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Interannual variability in krill abundance at South Georgia

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ABSTRACT: Interannual variability within the pelagic marine environment around South Georgia is a well-recognised phenomenon. A key aspect of this variability is interannual fluctuation in the abundance of Antarctic krill *Euphausia superba*. Here we describe a new acoustic survey programme to monitor krill abundance in the South Georgia region. We present biomass estimates for 2 survey boxes, located over the shelf-break to the northeast and northwest of the island, derived from the first of these surveys conducted in January 1996. We contrast these with the most recent previous estimates for the region obtained in January 1994. Weighted mean krill density (and weighted variances) estimates for the 1996 surveys were 40.57 g m^{-2} (13.37) and 26.48 g m^{-2} (54.30) for the eastern and western boxes respectively. These are high compared with those obtained in January 1994, when estimates for similar areas were 1.87 g m^{-2} (0.14) and 7.43 g m^{-2} (1.33) respectively. The greater than 20-fold difference between surveys reveals a very large interannual variability in krill abundance at South Georgia. In 1994 the low abundance resulted in greatly reduced breeding success in most habitual krill predator species there. In the 1996 season, however, breeding success of these species was normal. Instantaneous estimates of krill abundance using acoustic techniques are therefore consistent with measurements from predators, whose breeding performances provide a longer-term indication of prey abundance in the surrounding pelagic ecosystem in a particular season.

KEY WORDS: Antarctic krill · *Euphausia superba* · Acoustic survey · Interannual variability · Predators · Breeding success · South Georgia · Southern Ocean · Gentoo penguins

INTRODUCTION

Interannual variability within the pelagic marine ecosystem around the sub-Antarctic island of South Georgia has been apparent since the early decades of this century. In the period when commercial whaling operated from shore stations (see Bonner 1980), and before whaling levels began to affect stocks (Beddington & May 1982, Gambell 1985), year-to-year fluctuations in the abundance of whales close to South Georgia were evident from catch statistics (Kemp & Bennet 1932). Harmer (1931) suggested that these fluctuations were linked to local availability of food, predominantly Antarctic krill *Euphausia superba*, and to prevailing oceanographic conditions. In recognition of the fact that 'the habits of whales are intimately bound up with the whole economy of oceanic life' (Discovery Committee 1937) the 'Discovery' Investigations were instigated. These investigations included a series of detailed biological oceanographic studies around South Georgia (see Hardy 1967), and yielded a number of results supporting Harmer's observations (1931). Yearly fluctuations in zooplankton abundance were correlated with fluctuations in whale catches (Hardy & Gunther 1935), and interannual differences in the sizes of scientific catches of krill were correlated with years characterised by warm and cold sea surface temperatures (Mackintosh 1972), krill catches being substantially greater in colder years. Marr (1962) suggested that outflow from the Weddell Sea (cold water) was of great importance to the distribution of krill, and this provided a tenable explanation for the observed link at South Georgia between prevailing hydrographic conditions and fluctuating krill abundance (see Deacon 1977).

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More recent analyses of 'Discovery' and other historic data sets, in conjunction with contemporary biological, biogeochemical and physical observations, have suggested that variability within the pelagic ecosystem at South Georgia may be a manifestation of periodic variations throughout the Scotia Sea, and indeed throughout the Southern Ocean as a whole (Priddle et al. 1988, Sahrhage 1988, Murphy et al. 1995, Fedoulov et al. 1996, Whitehouse et al. 1996). These analyses have also provided the foundations for working hypotheses to further explain mechanisms underlying interannual variability in krill abundance at South Georgia. The extent of sea ice cover in the Southern Ocean, for example, has been shown to oscillate regionally with a 4 to 5 yr periodicity as the so-called Antarctic Circumpolar Wave rotates around the continent (Murphy et al. 1995, White & Peterson 1995). Recruitment of juvenile krill in the Antarctic Peninsula region has been linked to the extent and duration of ice in the previous season (Quetin et al. 1994, Siegel & Loeb 1995), the environment beneath winter sea ice apparently providing a favourable habitat for larval krill development (Daly 1990). If krill at South Georgia have their origins in the Peninsula region (Marr 1962, Maslennikov et al. 1983, Everson 1984), then seasons characterised by increased ice cover there could propagate high krill abundance to South Georgia and other downstream locations. Large numbers of small krill have in fact been observed in the vicinity of the South Shetland Islands following a season of extended ice cover (Kawaguchi & Satake 1994).

