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LONG-TERM MONITORING OF KRILL RECRUITMENT AND ABUNDANCE INDICES IN THE ELEPHANT ISLAND AREA (ANTARCTIC PENINSULA)

V. Siegel
Bundesforschungsanstalt für Fischerei
Institut für Seefischerei, Palmaille 9
D-22767 Hamburg, Germany

W.K. de la Mare
Australian Antarctic Division
Channel Highway, Kingston 7050
Tasmania, Australia

V. Loeb
Moss Landing Marine Laboratories
PO Box 450, Moss Landing, Ca. 95039, USA

Abstract

Krill distribution and density are reviewed for the Elephant Island area with regard to the representativeness of the study area (60°–62°30´S and 53°–57°30´W) for proportional recruit and density indices. Proportional recruitment indices were re-calculated applying the delta distribution approach introduced by de la Mare (1994a). The high interannual variability of krill recruitment is confirmed by the present analysis. Results are compared for one- and two-year-old krill (R_1 and R_2 respectively). Statistically significant fluctuations in krill density over the period 1977 to 1994 are also confirmed by this study using randomisation tests on an analysis of variance.

Résumé

Examen de la répartition et de la densité du krill de la zone de l'île Éléphant relativement à l'à-propos du secteur étudié (60°-62°30'S et 53°-57°30'O) pour les indices de recrutement proportionnel et de densité. Nouveaux calculs des indices du recrutement proportionnel par la méthode d'application de la distribution delta proposée par de la Mare (1994a). La présente analyse confirme la grande variabilité interannuelle du recrutement du krill. Comparaison des résultats des classes d'âge 1 (R_1) et 2 (R_2). Cette étude confirme également, au moyen de tests de randomisation sur une analyse de variance, l'importance sur le plan statistique des fluctuations de densité de krill pour la période de 1977 à 1994.

Резюме

Распределение и плотность криля в районе о-ва Элефант были рассмотрены с целью определения степени пригодности изучаемого района (60°–62°30´ю.ш. и 53°–57°30´з.д.) для вычисления индексов пропорционального пополнения и плотности. Индексы пропорционального пополнения были повторно рассчитаны с помощью дельта-распределения (de la Mare, 1994a). Результаты нашего анализа подтвердили высокий уровень межгодовой изменчивости пополнения криля. Были подвергнуты сравнению результаты для однолеток и двухлеток (R_1 и R_2 соответственно). При дисперсионном анализе с помощью критерия случайности также было подтверждено существование статистически значимых колебаний в плотности криля за период с 1977 по 1994 г.

Resumen

Se hizo un estudio de la distribución y densidad del kril en el área de la isla Elefante, para evaluar si ésta (60°–62°30´S y 53°–57°30´W) es representativa de los índices de reclutamiento proporcional y de densidad. Se calcularon nuevamente los índices de reclutamiento proporcional mediante la aplicación del enfoque de la distribución delta que fue introducido por de la Mare (1994a). El análisis actual confirma la alta variabilidad interanual del reclutamiento del kril. Se comparan los resultados para ejemplares de uno y dos años de edad (R_1 y R_2 respectivamente). Asimismo, éste estudio confirmó la ocurrencia de fluctuaciones estadísticamente significativas de la densidad del kril en el período comprendido entre 1977 y 1994, mediante el uso de pruebas de aleatorización en un análisis de variancia.

Keywords: abundance, Antarctic Peninsula, distribution, *Euphausia superba*, interannual variability, krill, monitoring, recruitment, spatial and temporal succession, CCAMLR

INTRODUCTION

Krill recruitment and abundance are two of the essential parameters that influence the results of the krill yield model developed for the management of Antarctic krill stocks (Butterworth et al., 1991). The original yield model was extended to integrate over the range of uncertainties associated with a number of model parameters, including recruitment (Butterworth et al., 1994). Proportional recruitment indices for krill were recorded in a time series database in the Elephant Island area (South Shetland Islands, Antarctic Peninsula) covering the years 1977/78 to 1994/95 (Siegel and Loeb, 1995). The proportion of recruits for age group 1+ (R_1) was calculated for a spatially limited station grid and was based on length frequency data applying the MacDonald and Pitcher (1979) distribution mixture analysis. Results on krill recruitment showed a high degree of interannual variability which would have a marked effect on the krill yield model.

Earlier studies in the Antarctic Peninsula region showed that krill size/age groups are not uniformly distributed within the distribution range of the stock, and that juveniles, subadults and adults (i.e. recruits and spawners) are geographically segregated (Siegel, 1988). The question arises whether the results of the mesoscale Elephant Island station grid reflect the stock composition of a much larger area (i.e. are representative of the krill stock of the broader Antarctic Peninsula region). Furthermore it is necessary to know if high variability of the R_1 index is a real phenomenon or is biased by sampling and/or data handling and if calculation of R_2 (proportion of recruits for 2-year-old krill) may indicate lower recruitment variability. Preliminary results on krill density estimates from the Elephant Island time series indicate that a substantial decrease has occurred since the early 1980s; this must be verified, as another assumption of the krill yield model is that the statistical distribution of the unexploited biomass does not change over time.

