

# Demographic studies of Antarctic krill *Euphausia superba* in the Cooperation and Cosmonaut Seas (Indian sector of the Southern Ocean)

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**ABSTRACT:** The reproductive state and size composition of *Euphausia superba* Dana collected in the Indian sector of the Southern Ocean from 1985 to 1990 were analyzed to estimate its growth, life span and mortality rates. The life span of *E. superba* exceeded 5 yr in the Cosmonaut Sea and 6 yr in the Cooperation Sea. Assuming growth for only 180 d per year, growth rates ranged from 0.120–0.133 mm d<sup>-1</sup> during the first year of life to 0.019–0.022 mm d<sup>-1</sup> during the fifth year. Von Bertalanffy growth curves calculated for different areas are similar to those obtained by Australian researchers in the Prydz Bay region for 1981 to 1985. In mid summer, *E. superba* of age 2+ to 4+ were predominant in all hauls made south of the Antarctic Divergence, while north of the Divergence the krill were clearly dominated by individuals of age 4+. The coefficients of natural mortality (*M*) of *E. superba* in the Indian sector of the Southern Ocean, calculated by the methods of Alverson & Carney, Richter & Efanov and Beverton & Holt, varied from 0.72 to 0.87, from 0.52 to 0.57 and from 0.76 to 2.92, respectively. The value of age-dependent natural mortality of *E. superba* derived using Zikov & Slepokurov's method ranged from 0.52 during the maturation period to 1.1–2.41 during the first and last years of life. Based on long-term observations, the relationship between *E. superba* age composition and its spawning success is examined for the coastal areas of the Cooperation and Cosmonaut Seas.

**KEY WORDS:** *Euphausia superba* · Krill · East Antarctica · Growth · Life span · Mortality rates

## INTRODUCTION

During the last 2 decades, intensive studies on Antarctic krill have produced a large volume of data on its distribution, biology and role in the Southern Ocean ecosystem. Most of the studies on the biology and ecology of Antarctic krill have traditionally been carried out in the Atlantic sector of the Southern Ocean, while little data is available from other regions of this circumpolar ocean (Miller & Hampton 1989, Makarov & Spiridonov 1993). For 14 yr (1977 to 1990), YugNIRO (Southern Scientific Research Institute of Marine Fisheries and Oceanography, Kerch, Ukraine) has carried

out research cruises in the Prydz Bay region (Cooperation Sea, East Antarctica) and adjacent areas to the north of this (e.g. Aseev 1983, 1990, Samyshev 1991). The Prydz Bay region has also been the focus of numerous investigations during the international BIOMASS (Biological Investigations of Marine Antarctic Systems and Stocks) Programme (Williams et al. 1983, 1986, Ikeda et al. 1984, 1986, Miller 1986, Hosie et al. 1987, 1991). However, despite the contribution of the BIOMASS programme, studies on krill demography carried out in East Antarctica are limited compared to other regions of the Southern Ocean (Hosie et al. 1988, Miller & Hampton 1989, Makarov & Spiridonov 1993). With the possibility of an imminent resumption of krill fisheries in the Cooperation Sea, it is necessary to obtain reliable estimates of important population parameters such as distribution, density, mortality, produc-

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tion, growth and age in order to apply successfully management strategies.

A common feature of the large-scale distribution of *Euphausia superba* Dana is the increase in density in 2 different zones of the Southern Ocean, designated as the southern and northern zone (Makarov & Spiridonov 1993). The southern circumpolar ring of high krill density is restricted to the zone of the Antarctic Coastal Current (East Wind Drift), north of the shelf edge and above the upper part of the continental slope. The northern zone of high krill density is connected with areas where waters characteristic of high latitudes are mixed with waters of the Antarctic Circumpolar Current. This zone is not as continuous as the southern one (Makarov & Spiridonov 1993) but is distinctly identified within the Weddell and Ross Sea gyres (Marr 1962, Mackintosh 1972), and may also be observed in the Bellingshausen, Lazarev, Riiser-Larsen, Cosmonaut, Cooperation and Dumont D'Urville seas around the Antarctic Continent (Makarov & Sysoeva 1983, Williams et al. 1983, 1986, Iganake et al. 1984, Hampton 1985, Miller 1986, Shirakihara et al. 1986, Bibik et al. 1988, Pakhomov 1993). Makarov & Spiridonov (1993) have concluded that some characteristics of the life span of krill are very different in the different regions and vary from year to year, in response to environmental conditions.

Despite its recognized importance, the population structure of *Euphausia superba* in the Southern Ocean is still poorly understood. It has been suggested that areas of steady, cyclonic water circulations around the Antarctic Continent (Treshnikov 1964) may constitute areas inhabited by different and separated (self-maintaining) populations of *E. superba* (Makarov 1972, Maslennikov 1980, Maslennikov & Solyankin 1980).

Data on the distribution of larvae, on the interannual fluctuations in krill age-size composition and on the infection of individuals with protozoan parasite indicator species (i.e. gregarines) allowed Dolzhenkov et al. (1987) to formulate a general model on the krill population structure and movements within the Southern Ocean. This hypothesis suggests the co-occurrence of one simple and one more complex population of *Euphausia superba* around the Antarctic Continent. The first population would inhabit only the eastern part of the Indian sector of the Southern Ocean (Mawson and Dumont D'Urville Seas), while the second population would be distributed throughout the rest of the Southern Ocean and would consist of at least 4 subpopulations. These

subpopulations would inhabit the Weddell Sea, the Riiser-Larsen and Cosmonaut Seas, the Cooperation and Davis Seas, and the Somov and Ross Seas.

From analyses of the size-frequency distribution of *Euphausia superba*, Latogursky et al. (1990) concluded that the reduction in the number of age groups in the northern parts of the eastern Antarctic supports the hypothesis of an advection of krill from the west. These krill are likely to originate in the Weddell Drift and may reach the Cosmonaut Sea (Latogursky et al. 1990, Danilov & Guretsky 1993). Latogursky et al. (1990) distinguished 3 groups of Antarctic krill: the Weddell Sea group, the Bellingshausen Sea group and a coastal group. However, based on biochemical and genetic data, Fevolden (1988) and Fevolden & Schneppenheim (1989) concluded that a single, genetically homogeneous population of *E. superba* occurs around the Antarctic Continent. This would be explained by an extensive gene flow between the major areas of krill distribution, facilitated by the main Southern Ocean currents.

The aim of this work is to present some results on the different demographic parameters of krill in the Indian sector of the Southern Ocean using data on sex and size composition of the krill groups collected during long-term observations, from 1985 to 1990.

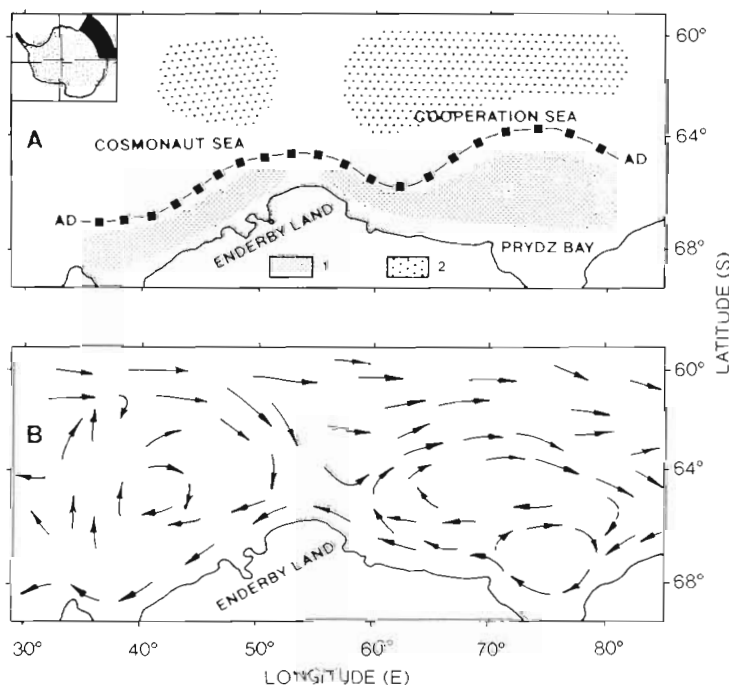


Fig. 1. (A) Position of the sampling areas and (B) the general surface circulation in the Indian sector of the Southern Ocean. Adapted from Treshnikov (1964), Bibik et al. (1988), Danilov & Guretsky (1993). 1: southern sampling area; 2: northern sampling area; AD: Antarctic Divergence

## MATERIALS AND METHODS

Krill samples were collected in the Cooperation Sea (south of 60° S and between 55 and 85° E) during the period 1985 to 1990 and in the Cosmonaut Sea (south of 60° S and between 30 and 50° E) during the period 1987 to 1990 (Fig. 1A). The subdivision into northern and southern zones was made in relation to the general position of the Antarctic Divergence (AD) as determined from hydrographic observations (Fig. 1A). Sampling was conducted during February of each year in the Cooperation Sea (with the exception of 1988 when data from January in the northern area was used) and March of each year in the southern Cosmonaut Sea. A single data set was collected during April 1989 in the northern part of the Cosmonaut Sea.

