

# An 8-year cycle in krill biomass density inferred from acoustic surveys conducted in the vicinity of the South Shetland Islands during the austral summers of 1991–1992 through 2001–2002

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## Abstract

Data from single and multi-frequency active acoustic surveys conducted annually in the vicinity of the South Shetland Islands, Antarctica were re-analyzed using updated procedures for delineating volume backscattering due to Antarctic krill, adjusting for signal contamination due to noise, and compensating for diel vertical migration of krill outside of the acoustic observation window. Intra- and inter-seasonal variations in krill biomass density and dispersion were derived from the re-processed data set for surveys conducted in the austral summers of 1991/1992 through 2001/2002. Estimated biomass density ranged from 1 to 60 g m<sup>-2</sup>, decreasing from mid-range levels in 1991/1992 to a minimum in 1992/1993–1993/1994, increasing to a peak in 1996/1997–1997/1998, and decreasing again through 2000/2001–2001/2002. Although this variability may be attributed to changes in the spatial distribution of krill relative to the survey area, comparisons with the proportion of juvenile krill in simultaneous net samples suggest that the changes in biomass density are consistent with apparent changes in reproductive success. A truncated Fourier series fit to the biomass density time series is dominated by an 8-year cycle and predicts an increase in krill biomass density in 2002/2003 and 2003/2004. This prediction is supported by an apparent association between cycles in the extent of sea ice cover and per-capita krill recruitment over the last 23 years and indications that ice cover in the winter of 2002 is seasonally early and extensive. © 2003 Éditions scientifiques et médicales Elsevier SAS and Ifremer/IRD/Inra/Cemagref. All rights reserved.

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## 1. Introduction

A series of active acoustic surveys were conducted in the vicinity of the South Shetland Islands as part of a larger effort to understand the relationships between krill and their predators, the influence of the environment and the potential effects of a fishery on krill. Aggregations of krill, moving past the islands with the Antarctic Circumpolar Current, are preyed on by land-breeding predators who consume approximately 800 000 ton annually (Croll and Tershey, 1998). The krill fishery operating in this area currently takes less than 10% of this estimate on an annual basis (Convention on the Conservation of Antarctic Marine Living Resources, CCAMLR, 2000); however, 90% of the catch is within 80 km of the breeding colonies (Agnew, 1992). Large variations in krill recruitment success and age structure have been de-

scribed from net samples obtained in the vicinity of the islands (Siegel and Loeb, 1995; Loeb et al., 1997; Siegel et al., 1998). Strong year classes appear to be auto-correlated in time such that several years of poor recruitment are followed by 1 or 2 good years, describing a repeating cycle with a 4–5-year period. Loeb et al. (1997) suggested a link between krill reproductive success and the extent of sea ice. Brierley et al. (1999) suggested that the similarities in results from krill surveys conducted in the South Shetland Islands and near South Georgia (ca. 1000 km to the east) implied large-scale physical influences on krill reproduction.

Data describing long-term trends and cycles in Antarctic krill (*Euphausia superba*) biomass density can be useful when making inferences regarding factors that may regulate the growth of the krill population (Loeb et al., 1997) and the spatial and temporal scales over which these factors may operate (Brierley et al., 1999). While relative estimates of biomass derived from a series of surveys conducted and analyzed in a consistent manner have value, accurate esti-

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mates are critical to comparisons between surveys conducted by different investigators in different locales (Brierley et al., 1999). Absolute estimates of biomass density are also important to the development of models underpinning an ecosystem approach to the management of the krill fishery (e.g. Constable et al., 2000; Constable, 2001).

The surveys reported here were originally conducted and analyzed following the methods described by Hewitt and Demer (1993) and reported in a series of annual reports available from the US Antarctic Marine Living Resources, AMLR Program<sup>1</sup>. For these analyses, contamination by noise was avoided by thresholding measurements of volume backscattering before integrating; bias due to diurnal vertical migration of krill (Demer and Hewitt, 1995) was ignored; and delineation of backscattering due to krill was accomplished by visual inspection of reconstructed echograms. The re-analyses of the surveys reported here improve accuracy by: (1) characterizing system noise for portions of survey transects and then subtracting it from reconstructed echograms; (2) deleting from consideration those portions of transects that were conducted after local sunset and before local sunrise when an unknown portion of krill were in the surface layers above the observation window; and (3) employing a multi-frequency technique for objectively delineating volume backscattering due to krill.

The time series of krill biomass densities generated from the re-analysis of the surveys in the South Shetland Islands are examined as they relate to variations in reproductive success. A truncated Fourier series is also fit to the data, following Brierley et al. (1999). The predictive value of such a model is dependent on the continuation of cycles apparent in the Antarctic Peninsula environment over the last 20 years.

## 2. Materials and methods

Two surveys were conducted each year during mid-January to early March. Although survey design varied between years, at least five transects were conducted in the vicinity of Elephant Island during each survey (Fig. 1, Table 1). During each survey, oceanographic profiles and net samples were obtained over a grid of regularly-spaced stations. Acoustic transects were conducted between stations. Transects were oriented across bathymetric gradients and for the purposes of estimating krill biomass density, transects between a line of stations were aggregated and treated as a single transect.

