Krill demography in the Atlantic Sector of the Antarctic during the CCAMLR Survey 2000

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1. Abstract

In January/February 2000 standard RMT net tows were carried out during midnight and midday stations between 20°W and 70°W south of the Antarctic Convergence. The presented overall mean numerical density and biomass of krill (247 krill 1000 m^{-3} and 18.7 g m^{-2} , respectively) were in the upper range of values estimated for the period 1984 to 1999 in the long-term study of the Elephant Island meso-scale survey. However, this period is known for its low krill abundance in general.

Analyses indicate that krill distribution showed three distinct geographical clusters of size frequency distributions. Small juvenile and immature krill occurred east of the South Orkney Islands. Adult krill predominately smaller than 50 mm mean length dominated in the shelf areas of the Antarctic Peninsula and to the north of the juvenile stock across the Scotia Sea. Adult krill larger than 50 mm mean size was mostly restricted to the area west of the South Orkney Islands. Adult maturity stages were well advanced demonstrating that the peak of spawning had already passed in early February. Dispersion of the spawning stock showed two hotspots, the first between South Shetland and South Orkney Islands, the second around the South Sandwich Islands. A large gap in the spawning stock occurred in the central Scotia Sea. Krill larvae concentrations were found slightly to the east of the spawning stock. Only scattered aggregations of larvae were recorded east of 36° W. Mean density of larvae in the western part was 2044 m⁻² and 2 m⁻² in the eastern sector.

Recruitment indices for one and two year old krill were low in the western part, the outflow of the Bellingshausen/Antarctic Peninsula region $R_1 = 0.0$, $R_2 = 0.11$). This indicates a failure of spawning success and/or poor recruitment for several years. In the eastern part of the survey area, mostly the outflow of the Weddell Sea, recruitment indices were high above average ($R_1 = 0.60$ and $R_2 = 0.72$). This could point towards a population with constant successful reproduction, recruitment and mortality in the eastern Scotia Sea. Implications are discussed arising from the stock composition and distribution patterns of larval and adult krill.

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2. Introduction

A commercial krill fishery developed in Antarctic waters in the early 1970's In 1981 a first international exercise (BIOMASS FIBEX) was carried out to estimate the large-scale krill biomass in the Antarctic (BIOMASS 1991, Trathan and Everson, 1994). Since then the results of this multi-ship exercise was used by CCAMLR to set limits to the commercial krill fishery on a larger scale. However, more recent meso-scale research surveys have shown a high amplitude in interannual fluctuations of krill biomass or even a possible decline in krill biomass over the past 15 years (Siegel *et al.*, 1998; Brierley *et al.*, 1999). New data were required by CCAMLR to justify changes in precautionary catch limits for the krill fishery. New technology as well as standardized equipment and methods were also thought to lead to more accurate estimates and reliable catch limits for the large scale region as well as for subdividing the potential yield to smaller management units.

Objectives of the net sampling programme

The international CCAMLR Survey 2000 was conducted to support an updated estimate of the large scale krill biomass in the South Atlantic Sector of the Antarctic. Four research vessels participated in the study and covered most of the Scotia Sea. 22 parallel hydroacoustic transects as well as four small scale shelf grids were investigated in this quasi-synoptic survey. Standard net tows were carried out during midnight and midday stations. Additional samples were taken by opening-closing nets for the identification of acoustic targets.

The RMT net sampling programme for krill was a central part of the CCAMLR Synoptic Survey 2000. This programme had three primary objectives:

- to validate and identify acoustic targets, confirming which targets can be considered as krill and obtaining krill length frequency data for target strength estimation
- to describe krill demography and large scale distribution patterns of size groups and maturity stages as well as regional recruitment indices
- to identify the reproductive success of krill during the current spawning season and study the occurrence of major zooplankton taxa such as salps and myctophids

The present contribution deals with aspects of krill density from net samples, large scale distribution patterns of size groups, development of maturity stages, spawning conditions, krill larvae occurrence and recruitment.

3. Material and Methods

Four vessels from CCAMLR member nations participated in the synoptic survey: Kaiyo Maru (Japan), Atlantida (Russia), James Clark Ross (UK) and Yuzhmorgeologiya (USA). Each vessel carried out standardized hydro-acoustic measurements along parallel transects across the Scotia Sea between 20° and 70° W (Figure 1). A minimum of two net sampling stations was conducted by each vessel every day.

3.1. Standard Gear

All participants of the international CCAMLR Survey 2000 agreed with the CCAMLR Working Group Ecosystem and Management recommendation to use the RMT1+8 (Rectangular Midwater Trawl; Baker *et al.* 1973) as the most appropriate type of net presently available. This decision was taken to avoid potential variation in catchability and selectivity of nets. Each net was equipped with a flowmeter to estimate the filtered water volume as accurately as possible, and a real-time time-depth-recorder (TDR) to follow the track of the net.

Station net tows were carried out around local midnight. The timing of the midnight sample was constrained by the period of darkness. A midday station net haul was also carried out if target fishing had not taken place since daybreak. At each station a quantitative standard double oblique tow was conducted from the surface down to 200 m (or to within 10 m of the bottom at stations shallower than 200 m). Such a depth range was considered to be the best compromise between the time available for sampling and the likely vertical depth range of krill. During the hauls a constant ship's speed of 2.5 ± 0.5 knots was suggested. A wire speed of 0.7 to 0.8 m/sec (42 to 48 m/min) was maintained during paying out and of 0.3 m/sec (18 m/min) during hauling. The net mouth angle is remarkably constant during hauling within the speed ranges given above. When the net reached maximum depth, the winch was to be stopped for about 30 seconds to allow the net to stabilize before retrieval.

