ESTIMATION OF KRILL (*EUPHAUSIA SUPERBA*) MORTALITY AND PRODUCTION RATE IN THE ANTARCTIC PENINSULA REGION

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Abstract

A net sampling survey for krill was carried out by RV *Meteor* along the Antarctic Peninsula from 26 December 1989 to 14 January 1990. Results were compared with data of an identical survey with RV *Polarstern* in 1987/88. Seasonal variation between summer and winter abundance/biomass data exceeded a factor of 1:35, while interannual variability between available surveys reached only a factor of 1:1.6. Krill mortality was calculated by linearized catch curve analysis and resulted a rate of Z = 0.88 (1989/90) and Z = 0.96 (1987/88). Production was estimated and resulted a P/B ratio of 0.88 to 0.94 for different years. The exchange rate of water masses and krill biomass within one summer season was roughly estimated as two times from which follows a maximum total effective biomass (including production) of 4.3 and 5.0 x 10^6 tonnes passing through the survey area during the respective summer.

Résumé

Du 26 décembre 1989 au 14 janvier 1990, le RV *Meteor* a effectué une campagne d'évaluation du krill par échantillonnages au filet le long de la péninsule antarctique. Les résultats ont été comparés avec les données d'une campagne identique effectuée par le RV *Polarstern* en 1987/88. La variation saisonnière entre les données d'abondance et de biomasse d'été et d'hiver dépassait un facteur de 1:35, alors que la variabilité interannuelle entre les données de campagnes disponibles n'atteignait qu'un facteur de 1:1,6. La mortalité du krill, calculée par l'analyse de la courbe de capture linéarisée, a produit un taux de Z = 0,88 (1989/90) et Z = 0,96 (1987/88). La production ayant été estimée, on est arrivé à un rapport de P/B de 0,88 à 0,94 selon les années. Le taux d'échange des masses d'eau et de biomasse de krill en une saison d'été était estimé, grosso modo, à deux fois, d'où une biomasse effective totale maximale (production comprise) de 4,3 et 5,0 x 10^6 tonnes traversant l'aire de la campagne pendant les étés respectifs.

Резюме

С 26 декабря 1989 г. по 14 января 1990 г. вдоль Антарктического полуострова НИС *Meteor* была проведена съемка по сбору проб криля сетями. Результаты были сравнены с данными идентичной съемки проведенной НИС *Polastern* в 1987/88 г. В результате сезонной изменчивости данных по численности/биомассе различие между зимними и летними месяцами составило 1:35, тогда как межгодовая

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изменчивость между имеющимися съемками достигла лишь фактора 1:1,6. Смертность криля была подсчитана при помощи анализа линеаризированной кривой улова. Были получены следующие результаты: коэффициент Z = 0,88 (1989/90) и Z = 0,96 (1987/88). Оценка продуктивности составила отношение P/B от 0,88 до 0,94 в разные годы. Коэффициент обмена масс воды и биомассы криля в течение одного лета был приблизительно равен 2, из чего следует, что в течении изученных летних сезонов, мигрирующая через данный участок максимальная общая фактическая биомасса (включая продуктивность) составит 4,3 и 5,0 x 10^6 тонн.

Resumen

El buque de investigación *Meteor* llevó a cabo una prospección con redes a lo largo de la península Antártica del 26 de diciembre de 1989 al 14 de enero de 1990. Se contrastaron los resultados con los datos obtenidos de una prospección idéntica hecha con el BI *Polarstern* en 1987/88. La variación estacional de los datos de abundancia y biomasa entre el verano y el invierno sobrepasó un factor de 1:35, mientras que la variación interanual de las prospecciones disponibles sólo alcanzó un factor de 1:1.6. La mortalidad del krill fue calculada mediante un análisis lineal de la curva de capturas y dio un índice de Z = 0.88 (1989/90) y Z = 0.96 (1987/88). El rendimiento estimado dio una razón P/B de 0.88 a 0.94 para distintos años. El índice de intercambio de las masas de agua y biomasa de krill dentro de una temporada estival se calculó, a *grosso modo*, en dos veces, de lo que se deduce una biomasa total efectiva máxima (incluida producción) de 4.3 y 5.0 x 10^6 toneladas que pasaron por el área prospectada durante los veranos respectivos.