Catch data from Isaacs-Kidd trawls (mouth area  $\approx 6 \text{ m}^2$ , mesh size  $\approx 4.5 \text{ mm}$ ) and Samyshev-Yevdokimov trawls (mouth area  $\approx 30 \text{ m}^2$ , mesh size  $\approx 5 \text{ mm}$ ) were analyzed. A total of 43 horizontal and oblique trawls in the Cosmonaut Sea and 250 in the Cooperation Sea were undertaken from the surface to ca 200 m

throughout the daily cycle. All tows were completed at a speed of 1.5 to 3.5 knots. The hauling time ranged from 10 to 30 min. Catches were subsampled and examined on board, with ca 100 krill from each haul randomly selected and analyzed. Krill length measurements were taken from the tip of the rostrum to the end of telson, with an accuracy of ca 1 mm. Biological analyses were carried out in accordance with the procedures described by Makarov et al. (1982). Following this method, the condition of the female reproductive system was assessed and postlarval developmental stages were differentiated (Table 1).

Altogether, 4128 *Euphausia superba* individuals from the Cosmonaut Sea and 20463 individuals from the Cooperation Sea (no subdivision into males and females) were analyzed for the length distribution. Preliminary estimates of means, standard deviations and relative proportions were carried out using the probability-paper method of Harding (1949). These values were then used in the distribution-mixture analysis employing the computer programme of MacDonald & Pitcher (1979) on an IBM PC. If the observed

Table 1. *Euphausia superba*. Reproductive stages defined according to Makarov et al. (1982) and Makarov & Denys's (1981) method

Stage according to Makarov et al. (1982)	Description	Equivalent to stages of Makarov & Denys (1981)
<b>Juveniles</b>	Secondary sexual characteristics are not visible	1
<b>Females</b>		
Stage 2	Developing thelycum present but not fully coloured and sometimes bears spermatophores. Ovary always present but not fully developed. All oocytes are transparent, though different in size	2b-3a
Stage 3	Thelycum fully developed and red. It usually bears spermatophores. Ovary larger than in stage 2, thorax may be slightly swollen. The cytoplasm of all or part of the oocytes is not transparent but nuclei are visible in the form of light small disks	3c
Stage 4	Thelycum fully developed and brick red. It usually bears spermatophores. Ovary fully expanded filling the whole thoracic space as well as the dorsal regions of the first and second abdominal segments. The thorax and first 2 abdominal segments are swollen. Ovary bears large, not transparent, oocytes with faceted contents	3d
Stage 5	Thelycum fully developed but may be slightly diminished and faint coloured, often without spermatophores. Thorax and first 2 abdominal segments swollen but no enlarged ovary is visible through the integument. The internal body cavities are empty, the eggs having been laid. A small ovary is situated in the middle of this space	3e
<b>Males</b>		
Stage 2	Developing petasma visible but not fully developed. Petasma with the middle and inner lobe not exceeding the length of the auxiliary lobe. There is no wing present	2a
Stage 3	Petasma fully developed. No fully formed spermatophores within the ejaculatory ducts	3a
Stage 4	Petasma fully developed. Ejaculatory ducts red and clearly visible through the gills. Fully formed spermatophores present within the ejaculatory ducts and are easily ejected by exerting pressure on the ducts	3b
Stage 5	Petasma fully developed but faint coloured. Spermatophores absent within the ejaculatory ducts	—

and computed distribution was not significant at the 5% level ( $p < 0.05$ ), the number of age groups was decreased with purpose of reducing the chi-squared value to a significant level. The Macdonald & Pitcher approach was designed to identify the maximum probability estimates from pooled data and to allow a more objective interpretation of modal values from overlapping size groups. It was assumed that size groups mixed in pooled data sets are normally distributed. Previous studies suggest that *E. superba* has a distinct seasonal spawning period and, consequently, a relatively narrow time of recruitment (Miller & Hampton 1989). Juveniles of *E. superba* are regarded as a single age group (1+) with a normal distribution (Ettershank 1985, Siegel 1987, Hosie & Stolp 1989). Subsequently, after much research (Ivanov 1970, Aseev 1983, Ettershank 1984, Siegel 1987), it was concluded that the size distributions of older krill follow the same pattern and are also normally distributed. Therefore, the modal peaks identified by the Macdonald & Pitcher method should represent year classes (called age groups). The separation of the 2 oldest age groups is more difficult since older stages are usually encountered less frequently than younger ones and also because they may overlap with the tail of preceding length/age classes. The possibility of body shrinkage further complicates the separation. In this study, it was, therefore, assumed that the age of the last group under consideration was equal to the maximum age of the bulk of the krill group in this region.

Since the degree of isolation of the krill group within the areas under investigation was unknown, the age-averaged natural mortality coefficients ( $M$ ) of *Euphausia superba* were estimated employing standard ichthyological methods:

$$\text{Alverson \& Carney (1975): } M = 3k/e^{t_m k} - 1 \quad (1)$$

where  $k$  is the coefficient of catabolism in the differential form of the von Bertalanffy growth equation, and  $t_m$  is the age corresponding to the biomass peak of a population. According to Babajan et al. (1984)  $t_m$  is equal to ca 0.38 of the estimated life span,  $T$ .

$$\text{Richter \& Efanov (1977): } M = 1.521/t_n^{0.72} - 0.155 \quad (2)$$

where  $t_n$  is the age at which 70% of individuals mature for the first time (Babajan et al. 1984).

$$\text{Beverton \& Holt (1956): } M = k(L_\infty - L_t)/(L_t - L_m) \quad (3)$$

where  $L_m$  is the minimum length of individuals fully represented in net catches;  $L_t$  is the mean length of individuals in the size range from  $L_m$  to the maximum length represented in catches;  $k$  and  $L_\infty$  are both parameters of the von Bertalanffy equation. The first size group entirely represented in the catches was assumed to be the one that follows the group with the maximum

relative abundance (Beverton & Holt 1956, Babajan et al. 1984).

For the calculation of age-dependent natural mortality rates, Zikov & Slepokurov's (1982) approach was used. This is based on the relationship between the natural mortality coefficient ( $M$ ) and age ( $t$ ). From the definition of the rate of natural loss, or annual extinction (survival) rate ( $\Theta = 1 - e^{-M}$ ), it is possible to derive a relationship between  $\Theta$  and age. This relationship can best be expressed by a U-shaped curve where the highest mortality rates coincide with the first and last years of life of the krill. During the period of maturity, mortality parameter values are close to their minima and remain relatively constant for some time. Peaks in the mortality curve may be displaced to asymmetric positions. Using the ratio  $t_n/T$  as an index of the asymmetry of the curve, it is possible to show that when  $t_n/T < 0.5$  the peak of the curve is shifted to the left, while when  $t_n/T > 0.5$  the peak is shifted to the right. When  $t_n/T = 0.5$ , the peak is symmetric to a value of  $T/2$ . Hence, if maturation takes place at an age  $t_n = 0.5T$ , the curve of the rate of annual extinction of a population or stock ( $\Theta$ ) may be described analytically by a parabolic equation. The dependence of  $\Theta$  on the age ( $t$ ) is approximated by:

$$\Theta = at^2 + bt + c \quad (4)$$

where  $a$ ,  $b$  and  $c$  are constants. When  $t = 0$  and  $t = T$ , the maturity remains maximal and  $c$  is equal to 1. Theoretically, this means 100% birth mortality, but even when just born, crustaceans already have some length and, correspondingly, some age (egg development time). Thus, the initial age will be close to but not equal to zero, and mortality will be close to but not equal to 1.