The present contribution reviews aspects of krill distribution which must be considered during net sampling operations to obtain adequate data for the calculation of proportional recruitment indices. Proportions of recruits are calculated for R_1 and R_2 using length density data and applying the maximum likelihood method described in detail by de la Mare (1994a). Net haul abundance estimates will be re-calculated by replacing the stratified mean method with the delta distribution approach introduced by de la Mare (1994b) and also by bootstrap replication (Efron and Gong, 1983). The statistical significance of observed variation in krill density is assessed by randomisation tests in an analysis of variance (Manly, 1991).

REVIEW OF KRILL DISTRIBUTION BY SIZE/DEVELOPMENTAL STAGES

Krill distribution is a function of time and space. The Antarctic Peninsula region and adjacent areas are characterised by a clear seasonal fluctuation in krill abundance. Figure 1 gives a conceptual view of the seasonal variation. Krill abundance/density is low in the region during winter. During November krill abundance in open water starts to increase rapidly and generally reaches its maximum at the end of December (Siegel, 1988). This maximum can be observed until late February. There is some interannual variation in this seasonal trend and the period can shift by approximately four weeks to give an earlier start or later end to the cycle. From March onward, the krill stock size along the coast of the Antarctic Peninsula shows a dramatic decline long before the winter sea-ice cover and the difference between the summer peak and winter minimum can be several orders of magnitude (Siegel, 1988 and 1992).

The krill spawning season occurs over the summer (Fraser, 1936) during the time of krill maximum abundance. However, the onset of spawning can be observed from early December to late March (Spiridonov, 1995). Interannual variation in the onset of spawning is described for the period 1978 to 1994 and has a marked effect on the reproduction and recruitment success of the stock (Siegel and Loeb, 1995).

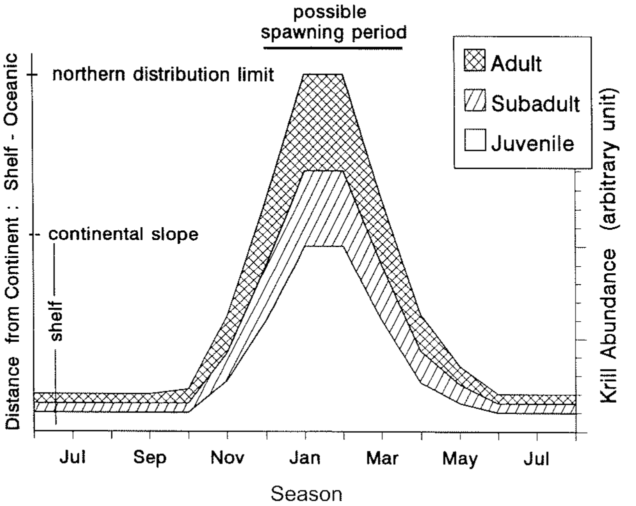

Figure 1: Generalised picture of seasonal fluctuations in the abundance and distribution of krill in waters of the Antarctic Peninsula and spatial succession of developmental stages from coastal to oceanic waters.

During the winter, when krill abundance and biomass along the Antarctic Peninsula are low, krill occurs mainly on the continental shelf. With the seasonal increase in abundance, krill distribution extends beyond the continental shelf break into oceanic waters almost as far north as 59°S (Nast, 1982; Siegel et al., 1990). This northern limit of krill distribution is reached only during the period when krill abundance is high in the area (i.e. in January/February), but it is generally low north of 60°S. Outside the peak season the northern limit of krill distribution is located well south of 60°S.

During the austral summer, spatial separation of krill developmental stages can be observed. Juveniles inhabit coastal waters (e.g. the Antarctic Peninsula shelf, Bransfield Strait) while adult spawning stages occur primarily in oceanic regions (Figures 1 and 2). This general picture is also observed in the Elephant Island survey area. Juveniles are concentrated south of Elephant and King George Islands and in a narrow band extending across the northern shelves where countercurrents flow from east to west in nearshore waters. The spawning stock is found north of the continental slope. The distribution range of medium-sized krill overlaps with those of the juvenile and adult stocks. The medium-sized group consists of immature and small adult stages and mostly belong to age group 2+, which therefore shows a distribution slightly more to the northern than the juvenile 1+ age group. In principal the seasonal aspect is a very dynamic process: krill abundance undergoes a strong seasonal fluctuation, the distribution range varies seasonally, and at the same time a spatial succession of size/age groups occurs in the area (Siegel, 1988).

To the east of Elephant Island these various discrete size groups are distributed over the shelf areas and in the oceanic waters of the Scotia Sea, but the north-south succession of developmental stages/age groups seem to occur further across the Scotia Sea (BIOMASS, 1991). This krill is thought to belong to the Antarctic Peninsula stock and probably originates from the Bellingshausen Sea (Everson, 1976; Siegel, 1986 and 1988). Krill in the upstream Bellingshausen Sea area shows similarly geographically separated size/age groups (Siegel and Harm, 1996).

A different juvenile size category is found regularly to the south and southeast of Elephant Island, along the permanent pack-ice zone. The mean length of these juvenile krill is 6 to 10 mm smaller than the length of Peninsula juveniles. Juveniles of this size are distributed south of 63°S, approximately from the tip of the Peninsula to the east; often they are found over the northern shelf of the Peninsula in southern Bransfield Strait. These juveniles are thought to originate from Weddell Sea stock (Makarov, 1980; Siegel et al., 1990; SC-CAMLR, 1995). The Elephant Island survey area includes the distributions of the two juvenile stocks and therefore data from south of 62°30′S are not included in the calculation of proportional recruitment.

