 WCB; (d) 1997/98 ECB; (e) 1998/99 WCB; and (f) 1998/99 ECB.



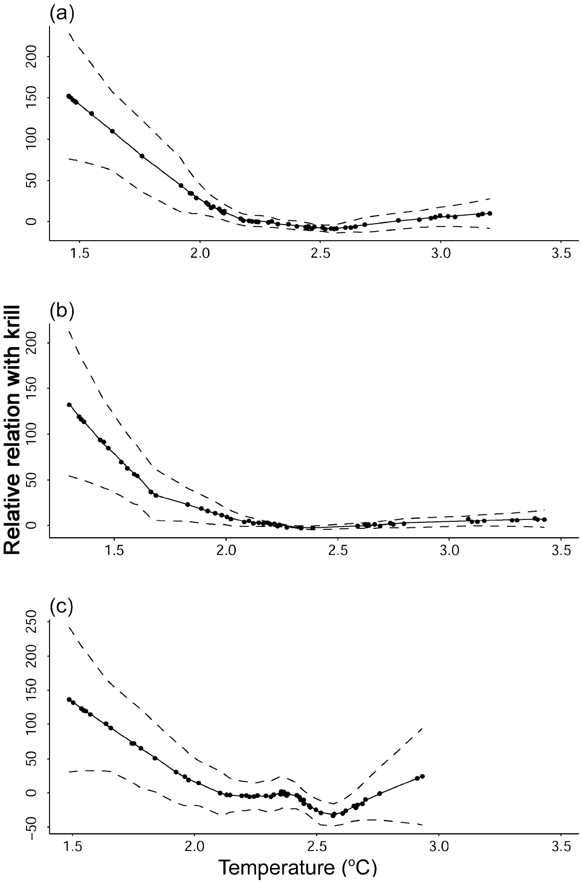
DISCUSSION

At South Georgia, differences in water properties were evident during the 3 years of the study. Both the ECB and the WCB showed considerable variation between years, with differences in both potential temperature and salinity. During each cruise, variability was present throughout the water column, with differences between off-shelf and on-shelf waters generally apparent (Table 2). Waters were predominantly cooler off-shelf than on-shelf (at the depth of the near-surface potential temperature minimum). Such a situation highlights the importance of local modification close to the island (cf. Brandon *et al.*, 2000). Surface modification was stronger in the WCB than in the ECB, indicative of either greater modification in the WCB, or transport of modified waters to the WCB (or both) (cf. Hardy and Gunther, 1935; Trathan *et al.*, 1997; Brandon *et al.*, 2000). Despite temperature and salinity differences between years, density anomaly differences across the shelf break front occurred within a narrow range. Thus, the shelf break front could generally be characterized at the θ minimum by a density anomaly surface within the range 27.22–27.26 kg m^{-3} in the ECB and 27.26–27.29 kg m^{-3} in the WCB.

Fine-scale relationship between krill and the environment

Various fine-scale and mesoscale relationships between krill abundance and environmental variables have been considered by a number of authors (e.g. see review by Miller and Hampton, 1989a). However, no single environmental factor, or group of factors, has been found that shows a reliable and predictable relationship with the fine scale or mesoscale distribution and abundance of krill. Various factors such as

Figure 6. Generalized Additive Models for estimating the mean weight density (g m^{-2}) of krill from temperature (°C) as a predictor. The ordinate represents the relative importance of the predictor on the response variable. The points show the partial deviance residuals for each acoustic transect; the predicted model is shown by the solid line and the 95% confidence intervals by the dashed lines. (a) Model using all acoustic intervals from a transect; (b) model using only off-shelf intervals (depths >500 m), and; (c) model using only on-shelf intervals (depths <500 m).



temperature, salinity, oxygen concentration and nutrient level have been considered, but none appears to have a consistently measurable or predictable effect upon krill (e.g. Weber and El-Sayed, 1985; Witek *et al.*, 1988). The fine scale results reported here support this, showing that even when relationships between krill abundance and the environment are sometimes apparent in a single year, or within a single Core Box, they are not always consistent between years or between Core Boxes.