Krill play a pivotal role in the ecology of the Southern Ocean. They are dominant primary consumers (e.g Miller & Hampton 1989) and constitute a crucial food source for many mammalian and avian predatory species (Everson 1984): in years when local krill abundance is low, near-complete failures in the breeding success of numerous of these predators have been observed (Croxall et al. 1988). Krill are additionally of interest to commercial fisheries (e.g. Everson & Goss 1991, Kawaguchi et al. 1996). Effective resource management for the species is therefore vital, but is complicated by the interannual variability in its abundance (Everson 1992). Assessment of krill abundance is difficult (Everson 1988) but, with the development of new target strength relationships (see Everson & Miller 1994), acoustic techniques have been able to provide estimates which are credible because, on a gross scale, they are in agreement with quantities thought to be required to sustain known predator consumption levels (Trathan et al. 1995). At Elephant Island a time series of acoustic data clearly shows yearly fluctuations in krill density there (e.g. Demer & Hewitt 1994). At South Georgia no annually continuous long-term acoustic data set yet exists, but the data that are available include widely varying estimates of abundance (e.g. Heywood et al. 1985, Murphy et al. 1991, Brierley & Watkins 1996, Goss & Everson 1996). Trawl data from South Georgia suggest that krill densities can vary by as much as 30-fold from year to year (Heywood et al. 1985).

A detailed understanding of the potential magnitude of the interannual variability in krill abundance is clearly essential for effective ecosystem management, and for further development of hypotheses attempting to explain mechanisms behind this variation. In a systematic effort to investigate the pelagic component of the now well-recognised phenomenon of interannual variability at South Georgia, the British Antarctic Survey conceived a new multi-disciplinary, 5 yr research programme for the region, which began in January 1996. Central to this 'Core Programme' are annual acoustic surveys within 2 clearly defined boxes to the northeast and northwest of South Georgia (Brierley et al. 1996). The eastern box is centred on an area of shelf-break to the northeast of Cumberland Bay encompassing Charlotte Bank. Elevated krill abundances have been recorded previously in this area (Priddle et al. 1986, Latogursky et al. 1990) and historically catches of mysticete whales there were high (reviewed by Everson 1984). In addition, numerous observations of krill swarms have been made there (Marr 1962) and the area is targeted by the krill fishing fleet (see Murphy et al. 1996). Oceanographic models (FRAM Group 1991) and observations of iceberg tracks (Trathan et al. in press) also suggest that currents may transport krill from the Antarctic Peninsula around the eastern end of South Georgia into this region. The western box is centred on an area of shelf-break to the north of Bird Island, a major breeding location for numerous avian and mammalian species predatory upon krill (see Croxall et al. 1984, 1985, Croxall & Prince 1980, 1987, Boyd 1993). Bird Island is the site of a long-running research programme in which diet composition and breeding performance of krill predators are regularly monitored (Croxall et al. 1988, in press a), and the western box includes a large area that direct (Hunt et al. 1992, Veit & Prince in press) and satellite tracking observations (Prince et al. in press) have shown to be within the effective foraging range of most of these predator species. The western box is therefore within an important predator feeding ground; in years when krill abundance in this region is low (e.g. 1983: see Heywood et al. 1985; and 1994: see Brierley & Watkins 1996), breeding success at Bird Island is much reduced (Croxall et al. 1988, in press a). Together the boxes also provide good oceanographic coverage of the important and annually variable water mass boundary between Weddell Sea water and Polar

Frontal water (Deacon 1977), and provide a basis for determination of improved estimates of rates of krill flux into the South Georgia region from both ends of the island and also from off- to on-shelf areas (see Murphy 1995).

Since this is the first instance in which the new acoustic survey programme has been reported, the protocols behind survey design, survey method, echo-signal analysis and biomass calculation are given in some detail. Such detail is important in facilitating valid quantitative comparisons with results from previous surveys and surveys from other regions (CCAMLR 1996).

MATERIALS AND METHODS

The outer bounds of the 2 acoustic survey boxes are shown in relation to South Georgia and to its surrounding bathymetry in Fig. 1. The bounding latitudes and longitudes of the 2 survey boxes are given in Table 1.

Survey design. A stratified random survey design incorporating a series of parallel transects was adopted in order to permit calculation of statistically valid variance estimates for mean abundance values within each survey box according to established sampling theory (Jolly & Hampton 1990). Geostatistical analysis of historic krill acoustic survey data from the South Georgia region has indicated that variability in distribution of krill increases to a plateau beyond a separation of 10 km (Murray 1996), suggesting that an inter-transect distance of about this order is appropriate for such surveys. Consequently each 100 km wide survey box was split into 10 equal strata, within each of which 20 possible parallel transects 0.5 km apart were defined. The positions of the 10 transects to be surveyed, one from within each of the strata, were then selected at random following a 2-stage procedure. This procedure both ensured that each possible track had an equal chance of selection, and that sampling intensity was spread reasonably evenly throughout each box by constraining transects from neighbouring strata from approaching any closer than 5 km. First a common offset for all transects was chosen at random from 0 to 5 km in 0.5 km steps. Next an individual transect offset within each stratum was chosen again at random from 0 to 5 km in 0.5 km steps. Fig. 2 shows a schematic representation of this survey design. Cruise tracks for the 1996 surveys in both boxes are given in Fig. 3a.