Measurements of volume backscattering strength were obtained using a Simrad EK500 echosounder and various

frequencies and transducer configurations. From 1992 through 1995, surveys were conducted aboard the NOAA Ship *Surveyor* using a 120 kHz transducer deployed on a towed-body (1992 and 1993) or installed in a hull blister (1994 and 1995). From 1996 through 2002, surveys were conducted aboard the R/V *Yuhzmorelogiya* using 38, 120, and 200 kHz transducers installed in a hull blister. System calibrations using standard spheres were conducted under ambient conditions before and after survey operations each year.

Echograms were reconstructed from samples of volume backscattering strength obtained at a vertical resolution of 0.5 m and a horizontal resolution of approximately 10 m, assuming 2 s ping repetition rate and nominal survey speed of 10 knots. Portions of the echograms corresponding to the surface layer (0–15 m depth), bottom (5 m above the bottom and deeper), and periods when the ship was on station were excluded from further consideration. Various methods to compensate for bias due to diel migration of krill into the surface layer (Demer and Hewitt, 1995) were explored. The additional uncertainty associated with applications of these methods was difficult to quantify, however, and it was decided to instead eliminate sampling periods between local apparent sunset and sunrise. The effects of this decision on sampling variance are discussed in Section 3. Post-survey adjustments for system calibration and water density effects on sound absorption, wavelength and two-way beam angle were made where appropriate.

Initial measurements of noise at each frequency under survey conditions were used to generate time-varied echograms of only noise. These were visually compared to echograms reconstructed from the original data using similar absorption coefficients and display thresholds. Noise levels were then adjusted until the effects of noise at long ranges appeared equal on each display; another 2 dB was then added in order to arrive at a conservative adjustment for noise. The time-varied noise echograms were subtracted from the original data in manner similar to that described by Watkins and Brierley (1995).

Regions of the noise-free echograms were attributed to backscattering from krill swarms and layers by making use of the expected frequency-specific target strength of krill over the size range of krill encountered during the survey. Volume backscattering strength from an aggregation of krill at 38, 120 and 200 kHz was modeled by Demer (2003) using a Distorted Wave Born Approximation model of krill target strength (McGehee et al., 1998) and assumed distributions for body orientation (Kils, 1981) and the density of animals within an aggregation. The distributions of expected differences of volume backscattering strength at 120 vs. 38 kHz ( $S_{V,120} - S_{V,38}$ ), and 200 vs. 120 kHz ( $S_{V,200} - S_{V,120}$ ) had modes of 11 dB (range ca. 4 dB) and –1 dB (range ca. 3 dB), respectively (Demer, 2003). In order to account for random variability in the sound scattering process, these ranges were expanded to 12 and 6 dB, respectively, and were used to construct filters. Regions of a noise-free echogram were

<sup>1</sup> US AMLR Program Field Season Reports, published on an annual basis from 1989 through 2002 as SWFSC Administrative Reports (1989–1999) and NOAA Technical Memoranda (2000–2002). See also a series of short papers under the general heading of US AMLR Program in the 1991–1997 review issues of the Antarctic Journal of the US published by the US National Science Foundation. Copies available from US AMLR Program, 8604 La Jolla Shores Drive, La Jolla, CA 92037, USA.

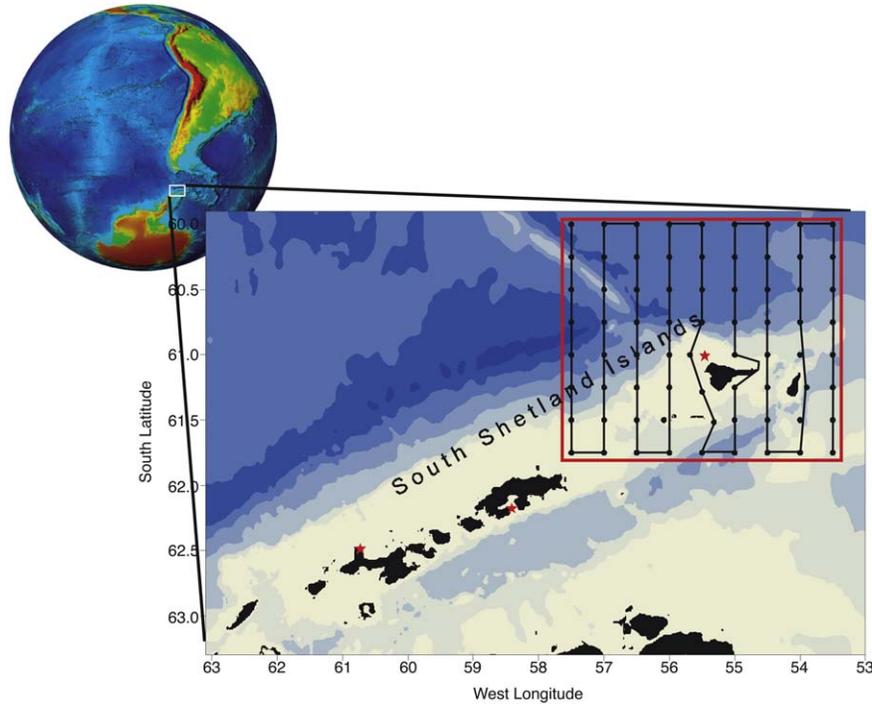


Fig. 1. Study area for the US Antarctic Marine Living Resources, AMLR Program. Solid circles indicate oceanographic and net sampling stations, solid lines indicate acoustic transects between stations, and stars indicate field camps where the reproductive success of land-breeding krill predators was monitored. Survey designs varied from year to year depending on the number of stations sampled in the grid. The most consistent sampling was conducted in the Elephant Island stratum delineated by the red rectangle.