The constants  $a$  and  $b$  can be determined from the following:

$$\begin{aligned} \Theta_T &= aT^2 + bT + 1 \\ \Theta_n &= at_n^2 + bt_n + 1 \end{aligned} \quad (5)$$

where  $\Theta_T$  is the mortality coefficient at age  $T$  ( $\Theta_T = 1$ ) and  $\Theta_n$  is the mortality coefficient at age  $t_n$ . To solve Eq. (5), it is necessary to determine the value of  $\Theta_n$ . Owing to the lack of sufficient experimental data, only a theoretical value for  $\Theta_n$  was determined. Richter & Efanov (1977) have suggested that the relationship between the age at maturation and the coefficient of natural mortality  $M$  [ $M = -\ln(1 - \Theta_n)$ ] at this age can be derived from Eq. (2). The  $t_n$  values were estimated from the literature. Siegel (1987) has shown that krill within the Antarctic Peninsula region are mature at a length class of 35 (age 2+) to 45 mm (age 3+). Hosie et al. (1988) reported for the Prydz Bay region that the smallest matured males and females were 39.4 and 39.2 mm in length, respectively. Similar results for the same area were obtained by Miller (1986) who calcu-



Table 2. *Euphausia superba*. Mean length and standard deviation of various age groups from the southern (March 1987 to 1990) and northern (April 1989) parts of the Cosmonaut Sea, calculated by mixture analysis (Macdonald & Pitcher 1979)

Age group	March 1987	March 1988	March 1989	March 1990	March 1987–1990	April 1989
1+	28.0 ± 2.70	30.6 ± 2.12	25.7 ± 3.01	29.0 ± 3.50	28.3	27.8 ± 3.80
2+	37.5 ± 4.37	–	32.8 ± 3.15	37.0 ± 3.00	35.8	40.7 ± 3.30
3+	48.3 ± 3.15	44.1 ± 4.01	40.9 ± 4.28	42.5 ± 3.50	44.0	49.3 ± 3.51
4+	–	–	49.2 ± 2.96	52.0 ± 4.00	50.6	55.0 ± 2.32
No. of ind.	800	563	296	2160		307
$\chi^2$	10.2	10.7	9.5	10.6		11.7
df	18	17	16	19		18

lated the regression of maturity stage versus body length for both sexes. Aseev et al. (1988) estimated that in the Cooperation Sea the length at which 70 % of individuals mature ( $l_n$ ) ranges from 41 to 43 mm. In the southern Cosmonaut Sea  $l_n$  was ca 40 to 42 mm, while in the region north of the Antarctic Divergence it reached a level of ca 44 mm. These values were used for the calculation of  $t_n$  according to the krill linear growth equation:

$$l = pt^q \quad (6)$$

where  $p$  and  $q$  are constants;  $l$  and  $t$  are krill length and age, which were obtained using Macdonald & Pitcher mixture analysis. From this it follows that:

$$t = (l/p)^{1/q} \quad (7)$$

Substituting  $\Theta_T = 1$ ,  $T$  and  $t_n$  in Eq. (5), a set of equations for the dependence of mortality on krill age is

obtained. Thus, the dependence of natural mortality on krill total length can be expressed by:

$$\Theta = a(l/p)^{2/q} + b(l/p)^{1/q} + 1 \quad (8)$$

## RESULTS

### Age composition and reproductive stage

**Cosmonaut Sea.** At least 4 age groups (excluding larvae), corresponding to 5 yr of life, were distinguishable in the curves of krill size distribution for the period 1987 to 1990, south of the AD (Table 2). Length ranged from 18 to 60 mm (Fig. 2). Two cohorts (krill hatched in 1985 and 1987) were clearly identified during the period of the investigation (Fig. 3, Table 2).

In the northern Cosmonaut Sea, krill length ranged from 26 to 64 mm in 1989 (Fig. 2) and, as for the south-

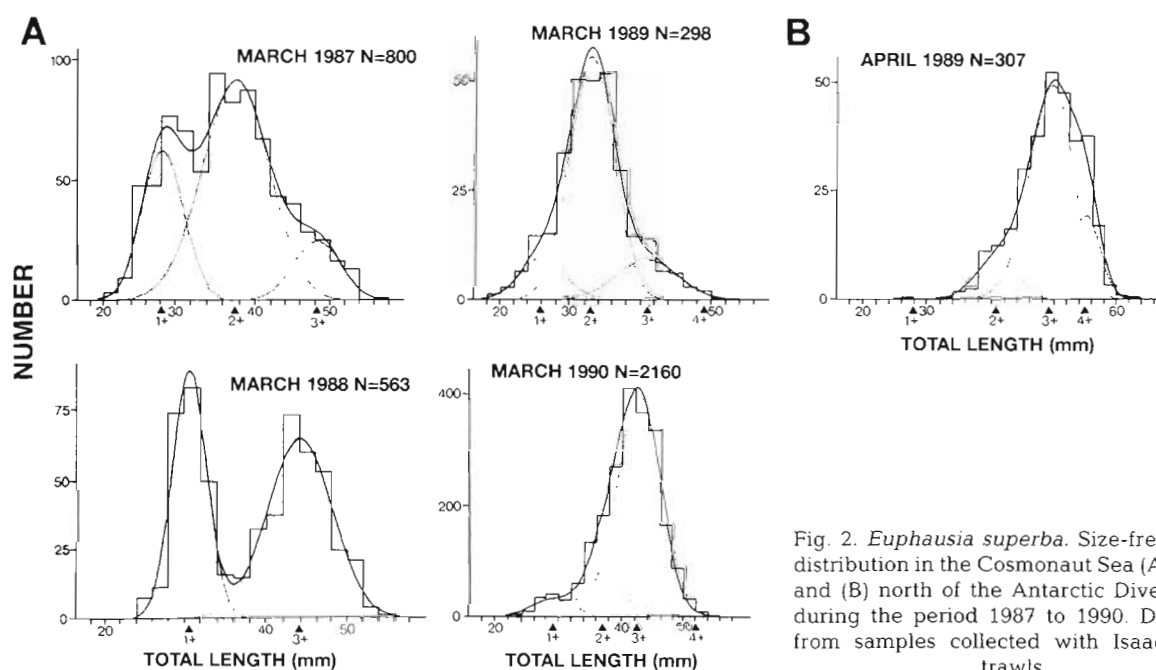


Fig. 2. *Euphausia superba*. Size-frequency distribution in the Cosmonaut Sea (A) south and (B) north of the Antarctic Divergence during the period 1987 to 1990. Data are from samples collected with Isaacs-Kidd trawls

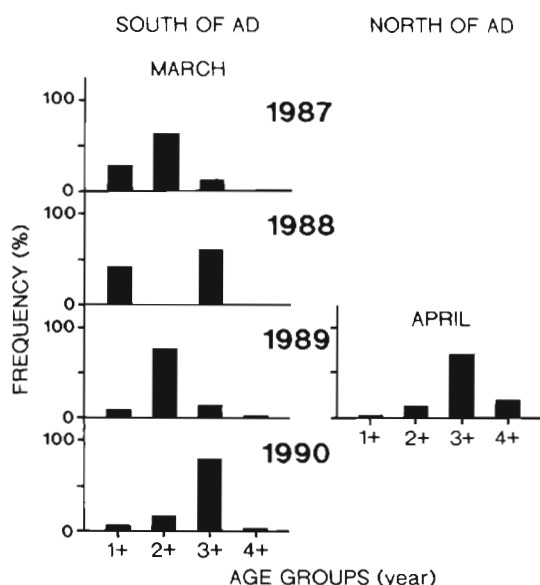


Fig. 3. *Euphausia superba*. Age distribution in the Cosmonaut Sea for the period 1987 to 1990

ern group, a life span of ca 5 yr was estimated (Table 2). The mean sizes of 2+ to 4+ age groups were 1 to 8 mm larger than those in the corresponding age classes of the southern group. Krill age distribution in the north was characterized by a marked predominance (69.7 %) of specimens of age 3+ (krill hatched in 1986).

The reproductive state of the southern group was characterized by a predominance of gonad maturity stage 2 in all years. Individuals of maturity stage 3 were abundant only in 1990 (19 % of males and 24 % of females; Table 3). The proportion of mated females never exceeded 13 %, and generally ranged from 0.2 to 9.7 %. Despite a high proportion of immature specimens north of the AD (18 % of males and 21 % of females at stage 2), a substantial number of individuals were ready to spawn (26 % of males and 17 % of females at stage 4). Approximately a quarter of the females (25.6 %) carried spermatophores.

**Cooperation Sea.** In the catches of 1985 to 1990, individual length ranged from 9 to 63 mm in the southern, and between 10 and 62 mm in the northern area (Figs. 4 & 5). At least 4 age groups were identifiable in the southern part of the Cooperation Sea, while 5 age groups were recorded in the northern, open oceanic part of this sea (Tables 4 & 5, Fig. 6). If the larval stages are included, a life span of no less than 5 yr for the south and 6 yr for the north could, therefore, be expected.

