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ACOUSTIC ESTIMATES OF KRILL DENSITY AT SOUTH GEORGIA, 1981 TO 1998

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Abstract

Acoustic estimates of densities of Antarctic krill, *Euphausia superba*, at South Georgia during 11 austral summers between 1981 and 1998 are presented. Krill density at the island fluctuated widely from year to year over that time, ranging from ≈2 to ≈150 g m^{-2} (fresh mass). The 1982, 1991 and 1994 austral summer seasons were characterised by particularly low densities of krill (upper 95% confidence limits <15 g m^{-2}). For five of the summers between 1990 and 1998 it was possible to calculate separate density estimates for northeastern and northwestern South Georgia, and in four of these seasons density was higher to the east.

Résumé

Estimations acoustiques de la densité du krill antarctique, *Euphausia superba*, en Géorgie du Sud au cours de 11 étés australs, entre 1981 et 1998. Pendant cette période, on assiste à une fluctuation importante de la densité de krill à cette île d'année en année, entre ª2 et ª150 g m^{-2} (poids vif). Les saisons d'été austral de 1982, 1991 et 1994 se caractérisent par une densité de krill particulièrement peu élevée (avec des limites supérieures de l'intervalle de confiance à 95% <15 g m^{-2}). Pour cinq des étés de 1990 à 1998, il est possible de calculer des estimations de densité séparées pour le nord-est et le nord-ouest de la Géorgie du Sud, et la densité de quatre de ces saisons est plus élevée à l'est.

Резюме

В работе представлены акустические оценки плотности антарктического криля (*Euphausia superba*) у Южной Георгии за 11 австральных летних периодов с 1981 по 1998 г. В течение этого периода плотность криля у острова менялась от ≈2 до ≈150 г м$^{-2}$ (сырая масса). Австральные летние периоды 1982, 1991 и 1994 гг. характеризовались особенно низкими показателями плотности криля (верхние пределы 95% доверительных интервалов <15 г м$^{-2}$). Для пяти летних периодов с 1990 по 1998 г. оказалось возможным рассчитать индивидуальные оценки плотности для вод северо-востока и северо-запада Южной Георгии; в четырех случаях плотность была выше на востоке.

Resumen

En este trabajo se presentan las estimaciones acústicas de la densidad de kril antártico, *Euphausia superba*, en Georgia del Sur durante 11 veranos australes, entre 1981 y 1998. La densidad de kril frente a la isla varió enormemente de un año a otro durante ese período, de ª2 a ª150 g m^{-2} (peso en vivo). Las temporadas estivales de 1982, 1991 y 1994 se caracterizaron por densidades extremadamente bajas de kril (límites superiores del intervalo de confianza del 95% <15 g m^{-2}). En cinco de los veranos entre 1990 y 1998 se pudo estimar por separado las densidades para el sector noreste y noroeste de Georgia del Sur, y en cuatro de estas ocasiones la densidad fue mayor hacia el este.

Keywords: Antarctic krill, density, *Euphausia superba*, interannual variability, South Georgia, CCAMLR

INTRODUCTION

Interannual variability in the abundance of Antarctic krill, *Euphausia superba*, at South Georgia has been apparent since the 1920s and 1930s when shore-based whaling took place from the island and when the early *Discovery* investigations were underway there (see Priddle et al., 1988). Since that time there have been numerous further reports of large year-to-year fluctuations in krill abundance in the vicinity of South Georgia, based on both commercial and scientific netting studies, and on observations of the breeding performance of krill-dependent predators (e.g. Bonner et al., 1978; Heywood et al., 1985; Croxall et al., 1988; Fedoulov et al., 1996). The phenomenon of interannual variability in krill abundance thus seems to be an integral feature of the South Georgian marine ecosystem (reviewed by Brierley et al., 1997a).