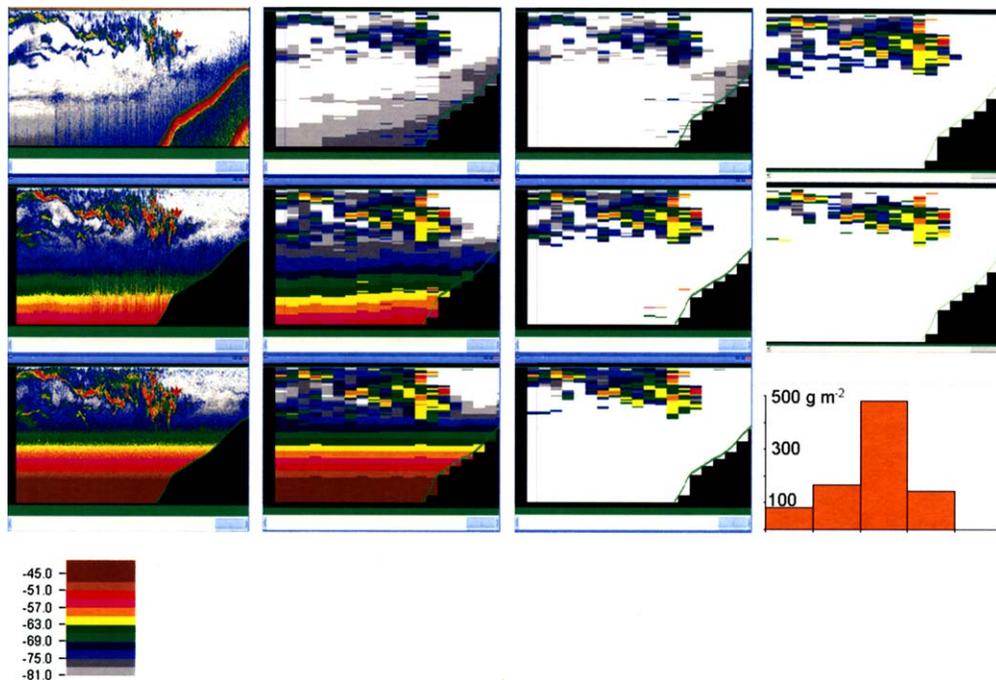


Fig. 2. The processing of samples of volume backscattering strength is illustrated by an example section of a transect. Echograms constructed from 38, 120 and 200 kHz data are shown in the first column. An irregular layer of krill is shown above the remnants of an extensive layer of myctophid fish and below more diffuse aggregations of zooplankton. Re-sampled versions of these echograms are shown in the second column where each block represents the average of 500 samples. Re-sampled noise-free echograms are shown in the third column. In the fourth column the re-sampled noise-free 120 kHz echogram is shown filtered for those regions where  $4 \leq (S_{V,120} - S_{V,38}) \leq 16$  dB (top, where most of the backscatter attributed to myctophids is eliminated), and for those regions where  $-4 \leq (S_{V,200} - S_{V,120}) \leq 2$  dB (middle, where backscatter attributed to zooplankton and the remainder of backscatter due to myctophids is eliminated). In the final step, volume backscattering strength at 120 kHz is vertically integrated, averaged over 1 nautical mile intervals and converted to krill biomass density (bottom).

Table 1  
US AMLR Program surveys in the vicinity of Elephant Island. CCAMLR: Convention on the Conservation of Antarctic Marine Living Resources

