Seasonal variability in the distribution of Antarctic krill, *Euphausia superba*, west of the Antarctic Peninsula

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Abstract

A unique Antarctic data set from four multidisciplinary cruises (spring, Nov 1991; summer, Jan–Feb 1993; fall, Mar–May 1993; winter, Aug–Sept 1993) was analyzed to provide a description of seasonal variability in the distribution and abundance of Antarctic krill, *Euphausia superba*, west of the Antarctic Peninsula. Analyses of acoustic observations revealed distinct seasonal variations in estimates of krill abundance, the dimensional parameters used to characterize individual krill aggregations, the geographic area over which krill were acoustically detected, and the depth distribution of krill biomass. Spatially averaged estimates of krill biomass were an order of magnitude higher in spring ($32 \, \mathrm{g \, m^{-2}}$) and summer ($95 \, \mathrm{g \, m^{-2}}$) compared to fall ($12 \, \mathrm{g \, m^{-2}}$) and winter ($8 \, \mathrm{g \, m^{-2}}$). In summer, krill were detected throughout the region and most of the krill biomass was associated with aggregations of small cross-sectional area ($< 2000 \, \mathrm{m^2}$) and high mean biomass ($> 150 \, \mathrm{g \, m^{-3}}$), which were positioned in the upper 50 m of the water column. Winter observations, in contrast, were characterized by the absence of krill throughout most of the region and aggregations occuring deeper than 100 m with large cross-sectional area ($> 10000 \, \mathrm{m^2}$) and low mean biomass ($< 10 \, \mathrm{g \, m^{-3}}$). Two features common to all seasons were the presence of higher krill biomass ($> 50 \, \mathrm{g \, m^{-2}}$) at selected locations on the inner shelf and the disproportionate contribution, in terms of total krill biomass ($> 80\%$), by a small number of aggregations ($< 20\%$). The length frequency distributions of krill collected by nets showed an across-shelf pattern of larger ($> 40 \, \mathrm{mm}$) krill positioned offshore of smaller krill (32–38 mm) in all seasons except winter. Synthesis of these data and historical observations suggest that there is a seasonal shift in the primary habitat of krill and that changes in krill behavior are an important factor affecting variations in krill distributions. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The Antarctic krill, *Euphausia superba*, is widely recognized as a major link between primary producers and many populations of Antarctic carnivores, including whales, seals, seabirds, penguins, and fishes (Marr, 1962; Knox, 1970; Laws, 1985). Krill became a commercially harvested species during the late 1960s and today is the subject of an active fishery by several nations. Concern over exploitation of Antarctic organisms prompted the establishment of the Biological Investigations of Marine Antarctic Systems and Stocks (BIOMASS) program in the late 1970s to study the marine living resources of the Southern Ocean (El-Sayed, 1977). As part of this 10-year international program, net and acoustic surveys were conducted to provide quantitative estimates of krill abundance. Large variations (several orders of magnitude) in krill biomass were observed between regions and years (e.g., Everson, 1983; Hampton, 1985; Priddle et al., 1988; Miller and Hampton, 1989; Everson and Miller, 1994).

A large degree of uncertainty still surrounds the assessment of krill biomass and production at global, regional, and even local scales (Everson, 1988; Ross and Quetin, 1988; Miller and Hampton, 1989), yet this information is integral to an improved understanding of the Antarctic ecosystem and to the successful management of the krill fishery. Some uncertainty stems from the bias of historical krill observations towards collections made during a single season, the austral summer, and towards selected regions, most notably those targeted by the BIOMASS program. Moreover, published descriptions of seasonal changes in the abundance of krill are few (Stepnik, 1982; Siegel, 1988, 1992).

The Palmer Long-Term Ecological Research (LTER) program (Smith et al., 1995) was established in 1990 to document interannual and seasonal variations in the pelagic marine ecosystem within continental shelf waters west of the Antarctic Peninsula (Fig. 1). Historical observations in this region are limited, especially south of Anvers Island. However, this area is considered a source of krill for regions to the northeast including Bransfield Strait and South Georgia, which were intensively sampled during and after BIOMASS (Siegel, 1988; Priddle et al., 1988; Everson and Miller, 1994).

The first four Palmer LTER cruises provide multidisciplinary observations that span all seasons, thus constituting a unique Antarctic data set for this region. In this study we examine the seasonal variability of krill distributions and abundances west of the Antarctic Peninsula. Acoustic measurements are used to estimate the abundance of krill and to characterize the size, shape, and biomass of individual krill aggregations. Net collections are used to describe the population structure of krill. Seasonal and mesoscale variations in the krill observations are compared to other krill surveys, and factors that may affect seasonal variability are discussed.

2. Methods

The sampling grid defined by the Palmer LTER program (Waters and Smith, 1992) consists of ten across-shelf transects extending from the southern end of Bransfield

Strait to the northern end of Alexander Island (Fig. 1). Transects are spaced 100 km apart and run offshore 200 km with primary stations positioned every 20 km along a transect. Each transect is designated by a three digit number (000–900), which identifies the distance (km) of a transect from the southern-most transect. Grid locations are identified by coordinates of the form $xxx.yyy$, where xxx is the transect number and yyy is the along-transect distance (km) from the innermost station. The 000.000 station is positioned at latitude 68.983°S and longitude 73.579°W.

Portions of this grid were surveyed during four research cruises: spring (7–21 November 1991), summer (8 January–7 February 1993), fall (28 March–12 May 1993), and winter (29 August–26 September 1993). Multidisciplinary data were collected at stations occupied sequentially along individual transects (Fig. 2). The sampling
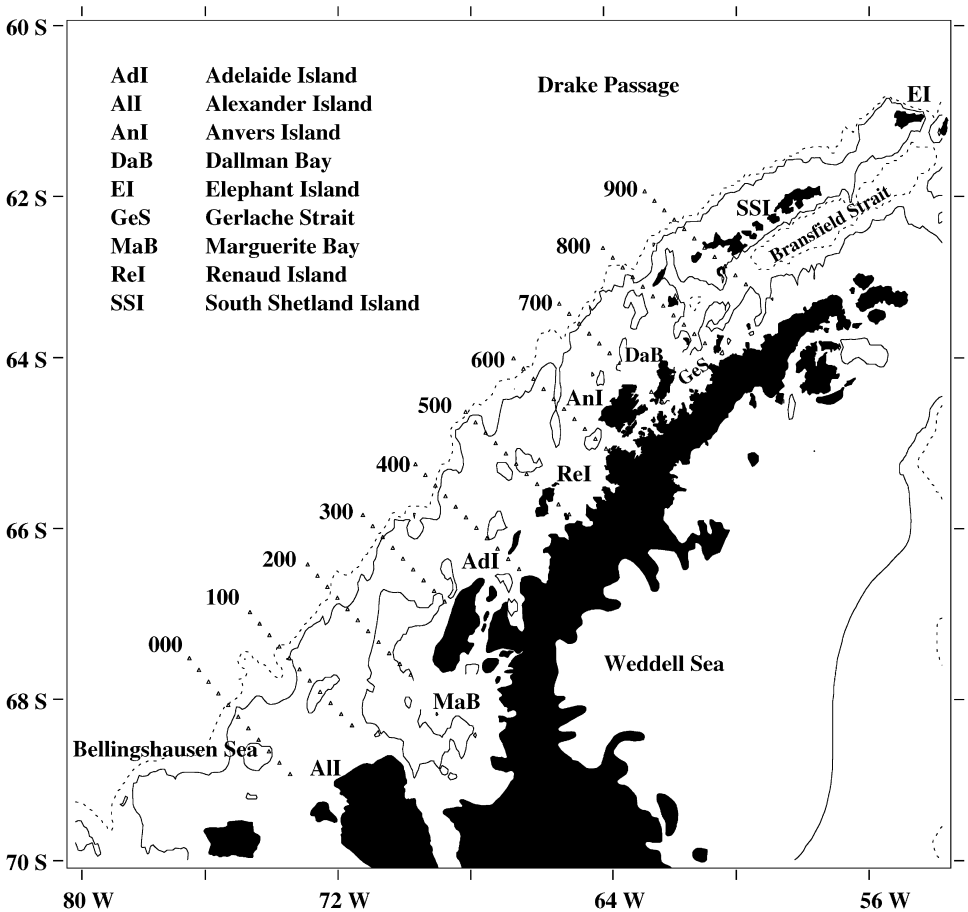

Fig. 1. Basemap of the study region along the west coast of the Antarctic Peninsula. Stations (△) are located at 20 km intervals along ten transect lines, which are spaced 100 km apart. The solid and dashed lines represent the 500- and 1000-m isobaths. The coastline and bathymetry were derived from the JEBCO and ETOPO5 data sets, respectively.
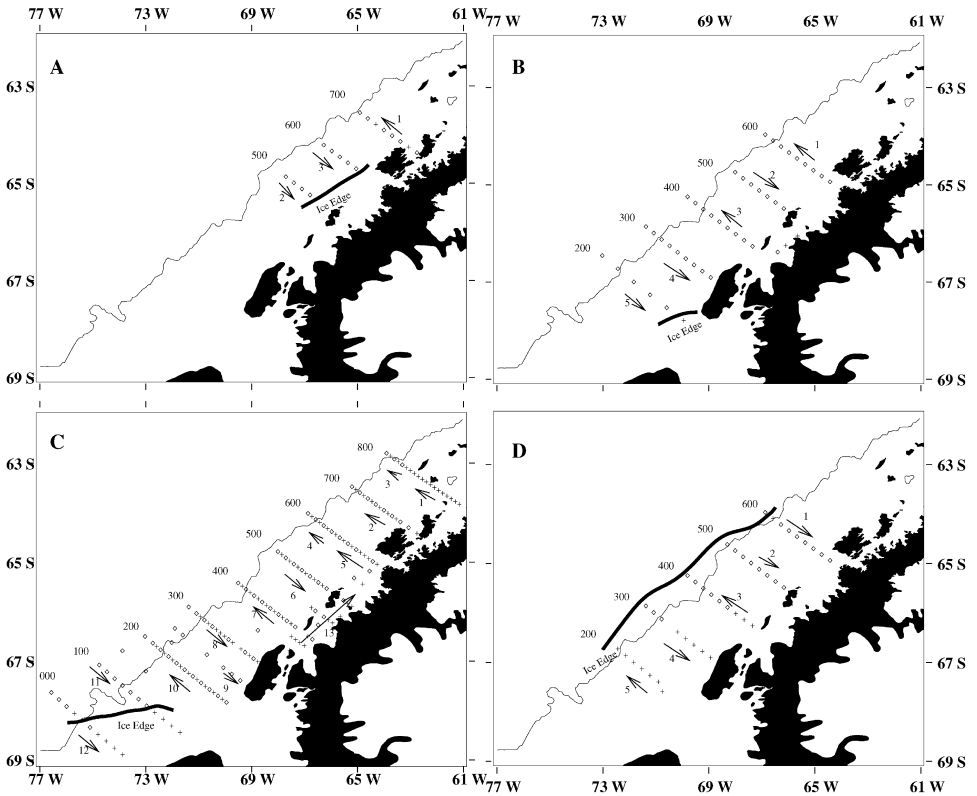
Fig. 2. Locations sampled during (A) spring: 7–21 November 1991, (B) summer: 8 January–7 February 1993, (C) fall: 28 March–12 May 1993, and (D) winter: 29 August–26 September 1993. The ◇ indicates stations where environmental and acoustic measurements were collected; the X indicates environmental measurements only. The 1000-m isobath is denoted by the solid line and the ice edge by the heavy line. Numbered arrows show the direction and the order in which across-shelf transects were occupied.

intensity and station coverage differed among cruises due to cruise duration and sea ice conditions. Ice conditions (type and thickness) were recorded at each station and used to identify the approximate location of the ice edge (Fig. 2), separating ice-free regions from ice-covered regions (positioned inshore of the ice edge). Typically, acoustic sampling was not accomplished at stations where ice thickness exceeded 0.5 m.