In the southern part of the Cooperation Sea catches were dominated in 1985 by individuals hatched in 1982, while during 1986 krill hatched in 1982 and 1983 were represented in equal proportions. The age structure during 1987 was fairly uniform. However, krill hatched in 1985 formed the bulk of the 1988 catches. Age classes 2+ and 3+ (hatched in 1986 and 1987) were the most abundant in 1989 and 1990 (Fig. 6). Unlike for the southern group, age distribution in the north (where all classes occurred) was almost always dominated by age 4+, and only once by 3+ (Fig. 6).

The reproductive state of krill was also different in the northern and southern groups, with northern specimens generally being in a more advanced stage of maturity than those in the south (Table 6).

### Growth rates

The von Bertalanffy growth curves calculated from data in Tables 2, 4 & 5 are presented in Fig. 7. The theoretical asymptotic length ( $L_{\infty}$ ) of the southern group is 60.1 and 59.1 mm for the Cooperation and Cosmonaut Seas, respectively. In the Cooperation Sea, individuals with a maximum length of 63 mm were observed only during February 1990. During other years, maximum length never exceeded 61 mm (Fig. 4). In the Cosmonaut Sea south of the AD, the maximum length observed was 60 mm (Fig. 2). The asymptotic length of individuals from the northern Cooperation Sea was 61.3 mm ( $L_{\max}$  observed in the samples of February 1985 to 1990 was 61 mm), while in the Cosmonaut Sea

Table 3. *Euphausia superba*. Percentage of krill at each reproductive stage in the Cosmonaut Sea in March, 1987 to 1990

Area	Year	Juv.	Males				Reproductive stage:				Proportion of mated females
			2	3	4	5	2	3	4	5	
South of AD	1987	14.9	35.1	0.4	0.4	–	45.1	4.1	–	–	9.7
	1988	26.9	20.9	1.1	1.1	–	44.2	1.1	0.7	4.0	12.9
	1989	6.9	46.9	1.5	0.9	0.4	31.1	12.2	–	–	0.2
	1990	3.5	26.7	18.6	1.2	–	26.0	23.6	0.3	–	5.0
North of AD	1989	–	18.3	3.6	26.1	2.0	20.7	11.1	16.6	1.6	25.6

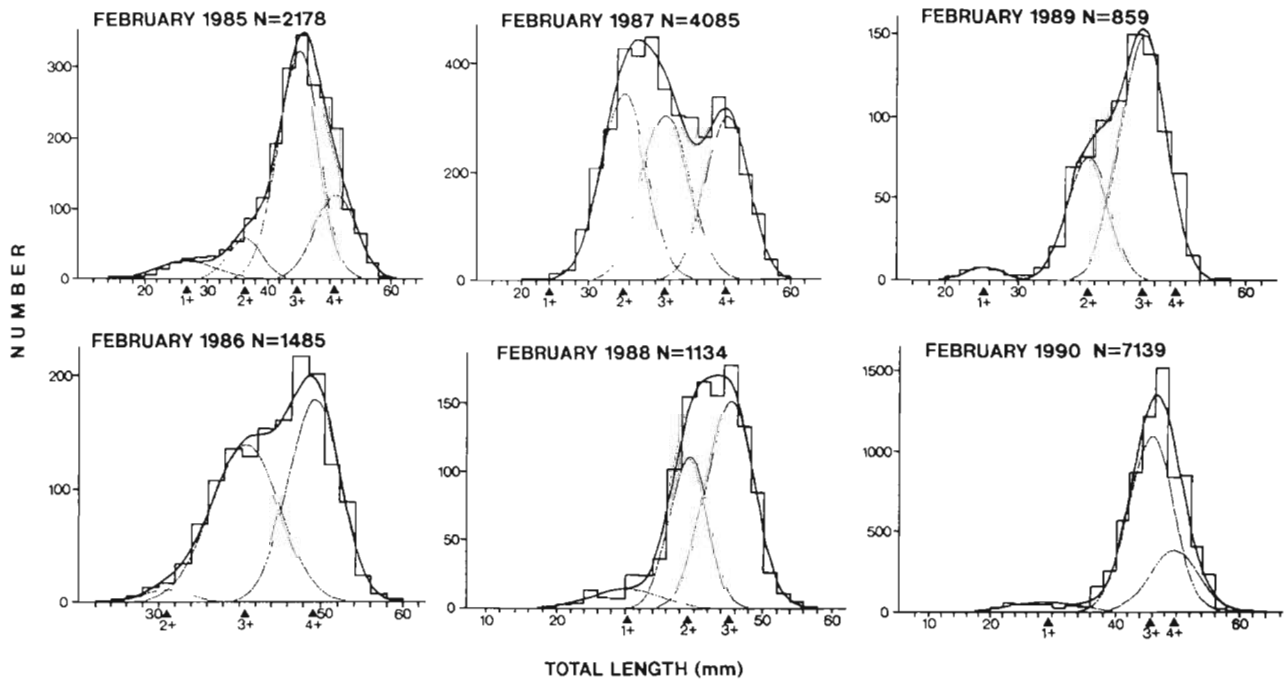


Fig. 4. *Euphausia superba*. Size-frequency distribution in the Cooperation Sea south of the Antarctic Divergence during the period 1985 to 1990. Data are from samples collected with Isaacs-Kidd and Samyshev-Yevdokimov trawls

it was 65.1 mm ( $L_{\max}$  observed in samples = 64 mm) (Figs. 2, 5 & 7). The growth performance in the southern ( $k = 0.47$ ) and northern ( $k = 0.42$  to  $0.44$ ) groups of both the Cooperation and Cosmonaut Seas was very

similar. The time at which 50% of the asymptotic length was attained by krill ( $t_{50\%} = 0.693/k + t_0$ ; Siegel 1987) was 1.48 to 1.53 and 1.55 to 1.56 yr for the southern and northern groups, respectively, in both seas.

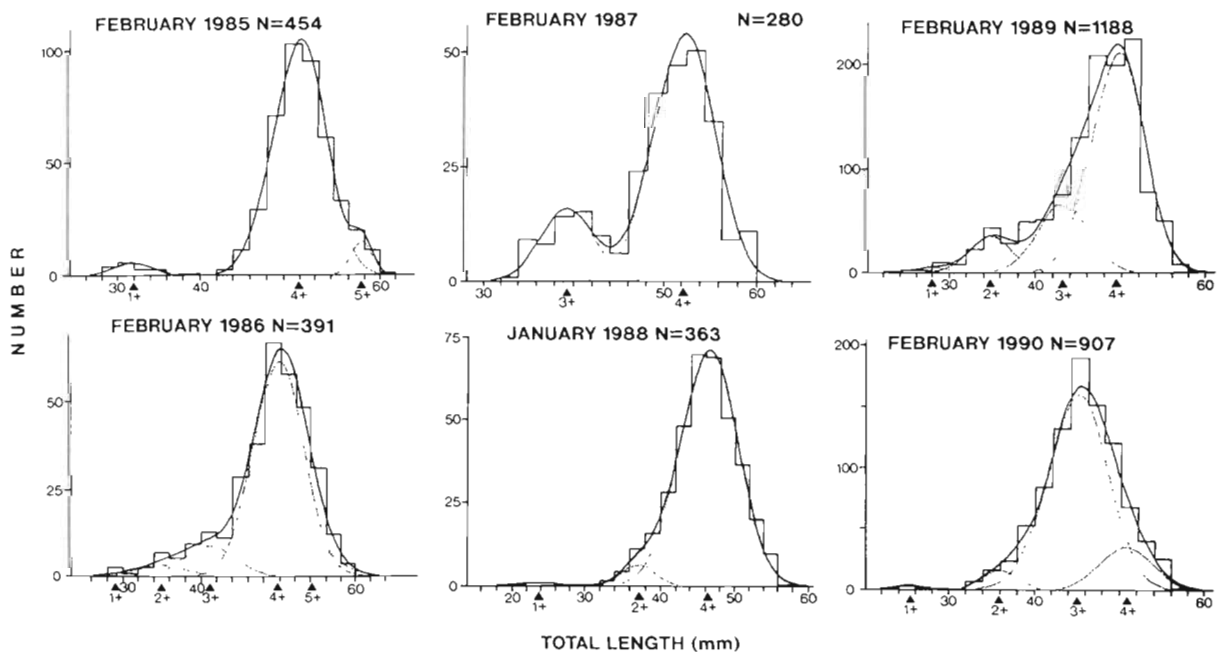


Fig. 5. *Euphausia superba*. Size-frequency distribution in the Cooperation Sea north of the Antarctic Divergence during the period 1985 to 1990. Data are from samples collected with Isaacs-Kidd and Samyshev-Yevdokimov trawls