The only fine scale relationship between krill and the environment that showed a consistent relationship, both between Core Boxes and across years, was the relationship between krill density and bathymetry (Fig. 5). In the WCB the relationship was very consistent indicating increased biomass over shelf and shelf break areas, particularly between 250 and 750 m, consistent with Murphy *et al.* (1991). In the ECB the relationship was less consistent though it was still marked, again it indicated increased biomass over the shelf and shelf break areas. The analyses of acoustic data for off-shelf transect sections and for on-shelf transect sections, supports this relationship for both Core Boxes (Table 4).

Although krill is generally assumed to be a planktonic species, the importance of bathymetry in relation to krill density has been recognized previously. For example, the First International Biological Investigations of Marine Antarctic Systems and Stocks (BIOMASS) Experiment (FIBEX) surveyed regions of known krill abundance in the South Atlantic; these areas were principally over the continental shelf (Anon, 1977). In the Scotia Sea, shelf areas and shelf break areas are also locations where commercial harvesting for krill has taken place (e.g. Everson and Goss, 1991; Murphy *et al.*, 1997; Trathan *et al.*, 1998). How and why krill aggregate in such regions remains unclear, although bathymetry could affect reproduction and spawning. For example, it has been suggested (Siegel, 1988; Trathan *et al.*, 1993; Lascara *et al.*, 1999) that reproductive behavioural responses to bathymetry west of the Antarctic Peninsula potentially explain spatial patterns in krill abundance, size segregation and maturity stage. As such, reproductive behaviour at South Georgia could result in similar spatial patterns of krill (cf. Siegel, 1988; Trathan *et al.*, 1993), even if the South Georgia population is not self sustaining (Marr, 1962; Mackintosh, 1972; Everson, 1977).

Other interactions with bathymetry are also possible. For example, Everson (1976, 1977 has suggested that enhanced primary productivity in regions of vertical upwelling may be a key factor in krill distribution. In contrast, Witek *et al.* (1988) have suggested that behavioural reactions to water velocity gradients tend to concentrate krill in quiescent areas to the side of strong flow fields (see also Macaulay *et al.*, 1984). Such quiet areas close to upwelling systems are generally known to be areas where plankton abundance is high, possibly as a consequence of the often highly productive stable water conditions (Mann and Lazier, 1996). At South Georgia, these conditions exist at the shelf break. Regions of upwelling occur along the shelf break, whilst water movement at the shelf break front, or off-shelf, is generally faster than over the shelf (Brandon *et al.*, 2000). Thus, movement of krill onto the shelf from off-shelf regions could be the result of behavioural responses and could result in elevated abundance levels over the shelf (cf. Witek *et al.*, 1988). Certainly, swimming speeds of krill are sufficiently fast (approximately 20 cm s^{-1}) that they may be able to maintain their position in favourable locations even in regions of relatively rapid water movement (cf. Kils, 1979; Hamner, 1984). At South Georgia, similar shelf break relationships would be anticipated in both the WCB and the ECB, so long as regions of upwelling occurred and flow patterns along the shelf break were maintained.

Broad-scale relationships between krill and the environment

In contrast to analyses carried out at the scale of the acoustic integration interval, analyses carried out at the scale of the acoustic transect showed strong evidence of relationships between krill and the environment. Thus, the negative relationship between krill biomass and temperature (Fig. 6) supports the hypothesis that krill is influenced by temperature over larger scales.

To the north and east of South Georgia, the SACCF approaches close to the island (Orsi *et al.*, 1995). This front is the southern-most of the deep fronts in the ACC and carries waters with circumpolar characteristics. It is a fast-flowing, narrow core that accounts for more than 15 Sv of transport (1 Sv = 10^6 m^3 s^{-1}) (Read *et al.*, 1995; Thorpe *et al.*, in press). The property indicators for the front include temperatures of below 0°C at the θ minimum, where the θ minimum is at depths shallower than 150 dbar (Orsi *et al.*, 1995). South of the SACCF, the southern ACC boundary (SACCB) is marked by the southward extent of Upper CDW (UCDW). Between the SACCF and the SACCB, the waters are marked by a θ minimum of below −0.18°C at depths of <100 dbar (Orsi *et al.*, 1995).