At each station, conductivity–temperature–depth (CTD) measurements were made using a SeaBird 911+ sensor, which was deployed from the surface to 500 m or to within 50 m of the bottom for shallower stations. These data were averaged into 1-m depth bins and processed according to algorithms described in UNESCO (1983) to provide vertical profiles of temperature, salinity, and density. Complete descriptions of the SeaBird sensor calibrations and data processing are given in Lascara et al. (1993a, b), Smith et al. (1993a, b), and Klinck and Smith (1994).

A 2-meter square trawl (700 µm mesh) was towed obliquely down to 120 m at each station (Quetin et al., 1992). These net samples were used to identify the taxonomic groups potentially responsible for acoustic scattering and to provide quantitative information on the size structure of the krill population. Length frequency distributions (LFD, bin size = 1.0 mm) of krill ($n = 100$) were computed for each station based on measurements of total length (mm, Standard Length 1 of Mauchline, 1980). A composite frequency distribution was created for groups of stations with similar LFDs based on visual examination. A length–weight regression, representing a random selection of individuals from all stations, was generated for each cruise.

Acoustic measurements were collected using a BioSonics Model 102 echo sounder (BioSonics, Inc., Seattle, WA) operating at 120 kHz. At each station, the transducer was deployed in a dead-weight body and towed 2–4 m below the surface along short (1–2 km) transects, in conjunction with net tows. Since several net tows were made, the total acoustic sampling effort for a station was typically 2–10 km within a 1–3 h period. The acoustic system was calibrated before the 1991 cruise and before the suite of 1993 cruises by the manufacturer in a calibration tank using standard methods.

The returned echo energy (volts) was corrected for spreading loss using a time-varied gain function ($20 \log R$). The voltage measurements were averaged over 2-m depth intervals for several pings and combined with calibration data to generate a two-dimensional (alongtrack, vertical) matrix of volume scattering data (VSD, $m^2 \, m^{-3}$) for each acoustic transect (BioSonics, 1990). The ship's position was time-keyed to the acoustics data and used to determine the total transect distance and mean horizontal resolution of cells in each acoustic data matrix (Table 1). Echograms were visually examined and data representing scattering from abiotic noise (e.g., pack ice, surface bubbles, bottom return) were excluded. A background noise level of -81 decibels (dB), which is roughly equivalent to $0.05 \, g \, m^{-3}$ of krill biomass, was removed from all acoustic observations.

Conversion of VSD to krill biomass ($g \, m^{-3}$) requires an expression for the back-scattering cross-sectional area (σ_{bs}, m^2) or target strength (TS, defined as $10 \log \sigma_{bs}$) of

Table 1
Summary of acoustic processing parameters

Parameter	Spring	Summer	Fall	Winter
Number of stations	15	40	81	25
Total acoustic sampling distance (km)	108	180	354	127
Ping rate (s^{-1})	2	1	1	1
Pings per record	5–10	3–5	3	3
Depth range (m)	17–189	17–189	17–189	17–189
Acoustic matrix cell size				
Vertical (m)	2	2	2	2
Horizontal (m)	6–13	2–9	2–7	2–8
L-W regression ($W = aL^b$)				
Coefficient (a)	0.0061	0.0040	0.0033	0.0093
Exponent (b)	3.078	3.202	3.231	2.940

krill. The TS-weight relationship used in this study is based upon the empirically derived linear regression equation of Wiebe et al. (1990), as modified by Greene et al. (1991) for 120 kHz:

$$\text{TS} = -98.64 + 10.28 \log \text{WW}, \tag{1}$$

where WW is krill wet weight. The TS–length relationship adopted by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Working Group on Krill (SC-CAMLR-X, 1991) is also derived from Greene et al. (1991). We chose a TS-weight relationship so that seasonal variations in length-weight regressions could be incorporated into krill target strength. For each station, a LFD-weighted mean σ_{bs} was computed based on the frequency distribution of krill sampled by nets at each station, the seasonal length–weight regression, and the TS-weight equation above. Estimates of krill biomass (g m^{-3}) were then computed by dividing VSD (m^2 m^{-3}) by the mean weight-specific σ_{bs} (m^2 g^{-1}).

Each two-dimensional matrix of krill biomass (g m^{-3}) was examined with an aggregation analysis procedure (Nero and Magnuson, 1989) designed to identify individual aggregations and characterize aggregation structure. A patch or aggregation was defined as a contiguous group of cells in the acoustic matrix with biomass values exceeding a minimum defined threshold value of 0.5 g m^{-3}. Cells within the data matrix with biomass values below this threshold were reset to zero, and all subsequent processing thus represented only krill biomass associated with an aggregation. This patch threshold value was chosen because it was the lowest value that resulted in aggregations with lengths and heights similar in scale to those described historically as krill aggregations (Miller and Hampton, 1989; Kalinowski and Witek, 1985). At lower threshold values, numerous small aggregations were observed, as well as many horizontally and vertically extensive aggregations of low scattering intensity. The total krill biomass observed at a location was typically reduced by < 5% using the patch threshold, 0.5 g m^{-3}, in comparison to the total krill biomass estimated using only the noise threshold (0.05 g m^{-3}).

The structure of individual krill aggregations was characterized with a set of five dimensional parameters as defined in Table 2. For each parameter, aggregations were grouped by size class to create two types of frequency distributions: by number of aggregations and by total aggregation biomass contained within each size class. Since the acoustic path randomly intersects aggregations, which may be irregularly shaped, some of the individual measurements may be poorly correlated with the true aggregation parameters. With this in mind, analysis of these data will be limited to a relative comparison of the frequency distribution of these parameters between seasons using a large number of aggregations.

Mean krill abundance per square m of sea surface (B_a) was calculated by vertically integrating over the depth range 17–187 m and horizontally averaging over 750 m of survey transect defined as the elementary distance sampling unit (EDSU, MacLennan and Simmonds, 1992):

$$B_a = \frac{1}{I} \sum_{i=1}^{i=I} \left(\sum_{j=1}^{j=J} (B_v)_j \Delta z_j \right)_i, \tag{2}$$

Table 2
Definitions of dimensional parameters computed for each aggregation

Parameter	Units	Definition
Length (L)	m	Intercepted length of aggregation along transect
Height (H)	m	Distance from top to bottom of aggregation
Area (A)	m^2	Cross-sectional area of aggregation in vertical plane
		$\sum$ area for each matrix cell within the aggregation
		Not equivalent to $L \times H$ for irregular aggregations
Mean biomass (B_v)	g m^{-3}	Mean volumetric biomass of the aggregation
Total biomass (B_t)	kg m^{-1}	Aggregation biomass estimated by $B_v \times A$

where I is the number of integration records in one EDSU, J is the number of depth strata, Δz is the stratum size in m, and B_v is the volumetric krill biomass (g m^{-3}). The EDSU-based estimates of krill biomass (B_a) were used to generate a mean krill biomass estimate at each station or region as

$$\bar{B}_a = \frac{1}{K} \sum_{k=1}^{k=K} (B_a)_k, \tag{3}$$

where K is the number of EDSUs for that station or region. The reliability of acoustically derived mean estimates is clearly an important issue, particularly for aggregating species, and several methods of estimating variance are described in MacLennan and Simmonds (1992). Most methods, however, require numerous randomly positioned parallel transects. Given the simple sampling design employed in the current study and the small number of EDSUs obtained per location, a simple estimator of variance, standard deviation (Snedecor and Cochran, 1978), was selected.

Acoustically-derived estimates of krill biomass are affected by uncertainties surrounding the identification of the species responsible for acoustic scattering and the determination of related target strength characteristics. Historically, the general practice adopted by krill survey programs using single-frequency, single-beam systems is to assume that all biotic scattering returns are due to krill and that target strength is a function solely of length (or weight) of the individuals (e.g., Hampton, 1985; Witek et al., 1988; Miller and Hampton, 1989a). Clearly the first assumption is not always valid, and the potential bias introduced by the inclusion of alternate scatterers is itself a function of the relative target strengths of the scattering types.

In this study, the entire biotic acoustic signal was attributed to krill scattering, which results in an unquantifiable overestimation of krill biomass for locations where scattering by non-krill taxa was important. Comparisons between paired net/acoustic observations indicated in all seasons that krill were the dominant acoustic scatterer in the study region. In addition, the highest net-derived krill density estimates were coincident with acoustic echograms characterized by strong scattering intensities (Lascara, 1996). Unfortunately, since the net samples represent integrated collections, there is no objective method for partitioning the acoustic data into krill and non-krill

targets. One possible alternate acoustic scatterer in this region is the salp, *Salpa thompsoni*. During this study, salps were found at very few stations and in low densities in spring 1991 and summer and winter 1993 (Ross et al., 1996). Only in fall 1993 on the 700, 800, and 900 transect lines and at stations beyond the shelf break were salps abundant (Ross et al., 1996). However during this study acoustic scattering was not strong at these stations, resulting in low acoustic estimates of krill biomass.

3. Results

3.1. Seasonal comparisons

3.1.1. Environmental observations

Sea ice conditions ranged from ice-free at most stations in the summer to ice-covered at most stations in the winter (Fig. 2b and d). In spring, the outer shelf was ice-free with a compacted ice edge positioned on the middle shelf of the 500 and 600 lines and near the mouth of Dallman Bay on the 700 line (Fig. 2a). Ice-free conditions were observed during fall throughout the region with the exception of newly forming ice found along the inner shelf of the 000 and 100 lines (Fig. 2c).

Temperature–salinity (T–S) diagrams from each season (Fig. 3) indicated the presence of two water masses, Antarctic Surface Water (AASW) and Circumpolar Deep Water (CDW). Warm temperatures ($>1.0°C$) and high salinities (>34.6) characterized CDW, which was found below the permanent pycnocline and exhibited little seasonal variability. In winter and spring, cold temperatures ($< -1.0°C$) and salinities of 33.8–34.0 characterized AASW, which occupied the upper 100 m of the ocean, extending from the permanent pycnocline to the water surface. In summer and fall, AASW spanned a wide range of temperature and salinity values, which reflected strong vertical gradients in hydrographic properties for this water mass. A portion of the water column directly above the permanent pycnocline retained the T–S character observed for AASW in the winter, and the water associated with this temperature minimum has been referred to as Winter Water (WW). Warm ($>0°C$) temperatures and low salinities (<33.8) characterized AASW near the surface (upper 50 m) in summer and fall, which was separated from WW by a seasonal pycnocline.

3.1.2. Vertically integrated krill biomass

Krill biomass estimates from all locations (Table 3) were averaged by season as a first attempt at characterizing seasonal variations in krill abundance (Table 4). Spatially-averaged estimates of krill biomass increased three-fold from spring to summer ($32–95 \text{ g m}^{-2}$) and then decreased an order of magnitude to the low values ($<12 \text{ g m}^{-2}$) observed during fall and winter. The dramatic decrease in krill biomass from summer to fall occurred over a 2–3 month period in 1993.