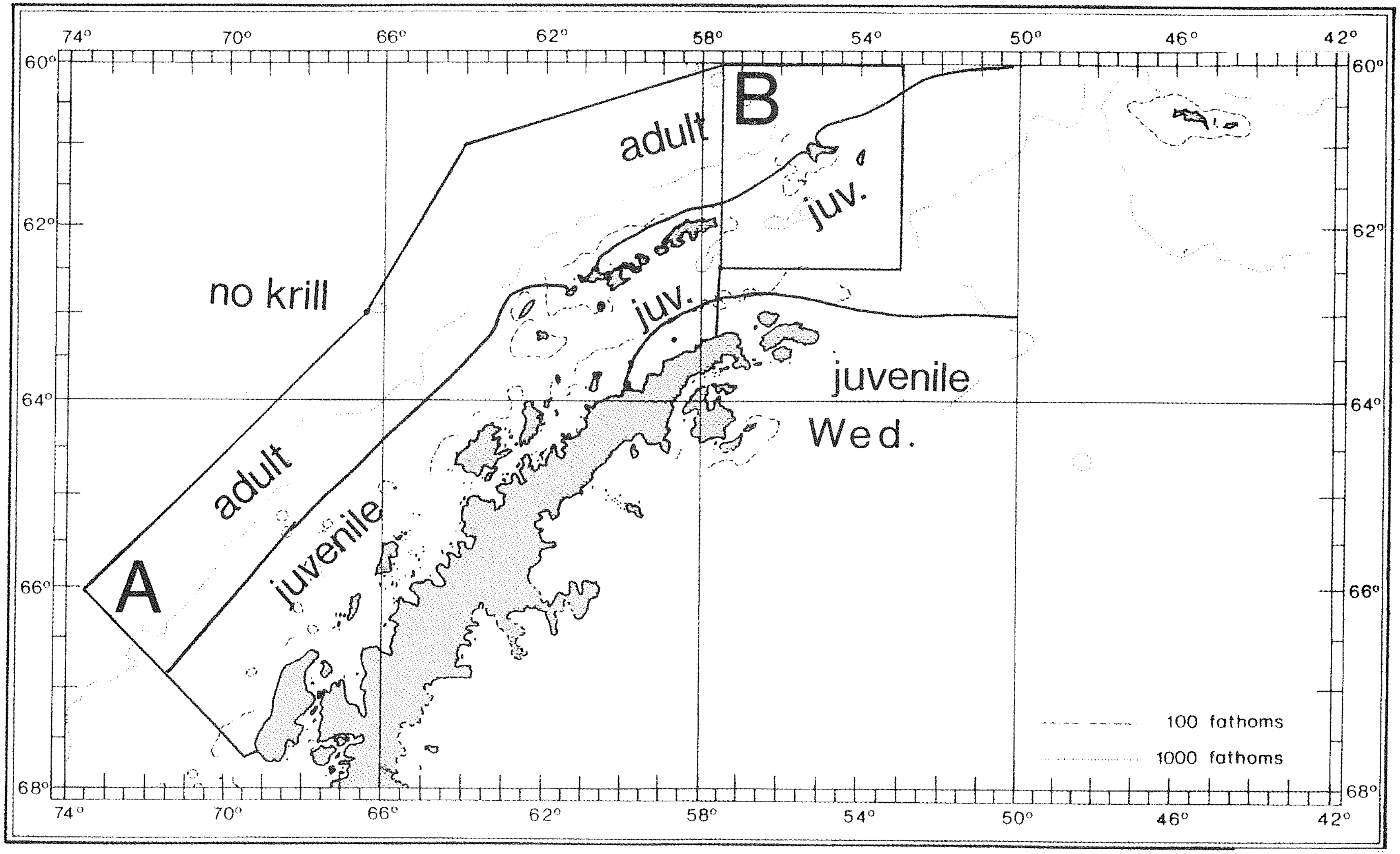

Figure 2: Elephant Island survey area (B) and large-scale survey area (A) (area A includes B) in waters of the Antarctic Peninsula with the generalised distribution pattern of juvenile (mostly age group 1+) and adult krill (mostly ≥3+ age groups). Wed. = juveniles of the Weddell Sea stock.

REVIEW OF KRILL MOVEMENT INTO AND OUT OF THE STUDY AREA

The Elephant Island survey area contains water masses from three different sources: in the west from Drake Passage north of the South Shetland Islands, in the southwest from the Bransfield Strait, and in the south from the Weddell Sea. The most striking oceanographic feature of the area is the Weddell-Scotia Confluence (WSC) with its northern boundary just north of Elephant Island crossing the area from southwest to northeast.