| Austral summer | Survey      | Dates                   | Number of transects | Frequencies (kHz) | Mean density ( $\text{g m}^{-2}$ ) | Coefficient of variation (%) | Original estimate of mean density ( $\text{g m}^{-2}$ ) |
|----------------|-------------|-------------------------|---------------------|-------------------|------------------------------------|------------------------------|---|
| 1991/1992      | Survey A    | 19 January–31 January   | 6                   | 120               | 38.0                               | 20.1                         | 61.2  |
|                | Survey D    | 29 February–10 March    | 9                   | 120               | 7.9                                | 14.3                         | 29.6  |
| 1992/1993      | Survey A    | 18 January–31 January   | 9                   | 120               | 1.2                                | 52.1                         | –   |
|                | No data     | –                       | –                   | –                 | –                                  | –                            | –   |
| 1993/1994      | Survey A    | 19 January–28 January   | 8                   | 120               | 3.1                                | 34.7                         | 9.6   |
|                | Survey D    | 26 February–5 March     | 9                   | 120               | 2.1                                | 33.7                         | 7.7   |
| 1994/1995      | Survey A    | 19 January–29 January   | 9                   | 120               | 7.5                                | 23.5                         | 27.8  |
|                | Survey D    | 16 February–23 February | 9                   | 120               | 13.2                               | 28.8                         | 35.5  |
| 1995/1996      | Survey A    | 25 January–4 February   | 9                   | 38, 120, 200      | 26.8                               | 29.0                         | 80.8  |
|                | Survey D    | 25 February–5 March     | 9                   | 38, 120, 200      | 17.0                               | 36.0                         | 70.1  |
| 1996/1997      | Survey A    | 31 January–9 February   | 9                   | 38, 120, 200      | 50.0                               | 21.4                         | 100.5   |
|                | No data     | –                       | –                   | –                 | –                                  | –                            | –   |
| 1997/1998      | Survey A    | 16 January–25 January   | 9                   | 38, 120, 200      | 60.2                               | 19.3                         | 82.3  |
|                | Survey D    | 16 February–25 February | 9                   | 38, 120, 200      | 20.8                               | 16.3                         | 47.1  |
| 1998/1999      | Survey A    | 22 January–28 January   | 5                   | 38, 120, 200      | 14.8                               | 38.1                         | –   |
|                | Survey D    | 16 February–23 February | 5                   | 38, 120, 200      | 13.4                               | 39.8                         | –   |
| 1999/2000      | CCAMLR 2000 | 29 January–1 February   | 8                   | 38, 120, 200      | 25.7                               | 25.2                         | –   |
|                | Survey D    | 26 February–5 March     | 9                   | 38, 120, 200      | 34.6                               | 28.6                         | –   |
| 2000/2001      | Survey A    | 17 January–24 January   | 9                   | 38, 120, 200      | 6.6                                | 19.1                         | –   |
|                | Survey D    | 17 February–25 February | 9                   | 38, 120, 200      | 5.6                                | 10.4                         | –   |
| 2001/2002      | Survey A    | 20 January–26 January   | 7                   | 38, 120, 200      | 3.3                                | ~60                          | –   |
|                | Survey D    | 28 February–6 March     | 7                   | 38, 120, 200      | 1.2                                | 31.2                         | –   |

attributed to krill when both of the following conditions were true:  $4 \leq (S_{V,120} - S_{V,38}) \leq 16$  dB and  $-4 \leq (S_{V,200} - S_{V,120}) \leq 2$  dB. The effects of these decisions are discussed in Section 3.

The multi-frequency filters were used to process survey data collected on surveys conducted in 1996 through 2002. The distribution of volume backscattering strength attributed to krill ranged between  $-50$  and  $-90$  dB, with approximately 80% of the integrated energy between  $-50$  and  $-70$  dB. For surveys conducted during 1992 through 1995, when data collection was limited to 120 kHz, volume backscattering strength was thresholded to include values  $>-70$  and  $<-50$  dB as a means of delineating regions of the echograms attributed to backscattering from krill. Visual inspection of the echograms indicated that this was an effective, but conservative, method of eliminating backscattering due to animals other than krill.

Comparisons of single samples of volume backscattering strength were too variable to allow contiguous regions of the echogram to be delineated as krill and it was judged necessary to average volume backscattering strength over bins of finite vertical and horizontal dimensions (resample). Bin size was set at 5 m vertical and 50 pings horizontal (ca. 500 m). The effects of this decision are discussed in Section 3.

Resampled, noise-free 120 kHz echograms were filtered to include only those regions where volume backscattering was attributed to krill. Volume backscattering coefficients ( $\text{m}^2 \text{m}^{-3}$ ) were vertically integrated and averaged over 1 nautical mile distance intervals. Integrated volume backscattering area ( $\text{m}^2 \text{m}^{-2}$ ) was converted to krill biomass density

( $\text{g m}^{-2}$ ) by applying a factor equal to the ratio of the weight of an individual krill (g) and its backscattering cross sectional area ( $\text{m}^2$ ) summed over the length frequency distribution of krill sampled in the survey area (Hewitt and Demer, 1993).

The procedures outlined above are illustrated in Fig. 2 for an example section of a survey transect. Mean biomass density and its sampling variance were estimated for each survey following Jolly and Hampton (1990) where the mean density along each transect is considered a representative sample of the survey mean (Shotton and Bazigos, 1984). It should be noted, however, that transect spacing was not random, and therefore, a violation of their requirement for a ratio estimate of sampling variance. Other investigators defend the validity of systematic transect spacing when using this method to estimate variance by noting that the surveyed population is most often randomly distributed relative to transect spacing (Williamson, 1982; Francis, 1984, 1985). In their manual for the conduct of acoustic surveys Simmonds et al. (1992) recommended a survey design of systematically spaced parallel transects for populations, exhibiting both high and low contagion in their spatial distribution, where the distribution can be assumed to be random with respect to transect location. No evidence to the contrary was discovered with respect to the surveys reported here.