Since the sampling intensity and region occupied differed between cruises, mean krill biomass was also determined by averaging the acoustic data for selected subsets of stations. Only nine stations were common to the sampling done during all four seasons primarily because of the ice conditions (Fig. 2) encountered during spring
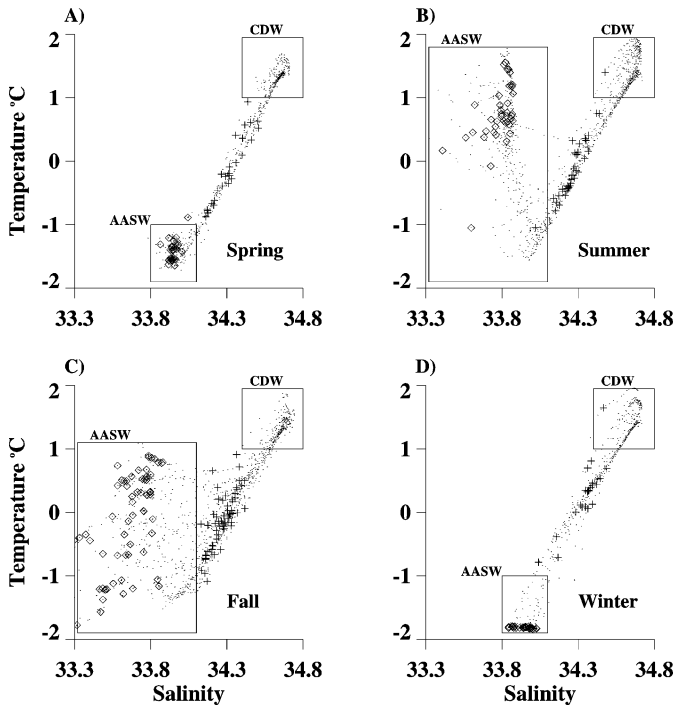
Fig. 3. Temperature–salinity diagrams based on observations from standard depth intervals of 10 m over the range 10–500 m: (A) spring, (B) summer, (C) fall, and (D) winter. The $T–S$ space occupied by the two principal water masses, Circumpolar Deep Water (CDW) and Antarctic Surface Water (AASW), is indicated by the solid lines. Observations from depths of 50 and 150 m are designated by the $\diamond$ and $+$ symbols, respectively. Analysis based on data sets in Lascara et al. (1993a, b), Smith et al. (1993a, b), and Klinck and Smith (1994).

1991, which limited acoustic sampling for this season. Based on this subset, which encompassed locations on the mid- and outer-shelf of the 500 and 600 lines, the summer mean krill biomass value was greatly reduced from that obtained for all locations and was similar in magnitude to that observed during the spring (Table 4). Mean krill biomass ($<2\,\mathrm{g\,m^{-2}}$) was also lower for observations from the winter and fall compared to the full data set. However, the basic pattern of higher krill biomass in summer and spring relative to fall and winter is apparent. Two additional comparisons were made using spatially-averaged krill biomass values for 22 common stations sampled in summer, fall, and winter and 35 stations sampled in summer and fall. These data sets further highlight the order of magnitude reduction in fall and winter krill biomass levels compared to summer observations.

3.1.3. Depth distribution

Seasonal differences were observed in the spatially-averaged depth distribution of krill biomass (Fig. 4). In spring, over 60% of the biomass was present in the upper

Table 3
Mean vertically-integrated krill biomass (g m^{-2}) by station. See Fig. 1 for station locations

Station	Spring	Summer	Fall	Winter	Station	Spring	Summer	Fall	Winter
000.100			0		400.080		575	6	
000.120			0		400.100		<1	1	0
000.160			0		400.120		<1	4	<1
000.180			0		400.140		307	<1	0
000.200			0		400.160		16	20	0
100.080			0		400.180		3	0	0
100.100			10		400.200		2		<1
100.120			62		420.000		582		
100.140			<1		430.015			28	
100.160			0		450.020			9	
100.180			5		450.040			2	
100.200			<1		500.020			56	
150.140			1		500.060		2	51	144
150.200			2		500.080		17	2	0
200.000			98		500.100	38	64	71	0
200.020			14		500.120	26	84	<1	0
200.040		878	8		500.140	11	68	0	0
200.060			1		500.160	30	41	0	0
200.080		<1	0		500.180		75	0	0
200.100			0		500.200				0
200.120		0	10		550.040			0	
200.140			35		580.030			29	
200.160		52	0		600.040		148	30	0
200.180			0		600.060		152		0
200.200		69	0		600.080	30	43	0	0
225.160			0		600.100	46	0	0	0
250.020			0		600.120	14	26	<1	0
250.040			0		600.140	15	15	0	1
250.060			0		600.160	24	21	<1	0
250.100			0		600.180		18	0	
250.160			40		600.200		0	<1	0
250.180			<1		700.020	105			
300.040		53	0		700.040			<1	
300.060		341	2		700.060	47		5	
300.080		55			700.080	17		5	
300.100		163	25		700.100	30		0	
300.120		2			700.120			0	
300.140		24	101		700.140	16		0	
300.160		56	0	0	700.160	47		0	
300.180		78	0	<1	700.180			0	
300.200		25	0	0	800.140			34	
350.080			0		800.160			0	
400.000			0		800.180			0	
400.040		225	64						
400.060		164	0						

Table 4
Summary of mean vertically-integrated krill biomass (g m^{-2}) by season for (A) all stations, (B) nine common stations sampled in all seasons, (C) 22 common stations sampled in summer, fall, and winter, and (D) 35 common stations sampled in summer and fall

Region		Spring	Summer	Fall	Winter
(A) All stations	Mean (g m^{-2})	32	95	12	8
	Standard deviation	43	188	47	66
	No. EDSU Samples	127	192	394	141
(B) Nine common stations	Mean (g m^{-2})	26	35	2	<0.1
All seasons	Standard deviation	33	52	10	1
	No. EDSU samples	84	35	47	40
(C) 22 common stations	Mean (g m^{-2})	—	57	7	10
Summer–Fall–Winter	Standard deviation	—	103	26	68
	No. EDSU samples	—	112	117	119
(D) 35 common stations	Mean (g m^{-2})	—	92	10	—
Summer–Fall	Standard deviation	—	178	41	—
	No. EDSU samples	—	173	199	—

70 m, with 20% deeper than 100 m. The summer distribution was skewed towards the ocean surface, and only 25% of the biomass was positioned deeper than 50 m. The fall profile was intermediate between the shallow summer and the deeper spring distributions. Krill were distributed deepest in winter, with only 10% of the total biomass located in the upper 70 m of the water column. Frequency distributions were also constructed using data from only the nine common stations sampled in all seasons. These distributions (not shown) were very similar to that described here using all data.

3.1.4. Aggregation characteristics

In total, over 3000 aggregations were acoustically-detected during this study. The seasonal pattern in number of aggregations per km was consistent with the seasonal pattern in mean vertically-integrated krill biomass. Aggregation abundance increased 2.5-fold from spring (4.8 no. km^{-1}) to summer (11.7 no. km^{-1}) and then decreased by an order of magnitude to the low values (<1 no. km^{-1}) observed in winter and fall.

In all seasons, the frequency distributions constructed for aggregation dimensional parameters based on number of aggregations within each size class were quite different from distributions based on total aggregation biomass (Fig. 5). Analysis of a composite data set consisting of randomly selected aggregations from all seasons revealed that over 70% of the aggregations were <40 m in length, <10 m in height, covered <250 m^2, and had mean biomass values <10 g m^{-3} (black bars in Fig. 5). However, most of the total krill biomass (>80%) was associated with a small number of aggregations (<20%) that were two- to four-fold larger and an order of magnitude more dense (gray bars in Fig. 5). Due to the skewness of frequency distributions based on number of aggregations, the frequency distributions based on total aggregation biomass were used to examine seasonal variability in aggregation dimensional parameters.
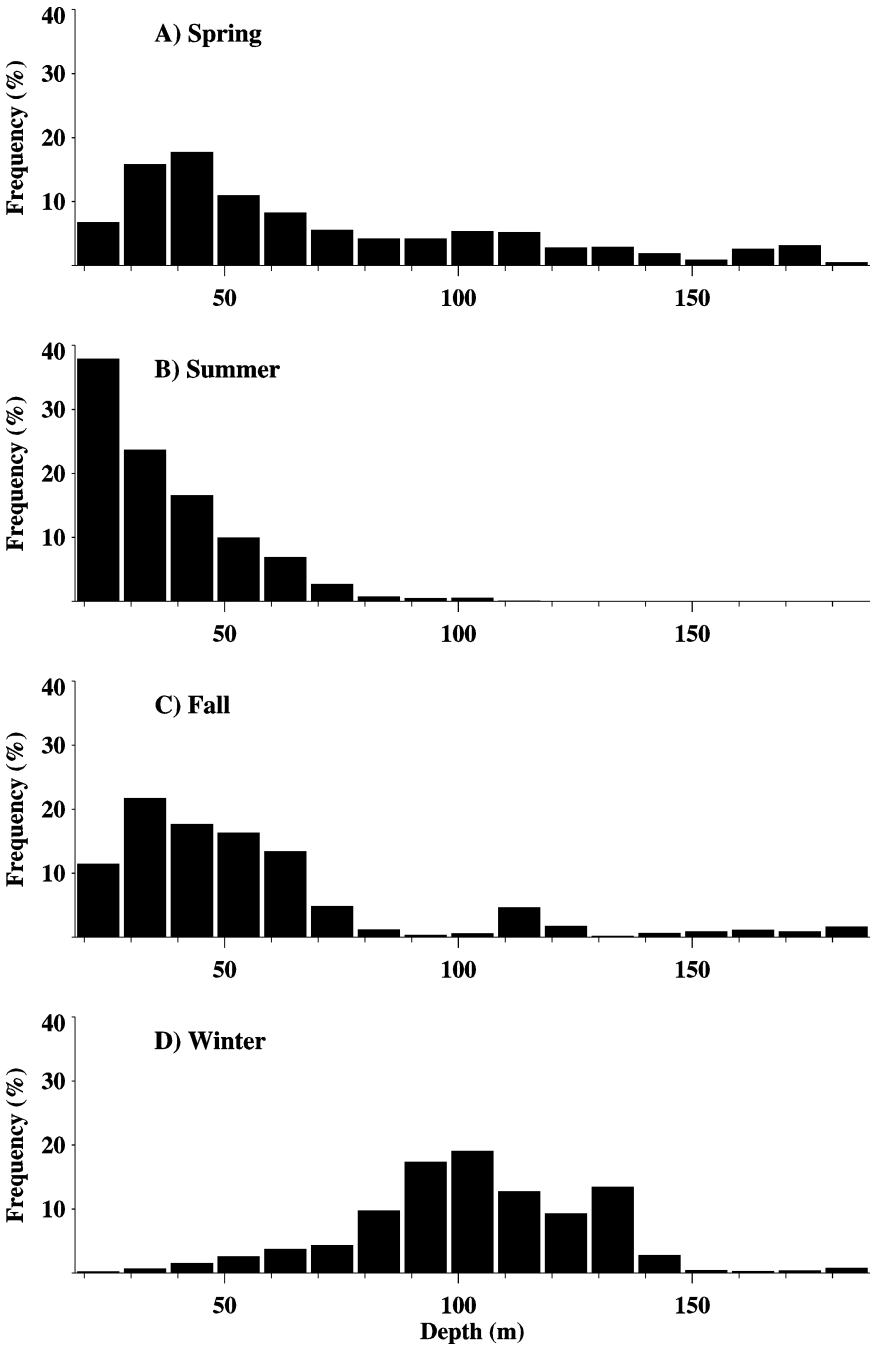
Fig. 4. (A) Frequency distribution of krill biomass as a function of depth by season: (A) spring, (B) summer, (C) fall, and (D) winter. Depth bin size is 10 m over the range 17–187 m.
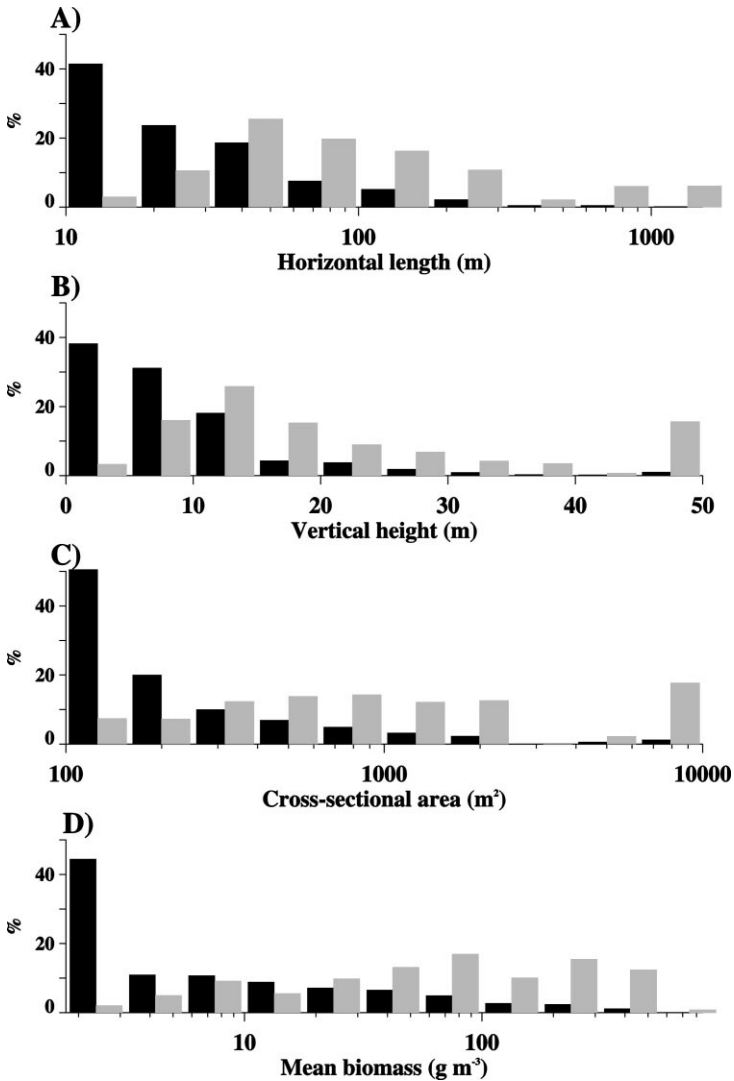
Fig. 5. Frequency distributions based on number of aggregations (black bars) or aggregation total biomass (grey bars) within size classes of the dimensional parameters: (A) horizontal length, (B) vertical height, (C) cross-sectional area, and (D) mean biomass. Data set consists of 950 aggregations, which were randomly selected from all seasons (spring = 300, summer = 300, fall = 300, and winter = 50). Bin sizes are 0.25, 0.20, 0.25 logarithmic units for length, area, and mean biomass, respectively, and 5 m for height.