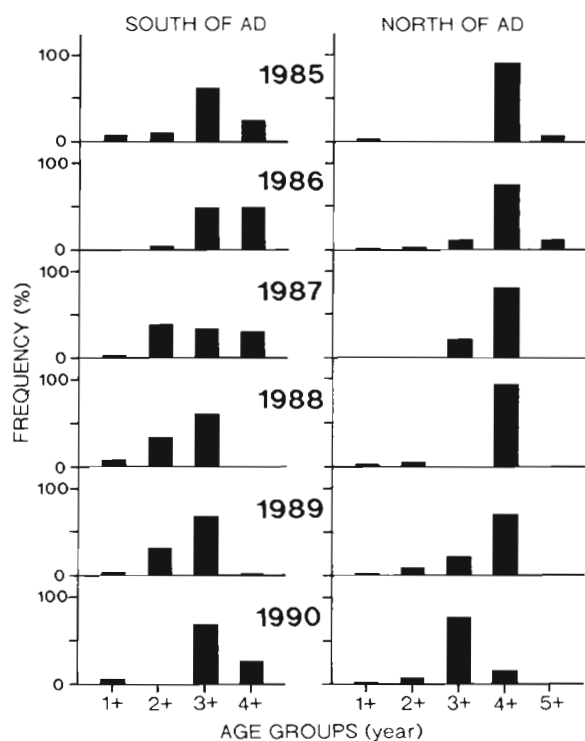
Table 4. *Euphausia superba*. Mean length and standard deviation of various age groups from the southern part of the Cooperation Sea during February 1985 to 1990, calculated by mixture analysis (Macdonald & Pitcher 1979)

Age group	1985	1986	1987	1988	1989	1990	Average
1+	26.8 ± 4.75	–	24.1 ± 3.40	30.3 ± 5.25	25.5 ± 2.52	29.3 ± 4.63	27.2
2+	36.3 ± 2.80	31.0 ± 3.00	35.0 ± 3.45	39.1 ± 2.79	39.2 ± 2.83	–	36.1
3+	44.8 ± 3.35	40.5 ± 4.20	41.3 ± 3.60	45.1 ± 3.44	46.4 ± 3.08	45.6 ± 3.56	44.0
4+	51.0 ± 3.37	48.9 ± 3.20	50.4 ± 3.20	–	50.9 ± 3.11	49.4 ± 3.85	50.1
No. of ind.	2178	1485	4085	1134	859	7139	
$\chi^2$	13.4	9.8	12.6	14.3	9.9	16.0	
df	22	18	18	19	18	27	

Table 5. *Euphausia superba*. Mean length and standard deviation of various age groups from the northern part of the Cooperation Sea during February 1985 to 1990, calculated by mixture analysis (Macdonald & Pitcher 1979)

Age group	1985	1986	1987	1988 <sup>a</sup>	1989	1990	Average
1+	29.9 ± 2.47	29.0 ± 2.10	–	23.6 ± 2.13	28.0 ± 2.10	25.4 ± 1.17	27.2
2+	–	35.0 ± 3.10	–	37.2 ± 2.33	34.8 ± 2.51	35.8 ± 2.06	35.7
3+	–	41.1 ± 3.30	39.3 ± 2.87	–	43.2 ± 3.00	44.9 ± 3.53	42.1
4+	49.9 ± 3.17	49.8 ± 3.29	51.9 ± 3.34	46.6 ± 3.90	49.5 ± 3.10	50.7 ± 3.13	49.7
5+	57.7 ± 1.29	54.2 ± 3.20	–	–	–	–	55.9
No. of ind.	454	391	280	363	1188	907	
$\chi^2$	9.0	6.5	7.6	11.6	10.4	9.5	
df	17	13	14	20	17	16	

<sup>a</sup>For 1988 only, data were taken in January

Fig. 6. *Euphausia superba*. Age distribution in the southern and northern sectors of the Cooperation Sea during February 1985 to 1990. AD: Antarctic Divergence

Based on a seasonal growth of 180 d (Ikeda 1985), the mean daily increase was calculated as 0.120 to 0.133 mm during the first year, 0.077 to 0.080 during the second, 0.048 to 0.057 during the third, 0.030 to 0.034 during the fourth and 0.019 to 0.022 mm during the fifth year (Table 7). Data from Aseev (1983) and Hosie et al. (1988) for the Cooperation Sea, as well as the available information on krill growth rates in the Southern Ocean obtained from both field and experimental data, are also given in Table 7 for comparison.

#### Mortality rates

The constants  $p$  and  $q$  (Table 8) in Eq. (6) were calculated using the length ( $l$ ) versus age ( $t$ ) relation obtained with Macdonald & Pitcher's (1979) mixture analysis and are presented in Tables 2, 4 & 5. The correlation coefficients for these relationships ranged between 0.8 and 0.9 and were significant at the level  $p < 0.01$ . The duration of the life span ( $T$ , Table 8) was calculated from the maximum krill total length ( $L$ ; Figs. 2, 4 & 5) using the linear growth Eq. (6). Similarly, the age at which 70% of individuals mature ( $t_n$ ) was calculated using data of  $l_n$  calculated by Aseev et al. (1988). Thus, if  $t_n$  ranges between 2.8 and 3.1 yr, from



Eq. (2)  $M$  ranges between 0.52 and 0.57. Consequently,  $\Theta_n$  ranges from 0.40 to 0.44. The constants  $a$  and  $b$  were also calculated (Table 8) from Eq. (5).

Krill age-averaged natural mortality rates ( $M$ ) in the Cooperation and Cosmonaut Seas varied considerably, ranging from 0.52 to 2.92. The lowest values (0.52 to 0.57) were obtained using Richter & Efanov's equation. Mortality rates calculated according to Alverson & Carney's model exhibited very little variability, 0.72 to 0.87, while mortality coefficients calculated following Beverton & Holt's approach varied considerably, from 0.76 to 2.92 (Table 9).

The age-dependent natural mortality rates in the Indian sector of the Southern Ocean calculated using Zikov & Slepokurov's approach (Table 8, Eqs. 4 & 8) ranged from 0.52 during the maturation period to 1.1 to 2.41 during the first and last years of life (Fig. 8).

## DISCUSSION

Several studies conducted in different regions of the Southern Ocean have concluded that Antarctic krill live for at least 4 to 6 yr (Ivanov 1970, Aseev 1983, Siegel 1986, 1987, 1991, Hosie et al. 1988), and may even live as long as 7 to 8 yr (Ettershank 1984, 1985, Ikeda 1985, Rosenberg et al. 1986). In the Cosmonaut Sea and in the southern part of the Cooperation Sea, only 5 age groups (including larvae) were clearly identified, while in the northern oceanic area of the Cooperation Sea 6 age classes were found. These results are consistent with previous estimates from the region (Hosie et al. 1988). However, in the southern Cooperation Sea remarkably large sized krill (larger than the

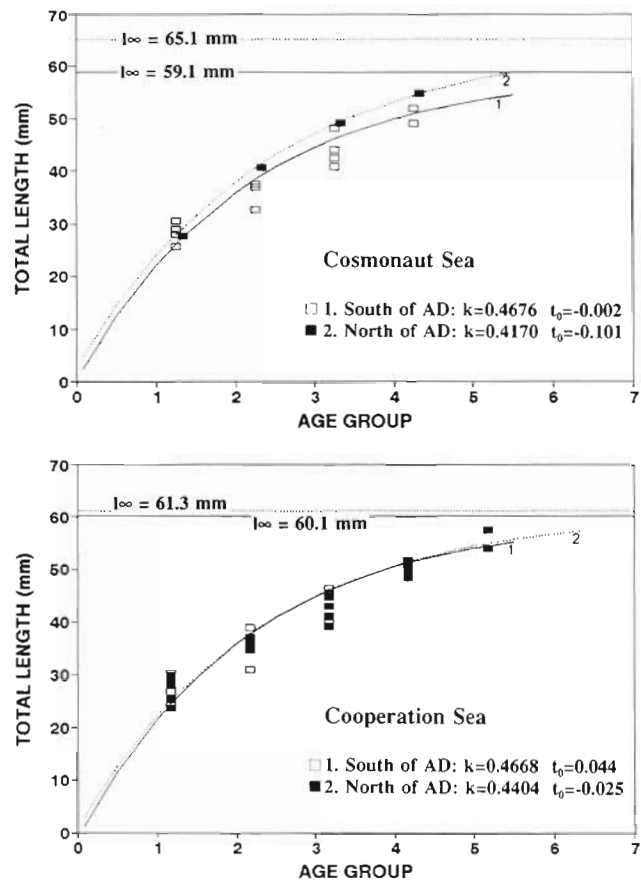


Fig. 7. *Euphausia superba*. Theoretical length growth curves in the Cosmonaut and Cooperation Seas derived from data presented in Tables 2, 4 & 5. Parameters of the von Bertalanffy growth formula [ $l_t = l_\infty(1 - e^{-k(t-t_0)})$ ], where  $l_t$  = krill length at age  $t$  in years] are given