### 3. Results

Estimates of mean krill biomass density and coefficient of variation are listed for each survey in Table 1. The second

surveys in 1992/1993 and 1996/1997 were compromised due to problems with the towed-body (1993) and the ship's propulsion system (1997); consequently, no results for these surveys are presented. The results presented for the first survey in 2000 were estimated from data collected in the South Shetland Island stratum of the CCAMLR 2000 Survey (Hewitt et al., 2002). The large error associated with the first survey of 2001/2002 is a combined error due to sampling error between transects plus measurement error due to equipment malfunction during a portion of the survey (estimated by processing the entire survey twice using gain settings before and after replacement of a faulty power supply). With the exception of 1991/1992 and 1997/1998 the first and second surveys of each year are not significantly different from each other. In both 1991/1992 and 1997/1998 krill biomass density decreased sharply from the first to second surveys and continued to decrease in subsequent years.

Survey estimates of krill biomass densities and coefficients of variation were re-calculated using all of the data and compared to results where nighttime sampling was excluded. As expected, mean density was consistently higher when sampling during the dark hours was not considered. It should be noted, however, that the Jolly and Hampton (1990) method used to estimate mean density assumes that the transect mean is a representative sample of the survey mean. Thus a reduction in the number of intervals in a single transect does not impose a penalty with regard to the estimate of sampling variance between transects. The increased density estimates when only daytime sampling is considered, however, confirms the expected negative bias when sampling krill at night and justifies their exclusion.

The ranges for the multi-frequency filters used to delineate regions of the echogram attributed to krill scattering were initially selected based on theoretical expectations of the frequency-specific differences in volume backscattering strength from aggregations of krill (Demer, 2003). Selected echograms were processed using these initial values and the resulting echograms were compared against the original echograms. The initial ranges were judged to be too conservative and were expanded so that more aggregations presumed to be composed of krill were included. Aggregations were presumed to be composed of krill based on their size, shape, intensity, edge gradient and depth as verified by directed net sampling. Application of the first filter ( $4 \leq (S_{V,120} - S_{V,38}) \leq 16$  dB) captured most aggregations visually identified as krill, but also included aggregations identified as myctophid fish and smaller zooplankton. Narrowing the filter range excluded the non-krill scatterers at the expense of excluding more krill aggregations. Application of the second filter ( $-4 \leq (S_{V,200} - S_{V,120}) \leq 2$  dB) eliminated the non-krill scatterers while retaining most of the krill aggregations. The multi-frequency filters used here should be considered conservative; that is, their application will result in an underestimate of the krill biomass density.

The effect of changing the dimensions of the re-sampling bins was investigated. It was expected that the selection of

bin size would necessitate a tradeoff: if the bins were too small the variability between samples of volume backscattering strength would cause the continuous nature of krill swarms and layers apparent on the original echograms to be lost; if the bins were too large the power to distinguish krill would be diminished because backscattering from krill and non-krill scatterers would be averaged together. Experimentation with bin size on selected echograms indicated little change in integrated energy attributed to krill when the bin size was larger than some nominal dimensions and smaller than very large regions of the echograms. Bin size was selected at 5 m vertical and 50 pings in the horizontal direction, but comparable results could have been obtained if the bin size was half or double these dimensions.

#### 4. Discussion

The revised estimates of krill biomass density in the Elephant Island area were consistently lower than the original estimates (Table 1). As noted above the filter ranges used in the current analysis were chosen such that aggregations that were presumed to be composed of krill were included and all else was excluded. In contrast, the visual classification procedure used in the original analyses lumped krill and non-krill zooplankton; although, the non-krill zooplankton component (including other euphausiids, copepods, amphipods, chaetognaths, pteropods, and ostracods) was estimated to contribute less than 10% of the total volume backscattering strength at 120 kHz (Hewitt and Demer, 1993). Not included in this estimate were contributions from salps and myctophid fish. The numerical abundance of the non-krill zooplankton component was an order of magnitude higher in 1994/1995 and 1995/1996 than it was in 1991/1992 and 1997/1998 (V. Loeb, personal communication). The largest discrepancies between the current estimates of krill biomass densities and the original estimates also occur during 1994/1995 and 1995/1996, suggesting that the proportion of volume backscattering attributed to non-krill zooplankton was underestimated and variable from survey to survey. Variations in the abundance of myctophid fish (primarily *Electrona antarctica* and *Gymnoscopelus nicholsi*) and salps (primarily *Salpa thompsoni*) may have also contributed to the variations in the difference between the original estimates (which included a portion of the backscatter from these taxa) and the current estimates (which did not). Perhaps the largest and least quantifiable source of variability was the subjective nature of the visual interpretation of the original echograms.