Table 1. Bounding longitudes and latitudes of the two 100 × 80 km survey boxes

Box	Corner	Longitude °W	Latitude °S
East	Southwest	36.2968	54.0665
	Northwest	35.2827	53.6695
	Northeast	34.4232	54.4121
	Southeast	35.4472	54.8160
West	Southwest	38.9915	54.0128
	Northwest	39.2081	53.3054
	Northeast	37.7370	53.1369
	Southeast	37.4969	53.8415

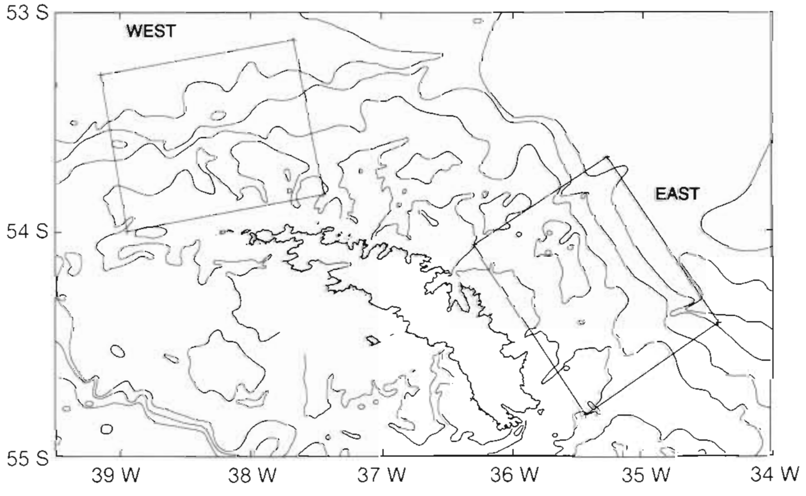

Fig. 1. Location of the 2 acoustic survey boxes in relation to South Georgia and its surrounding bathymetry. Depth contours are at 1000, 500, 200 and 100 m

Acoustic surveys. All acoustic surveys were conducted during hours of daylight to avoid the possibility of bias due to diel vertical migration (Demer & Hewitt 1995) or change in target orientation (Everson 1982, 1983). At a nominal survey speed of 10 knots, 2 transects, each 80 km long, plus an inter-transect track could be run each day within the daylight available at South Georgia during the austral summer. Transects were run alternately in on- and off-shelf directions, with the starting order also being alternated on a daily basis (Fig. 2). Successive transects were surveyed sequentially from west to east in the eastern box and from east to west in the western box, in the general along-shelf directions believed to be against the prevailing current flow (see Deacon 1937, Trathan et al. in press) in an attempt to avoid aliasing flow-mediated horizontal krill transport (MacLennan & Simmonds 1992).

Acoustic data were collected using an EK500 echo sounder (software version 4.01, Simrad 1993) linked to hull-mounted 38 and 120 kHz split beam transducers. The echo-sounder was operated in 'ping mode' to avoid documented software problems (Watkins

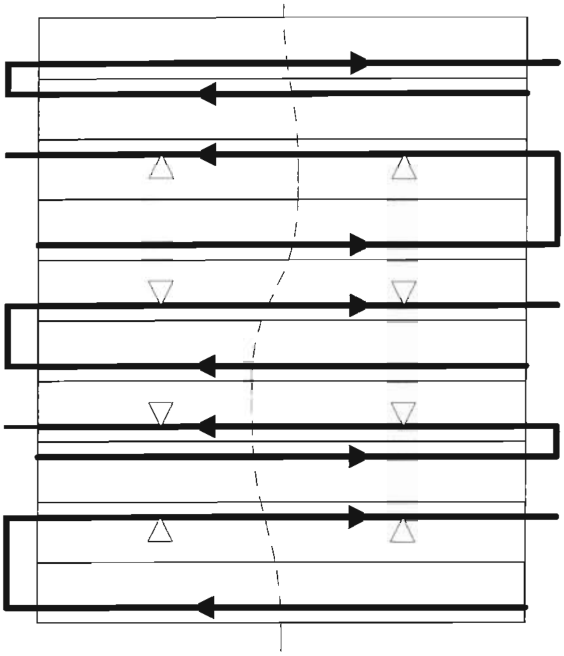

Fig. 2. Schematic representation of the acoustic survey design. The bounding box represents the 100 × 80 km survey box perimeter. Heavy lines indicate the positions of the randomised survey transects within each of the 10 strata. Solid arrows indicate direction of travel and show transect pairs on subsequent days starting alternately on and off shelf. The broken line represents the continental shelf break, and the open arrowheads show the positions of the net sampling sites

et al. 1995). A 'ping interval' of 2.5 s was employed, this being the fastest that could be achieved without provoking a 'ping interval warning'. Mean volume backscattering strength (mvbs) data were collected in 124 × 2 m depth bins from 2 to 250 m (depths relative to transducers in the ship's hull; approximate depth 6 m) and integrated over 100 s intervals, subsequently termed resets (40 pings per sample, ≈0.5 km at 10 knots). Integrated data were recorded in binary format over an ethernet link to a Sun workstation using custom-written logging software.