Directed or targeted net sampling was necessary to reduce the uncertainty associated with the delineation of krill in the acoustic data record. This sampling was directed at a variety of "acoustic morphs", some presumed to be krill and some presumed not to be krill.

3.2. Laboratory Sampling

Samples from RMT ranged from a few grams to several kilograms in weight. The total volume of the net catch was measured as total drained sample volume. The minimum requirement for samples less than one litre was that all the krill and salp specimens were to be counted and measured immediately after the catch. The rest of the zooplankton was stored in 10% buffered formalin solution for later analyses.

Samples that were too large to be sorted completely were subsampled volumetrically immediately after the catch. Due to differences in catch composition, subsampling was carried out differently. If the sample size was larger than 1 litre and the sample mainly consisted of krill, first the total drained sample volume was determined and recorded. Afterwards a quantitative subsample was taken randomly from the total samples and all krill and salp specimens were counted from this subsample. If the sample size was larger than 1

litre and the sample mainly consists of salps, then first the total drained sample volume was determined and recorded, afterwards all krill were removed from the total sample, counted and measured. Finally a 1 litre subsample was taken randomly from the total samples and all salp specimens are counted from this subsample.

The reductions in sample size were recorded properly to allow extrapolation from the subsample to total sample size for each of the components (krill, salps, zooplankton). These data together with information on fishing depth and filtered water volume allowed the necessary standardization of krill densities and length density data (per m^2 or per 1000 m^3)

The standard length measurement was total length as defined by the `Discovery' method (AT) from the anterior margin of the eye to the tip of the telson without the terminal spines . The standard unit is given in mm below , with an accuracy of 1 mm size classes. All measurements on each vessel were done by one person to remove observer variation (see Watkins *et al.* 1985). Samples which contain less than 100 krill were used in total for length measurements and maturity stage identification. For larger krill catches a minimum of 100 krill was measured and staged. Krill sex and maturity stages were identified using the classification of Makarov and Denys (1981) . A subsample of krill that had not been processed was preserved in formalin as a back-up data set; krill that had been measured and staged were also preserved.

3.3. Data recording and analysis

Relevant data on station parameters as well as krill counts and measurements were recorded and stored on PC in standardized EXCEL[®] spread sheet formats.

Data analysis was done using Statistica[®] software package. The spatial distribution of the krill population was analysed using a cluster analysis to compare between station similarities in krill size. A similarity matrix was computed based on the relative frequency of each krill length class. The hierarchical fusion of clusters was preferred using Ward´s method to link homogeneous clusters and the Euclidean distance coefficient was applied for the diversity analysis. Only stations with a minimum of 20 measured specimens were submitted to cluster analysis to avoid random fluctuations caused by stations with few length groups. A total of 135 net sampling stations was carried out during the cruise. 66 of these caught krill in sufficient numbers so that they could be used for the computation of the similarity matrix.

Each length frequency distributions was weighted by size of the catch and the filtered water volume before data were combined for the composite length frequency distributions on a Subarea or Area basis. To avoid over-representation of single samples, only random and no target haul data were used to produce the relevant composite length frequency distribution. The analysis of length frequencies had been undertaken in two parts: an agglomerative hierarchical cluster analysis to determine whether there were recognisable

groupings of krill length frequency distributions over the survey area, and a geographical consideration of the distribution of such clusters.

Four types of linkage methods were used to compare the results of the different fusion methods on the station groupings: Single linkage, Complete linkage, Unweighted Pair Group Average and Ward's method. In the first step each object (station) represents a cluster of its own. The distance between objects is determined by the distance measure (e.g. Euclidean Distance). In principal those objects are fused which have a minimal distance value (single linkage). Another way is to group objects (stations) into different (dissimilar) clusters by identifying the maximum distance (furthest neighbour, complete linkage). The latter method is usually recommended for data which naturally form groupings of objects.

Krill recruitment was estimated using length density data from routine trawls and applying the method described by de la Mare (1994a). From the oblique net hauls proportions of recruits were calculated for ages 1 and 2 (R_1 and R_2). The densities of krill in 1-mm length classes were estimated using the measured filtered volume for each haul. A mixture distribution was fitted to these data by maximum likelihood to estimate the proportion of recruits.

4. Results

4.1. Distribution, abundance, biomass

Krill numerical density was calculated in two different ways. The first was the simple arithmetic mean to allow comparisons with earlier published results as well as results from the Australian large scale survey in the Indian Ocean. The second method was the approach described by de la Mare (1994b) using the delta distribution and the maximum likelihood fitting (TRAWLCI software) which can be compared with results from the long-term time series of Elephant Island.

Highest numerical krill densities in the survey area were observed to the south-east of South Georgia, close to the southern extent of the South Sandwich Islands and on the northern shelf of the South Orkney Islands (Figure 2). Relatively low catches were recorded from the central Scotia Sea and the north-eastern Drake Passage/Antarctic Peninsula. According to the net samples, the survey transects run across large areas where obviously no krill were present. The northernmost stations, and especially the samples from the north-western Scotia Sea and the south-western Drake Passage yielded mostly zero krill. Some stations in the outflow of the Weddell Sea also yielded zero krill. A very similar picture can be derived for the distribution from krill biomass densities in the survey area, except for the high density patch in the southern South Sandwich region. Here numerical densities were very high, whereas biomass was

moderate. This is due to the krill size spectrum in that area, where small krill were highly abundant but due to their small size did not adequately contribute to the biomass.