Acoustic survey techniques are now the favoured means for assessing krill abundance, allowing detailed sampling over large areas in short periods of time. The BIOMASS FIBEX experiment in 1981 included acoustic surveys at South Georgia (Everson and Miller, 1994). Subsequent to that study, the British Antarctic Survey (BAS) has undertaken numerous cruises to investigate the marine environment around the island. This paper presents the best estimates of krill density at South Georgia between 1981 and 1998 based upon acoustic data collected there during those cruises. The resulting time series includes estimates arising from cruises where determination of krill biomass was a primary objective, and estimates derived from acoustic data collected subsidiarily during other studies of the pelagic ecosystem at South Georgia.

MATERIALS AND METHODS

A summary of acoustic survey details for all years considered is presented in Table 1. In all instances echosounders were fully calibrated. From 1989 onwards all calibrations were carried out at or near Stromness Bay, South Georgia, using standard sphere techniques. Water temperature and salinity were recorded on each occasion so that the expected target strengths of the standard spheres could be adjusted for ambient conditions. These records also enabled the impact of sea temperature on echosounder system performance to be monitored (see Brierley et al., 1998).

Survey Design

Since the 1996 austral summer (austral summer seasons include months from two calendar years; by convention the year given refers to the year in which the season ended) BAS has conducted annual (i.e. 1996, 1997 and 1998) acoustic surveys at South Georgia within two defined 80 x 100 km boxes which span the continental shelf-break to the northwest and northeast of the island (see Brierley et al., 1997a). Where cruise tracks allow, we have calculated krill density estimates from earlier cruises for areas corresponding to those boxes. For some years, however, data were not available for those exact regions, and for such occasions we have used the geographically nearest data we have. Transects considered in krill density estimates reported here are shown for some of the more recent cruises (Figure 1). From this it can be seen that before 1996, data were available from areas broadly equivalent to both the present-day survey boxes in two seasons, 1990 and 1994. Data for 1986 were available for an area equivalent to the western box. In three other of the years considered here data were available only for restricted areas along the north coast of South Georgia (1981, 1991 and 1993). For the remaining two years, 1982 and 1992, density estimates were derived from surveys around the whole island. The area covered by the 1982 cruise was very extensive and included long transects in oceanic water: the 1992 survey, however, was restricted to on-shelf locations where water depth was <500 m. Krill density at South Georgia is often elevated on-shelf and in the vicinity of the shelf-break (see Atkinson et al., 1999; Reid et al., 1999), and inclusion of differing proportions of such areas in surveys in different years may bias relative density estimates. Survey tracks and other details of those cruises not depicted in Figure 1 (i.e. 1981, 1982 and 1992) are given in Trathan et al. (1992), Murphy et al. (1991) and Goss and Everson (1996) respectively.

Krill often exhibit pronounced diel vertical migrations (e.g. Godlewska, 1996), and because of the documented negative bias this behaviour has on acoustic survey estimates of krill density (Demer and Hewitt, 1995), surveys ought only to be conducted in hours of daylight. With the exception of the 1982 value, all biomass estimates reported here were derived only from acoustic data gathered during daylight.

Target Identification

Krill are not the only organisms inhabiting the pelagic realm around South Georgia that are detected by scientific echosounders. In order for accurate krill biomass estimates to be derived from acoustic data it is therefore necessary for echoes due to krill to be distinguished from those caused by other scattering sources. In krill studies, such echo-partitioning has been achieved by visual classification of echo traces and, more recently, using dual-frequency (ΔMVBS)

Table 1: Summary of similarities and differences between acoustic surveys of krill density at South Georgia, 1981 to 1998, and estimates of weighted mean krill density (and variance). Cruise codes prefixed JB refer to cruises aboard the British Antarctic Survey ship RRS *John Biscoe*, JR identifies cruises aboard its successor, RRS *James Clark Ross*. * indicates very few krill caught, TS for this year was taken as the mean value expected for krill spanning the size range 25 to 55 mm (see Brierley and Watkins, 1996).