Calibration. Standard-target echo sounder calibrations (Foote et al. 1987) were conducted in Stromness Bay, South Georgia, immediately after each of the box surveys. Calibration results from both occasions revealed no significant change in echo sounder performance over the duration of the 2 surveys (38 kHz: number of calibrations = 7, standard error = 0.06 dB. 120 kHz: n = 6, SE = 0.04 dB).

Net sampling and length-frequency estimation. Station net sampling to provide krill samples for estimates of mean box-specific length-frequency distributions took place at night following the completion of each pair of acoustic survey transects. Net sampling at night was a logistical necessity given time limitations and the desire to conduct all acoustic surveys in hours of daylight, but did convey the advantage of reducing net avoidance (Everson & Bone 1986). The necessity of night time sampling prevented individual acoustic targets observed on transect from being sampled immediately, but is unlikely to have introduced significant error into our assessment of mean krill length frequency distribution within each box (see Watkins et al. 1990). Hauls were taken with a multiple 8 m^2 rectangular mid-water trawl (RMT8; Roe & Shale 1979). Two hauls per night were taken at fixed on- and off-shelf locations, 20 km in from either end of the final transect of the day (see Fig. 2). These were fished obliquely from the surface to 250 m and back again. Up to 2 additional hauls per night were targeted at dominant acoustic targets, and synchronous surface hauls with a 1 m^2 frame net were taken from a boom deployed from the foredeck. A random subsample of 100 individuals was taken from each haul and for each krill the total length (AT), rounded to the mm below, was measured from the anterior edge of the eye to the tip of the telson (Morris et al. 1988). A mean krill length, weighted to take account of the number density of krill in each net haul, was derived for each survey box and these values are given in Table 2.

Target strength. In order to relate the magnitude of the detected echo signals to krill biomass a target strength (TS) value was derived for each survey box. Box-specific mean TS values were calculated using the box-specific weighted mean krill length estimates in conjunction with the TS/mass relationship described by Brierley & Watkins (1995a, 1996). This generic TS/mass relationship has the advantage of being less sensitive to errors in estimation of krill length than are traditional TS/length relationships (Hewitt & Demer 1993). TS values (dB kg^{-1}) used for each box are given in Table 2.

Acoustic data processing. Binary data were converted to a format compatible with the data-visualisation software AVS (Upson et al. 1989). In this environment erroneous data points, due for example to bottom integration, false bottom echoes or surface noise, were removed (Socha et al. 1996), and time varied gain (TVG) amplified background noise was subtracted using an algorithm described by Watkins & Brierley (1996). Cleaned data were exported to the statistical package Genstat (Payne et al. 1993), where the appropriate calibration correction was made (Simrad 1993). A biomass value for each time/depth integration cell was then calculated from the corrected 120 kHz echo intensity using the target strength values given in Table 2 and the distance run during each integration interval determined with reference to position data collected continuously by GPS.