The CCAMLR Workshop on Evaluating Krill Flux Factors (SC-CAMLR, 1994) estimated a water retention time of 18 to 44 days for the Elephant Island area based on influx and efflux rates from oceanographic data (CTD samples). Direct measurements of flow are available from Japanese satellite-tracked drifter buoy studies (Ichii and Naganobu, 1996). In 1991 one drifter buoy was released in oceanic waters north of the South Shetland Islands. It entered the survey area and drifted north of the continental slope to the northeast and crossed the eastern boundary of the area after 25 days. In 1995 another buoy was released close to the continental slope in Drake Passage. This drifter followed the contours of the slope and reached the northeastern part of the study area after 13 days, but was then trapped in an eddy system for another 30 days before leaving the area in a northeasterly direction after a total retention time of 43 days. A third drifter buoy, which is of interest, was released on the northern shelf of the South Shetland Islands. This buoy showed rotating and irregular movements but finally entered the Elephant Island shelf area within the WSC zone. It continued its drift south of the island, travelled around Elephant Island anticlockwise, and was finally trapped near Gibbs Island after more than 48 days in the area.

These experiments demonstrate the existence of complex eddy formation and prolonged water retention times on the island shelves in contrast to the oceanic waters north of the WSC. As mentioned above, the oceanic waters are inhabited mostly by adult krill and these show the shortest retention times. The northern shelf/ continental slope/WSC boundary areas are a transition zone between adults in the north and juveniles in the south and are often dominated by subadult krill, but distributions of adults and juveniles also overlap in this meandering and eddy-rich system with prolonged water retention. Juveniles enter the survey area from Bransfield Strait and clearly dominate shelf areas south of the islands and therefore are at least partly under the influence of prolonged retention times. Little information is available about retention times in the southern part of the survey area, particularly over the deep basins east of the Bransfield Strait where juvenile krill dominate. However, preliminary results from indirect oceanographic data presented at the CCAMLR Workshop on Evaluating Krill Flux Factors indicate that the retention times are in the higher range of oceanic measurements (25 to 39 days) but shorter than in eddy-rich shelf areas north of the island.

RECALCULATION OF PROPORTIONAL RECRUITMENT INDICES

The proportional recruitment R_1 calculated by Siegel and Loeb (1995) was based on standardised length frequency data using the MacDonald and Pitcher (1979) distribution mixture analysis. It was assumed that the frequencies of each length class have a Poisson distribution, which would imply that krill are randomly and independently distributed. However, survey densities do not show these properties and the use of Aitchison´s delta distribution was recommended for analysing net haul data (de la Mare, 1994b). A new approach was developed which uses density-at-length data and the maximum likelihood estimation method (for details see de la Mare, 1994a and 1994b).

Table 1 summarises the recalculated proportion of recruits for 1-year-old krill. The R_1 recruitment value is the proportion of 1-year-old animals in the population in that year. In a few cases the recalculated values differ substantially from those in Siegel and Loeb (1995), e.g. November 1987 and January 1988. For these surveys, single stations with extremely high density values were excluded from the first analyses, but included in the present dataset, which explains the difference in results.

The Elephant Island surveys covered an area between 60°S and 62°30´S. The known maximum range of krill distribution in this area extends northward to approximately 59°S, however, as mentioned above, krill are generally sparse north of 60°S and this maximum range is observed only during high summer. Due to the spatial separation of developmental stages the reduced coverage of the distribution range causes an under-representation of the adult stages during January/February surveys. As mentioned earlier, the southern limit of the Antarctic

Table 1: Proportional recruitment index R_1 for 1-year-old krill calculated using the method described by de la Mare (1994a).

Survey	Siegel and Loeb (1995)	Maximum Likelihood Method		Number of Hauls
	R_1	R_1	S_E	
JAN 78	0.087	0.048	0.0256	17
FEB 82	0.677	0.757	0.1373	40
MAR 83	0.329	0.470	0.0990	8
NOV 83	0.028	0.030	0.0230	33
MAR 85	0.000	0.0001	0.0062	36
MAR 85A	-	0.028	0.0162	105
MAY 86	0.132	0.175	0.1049	25
MAY 86A	-	0.186	0.2089	73
NOV 87	0.230	0.143	0.0917	14
NOV 87A	-	0.181	0.0340	70
JAN 88	0.218	0.141	0.0339	41
FEB 89	0.673	0.651	0.1950	50
DEC 89	0.000	0.011	0.0125	20
DEC 89A	-	0.057	0.0390	86
JAN 90	0.000	0.000	-	
FEB 90	0.000	0.000	-	
JAN 91	0.167	0.099	0.0999	42
MAR 91	0.064	0.000	-	
JAN 92	0.426	0.471	0.0596	63
MAR 92	0.276	0.264	0.0619	68
JAN 93	0.000	0.000	-	72
FEB 93	0.000	0.000	-	68
JAN 94	0.046	0.061	0-0368	66
MAR 94	0.083	0.076	0.0390	73
DEC 94	0.060	0.046	0.0141	74

Table 2: Proportional recruitment R_2 for 2-year-old krill calculated using the method described by de la Mare (1994a).