Year of Survey	Cruise Code	Area of Coast	Dates of Survey	Echosounder/ Integrator	Day/ Night	Krill ID Method	Mean Length (mm)	Target Strength	Krill Density			Reference
									Mean ($g\,m^{-2}$)	Variance	CV (%)	
1981	FIBEX	North	25/2–7/3	EK120 analogue	Day	All signal	37.0	-72.80 dB per krill (weight = 0.36 g)	59.70	511.95	37.90	BIOMASS, 1986 Trathan et al., 1992
1982	JB03	All	24/11–19/12	EKS120 QM	Day + night	All signal	29.7	-75.00 dB per krill (weight = 0.18 g)	11.70	1.24	9.50	Murphy et al., 1991
1986	JB06	West	6–12/2	EK400 QD	Day	Visual	52.5	-38.39 dB kg^{-1}	29.71	196.78	47.22	Goss and Grant, 1999
1990	JB10	West East	5–18/1 4–6/2	EK400 ESP	Day	Visual	40.3 40.3	-38.73 dB kg^{-1} -38.73 dB kg^{-1}	45.08 75.06	392.67 247.80	43.96 20.97	BAS, unpublished
1991	JB11	North	19/1	EK400 ESP	Day	Visual	39.0	-38.77 dB kg^{-1}	6.36	11.43	53.16	BAS, unpublished
1992	Fish survey	All, on shelf	8–27/1	EK400 ESP	Day	ΔMVBS	34.0	-74.08 dB per krill (weight = 0.31 g)	94.96	202.58	14.99	Goss and Everson, 1996
1993	JR03	North	6–7/1	EK500	Day	Visual	43.1	-38.65 dB kg^{-1}	65.82	518.70	34.60	BAS, unpublished
1994	JR06	West East	9–10/1 5–9/1	EK500	Day	ΔMVBS	* *	-38.77 dB kg^{-1} -38.77 dB kg^{-1}	7.43 1.87	1.33 0.14	15.54 20.28	Brierley and Watkins, 1996
1996	JR11	West East	18–22/1 12–15/1	EK500	Day	ΔMVBS	32.0 29.5	-39.03 dB kg^{-1} -39.13 dB kg^{-1}	26.72 40.57	59.00 13.37	28.75 9.01	Brierley et al., 1997a
1997	JR17	West East	29/12–2/1 23–27/12	EK500	Day	ΔMVBS	45.4 36.1	-38.59 dB kg^{-1} -38.89 dB kg^{-1}	25.17 54.65	18.44 36.55	17.06 11.06	Brierley et al., 1997b
1998	JR28	West East	24–28/1 30/1–3/2	EK500	Day	ΔMVBS	40.4 39.7	-38.73 dB kg^{-1} -38.75 dB kg^{-1}	21.41 150.99	17.96 879.68	19.80 19.64	BAS, unpublished