During the spring, much of the total krill biomass was associated with aggregations characterized by cross-sectional areas ranging from 700 to 2200 m^2 (Fig. 6A) and mean biomass ranging from 20 to 100 g m^{-3} (Fig. 7A). The frequency distributions in summer were shifted towards aggregations with smaller areas (< 1000 m^2) and higher
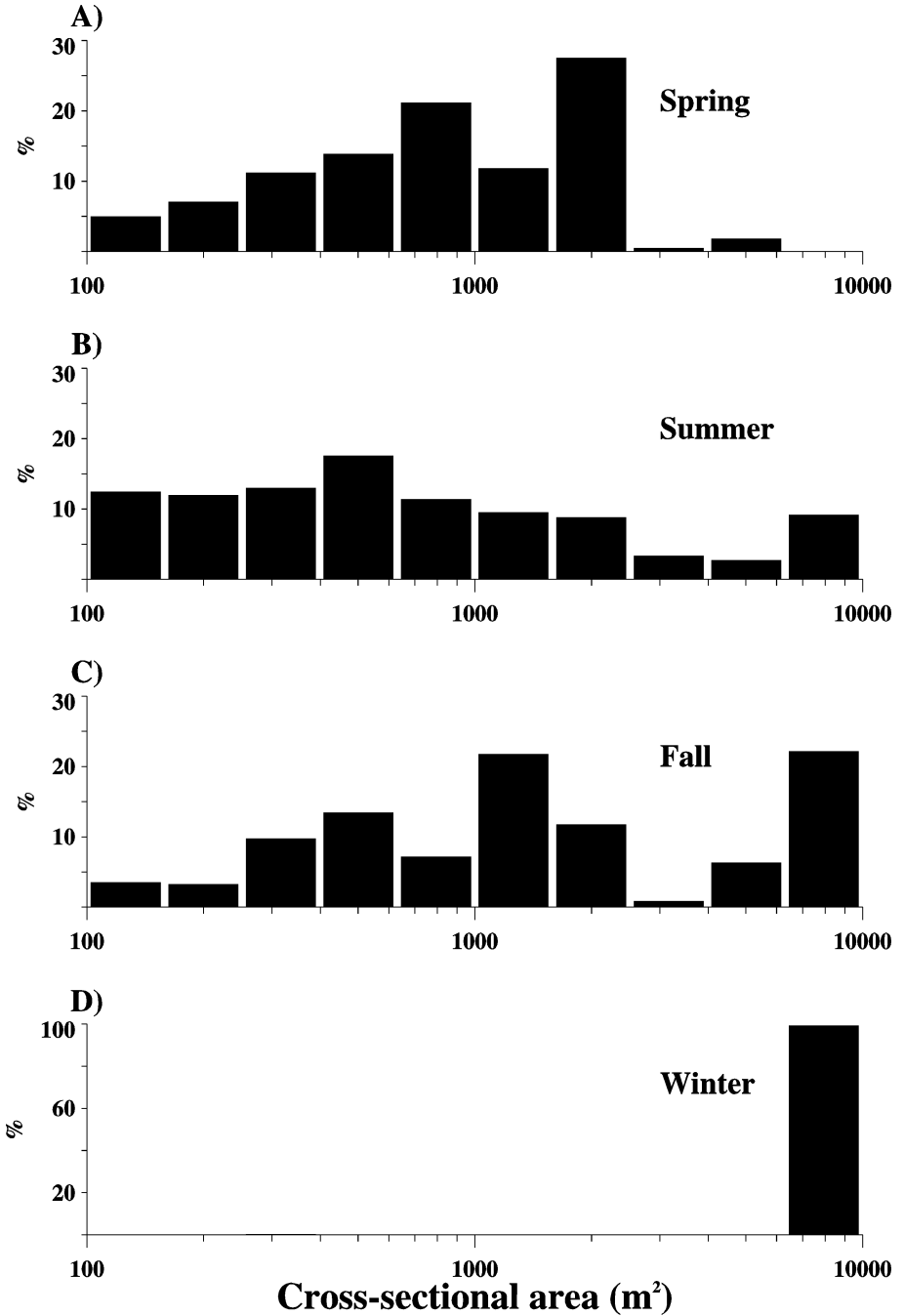
Fig. 6. Frequency distributions based on aggregation total biomass within size classes of the dimensional parameter, cross-sectional area: (A) spring $n = 519$, (B) summer $n = 2106$, (C) fall $n = 354$, and (D) winter $n = 56$. Bin size is 0.2 logarithmic units.
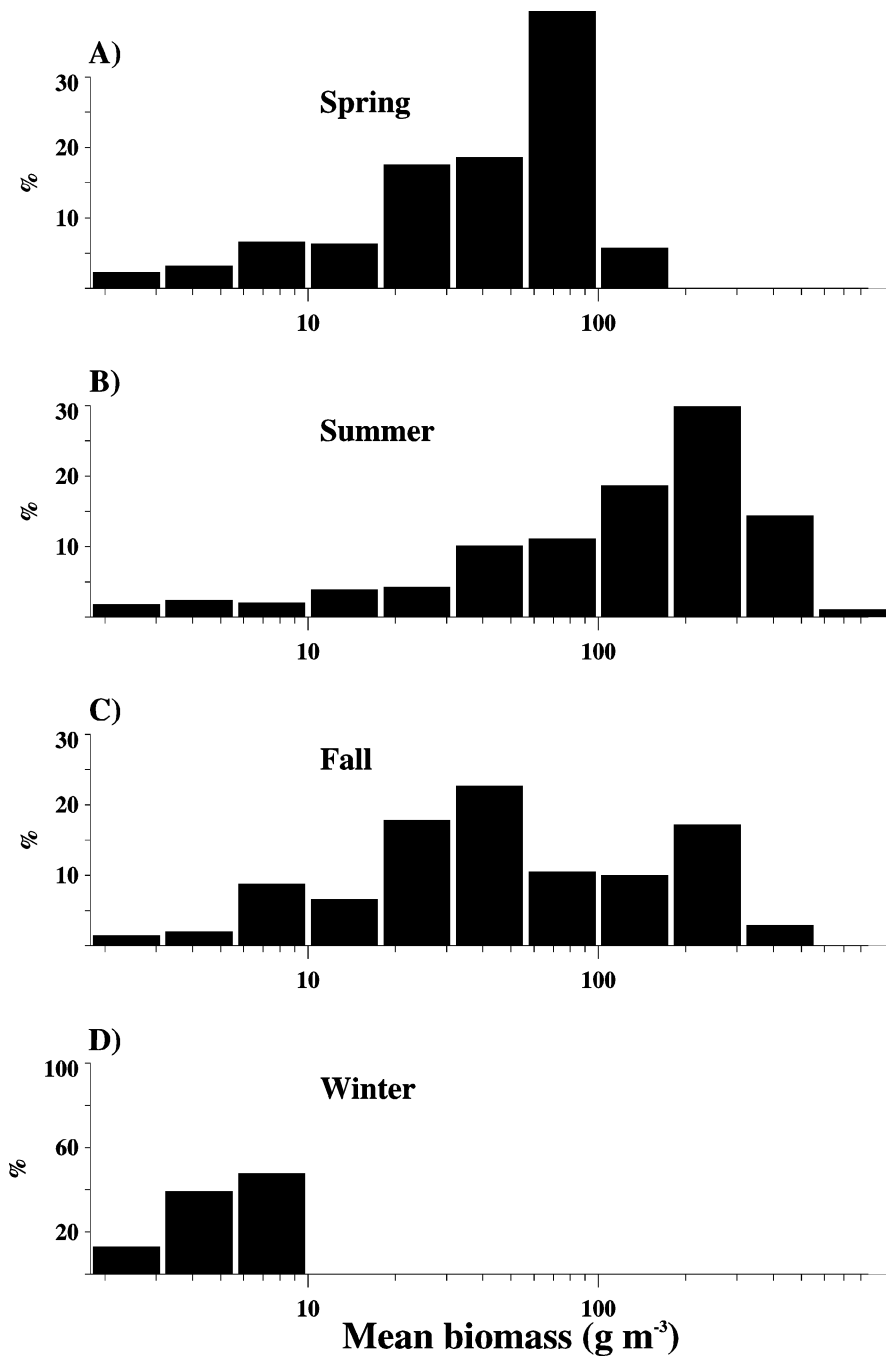
Fig. 7. Frequency distributions based on aggregation total biomass within size classes of the dimensional parameter, aggregation mean biomass: (A) spring *n* = 519, (B) summer *n* = 2106, (C) fall *n* = 354, and (D) winter *n* = 56. Bin size is 0.25 logarithmic units.

mean biomass values (150–500 g m^{-3}) (Figs. 6B and 7B). Fall observations were characterized by proportionately more total biomass contained within large aggregations exceeding 4000 m^2 (Fig. 6C). In fall, the mean biomass frequency distribution was also shifted towards less dense (<60 g m^{-3}) aggregations (Fig. 7C). The frequency distributions in winter were skewed towards very large aggregations (>7000 m^2) and very low mean biomass values (<10 g m^{-3}, Fig. 7D).

