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Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability

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ABSTRACT: Between-year variability of krill *Euphausia superba* year class success and recruitment during the 1977 to 1994 period are described based on data from German expeditions and U.S. Antarctic Marine Living Resources Program cruises in the Elephant Island area. The recruitment index (R_1), based on the relative abundance of the 1+ age class, varies substantially between years, whereas it is quite similar between different surveys within the same field season. The overall mean recruitment index for all years was $R_{mean} = 0.210$. Good recruitment was observed for the 1980/81, 1985/86, 1987/88, and 1990/91 year classes; exceedingly poor recruitment occurred for the 1976/77, 1982/83, 1983/84, 1988/89, 1991/92 and 1992/93 year classes. Pairwise correlations between the stock parameters, recruitment indices, and available environmental data indicate that good and poor year class success are directly and indirectly related to sea ice conditions during the preceding winter season, the timing of krill spawning, and the occurrence of dense salp concentrations. No correlation is shown with upper water column temperature or krill stock/spawning stock size. A concept is developed describing the interactions of various parameters leading to good or poor krill recruitment.

KEY WORDS: Antarctic krill · *Euphausia superba* · Recruitment · Salps · *Salpa thompsoni* · Sea ice

INTRODUCTION

Since the early 'Discovery' expeditions, the Atlantic Sector has been described as an area where large concentrations of krill occur regularly and in higher densities than in other parts of the Southern Ocean (Marr 1962, Mackintosh 1973). Therefore, the virtual absence of krill from the South Georgia area during the 1977/78 field season, reported by British and German research cruises, was unexpected (Bonner et al. 1978, Hempel et al. 1979). The extremely low abundance of krill during this time resulted in high mortality of penguin and albatross chicks in the local populations (Croxall et al. 1988).

A similar paucity of krill characterized winter 1983, summer 1983/84 (Heywood et al. 1985) and summer 1990/91 (Everson 1992). During winter 1983 krill were rare both at South Georgia and in the waters off Elephant Island, normally a productive krill fishing ground. Speculations about the possible causes included high krill mortality rates, overfishing, and highly fluctuating stock sizes as a normal phenomenon. However, a total stock breakdown in one year and complete recovery the following year is not compatible with the species life span of 6 or more years. Overfishing can also be excluded because even higher catch rates in years subsequent to the 'bad krill years' indicated no evidence for krill stock size reduction.

Later detailed data analyses showed that the absence of krill around South Georgia and the shortage reported for Elephant Island during winter 1983 were caused by different factors. For the 1983/84 season there is strong evidence that large-scale southward airflow produced movements of the frontal structure in the northern Scotia Sea (including the South Georgia area) and the southward displacement of near surface water masses removed krill from the area (Priddle et al. 1988). This extreme atmosphericoceanographic large-scale event satisfactorily explains occasional dramatic changes in krill stock densities in South Georgian waters because here the species is living close to its northern distribution limit.

The situation is different for krill off the Antarctic Peninsula, where stock densities show less extreme between-year changes. However, strong seasonal fluctuations in krill abundance are regularly observed in this southern region, with minima in winter and maxima in summer (Siegel 1988). It was therefore suggested that the scarcity of krill *Euphausia superba* in the Elephant Island area during in winter 1983 reflected normal winter conditions when these krill disappear from open water areas and overwinter under the ice (Siegel 1988). This is supported by the fact that krill have regularly been observed under the winter ice ever since this has been researched as a krill habitat (e.g. Spiridonov et al. 1985, Kottmeier & Sullivan 1987, Marschall 1988, Stretch et al. 1988, Bergström et al. 1990). Interannual variation in stock size does occur in the Peninsula region but is overshadowed by the magnitude of seasonal abundance fluctuations (Siegel 1992).

Between-year variability in krill abundance observed in the Peninsula region during spring-summer seasons could result from conditions prevailing in a previous season. Possible reasons for changes in regional stock size of this relatively long-lived species are spawning success/failure during the preceding season and/or the survival/mortality of recruits during the winter. Indications of 'poor' or 'good' year classes (e.g. the extremely strong year class from 1980/81 which dominated the stock in 1982) were first tabled by Siegel (1989) and continued by Loeb & Siegel (1994), but this information was purely qualitative.

The present contribution concentrates on aspects of krill stock size variability associated with differences in recruitment rates derived from survey data collected in the Antarctic Peninsula area during spring and summer field seasons, 1977/78 through 1993/94. It also includes consideration of possible biological and environmental proximate causes to indicate trends in important ecosystem components which may be of relevance for krill recruitment success or failure and strengthen the possibility of formulating a well-defined hypothesis on the natural variability of krill stocks.

MATERIALS AND METHODS

Our data are derived from net sampling operations in the Antarctic Peninsula area by German expeditions and U.S. Antarctic Marine Living Resources (AMLR) Program survey cruises conducted between 1977 and 1994 (Table 1). Of the 28 surveys 21 were made during austral summer (January to March); 6 were made during spring (November to December) and 1 during late fall (May) months. Although most of these surveys covered a larger area, the sampling effort concentrated in the vicinity of Elephant Island and the area between 60° S to 62° 30' S and 52° W to 57° 30' W (Fig. 1) was sampled during all cruises. We consider here the survey data from samples collected within this 'Elephant Island area'.

Different sampling gear was used over the 16 yr period (Table 1). The German surveys (RV 'Walther Herwig', 'John Biscoe', 'Polarstern' and 'Meteor' cruises) utilized Rectangular Midwater Trawl (RMT

Table 1. *Euphausia superba*. List of krill surveys in the Elephant Island area (60° S to 62° 30' S and 52° W to 57° 30' W) during 1977 to 1994. RMT: Rectangular Midwater Trawl; BGO: Bongo, IKMT: Isaacs Kidd Midwater Trawl