The procedures described here provide a more objective method for delineating backscatter from aggregations of Antarctic krill. Verification of the method, however, is dependent on an accurate and unique characterization of krill aggregations derived from a comparison of acoustic records and net sampling. Underestimates of krill biomass density will arise if unknown forms of krill aggregations (or mixed species aggregations) have not been characterized and hence not considered when comparing the performance of various filter

ranges in delineating krill aggregations. Dispersed krill were also not explicitly considered when selecting the filter ranges, although it was noted that low density regions of krill were often delineating in the vicinity of denser krill aggregations when the filters were applied. The advantages of the method are that it can be described in specific terms, and therefore, applied consistently to a series of surveys; the filters can be adjusted, new ones added and analyses redone as warranted; and it can be used in a complementary way to other techniques for delineating krill aggregations such as discriminate functions and neural networks (Woodd-Walker, 2003).

The coefficients of variation reported here represent sampling error as distinguished from measurement error (Hewitt and Demer, 2000). Demer (2003) analyzed the total uncertainty associated with a similar survey of Antarctic krill across the Scotia Sea. He considered errors associated with system calibration, characterization of krill target strength, probability of detection, and the efficiency of algorithms used to delineate backscatter attributed to krill. He concluded that measurement variance was negligible relative to sampling variance. Demer (2003) also noted a disparity in krill target strength predicted by an empirical model (Greene et al., 1991) vs. a theoretical model (McGehee et al., 1998), and concluded that uncertainty with regard to krill target strength remains the largest source of potential bias. The empirical model, where target strength is estimated as a function of body length, is used in the current analyses to convert integrated volume backscattering strength to krill biomass density. The theoretical model, where target strength is a function of body length, shape, curvature, orientation angle and material properties, is impractical to apply under survey conditions because so many parameters must be characterized. One approach is to randomize the sound scattering process by assigning appropriate probability density functions to various parameter values and estimating a range of target strength values for various body lengths (Demer and Conti, 2003). The results of this and similar work will be improved estimates of krill target strength under natural conditions and the possibility of systematic changes in estimates of krill biomass density.

Assuming that the character of krill aggregations and their target strength are not influenced by overall abundance, the trends apparent in the time series presented here may be helpful when making inferences regarding factors that control the growth of the krill population. One must also assume that a representative sample of the krill population (both biomass density and demographic structure) can be obtained from sampling in the vicinity of Elephant Island.

Siegel (1988) proposed a model of spatial succession of age groups in the vicinity of the South Shetland Islands. He described an order of magnitude increase in krill abundance as the austral spring progressed into summer and fall, and then a sharp decline as krill apparently left the area before the expansion of sea ice into the region. The seasonal change in abundance has a spatial component with an increase in the

numbers of juvenile krill near the islands and in the Bransfield Strait between the islands and the Antarctic Peninsula, and by an influx of sexually maturing adults farther offshore. Siegel further proposed that, as the summer progresses, post-breeding adults move shoreward and juveniles leave the area. Lascara et al. (1999) suggested that shoreward migration could explain large differences between summer and winter krill densities observed along the western Antarctic Peninsula south west of the South Shetland Islands. Results from net sampling in the Elephant Island area have confirmed that this movement is a consistent phenomenon from year to year (V. Loeb, personal communication). The juvenile and immature component of the population is reduced from the first survey to the second survey of each year. Over the course of four surveys conducted in the vicinity of the South Shetland Islands from mid-December 1999 through early March 2000, small and intermediate krill length modes were reduced, but differences in biomass density were not detectable (Gutierrez et al., 2003). Similarly, krill biomass density, as estimated from acoustic surveys reported here, does not describe a consistent pattern from the first to second surveys. Only in 1991/1992 and 1997/1998 were significant differences detectable between the first and second surveys.

Although krill are only seasonally abundant in the South Shetland Islands (Siegel, 1988; Siegel et al., 1997), results from net sampling during the early summer suggest that the relative contribution of year classes, and their effect on population size, can be tracked over several years (Fig. 3). The strong 1987/1988 year class (45 mm mode following Siegel, 1987) was still evident in the population when the first acoustic surveys reported here were conducted. Also evident was another strong year class (27 mm mode) produced by spawning in 1990/1991. Recruitment from spawning in 1991/1992 was negligible and biomass density sharply declined. Weak recruitment from spawning in 1992/1993 and 1993/1994 was associated with modest increase in biomass density. The 1994/1995 year class was very strong, followed by moderately successful recruitment from spawning in 1995/1996 and 1996/1997, and biomass density rapidly increased peaking in 1997/1998. Recruitment from spawning in 1997/1998 was negligible and biomass density sharply declined. The increase in biomass density in 1999/2000 was associated with moderate reproductive success from spawning in 1998/1999 but was not sustained in 2000/2001. The most recent surveys in 2001/2002 suggest a slight decrease in biomass density associated with relatively good reproductive success from spawning in 2000/2001. Reid et al. (1999a, b) also demonstrated a correlation between krill abundance and the length-frequency distribution of krill in the diets of krill predators breeding at South Georgia.