Survey	Siegel and Loeb (1995)	Maximum Likelihood Method		Number of Hauls
	R_2	R_2	S_E	
NOV 77	0.128	0.314	0.4710	16
DEC 77	0.136	0.135	0.0904	14
JAN 78	-	0.297	0.5386	17
FEB 81	-	0.069	0.0050	9
NOV 83	-	0.663	0.0212	33
MAR 85	-	0.0001	0.0200	36
MAR 85A		0.119	0.0841	105
MAY 1986		0.214	0.0970	25
NOV 87	0.407	0.572	0.2434	14
NOV 87A		0.633	0.0205	70
FEB 89		0.291	0.1990	50
DEC 89		0.309	0.1237	86
JAN 90		0.421	0.3637	37
FEB 90		0.195	0.1377	41
JAN 91		0.040	0.0320	42
MAR 91		0.191	0.0791	39
MAR 92		0.345	0.1137	68
JAN 93		0.474	0.1375	72
FEB 93		0.648	0.1033	68
JAN 94		0.147	0.1424	66
MAR 94		0.012	0.0078	73
DEC 94		0.029	0.0215	74

Peninsula krill stock extends roughly to 63°S in this area. Since the survey grid did not extend further south than 62°30'S, the juveniles drifting out of Bransfield Strait are not completely spatially covered and the proportion of 1-year-old krill is also underestimated.

Additional data were analysed for four surveys and these are marked with 'A' in Table 1. These data sets include stations which covered a large-scale area along the Antarctic Peninsula (see Figure 2). In the region to the southwest of Elephant Island the station grid extended as far as the oceanic distribution limit of postlarval krill. The proportion of recruits calculated from these surveys are all higher than for the Elephant Island area, however, the proportional recruitment index R_1 differs by less than 5% compared to the large-scale surveys. The two effects (incomplete coverage for adults as well as juveniles) seem to balance each other to some extent.

Table 2 summarises results for the second component of the distribution mixture. Not all survey data used for the R_1 calculation led to a significant fitting of observed and expected length density components for R_2. Therefore, some surveys, like MAY 86A and DEC 89A are missing in this table. It is obvious that variability of R_2 between surveys of the same season and between large-scale (A) and small-scale surveys is much higher than that of R_1. Very often the results differ by more than 10%, while the difference is generally less than 5% for the R_1 index. The R_2 values are generally higher than those of R_1 for the same year class. There are several possible explanations for this discrepancy.

(i) The station grid does not cover the juvenile distribution range adequately and therefore results in an underestimation of the proportion of 1-year-old krill. It was shown above that this effect does occur, but is minimal.

(ii) Age group 1+ is influenced by net selection and under-represented in the catches. This effect may occur for the RMT8 net with a mesh size of 4 mm, although comparisons with RMT1 catches (330 µm mesh size) indicate that mesh selection occurs for krill smaller than 20 mm (Siegel, 1986), which is the lower end of the length frequency distribution of juvenile krill in summer. Furthermore the same differences between R_1 and R_2 resulted from catches made with the IKMT net, and with 0.5 mm mesh size net selectivity is certainly no problem for postlarval krill.

(iii) Estimating the proportions of the distribution mixture. Separating the first component from the rest of the distribution mixture is generally not a difficult task, because this component is easily distinguishable from the rest of the distribution mixture, even if the 1+ age group length classes overlap to some degree the second age group. The second component is often less well defined, because there is a strong overlap between the two components especially during summer when juvenile krill have already grown to their maximum size and in years when the first component is represented by a strong age group 1+ and completely masks the ascending tail of the distribution of the second age group. This size distribution may result in a bias in fitting the distribution mixture. The standard error of the R_2 estimates is generally higher than for R_1, and this may indicate that the analytical procedure is more reliable for the R_1 values.

(iv) Environmental parameters influence the different age groups differently. Two-year-old krill consist of medium-sized subadult and early-adult stages. In the Elephant Island area this size/maturity stage group shows a spatial distribution overlapping partly with juvenile and partly with adult stages. This central geographical distribution conforms to the area of the WSC zone, which creates a dynamic flow pattern with eddies and meanders. It may be that the mean retention time for krill is much longer in this area, resulting in a higher concentration of subadult stages, whereas further north or south more laminar currents create less concentration effects for adult and juvenile krill, respectively. Since mesoscale oceanographic features change on a weekly to monthly time scale, this would also explain high variability of the R_2 index between surveys of the same season and between large- and mesoscale surveys.

Table 3 presents R_1 and R_2 for each season. These indices are pooled values for seasons represented by more than one survey. The

Table 3: Results for R_1 and R_2 for different krill year classes, calculated as the inverse variance weighted mean for the various surveys.

Year Class	R_1	R_2
1975/76		0.144
1976/77	0.048	
1977/78		
1978/79		0.069
1979/80		
1980/81	0.757	
1981/82	0.470	0.663
1982/83	0.030	0.0001
1983/84	0.0001	0.214
1984/85	0.175	
1985/86		0.633
1986/87	0.156	0.291
1987/88	0.651	0.275
1988/89	0.057	0.063
1989/90	0.099	0.345
1990/91	0.375	0.587
1991/92	0	0.012
1992/93	0.068	0.029
1993/94	0.046	0.125

large-scale surveys (marked with A in Tables 1 and 2 are not included in the calculation of the mean, because the small-scale survey was part of the total survey. To be consistent with the other seasons, only the Elephant Island survey estimates were used for the overall mean.

The estimates of the inverse variance weighted mean and variance of R_1 and R_2 estimates are:

Mean R_1	0.214
SD	0.5103
SE	0.1275

and

Mean R_2	0.291
SD	1.2010
SE	0.2620

The simple arithmetic means are slightly smaller ($R_1 = 0.197$ and $R_2 = 0.255$), because of the inclusion of zero values which were not considered for the inverse variance weighted mean calculation.