Table 6. *Euphausia superba*. Percentage of krill at each reproductive stage in the Cooperation Sea in February, 1985 to 1990

Area	Year	Juv.	Reproductive stage:								Proportion of mated females
			Males				Females				
			2	3	4	5	2	3	4	5	
South of AD	1985	15.1	22.6	7.8	6.7	0.4	23.1	19.5	4.0	0.9	43.5
	1986	7.1	25.1	6.2	11.0	0.2	24.2	23.3	2.2	0.1	73.1
	1987	14.6	22.4	11.8	5.9	–	24.4	17.8	2.8	0.2	30.2
	1988	1.3	37.2	5.6	5.9	–	34.2	13.7	1.6	0.1	42.4
	1989	3.6	43.2	3.6	2.0	–	19.4	25.0	3.1	0.6	25.8
	1990	3.2	16.4	20.4	10.0	–	25.3	14.4	9.9	0.4	55.8
North of AD	1985	5.3	3.6	5.7	34.9	0.4	0.8	29.9	18.5	0.8	91.9
	1986	5.5	14.5	2.3	25.3	2.8	3.1	13.8	28.5	4.2	93.8
	1987	1.2	6.5	1.6	41.9	–	4.5	15.0	19.5	–	45.5
	1988 <sup>a</sup>	5.1	25.2	6.5	13.2	–	34.2	13.2	2.6	–	37.0
	1989	–	22.1	7.3	20.6	–	15.6	15.3	16.5	2.6	53.9
	1990	0.9	23.1	17.0	8.9	–	21.0	27.4	1.6	–	14.3
<sup>a</sup> For 1988 only, data were taken in January											

<sup>a</sup>For 1988 only, data were taken in January

Table 7. *Euphausia superba*. Daily growth of Antarctic krill according to data reported in the literature. E: experimental data; FD: field data; GC: growth curve data

Length, age	Observation period, conditions	Daily growth, mm	Source
16.6–29.5 mm	E	Max 0.047	Ikeda & Thomas (1987)
16–34 mm	E	Max 0.031 – 0.033	Segawa et al. (1983)
20–30 mm	E	0.023 – 0.033	Morris & Keck (1984)
20–33 mm	E	Max 0.07 – 0.14	Mackintosh (1967)
22–30 mm	E	0.034	Murano et al. (1979)
22–44 mm	E	0.070	Ikeda et al. (1985)
22–50 mm	E, feeding	Very small	Ikeda & Dixon (1982a)
22–50 mm	E, not feeding	Negative	Ikeda & Dixon (1982a)
25–47 mm	E, not feeding	0.002 – 0.007	Ikeda et al. (1983)
32 mm	E	0.083 – 0.156	Buchholz (1985)
?	E, late summer-autumn	0.024 – 0.060	Quetin & Ross (1991)
?	E, winter	–0.002 to –0.028	Quetin & Ross (1991)
Adult	E, good nutrition	0.070	Ikeda (1985)
Adult	E, poor nutrition	0.033	Ikeda (1985)
Adult	E, feeding specimens	0.033	Maiharu & Endo (1986)
Adult	E, not feeding specimens	0.004	Maiharu & Endo (1986)
23.5–30 mm	E	Max 0.037 – 0.068	Polek & Denys (1982)
0+	FD, from March to September	0.047	Hosie & Stolp (1989)
Furcilia 3–6	FD, winter under ice	0.07	Daly (1990)
Juveniles	FD, summer	0.106 – 0.180	Spiridonov (1987)
Adult	FD, summer	0.040 – 0.107	Spiridonov (1987)
0+	FD, summer	0.130	McClatchie (1988)
>3+	FD, summer	0.025	McClatchie (1988)
>3+	FD, winter	0.010 – 0.048	McClatchie (1988)
All ages	FD, summer	0.033	Siegel (1986)
1+	FD, summer	0.120	Siegel (1986)
2+	FD, summer	0.070	Siegel (1986)
30 mm	FD, summer	0.105 – 0.179	Rosenberg et al. (1986)
>30 mm	FD, January	0.170 – 0.190	Ikeda (1989)
Mean 40–45 mm	FD, summer	0.063	Kanda et al. (1982)
24–36 mm	FD, summer	0.133	Clarke & Morris (1983)
?	FD, November–March	0.089	Brinton et al. (1987)
1+	GC, Cooperation Sea	0.172	Aseev (1983)
2+		0.038	Aseev (1983)
3+		0.035	Aseev (1983)
4+		0.029	Aseev (1983)
5+		0.027	Aseev (1983)
1+	GC, Prydz Bay region	0.109	Hosie et al. (1988)
2+		0.078	Hosie et al. (1988)
3+		0.044	Hosie et al. (1988)
4+		0.039	Hosie et al. (1988)
1+	GC, Cosmonaut and Coopera- tion Seas	0.120 – 0.133	This study
2+		0.077 – 0.080	This study
3+		0.048 – 0.051	This study
4+		0.030 – 0.034	This study
5+		0.019 – 0.220	This study

Table 8. *Euphausia superba*. Parameter values of natural mortality rates estimated using Eqs. (4), (6) & (7). AD: Antarctic Divergence

Area	Sector	$p$	$q$	$L$	$T$	$I_n$	$t_n$	$a$	$b$
Cooperation Sea	South of AD	22.71	0.578	63	5.8	42	2.9	0.069	–0.400
	North of AD	23.70	0.526	62	6.2	43	3.1	0.062	–0.387
Cosmonaut Sea	South of AD	23.14	0.554	60	5.6	41	2.8	0.073	–0.408
	North of AD	24.91	0.547	64	5.6	44	2.8	0.073	–0.408

Table 9. *Euphausia superba*. Natural mortality rates in the Cosmonaut and Cooperation Seas calculated using Beverton & Holt's (1959) approach

Region	Area	1985	1986	1987	1988	1989	1990
Cosmonaut Sea	North of AD	–	–	–	–	2.20	–
	South of AD	–	–	1.17	0.82	2.52	0.76
Cooperation Sea	North of AD	1.68	2.17	1.84	2.17	2.23	2.15
	South of AD	1.61	1.02	0.94	0.83	2.92	2.00

mean size of the 3+ and 4+ groups) were collected (Fig. 4). These animals did not exhibit distinct peaks in the length-frequency distribution and, unfortunately, could not be conclusively isolated using Macdonald & Pitcher's (1979) mixture analysis. It is assumed, therefore, that they belonged to a 5+ age group. This assumption is consistent with the results of Aseev (1983) and Ettershank (1983, 1985) who also found 5 adult year groups in Prydz Bay employing various methodologies.

The method of determination of krill age from the size structure of a population has several drawbacks. It is evident from Table 7 that growth rates in summer change within a broad range, and presumably depend on water temperature, size of individuals and food concentration (see also Quetin et al. 1994). The coefficients of daily increase, calculated for a growth period of 180 d during this study, agree with results of field observations and exceed values obtained from laboratory experiments (Table 7). There are, however, indications of possible negative growth in winter and, as a result, of possible mixing of age classes (Ikeda & Dixon 1982b, Ettershank 1984). Furthermore, low growth rates in older age-groups and their small numbers may make their separation by Macdonald & Pitcher's (1979) approach impossible (Hosie et al. 1988, Siegel 1991, this study). The suggestion that total size may decrease in winter was originally based on aquarium experiments (Ikeda & Dixon 1982b, Thomas & Ikeda 1987). However, recent underwater observations show that krill can change biotope and foraging strategy and are able to reduce their metabolic level in winter (Kawaguchi et al. 1986, Marschall 1988, Quetin & Ross 1991). Furthermore, research on floating ice has proved that krill larvae and juveniles live under the ice surface in winter where they find shelter and food (>90 %

were observed feeding) and continue to grow (Nau-mov & Chekunova 1985, Daly & Macaulay 1989, Hosie & Stolp 1989, Daly 1990). In addition, during winter krill may consume microzooplankton and copepods (Tanoue & Hara 1986, Price et al. 1988, Bathmann et al. 1993, Huntley et al. 1994). Thus, no conclusive evidence for the occurrence of negative growth under natural conditions has yet been found.

