Variation in the biomass density and dispersion of Antarctic krill in the vicinity of the South Shetland Islands throughout the 1999/2000 austral summer

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Abstract

Vessels from Japan, Republic of Korea, Peru and the USA conducted five surveys designed to estimate the biomass density and dispersion of Antarctic krill in the vicinity of the South Shetland Islands from late December 1999 through early March 2000. These surveys were conducted in conjunction with the CCAMLR 2000 Survey across the Scotia Sea (Watkins et al. this volume), and data were analyzed in a similar fashion. Excluding one survey with suspected measurement errors, biomass densities were not significantly different between surveys conducted over an eleven-week period of time during the austral summer of 1999/2000, and averaged 49 g m⁻². Examination of maps of biomass dispersion suggests three consistent area of high krill density: near the east end of Elephant Island, mid-way between Elephant and King George Islands, and near Cape Shirreff on the north side of Livingston Island. Highest densities of krill appear to move closer to the shelf break as the season progresses. This apparent movement is complemented by a change in the demographic structure of the population, with smaller length modes absent and a larger proportion of sexually mature animals later in the summer.

Introduction

During the summer months swarms of Antarctitc krill (*Euphausia superba*) sweep past the South Shetland Islands, moving with the Antarctic Circumpolar Current as it concentrates and accelerates though Drakes Passage transporting massive quantities of water (130 Sverdrups, Deacon 1984) from the south Pacific to the south Atlantic Oceans (Figure 1). Krill predators breeding in the South Shetland Islands, such as chintrap penguins, Adelie penguins, gentoo penguins and Antarctic fur seals, consume approximately 0.83 million tonnes of krill during the reproductive season (Croll and Tershey 1998). The krill fishery operating in the area has taken on the order of 50,000 tonnes each year between 1990 and 2000 (CCAMLR 2000, SC-CAMLR-XIX), less than 10% of the estimated consumption by land-breeding krill predators. However, Agnew (1992) estimated that 90% of this catch was within 80 km of the breeding colonies.

Consumption of krill by pelagic predators, such as baleen whales, crabeater seals, fish and other seabirds is more difficult to estimate but may be on the order of 1 million tonnes per annum in the vicinity of the South Shetland Islands. In January 2000 the standing stock of krill along the north side of the South Shetlands was estimated at 1.84 million tonnes, average density 38 g m⁻² (Hewitt et al. this volume). Average krill densities in the area, as measured by acoustic surveys conducted from 1992 through 2000, ranged from 7 to 100 g m⁻² resulting in estimates of standing stock ranging from 0.3 to 4.0 million tones (Emery et al. 2000).

Unlike the region around South Georgia, 1000 km downstream from the South Shetlands, where krill consumption is on the order of 10 times the standing stock (Everson and de la Mare 1996, Trathan et al. 1995, Hewitt et al. this volume, Boyd in press) and where reproductive failures among krill predator populations are associated with occasional low levels of krill availability (Brierley et al. 1999, Croxall et al. 1999, Boyd and Murray 2001), annual consumption of krill in the vicinity of the South Shetland Islands is on the same order as the standing stock.

Siegel 1988 proposed a model of spatial succession of krill 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 dramatic decline as krill apparently left the area before winter. This seasonal change in abundance is characterized by an increase in the numbers of juvenile krill near the islands and in Bransfield Strait between the islands and the Antarctic Peninsula, and by in influx of sexually maturing adults further offshore. As the summer progresses post-breeding adults move shoreward, displacing the juveniles.

In addition to seasonal changes in krill abundance, large inter-annual variations in krill density and recruitment have been described from net samples obtained in the vicinity of the South Shetland Islands (Siegel and Loeb 1995, Loeb et al. 1997, Siegel et al. 1998). During any particular year the age structure of the population appears to be dominated by one or two age classes. These strong year classes appear to be auto-

correlated in time such that several poor years of reproduction are followed by one or two good years, describing a repeating cycle with a four to five year period. Krill abundance, viewed as the sum of all age classes in the population, is cyclic as well, declining with successive decreases in reproductive success and increasing dramatically with the recruitment of strong year classes. Three relatively strong year classes, produced from spawning in 1986/87, 1990/91 and 1994/95 have apparently sustained the population during the late 1980's and 1990's. Krill appear to be seasonal visitors to the South Shetland Islands, but the data presented by Siegel, Loeb and their colleagues suggest that the relative contribution of year classes, and their effect on population size, can be tracked over several years by sampling in the area during the spring and summer months.