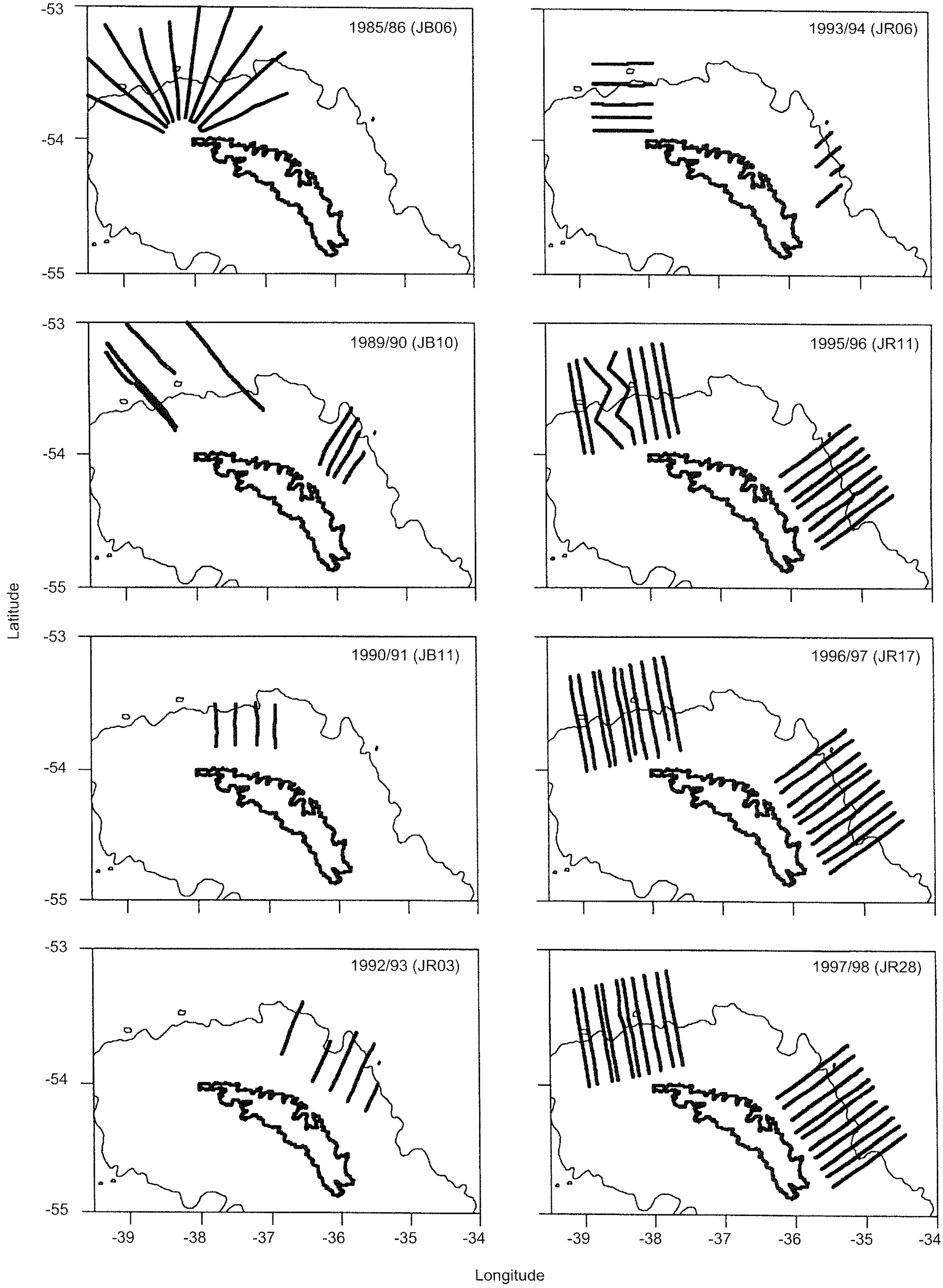

Figure 1: Maps showing South Georgia, the approximate position of the shelf-break as defined by the 1 000 m isobath, and sections of cruise track from which acoustic data for krill density estimation were taken.

echo-classification techniques: both give broadly similar results (see Watkins and Brierley, 1997). In all except the 1981 and 1982 surveys, for which biomass estimates are based on all backscattered signal, data have been partitioned using one or other of these approaches, and values reported for cruises after this time are thus what we consider to be the best estimates of krill density. Because they are based on all backscattered energy, 1981 and 1982 values are likely to be overestimates of krill density.

Target Strength

Both echosounder technology and understanding of the acoustic properties of krill (e.g. target strength (TS), multifrequency signature) have advanced considerably since the FIBEX survey in 1981. Trathan et al. (1992) re-analysed the FIBEX acoustic data using the CCAMLR-recommended TS/krill-length relationship (Greene et al., 1991), and their revised estimate for South Georgia is the first point in the time series presented here. Although several echosounders have been used over the years, all surveys reported here have similarly been conducted at 120 kHz and interpreted using the Greene et al. (1991) TS relationship (Table 1). In some instances this relationship has been applied as a TS per kilogram of krill, rather than as a TS per individual, because this approach is less sensitive to errors in krill length estimation (see Hewitt and Demer, 1993; Brierley and Watkins, 1996).