3.2. Mesoscale comparisons by season

In this section, spatial variations in krill biomass (g m^{-2}) and length frequency distributions (LFD groups) will be described by season. As an index of environmental variability, contours of mean salinity over the upper 40 m of the water column will be provided on the seasonal maps of krill biomass. This depth range (0–40) was chosen because it represents the portion of the water column within the acoustic sampling depth range (0–200) that exhibited the greatest variability in environmental conditions (Fig. 3).

3.2.1. Spring
Spatial variability in hydrographic properties was low throughout the region sampled in spring 1991 as shown by contours of salinity (Fig. 8). Krill aggregations were detected at all stations (Table 3), with mean biomass ranging from 10 to 47 g m^{-2} over the middle and outer shelf (Fig. 8). The highest krill biomass (105 g m^{-2}) was found on the inner shelf within Dallman Bay (station 700.020) and was spatially coincident with the lowest surface salinity (33.85) observed in spring.

Krill length frequency distributions (LFD) during spring 1991 fell into two LFD groups (Fig. 9). Group A occurred throughout the region and was numerically dominated by small (10–20 mm) krill. However, most of the krill biomass for group A was attributed to larger krill observed in the secondary LFD mode between 30 and 36 mm. Group B was restricted to two locations on the outer shelf of the 500 line and was dominated numerically by large (40–50 mm) krill (Fig. 9).

3.2.2. Summer
Across-shelf gradients were a dominant feature of the spatial distribution of hydrographic properties in summer 1993 (Fig. 10). Differences in surface salinity were used to partition the region into two hydrographic regimes. The 33.8 isohaline was chosen as the transition value distinguishing the fresher, inner shelf regime from the saltier, outer shelf regime. This salinity value represents the freshest AASW observed in winter and spring, thus waters exhibiting lower salinity values (e.g., the inner shelf regime) have been modified by seasonal inputs of freshwater. Alongshelf variations in the offshore distribution of waters associated with the inner shelf regime were also apparent (Fig. 10).

Estimates of krill biomass ranged from 0 to >800 g m^{-2} in summer (Table 3), with krill abundance notably different between the two hydrographic regimes. The outer shelf regime was characterized by biomass values typically ranging between 20 and 80 g m^{-2} in comparison to half of the stations exhibiting values >180 g m^{-2} within
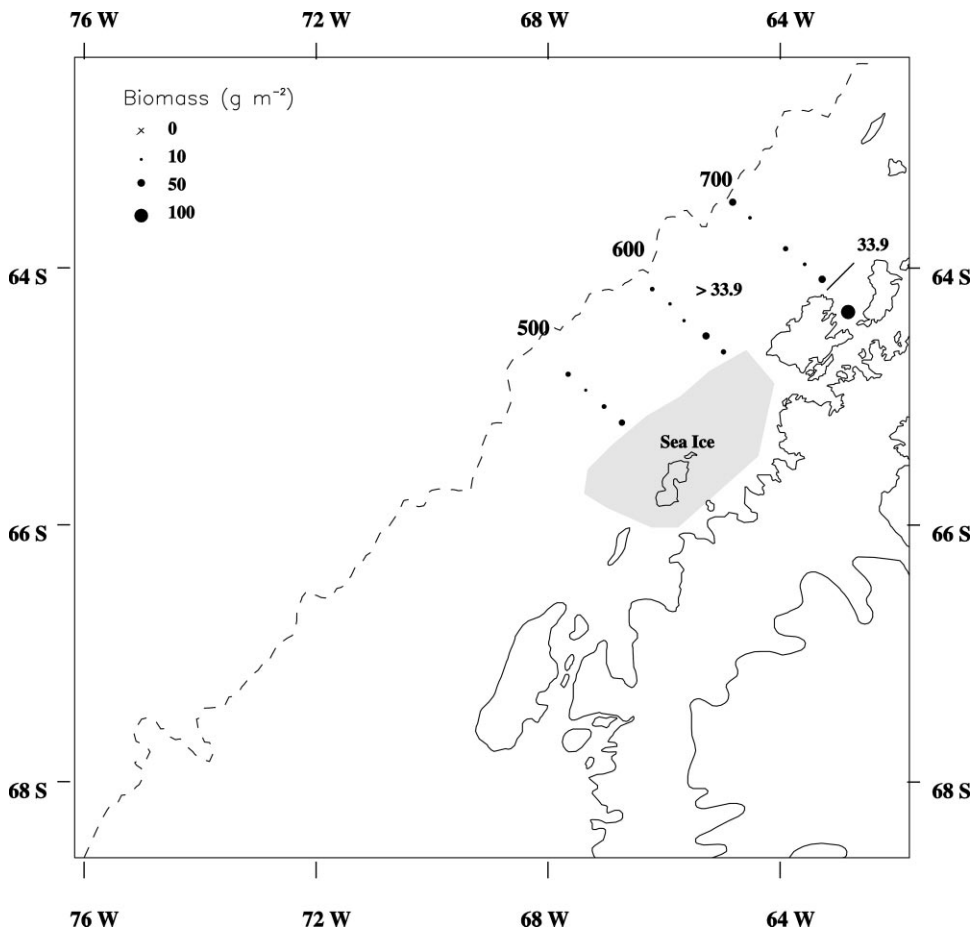
Fig. 8. Distribution of vertically-integrated krill biomass (g m^{-2}) in spring 1991. The dashed line is the 1000-m isobath and the shaded region represents sea ice cover. The solid lines are contours (0.1 intervals) of salinity averaged over the upper 40 m.

the inner shelf regime. The mean krill biomass computed from all stations within the inner shelf regime (180 g m^{-2}) was five-fold higher than the mean for the outer shelf regime (40 g m^{-2}).

Three LFD groups were identified during summer 1993 (Fig. 11). Group A was characterized by small individuals (33–37 mm), whereas groups B and C were dominated by large individuals (>40 mm). Spatial separation of the LFD groups was apparent (Fig. 11), with groups B and C confined to the outer shelf hydrographic regime. All of the stations within the inner shelf regime were characterized by group A, and thus the high krill biomass (>180 g m^{-2}) observed on the inner shelf in summer 1993 (Fig. 10) was due to krill smaller than 40 mm.
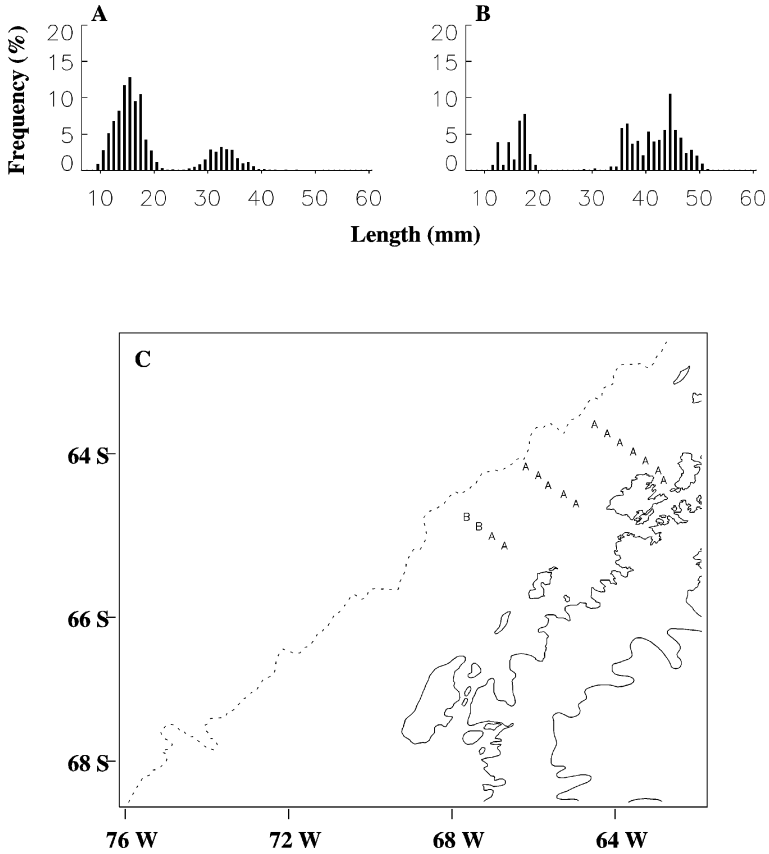
Fig. 9. Length frequency distributions (LFD) of krill collected in spring 1991: (A) group A, (B) group B, and (C) spatial distribution of LFD groups. The dashed line indicates the 1000-m isobath.

3.2.3. Fall

Across-shelf variation in hydrographic properties was also evident in fall 1993 (Fig. 12). Surface salinity values were generally lower throughout the region than observed during the preceding summer. The 33.8 isohaline was positioned beyond the shelfbreak in the fall, representing an offshore movement of 50–100 km, depending on transect line (Figs. 10 and 12). Krill aggregations were not detected at over half of the stations sampled in fall 1993 (Table 3), and low biomass values (<10 g m^{-2}) prevailed over much of the region (Fig. 12). The patchy distribution of krill was not correlated with variations in surface hydrographic properties; however, most of the stations exhibiting biomass values >20 g m^{-2} were geographically positioned either within 20 km of the shelfbreak or on the inner shelf within 40 km of the Antarctic Peninsula.