The surveys reported in this paper were conducted in the vincity of the South Shetland Islands by scientists aboard ships from Japan, Korea, Peru and the USA during the austral summer of 1999/2000 (Table 1). The surveys were designed to coincide with and complement the CCAMLR 2000 Survey of krill across the Scotia Sea (Watkins et al. this volume). Two surveys were conducted by the Japanese R/V *Kaiyo Maru*: one in mid-December (Survey 1) and another in late January-early February (Survey 4). The Korean R/V *Onnuri* conducted a survey in mid-January (Survey 2); the Peruvian R/V *Humboldt* conducted a survey in late January; and the USA chartered R/V *Yuzhmorgeologiya* conducted a survey in late February-early March. This report complements that of Kim et al. (1998) who described the results of another series of surveys conducted in the vicinity of the South Shetland Islands during the austral summer of 1994/95. Numbers of post-larval krill declined as the season progressed while the numbers of larval krill increased dramatically (Kim et al. 1998). Spawning during this summer ultimately produced a very strong year class.

Historically the krill fishery has operated near South Georgia in the winter (Constable et al. in press). With the retreat of sea ice in the late spring and summer months the fishery moved south and west to the South Orkney Islands and South Shetlands Islands. In recent years a reduction in the development of winter-time sea ice (Stammerjohn and Smith 1996, Smith et al. 1998), coincident with a warming trend in the

Antarctic Peninsula (Vaughan and Doake 1996), has allowed the winter fishery access to the more predictable concentrations of krill in the vicinity of the South Shetland Islands. As the probability of interactions between the krill fishery and krill predators increases in this region, the need for proactive management becomes more urgent. However, any management option will require quantitative knowledge of the seasonal and ontogenic movements of krill through the region. This report is a step is this direction.

Methods

All of the survey vessels were equipped with Simrad EK500 echosounders and hull-mounted transducers operating at 120 and 200kHz. Standard sphere calibrations were conducted before and after each survey with the exception of Survey 3 when a single calibration was conducted before the survey. Ping intervals were 2 sec and pulse durations were 1 msec for all frequencies. Samples of volume backscattering strength were obtained every 0.71 m from the transducer faces to 500 m depth for Surveys 1, 4 and 5. Samples of volume backscattering strength were obtained every 0.5 m from the transducer faces to 250 m depth for Surveys 2 and 3. During Surveys 1, 4 and 5 acoustic data was collected SonarData's EchoLog software. During Surveys 2 and 3 acoustic data was collected using Simrad's BI500 software.

The analytical protocol used to estimate the dispersion of krill biomass across the survey areas was similar to that used for the CCAMLR 2000 Survey of krill biomass across the Scotia Sea (Hewitt et al. this volume). The protocol consisted of four general steps: 1) delineation of volume backscattering by krill from all other scattering; 2) conversion of integrated volume backscattering (attributed to krill) to krill biomass density; 3) summing of krill biomass density over the survey area; and 4) estimation of sampling error.

 With regard to delineating krill, backscattering was attributed to krill when the difference between mean volume backscattering at 120 kHz and 38 kHz was greater than 2 dB but less than 16 dB. SonarData's EchoView Version 2.1 software was used to: 1)

reconstruct and filter echograms for the transect periods between stations; 2) remove echoes due to surface turbulence and the bottom; 3) resample the echograms using 5 m (vertical) by 50 ping (horizontal) bins; 4) create time-varied noise echograms and subtract from the resampled echograms; 5) subtract the noise-free resampled 38 kHz echogram from the noise-free resampled 120 kHz echogram; 6) mask portions of the 120 kHz noise free resampled echogram to exclude regions where the difference between the mean volume backscattering strength at 120 kHz and that at 38 kHz was less than 2 dB or greater than 16 dB; and 7) integrate the masked noise-free resampled 120 kHz echogram from the bottom of the surface exclusion layer to vertical extent of acoustic sampling at 120 kHz (500 m for Surveys 1, 4 and 5; 250 m for Surveys 2 and 3; or 5 m above the bottom if shallower) and average over 1852 m horizontal distance (1 n. mile). The output of this was a series of integrated volume backscattering area values (expressed as nautical area scattering coefficient, *NASC*, MacLennan and Fernandes 2000), one for each n. mile of survey transect.