Sensitivity Analysis

The South Georgia boxes, from within which acoustic estimates of krill density are now derived, are surveyed along 10 randomly spaced parallel transects that run normal to the continental shelf-break (see Brierley et al., 1997a). Random, parallel transects are required for the mean and variance of krill density to be calculated using standard statistical theory (Jolly and Hampton, 1990). We were able to obtain data from essentially parallel transects for cruises in all seasons prior to 1996 (with the exception of 1986 when a radial survey design was adopted). Since these transects were not run with reference to any preconceived notions relating to krill distribution, and since their effective start and end positions for the analyses reported here were often constrained only by persistence of daylight, we believe that it is also reasonable to consider these transects as random relative to the patchy distribution of krill within a dynamic physical environment. In most instances, however, only four such transects were available. In order to establish the likelihood that data from only four transects would yield a mean density estimate falling within the 95% confidence limits of the mean arising from 10 transects, we conducted the following simulation. Using individual transect means for the 10-transect surveys exhibiting both the highest and lowest variances (1998 east and west South Georgia box surveys respectively; see Table 1), for each survey we calculated mean krill density estimates for each of the 210 possible combinations in which four transects could be selected from 10. The 210 four-transect means resulting from each survey were then inspected to determine how many fell outside the 95% confidence limits for the mean for all 10 transects.

RESULTS

Best estimates of krill density at South Georgia from 1981 to 1998 are given in Table 1. Mean values ±95% confidence limits (from sampling variance) are presented graphically in Figure 2. Over the period for which data are available, mean density of krill at South Georgia has varied between years from <2 g m^{-2} to >150 g m^{-2}, i.e. by two orders of magnitude. Variances associated with means are, however, typically high, with most coefficients of variation (CV) being of the order of 20%. Demer (1994) has shown that in addition to sampling variance, survey methods and acoustic apparatus can also contribute uncertainty to acoustically derived krill density estimates. The confidence intervals reported here do not include contributions from these sources.

Sensitivity analyses suggest that four-transect surveys will yield mean krill density estimates falling within the 95% confidence limits of the mean determined from 10 transects in ≈93% of cases. For the 1998 box survey to the east of South Georgia (high variance) only 15 of the possible 210 four-transect means fell outside the 95% confidence limits for the 10-transect mean; in the west (low variance) only 16 instances fell outside these bounds.

For five years (1990, 1994, 1996, 1997 and 1998) it was possible to calculate separate density estimates for east and west South Georgia. In all except 1994 mean density was higher in the east.