Table 1 and 2 summarize the average numeric and biomass densities for the entire survey area as well as for the different statistical Subareas or survey strata. Accepting the observation that the northernmost stations with zero catch rates were located beyond the krill distribution range then these stations can be excluded from the calculation of mean densities. The overall mean numerical density within the krill distribution area was calculated as 247 specimens 1000 m⁻³. This would compare to a the biomass density of 18.7 g m⁻² on average (Table 2). Numerical and biomass densities seem to be substantially higher in the South Orkney (Subarea 48.2) and especially South Sandwich Island (Subarea 48.4) areas than in the Antarctic Peninsula and South Georgia regions. Furthermore, krill densities appear to be threefold higher in shelf areas than in open oceanic waters (Table 1).

4.2. Length frequencies

The results of the cluster analysis applying the Single Linkage method showed no separation of stations into distinct clusters, but the dendrogram was forming a "chain" of stations. This often occurs if few objects have similar distance values. Results from all other three linkage methods clearly indicated a separation of stations into at least three distinct clusters. Interpretation of the results using Ward's method caused some difficulty, because from the dendrogram cluster 2 appeared to be more similar to cluster 3 than to cluster 1, although the resulting overall length frequencies of cluster 1 was distinctly different from cluster 2 and 3 (see below). The Unweighted Pair Group Average (UPGA) method uses the average distance between all pairs of objects (stations). The dendrogram of this linkage showed a greater similarity between clusters 2 and 3 and a greater dissimilarity of these two to cluster 1. This was in concordance with the resulting composite length frequency distributions of the relevant clusters. The Complete Linkage method (using the greatest instead of the average distance) provided a dendrogram very similar to the UPGA method, and the three clusters were even more distinct then for the previous method. Therefore, the result of the Complete Linkage method (Figure 3) was thought to be the most appropriate to describe the geographical distribution of the various clusters and the related composite length frequency distributions.

The analysis resulted in three size clusters (Figure 4). Cluster 1 was composed primarily of krill < 35 mm. The unimodale length frequency distribution had a mode at 26 mm. The majority of these krill were juveniles (79%) and fewer immature animals (see below) The skewed unimodale length frequency distribution of cluster 3 represented primarily by large adult mature krill (82%) with a mode at 52 mm length (a mixture of = 4 year olds). Cluster 2 krill showed a slightly smaller modal size of 48 mm and a higher frequency of intermediate size classes. This size mode usually represents mainly 4 year old krill.

During the survey 55% of the krill in this intermediate cluster were immature, while 39% were mature stages. The length frequency was skewed by size classes between 30 to 45 mm which usually represent 2 and 3 year old krill, but frequency of these size/age groups was relatively low in cluster 2.

An overall spatial succession of length and maturity stages (Figure 5) is typical for the area along the Antarctic Peninsula, but had also been described from the Scotia Sea (Siegel 1988, BIOMASS 1991). In summer 2000 a similar pattern of segregation was observed across the Scotia Sea. Small, juvenile and immature krill (cluster 1) occurred primarily in the eastern part of the survey area and adjacent to the western side of the South Sandwich Islands and reached the south-eastern side of South Georgia. However, this cluster and the related krill size classes did not occur in the western survey area, where it can usually be found on the shelf of the Antarctic Peninsula.

Cluster 3 with the largest mature krill occurred in western oceanic waters of Drake Passage, north of the South Shetland and South Orkney Islands. A few scattered stations to the east of the South Sandwich Islands also belonged to cluster 3. In summer 2001 this cluster was missing from the central Scotia Sea. The relatively large intermediate krill of Cluster 2 formed a continuous band, extending south of cluster 3 from the Bransfield Strait across the Scotia Sea to the north of South Georgia and cluster 1 and bent south again east of the South Sandwich Islands.

The composite length frequency distributions of each cluster give a generalized picture, however, length frequency distributions were not uniform within a cluster, but showed some variability in the composition of size classes involved. From the dendrogram (Figure 3) there was already some indication on sub-groupings of stations for at least cluster 1 and 2. To demonstrate the possible degree of variability in length frequencies within each cluster Figure 4 also illustrates the size composition of krill for the relevant subgroups.

Sub-group 1a reflects entirely the composite length frequency distribution with a modal size of 28 mm (Figure 4a), because these stations with high krill densities dominated cluster 1. The unimodale length frequency distribution of sub-group 1b had a slightly larger mode of 31 mm. However, stations with this size composition had relatively low densities so that they contributed very little to the overall length frequency of cluster 1. The smaller sub-group 1a covered stations in the south-eastern corner of cluster 1, whereas the slightly bigger sub-group 1b occurred in the south-western corner of cluster 1 and south-east of South Georgia. However, there was no clear latitudinal effect which could be interpreted as a continuum in growth from south to north.

Cluster 2 is more variable than cluster 1 and shows three potential sub-groups. The length frequency for sub-group 2a is very similar to the overall composite distribution of cluster 2 with a strong mode at 48 mm

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(Figure 4b). Size classes smaller than 43 mm are hardly present in sub-group 2a length frequencies. Stations belonging to this sub-group are mainly located in the Antarctic Peninsula area with a few scattered stations around South Georgia and the South Sandwich Islands. Length frequencies of sub-groups 2b and 2c show a broader distribution between 30 and 45 mm with a slightly higher proportion of bigger size classes in sub-group 2b. In general these length frequency distributions represent the left shoulder of the composite length frequency distribution of cluster 2. Stations with the medium sized krill and belonging to sub-groups 2b and 2c were found east of the South Orkney Islands, north of South Georgia and around the South Sandwich Islands.