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1. INTRODUCTION

During recent years research on Antarctic krill has led to a deeper understanding of the species life cycle and a more refined knowledge on distribution patterns and the variability with time. First attempts had been carried out to estimate population dynamic parameters as there are age, growth, mortality and production. A comprehensive review of the present state of knowledge was undertaken by Miller and Hampton (1989) who documented the progress since the report by Everson (1977). On the other hand this review also elucidated the problems of diverting published results which are often derived from different methodological approaches.

For a long time krill was thought to live only for two or three years and spawn only once during the life-cycle. Studies on 're-maturation' and 're-juvenation', however, led to the conclusion of a multiple spawning during a longer life span. Meanwhile a longevity of five to seven years (6 to 8 age groups) is accepted in principal (Ettershank, 1984 and 1985; Siegel, 1986 and 1987; Rosenberg *et al.*, 1986; Hosie *et al.*, 1988) which changed the basis for the calculation of basic population dynamic parameters.

Since the establishment of a commercial krill fishery there is an increasing need for reasonable estimates on age, growth, mortality and productivity. The present study intends to support data from a survey covering the area of the krill distribution range from juvenile to adult stages. A representative sample of all age groups can be expected which overcomes shortcomings of earlier locally restricted investigations. Determination of mortality as well as productivity will support more reliable results than it would be possible from an unknown, smaller part of the population with an unknown age structure.

2. MATERIAL AND METHODS

A net sampling survey for krill was conducted by RV *Meteor* during 26 December 1989 and 14 January 1990. The survey area was located along the Antarctic Peninsula between Elephant Island in the northeast and Adelaide Island in the southwest. The station grid was based on the extended BIOMASS-SIBEX grid, which was already surveyed during previous years, March 1984/85, winter 1986, and November/December 1987/88.

A total of 88 stations were sampled (Figure 1) by a multiple RMT 8 net with a mesh size of 4.5 mm (Roe and Shale, 1979). Flow-meter data, net angle, fishing depth and temperature were monitored continuously and the data stored on a personal computer (Dimmler and Klindt, 1990). Filtered water volumes were calculated from the net parameters applying formulas given by Rose and Shale (1979) and Pommeranz *et al.* (1982).

Plankton samples were preserved in 4% buffered formalin seawater solution. Krill was always sorted completely from the entire sample. Total length (AT) was measured from the anterior margin of the eye to the tip of the telson to the nearest millimetre below. All measurements were carried out by a single observer to avoid methodologically biased differences in length frequency data (Watkins *et al.*,1985). A total of 12 933 krill specimens were measured and their developmental stages determined.

Statistical analyses were carried out using the CSS statistical computer package. Age groups were derived from length frequency data by application of the distribution mixture analysis presented in detail by MacDonald and Pitcher (1979). The MIX computer program was run in an interactive session to estimate, by stepwise optimization, certain variables of single components of the distribution mixture (means, standard deviations and proportions) as well as the chi-square goodness of fit test.

3. RESULTS

The survey covered an area of approximately 93 800 n miles^2. Abundance values were integrated for the 200 m depth zone.

3.1 Stock Composition

The composition of the krill stock and its spatial distribution pattern was investigated applying a cluster analysis to compare similarity between stations. A similarity matrix was computed based on the relative frequency of each krill length class as station parameters as described by Siegel (1986 and 1988). Results of this analysis were plotted as a dendrogram. A similarity level of 70% led to four geographical coherent clusters which were interpreted to be biologically meaningful.

Since number of stations and the abundance of krill were different in these clusters, a simple unweighted mean length frequency distribution calculated from the above relative distribution would bias the absolute abundance and the composition of the overall length composition. Therefore krill density strata were established in each cluster. The stratified mean (Saville, 1977) was then determined for each cluster separately and multiplied by the size of the respective cluster. The sum of all four clusters finally led to the absolute abundance of size classes within the entire survey area.