The mean size of age classes presented in this paper do not differ significantly from those already published for the Cooperation Sea and the Antarctic Peninsula (Table 10). However, in general the length of the 1+ group obtained in this study exceeds the size range reported by Miller (1986) and Hosie et al. (1988) for the Prydz Bay region. This supports Siegel's (1986) results

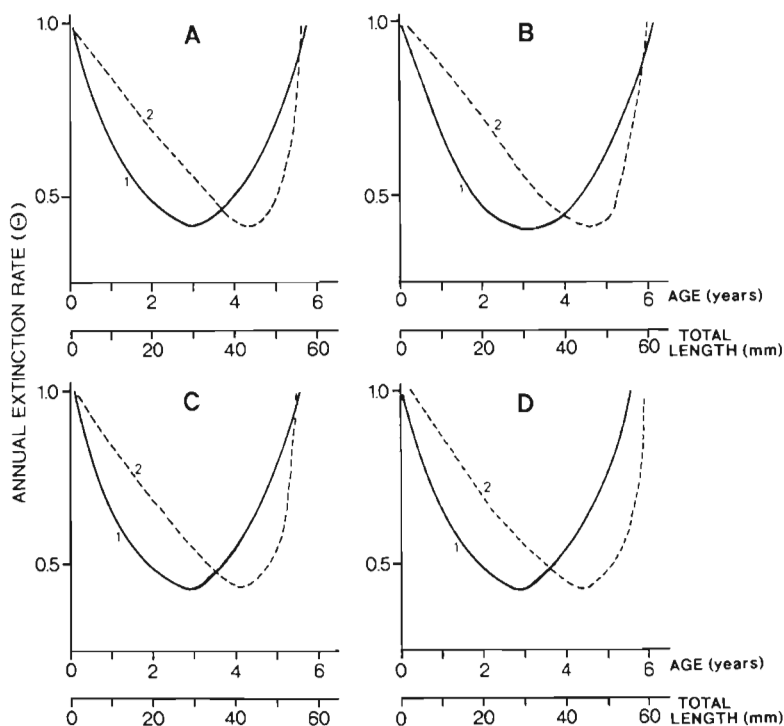


Fig. 8. *Euphausia superba*. Curves of the mortality rates ( $\Theta$ ) in the southern and northern parts of the Cooperation (A and B) and Cosmonaut (C and D) Seas estimated by Zikov-Slepokurov's (1982) method. 1: mortality versus age; 2: mortality versus total length

Table 10. *Euphausia superba*. Mean size of krill age classes in different areas of the Southern Ocean

Area	1+	2+	Age class 3+	4+	5+	Source
Antarctic Peninsula	29.0–31.8	38.0–41.3	45.5–47.6	51.0–52.3	55.5–57.1	Siegel (1986)
Antarctic Peninsula	20.8–30.5	36.0–40.0	43.6–46.0	50.0–50.3	54.2	Siegel (1987)
Antarctic Peninsula	26.5	35.9	44.3	50.8	55.4	Siegel (1991)
Cooperation Sea	29.6–32.2	37.4–38.3	43.4–44.6	47.8–50.7	52.4–55.7	Aseev (1983)
Prydz Bay region	19.1–30.8	34.3–41.0	41.3–48.8	51.1–54.9	?	Hosie et al. (1988)
Prydz Bay region	~20.0	33.5	41.2–42.3	~50.0	?	Miller (1986)
Cooperation Sea:						
South of AD, Feb.	24.1–30.3	31.0–39.2	40.5–46.4	48.9–51.0	?	This study
North of AD, Feb.	23.6–29.9	34.8–37.2	39.3–44.9	46.6–51.9	54.2–57.7	
Cosmonaut Sea:						
South of AD, March	25.7–30.6	32.8–37.5	40.9–48.3	49.2–52.0	–	
North of AD, April	28.7	40.7	49.3	55.0	–	

which indicate that krill juveniles <21 mm in size (age class 1+) are undersampled by the 4.5 mm mesh size trawl. The growth curves of *Euphausia superba* for the Cosmonaut and Cooperation Seas were similar to each other and, indeed, to those for the Prydz Bay region during 1981 to 1985 (Hosie et al. 1988), the Antarctic Peninsula region (Siegel 1987) and the Atlantic sector of the Southern Ocean (Rosenberg et al. 1986). In addition, the results of this study support the theoretical curve of Ikeda (1985) for krill seasonal growth (6 mo).

Catches of krill of age 1+ were generally poor in the Cooperation and Cosmonaut Seas. Similar results were observed by Siegel (1991) in the Antarctic Peninsula area. However, this was found to be the result of methodological problems as noted above. Recent data suggests that krill recruits (1+) are dispersed in surface layers (0 to 1 m or 0 to 10 m) throughout the Cooperation Sea during both day and night (Miller 1986, Krakatitsa et al. 1993). In the northern part of this area, conditions favourable for larval and juvenile accumulation seldom occur. Consequently, young krill usually remain dispersed (Krakatitsa et al. 1993). Only older individuals, which can withstand current transport, are able to swarm and consequently dominate catches. However in the southern part of the sea, coastal circulation may cause passive accumulation. Seasonal changes in the horizontal and vertical distribution of juvenile krill further result in the cause for the absence of the recruits. According to the literature (Hosie et al. 1988, Bibik 1989, Hosie & Stolp 1989) and our unpublished data, krill recruits (1+) were well represented in the catches of spring and early summer (November to January).

Krill with a maximum length of 63 and 64 mm (in the southern and northern groups of the Cooperation Sea, respectively) were observed during the 1990 survey, while Miller (1986) and Hosie et al. (1988) did not find

krill larger than 59 mm in the Prydz Bay region. During April 1989, the largest krill found in the northern part of the Cosmonaut Sea attained a size of 64 mm, while south of the AD no size classes larger than 60 mm were represented in this region during the period 1987 to 1990 (Fig. 2). Any artefact due to analytical strategy can probably be excluded as the same method was used throughout the investigation. Although we were not able to avoid methodological problems, due to the contribution of length-frequency data obtained from different workers, it is worth noting that krill of the same length (up to 63–66 mm) has periodically been observed in both the Cooperation and the Cosmonaut Seas (see results of Aseev 1983, Bibik et al. 1988). Interestingly, both the South African and Australian krill surveys have neglected or underinvestigated the northern part of the Cooperation Sea (between 59 and 62° S), where the largest krill individuals were generally collected during this study.

Two abundant generations of krill, hatched in 1985 and 1987, were recorded in the southern part of the Cosmonaut Sea during the period 1987 to 1990. Longer observations in the Cooperation Sea (Australian and present data) cover the period from 1981 to 1990. Combining the data sets from all these studies, it is clear that the fluctuations in larval abundance indicate alternation of years with low (1983, 1984), medium (1979, 1980, 1982, 1988, 1989) and high (1978, 1981, 1985, 1986, 1987) spawning success (Bibik 1989, Hosie et al. 1991, Samyshev 1991).

The data collected by Australian researchers suggest that krill hatched in 1978 to 1980 and 1981 to 1982 were predominant in the Prydz Bay region in 1981 to 1982 and 1984, respectively. During January 1985, catches were dominated by individuals hatched in 1984, particularly in the extreme eastern and north-eastern parts of the Cooperation Sea (Hosie et al.



1988). According to our data, however, a rich cohort hatched in 1982 was observed in February 1985 and 1986 in the southern part of the Cooperation Sea. The generation of 1985 was predominant in 1987, and especially in 1988, but virtually disappeared in 1989, when krill hatched in 1986 dominated the catches. Krill hatched in 1987 and 1986 were predominant in the catches of 1990 (Fig. 6).

It should be noted that the appearance of abundant generations in the Cooperation Sea coincided with high and medium success spawnings. For example, the results of successful spawnings in 1978, 1981, 1985, 1986 and 1987 and medium success spawnings in 1980 and 1982 can be clearly traced for ca 2 to 3 yr. Unfortunately, no data on larval distribution and abundance in the Cosmonaut Sea is available. However, the occurrence of abundant generations in this sea, with successful spawnings in the Cooperation Sea during 1985 and 1987, must be stressed. It is reasonable to assume that krill larvae from the Cooperation Sea may be recruited into the southern group of the Cosmonaut Sea through the East Wind Drift (Fig. 1B).