As mentioned earlier, krill densities were substantially different in various parts of the South Atlantic. Highest densities were found in the eastern stratum and much lower densities to the west of the South Orkney Islands. These regional differences in densities across the survey area have a strong effect when standardizing length frequencies and set up a composite length frequency distribution for the krill stock in the South Atlantic (Figure 6). The krill stock(s) of the large-scale survey area were clearly dominated by the presence of small krill with a mode of 26 mm, although these occurred only in parts of the eastern sector. The second mode at around 48 mm also showed the strong influence of the relatively high densities in parts of cluster 2.

4.3. Maturity stage composition

Figure 6 shows that the small size group consisted exclusively of juvenile krill. Interestingly, the juvenile stage had a second but smaller mode at 35 mm length. This would indicate that part of the juvenile stage would be two years old (in January mean length-at-age for two year old is usually 36 mm). Immature stages reached a maximum size of over 50 mm. The mean expected length-at-maturity for males is 42 mm (Siegel and Loeb, 1994), while it is even smaller for females. Adult krill was mostly bigger than 48 mm.

The relative frequency of the various maturity stages is given in Figure 7. Approximately 45 % of the entire stock were juveniles. Adult female stages showed an increasing frequency with progressed maturity from early to gravid to spent stages. More than 6 % of the total stock consisted of spent females, i.e. almost half of the adult females were spent during the survey period from end of January to early February (Figure 8).

The maturity index is based on the data shown in Figure 8 and calculates the proportion of sexually advanced female maturity stages in January (stages 3C to 3E) from the total number of all adult female stages (3A to 3E). A high index in January can be used as an indicator for an early spawning season (Siegel and Loeb 1995). For the CCAMLR survey 2000 the overall index was 0.79, whereas it was comparatively low for the South Georgia region (G = 0.30).

The cluster analysis has shown geographical differences in krill length composition. Since length and maturity are closely related, it is not surprising to see a similar geographical pattern in the spatial distribution of maturity stages (Figure 9). The relative frequency of juvenile krill reached a maximum in cluster 1 (80 %). Adult stages contributed only 1 % to the krill stock in this region to the south-east of South Georgia. Immature and early pre-spawning adult stages dominated cluster 2 by 85 %. This cluster covered the Bransfield Strait and its eastern outflow of the Scotia Sea, as well as the wider regions north of South Georgia and part of the South Sandwich Island area. Less immature but mostly advanced adult size classes occurred in the samples from the north-western Scotia Sea and off the Antarctic Peninsula. This cluster 3 can clearly be described as the spawning stock, more than 85 % of the krill in this area were gravid stages close to spawning or had recently spawned .

From these observations it is obvious, that the dispersion of the spawning stock across the Scotia Sea was far from even. Two hotspots can be detected for the occurrence of gravid/spent krill in the season 2000 (Figure 10). The first concentration of spawning krill extended in a narrow band from the northern side of the South Shetland Islands to just north of the South Orkney Islands. Mean concentration of gravid/spent females was above 12 per 1000 m³ (Table 3). The second spawning concentration was located in the central and south-eastern part of the South Sandwich Islands. However, density of spawning krill was much lower in the eastern Scotia Sea. From Figure 10 it is evident, that there was a big gap in krill spawning activity in the entire central Scotia Sea, around South Georgia and in the northern part of the South Sandwich Islands.

As a result of the occurrence of spent female stages it could be expected that krill larvae were already present in the water column. The quantitative analysis of RMT 1 samples shows that more than 40 % of the total number of larvae were in the calyptopis 1 stage, 32 % in the C2 stage and less than 10 % accounted for all furcilia stages F1 to F3. Figure 11 demonstrates a clear disparity in larval distribution between different strata of the survey area. Highest concentration of larvae were found in the western sector, i.e. the central Scotia Sea between Elephant Island, east of the South Orkneys and south-west of South Georgia. There were some scattered stations with records of calyptopis larvae in the South Sandwich Islands region, but there was a sharp boundary around 36°W where larval distribution rapidly declined cease out. RMT 1 samples yielded a maximum of 36000 krill larvae per m² in the western sector, but only 25 to the east of 36°W. Table 4 summarizes average larvae densities and makes the difference quite evident between the western and eastern sector. Interestingly the very western upstream areas along the Antarctic Peninsula also showed relatively low larval densities.

4.4. Age structure and recruitment

Results on krill recruitment obtained by the analysis of the length density distributions applying the method described by de la Mare (1994) are summarized in Table 5 for the Subareas and larger geographical regions. It is obvious that no one-year-old krill recruits (R_1) were observed in the Antarctic Peninsula region (Subarea 48.1) and that krill recruitment was relatively low in the South Orkney Islands and South Georgia regions, with slightly more than 4 and 6 % of the stock consisting of age group 1+ krill. Those one-year-olds found in the later two Subareas had come from the eastern part of the Subareas, the area west of $45^{\circ}W$ showed a complete absence of this krill age-class.

Recruits were exclusively found east of 45°W with the highest proportion in the South Sandwich Island area, where they dominated the stock. The actual very high absolute number of these animals in the eastern part of the survey area also strongly influenced the overall index for the entire survey area. Compared with other recruitment values (Siegel and Nicol, 2000) a value of $R_1 = 0.568$ has to be regarded as a very successful year-class 1999/2000 at least in the eastern sector of the South Atlantic.

 R_2 values of Table 5 indicate that recruitment of the two year old krill in the Peninsula area was also poor, leaving us with at least two weak year-classes in a row in the western sector, while krill in the east again showed a recruitment success far above average for the eastern part of the South Atlantic.

These poor and successful year-classes had a determining effect on the age structure of the stocks in the different parts of the South Atlantic (Table 6). In the western sector the stock was clearly dominated by relatively old, large and adult krill (see also length frequencies and maturity stages above). During the past years failure of reproduction and/or poor recruitment of the stock had obviously turned the population age pyramid upside-down.