2) With regard to converting integrated volume backscattering area to krill biomass density, a conversion factor was calculated equal to the quotient of the weight of an individual krill and its backscattering cross-sectional area summed over the length frequency distribution (Hewitt and Demer 1993). Krill were directly sampled using Bongo, Isaacs-Kidd Mid-Water Trawl (IKMT), Rectangular Mid-Water Trawl (RMT-8) and Engel Mid-Water Trawl gears as summarized in Table 2. Post-larval krill were removed from the catches (large catches were sub-sampled for at least 100 animals) and processed at sea. Length measurements were made from the tip of the rostrum to the tip of the telson; maturity stages were determined following Makarov and Denys (1981).

Net samples were categorized into three time periods: early summer (mid-December; Survey 1), mid-summer (mid- January to early February; Surveys 2, 3 and 4), and late period (late February to early March; Survey 5). Length frequency distributions were analyzed using a cluster analysis to compare similarities between stations. Hierarchical fusion of clusters was performed using Ward's method to link homogeneous clusters, and the Euclidean distance coefficient was applied for the dissimilarity

measures. Siegel and Loeb (1995) report negligible differences between the RMT-8 and the IKMT in their efficiency to sample post-larval krill. Therefore, the length data obtained with these two nets (Surveys 1, 4 and 5) were used for the cluster analysis. Length frequency data obtained with the Bongo and Engel nets were used as qualitative information to support the determination of cluster boundaries during the mid-summer period.

Calculation of conversion factors using length frequency distributions requires assumptions of relationships of target strength (and by inference acoustic backscattering cross-sectional area) and weight as a function of length. The target strength/length relationship adopted by CCAMLR in 1991 (SC-CAMLR 1991) was used where:

$$TS(L) = -127.5 + 34.85 \log(L)$$

The weight/length relationship used for the analysis the CCAMLR 2000 Survey of krill biomass across the Scotia Sea (Hewitt et al. this volume) was used where:

$$W(L) = 0.002236(L)^{3.314}$$

and animal weight (W) is expressed in g and animal length (L) is expressed in mm.

Conversion factors were calculated for each cluster following the algorithm developed in Appendix 1 and listed in Table 4. Transects were subdivided where they crossed cluster boundaries and *NASC* values from portions of the transects in each cluster were multiplied by the appropriate conversion factor (*CF*) in order to generate a series of areal krill biomass densities (ρ).

3) With regard to summing krill biomass density over the survey area, the method proposed by Jolly and Hampton (1990) was employed, where the mean density over each transect was assumed to be representative of the mean density of the survey area. The mean density of the survey area was thus calculated as the weighted average of all transects within the survey area, where the weighting was proportional to the length of each transect:

$$\overline{\rho} = \frac{1}{N} \sum_{j=1}^{N} w_j \overline{\rho}_j$$

where $\overline{\rho}$ is the mean areal krill biomass density of the survey area, *N* is the number of transects in the survey area, and w_j is the normalized weighting factor for the *j*th transect as defined below, and $\overline{\rho}_j$ is the mean areal krill biomass density on the *j*th transect as defined below.

For several reasons ships deviated from the planned transects. Such deviations included random effects caused by strong winds and ocean currents, and larger systematic deviations caused by avoidance of icebergs and islands. To correct for these larger deviations, an expected change in latitude per nautical mile of transect, Δlat , was calculated for each transect in the survey design. The actual latitude made good, $\Delta l\hat{a}t$, was derived by differencing the latitudes of the beginning and end of each interval. An interval weighting W_I was calculated as:

$$W_{I} = \frac{\left|\Delta lat\right| - \left|\left(\Delta lat - \Delta l\hat{a}t\right)\right|}{\left|\Delta lat\right|}$$