Brierley et al. (1999) concluded that variations in krill abundance were influenced by broad-scale variations in the physical environment. They documented 2-, 3-, 4-, 5- and 8-year cycles in the power spectra of a 15-year record of air temperature and a 17-year record of sea-ice extent in the Antarctic Peninsula region, and a 15-year record of sea-

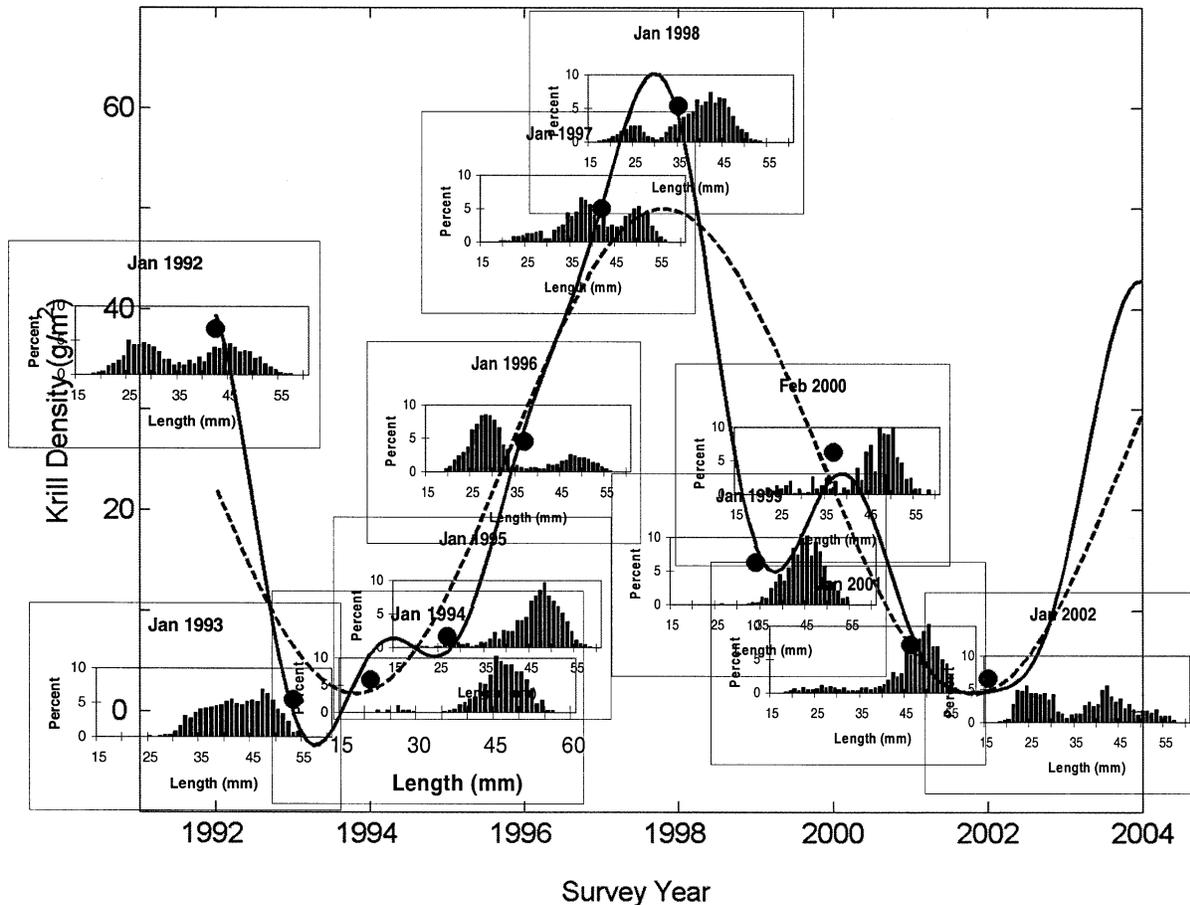


Fig. 3. Annual estimates of krill biomass density in the vicinity of Elephant Island from the first survey of each year (filled circles). Also shown are krill length frequency distributions corresponding to the surveys (number of net tows per survey ranged from 75 to 105; 150 krill or less measured per tow). The solid line is a truncated Fourier series fit to the data, using cycles of 2, 3, 4, 5 and 8 years, which explains 98% of the variability in the time series. Of these, the 8-year cycle (dashed line) dominates explaining 75% of the variance; addition of a 3-year cycle explains another 9%.

surface temperatures near South Georgia. They then fit a truncated Fourier series to a time series of acoustic estimates of krill biomass density in the Elephant Island area drawn from a variety of sources. A majority of the variance between annual surveys was explained by 5- and 8-year cycles. Similar analyses were applied to the data in Table 1, considering all of the surveys, only the first surveys in each year, only the second surveys in each year and the mean of both surveys in each year. In all cases, 3- and 8-year cycles explained the majority of the variance in the time series (Fig. 3). The model also suggests an increase in krill biomass density over the next 2 years. This prediction is dependent on the continuation of cycles in the environment and associated changes in krill reproductive success.

An association between the extent of sea ice cover and per-capita krill recruitment is apparent in indices derived from satellite imagery of sea ice concentrations west of the Antarctic Peninsula and net sampling data in the vicinity of the South Shetland Islands over the last 23 years (Fig. 4). These records suggest cyclical variation, and mechanisms have been proposed to link sea ice extent and krill reproductive success (e.g. Loeb et al., 1997). However, the period is irregular and the association is not perfect. Interestingly,

although the extent of ice cover in 2001 was low, the most current satellite images indicate seasonally early and extensive sea ice cover in the Antarctic Peninsula area through the winter and early spring of 2002<sup>2</sup>. Recruitment from spawning in 2000/2001 and a second good or stronger year class from spawning in 2001/2002 could be expected to increase krill biomass density over the next 2 years as happened following the recruitment of the 1994/1995 year class.