The eastern sector was inhabited by a stock of a more conventional population structure, from which one expects a high proportion of young animals and a continuously decreasing number of older age groups. This would reflect a population with constant successful reproduction, recruitment and mortality. Variability in these parameters seems to be much lower in the eastern than in the western sector or in the upstream regions of these areas.

5. Discussion and Conclusions

5.1. Density from net hauls

The presented average density of krill from net samples was in the range of values estimated for the period 1985 to 1999 (7 to 637 krill 1000 m⁻³) in the long-term study of the Elephant Island meso-scale survey (Siegel 2000). However, before that period density was regularly above this level (188 to 1681 krill 1000 m⁻³), thus the present density would still be below the lowest value of the high density period before 1985. Interestingly, the Subareas around South Georgia and the Antarctic Peninsula had the lowest krill densities during the present survey, while these are thought to be predictably high density areas for the krill fishery. The density results for South Georgia and the Peninsula are around the low density means of the krill poor period of the 1990'ies. Different to these observations are the high density values from the South Sandwich Island. Unfortunately, no directly comparable data are available from other years to which the new estimate could be related to. The high numerical density in 48.4 is a direct consequence of the high number of young, juvenile krill in that area.

There are only few other recent large-scale survey for krill in the Southern Ocean. Unfortunately the FIBEX survey used completely different types of gear so that a direct overall comparison of net sampling densities is impossible. Several surveys were conducted in the Scotia Sea during the mid 1980 and using nets of similar opening and mesh size. Sushin and Shulgovski (1999) reported krill densities from summer seasons 1984, 1985 and 1988 from an area similar to the survey 2000, but not covering the South Sandwich Island region. If converting the biomass estimates given by Sushin and Shulgovski (1999) to biomass per m² we would obtain the following mean biomass densities:

1984: 7.7 g m⁻²

1985: 10.2 g m⁻²

1988: 10.1 g m⁻².

These data should be best compared with the ones given in Table 2 for the Scotia Sea (SS) and Antarctic Peninsula (AP) strata or the subareas 48.1 to 48.3 (6.2 to 29.3 g m⁻²). Keeping in mind that the surveys from the 1980'ies sampled the high-density upper-100-meter surface layer, then those values have to be regarded as overestimates. The conclusion is that the year 2000 estimates are slightly above the older biomass densities, although it is difficult to quantify this difference.

Although biomass estimates for the entire area seemed to be stable over the studied years, the dispersion of biomass showed some dynamic peculiarities. Different scenarios in krill dispersion can be detected from the distribution maps given by Sushin and Shulgovski (1999):

- a) a homogeneous distribution of krill density was found across the Scotia Sea and South Georgia region in 1984, but with higher densities east of 38°W,
- b) a relatively homogeneous distribution occurred in the west and south-east in 1985, but densities were substantially reduced around South Georgia,
- c) relatively high and evenly distributed krill densities were recorded in 1988 all over the Scotia Sea survey area.

Priddle *et al* (1988) already suspected a large-scale influence of weather (wind) on the krill distribution Against this background it seems reasonable to expect that krill is regularly drifting into the South Georgia area, but in some years krill occurrence can change dramatically in the area due to strong and persistent northerly wind effects displacing the water masses further to the south (Priddle *et al.*, 1988). The high variability in occurrence and abundance of krill in the waters off South Georgia seems explainable by the fact that these waters are at the extremes of the geographical range of *Euphausia superba* rather than in the centre of its distribution.

Another large-scale study was carried out in the Indian Ocean in summer 1996. Even if the estimated average krill density in the South Atlantic was classified as average for a low density period, these results are high compared to the large-scale Indian Ocean survey. In this regard the results of the present net sampling assessment correspond well with that produced from the examination of the acoustic data (Hewitt *et al.*, this volume). Nicol *et al.* (2000) reported 1.07 to 4.73 krill 1000 m⁻³ and 0.39 to 0.97 g m⁻² from RMT net samples. The results were obtained from catches containing krill and excluding more oceanic water stations devoid of krill. These values from the Indian Ocean are more than one order of magnitude lower than the Atlantic krill densities, especially if we also exclude those areas in our estimate which are thought to be located to the north beyond the krill distribution range. The difference cannot be attributed to the fact that the Atlantic sector has more shelf areas with larger krill aggregations, because the results from oceanic waters of the Atlantic show the same discrepancy. Similar observations were recorded by Miller et al. (1989) from acoustic data, who found a much smaller swarm density, swarm size and a larger interswarm distance for the Indian Ocean. Either the total biomass is lower in the Indian Ocean with generally lower overall densities or because krill are dispersed over a wider latitudinal range in the Indian Ocean than in the Atlantic. The second argument was used by Siegel and Harm (1996) to explain the lower krill density but wider geographical range of krill in the Bellingshausen Sea compared to the Antarctic Peninsula region, where the krill aggregations are compressed in a narrow belt of occurrence and a possibly longer retention time due to bathymetric features.