The overall length frequency distribution is shown in absolute numbers in Figure 2 for the summer cruise 1989/90. The scarcity of juvenile krill of 23 to 30 mm became quite obvious, while 30 to 44 mm medium sized subadults represented the bulk of the krill stock. Largest adult specimens were 61 mm in size, which is generally the maximum length reached by this species.

The above described procedure was also undertaken for other surveys from different years to detect the degree of interannual variation in krill abundance. The occurrence of different cluster and their related length frequency distributions during various cruises had been published earlier (Siegel, 1988 and 1989). Data and results are summarized in Table 1.

In summer 1989/90 the total amount of krill reached 2 700 x 10^9 individuals in the survey area (Figure 3). Abundance was higher during the post-spawning season 1984/85 with 3 795 x 10^9 krill and highest in early summer pre-spawning season 1987/88 with more than 4 400 x 10^9 krill. During winter 1986 the stock was at its lowest level with 124 x 10^9 individuals. Juvenile krill was scarce in 1984/85 and 1989/90, indicating poor 1^+ age groups. Subadult stages observed in lower numbers during the 1987/88 season indicating a missing of a middle aged class (see below).

3.2 Biomass

Krill biomass was mapped as g/m² and contoured and size of biomass density strata were measured. The stratified mean and variance were determined for the area within the krill distribution range using the method described by Saville (1977). Data from earlier surveys were reanalysed in the same manner, because in some cases the area of zero catches beyond the distribution range - but inside the survey area were included for the calculation of the overall stratified mean. This reduces the value of the stratified mean and would not give a real impression on the variability of biomass density within the distribution limits of the species. Results of all estimations are given in Table 2.

During summer the total estimated biomass ranged from about 1 million tonnes to more than 1. 6 million tonnes regarding the fact that the size of the survey area slightly differed from year to year.

3.3 Population Dynamic Parameters

3.3.1 Age Composition

The estimation of population dynamic parameters require a representative sample of the stock. It is important, therefore, to know that during summer krill distribution has its furthest northern extent into oceanic waters along the Peninsula. During this time the stock presents a complete set of developmental stages/age groups (Siegel, 1988). The survey grid considers the distribution pattern and included shelf as well as oceanic waters and covers most of the krill distribution range or even extended beyond this range. The overall length frequency distribution given in Figure 2 was computed by the stratified means and the size of the cluster subareas and thus is representative for the krill stock in the Peninsula area. The data of this length frequency distribution were used to analyse the age class composition and the strength of age classes in the stock. The separation of normal distributions from a distribution mixture was conducted by applying the method described in detail by MacDonald and Pitcher (1979). The basic assumption on normal distribution of size classes for krill age groups had been discussed and analysed by Siegel (1986).

The results with best goodness of fit of observed and expected values for the least number of components are summarized in Table 3 (chi-squared = 11.1, df = 25, P = 0.992). At least five age groups could be distinguished from the distribution mixture. Since age class 0 was only present as recently spawned eggs or hatched nauplii, the smallest group of 26.5 mm size can be regarded as age class 1^+. The largest group of 55.4 mm mean size represented only a small number (3.3%) of individuals and a high degree of overlapping occurred with the preceding group. Since it was not possible to split this group into further components, the largest group is defined as $\geq 5^+$, because this group might include more than one undetected age class - although these would be very rare ones and strongly overlapping in size.

The total number of krill in the survey area (Table 1) and the calculated proportions of the components (Table 3) were used to estimate the number of krill for each of the age classes. The same procedure was undertaken for the data of the 1987/88 summer cruise, which also resulted at least five components. Results on the abundance of each age group are given in Table 4.

In both seasons 1987/88 as well as 1989/90 age group 1^+ was scarce and represented only 1.5% and 2.3% of the krill stock, respectively (Table 4). Age class 2^+ was by far the most abundant group (75.8%) in 1989/90 and showed even higher proportions (78.4%) in summer 1987/88. The results of 1989/90 further showed a steady decline in number of krill for the older age classes. From Table 3, however, it is obvious that in 1987/88 the age group 3^+ with a mean length of 44.7 mm contributed only 4.4% to the stock size which was much less than the proportion of the older 4^+ age group (11.3%).