The present overall mean recruitment proportion is lower than that calculated by the CCAMLR Working Group on Krill (WG-Krill) (de la Mare, 1994a). However, a number of surveys were excluded from that calculation, because some low recruitment values were thought not to be representative for the age class. However, examples from the time series show that years of poor to almost zero recruitment do exist. These results were observed not only on a local scale (e.g. Elephant Island survey area), but, in the same year, on a much larger scale throughout the Antarctic Peninsula region. For example, in 1985 and 1989 (Table 1) the proportional recruitment indices were very low and similar for the meso- and large-scale survey. Values like these were excluded from calculation of the overall mean in de la Mare's analysis (when R_1 was smaller than 0.1). The present analysis however confirms the occurrence of such low recruitment, and therefore these values must be included in calculations of the overall mean proportion of recruits.

NET HAUL ABUNDANCE ESTIMATES

Krill density estimates were listed by Siegel and Loeb (1995) for the Elephant Island area. The method applied was the stratified mean (Saville, 1979) of standardised non-targeted net catches ($N/1\,000\ m^3$) carried out during summer, between mid December and late February. This time restriction reduces the seasonal aspect of krill abundance fluctuations. The present analysis uses the Aitchison's delta distribution method and calculates confidence intervals as described by de la Mare (1994b). The results of both studies are listed in Table 4.

Table 4: Krill density estimates for the Elephant Island area from standardised non-targeted net catches ($N/1\,000$ m^3) taken during the summer season between mid December and late February. The present analysis applies the delta distribution method and calculates the confidence intervals described by de la Mare (1994b) and also uses a bootstrap procedure to calculate means and confidence intervals.

Year	Siegel and Loeb (1995)		Maximum Likelihood				Bootstrap				*N*
	Str. Mean	CV	Density	SE	Lower CI	Upper CI	Density	SE	Lower CI	Upper CI	
1977/78	101.2	0.732	697.53	507.26	139.42	8282.8	348.29	177.63	90.72	751.57	45
1980/81	66.1	1.429	358.57	276.64	60.95	7683.4	161.38	86.09	39.87	357.09	23
1981/82	*510.9*	*0.525*	*1681.15*	*1225.39*	*334.28*	*20366.9*	*324.87*	*96.47*	*156.29*	*530.04*	42
1982/83	90.6	1.623	306.28	216.95	67.28	6058.3	276.70	166.56	48.32	646.24	12
1984/85	11.5	0.367	22.63	14.11	6.35	170.1	85.85	65.31	10.05	225.9	37
1987/88	20.1	0.926	35.29	12.38	18.57	90.2	27.64	5.57	17.26	39.14	38
1988/89	41.7	0.509	65.31	27.26	29.96	205.0	79.84	31.58	28.32	149.58	49
1989/90	21.4	0.348	20.27	6.10	11.59	42.3	15.39	3.47	9.11	22.77	97
1990/91	5.3	0.355	6.76	2.15	3.75	15.3	6.46	1.67	3.51	10.01	42
1991/92	20.8	0.559	15.84	4.46	9.46	31.7	19.86	8.21	8.02	38.64	63
1992/93	29.6	0.368	37.32	12.17	20.50	84.1	29.17	7.52	16.67	45.80	72
1993/94	29.7	0.535	28.86	11.40	13.82	81.6	32.96	11.37	13.49	57.45	66
1994/95	19.5	0.522	25.03	7.45	14.41	50.3	73.31	54.07	12.39	186.83	147

The difference between the periods 1978–1983 and 1985–1995 can be seen in the results of both analyses. Mean krill density was much higher during the early period. Even the lower confidence interval of the early period is generally higher than the mean during the period after 1985. The time difference is less obvious for the median values, but it is interesting that the 75% percentile is much higher in the 1978 to 1983 period. Obviously large krill catches occurred more frequently during this time but have rarely been made during the past 11 years.

The four highest density values were observed at the beginning of the time series. The hypergeometric distribution gives a low probability (0.001) that the four highest values occurred by chance at the beginning of the time series. Kendall's Tau correlation analysis was carried out, testing krill density versus year. The result showed a significant negative trend of the density over years (T = -0.615 , p-level = 0.0034) for the period 1978 to 1995.

These analyses however are based only on the means of the abundance indices. A method which makes use of all the data is the usual one-way analysis of variance, with year as a factor. However, because the density data depart very markedly from normality and homescedasticity, and the number of observations for each level of the year factor vary substantially, the significance levels based on the usual F test in any hypothesis testing will be inaccurate. Nevertheless, accurate tests of significance can be obtained by calculating the distribution of an appropriate test statistic over a large number of random permutations of the observed values of the dependent variable to the levels of the treatment variable (for details see Manly, 1991).

The significant level for the null hypothesis is determined from the frequency of obtaining more extreme values of the test statistic in the distribution obtained by random permutation. Such significance tests have a high level of accuracy when a full enumeration of the distribution over all permutations is undertaken. When full enumeration is not practical, the test can be made arbitrarily precise by sufficient re-sampling (500 permutations are adequate for a significance level of 0.05 and 5 000 for a level of 0.01). The approach can be extended to examine *a posteriori* contrasts in the experiment, provided, of course, that the null hypothesis of homogeneity is rejected in the overall analysis of the experiment (see Petrondas and Gabriel, 1983; Edwards and Berry, 1987).