Part of the CCAMLR 2000 large-scale survey has regularly been studied by a long-term meso-scale survey around Elephant Island. The krill biomass in this local area has undergone substantial fluctuation in the past 20 years. The three Soviet large scale surveys from the 1980'ies mentioned above would fall into a period of clearly declining biomass densities in the Antarctic Peninsula region, from 26.7 g m⁻² in 1984 to 2.6 gm⁻² in 1988 (Siegel *et al.*, 1998). For Subarea 48.1 the present CCAMLR 2000 survey (8 g m⁻²) would be closer to the lower end of these biomass indices of the earlier meso-scale surveys. This strong variability in the Peninsula area is obviously not really reflected in the Soviet large-scale surveys of the Scotia Sea. Possibly the stock around the Antarctic Peninsula region is subject to much higher variability in biomass than the overall stock. An alternative could be an effect derived from the existence of two stocks

in the Scotia Sea with alternating / opposing development. The result for the Scotia Sea would be that a decline in one stock (possibly Bellingshausen/Peninsula) would be balanced by a simultaneous stronger influence of the second stock (possibly Weddell Sea) and *vice versa*. In this case the overall biomass in the Scotia Sea would appear to be stable despite large variability in the source regions. The potential existence of two stocks in the area was already discussed by Mackintosh (1973) and Everson (1976), and the hypothesis was supported by Siegel *et al.* (1990) describing differences in demographic parameters as indicators for krill stocks with different origin.

5.2. Overall population structure and distribution

Length frequency distributions and maturity stage composition showed some peculiarities across the survey area. Gravid and spent females were not evenly distributed across the Scotia Sea. The distribution spawning stock showed two hot spots, the first along the outer shelf/open ocean region between the Antarctic Peninsula and South Orkney Islands and the second around the central and southern South Sandwich Islands. However, noteworthy is the large discontinuity in the distribution of the spawning stock between 30° and 45° W, the central Scotia Sea and South Georgia.

Furthermore, in parts of the area where gravid stages occurred frequently, immature developmental stages were often proportionately large (Figure 6). This probably indicates that many of the immature krill (at least according to their external sexual characteristics) were undergoing post-spawn regression. The phenomenon of a recovery and possible later re-maturation of adult specimens after spawning was described in detail by Makarov (1975). He found that several moults after spawning krill no longer show clear characteristics of spawning and these specimens are difficult to distinguish from pre-spawning stages. This interpretation is supported by the high abundance of krill larvae in the central Scotia Sea during the survey time. It is therefore possible that the number of spent animals might have been even higher than the number of females simply recorded as stage 3E might suggest. Many of the 'externally pre-spawning' stages might in fact had already finished spawning and recovered from the process. The conclusion which can be drawn from the observations is that the spawning season had already passed its peak in early February.

Although the spawning timing for Antarctic krill is thought to occur between late November and April, it was shown that the onset and duration of spawning within this time window may change inter-annually (Siegel and Loeb, 1995; Spiridonov, 1995). The high maturity index of 0.79 (Siegel and Loeb, 1995; Loeb *et al.*, 1997) strongly suggests that the spawning season 1999/2000 had started very early. The early spawning event is supported by the abundance of surface larvae of calyptopis and furcilia stages in the RMT 1 samples. It takes krill about 85 days to develop to furcilia 3 stage and 30 to 45 days to calyptopis 1 or 2 (Ikeda, 1984). The approximate timing of spawning due to the average (calyptopis 1 and 2) and oldest

(furcilia 3) larval stages would be 15 November as the earliest possible date and 15 to 30 December on average. The situation seemed to be comparable to the one in 1981, the FIBEX survey. At the end of January /beginning of February about 63 % of the larvae were in the C1 and 25 % in the C2 stage which is similar to the situation of the present study. Working backwards from the composition of calyptopis stages, Rakusa-Suszczewski (1984) concluded that in 1980/81 the most intense spawning occurred in late December. According to Siegel and Loeb (1995) early spawning events are advantageous for a promising reproductive season. Therefore, one would expect a high spawning success and depending on the survival rate of larvae during the following winter, this positive stipulation gives the 1999/2000 year-class the potential for a high recruitment and a strong age group.

Quantitative large-scale larval surveys are scarce in the published literature. The Australian survey from 1996 recorded 2.5 larvae m⁻² (adjusted from n 1000m⁻³) in the western sector of the Indian Ocean and 637 larvae m⁻² in the eastern sector (Nicol *et al.*, 2000). Brinton *et al.* (1986) mentioned average larval densities of 35 m-2 in the Scotia during summer 1984, and called these concentrations fewer than observed in 1981 (FIBEX year) but still substantial for the 1984 season. Therefore, krill larval concentrations of the magnitude reported here from the CCAMLR survey have to be considered to be high. However, the spawning season 1981 was quite unusual, in that spawning season krill larval densities were even one order of magnitude higher than during 2000. The 1981 year-class was the most successful one since 1975, in terms of proportional as well as absolute recruitment.

Interestingly, during the FIBEX survey the highest numbers of larvae were recorded in the central part of the Scotia Sea, in the open ocean and along the shelf slopes (Rakusa-Suszczewski, 1984). This coincides with the observed distribution of larvae during the present CCAMLR survey. Unfortunately the areas around South Georgia and South Sandwich Islands were not sampled during FIBEX. Therefore, it is not possible to see whether during FIBEX this sharp decline in larval density also occurred around 36°W and south of South Georgia. However, going back into historic 'Discovery' data, the large-scale krill larvae distribution looks very similar. The maps produced by Marr (1962) show a concentration of calyptopis and furcilia between 27° (South Sandwich Islands) and 60°W (South Shetland Islands) for the period January to February (Marr, 1962, figure 100).

Even for the short period of the time between spawning and the occurrence of surface larvae, some rough idea can be formulated on the drift of larvae. As mentioned above, the western spawning stock showed a sharp decline at 45°W. Through the time of their development of 30 to 53 days (because 90 % of the larvae were calyptopis stages) krill larvae covered a much wider range than the spawning stock. Larvae had dispersed further to the north from approximately 59°S to 55°S (240 miles) and further to the east from 45°W to 36°W (about 250 miles). Following Marr's sequence of larval data over the summer and autumn into the winter period, there is clear evidence for a gradual spreading to the east far beyond the South

Sandwich Islands (his figure 130). Marr (1962) called this the surface drift along the 'Weddell stream', but which is probably better described as the West Wind Drift. In principal it seems noteworthy that the origin of the mass surface larvae in the central to western Scotia Sea and the gradual north-eastward spreading observed during the season 2000, very much resembled the situation described from the 'Discovery' investigations.