The sum of the interval weightings along each transect was used to weight the transect means to provide a stratum biomass, such that:

$$L_j = \sum_{i=1}^{N_j} \left(W_I \right)_i$$

where L_j is the length of the *j*th transect, $(W_I)_i$ is the interval weighting of the *i*th interval, and N_j is the number of intervals in the *j*th transect. The normalized weighting factor for the *j*th transect (w_i) was defined as:

$$w_j = \frac{L_j}{\frac{1}{N}\sum_{j=1}^N L_j} \quad \text{such that} \quad \sum_{j=1}^N w_j = N$$

The mean areal krill biomass density over all intervals on the jth transect ($\overline{\rho}_j$) was defined as:

$$\overline{\rho}_{j} = \frac{1}{L_{j}} \sum_{i=1}^{N_{j}} (NASC)_{i} (CF)_{i} (W_{I})_{i}$$

where $(NASC)_i$ is the integrated backscattering area for the *i*th interval and $(CF)_i$ is the conversion factor for the *i*th interval.

4) Sampling error was assumed to be proportional to the weighted variance between transects (Jolly and Hampton 1990). The variance of the mean areal krill biomass density over the survey area was thus calculated as:

$$Var(\overline{\rho}) = \frac{N}{N-1} \frac{\sum_{j=1}^{N} w_j^2 (\overline{\rho}_j - \overline{\rho})^2}{\left(\sum_{j=1}^{N} w_j\right)^2} = \frac{\sum_{j=1}^{N_k} w_j^2 (\overline{\rho}_j - \overline{\rho})^2}{N(N-1)}$$

Maps of the dispersion of krill biomass were constructed by generating estimates of mean areal krill biomass density using the procedures outlined above, but averaging over 5 n. miles instead of 1 n. mile. These data were interpolated onto a square grid, whose dimensions were one-half the spacing between transects, and then contouring the grid values. Interpolation was accomplished by Krigging assuming a linear model of variance between points as a function of distance.

Results

Aggregated length-frequency distributions, weighted by catch rates, indicated that each of the clusters had a reasonably tight length frequency distribution (Figure 3). In the early summer, three distinct clusters were observed: a small mode (with median length of 34mm), a medium mode (with median length of 40mm), and a large mode (with median length of 50mm) were observed. During mid-summer, two clusters were observed: a medium mode (with median length of 44mm), and a large mode (with median length of 51mm). Although three clusters were detected during the late summer, their size composition was very similar (with median length of 49, 50, and 51mm respectively) and the catches were combined to describe a single large mode cluster for the entire survey area.

Geographical distributions of each cluster are shown in Figure 4. During the early summer, segregation among different size clusters was detected with smaller krill to the inshore and the larger to the offshore. During the mid-summer period the boundary separating medium length and large length krill moved shoreward. During the late-summer period only large krill were sampled over the entire survey area. The latitudinal positions of cluster boundaries along each survey transect are indicated in Table 3. The range of conversion factors varied by less than 7% (Table 4). The highest factors corresponded to length frequency distributions with smallest size modes and lowest factors corresponded to length frequency distributions with largest size modes.

Sampled krill were also more sexually mature as the season progressed (Table 5). During Survey 1, conducted in mid-December, 33% of the sampled krill were juveniles and another 37% were immature adults. The proportion of juveniles in the samples decreased as the season progressed, falling to 1% in Survey 4 (late January – early February) and negligible in Survey 5 (late February). The proportion of adults in advanced stage of sexual maturity increased as the season progressed. Only 30% of the krill sampled during Survey 1 were classified as Stage 3, increasing to 83% and 99% in Surveys 4 and 5.

Biomass densities, coefficients of variation, and total biomasses are listed for each of the surveys in Table 1. Detailed transect-by-transect data from each survey are listed in Table 6. Biomass densities on four out of the five surveys were of the same order of magnitude (44 to 54 g m⁻²). Estimated biomass density on the other survey was less than 2 g m^{-2} (see discussion below). Coefficients of variation ranged from 14% to 23.2%, with the highest coefficient of variation associated with the highest biomass density (Survey 3). During this survey a local region of very high biomass density was observed east of Elephant Island (Figure 5c). The survey transect in this area deviated substantially to the east in order to navigate around the island, and the over sampling was corrected by the use of interval weighting factors. Even with this adjustment, the mean biomass density on this transect was double the overall survey mean, which contributed to the higher coefficient of variation.