The results of an ANOVA for the overall dataset based on 5 000 permutations are given in Table 4. The analyses of variance were calculated using the statistical package S-Plus. The null hypothesis that there is no difference between years is rejected at $P < 0.01$.

Given that the overall differences are statistically significant, the next question is which years are the main contributors to the significant year effect. This is examined by testing the following null hypothesis for each year:

$$H_0 : 12 * d_j - \sum_{i \neq j} d_i = 0$$

where d_j is the density in the year under examination, and d_i is all the other years. This results in 13 *a posteriori* tests. In multiple comparisons, the significance level has to be adjusted so that the probability of type I error is maintained at the appropriate level across the entire experiment (Winer, 1971). The adjusted significance level α' is given by:

$$\alpha' = 1 - (1 - \alpha)^{1/N}$$

where α is the significance level for the experiment-wise error rate and N is the number of comparisons to be drawn. Since there are 13 comparisons, the adjusted significance level is $\alpha' = 0.0039$ for $\alpha = 0.05$ and $\alpha' = 0.0081$ for $\alpha = 0.10$.

The results of the individual comparisons are given in Figure 3 and Table 5. Although none of the comparisons are statistically significant at the $\alpha = 0.05$ level, the years 1977 and 1981 are significant at the $\alpha = 0.10$ level.

The final analyses undertaken on the data were pairwise comparisons to determine which groups of years among the data could be classified as having homogeneous densities. In this case the test procedure was to form pairwise contrasts where the null hypothesis is given by:

$$H_0 : d_i - d_j = 0 .$$

The first test series is to compare the year in which the highest mean density occurred with each other year, from lowest to highest until H_0 is accepted. The random permutations of the data are now carried out only between the pairs of years being compared; the other data are not permuted in any way. As before, the significance

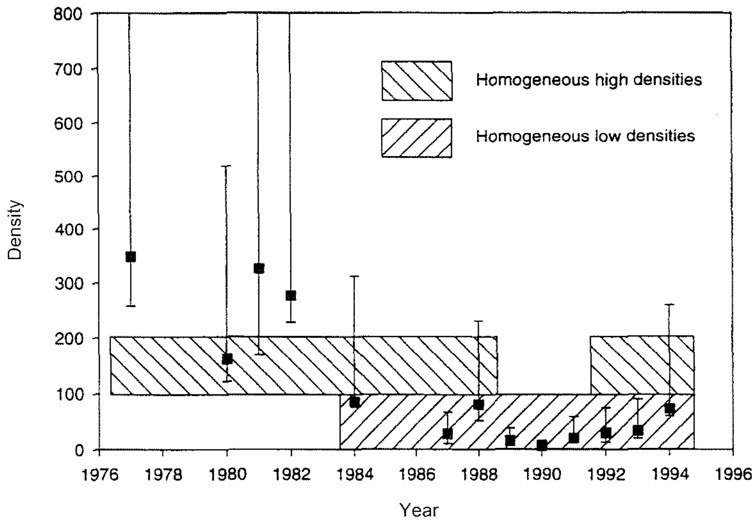

Figure 3: Results from the randomisation analyses for krill densities. The plotted mean densities and the error bars are from the bootstrap analyses. The error bars enclose the 95% confidence intervals. The hatched boxes show the years which can be homogeneously grouped.

Table 5: Analysis of variance for Elephant Island krill net haul density data for the seasons 1977/78 to 1994/95. The statistical significance is tested by random permutation of the densities from hauls among the years.

H_0: Density distributions are homogeneous across years (year taken as factor).

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	*F* Ratio	Nominal[1] Significance
Year	12	7 666 672	638 889.3	2.903	$p < 0.00062$
Error	718	158 018 102	220 080.9		

[1] This probability level is based on normal theory and is not accurate. Shown for comparison purposes only.

Table 6: Single degree of freedom comparisons to examine which years, taken one at a time, are significantly different from the remainder. Significance tests are by random permutation. Adjusted significance levels are $\alpha' = 0.0039$ for $\alpha = 0.05$ and $\alpha' = 0.0081$ for $\alpha = 0.10$.

Year under Test	*F* Value from ANOVA	Number of Permutations	Frequency of Higher *F* Value	Probability of Higher *F*	Significance
1977/78	15.068	5000	26	0.0052	~sig. ($p < 0.10$)
1980/81	0.6293	200	34	0.17	n.s.
1981/82	11.6855	5000	32	0.0064	~sig. ($p < 0.10$)
1982/83	2.0150	500	33	0.066	n.s.
1984/85	0.00005	100	99	0.99	n.s.
1987/88	0.6051	100	27	0.27	n.s.
1988/89	0.0058	100	95	0.95	n.s.
1989/90	2.4530	500	45	0.09	n.s.
1990/91	1.2587	500	57	0.114	n.s.
1991/92	1.3411	200	34	0.17	n.s.
1992/93	1.1428	100	25	0.25	n.s.
1993/94	0.9057	100	28	0.28	n.s.
1994/95	0.1415	100	78	0.78	n.s.

Table 7: Single degree of freedom comparisons to examine which pairs of years, taken two at a time, are significantly different, (a) comparing the year with highest mean density (1977/78) with the remainder, beginning with the year with lowest density, (b) comparing the year with lowest mean density (1990/91) with the remainder, beginning with the year with highest density. Significance tests are by random permutation. The comparisons are presented until H_0 (see text) is accepted. The adjusted significance level is $\alpha' = 0.0043$ for $\alpha = 0.05$.