Survey	Date	Type of net	No. of samples
'Walther Herwig' 1977/78	16-23 Nov 1977	RMT8	18
	1-7 Dec 1977	RMT8	15
	14-20 Jan 1978	RMT8	19
	3-8 Mar 1978	RMT8	16
'Walther Herwig' 1980/81	26 Jan-1 Feb 1981	RMT8	7
	17-28 Feb 1981	RMT8	14
	17-19 Mar 1981	RMT8	12
'John Biscoe' 1981/82	2-23 Feb 1981	RMT8	52
'Polarstern' 1982/83	13-15 Mar 1983	RMT8	12
'Polarstern' 1983/84	3-9 Nov 1983	RMT8	36
'Polarstern' 1984/85	22-30 Nov 1984	RMT8	35
'Walther Herwig' 1984/85	21-27 Feb 1985	RMT8	34
	1-18 Mar 1985	RMT8	34
'Polarstern' 1985/86	14-20 May 1986	RMT8	25
'Polarstern' 1987/88	3-5 Nov 1987	RMT8	14
'Siedlecki' 1987/88	24 Jan-3 Feb 1988	BGO	42
'Surveyor' 1988/89	15-28 Feb 1989	BGO	50
'Meteor' 1989/90	26-30 Dec 1989	RMT8	19
'Surveyor' 1989/90	6-26 Jan 1990	BGO	38
	7-22 Feb 1990	BGO	41
'Surveyor' 1990/91	21 Jan-1 Feb 1991	BGO/IKMT	42
	27 Feb-7 Mar 1991	BGO/IKMT	39
'Surveyor' 1991/92	19 Jan-2 Feb 1992	IKMT	63
	29 Feb-9 Mar 1992	IKMT	67
'Surveyor' 1992/93	18-31 Jan 1993	IKMT	71
	21 Feb-3 Mar 1993	IKMT	66
'Surveyor' 1993/94	19-28 Jan 1994	IKMT	63
	25 Feb-6 Mar 1994	IKMT	70

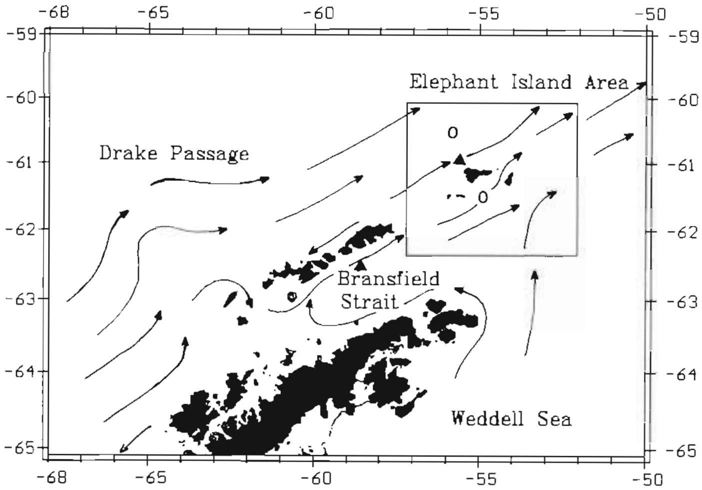

Fig. 1. The 'Elephant Island area' used for between-year analysis of krill stock composition and recruitment. Major current flows are illustrated. (○) Location of sites north and south of Elephant Island used for upper water column temperature values; (▲) location of reference sites north of Elephant Island and south of King George Island used for ice condition indices

1+8) nets (Baker et al. 1973); krill data were obtained from the RMT 8 net. The 1988 to 1990 U.S. AMLR surveys (RV 'Siedlecki' and 'Surveyor' cruises) utilized bongo nets (0.6 and 0.7 m diameter) fitted with 333 and 505 µm mesh (Loeb et al. 1993). Data from the 1991 AMLR survey was derived from a 1.8 m Isaacs-Kidd Midwater Trawl (IKMT) fitted with a multiple mesh net, grading from 2.5 to 1.2 cm, and a 1 mm mesh cod end. Material from subsequent AMLR Surveyor cruises was collected by the IKMT fitted with a 505 µm mesh Nitex plankton net.

Krill demographic analyses were based on samples recently preserved in buffered 10% formalin or from fresh or freshly frozen krill. The samples were analyzed at sea, and shrinkage of the formalin-preserved material was found to be negligible. All postlarval krill from samples with ca 150 or fewer individuals were analyzed; a minimum of 100 krill were analyzed for larger samples. Total counts were made of samples with up to ca 2000 krill; for larger samples, counts were made of the numbers of krill in two 1 l aliquots to make estimates for the entire volume of krill collected. Krill were measured with an accuracy of 1 mm (total length) and sexed and staged according to the scheme of Makarov & Denys (1981).

Calculation of the krill recruitment parameters requires quantitative length frequency data (i.e. the length frequencies adjusted to numbers per 1000 m^3). There are several potential problems in producing these data. Gear selectivity may result in under- or over-representation of the smallest age class. This source of bias is minimized by basing the recruitment index on the 1+ age class, which is the first age class that is fully represented in the larger mesh sampling nets (e.g. the RMT 8). The larval (0) age class attains a mean length of about 18 mm at the end of the first year, while the mean length of age class 1+ ranges from 24 to 28 mm during summer (Siegel 1987). Therefore, age class 0 was not considered because sizes <20 mm are under-represented in the samples (Siegel 1986). Changes in gear types over the study period undoubtedly bias the survey results. Krill size and maturity stage composition are probably not seriously affected by gear differences. Catch comparisons between RMT, bongo and IKMT nets (Anonymous 1991) indicate that gear-related differences in krill size are insignificant in relation to the large seasonal and spatial differences. Krill abundance estimates, especially those derived from the bongo net collections, are probably more seriously affected by gear type. Such bias is taken into consideration in our discussion of the results.