Excluding the survey associated with the very low estimate of biomass density, biomass densities on the four remaining surveys were 50.4 g m⁻² (CV 20.3%), 54.2 g m⁻² (CV 23.2%), 46.5 g m⁻² (CV 20.4%) and 44.2 g m⁻² (CV 14.0%) over an eleven-week period of time, mid-December through late-February (Table 1).

Maps of biomass density for each of the surveys are shown in Figures 5a through 5e. Examination of these maps suggests three consistent areas of high krill biomass density: near the east end of Elephant Island, mid-way between Elephant and King George Islands, and near Cape Shirreff on the north side of Livingston Island. It also appears that highest densities of krill move closer to the shelf break as the season progresses. This apparent movement is complemented by a change in the demographic structure of the population. The smaller size modes disappear and krill are more sexually mature later in the summer.

Discussion

With the exception of Survey 2, biomass densities were not significantly different between surveys conducted over an eleven-week period of time during the austral summer of 1999/2000 and averaged 49 g m⁻². This value is mid-way between the lowest and highest values of krill biomass densities observed during German and USA acoustic surveys in the South Shetland Islands since 1981 (Hewitt and Demer 1994, Emery et al. 2001).

The low variation in krill biomass density over this period of time is remarkable given the more dramatic change in the demographic composition of the surveyed population. The sampled krill represent 5 age classes: 1999 as juveniles; 1998 and 1997 - relatively weak year classes; 1996 - a moderate year class; and 1995 - the last strong near class represented in the population (Loeb 2000). The demographic changes observed over the course of the surveys could not have been caused by seasonal growth. Rather they were the result of movement of the adult population shoreward, displacing the

juveniles perhaps southward (as observed in 2001 by Siegel et al. in press), and immigration from the southwest of large animals in advancing stages of sexual maturity. In spite of these changes in the composition of the population, the mean biomass density remained constant. A 25 mm juvenile krill reflects approximately ¹/₄ of the sound reflected by a 50 mm adult krill, implying that numerical densities of krill were 2 to 4 times higher during the early and mid-summer than they were during the late summer, particularly in the near-shore areas

Sound scattering aggregations of presumed biological origin were observed on Survey 2 with the lowest estimated krill biomass density. However, for most of the aggregations the difference between mean volume backscattering at 120 and 38 kHz was less than 2 dB and therefore not classified as krill. Both theoretical models (McGehee et al. 1998) and experimental evidence (Wiebe et al. 1990) demonstrate stronger sound scattering from krill at 120 kHz than from 38 kHz under all natural conditions. Two explanations are therefore possible: 1) the aggregations are krill but one or both of the acoustic transceivers was operating sub-optimally (calibration was conducted before but not after this survey); or 2) the acoustic equipment was not mal-functioning and the aggregations were not composed of krill.

The only other biological candidate for similar sound scattering at both frequencies is mesopelagic myctophid fish. However, aggregations were often found in the upper portion of the water column and in a few cases, the net actually caught krill nearby. Furthermore, if the aggregations are not krill, the implication is that krill abundance was very low during this survey. This further implies that krill left the survey area sometime over the three-week period since the preceding survey. It also implies that a substantial amount of krill entered the survey area during the 10-day period before the subsequent survey. There was insufficient information on hand to distinguish between the two explanations. Measurement error due to instrument malfunction seems, however, to be the most probable. This implies that absolute estimates of krill density are not possible from the data collected. If the lowest estimate is treated as the result of measurement errors, then the consistency between the other four surveys suggests low variability in krill biomass north of the South Shetland Islands throughout the summer of 1999/2000. However, the demographic composition of krill present in the survey area changed as the summer progressed from a mixture of juvenile, immature and mature animals to one of a single mode of large, mature animals. These changes are consistent Siegel's (1988) description of ontogenic seasonal movements of krill in the vicinity of the South Shetland Islands.