(a)

Year under Test	*F* Value from ANOVA	Number of Permutations	Frequency of Higher *F* Value	Probability of Higher *F*	Significance
1990/91	11.982	10000	1	0.0001	Reject H_0
1989/90	11.369	10000	0	<0.0001	Reject H_0
1991/92	10.756	10000	4	0.0004	Reject H_0
1987/88	10.776	10000	57	0.0057	Accept H_0

(b)

Year under Test	*F* Value from ANOVA	Number of Permutations	Frequency of Higher *F* Value	Probability of Higher *F*	Significance
1977/78	11.982	10000	1	0.0001	Reject H_0
1981/82	9.715	10000	0	<0.0001	Reject H_0
1982/83	2.700	10000	0	<0.0001	Reject H_0
1980/81	1.809	10000	0	<0.0001	Reject H_0
1984/85	0.647	10000	117	0.0117	Accept H_0

level has to be adjusted to maintain the experiment-wise error rate at the selected level. There are 12 possible pairwise comparisons, and so the adjusted significance level is $\alpha' = 0.0043$ for $\alpha = 0.05$. The results shown in Table 6 show that across all years the higher densities can be considered homogeneous. The group of lower densities excluded are those in the three years 1989, 1990 and 1991, which form a statistically significantly different subset of densities.

The second comparison is between the year with the lowest mean density with each other year, from the highest to the lowest, until H_0 is accepted. As before, there are 12 possible pairwise comparisons. The results given in Table 7 show that across all years in the lower densities can be considered homogeneous. The group of higher densities excluded are those in the four years 1977, 1980, 1981 and 1982, which form a statistically significantly different subset of densities.

The results of these analyses are difficult to interpret. While it is clear that there is more variability in the density data than would be expected on purely statistical grounds, the precision of estimates of density from the net hauls is low. It is possible to conclude that the three low years 1989–91 represent a period of anomalously low density, but that otherwise the observed fluctuations are not statistically significant, and that, while there is evidence of a transient change, there is no evidence of a persistent change in krill density. It is equally possible to conclude that the early years 1977, 1980, 1981 and 1982 represent anomalously high densities, and that the fluctuations in the later period are not significant, which suggests that there may be a persistent change in krill density. Of course, a combined hypothesis is also supportable, i.e. that local krill abundance is subject to high degrees of variability which can cause local fluctuations in krill abundance which in turn can persist for periods of the order of three to four years or more.

The power of these analyses is likely to be low, so that the assumption that there has been no persistent change in krill density should be tempered with the caution that the statistical power of a time series of net hauls is likely to be only sufficient to detect quite gross changes in krill density. Given that there are variations in other indicators of krill abundance (e.g. the decrease in abundance of krill-dependent Adélie penguins in the area for which we have sufficient long-term information (Trivelpiece and Fraser, 1996) over this period, we favour the conclusion that krill abundance is indeed much lower during the recent years of the study period.

SUMMARY AND CONCLUSIONS

High interannual variability was observed for both R_1 and R_2 indices over the time series of the past 19 years, ranging from (almost) zero to $R > 0.75$. Comparisons between the Elephant Island area and a much larger survey area showed that the occurrence of very low krill recruitment is a recurrent and real event. Therefore, the low recruitment values must be considered when pooling estimates and calculating an overall mean proportional recruitment index.

The spatial succession of developmental stages/age groups demands complete coverage of the north-south distribution range during krill surveys. During the austral summer the distribution range is at its maximum and the Elephant Island survey grid does not completely cover this range. However, results for R_1 seem to be biased by less than 5% compared to large-scale Antarctic Peninsula surveys. Intersurvey differences occur during the same season, but are generally higher for the R_2 index than forR_1. Generally R_2 is higher than R_1, but the standard error is also much higher for R_2. The influence of a longer retention time of subadult krill in the area is discussed as a possible reason. Obviously the different developmental stages/age groups are under different water current influences and retention times.

Krill abundance shows a clear seasonal trend with highest abundance during summer (mid December to late February). This seasonal trend demands that biomass/abundance estimates for krill stocks are carried out during this time to obtain comparable results.

Results from summer surveys show high interannual variability of krill density in the Elephant Island area. Krill density was much higher during the early part of the time series (late 1970s – early 1980s) and much lower and less variable during the later part (late 1980s – early 1990s). These significant fluctuations will certainly have implications for krill predators. Reasons as well as consequences for these fluctuations are discussed elsewhere (Siegel and Loeb, 1995; Loeb et al., 1997; Trivelpiece and Fraser, 1996).

Whatever the interpretation of this particular series, the results have implications which need to be taken into account in the revision of precautionary krill catch limits. Leaving aside whether or not the results indicate a persistent change in krill density, they do at least suggest that local krill density may vary by nearly two orders of magnitude and that the effects can persist for several years. Such behaviour is not explicitly modelled in the current krill population model, and so outputs of the model should be examined to determine whether it generates fluctuations in krill biomass consistent with the observations reported in this paper. If the fluctuations generated are substantially less, the model may require modification so that the implications for precautionary krill catch limits of the fluctuations in krill density of the order of the observed scale and duration can be examined.

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