A second source of bias is the spatial segregation of krill age/length groups which may cause non-representative data if only a portion of the stock is sampled. This bias is minimized by the location of the Elephant Island survey area which covers the distribution range of all krill life stages and size groups from juveniles to large adults (Siegel 1988, 1989). A third potential problem affecting krill recruitment data is the patchiness of krill distribution, which causes a non-normal distribution of the abundance/density data. The effects of krill patchiness, as well as the spatial segregation of age/length groups, are reduced here through adjustments to the data obtained from each survey. A cluster analysis was performed on all stations within the survey area to determine the size and proportion of the area in which different length/maturity components of the stock occurred (see Siegel 1988 for details). The krill length frequency of each of the resulting clusters (e.g. krill length classes) was calculated as the stratified mean from individual haul data using the method of Saville (1977); this procedure takes into account the non-normal distribution pattern of abundance and also includes zero catches of krill. The data were then pooled, the density of each of the krill length classes reflecting the extent of their spatial distribution. The overall pooled length frequency distribution (Fig. 2) was then subjected to distribution mixture analysis (Macdonald & Pitcher 1979) to decompose the mixture of age/length distributions into their separate components. Recruitment indices (R_1) were based on the numerical densities at length data from random samples. Here it was only necessary to separate the first fully represented age class (1+) from the older classes (Fig. 2) because the proportion of recruits (R_1) is the ratio of numbers in this first age class to the numbers of all age classes combined according to:

$$R_1 = \frac{A_i}{\sum_{i=1}^{n} A_i} \qquad (1)$$

where A_i is the number of animals in age class i, and n is the age of the oldest individuals in the stock (de la Mare 1994).

Krill abundance (numbers per 1000 m^3) is presented as total stock density (all krill stages); spawning stock density includes sexually mature stages only (stages 3B to 3E). S_1 is the relative proportion of spawning stock to total stock minus the 1+ age class during each survey (Table 2). In this case the 1 yr old krill were excluded to reduce the effect of strong year classes dominating the overall stock size.

Various biological and physical parameters which might influence krill recruitment are considered. Among the biological parameters are an index for the proportion of advanced gravid maturity stages (stages 3C, D, E) in January and February describing early or late spawning progress and salp density (median numbers per 1000 m^3) derived from the net tows. Physical parameters include water temperature and sea ice conditions. Upper water column (0 to 50 m) temperatures were derived from conductivity, temperature and depth (CTD) casts made north and south of Elephant Island (60° 30′ S, 56° W; 61° 30′ S, 55° W) during each survey period. Seasonal sea ice conditions were derived from weekly ice charts obtained from the U.S. National Ice Center. Indices were developed for each year based on the ice conditions present at 2 reference sites, one north of Elephant Island (61° 04′ S, 55° 30′ W) the other south of King George Island (62° 30′ S, 58° 28′ W) representing more inshore waters in the Bransfield Strait.

To examine the possible relation between year class success and sea ice condition, indices were established to denote the seasonal appearance, disappearance, and duration of ice cover and ice-free conditions for each year. These indices were based on sea ice observations during 49 (7 to 9 d) periods each year and include the number of the week (e.g. 1 to 49) when persistent ice cover and persistent ice-free conditions

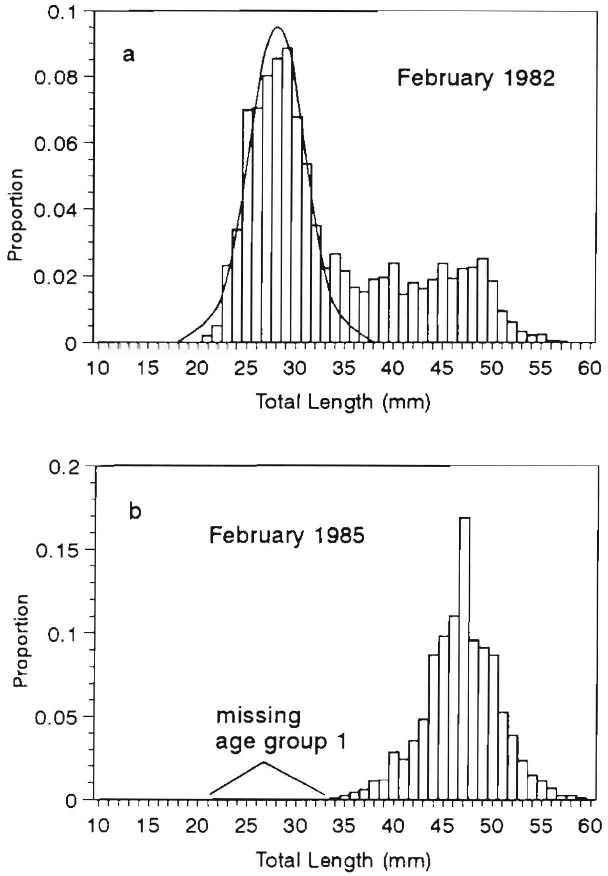

Fig. 2. *Euphausia superba*. Krill length frequency composition during years with (a) strong recruitment, age class 1+ indicated by continuous line, (b) weak recruitment

Table 2. *Euphausia superba*. Indices for krill stock and spawning stock densities and the proportion (S_1) of spawning stock to total stock excluding age group 1+. CV: coefficient of variance associated with the stock density estimate; –: representative data not available

Survey period	Stock density (no. per 1000 m^3)	CV	Spawning stock (no. per 1000 m^3)	S_1
Dec 1977	215.4	0.994	–	
Jan 1978	101.2	0.732	37.48	0.406
Mar 1978	105.3	0.653	31.13	0.305
Jan 1981	66.1	1.429	19.34	0.329
Feb 1981	54.9	1.641	13.50	0.250
Mar 1981	27.5	1.689	–	
Feb 1982	510.9	0.525	76.68	0.465
Mar 1983	90.6	1.623	32.98	0.543
Feb 1985	11.5	0.367	8.20	0.718
Mar 1985	2.2	0.241	–	
Jan 1988	20.1	0.926	7.77	0.494
Feb 1989	41.7	0.509	5.55	0.535
Dec 1989	21.4	0.348	3.47	0.250
Jan 1990	14.9	0.976	10.89	0.731
Feb 1990	9.9	0.413	7.98	0.806
Jan 1991	5.3	0.355	3.96	0.896
Mar 1991	4.2	0.566	2.77	0.705
Jan 1992	20.8	0.559	9.44	0.790
Mar 1992	29.7	0.344	8.88	0.413
Jan 1993	23.6	0.474	10.85	0.459
Feb 1993	29.6	0.368	16.92	0.571
Jan 1994	29.7	0.535	17.76	0.628
Mar 1994	28.1	0.374	18.28	0.709

were first established. For years with no ice a value of 49 was used to denote no ice development. An index of the duration of ice cover was based on the total number of weeks ice was present each year (0 for years with no ice). The duration of ice-free conditions was the total number of weeks that continuous open water conditions occurred prior to January each year. For periods of extended ice-free conditions, this index included the numbers of weeks from the previous year(s) since ice cover last occurred. This index therefore reflects possible cumulative effects from prolonged (e.g. multi-year) absence of sea ice from the survey area. Considerations were also made of ice concentration each year. Ice concentration was measured as the mean proportion of total cover during the period when ice was continuously present. One more index was established based on the product of mean ice cover and the duration in weeks, because in some years ice cover was prolonged but the concentration was rather low, which may have additive effects or different implications for krill if these parameters were only considered independently.