Transect-to-transect variation in mean krill biomass density was similar among the surveys, suggesting similar dispersion patterns on the scale of the transects. This may be interpreted as relatively constant prey availability to predators, although the numerical density and size composition of prey changed as the season progressed. There is also the suggestion that prey may have been moved closer to the shelf break as the season progressed.

These surveys cannot resolve where the juvenile krill went after moving through the survey area. Siegel et al. (in press) sampled high densities of juvenile krill in the southeastern portion of Bransfield Strait during January-February 2001. They acknowledged that these krill may have been transported from the Weddell Sea, but concluded that their observations were more likely the result of a southern shift in the position of krill from the Bellingshausen Sea moving with the Antarctic Circumpolar Current.

In addition, these surveys cannot unambiguously resolve the rate of movement of krill through the South Shetland Islands region. At least two models of krill transport are possible. The first is where large aggregations of krill move cohesively through the region. With this model it may be possible to identify and track the movement of the aggregations and thus quantify the flux of krill through the region and the amount of prey available to predators over a period of time, such as the breeding season. The second model of movement is where much smaller aggregations of krill are transported into areas where their movement is stalled and they join other small aggregations to form

persistent localized areas of high krill density. These areas may coincide with places where currents have been influenced by topographic features creating eddies, convergence zones and other diversions of the water flow, which may act to concentrate krill (Witek 1988). Finer-scale observations, both in space and time, would be required to resolve this model of krill transport.

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Appendix 1. Calculation of conversion factor

The conversion factor (CF) was defined as the quotient of the weight of an individual krill (W) and its backscattering cross-sectional (σ) area summed over the length frequency distribution:

$$CF = \frac{W(L)}{\sigma(L)} \left(\frac{g}{m^2}\right)$$

The biomass density of krill (ρ) is thus computed as the integrated volume backscattering area for each interval multiplied by the CF. Integrated volume backscattering area for each interval is expressed by the EchoView software as the Nautical Area Scattering Coefficient (NASC) in units of m² of backscattering area per n.mile² of sea surface following the definition of s_A established by Simrad.

The weight/length relationship assumed was the same as used in the analysis of the CCAMLR 2000 Survey (Hewitt et al. this volume):

$$W(L) = 0.002236(L)^{3.314} x 10^{-3}(g)$$

Backscattering cross-sectional area is defined as a function of target strength (TS): $\sigma(L) = 4\pi 10^{TS(L)/10} (m^2)$

where the TS/length relationship was that adopted for krill by CCAMLR in 1991 (SC-CAMLR 1991):

Thus:

$$\sigma(L) = 4\pi 10^{(-127.5+34.85\log(L))/10}$$

= $4\pi 10^{-12.75} 10^{3.485\log(L)}$
= $4\pi 10^{-12.75} L^{3.485}$

 $TS(L) = -127.5 + 34.85 \log(L)$

Substituting these relationships into the expression for CF and adjusting for units:

$$CF = \frac{0.002236(L)^{3.3314} x 10^{-3}}{4\pi 10^{-12.75} L^{3.485}} \left(\frac{g}{m^2}\right) \left(\frac{1n.mile^2}{1852^2 m^2}\right)$$
$$= \frac{2.236x 10^{-6}}{4\pi 1852^2 x 10^{-12.75}} \left(\frac{L^{3.314}}{L^{3.485}}\right)$$
$$= 0.2917 L^{-0.171}$$

The final expression for CF is calculated by summing over the length frequency distribution:

$$CF = 0.2917 \sum f_i(L)^{-0.171}$$

where $\sum f_i = 1$.

Table 1. Survey numbers, research vessels, survey dates, number of transects, are surveyed, krill density, sampling error, and estimated biomass over the survey area. Data from Survey 5 (West Area) are included in the comparisons of survey results discussed in the text. Data from Survey 5 (Elephant Island Area) and Survey 5 (South Area) are included for completeness.