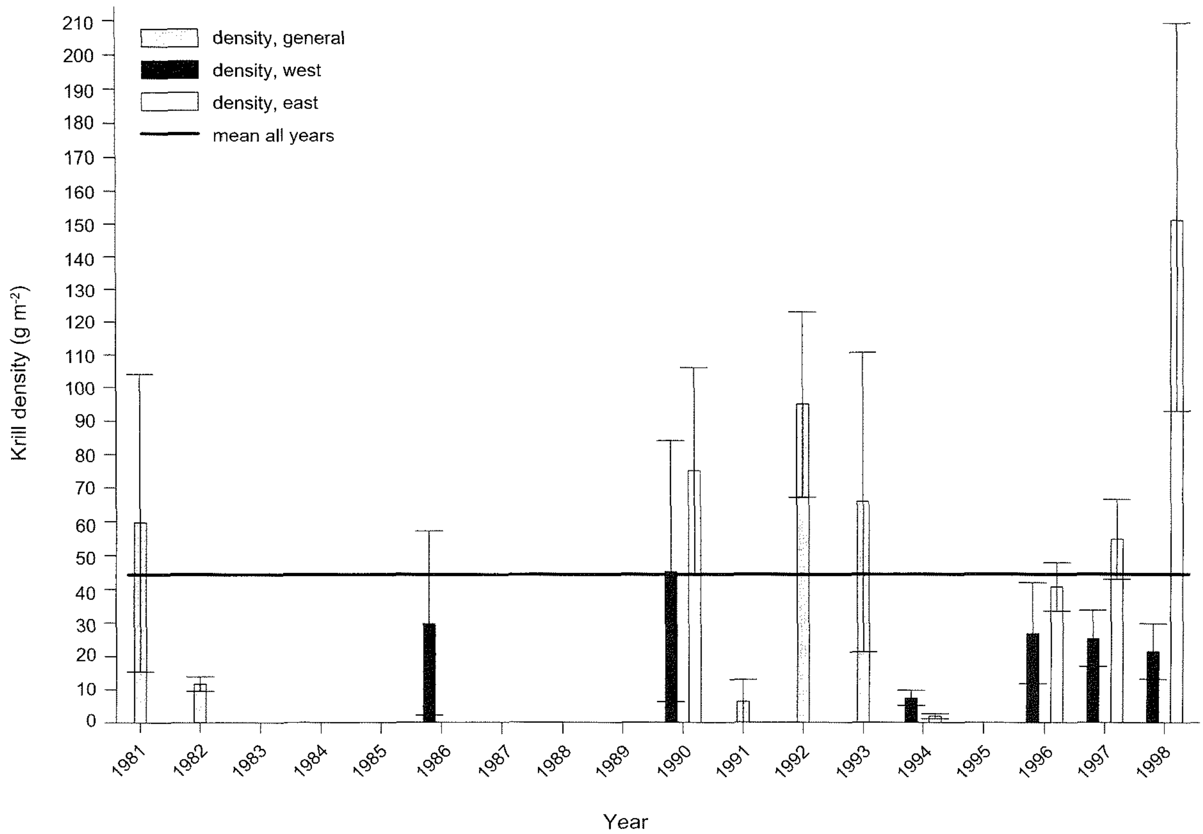

Figure 2: Bar chart showing acoustically determined krill density estimates at South Georgia between 1981 and 1998. Values shown are weighted means (Jolly and Hampton, 1990) ±95% confidence intervals.

DISCUSSION

Despite some major differences in cruise objectives and method of execution over the years, it has been possible here to derive a time series of comparable acoustic estimates of krill density at South Georgia spanning almost two decades. Although method-related caveats exist, the variability evident within this time series supports the generally held impression gained from previously reported observations of net catches, commercial fishing success and predator performance, that large between-year fluctuations in krill abundance are a regular feature of the South Georgian pelagic marine ecosystem. The causes of this variability are likely to be complex and involve interactions of numerous physical and biological factors (Murphy et al., 1998). These factors are not discussed in this paper. Instead, all relevant acoustic survey data for South Georgia are summarised to allow the phenomenon of interannual variability in krill density at the island to be ascribed some quantitative bounds. Previously it has been possible only to describe krill density at South Georgia during a particular season in somewhat subjective terms as being, for example, 'good', 'bad' or 'unusual' (e.g. Priddle et al., 1997). Such descriptions may be misleading, and subjective impressions have not always reflected accurately the picture that later becomes apparent from quantitative analyses.