Because of gaps in nearly all of the parameter data sets, we were not able to utilize multivariate statistical analysis techniques across the 16 yr survey data base. Instead nonparametric pairwise correlation tests (Kendall's tau; Snedecor & Cochran 1982) were applied to the available data to elucidate trends of association between krill stock and recruitment success and environmental parameters across the survey period.

RESULTS

Stock density

Information on krill stock density from the surveys is presented in Table 3. November and May survey data are excluded from consideration because of the seasonal variation in stock density as well as the maturity stage composition during those months which is not representative of the actual composition during the typical December to March spawning period. Due to interannual variations in timing of spawning, the maturity stage information from December 1977 (extremely late start of the spawning season), and from March 1981 and March 1985 (postspawning situation), were not representative of the actual spawning stock and are also excluded. Results for the 1985/86 year-class are obtained from 2+ krill of the 1987/88 season. Analyses carried out by de la Mare (1994) indicate that results for 1+ and 2+ krill are comparable, although the separation of 2+ age group from the mixture distribution is more difficult.

Table 3. *Euphausia superba*. Krill year class recruitment index (R_1) and associated standard error (SE) values derived from survey data collected in the Elephant Island area from 1977 to 1994. *Results based on 2+ krill

Survey data source	Year class	R_1	SE
Nov 1977	1975/76	0.128	0.086
Dec 1977	1975/76	0.136	0.006
Jan 1978	1976/77	0.087	0.003
Mar 1978	1976/77	0.030	0.009
Jan 1981	1979/80	0.112	0.011
Feb 1981	1979/80	0.000	0.000
Mar 1981	1979/80	0.000	0.000
Feb 1982	1980/81	0.677	0.005
Mar 1983	1981/82	0.329	0.011
Nov 1983	1982/83	0.028	0.006
Nov 1984	1983/84	0.085	0.011
Feb 1985	1983/84	0.008	0.010
Mar 1985	1983/84	0.000	0.000
May 1986	1984/85	0.132	0.022
Nov 1987*	1985/86	0.407	0.027
Jan 1988*	1985/86	0.490	0.069
Nov 1987	1986/87	0.230	0.006
Jan 1988	1986/87	0.218	0.056
Feb 1989	1987/88	0.673	0.024
Dec 1989	1988/89	0.000	0.000
Jan 1990	1988/89	0.000	0.000
Feb 1990	1988/89	0.000	0.000
Jan 1991	1989/90	0.167	0.004
Mar 1991	1989/90	0.064	0.003
Jan 1992	1990/91	0.426	0.006
Mar 1992	1990/91	0.276	0.005
Jan 1993	1991/92	0.000	0.000
Feb 1993	1991/92	0.000	0.000
Jan 1994	1992/93	0.046	0.005
Mar 1994	1992/93	0.083	0.007

Greatest overall stock densities were encountered during the earlier part of the 16 yr study period (Fig. 3a). Highest densities (90 to 511 per 1000 m^3) occurred in December 1977 to March 1978, February 1982 and March 1983. The 1985 to 1994 period was characterized by lower overall densities. Lowest values (2 to 5 per 1000 m^3) were encountered during March 1985 and January to March 1991. The January 1988 survey and all January to March surveys from 1992 through 1994 had similar densities ranging from 20 to 30 per 1000 m^3. Spawning stock densities (Table 2) generally mirrored this trend [Kendall's tau (T) = 0.673, $p < 0.01$] with greatest values (31 to 77 per 1000 m^3) occurring in 1977/78, 1982 and 1983 and lowest values (2 to 4 per 1000 m^3) in 1991.

The proportions of spawning stock to total stock minus new recruits (S_1) were relatively low during the 1977/78, 1981, 1982, and 1988 surveys (0.3 to 0.5). Higher S_1 values (0.6 to 0.9) characterized the January to March surveys of 1985, 1990, 1991 and 1994. The

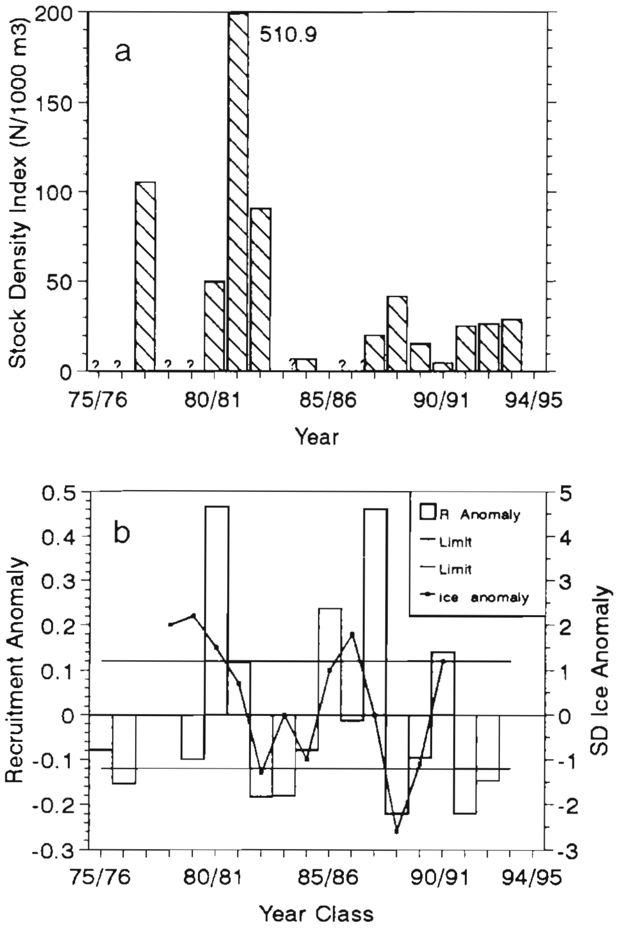

Fig. 3. *Euphausia superba*. (a) Mean overall krill stock densities in the Elephant Island area 1978 to 1994. (b) Anomalies of the long-term running mean krill recruitment index (R_1) and standard deviation of winter ice extent anomalies for the Antarctic Peninsula region (modified from Stammerjohn 1995). Mean R_1 = 0.210; horizontal lines indicate half the standard deviation of the mean ± 0.11. ?: data not available

S_1 values show a significant negative correlation with overall stock density ($T = -0.49$; $p = 0.035$) reflecting large proportions of juvenile krill when overall stock abundance was quite large (Fig. 2a).