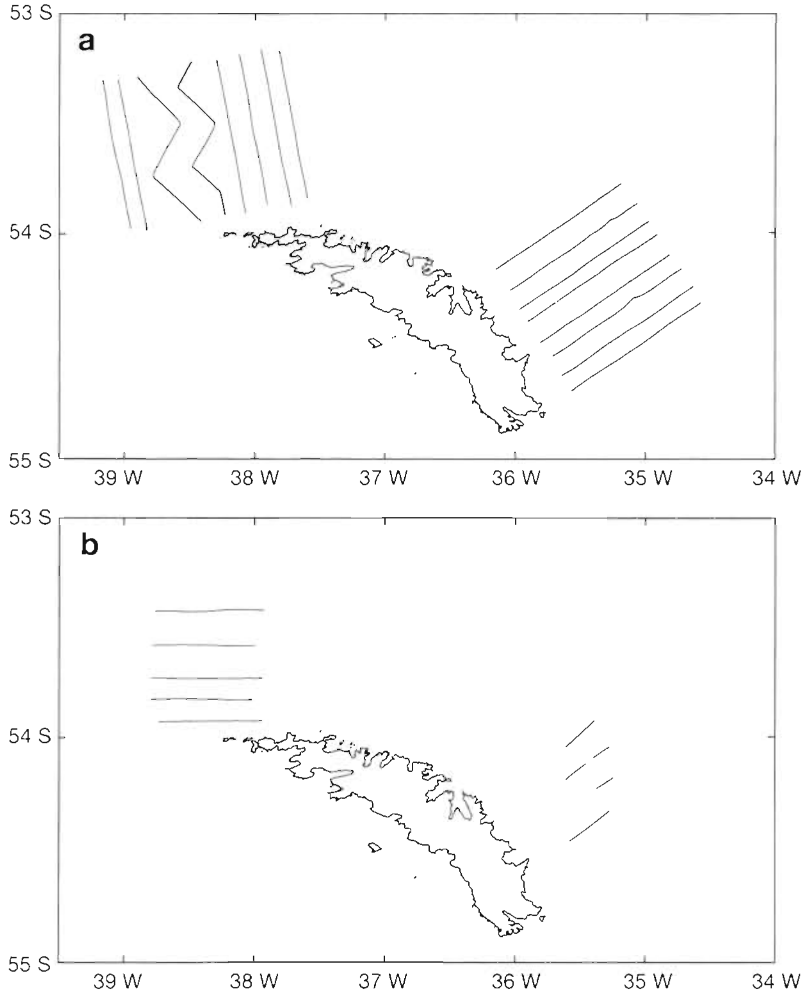

Fig. 3. (a) Cruise tracks within the 2 survey boxes during January 1996. (b) Cruise tracks during surveys conducted in January 1994

Madureira et al. (1993a) described 3 biological acoustic target types, corresponding to krill, zooplankton (smaller than krill) and nekton (fish/squid), which can be distinguished routinely on echo charts recorded in the vicinity of South Georgia. Madureira et al. (1993a) have also demonstrated that these and other targets (Madureira et al. 1993b) can be discriminated on the basis of their different echo strengths at 120 and 38 kHz. Madureira et al. (1993a) suggest that a difference in signal strength between 120 and 38 kHz echoes (δmvbs = mvbs 120 kHz − mvbs 38 kHz) in the range 2 to 12 dB is indicative of krill. Our own observations during the 1996 survey, and those of other authors made during acoustic studies of wild (Hampton 1990, Everson et al. 1993) and caged (Foote et al. 1990) krill, and calculations on the basis of theoretical models describing sound scattering from euphausiids (Greene et al. 1991) support this dual frequency relationship being a robust descriptor of krill which remains linear over a wide numerical range of krill densities, and hence over a wide dynamic range of echo signal intensities. Therefore, in accordance with Madureira et al. (1993a), the following criteria were used to partition all acoustic signals into 3 biological categories:

δmvbs between 2 and 12 dB
Antarctic krill *Euphausia superba*

δmvbs >12 dB
Zooplankton smaller than krill

δmvbs <2 dB
Nektonic organisms larger than krill

In order to remove multiple low intensity signals which skewed the frequency distribution of observed δmvbs values, Madureira et al. (1993a) imposed a −70 dB threshold on their 120 kHz data before applying these signal recognition criteria. Their data were collected using a Simrad EK400 and integrated over quite large intervals (20 m × 1.852 km). Within integration intervals where few targets were observed, the mvbs value reported therefore had the potential to be very low and to be obscured by noise. Data in the current study were collected using an EK500, reputed to have superior signal to noise characteristics, and were integrated over much smaller intervals (2 m × 0.5 km) In addition we now have the ability to remove much background noise from our echo-signals (see Watkins & Brierley 1996). We consequently believe that it is not necessary to apply such a stringent threshold; in this study all echo pairs where the 120 kHz signal exceeded −100 dB were considered. This approach results in a much reduced number of data points being rejected, although because of the logarithmic nature of the dB scale and the inherent aggregated nature of krill distribution, we have observed that echoes with an intensity of less than −70 dB contribute less than 10% to total krill biomass within a typical survey transect.

Table 2. Weighted mean krill length and associated target strength (TS) dB kg^{-1} of krill for each survey box

Box	Length (mm)	TS (dB kg^{-1})
East	29.5	−39.13
West	32.0	−39.03

Density estimation. Density estimates for each faunal class (krill, small zooplankton and nekton) were calculated by selecting all density values within each reset matching the required δmvbs criteria for that class. The density values (g m^{-3}) from each 2 m depth horizon within a reset were then doubled to account for bin depth, summed to provide a within-reset mean density, and multiplied by their respective integration interval lengths (km) to give a total density for each reset. Reset totals were summed within transects and divided by total transect length (km) to yield a mean transect density in g m^{-2} (Jolly & Hampton 1990). Transect totals were weighted by transect length, and weighted mean and variance estimates derived for each survey box according to Jolly & Hampton (1990) Mean and variance estimates for each faunal class for each survey box are given in Table 3.

Data from surveys carried out in similar regions during 1994, previously reported by Brierley & Watkins (1995a, b, 1996) were re-analysed using the above signal recognition and thresholding criteria in order to facilitate a direct between-year comparison of abundance. Density estimates and their variances from these re-analysed data are presented in Table 4 alongside equivalent 1996 estimates. Cruise tracks for the 1994 surveys are given in Fig. 3b.