Survey	Country Vessel	Survey dates	Number Transects	Area surveyed (km ²)	$\overline{ ho}$ (g m ⁻²)	CV (%)	Biomass (10 ³ tons)
Survey 1	Japan R/V <i>Kaiyo Maru</i>	14 to 18 Dec 1999	7	30,704	50.45	20.3	1,549
Survey 2	Korea R/V <i>Onnuri</i>	10 to 15 Jan 2000	8	38,803	1.68	21.2	65
Survey 3	Peru R/V <i>Humboldt</i>	24 to 28 Jan 2000	8	37,319	54.22	23.2	2,023
Survey 4	Japan R/V <i>Kaiyo Maru</i>	29 Jan to 2 Feb 2000	8	37,319	46.50	20.4	1,735
Survey 5	USA R/V Yuhzmorgeologiya	22 to 26 Feb 2000 (West Area)	7	34,149	44.25	14.0	1,511
	USA R/V Yuhzmorgeologiya	26 Feb to 5 Mar 2000 (Elephant Island Area)	9	41,673	39.77	19.1	1,657
	USA R/V Yuhzmorgeologiya	5 to 6 March 2000 (South Area)	3	8,102	23.46	46.1	190

Table 2. Net sampling periods, timing, survey, sampling gear and deployment method.

Sampling period	Timing	Survey	Net	Cross-sectional area of mouth and mesh size	Sampling method
Early Summer	mid-Dec	Survey 1	RMT-8	8 m ² , 5 mm	Oblique tow 200 m to surface
	mid-Jan	Survey 2	Bongo	1 m^2 , 0.5 mm	Oblique tow 200 m to surface
Mid-Summer	late Jan	Survey 3	Engel	14 mm	Directed at acoustic targets
	late Jan to Early Feb	Survey 4	RMT-8	8 m ² , 5 mm	Oblique tow 200 m to surface
Late Summer	late Feb to Early March	Survey 5	IKMT	$2.5 \text{ m}^2, 0.5 \text{ mm}$	Oblique tow 170 m to surface

		Large	Medium	Small
Early Summer	Transect 1	North of 60.701	South of 60.701	
	Transect 2	North of 60.883	South of 60.883	
	Transect 3	North of 61.175	South of 61.175	
	Transect 4	North of 61.404		South of 61.404
	Transect 5		All Medium	
	Transect 6	North of 61.846	South of 61.846	
	Transect 7	North of 61.974	South of 61.974	
Mid-Summer	Transect 1	All Large		
	Transect 2	South of 61.091	North of 61.091	
	Transect 3	North of 61.573	South of 61.573	
	Transect 4	North of 61.610	South of 61.610	
	Transect 5	North of 61.795	South of 61.795	
	Transect 6	North of 62.111	South of 62.111	
	Transect 7	North of 62.244	South of 62.244	
	Transect 8	North of 62.691	South of 62.691	
Late Summer	All transects	All large		

Table 3. Latitudinal position at which krill size clusters change along acoustic transects.

Table 4. Conversion factors for each length frequency cluster

Time Period	Size Modes	CF
Early summer	Large mode	0.1494
	Medium mode	0.1555
	Small mode	0.1594
Mid-summer	Large mode	0.1488
	Medium mode	0.1527
Late summer	Large mode	0.1496
Average		0.1526

	Survey 1	Survey 4	Survey 5
Juvenile	0.3350	0.0141	0.0000
Adult male			
M 2A1	0.1853	0.0280	0.0004
M 2A2	0.0936	0.0841	0.0090
M 2A3	0.0074	0.0450	0.0021
M 3A	0.0081	0.0126	0.0598
M 3B	0.0335	0.3175	0.4159
Adult Female			
F 2	0.0834	0.0000	0.0000
F 3A	0.2374	0.1409	0.0004
F 3B	0.0163	0.1851	0.0057
F 3C	0.0001	0.1223	0.1782
F 3D	0.0000	0.0504	0.2993
F 3E	0.0000	0.0000	0.0293

Table 5. Krill maturity stages sampled on Surveys 1, 4 and 5.