Recruitment indices

Recruitment indices (R_1) calculated for each survey were highly variable and ranged from 0 to 0.677 (Table 2). Multiple surveys within 1 field season demonstrated similar R_1 values, indicating minimal seasonal bias in this index. The constancy of the R_1 values resulting from the 1987/88 and 1989/90 surveys is especially noteworthy since it also indicates minimal gear-related (i.e. bongo nets vs RMT 8) bias in assessment of year class success.

Interannual differences in R_1 (Table 3) reflect highly variable year class success. Recruitment anomalies from the overall mean for all years ($R_{mean} = 0.210$) are illustrated in Fig. 3b; here the range of ± half the standard deviation ($SD_{0.5} = 0.112$) is defined as the range of normal (intermediate) recruitment rates. The highest values (0.677 and 0.673) and strongest year class success resulted from the 1980/81 and 1987/88 spawning seasons. An analysis of the 2+ age/length class which was prominent in the November 1987 and January 1988 survey data sets yielded relatively high R_1 values of 0.407 and 0.490 (Table 3), suggesting strong recruitment of the 1985/86 year class. The 1990/91 spawning season also had relatively strong recruitment (mean $R_1 = 0.351$). Extremely weak recruitment resulted from the 1988/89 and 1991/92 spawning seasons, as indicated by 0 R_1 values from all surveys made the following year (Table 3). Low R_1's (<0.1) and weak recruitment also characterized the 1976/77, 1982/83, 1983/84, and 1992/93 spawning seasons. Recruitment from the remaining years 1975/76, 1979/80, 1981/82, 1984/85, 1986/87, and 1989/90 was intermediate (Fig. 3b).

Recruitment relative to krill stock and environmental parameters

The mean krill R_1 for each year showed no correlation with the previous year's overall stock density ($T = -0.135$), spawning stock density ($T = +0.045$), or the spawning stock index S_1 ($T = -0.225$; $p > 0.35$ in all cases). This establishes that for the observed stock levels there is no relationship between krill stock or spawning stock density in one year and recruitment in the next year.

Overall krill stock density showed no correlation with the mean R_1 value from the preceding year ($T = +0.22$; $p = 0.34$). From this it is obvious that low or moderate recruitment success has no major impact on the overall density of the krill stocks the following year. This results from the fact that krill stocks are cushioned against poor recruitment of limited (e.g. 1 or 2 yr) duration because of their multi-age class composition. Only in cases where there is extraordinarily high recruitment would the total stock abundance be significantly increased, like in the 1981/82 survey season. As previously noted, the largest krill stocks included in the present data base contained high proportions of age 1+ juveniles (Fig. 2a).

Seasonal variations in the timing of spawning may affect recruitment success. Krill spawn during the summer season between mid-December and March; however, there is great deal of interannual variability in the time of the major spawning effort (Witek et al. 1980, Spiridonov 1995). In our data set the years char-

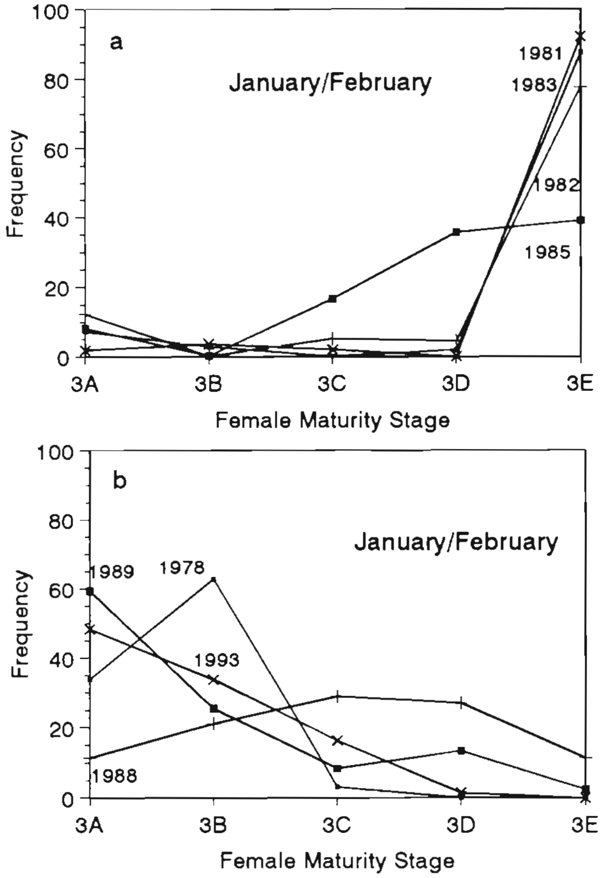

Fig. 4. *Euphausia superba*. Examples for maturity stage composition of adult female krill showing (a) early and (b) late spawning events from January/February survey periods. Stages 3C to 3E are advanced: 3C have developing ovaries; 3D are gravid; and 3E have recently spawned

Table 4. *Euphausia superba* and *Salpa thompsoni*. Biological and environmental parameters associated with krill recruitment index (R_1); mean recruitment index is based on all R_1 values available for that year class. Median salp density is derived from net tows taken during the period of larval krill development. Mean surface layer (0 to 50 m) temperature values are derived from CTD casts made at 2 reference sites north and south of Elephant Island during the January/February krill spawning season