Since 1981, mean krill density at South Georgia appears to have fluctuated between a maximum of 150.99 g m^{-2} and a minimum of 1.87 g m^{-2}. From Figure 2, 1982, 1991 and 1994 stand out as years of particularly low abundance. Indeed, in these years the breeding performance of most krill-dependent predators at South Georgia was poor, and the proportion of krill in the diet of such species was reduced significantly (e.g. Croxall et al., 1988; Boyd et al., 1994; Croxall et al., 1998). These predator-based observations provide independent corroboration that krill abundance was abnormally low during these seasons. In each of 1982, 1991 and 1994 the upper 95% confidence limit for the acoustic estimate of mean krill density (μ + 1.96σ) fell below 13.9 g m^{-2}. The mean of all combined annual density estimates for South Georgia given here is 44.3 g m^{-2} (σ = 29.3). Thus we can say that if the upper 95% confidence limit for the mean krill density within any given year is less than μ - σ for all years, then the year in question can be considered one of unusually low abundance. From standard sampling theory, and assuming that the distribution of mean density estimates for all years remains normal (the distribution of the 11 means reported here is not significantly not-normal: Anderson–Darling test $p > 0.05$), we might expect to experience seasons of poor krill abundance at South Georgia by this criterion on average in one year out of every six or seven[1]. Survey timing, however, may influence the perception one gains of krill abundance in a particular season. During the 1997/98 season, for example, an acoustic survey to the northwest of South Georgia in October suggested that krill density was ≈5 g m^{-2} (Brierley and Watkins, unpublished data). This exceedingly low value contrasts markedly with the value of ≈21 g m^{-2} reported here for the western South Georgia box derived from a survey in January. The possibility of large, mid-season recruitment events predicates that long-term studies, or studies within the same season attempting comparative assessments of krill abundance in different areas should, where possible, be conducted at the same time of year. This aside, Loeb et al. (1997) suggested that the significant reduction in krill abundance they observed using net sampling techniques in the Antarctic Peninsula region between the mid-1970s and 1990s might be due to an increasing frequency of years of weak krill recruitment over that time. Unfortunately, because of the gaps in the early part of our time series, we are not able to assess this possible frequency change for the South Georgia region. There is, though, no evidence of a general decline in krill abundance at South Georgia within our density time series. If the decline at the Peninsula reported by Loeb et al. (1997) was real, it is perhaps surprising that no similar decline was observed at South Georgia given the demonstrated concordance in krill abundance between the two areas (Brierley et al., 1999). More recently, however, Siegel et al. (1998) have observed an upturn in abundance for the Elephant Island area and conclude that variability there is associated with 'high interannual fluctuations in stock size and not with a persistent change in krill density'. This latter interpretation is consistent with our observations at South Georgia.

On the five occasions for which it has been possible to estimate krill density separately for the eastern and western ends of South Georgia (1990, 1994, 1996, 1997 and 1998), four years exhibited greater density in the east. The year deviating from this pattern, 1994, was the year in which krill density at the island was the lowest of all years for which data are available. The east/west variability could be caused by differing rates of krill flux, differing predation pressure, or both. Lubimova et al. (1982), amongst others, have suggested that krill to the east and west of South Georgia may have arrived at the island via different routes, possibly from different locations of origin. This suggestion is supported to a certain extent by models of ocean currents (Latogursky et al., 1990; FRAM group, 1991) and by satellite observations of iceberg drift (Trathan et al., 1997). At the island, retention times may differ at opposite ends (Brandon et al., 1999). Observations of generally warmer waters in the western survey region, and of generally larger krill there (Watkins et al., 1999), also suggest that oceanographic and krill population processes may not be the same at both ends of the island. Such processes may be responsible for the observed differences in density. Alternately, it is possible that the reduced relative density of krill to the west of the island is due to increased predation pressure there. Far greater numbers of krill predators inhabit the western end of South Georgia than the east (Everson, 1984; Boyd, 1993; Trathan et al., 1998), and the reduced instantaneous krill density at the west may be due to greater levels of predator-induced mortality there.

Spatial and temporal variability in krill abundance may together confound understanding of ecological processes in the South Georgia marine ecosystem. As the first attempt to set such yearly and areal variability within a common quantitative framework, this study may serve to expedite efforts to understand this ecosystem and its response to environmental forcing factors, and hence might aid conservation and management of living marine resources at and beyond South Georgia.

CONCLUSION

Acoustic surveys at South Georgia over the past 20 years suggest that krill density around the island fluctuates markedly between years, ranging from a maximum of 151 g m^{-2} to a minimum of 2 g m^{-2} wet mass. There is no evidence of a general decline in krill density over this period.

[1] 15.87% of measurements from a normal population (i.e. between one year out of six and one year out of seven) fall below $\mu - \sigma$.

Years when the upper 95% confidence limit for mean krill density falls below 15 g m^{-2} correspond to years when the reproductive success of krill-dependent predators is poor. Such years can be considered as years of abnormally low krill density and, on average, occur once in every six or seven years.

Krill abundance is usually higher to the east of South Georgia than to the west. This may be due to differing levels of predation at each end, or may indicate the existence of different populations at, or differing sources of immigration to, the two ends of the island.

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