Table 3. Lengths of each transect, and transect densities for each faunal class within each 1996 survey box with their weighted mean and variance estimates

Box	Transect	Length (km)	Density estimate (g m^{-2}) Krill	Zooplankton	Nekton
East	1	78.69	45.85	36.45	0.76
	2	80.66	48.46	49.40	0.82
	3	79.38	35.85	29.24	0.42
	4	79.84	36.23	22.74	0.40
	5	80.12	33.98	26.48	0.54
	6	79.91	60.47	38.82	0.27
	7	80.38	35.40	28.63	0.36
	8	79.68	28.31	20.70	0.51
Mean			40.57	31.57	0.51
Variance			13.37	11.36	0.00
West	1	77.66	24.41	10.64	0.64
	2	81.00	14.81	5.20	0.42
	3	79.14	39.01	31.45	0.64
	4	80.74	16.11	21.75	0.94
	5	106.25	64.28	39.13	2.48
	6	98.52	13.65	2.57	0.48
	7	80.36	12.25	7.09	1.03
	8	77.94	18.05	10.01	1.29
Mean			26.48	16.51	1.03
Variance			54.30	27.35	0.08

Table 4. Comparison of krill density estimates (± variance) for the eastern and western boxes for January 1994 and January 1996

Year	West	East
1994	7.43 (± 1.33)	1.87 (± 0.14)
1996	26.48 (± 54.30)	40.57 (± 13.37)

RESULTS AND DISCUSSION

Acoustic surveys

Rough weather at the beginning of the eastern box survey reduced the time available and so the 2 outermost transects were omitted, reducing the area covered by the survey by 20% but retaining its centre of location. Preliminary inspection of echo charts from the eastern box revealed that the abundance of krill in on-shelf regions was higher than that in deep water off-shelf. Given that adjacent transect pairs were begun alternately at the on- and off-shelf ends of the box, this suggests that the distributional variation was of a geographic rather than temporal nature. Evidence from elsewhere has suggested that the distribution of krill (Orlowski 1983) and other pelagic species (Rogers 1994, Dower & Mackas 1996) are linked to bathymetric features. For this reason it is intended that each of the subsequent annual acoustic surveys will be conducted along the same transects as those run here. Collecting data from the same transects each year should prevent any genuine interannual abundance variation from being confounded with and possibly masked by the influence of otherwise varying bathymetry on krill distribution.

The first 2 acoustic survey transect pairs of the western box were run successfully as planned. By Day 3, however, developing swell running at 45° to the transects caused excessive ship roll which compromised the quality of the acoustic data, resulting in numerous signal dropouts and increased surface noise. To overcome this problem transects were run in the prescribed on/off-shelf direction, but at an angle to the sea chosen to reduce the motion of the ship (see Fig. 3a). The poor weather continued on Day 4, and a zig-zag survey track was again adopted. Zig-zag transects provide increased sampling effort per unit area in the region at which they converge. In an effort to minimise the bias that this may potentially have caused, an analysis of autocorrelation was conducted to determine over what distance biomass between adjacent resets was correlated. This analysis suggested that within the western box there was no distance-dependent correlation of biomass between resets. No transect truncation was therefore deemed necessary, and vertices of zig-zags were merely cut to discard data from the turn points where entrainment of bubbles under the ship's hull compromised signal integrity. Daily zig-zags were then considered as single transects, and their contribution to overall mean density was simply weighted by overall length (see Table 3). By Day 5 the weather had improved, and the straight survey tracks originally proposed for that day were run.

Biomass estimates

The mean weighted krill density within the eastern survey box was calculated as 40.57 g m^{-2}, with a weighted variance of 13.37. The mean krill density for the western box was lower, at 26.48 g m^{-2}, but the variance associated with this mean, 54.30, was substantially higher. Weighted mean krill biomass estimates for each survey box, and estimates of their variance, are presented in Table 3, along with similar estimates for the small zooplankton and nekton fractions. Biomass estimates can be attached to the small zooplankton component at each site as the generic target strength relationship used is likely to approximate a plausible TS value for a heterogeneous aggregation of small crustacean zooplankters. In the absence of any other appropriate general TS value for the nektonic fraction, which was likely to be composed of fish with and without swim bladders (Marshall 1979) and of various squid species, the generic TS value was applied here also. Although an absolute biomass estimate cannot be attached to this proportion with any degree of confidence, the measure is useful to the extent that it provides a comparable indication of the relative abundance of this pelagic size fraction at each location. This approach essentially has the effect of scaling all backscattering density values by a common factor, and could be considered in broad terms as portraying densities in units of equivalent krill biomass. A number of nations currently conduct acoustic surveys in various regions of the Southern Ocean, but there is as yet no agreed standard for discriminating that fraction of the biomass attributable to krill; direct comparisons of krill biomass estimates are therefore not always possible. Consequently it has been suggested (CCAMLR 1996) that reports on acoustic estimation of krill biomass should include a measure of total estimated biomass for the survey region. This would facilitate direct gross comparisons between surveys. Employment here of a generic TS relationship allows our 3 partitioned biomass components to be summed to satisfy this suggestion.