Northwest of South Georgia, the mean climatological position of the SACCF is unknown, though variability in the location of the front in this region has been suggested (Trathan *et al.*, 1997, 2000; Thorpe *et al.*, in press). The results reported here support this suggestion. Thus, during 1997/98 water properties close to South Georgia were consistent with water from south of the SACCF: the average depth of the θ minimum was approximately 100 dbar and mean temperatures (Tables 2 and 3) were −0.49°C in the ECB and −0.75°C in the WCB. In contrast, water properties during 1996/97 and 1998/99 were consistent with water from north of the front; the θ minimum was deeper and the water temperature warmer. The deep CTD station occupied at the northeast corner of the ECB further supports this suggestion. During 1997/98 the θ minimum was cold (−0.65°C) and shallow (85 dbar). This station also indicated the presence of considerable interleaving in the deeper waters, consistent with shoaling of UCDW south of the SACCF (cf. Orsi *et al.*, 1995).

Oceanic fronts have long been recognized as an important factor in the distribution of Antarctic krill (e.g. Witek *et al.*, 1988; see also Miller and Hampton, 1989a). In particular, mesoscale variability in the SACCF has been highlighted as an important feature in the transport of krill to South Georgia. Hofmann *et al.* (1998) emphasized the importance of the SACCF in the transport of krill, and concluded that the southern portion of the ACC was the primary mechanism for transporting krill from the Antarctic Peninsula to South Georgia. Others have also highlighted the biological importance of the southern reaches of the ACC. For example, Tynan (1998) suggested that the SACCB was an important oceanographic feature associated with elevated seasonally averaged primary production, krill biomass and a variety of top marine predators. Similarly, Nicol *et al.* (2000) also highlighted the biological importance of the southern portion of the ACC, but suggested that biological activity (including krill) was distributed between the ice edge and the SACCB, and not associated with the SACCB itself. The θ minimum parameter values recorded during 1997/98 suggest that the water to the north of South Georgia was from the southern-most reaches of the ACC, and possibly from south of the SACCB. This accords well with Nicol *et al.* (2000) and highlights the suggestion that variability in the southern ACC accounts for variability across a range of trophic levels in the Antarctic marine ecosystem.

Large-scale movements in the frontal regions of the ACC have been considered previously, and put forward as a possible mechanism affecting the abundance of krill at South Georgia. For example, Priddle *et al.* (1988) identified movements in the Polar Front (PF) as the most probable source of physical variability. However, the location of the PF to the north of South Georgia has subsequently been shown to be relatively invariant (Trathan *et al.*, 1997, 2000), whereas the position of the SACCF is potentially much more mobile (Trathan *et al.*, 1997, 2000; Thorpe *et al.*, in press). Therefore, the results presented here are consistent with the mechanism suggested by Priddle *et al.* (1988), albeit with variability in the southern portion of the ACC, rather than with the PF.

Long-term variability

At South Georgia, acoustic surveys for krill have been reported since 1981 when the FIBEX survey was carried out (see Trathan *et al.*, 1995). Since then, the biomass of krill at South Georgia has been known to fluctuate, with periods of relative scarcity and periods of much higher abundance (Heywood *et al.*, 1985; Priddle *et al.*, 1988; Brierley *et al.*, 1997, 1999b). For example, at the eastern end of South Georgia, the biomass of krill has varied from approximately 2 to 151 g m^{-2} (Brierley *et al.*, 1999b). Periods of particular scarcity include January 1991 and January 1994, with 6.4 and 1.9 g m^{-2} respectively. Conversely, periods of particularly high abundance include January 1992 and January 1998, with 95.0 and 150.5 g m^{-2} respectively. These latter values are particularly extreme and reflect estimates that are approximately 20 g m^{-2} higher than the next nearest value.

If the southern portion of the ACC is the primary mechanism for transporting krill to South Georgia (Hofmann *et al.*, 1998), then signals reflecting large-scale physical variability within the ACC may be evident, either at times of krill scarcity, or at times of krill abundance. However, physical data at the spatial and temporal resolution necessary to identify possible relationships with krill biomass are not available. Furthermore, proxies derived from remotely sensed satellite data may not reflect detailed frontal positions, particularly where the fronts are not associated with surface water masses. Nevertheless, satellite data do provide evidence about surface variability in the southern portion of the ACC. In addition, they could provide information about variability in the location of the SACCF, if it has a surface signature as suggested by Read *et al.* (1995) and Holliday and Read (1998).