Transect krill Densities					Survey Krill Densities				
Survey	Transect	Number of Intervals	$\overline{\rho}_j$ without interval weighting	$\overline{\rho}_j$ with interval weighting	L_j	Wj	$\overline{ ho}$ (g/m ²)	$\operatorname{var}(\overline{\rho})$	CV (%)
1	1 2 3 4 5 6 7	96 61 56 40 45 45 45 49	(g/m ²) 31.91 31.12 82.17 101.76 32.01 51.48 43.18	(g/III ⁻) 27.24 31.19 84.30 100.49 33.50 49.72 46.89	50.54 43.86 39.94 27.38 32.84 31.54 35.25	1.35 1.17 1.07 0.73 0.88 0.84 0.94	 50.45	104.56	20.3
2	1 2 3 4 5 6 7 8	84 74 58 36 41 40 41 53	1.02 0.94 0.76 2.76 1.99 3.23 2.82 1.91	0.95 0.80 0.54 2.89 1.94 3.23 2.54 2.09	43.54 50.25 41.40 26.12 29.32 28.42 29.52 37.51	1.22 1.41 1.16 0.73 0.82 0.79 0.83 1.05	 1.68	0.13	21.2
3	1 2 3 4 5 6 7 8	88 68 54 60 52 55 55 52 54	176.16 36.62 19.50 34.41 28.59 60.41 88.24 39.67	116.38 37.05 18.94 35.16 30.01 61.47 90.80 37.15	45.29 44.09 37.85 40.70 33.82 38.93 34.36 39.04	1.15 1.12 0.96 1.04 0.86 0.99 0.88 0.99	 54.22	158.22	23.2
4	1 2 3 4 5 6 7 8	76 50 54 42 45 47 50 55	57.64 27.68 62.96 38.18 26.54 29.84 99.57 22.69	56.13 27.90 62.10 41.83 25.82 29.80 100.50 23.54	37.70 34.78 38.01 28.21 31.70 32.92 35.15 37.88	1.09 1.01 1.10 0.82 0.92 0.95 1.02 1.10	 46.50	89.95	20.4
5 (West)	1 2 3 4 5 6 7	41 45 66 71 73 89 99	79.77 35.41 43.03 44.54 36.73 54.59 27.37	80.58 36.37 45.20 46.42 35.35 56.72 24.91	30.30 30.86 49.26 46.14 53.85 62.41 67.45	0.62 0.63 1.01 0.95 1.11 1.28 1.39	44.25	38.49	14.0
5 (EI)	1 2 3 4 5 6 7 8 9	111 118 116 109 128 126 125 115 112	42.64 66.65 16.49 54.39 17.50 82.46 55.81 25.48 11.65	43.79 64.62 16.97 53.60 18.55 76.40 47.84 26.60 10.61	76.13 80.95 78.09 75.71 80.66 76.39 85.53 77.48 80.29	0.96 1.02 0.99 0.96 1.02 0.97 1.08 0.98 1.02	 39.77	57.48	19.1
5 (South)	1 2 3	20 44 40	1.69 34.74 27.07	1.70 37.63 29.98	15.24 28.50 28.35	0.63 1.19 1.18	27.03	71.39	31.3

Table 6. Krill biomass densities and coefficients of variation by transect and survey.



Figure 1. Scotia Sea sector of the Southern Ocean. Krill Spawning areas (cross-hatched), major currents and frontal zones where PF indicates Polar Front, SACCF indicates Southern Antarctic Circumpolar Front and SBACC indicates the southern boundary of the Antarctic Circumpolar Current. (from Hewitt and Linen Low 2000; sources: Marr 1962, Orsi et al. 1995, Hofmann et al. 1998).



Figures 2a through 2e. Survey transects and net sampling stations indicated by stars. Islands are indicated by gray-shaded polygons. Bottom topography indicated by shades of gray: 0-500 m, 500-2000 m, 2000-4000 m and 4000-6000m. Gray polygons indicate boundaries of survey areas for Survey 5.



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Figure 3. Aggregated length-frequency distributions of krill from each sampling period.



Figure 4. Geographic distribution of length-frequency clusters shown in Figure 3. Circles indicate Survey 1 samples, stars indicate Survey 3 samples, and triangles indicate Survey 4 samples. Light gray shading indicates small mode cluster, medium gray shading indicates medium mode cluster and black shading indicates large mode cluster. Late summer period was classified as a single cluster and is not shown.



Figures 5a through 5b. Dispersion of krill biomass density in the vicinity of the South Shetland Islands. Islands are indicated by gray-shaded polygons; shelf break is approximated by the 500 m isobath and indicated by thin black line. Note change of density scales for Survey 2.



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