Krill distribution

Given the large predator biomass and diversity of predatory species foraging from Bird Island and elsewhere within the western box region (Croxall et al. 1984, Croxall & Prince 1987, Hunt et al. 1992, Boyd et al. 1994), one might expect to observe lower densities of krill there than within the eastern box if the flux of krill into the 2 areas were equal. The eastern box is adjacent to smaller populations of breeding seabirds and seals (especially penguins and fur seals; see Boyd 1993) and lies within the effective foraging range of a much reduced predator biomass. Therefore krill within the eastern box are likely to be subject to a reduced predation pressure in comparison with those in the western box, where krill extraction rates may be higher (see Murphy 1995). Although the mean krill density estimate for the western box is lower than that for the eastern box, the high variance associated with the western box mean prevents the densities from the 2 boxes from being statistically separable. The observed difference in mean krill size between the 2 survey regions (mean length eastern box = 29.5 mm, western box = 32.0 mm) is unlikely to have been caused by prey selection. Studies of krill within penguin, albatross and fur seal diets (Croxall & Pilcher 1984, Hill et al. 1996, Reid et al. 1996) suggest that predators preferentially target larger krill: our length-frequency estimates however suggest that krill within the western box were ~2.5 mm larger than those in the eastern box. Differences in mean krill size between the 2 boxes are also unlikely to be attributable entirely to growth achieved in the period between the 2 surveys; the required growth rate of ~2.5 mm over 1 wk, although similar to that reported in a krill patch around South Georgia (Clarke & Morris 1983), exceeds other published growth rates by a factor of ~3 (reviewed by Quetin et al. 1994). The observed difference in size between krill from the 2 regions is possibly an indication that krill within both regions have different geographic origins, or have possibly been resident within water masses with differing levels of food availability (see Trathan et al. 1993). A number of genetic studies have been conducted in attempts to distinguish discrete populations of krill with different possible geographic affinities (for example Ayala et al. 1975, Fevolden & Schneppenheim 1989) but to date, at the resolution available with allozyme techniques (see Ferguson 1980), no such differentiation has been conclusively detected.

Interannual variability

Although krill abundances are known to fluctuate markedly at South Georgia (Heywood et al. 1985, Priddle et al. 1988), a continuous time series of directly comparable krill density estimates does not yet exist for the region. It is therefore difficult to classify estimates from a particular year within a quantitative framework as being for example 'high', 'low', or 'normal' Previous acoustic estimates of krill abundance at South Georgia range widely, for example from 11.7 g m^{-2} for a survey conducted in November/December 1981 (Murphy et al. 1991) to 95 g m^{-2} for a January 1992 survey (Goss & Everson 1996). This range includes the value of 59.7 g m^{-2} re-calculated by Trathan et al. (1992, 1995) from data collected during the FIBEX survey of the BIOMASS (Biological Investigations of Marine Antarctic Species and Stocks) programme in 1981 (Anonymous 1986), using the current CCAMLR recommended target strength relationship (CCAMLR 1991, derived from Greene et al. 1991). Difficulties arise in attempting to draw direct comparisons either between some of these previous studies, or with our current estimates, because of differences in survey coverage, design, and in data analysis. Murphy et al. (1991) included data from the entire perimeter of South Georgia in their analysis and, as with Trathan et al. (1992, 1995), assumed that all acoustic targets were krill. Goss & Everson (1996), on the other hand, partitioned echo energy, isolating the krill component, but based their estimate only on data collected on-shelf. If the density estimates for each of the 3 faunal classes discriminated in the present study are summed (a possibility since the same TS was used to calculate the biomass for each fraction), then the totals for the eastern and western boxes in January 1996 are 72.7 and 44.0 g m^{-2} respectively, values which are not dissimilar to those recalculated from the 1981 FIBEX data. It is generally considered (e.g. Trathan et al. 1995) that the FIBEX survey occurred during a year of high krill abundance around South Georgia. With reference to the abundance estimate for that year it would appear that the present (1996) survey also coincided with a period of elevated krill abundance. High levels of abundance were prevalent at Elephant Island, also within the Atlantic Sector of the Southern Ocean, at this time (Hewitt et al. 1996) and our own observations of the occurrence of krill swarms at the surface in the Polar Frontal region in 1996 also tend to suggest that the 1995/96 austral summer season was a season of 'high' krill abundance. Given current hypotheses on factors affecting krill recruitment (Siegel & Loeb 1995), the extended ice distribution during the preceding winter might anyway lead to the expectation that the 1995/6 austral summer season would be characterised by an elevated krill biomass and by the predominance of juvenile krill. Such expectations are supported by our net haul data which revealed a predominance of small krill at this time.