Reynolds and Smith (1994) describe the United States National Oceanographic and Atmospheric Administration (NOAA) operational global sea surface temperature (SST) analysis carried out by optimum interpolation. Data include monthly global SST grids generated at a resolution of 1° latitude by 1° longitude. These data are sufficient to resolve surface variability in the southern portion of the ACC, though not variability in frontal locations. These SST grids are available from the US National Centre for Atmospheric Research (NCAR) (ftp://ncardata.ucar.edu/datasets/ds277.0/oi/mnly/data), starting from November 1981. Monthly anomalies for the grid position located east of South Georgia (53°30′S, 38°30′W) are shown in Fig. 7; these anomalies were derived using a climatology based on the long term monthly averages from the data at this location.

During the periods of krill scarcity (January 1991 and January 1994) and the periods of high krill abundance (January 1992 and January 1998), temperature values were unusual. For example, SST values during the periods of scarcity were within the upper 20% of recorded values ($N = 212$ months), whilst values during the periods of abundance were within the lower 5% of values. At present, the number of periods for which any comparison can be made are very few and conclusions must be, at best, preliminary. Nevertheless, the available data do support the suggestion that temperature variability resulting from large-scale variability in the southern portion of the ACC does influence the biomass of krill reaching South Georgia. That the extreme high values of krill biomass correspond to extreme low values of temperature suggests that temperature variability (or other factors for which temperature is an alias, for example,

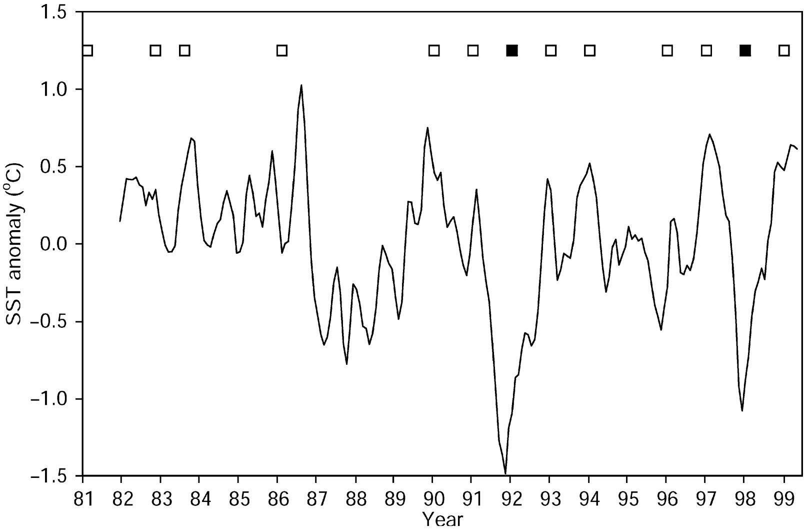


Figure 7. Sea surface temperature anomaly data for November 1981 to June 1999 for a grid position to the east of South Georgia (53°30′S, 38°30′W); a 3-month running average has been applied to the data. Months when acoustic surveys were carried out at south Georgia (□); high abundance surveys (■).

production and food availability) is an important determinant.

A wide range of factors may influence krill abundance; therefore a simple linear relationship between temperature and biomass is unlikely to exist (cf. Brierley *et al.*, 1999a). This may be further complicated if variability in the southern portion of the ACC is affected by processes such as the Antarctic Circumpolar Wave (White and Peterson, 1996), whereby interannual anomalies in a variety of physical factors propagate eastwards at speeds consistent with the ACC (see also Trathan and Murphy, in press). Such anomalies include atmospheric pressure, wind stress, SST, sea-ice extent (White and Peterson, 1996) and sea height (Jacobs and Mitchell, 1996). Notwithstanding, insights into the mechanisms that control variability in the abundance of krill at South Georgia are important for both conservation and management purposes (Everson, 1992).

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