South Georgia seems to be a special case, where in summer 2000 the maturity index and the larval density were extremely low. Either spawning was delayed or females do not spawn in this area. Furthermore, the actual numerical density of gravid and spent females was very low in 48.3. Even if spawning would culminate later in the season around South Georgia, these two observations together (possible late spawning if any and low mature adult stock size) lead to the conclusion that this area would not contribute substantially to a high recruitment in the South Atlantic.

Again the situation around South Georgia seems to be more variable than the more central Scotia Sea due to its proximity to the northern limits of krill distribution and its proximity to the Polar Front. Northerly physical oceanographic and atmospheric influences from beyond the Polar Front point towards the complexity of dynamic processes in at least part of the area and add a further complication to a generalized picture of krill dispersion in the South Atlantic.

The analysis of length frequency data indicated certain similarities in the krill stock composition across the Atlantic sector, but even more pronounced dissimilarities between subareas or larger geographical units. Interestingly in most of the Scotia Sea / Peninsula region large krill were proportionately abundant in the population. These modal size classes of 48 and 52 mm (4 to 5 year old) krill represent the 1995 and 1996 year-classes, which had been described earlier as the most successful year-classes during the 1990's. Since then recruitment was obviously poor at least in waters under the influence of the outflow of the Drake Passage / Antarctic Peninsula region. However, as mentioned above, there are signs from the spawning stock that during the 2000 season krill may produce a successful recruitment in future.

The differences in length frequencies described above for the various subareas could be interpreted in a way that each Subarea is inhabited by different or independent krill stocks. However, it is obvious that length frequency distributions vary substantially between Subareas, because the spatial extent of the various size clusters differed within and between Subareas. Despite the observation that Statistical Subareas are not representing natural boundaries for the krill population, there are obviously ecological units in the Scotia Sea which are of importance to krill demography and distribution. Figure 4 and 5 for example demonstrate that the distribution of small krill covered a large proportion of Subarea 48.2 and 48.4. This size cluster formed a big intrusion and almost separated the western stock (cluster 2a and 3 with mostly 4 and 5 year old adults) from the eastern adult stock (cluster 2b, 2c, 3 east with mostly 2,3,4 and

5year old krill). Obviously west of 45° the stock was dominated by old krill, while the eastern section of the area had a more complete set of age classes present. This 45°W natural boundary could be identified from krill demographic parameters such as recruitment, length frequency distributions, as well as density and dispersion of the spawning stock. At 36°W we found a boundary for the larval population originating from the South Shetland – South Orkney spawning event. However, these meridional oceanic boundaries are variable and move during the proceeding season as well as from year to year. This can be concluded from the dynamic dispersion of krill larvae described already by the 'Discovery' data (Marr, 1962).

From time to time these regular developments appear to be superseded by sporadic events. Obviously not only northerly large-scale event influence the density patterns and distribution of the krill stock(s) as described for Soth Georgia, but also occur at the southern extensions of the Scotia Sea generated by changes in the influence of the Weddell Sea. In some years, like obviously in 2000, intrusion of different krill into the central Scotia Sea from the south are much stronger than in others.

Some differences in the length and maturity composition point to the possibility of a different origin of the krill aggregations in the area. The juvenile fraction was completely missing in the area west of 45°W. This size class was well represented east of the South Orkney Islands in the outflow of the Weddell Sea gyre and extended as far north as South Georgia. The southern part of this area was still covered by seasonal pack-ice in late December (see ice-edge in Figure 1). The largest adult size fraction dominated the stock in Drake Passage water and extended east to the South Orkneys into Subarea 48.2. Since intermediate sized krill bordered on the southern side, it separated the large sized krill from the outflow of the Weddell Sea. It can therefore be concluded that the largest size component originated from the area west of the Antarctic Peninsula and was obviously of Bellingshausen origin, while juveniles had their source mainly in the Weddell Sea,

Subareas are obviously directly linked to each other by the continuous flow of krill (e.g. cluster 2), but at the same time Subareas are also inhabited by size components of krill from different sources, e.g. subgroups of cluster 2 or cluster 1 in different parts of the Scotia Sea. This has serious implications for meso-scale surveys in CCAMLR Subareas. It seems that at least in some years these meso-scale surveys do not adequately represent the composition and abundance of the krill populations in the entire Atlantic sector of the Antarctic. On the other hand in other years teleconnections and a high degree of similarity have been found between Subarea 48.1 and 48.3 (Brierley *et al.*, 1999). Furthermore, Siegel and Harm (1996) have shown that the meso-scale surveys around Elephant Island/Antarctic Peninsula represented the stock composition along the western side of the Antarctic Peninsula well into the Bellingshausen Sea. However, the Atlantic Sector seems to be under variable interannual influence from the Peninsula and the Weddell Sea, causing differences for the two krill stocks in abundance, age/size composition and recruitment success. These highly dynamic structures create regional differences and consequently severe

difficulties for the krill management of the South Atlantic (Area 48) in its entirety and argues for further

large scale surveys as well as a subdivision of the Area into smaller management units.