Year class	Mean R_1	Median salp density (no. per 1000 m^3)	Mean temp. North	Mean temp. South
1975/76	0.132	344.7	–	–
1976/77	0.058	–	–	–
1977/78	–	0.1	2.09	1.00
1978/79	–[a]	–	–	–
1979/80	0.037	–	–	–
1980/81	0.677	0.0	–	–
1981/82	0.329	0.7	1.58	1.09
1982/83	0.028	–	–	–
1983/84	0.031	122.9	–	–
1984/85	0.132	12.0	3.17	1.30
1985/86	0.448	27.0	–	–
1986/87	0.224	–	–	–
1987/88	0.673	0.3	–	–
1988/89	0.000	–	–	–
1989/90	0.115	947.8	2.91	1.92
1990/91	0.351	–	1.36	1.31
1991/92	0.000	15.9	1.34	0.67
1992/93	0.064	696.2	2.91	1.36
1993/94	–	582.5	2.04	1.25

[a] Poor spawning, according to Witek et al. (1980)

acterized by large proportions of advanced female maturity stages during January (stages 3C, D, E) and February (stages 3D, E; Fig. 4) were also ones of strong recruitment success. Across the years the mean R_1 values were significantly correlated with the proportions of these advanced maturity stages ($T = +0.648$; $p = 0.015$). This suggests that late spawning periods may lead to poor larval production and/or survival.

Salps *Salpa thompsoni* were extremely abundant zooplankton components in the Elephant Island area and in the broader Antarctic Peninsula region during several of the survey years (Table 4). The large salp concentrations observed during recent years appeared to have affected the distribution, aggregation behaviour, and recruitment of krill, and it was hypothesized that this could result from competition for similar food resources (Loeb & Siegel 1994). Because of this, we examined the relation between the krill stock parameters and R_1 values and salp abundance (Table 4). Across the years for which we have salp data we found no meaningful correlations between median salp abundance and mean krill stock density ($T = -0.288$; $p = 0.245$). The correlation between salp density and coefficient of variance (CV) values associated with mean krill stock density was not significant ($T = -0.422$; $p = 0.089$). However, relatively low salp densities were associated with a wide range of CV values while the highest salp densities (e.g. >200 per 1000 m^3) were only associated with very low CV values, indicating that the relationship is not linear. Therefore, it is possible that there is a salp density threshold level above which the krill distributional attributes are negatively affected. This could be effected through disruption of krill swarm structure leading to more evenly distributed krill and a low associated CV. The R_1 values had a fairly strong negative correlation with salp abundance ($T = -0.463$; $p = 0.047$) indicating a trend for lower recruitment success with increased salp concentrations.

As indicated above, environmental factors rather than krill stock parameters may be important in affecting year class success. Potentially important variable environmental factors in the Elephant Island area are water mass influence (e.g. Bransfield Strait, Weddell Sea, and Drake Passage waters), overall temperature regimes, and seasonal sea ice cover. Different water masses and warm versus cold summer seasons could influence the distribution and abundance of the different maturity stages and possibly affect spawning success and/or larval survival. Variations in the timing of sea ice development/retreat, duration and concentration of ice cover, and duration of ice-free conditions may affect the timing and intensity of spawning and larval survival.

Integrated upper water column (0 to 50 m) temperature values measured at standard reference sites north and south of Elephant Island were used to indicate between-year differences in overall temperature regimes. Only temperature data from the mid-January/mid-February krill spawning period were used to minimize the effects of seasonal warming and cooling. Although this data set is limited, the mean temperature showed substantial variability between the years (2.2°C range north of Elephant Island). Despite this variability, no relationship was found between these values and any of the krill parameters measured during the same or the following season (all correlations showed $p > 0.2$). The observed range of temperature seems to fall within the optimum range of the species so that the summer water temperature does not appear to influence present krill densities, maturity stage development, or spawning success, nor does it appear to have a long-term influence on krill recruitment or abundance in the following season.

Table 5. *Euphausia superba*. Results of pairwise correlations between biological and environmental variables to show trends in association. n: number of paired data sets used; T: Kendall's tau; p: probability level; R_1: mean krill recruitment index for each year; Salps: median salp density; Stock: krill stock density (stratified mean no. per 1000 m^3); CV: coefficient of variance for stock density; Spawn: mean spawning stock density; Gravid: proportion of advanced krill maturity stages in January/February; El: Elephant Island region; Br: Bransfield Strait. See 'Results' for further explanations

Pair of variables	Valid n	T	p
R_1 & Salps	11	−0.463	0.047
R_1 & Gravid	9	0.648	0.015
Stock & Spawn	11	0.673	0.004
Salps & CV	10	−0.422	0.080
Salps & Gravid	8	−0.643	0.026
R_1 & Ice opening date El	12	0.462	0.037
R_1 & Ice opening date Br	12	0.615	0.005
R_1 & Ice open duration Br	12	−0.698	0.002
R_1 & Ice close duration El	13	0.520	0.013
R_1 & Ice close duration Br	13	0.474	0.024
R_1 & Ice extent Peninsula area	11	0.587	0.010
Gravid & Ice concentration El	9	0.535	0.045
Gravid & Ice concentration Br	9	0.611	0.021
Gravid & Ice concentration × Duration El	9	0.555	0.037
Gravid & Ice concentration × Duration Br	9	0.500	0.060
Salps & Ice closing date El	9	0.592	0.026
Salps & Ice closing date Br	9	0.589	0.027
Salps & Ice open duration El	9	0.535	0.044
Salps & Ice close duration El	10	−0.600	0.015
Salps & Ice concentration El	10	−0.854	0.001
Salps & Ice concentration Br	10	−0.600	0.016
Salps & Ice concentration × Duration El	10	−0.778	0.002
Salps & Ice concentration × Duration Br	10	−0.778	0.002

Pairwise comparisons of the recruitment values and ice indices from the period of larval to juvenile development resulted in significant positive correlations between R_1 and the time of ice retreat north of Elephant Island and in Bransfield Strait (Table 5), indicating increased recruitment during years with late ice retreat. Positive correlations occurred between R_1 and the duration of ice cover for both areas ($T = +0.519$, $p = 0.013$ and $T = +0.474$, $p = 0.024$, respectively), reflecting strong recruitment in the region during years of prolonged ice cover. A significant negative correlation was obtained for R_1 versus duration of ice-free conditions in the Bransfield Strait ($T = -0.698$, $p = 0.001$). The annual ice cycles around Elephant Island represent more than just local conditions; they reflect the winter ice cover extent for a much larger area extending to the west of the Antarctic Peninsula and south to the Bellingshausen Sea (Stammerjohn 1995). We used ice anomaly data from the Peninsula area presented by Stammerjohn and found a significant positive correlation between the krill recruitment index and standard deviation of the ice coverage (spatial extent) anomalies from the following winter ($T = 0.587$, $p = 0.01$). This correlation indicates strong krill recruitment success for years when spatial ice coverage/extent was well above average.