Four LFD groups were identified in fall 1993 (Fig. 13). Groups A and B were dominated by small adults (34–38 mm), with individuals >40 mm more prevalent in
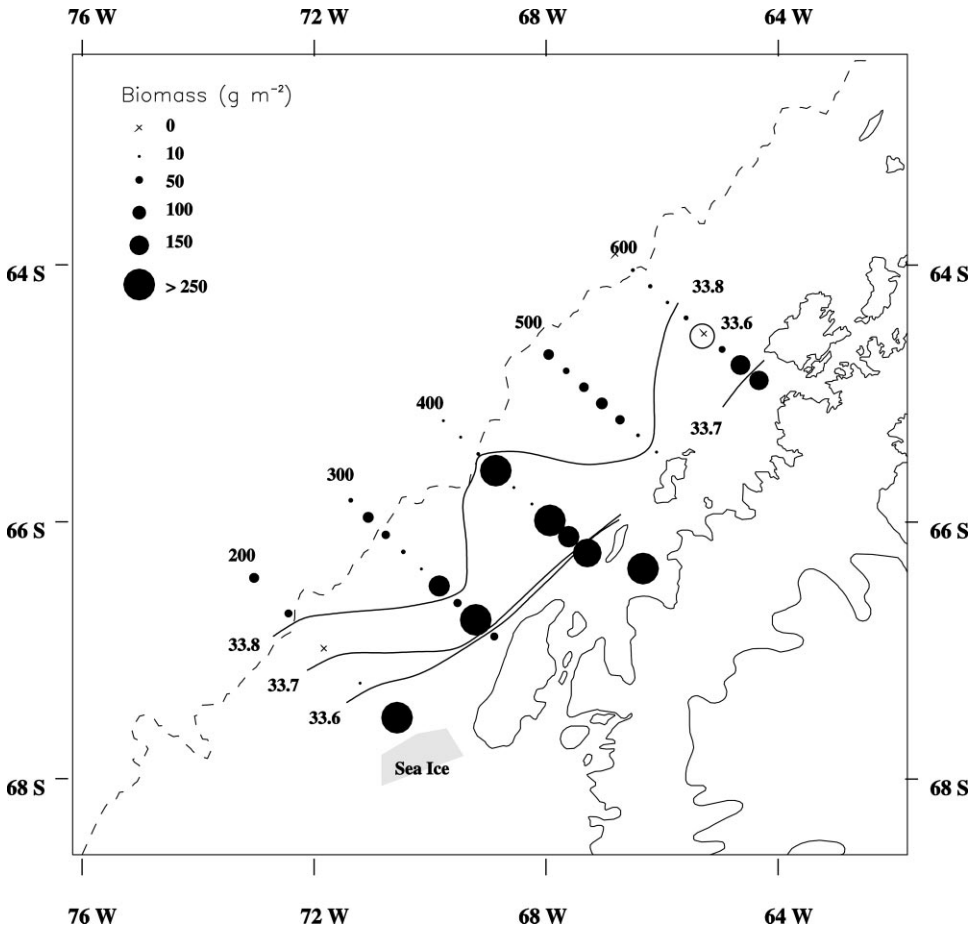
Fig. 10. Distribution of vertically-integrated krill biomass (g m^{-2}) in summer 1993. The dashed line is the 1000-m isobath and the shaded region represents sea ice cover. The solid lines are contours (0.1 intervals) of salinity averaged over the upper 40 m.

group B. Larger krill (46–53 mm) dominated groups C and D, with animals <40 mm rare in group D. The across-shelf differences in the distribution of LFD groups (Fig. 13) was consistent with other seasons, i.e., large krill were positioned offshore of small krill. However, the entire pattern was shifted inshore such that large krill (>40 mm) were found over the middle and inner shelf with the exception of the two southern-most transect lines (000 and 100).

3.2.4. Winter

Surface salinities observed in winter 1993 (Fig. 14) were higher and less variable (33.85–34.0) throughout the region in comparison to the previous fall. Estimates of
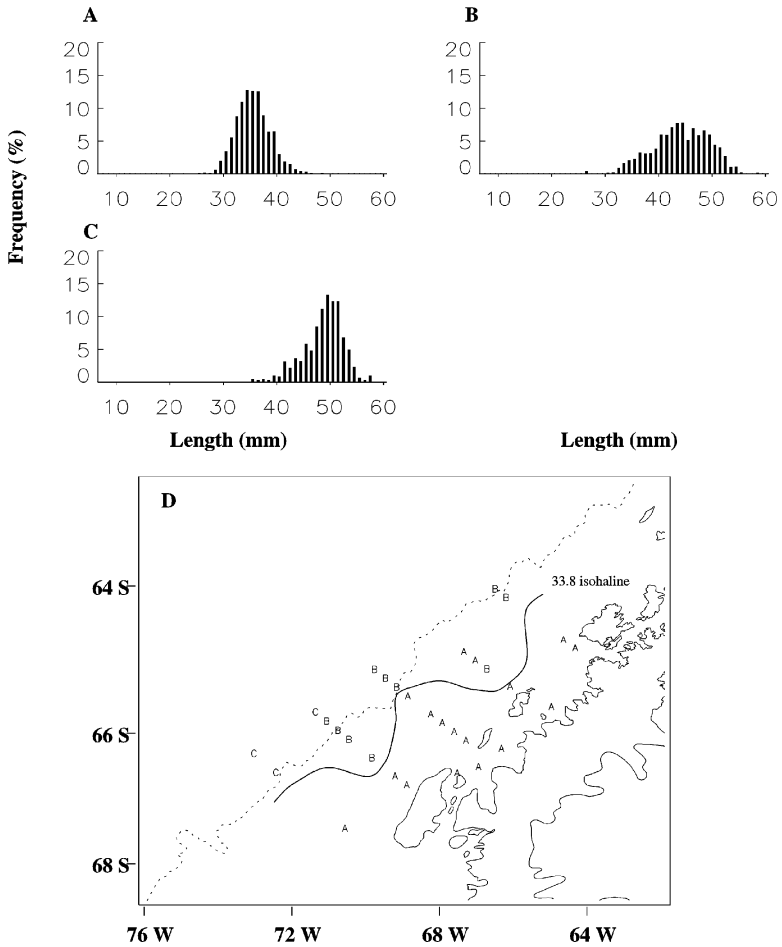
Fig. 11. Length frequency distributions (LFD) of krill collected in summer 1993: (A) group A, (B) group B, (C) group C, and (D) spatial distribution of LFD groups. The dashed line indicates the 1000-m isobath and the solid line represents the 33.8 salinity isohaline.

krill biomass ranged from 0 to 1 g m^{-2} at all but one station (Fig. 14). Several large aggregations were detected at an inner shelf station located near Renaud Island (500.060), resulting in a mean krill biomass of 144 g m^{-2}. This station was revisited two days later, and large aggregations and high biomass values were observed on both days. The LFD of krill captured by net at station 500.060 was bimodal, with peaks at 35 and 45 mm, indicating that several size classes were located on the inner shelf (not shown). A similar LFD was observed for the few krill collected at stations on the middle and outer shelf.
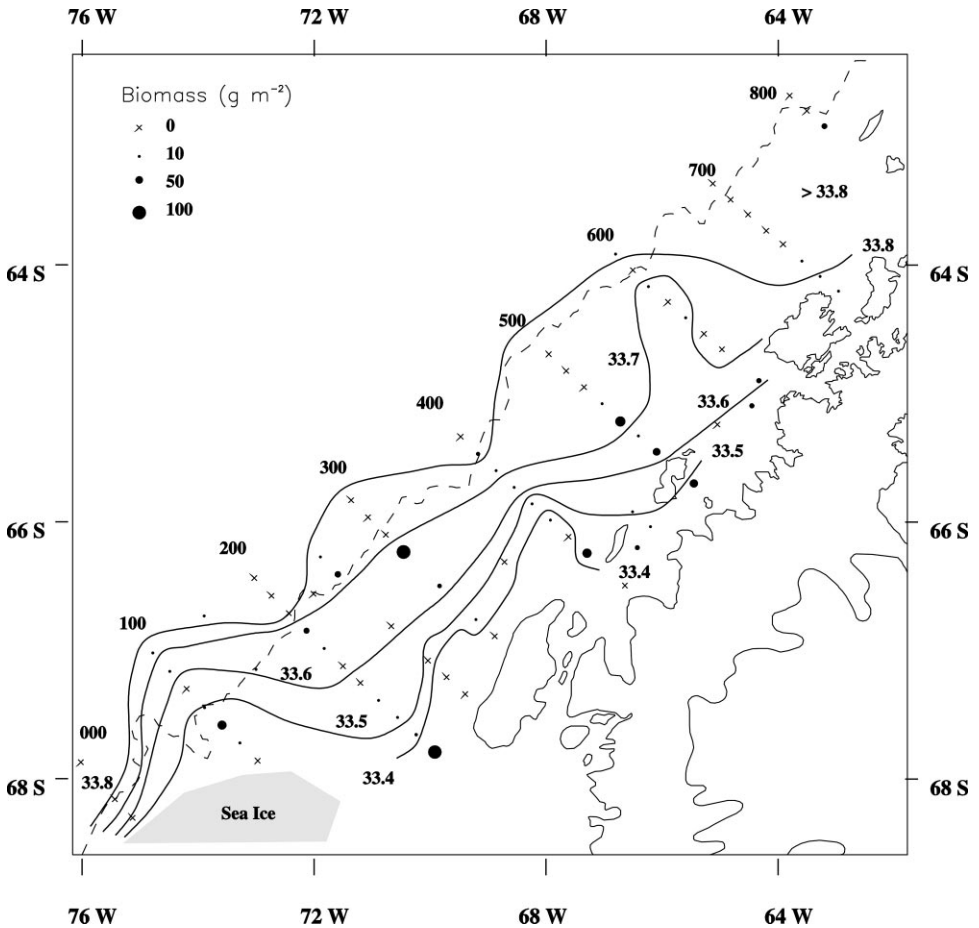
Fig. 12. Distribution of vertically-integrated krill biomass (g m^{-2}) in fall 1993. The dashed line is the 1000-m isobath and the shaded region represents sea ice cover. The solid lines are contours (0.1 intervals) of salinity averaged over the upper 40 m.

4. Discussion

4.1. Distribution and abundance of krill

The acoustic observations collected in this study document temporal and spatial variability in the distribution and abundance of krill for the region west of the Antarctic Peninsula. The degree to which these observations represent typical seasonal and mesoscale patterns or represent an extreme due to interannual variability is explored in this section. In the context of environmental conditions, the seasonal variations in the thermohaline character of the upper ocean (AASW) and the
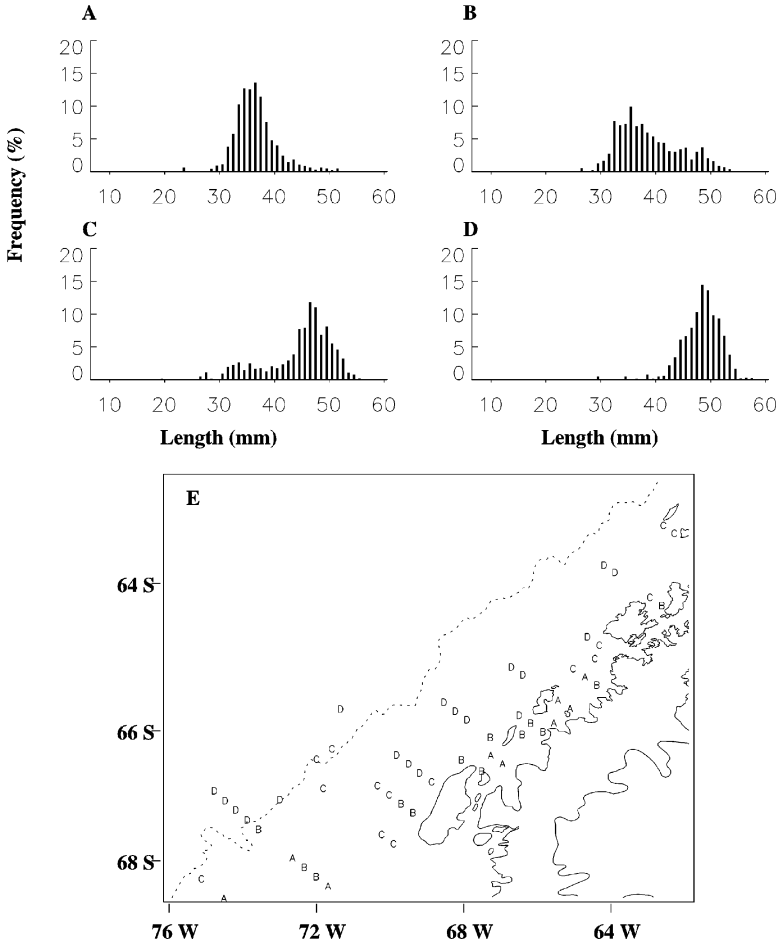
Fig. 13. Length frequency distributions (LFD) of krill collected in fall 1993: (A) group A, (B) group B, (C) group C, (D) group D, and (E) spatial distribution of LFD groups. The dashed line indicates the 1000-m isobath.

ubiquitous occurrence of CDW throughout the region are consistent with historical hydrographic observations (Hofmann et al., 1996; Hofmann and Klinck, 1998). Thus based on water mass distributions, the environmental conditions observed during this study were typical of the region and are not considered representative of an anomalous time period.