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Table 1: Krill numerical densities from routine RMT net samples ; average density is the simple mean, densities from the "TRAWLCI method" are calculated according to de la Mare (1994b); EES = Eastern Scotia Sea, SSI = South Shetland Islands, SOI = South Orkney Islands, SG = South Georgia

Stratum		Average krill density			"TRAWLCI me	ethod"
	all samples		excl. zero catches		density within distribution range	
	N 1000m ⁻³	$S_{\rm E}$	N 1000m ⁻³	S_{E}	N 1000m ⁻³	\mathbf{S}_{E}
48 all strata	124.2	35.9	158.9	45.4	247.5	136.4
SS (Scotia Sea)	53.8	35.2	77.9	50.6	38.3	23.4
AP (Ant. Pen)	44.8	25.4	58.8	32.8	90.3	68.2
Subarea 48.1	37.2	17.0	45.8	20.7	64.4	39.6
Subarea 48.2	134.0	94.3	201.0	139.3	127.3	113.1
Subarea 48.3	74.8	50.2	101.5	67.7	75.4	52.9
EES = 48.4	268.9	106.8	308.8	121.0	754.3	615.1
Oceanic region	89.5	37.0	120.7	49.4	153.3	91.0
Shelf (SSI,SOI,SG)	236.2	102.7	256.7	110.8	487.1	379.1

Table 2: Krill biomass densities within the distribution range from routine RMT net samples in different parts of the survey area; biomass densities were calculated as simple arithmetic means and applying the "TRAWLCI method" according to de la Mare (1994b); acronyms see Table 1

Stratum	Mean biomass density				
	Arith. mean		"TRAWLCI n	"TRAWLCI method"	
	g m ⁻²	\mathbf{S}_{E}	g m ⁻²	\mathbf{S}_{E}	
48 all strata	14.0	5.0	18.7	9.4	
SS (Scotia Sea)	6.2	4.0	3.6	2.1	
AP (Ant. Pen)	10.3	5.7	12.0	8.2	
Subarea 48.1	8.0	3.6	10.0	5.7	
Subarea 48.2	29.3	23.8	13.6	11.9	
Subarea 48.3	7.0	5.1	6.0	4.1	
EES = 48.4	20.2	12.1	27.3	20.3	
Oceanic region	10.4	5.2	10.6	5.8	
Shelf (SSI,SOI,SG)	25.7	13.5	47.9	35.5	

Table 3: Numerical densities from routine RMT net samples for gravid and spent female krill; average density is the simple mean, densities from the "TRAWLCI method" are calculated according to de la Mare (1994b);

Stratum	Average krill o	density	"TRAWLCI me	"TRAWLCI method"	
	N 1000m ⁻³	SE	N 1000m ⁻³	$S_{\rm E}$	
West of 45°W	24.9	18.50	12.4	7.07	
Central Scotia Sea 30° - 45° W	0.2	0.08	0.2	0.14	
Eastern Scotia Sea East of 30°W	7.1	5.12	3.8	2.56	

Table 4: Density of krill larvae during the CCAMLR survey 2000 and the FIBEX survey in 1981. Division of the area into west (= west of 36°W) and east is explained in the text.

Stratum	CCAMLR 2000		FIBEX 1981
	$N m^{-2}$	S_{E}	$N m^{-2} S_E$
Calyptopis West	1841.7	674.7	19307.9 9357.3
Calyptopis East	2.2	0.9	
Furcilia West	202.6	109.2	435.2 222.2
Furcilia East	0.2	0.1	
Total Larvae West	2044.3	749.3	18601.8 8322.6
Total Larvae East	2.4	1.0	

Table 5: Proportional recruitment indices R_1 and R_2 (one and two year olds, respectively) from krill length density distributions; indices calculated according to de la Mare (1994a)

Area	R ₁	S _E	R ₂	S _E
48.1	0	-	0.081	0.1975
48.2	0.043	0.1258	0.2953	0.5300
48.3	0.066	0.0452	0.9212	0.1725
48.4	0.7198	0.1738	0.5632	0.2576
West of 45 W	0	-	0.111	0.0635
East of 45 W	0.6017	0.2663	0.7280	0.1858
Total	0.5680	0.2265	0.4945	0.2006

Age Group	West of 45°W	East of 45°W
1	0	60
2	10	26
3	20	12
= 4	70	2

Table 6: Age structure of the krill stocks in the South Atlantic in January/February 2000, frequency of age groups in %

Figure captions

Figure 1: Map of RMT stations covered during the international CCAMLR Survey 2000 in January/February 2000. CCAMLR Subarea 48.1 = Antarctic Peninsula, 48.2 = South Orkney Islands, 48.3 = South Georgia, 48.4 =) South Sandwich Islands. The northern limit of the ice-edge is given for 20 November 1999 and 20 January 2000 (data source: www.natice.noaa.gov/pub/Antarctica/).

Figure 2: Distribution of krill numerical densities (N 1000 m⁻³) across the Scotia Sea during January/February 2000 derived from RMT8 samples

Figure 3: Dendrogram resulting from cluster analysis of krill size groups

Figure 4 : Krill length frequency distributions grouped according to different size clusters

Figure 5: Geographical distribution of krill size clusters in the Atlantic sector of the Antarctic in January/February 2000

Figure 6: Composite krill length density distribution (in N 1000 m⁻³) distinguishing between the various developmental stages for the entire survey area.

Figure 7: Overall krill maturity stage composition for the South Atlantic survey area; maturity stages according to the classification of Makarov and Denys (1981)

Figure 8: Development of adult female maturity stages during the spawning season at the end of January/beginning of February 2000 (3A pre-spawning, 3B and 3C developing, 3D gravid, 3E spent females.

Figure 9: Krill maturity stage composition in the South Atlantic according to the results of the cluster analysis.

Figure 10: Map of the geographical dispersion of gravid/spent female krill

Figure 11: Map of the geographical dispersion of larval krill