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<sup>2</sup> Near Real-Time DMSP SSM/I Daily Polar Gridded Sea Ice Concentrations from National Snow and Ice Data Center (<http://www.nsidc.org>).

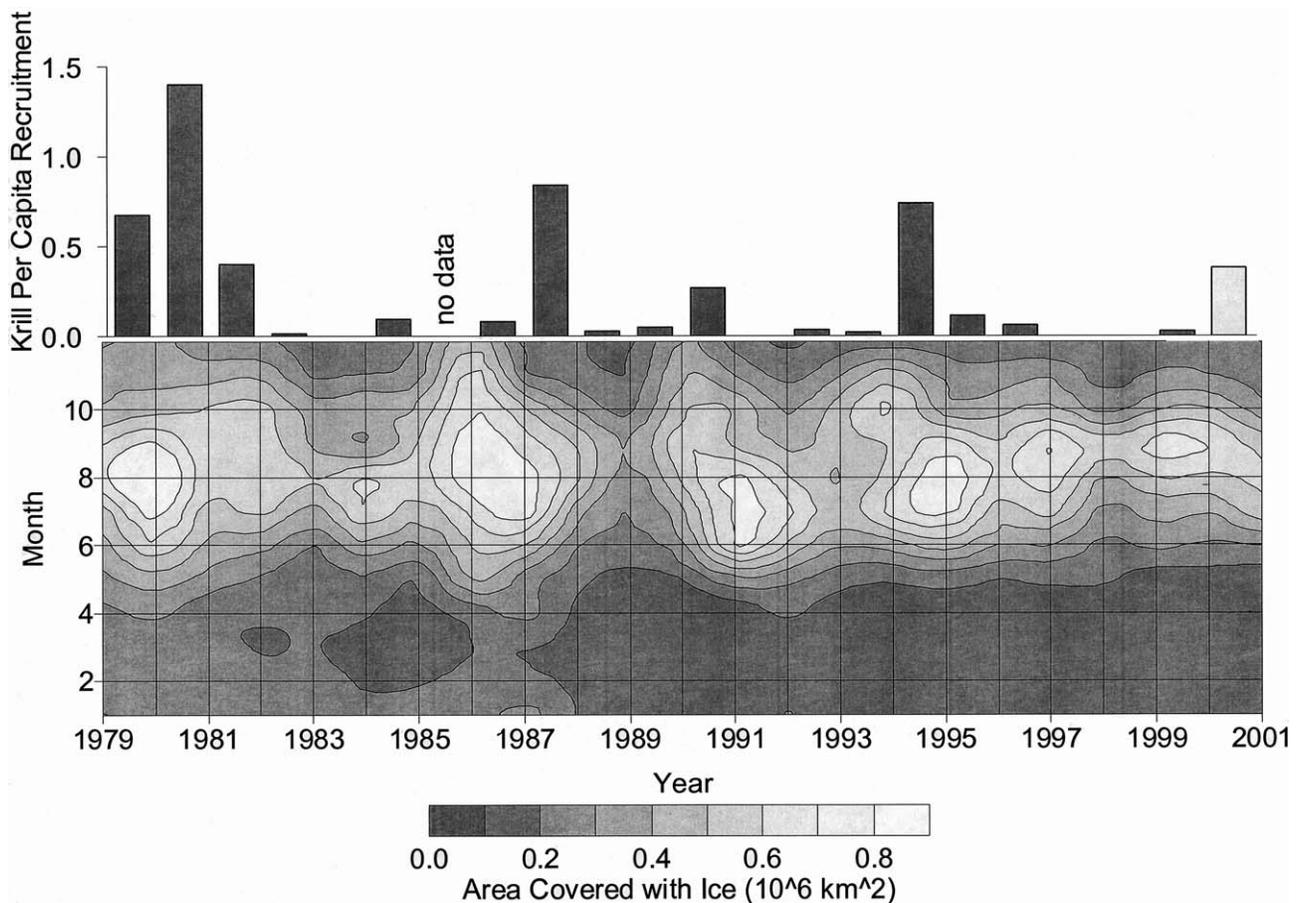


Fig. 4. Area covered by sea ice off the northwestern side of the Antarctic Peninsula (updated from Hewitt, 1997) and per capita krill recruitment as calculated from the proportion of age one krill (Siegel, personal communication) following Hewitt (2000). The estimate of per capita recruitment from spawning in 2001 (shaded in light gray) should be considered preliminary.

leagues who have used acoustic technology to assess marine resources in the Southern Ocean, including A. Brierley, I. Everson, K. Foote, C. Greene, C. Greenlaw, I. Hampton, I. Higgenbottom, V. Holliday, M. Macaulay, T. Pauly and J. Watkins.

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