The proportions of advanced female maturity stages during January and February showed a significant positive correlation with mean ice concentration in the previous winter (Table 5). To describe possible additive effects, a parameter was established combining duration and concentration of ice cover. The proportions of advanced maturity stages also correlate with the duration of heavy ice cover prior to the spawning season especially in the Elephant Island area ($T = +0.555$, $p = 0.037$). These results lead to the conclusion that long duration of heavy sea ice cover during winter and late opening of the seasonal pack ice in spring favour earlier onset of the krill spawning season in the Peninsula region.

In contrast to the krill-ice associations, salp density in spring/summer was negatively correlated with the duration of winter ice cover and positively correlated with the duration of ice-free conditions north of Elephant Island (Table 5). Salps are components of the oceanic zooplankton community (Siegel & Piatkowski 1990) and are, therefore, most affected by ice conditions in more northerly offshore waters. Furthermore, salp density had a significant negative correlation with ice concentration in the previous winter. Salp density also showed a strong negative correlation with the combined duration and concentration of winter ice cover ($T = -0.778$, $p = 0.002$). These results strongly support the conclusion that high salp densities occur after a winter with little or no ice concentration and short (if any) ice cover duration.

DISCUSSION

The 16 yr span of the survey data indicates that stock density was generally higher, and the density fluctuations much wider, during the earlier 1977–1983 period than during 1985–1994 (Fig. 3a). Within recent years the stock density has appeared to be especially constant. The apparent dichotomy in krill stock abundance characteristics between 1977–1983 and 1985–1994 is surprising given the similar range of R_1 values within the 2 periods. One possible explanation is that the abundance changes are artifacts resulting from differences in sampling gear. However, relatively similar low stock density values resulted from both RMT 8 and bongo net samples collected during 1987/88 and 1989/90. Additionally, comparatively small stock densities during 1984/85 and 1988/89 were derived from RMT 8 samples. Another possible explanation is the sample size representing the different surveys. The earlier stock density estimates were generally derived from less than 20 samples each, while the estimates from later years were generally based on at least 40 samples. The uncertainty associated with the earlier mean stock density estimates is reflected by their large associated CV values. However, multiple surveys during the 1977/78 and 1980/81 field seasons gave relatively similar and high density estimates. Everson & Miller (1994) noted exceedingly large average catch rates by the commercial krill fishery in the Atlantic sector during the early 1980s and speculated that they may have been associated with recurring krill 'superswarms' during those years. These considerations suggest that relatively large krill stocks did indeed occur during the earlier years and that these larger densities must have resulted from something other than what is reflected by the recruitment indices from that period. Possible reasons for this include higher primary productivity levels supporting larger krill stock densities, higher immigration rates from other areas, and/or longer retention time in the area due to long-term or large-scale hydrographic conditions. None of these parameters was surveyed on a long-term basis, and no information is available in the literature that changes occurred over a longer time period.

Analysis of the survey data set established the independence of stock density and recruitment from the preceding season except for those years where recruitment was extraordinarily high. On the other hand, recruitment was found to be independent of both total stock density and spawning stock density. From these latter results is obvious that for the stock levels observed there is no direct relationship between stock size and eventual recruitment.

From our results it is obvious that krill recruitment is highly variable. In some years the density of the 1 yr old age group was extremely low. One may think of pulses of juveniles drifting through the area and missed during the survey time. However, repetitive surveys during 1 season show very similar results. Furthermore, the Elephant Island area was only part of a large-scale survey, covering the upstream region as well. Since the stock composition was the same in this large-scale region, the absence of 1 yr old krill can be regarded as a realistic phenomenon. Large variation of the same magnitude in recruitment rates were also reported by de la Mare (1994) from the Indian Ocean sector. However, the results of the Indian Ocean do not correspond with our findings from the Atlantic sector. De la Mare (1994) calculated $R_1 = 0.001$ for the year class 1980/81, while this was the strongest observed recruitment ($R_1 = 0.677$) in the Atlantic. The year class 1983/84 was known to be extremely poor in the Atlantic ($R_1 = 0.031$) but well established in the Indian Ocean ($R_1 = 0.528$). It is unknown if a spatial separation of krill size groups like that which is found in the Atlantic also occurs in the Indian Ocean and if the Indian Ocean surveys always covered the same geographical area; if not, they might have missed part of the krill stock in some years. Further analysis is needed, before we can accept an indication of an inverse relationship between these 2 areas.

Our measurements on ice condition parameters obtained from 2 reference sites reflected conditions in the larger Antarctic Peninsula region during 1978 to 1991 (Stammerjohn 1995). Stammerjohn reported an oscillation of ice coverage/extent in the Bellingshausen and Antarctic Peninsula regions from above average to below average values on time scales of a few years. The Peninsula region had above average ice coverage from 1979 to 1983 and from 1986 to 1988; below average ice coverage occurred there from 1983 to 1986 and from 1988 to 1991 (Fig. 3b). For the Southern Ocean as a whole interannual trends in regional sea ice variability are averaged out. For example, from 1982 to 1987 there were more years with below mean than above mean ice coverage in the Weddell Sea region, whereas an opposite trend occurred in the Ross Sea region. The net result of such oscillations is no evident interannual trend in sea ice coverage for the Southern Ocean

(Stammerjohn 1995). Given the strong association between krill recruitment success and sea ice conditions, it is quite likely that krill recruitment varies regionally within the same year and that a uniform recruitment pattern may not be expected for the entire Southern Ocean. Therefore, determination of krill recruitment rates should only be carried out on a regional scale (e.g. Antarctic Peninsula, Weddell Sea, Ross Sea or Bellingshausen Sea).