Although there are difficulties in making direct comparisons between data from this study and that from most previous acoustic surveys at South Georgia, a meaningful direct comparison can be made with a 1993/4 survey there (Brierley & Watkins 1996). The 1993/4 survey was conducted within similar regions (see Fig. 3b) using the same echo sounder, and re-analysis of data from that survey using the same target recognition criteria as those used here allows a direct comparison to be made. The survey carried out in January 1994 revealed remarkably low levels of krill (Brierley & Watkins 1995a, b, 1996), with abundance estimates of 1.87 and 7.43 g m^{-2} for the eastern and western box equivalent areas respectively (see Table 4). Taken together this pair of estimates indicate a greater than 20-fold fluctuation in abundance. Such fluctuations are extreme and, as Heywood et al. (1985) have pointed out, are not compatible with a documented life span of over 5 yr for a locally maintained population. This observation emphasises the importance of transport processes to krill abundance at South Georgia, and in turn the importance of such processes to predator performance and to the state of the pelagic marine ecosystem at South Georgia in general (Murphy et al. 1991, Murphy 1995).

Krill abundance and predator performance

The 1993/4 krill density estimates are the lowest values recorded for South Georgia, and correspond with a season of major breeding failure for numerous krill predators there (see Brierley & Watkins 1996, Croxall et al. in press a). Acoustic surveys provide instantaneous abundance estimates for the period during which the surveys were conducted, but it may be argued that they reveal little concerning potential variations outside that time. Our acoustic estimates of krill abundance from both 1994 and 1996 are however supported in relative terms by evidence from diet composition and breeding performance from a number of avian and mammalian species normally dependant upon krill for food (see Brierley & Watkins 1996). Predator meal contents have been shown to reflect regional planktonic resource availability (Bost et al. 1994), and performance indices from habitual krill predators reflect levels of krill availability throughout the duration of the breeding season (Croxall et al. 1988): as such these indices can be considered as a measure of krill abundance integrated over time. At Bird Island, during the 1993/4 austral summer, at a time when acoustic surveys revealed very low levels of krill abundance (Brierley & Watkins 1995a, 1996), Gentoo penguins achieved only 4 % breeding success, amongst the lowest values recorded for the species since records began in 1976 (Croxall et al. 1988, Croxall & Rothery 1995). In 1995/6 breeding success for Gentoo penguins was, at 80 %, well above the mean for the species (44% over 19 seasons between 1976 and 1995), indicating favourable levels of krill availability (Croxall et al. in press a). Macaroni penguins, which target krill preferentially but have the ability to switch prey to exploit other zooplankton in years of krill absence (Croxall et al. in press b, unpubl.), had a high krill content in their diet in 1995/6 (>99% by mass compared to 13% in 1993/4) and produced offspring with a fledging weight of 3.179 kg (n = 100, SEM ± 0.04), significantly higher (ANOVA $F_{1,198} = 22.88$, $p < 0.001$) than the 2.913 kg (n = 100, SEM ± 0.04) achieved in 1993/4 (Croxall et al. unpubl.). The broad similarity between data from the different sources therefore suggests that acoustic estimates can be reliable indicators of krill availability around South Georgia on a year to year basis, at least within the summer season, and have a value as environmental indicators beyond that of an instantaneous measure. Congruence between data from such disparate sources as predator performance and acoustics also serves to highlight the benefit of integrated studies using multiple approaches to assess magnitudes of variation within ecologically and commercially important species.

It seems likely that the 1993/4 density estimates (1.87 and 7.43 g m^{-2}) fall towards the extreme low end of the potential krill abundance spectrum at South Georgia, and are not much greater than the acoustically detectable minimum (Everson & Miller 1994). As our time series lengthens it will become possible to judge krill abundance in a particular year relative to the expected maxima or minima for the region. It should then become clear whether our 1995/6 estimates (40.57 and 26.48 g m^{-2}) represent 'high' values or are perhaps 'normal'. Predator performance data are good at revealing seasons of poor abundance but, in seasons of high abundance, provide little information on the amount by which krill abundances may exceed dietary requirements (Cairns 1987, Monaghan 1996). Acoustic techniques have an inherent minimum detection threshold (Everson & Miller 1994) but are able to quantify high abundances which are not apparent from predator performance data alone because of saturation effects. Predator-based and acoustic studies are therefore complementary to investigations of variations within the pelagic marine ecosystem, and together should enable a framework describing the magnitude of the expected maximum fluctuation in krill abundance at South Georgia to be developed.

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