Quantitative acoustic measurements are available for a few krill surveys conducted primarily in the region encompassing Bransfield Strait, South Shetland Islands, and Elephant Island (Fig. 15). Even though these surveys represent different environmental regions and strong interannual variability is apparent during the summer, a seasonal pattern is evident. In addition, the magnitude of the biomass estimates for
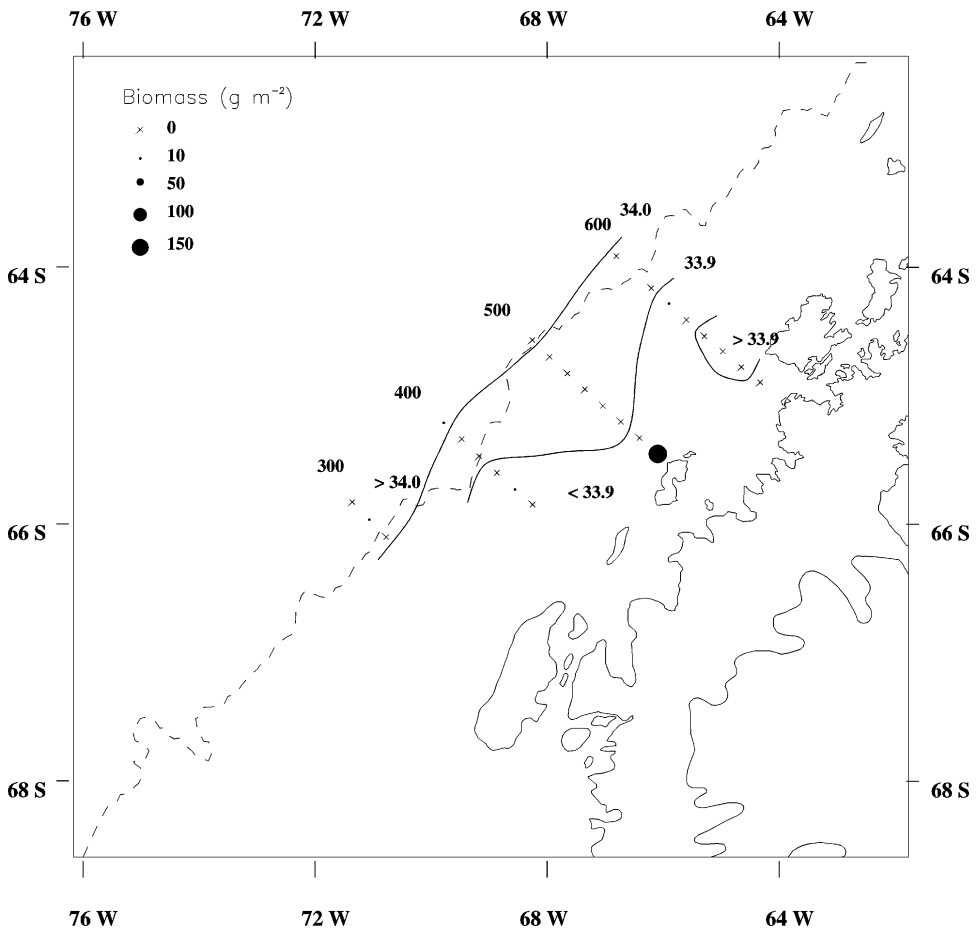
Fig. 14. Distribution of vertically integrated krill biomass (g m^{-2}) in winter 1993. The dashed line is the 1000-m isobath. The solid lines are contours (0.1 intervals) of salinity averaged over the upper 40 m. Sea ice covered the entire region sampled.

the LTER region are consistent with the other observations. Moreover, based on net-derived estimates of krill density obtained as part of the BIOMASS program in Bransfield Strait and adjacent areas, Siegel (1988, 1992) described a general trend of increasing krill density from December (< 50 ind. per 1000 m^3) to late summer (140–180 ind. per 1000 m^3) with very low densities observed in a single winter cruise (< 10 ind. per 1000 m^3). A time-series of net collections made over a one-year period within Admiralty Bay on King George Island (Stepnik, 1982) also showed a similar seasonal pattern.

Aggregation parameters were observed to vary between seasons, with small, dense aggregations dominant during the summer and large, less dense aggregations prominent
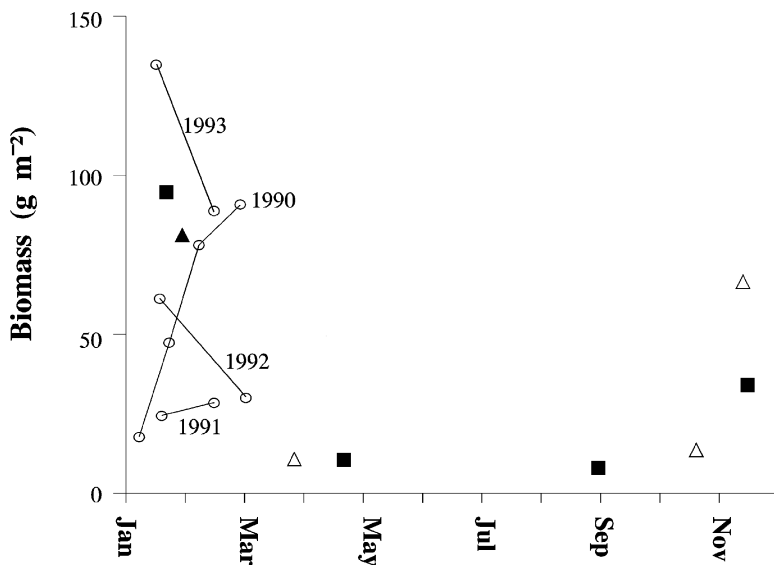
Fig. 15. Comparison of acoustically derived, spatially averaged estimates of krill biomass ($g\,m^{-2}$) by month. Datasets are denoted as: solid squares – this study, using all stations; open circles – AMLR study region near Elephant Island (Hewitt and Demer, 1993a, b), estimates collected within the same year are connected by lines and labelled; open triangles – Elephant Island (Klindt, 1986 as adjusted by Hewitt and Demer, 1993a); and solid triangle – southwest Atlantic survey region during FIBEX (Trathan et al., 1995).

in fall and winter (Figs. 6 and 7). In the only other published analysis of acoustic observations from all seasons, visual examination of echograms collected near Anvers Island and within Bransfield Strait also showed a seasonal pattern of maximum aggregation size in winter (Ross et al., 1996).

Krill abundance varied spatially in this study and, in all seasons, relatively higher krill biomass values were observed on the inner shelf within coastal waters near the Peninsula compared to the outer shelf (Figs. 8, 10, 12 and 14). An across-shelf gradient in krill biomass was described by Ichii et al. (1992), based on acoustic measurements made during summer 1991, north of the South Shetland Islands, where krill were an order of magnitude more abundant in inshore waters ($138\,g\,m^{-2}$), within the 150-m isobath, compared to oceanic waters ($8\,g\,m^{-2}$), beyond the shelfbreak. Net-based estimates of krill density obtained during several spring and summer surveys within Bransfield Strait and the Scotia Sea (Siegel, 1989, 1992; Brinton, 1991) have also shown differences in abundance between coastal and oceanic waters.

Few observations are available for the fall and winter seasons that can be used to describe mesoscale variations in the distribution of krill. During a winter cruise in 1992, net estimates of krill density were relatively higher (100–1000 ind. per 1000 m^3) on the inner shelf along a transect from Anvers Island to Crystal Sound (Nordhausen, 1994). Qualitative ADCP measurements obtained on the same cruise indicated the frequent presence of krill aggregations within Gerlache Strait (Zhou et al., 1994).

During a net survey of krill in winter 1986 (Siegel, 1989), krill were found to be most abundant (>200 ind. per $1000 \, \text{m}^3$) at a location on the inner shelf, which was positioned in the same general area near Renaud Island where large krill aggregations were acoustically observed during the winter of 1993 in this study (Fig. 14).

An across-shelf pattern in the length frequency distribution of krill was observed in all seasons except winter (Figs. 9, 11 and 13). Larger ($>40 \, \text{mm}$) individuals were typically offshore of smaller individuals, which resulted in a general correlation between animal size and environmental conditions. Net collections from summer 1993 indicated that small adults (32–38 mm) were associated with the inner shelf hydrographic regime which was characterized by lower surface salinity (<33.8) and was located over the inner and middle shelf. Large adults (45–60 mm) predominated offshore, beyond the shelfbreak in a region that was characterized by higher surface salinity (>33.8) and the presence of warm CDW ($>1.5°C$) at depth. During the fall, the geographic extent of the region occupied by small adults ($<40 \, \text{mm}$) was reduced and confined to the inner shelf and as such was associated with the lowest surface salinities observed at any time during this study. Large adults in fall were found over the broad region, extending from slope waters onto the middle shelf and including several locations on the inner shelf. Although large animals were located offshore of smaller individuals, the distribution in the fall was no longer correlated with the outer shelf hydrographic regime or with CDW.

The spatial pattern in size separation observed in this analysis was consistent with previous observations reported for the Antarctic Peninsula and Bransfield Strait (Quetin and Ross, 1984; Siegel, 1988; Brinton, 1991; Trathan et al., 1993). Furthermore, the correlation between the distribution of krill aggregations containing large animals and the presence of CDW observed in summer 1993 is consistent with similar observations from the Bransfield Strait and South Shetland Islands (Hofmann et al., 1992).

4.2. Implications of variability

These combined data sets suggest that the temporal and spatial changes in krill distribution and abundance observed in this study are a recurrent annual pattern at least for the broad region from Adelaide Island to Elephant Island along the Antarctic Peninsula. The order of magnitude, seasonal and mesoscale, variations in krill abundance have direct implications for large-scale, multi-year survey programs, such as those conducted by the Palmer LTER and the Committee for the Conservation of Antarctic Marine Living Resources (CCAMLR). This variability will also affect process-oriented research programs, including on-going and future activities within the Southern Ocean sponsored by the Joint Global Ocean Flux Study (JGOFS) and Global Ocean Ecosystem Dynamics (GLOBEC) programs. The ability to detect long-term trends or quantify interannual and interregional differences in krill abundance and productivity depends upon the identification of data sets for which appropriate comparisons can be made. As such, the time of the collection and the relative proportions of inner shelf, outer shelf, and slope within a survey region should be considered before comparison with other measurements are made.

In all seasons, large standard deviations were associated with the spatially-averaged estimates of krill biomass (Table 4); moreover, a small number of aggregations represented a large percentage of the total biomass (Fig. 5). These aggregations were typically larger in cross-sectional area or contained higher volumetric densities compared to the most frequently observed aggregations (Figs. 6 and 7). Highly variable biomass distributions where a few aggregations contained a significant portion of the total biomass have been reported for other krill surveys conducted in Bransfield Strait (Miller and Hampton, 1989; Hewitt and Demer, 1993a) and the Bellingshausen Sea (Murray et al., 1995). Towed, downward-looking acoustic systems provide a two-dimensional view of dynamic three-dimensional aggregations in which each acoustically detected aggregation is represented by only that portion of the aggregation that is intercepted by the acoustic survey track. The degree to which the observed variability in krill biomass is attributed to the true distribution of krill or to the sampling error imposed by the two dimensional acoustic representation of aggregations has not been quantified. Improving the confidence level associated with krill biomass estimates may depend on technological advancements in acoustic methods, which provide simultaneous along- and across-transect measurements of aggregations as recently demonstrated for herring schools in the North Sea (Misund et al., 1995).