The significant correlations between krill biological parameters, salp abundance, and ice condition indices are established on different levels of interaction. Some parameters are directly linked with krill recruitment; others are indirectly related. To facilitate an overview of all the significant correlations a concept is developed which describes the various interactions leading to good or poor krill recruitment (Fig. 5).

Our results show that ice concentration and duration of ice cover during winter directly influence salp abundance the following spring and summer seasons. If ice concentration is high and of long duration, then salp density can be expected to be relatively low. Salps are facultative phytoplankton filter feeders and are not able to use the ice algae resource. Development of high spring/summer salp densities is probably dependent on sufficient food resources during early spring, allowing rapid early reproduction and a prolonged period of population growth. Dense and prolonged ice cover cause a delayed seasonal peak of phytoplankton production (El-Sayed 1988) and thus provide suboptimal conditions for salp population growth.

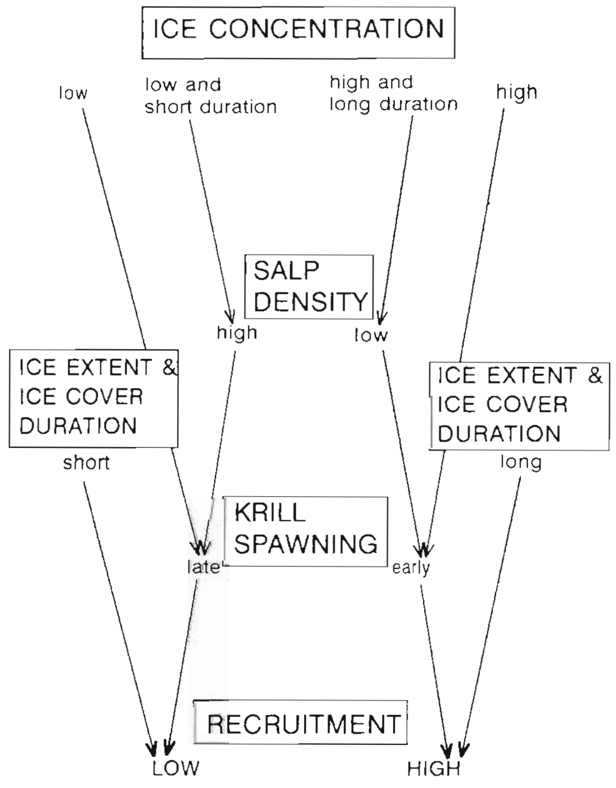

Fig. 5. *Euphausia superba*. Concept of the relationships between krill recruitment and sea ice parameters, timing of krill spawning, and salp abundance. (See 'Results' and Table 5 for further details)

In contrast to salps, extensive and long duration ice conditions favor krill maturation (Fig. 5). Dense winter ice concentrations apparently promote early female gonadal development and spawning. Krill undergo a seasonal shift from phytoplankton feeding in spring and summer to grazing on ice algae in winter (Spiridonov et al. 1985, Kottmeier & Sullivan 1987, Marschall 1988, Stretch et al. 1988, Bergström et al. 1990). During winters with low concentration and short duration of ice cover there may be insufficient food supplies for krill to satisfy their energy requirements and to initiate early gonadal development. At the same time, salps may act as strong competitors for limited food resources before the onset of the phytoplankton bloom. Krill gonadal development would then be negatively affected and postponed.

The final step in Fig. 5 is the success or failure of krill recruitment. Early seasonal maturity development and spawning by adult krill could result in high recruitment the following year through 2 means: increased spawning success and increased larval survival. Greater spawning success may be associated with early versus delayed spawning. Early spawning may be an indication of favourable environmental conditions including sufficient food supplies for both the adults and larvae; late spawning may occur when the females cannot fulfill the energetic cost of reproduction before late in the season. Under favorable circumstances krill reproduction is characterized by multiple spawning and high fecundity, whereas under less than optimal conditions fecundity may be significantly lower or reproduction may not occur at all (Quetin et al. 1994). Early spawning permits larval growth and development over a much longer portion of the summer season than late spawning. The resulting larvae would be in more advanced stages and presumably in better condition to survive food-limited winter conditions (Ross & Quetin 1989). Early spawning would also allow production of multiple batches of larvae during the period when sufficient food resources are available to the first feeding stages (Quetin & Ross 1991).

It appears that the survival/mortality rate of the 0 age group over winter is the dominating proximate cause of recruitment success/failure because, aside from the timing of krill spawning, the subsequent winter ice conditions are directly correlated to the recruitment rate. Long ice cover duration and large ice extent result in a high recruitment rate. Our findings confirm the observation of Kawaguchi & Satake (1994) that abundance of small krill in the Japanese krill fishery is very high after a season of heavy ice cover. *In situ* observations suggest that the winter sea ice may serve as an important nursery/feeding ground not only for larger krill but also for larval stages (Kottmeier & Sullivan 1987, Hamner et al. 1989, Daly 1990). Additionally, studies of the physiological condition of larval krill collected in winters characterized by light and heavy ice showed that the heavy ice favored higher lipid contents, higher condition factors and growth compared to the light ice conditions (Quetin et al. 1994). Dense and long ice cover may therefore establish the basis for a minimum, but necessary, food resource for larvae to survive the winter and reduce the risk of starvation and increased mortality. Prolonged ice cover may also protect the stock from strong predation and lower mortality rates. The cumulative effects of these possibilities result in high krill recruitment.

On a short-term basis the krill stock size is not greatly influenced by recruitment success or failure of a single year class because the effect is buffered by the multi-year age stock structure. Exceptions to this occur in extreme years, like the 1981/82 season, when the incoming year class is exceedingly strong. However, given a sequence of 3 or more years with reduced winter ice cover, ice extent, ice concentration and reduced recruitment, a dramatic gradual decline in krill stock size must be expected. With the oscillation back to a 2 to 3 yr period of heavier than average ice conditions, krill have the opportunity to rebuild the stock size, benefiting from improved feeding conditions and early spawning after the first winter season and improved larval and juvenile survival during the second and subsequent winter seasons. Given sufficient duration and concentration of the ice during the second winter, a successful year class could result, greatly augmenting the overall stock size. Such oscillations in ice coverage and duration, and associated fluctuations in krill and salp population size, most likely have occurred at varying frequencies throughout the evolution of the Antarctic marine ecosystem.

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