According to the age distribution of krill larvae, spawning takes place from December to March (Hosie et al. 1988, Hosie 1991, Samyshev 1991), but is most intense in late December and January (Pakhomov & Karpenko 1988, 1992). This accounts for the low percentage of mature females usually found during February and March (Tables 3 & 6).

In the northern part of the 2 seas, a different age structure was identified. In all cases, the first 2 age groups' (1+ and 2+) contribution was negligible, while the 4+ specimens dominated. In only one survey did the 3+ age group dominate. This suggests that krill were being transported from elsewhere, possibly through advection of waters from the south and west of these regions (Marr 1962, Aseev et al. 1988, Bibik et al. 1988, Latogursky et al. 1990). For the Cooperation Sea, this is supported indirectly by the similarity in the mean size of age classes of krill between the northern and the southern groups (Tables 4 & 5). However, the mean size of the age classes in the northern group of the Cosmonaut Sea was ca 1 to 8 mm larger than in the southern group. These data confirm an earlier suggestion of Aseev et al. (1988), that krill from the Weddell Drift may be advected to the northern part of the Cosmonaut Sea. Furthermore, data from the present study show that krill from the Weddell Drift may also be found in the northern part of the Cooperation Sea, where they constituted the 5+ age class. The presence in February of many females ready to spawn suggests the occurrence of a prolonged spawning period with no definite peak.

The age-averaged values of krill natural mortality ( $M$ ) estimated in previous studies vary between 0.45

and 5.5 (Kawakami & Doi 1979, Siegel 1986, 1991, Priddle et al. 1988, Basson & Beddington 1989). The wide range of mortality estimates appears to be the result of the different methodologies employed. A critical analysis of these approaches has been discussed by Miller & Hampton (1989), and is also stressed in Siegel's (1991) work. One of the main drawbacks of most approaches is the underestimation of krill age. Consequently, the realistic value of natural mortality may range between 0.66 and 1.35 (Siegel 1986, 1991, Priddle et al. 1988).

Age-averaged estimates of natural mortality obtained in this study range from 0.52 to 2.92. The lowest values, corresponding the age of maturity, were estimated using Richter & Efanov's method. Slightly higher, less variable values were calculated when considering the age at which the biomass peak of a population is reached (Alverson & Carney's method). Unlike previous models, Beverton & Holt's approach takes into account the size composition of the catches. The mortality coefficients calculated with this method were among the highest obtained, ranging between 0.76 and 2.92 (Table 9). The drawback of this method is that for the estimation of mortality it is necessary to assume that the population is fully represented in the catches. Generally, in net catches the peak of the curve of size composition is shifted to the right, especially in the northern parts of the Cosmonaut and Cooperation Seas. Krill with a total length >40 mm are usually more commonly represented in catches (Figs. 2, 4 & 5) and, consequently, the coefficients obtained are most accurate for the older age groups.

The ichthyological methods employed to estimate krill mortality rates in the Atlantic sector of the Southern Ocean provide a range of mortality rates, 0.75 to 1.13, similar to that obtained in previous studies (Maklygin pers. comm.). Alagaraja (1984) suggested that the life duration of animals is the age at which 99% of individuals die. Therefore,  $M_{1\%} = -\ln(0.01)/T = 4.605/T$  (Siegel 1991), and considering the different values for  $T$  obtained in Table 8,  $M$  will vary from 0.74 to 0.82. These estimates are similar to the results of this study obtained using Alverson & Carney's model.

The natural mortality rates obtained with Zikov & Slepokurov's approach are difficult to compare since the present study represents the first attempt where age-dependent mortality rates are estimated. The work of Brinton & Townsend (1984) represents the only study where a constant mortality rate for all age groups was not applied. They assumed survival rates of 10% from furcilia to sub-adults (20 to 43 mm length) and of 60% from sub-adults to adults (44 to 58 mm). Their estimates of  $M$  were 2.31 and 0.6 for the 1 to 2 and 2 to 3 yr old krill, respectively. However, as stressed by Siegel (1991), the calculations of Brinton & Townsend



(1984) are based on values for the life span of krill which are substantially underestimated. Their upper values of the mortality rate ( $M = 2.31$ ) are, therefore, too high. Using a regression of number-at-age against age (excluding 0+ and 1+ year old individuals), Siegel (1986, 1991) derived the average survival rate of 0.36 to 0.41 for krill in the Antarctic Peninsula region. Estimates of survival rate ( $= \Theta$ ) presented in this paper were not constant during this period of life (2+ to 5+), ranging from 0.40 to 0.78. These values are higher than those calculated by Siegel (1986, 1991). This may be explained as follows. Siegel used number-at-age data collected during a single survey only and could not identify and separate the different recruitment levels which might have occurred during the previous years. Furthermore the krill life span in the Cooperation (south part) and the Cosmonaut Seas during this study was 1 yr shorter when compared to the population from the Antarctic Peninsula region analyzed by Siegel (1986, 1991).

Results of many hydrographic studies (Smith et al. 1984, Klyausov & Lanin 1987, Bibik et al. 1988, Lanin 1993) suggest that the Cooperation Sea is a unique macroscale biotope due to its relatively closed circulation and higher heat background, when compared to the Cosmonaut and Davis Seas. In addition, biological studies (Dolzhenkov et al. 1987, Gerasimchuk & Lanin 1988) have provided some evidence that the fish and krill groups of the Cooperation Sea may indeed be isolated. However, neither latitudinal genetic differences in the region (MacDonald et al. 1986) nor meridional differences between the Cooperation Sea and other regions surrounding the Antarctic Continent have been documented (Fevolden 1988, Fevolden & Schneppenheim 1989). The demographic parameters obtained in this study (except those relative to the northern part of the Cosmonaut Sea) did not differ significantly from those in the other sectors of the Southern Ocean. The data presented suggest that larvae from the Cooperation Sea may be recruited into the Cosmonaut Sea. Similarly, larvae and juveniles from the Davis Sea may be recruited into the Cooperation Sea through the East Wind Drift, as suggested by Bibik (1989), Hosie (1991) and Lanin (1993). However, the long-term age structure of the krill groups and their spawning success in the Cooperation Sea covaried, suggesting the occurrence of a self-sustaining group. This would be consistent with the relatively closed circulation system of the Cooperation Sea (Bibik et al. 1988, Gerasimchuk & Lanin 1988, Lanin 1993, Solyankin 1993). The periodic resultant gene flow from recruits from the other regions, however, seems to prevent the establishment of a distinct endemic subpopulation in this area.

Some studies of krill biomass distribution and environmental variables in the Cooperation Sea suggest the hypothesis that this region exhibits unique features. Bibik (1989) has shown that within the circulation system of the Prydz Bay region, in the western part of the Cooperation Sea, the export of krill may be greater than the import, while in the eastern part of this sea, the reverse situation seems to occur. It appears, therefore, that krill is imported from the north by the return branch of the circulation as well as from the Davis Sea with the East Wind Drift from the east. On the basis of long-term observations within the Cooperation Sea, Bibik (1989) and Bryantsev et al. (1991) suggest that variations in krill biomass in the area may be the result of annual variations in the circulation pattern of the atmosphere and hydrosphere. These environmental parameters are important factors affecting the conditions for the reproduction and replenishment of the southern krill group. The spawning success and the return of juveniles to the coastal zone from the open ocean appear to be the main cause of variability in total krill stock (Bibik 1989, Bibik & Yakovlev 1991). Similar mechanisms have been proposed for other areas (Priddle et al. 1988).

The main factor responsible for inter-annual variability in krill biomass appears, therefore, to be the atmospheric circulation which determines the level of isolation of the Cooperation Sea from adjacent waters (Bryantsev et al. 1991). When the level of isolation increases, the biomass of krill may grow gradually, but when this level decreases a sharp decline in krill stock may be observed. For example, in contrast to the situation observed during the period 1986 to 1988, since 1988 a remarkable growth in atmospheric circulation activity has been observed over the Cooperation Sea (Bibik 1989, Bryantsev pers. comm.). This has led to an increased meandering of the current fields to the south of the AD and, therefore, a reduction in the rates of emigration of krill from the Cooperation Sea, resulting in build-up of biomass in the area, particularly in 1990 (Bibik & Yakovlev 1991, Samyshev 1991, Bibik pers. comm.). Further studies should, therefore, be directed towards the investigation of the degree of isolation within the Cosmonaut, Cooperation and Davis Seas, in terms of its influence on the level of krill recruitment both within these regions and from surrounding areas.

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