4.3. Factors affecting seasonal variations in krill distributions

Temporal and spatial variability in the abundance of marine organisms is typically assumed to be controlled primarily by three factors, circulation, population dynamics, and behavior, all of which are affected by environmental variability. Order of magnitude changes between seasons in estimates of krill abundance are not consistent with the time scales of recruitment and growth exhibited by this species, which takes 2–3 yr to become reproductively mature (Quetin et al., 1994) and lives for 5–7 yr (Ettershank, 1984). For this reason, population dynamics are not considered the driving force behind seasonal changes in krill abundance. Instead, the temporal change in the mesoscale distribution and abundance of krill over an annual cycle suggests a shift in the primary habitat between seasons.

Unfortunately, the existing data sets cannot be used to identify the habitat(s) occupied by krill in the fall and winter. Instead, observations from this study are combined with historical descriptions to examine the potential effects of circulation, sea ice, aggregation dispersal, and vertical and horizontal migrations on seasonal changes in the distribution of krill west of the Antarctic Peninsula.

4.3.1. Circulation

In the absence of direct measurements of circulation patterns during this study, several indirect measures will be used to suggest that advection is not the prime factor affecting seasonal changes in krill abundance west of the Antarctic Peninsula. First, krill biomass decreased by an order of magnitude over a two-month period in 1993 for a geographic region extending 1000 km along the Peninsula. Transport of krill from this region would require residual alongshelf flows exceeding $25\,\mathrm{cm\,s^{-1}}$ over the

continental shelf. Historical summer hydrographic observations have been used to construct dynamic topography contours, which indicate the presence of large-scale clockwise flow over the continental shelf west of the Antarctic Peninsula (Stein, 1988; Stein and Heywood, 1994; Hofmann et al., 1996). This pattern results from northeastward flow of the Antarctic Circumpolar Current (ACC) beyond the shelfbreak and southwestward flow along the coast due to buoyancy and wind forcing (Hofmann et al., 1996). In addition, dynamic height fields indicate complicated flow patterns on the inner and middle shelf region which are assumed to result from complex bottom topography and show baroclinic flows of less than $10 \, \mathrm{cm \, s^{-1}}$ (Smith et al., in press). These circulation patterns are not consistent with the space and time scales associated with the observed changes in krill biomass.

Additionally, analysis of hydrographic measurements collected in this study indicate a stable distribution of water masses in the region. Seasonal variability in hydrographic properties was limited to the upper portion (0–50 m) of AASW, which transitioned from well-mixed conditions in winter and spring to vertically-stratified conditions in summer and fall (Lascara, 1996; Hofmann and Klinck, 1998). These changes can be accounted for by surface fluxes of heat and salt due to seasonal changes in solar irradiance and sea ice conditions (Klinck, 1998).

4.3.2. Sea ice

The seasonal change in the areal extent of sea ice affects more than 20 million km^2 of the sea surface (Zwally et al., 1983). Krill has been characterized as leading a double life, alternating between two different habitats: the pelagic upper ocean and the undersurface of sea ice (Laws, 1985; Siegel et al., 1990; Marschall, 1988). However, the abrupt decrease in acoustically detectable krill biomass observed over the 2-month period between the summer and fall 1993 cruises preceded ice formation in this region. Since most of the region was ice-free during both cruises a simple characterization of krill alternating between pelagic and under-ice habitats is inappropriate for the waters west of the Antarctic Peninsula. In addition, under-ice observations obtained during several winters (including 1993 of this study) from west of the Antarctic Peninsula (Quetin et al., 1996) indicate that the abundance of adult krill observed directly beneath sea ice does not account for the change in abundance levels in the upper ocean from the ice-free season.

4.3.3. Swarming behavior

Foraging behavior and predator avoidance are often cited as biological factors that influence the formation and maintenance of krill aggregations (Miller and Hampton, 1989). The tendency to form aggregations is expected to be highest under conditions of high food availability and high predation pressure (Daly and Macaulay, 1991). Consequently, spatial and temporal changes in the relative abundance of food and predators should affect the swarming behavior of krill.

In this study, aggregations were most abundant in the summer (Table 4), the season with the highest pigment concentrations (B. Prézelin, unpublished data). Based on historical observations for this region, summer is also the time period of highest predation pressure (Fraser and Trivelpiece, 1996; Costa and Crocker, 1996). Thus, the

difference in the abundance of krill aggregations observed between summer and winter is consistent with the expected change in swarming behavior relative to differences in food availability and predation pressure. Moreover, most of the krill biomass observed during the summer 1993 was attributed to aggregations that were smaller (<500 m^2) and denser (>100 g m^{-3}) compared to the other seasons analyzed in this study (Figs. 6 and 7). This change in the character of the aggregations could be interpreted as a behavioral response to the high predation pressure during the summer, e.g., whales feeding on entire aggregations, as well as other carnivores feeding on individuals within aggregations.

Seasonal changes in krill swarming behavior will directly affect small-scale distributions, which in turn alter the ability to accurately estimate the local abundance of krill according to the capabilities of the sampling equipment employed. A change in behavior that favors dispersal rather than swarming would lead to a more uniform spatial distribution, and krill densities may become too low to be detected acoustically. The effect of dispersal on net sampling would be to increase the probability of capturing some krill each net tow, which in turn would decrease the variance observed between samples. The net-derived estimates of krill density obtained during the fall and winter 1993 cruises are not consistent with this expectation, e.g., krill were absent from net collections at most of the stations (R. Ross and L. Quetin, unpublished data). Since the abundance of acoustically detected aggregations and the net-derived estimates of dispersed krill individuals were both very low in the fall and winter, the seasonal change in krill biomass cannot be explained by dispersal of aggregations without also requiring additional changes in behavior that move krill individuals out of the acoustically sampled water column.

The presence of large aggregations observed during the fall and winter by this study and others (Zhou et al., 1994; Ross et al., 1996) indicates that some portion of the population remains in aggregations year-round. The disadvantages to living within large aggregations might include competition for limited food and oxygen resources and the potential for accumulation of toxic waste products. One potential advantage is that the time scale of swarm formation may be too long to facilitate annual re-swarming in the spring, hence some individuals remain in aggregations year-round. Unfortunately, little is known concerning the temporal integrity of individual aggregations or how much of an individual krill's life is spent in swarms versus how much is spent in a dispersed state.

4.3.4. Vertical movements

Movement into the upper 10 m of the water column during the fall would position krill in proximity to newly forming sea ice, although at the cost of increased predation risk, and would effectively remove krill from acoustic detection. Analysis of net-derived krill density estimates obtained during the fall 1993 cruise (R. Ross and L. Quetin, unpublished data), however, does not support relocation of the summer abundance levels of krill into the near surface waters by fall. In addition, extensive swarming by krill at the surface has never been reported during the fall or winter by any program in the Southern Ocean to date.

The downward migration of krill, either as individuals or aggregations, to depths typically not sampled by nets and acoustics could explain the reduced abundance

estimates of krill during the fall and winter. This type of movement is supported by several historical observations. A shift from the pelagic to the benthopelagic habitat was observed by Kawaguchi et al. (1986) for krill (20–45 mm) overwintering under fast ice in a shallow coastal region (Lutzow-Holm Bay, near 40°E latitude). Off South Georgia during the winter of 1983, a combination of acoustic measurements and net collections revealed that krill were present in layers up to 20 m thick near the bottom over parts of the shelf area (Heywood et al., 1985). In the southwest Weddell Sea, Gutt and Siegel (1994) used a video camera attached to a benthic remotely-operated vehicle to document the existence of scattered krill and krill aggregations positioned within 200 cm of the bottom near the shelfbreak in water depths of 400–500 m. Depth-stratified net samples have also shown the occurrence of krill down to 400 m in continental shelf waters along the Antarctic Peninsula (Siegel, 1985).

In the current study, krill were distributed deepest during the winter (Fig. 4), and a few of the largest aggregations observed during the fall and winter extended below the limit of acoustic detection (Lascara, 1996). However, the acoustic measurements were restricted to the depth range from 10 to 200 m, and net collections were derived from tows over the upper 120 m. Consequently, the abundance of krill in deeper waters cannot be described with these data sets, and the extent to which krill move below 200 m during the fall and winter remains unknown.

4.3.5. Horizontal migration

Krill have been characterized as highly mobile animals and, based on experimental and field observations, adults appear capable of sustained swimming at speeds between 10 and 15 cm s^{-1} over time scales of hours to days (Marr, 1962; Kils, 1981; Kanda et al., 1982). Siegel (1988) was the first to suggest that active migration played a role in establishing the spatial segregation in krill size class. Specifically, he hypothesized that large, reproductive adults migrate offshore in spring and return to coastal waters in the fall. Similarly, Sprong and Schalk (1992) described the migration of aggregations northwards away from the ice edge in the Weddell Sea from late November to early January, based on repeated acoustic surveys within this area.

To date, horizontal migration has been described only in terms of the mesoscale movements (100–200 km) of large, reproductively active adults, which represented only a small percentage of the total krill biomass observed during this study. The observed seasonal changes in the geographic area over which krill were detected and the spatial placement of specific size classes are consistent with an inshore movement of not only large (>40 mm) but also small (30–40 mm) adult krill with the scale of movement varying from roughly 100 km for large adults to less than 50 km for small adults.

Traveling at speeds between 10 and 15 cm s^{-1}, it would take 8 to 12 days for krill to move a distance of 100 km if the movement was directed. This time scale would increase as a function of the random component of movement. Evidence of directed swimming has been observed for krill aggregations by divers (Hamner et al., 1983; Hamner, 1984) over small spatial scales. Directed movement over larger scales is supported by the description provided by a Japanese fishing trawler (Kanda et al., 1982), which tracked two large krill aggregations over distances of 116 and 46 miles in

time periods of 18 and 8 days, respectively ($10–12 \text{ km da}^{-1}$). The time and space scales of the krill movements described in these studies are consistent with those required to support seasonal across-shelf migrations.

The acoustic measurements used in this study were not designed to provide direct observations of horizontal movements, and thus across-shelf migrations remain an unquantifiable possibility. However, the integrated krill biomass observed on the inner shelf in fall and winter 1993 does not account for the total biomass observed during the summer. One explanation is that adult krill moved further inshore than the region occupied by this sampling program. Alternately, it may suggest that only a portion of the krill population resides on the inner shelf in the fall and winter.

5. Summary

Acoustic surveys of the region west of the Antarctic Peninsula revealed distinct seasonal variations in spatially averaged estimates of krill biomass and aggregation abundance, the dimensional parameters used to characterize individual aggregations, the geographic area over which krill were acoustically-detected, and the depth distribution of krill. The absence of acoustically detected krill from the depth range 10–200 m over the study region in fall and winter is consistent with the hypothesis of a shift in the primary habitat of krill between seasons. Synthesis of the multidisciplinary observations collected as part of this study, along with published descriptions of krill distribution, suggests that changes in krill behavior, most notably dispersal, downward movement, and horizontal migration, may be responsible for a large part of the observed seasonal variability. In addition, the results suggest that the timing and nature of behavioral responses may be affected by varying environmental conditions and may change ontogenetically.

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