3.3.2 Mortality

Since data of consecutive years were not available, the static model was taken as an alternative way. This involves examining the age structure of the stock at one period in time. Working with these 'pseudo-cohort' data we can apply the linearized catch curve equation with constant time intervals (Sparre *et al.*, 1989)

$$\ln C_{(t1\,,\,t2)} = g - Zt$$

Figure 4 shows the linearized catch curve analysis for the particular years 1987/88 and 1989/90. As appears from the figure data points from the age group 1^+ and 3^+ (in 1987/88) show a sufficiently large deviation from the straight line to justify the exclusion from the regression analysis (Sparre *et al.*, 1989). The reason is that these age groups can be suspected to be extremely poor year classes most probably due to a failure of spawning in preceding years.

From the 1987/88 age group composition a total mortality of Z = 0.96 (r = -0.999) was calculated, which corresponds with a survival rate of 38 % from one year to the next. The 1989/90 data resulted a slightly lower mortality of Z = 0.88 (survival rate 41%) and a slightly lower correlation coefficient (r = -0.969), because the abundance of the age groups varied more and data points deviate more from the theoretical straight line than in 1987/88.

3.3.3 Production

For this analysis production was defined as the sum of growth increments (weight increase of all individuals during a one year period) of all post-larval age groups. The annual production of a monocyclic species (the population is represented by one age group and the reproductive period is of limited duration) can be calculated by

$$P = B_2 - B_1 + E$$

when the eliminated (E) part of the population is added to the difference in biomass from the starting and the end of the cycle. Elimination is defined as the difference between original and final abundance multiplied by the arithmetic mean of the starting and final individual weight of the respective age group (Winberg, 1971):

$$E = (N_1 - N_2) \cdot 0.5 \cdot (B_1/N_1 + B_2/N_2)$$

The production of a species with a multi-year life-cycle can be obtained by summing up the results for single age groups.

In the present study the results of the age group composition analysis were introduced as parameters in the krill production estimation. Mean size of age classes and their proportion of total abundance are given in Table 3. Table 4 includes the number of individuals and the biomass for each age group. Data indicated by asterisks represent theoretical values derived from the linearized regression in Figure 4, to allow the calculation of the elimination. Elimination and production of biomass within a one year cycle are also given for each age group in Table 4.

Since age class 1^+ was almost completely missing in 1987/88 and 1989/90 seasons, this group was not considered for the total production in either year. Furthermore, the 3^+ age class elimination and production figures were only of theoretical interest in 1987/88, because this group was almost missing in this season. Absolute krill production was 2.522×10^6 tonnes for 1987/88 excluding 3^+ age group, and the relative relationship between production and biomass can be calculated as $P/B = 0.94$ or 1.1 if the theoretical values for age group 3^+ are considered. In 1989/90 a biomass of 1.159×10^6 tonnes was estimated for the krill stock including age groups older than 1^+. Krill production was calculated as 0.967×10^6 tonnes/year in the survey area, resulting an index of $P/B = 0.83$.

4. DISCUSSION

The present net sampling surveys as well as the analysis were carried out in a standardized way, which allows a direct comparison of the results. Overall mean biomass in summer ranged from 6.1 g/m^2 in 1987/88 to less than 4.5 g/m^2 in 1989/90, but it was at its minimum in winter 1986 (0.55 g/m^2). Seasonal variation between summer and winter exceeded a factor of 35 times, i.e. the winter stock was at a minimum level of 2.8% of the maximum observed summer stock. The interannual variability between the krill summer stock was less pronounced, the total number of krill varied by factor 1.6, which means the lowest summer value still reached 61% of the amount observed in a year of maximum abundance. Results from hydroacoustic surveys (summarized by Godlewska and Rakusa-Suszczewski, 1988) indicate differences within the same season (1984/85) of 1.78 to 37.58 tonnes/n miles^2, which is a factor of at least 21 between spring and late summer. Maximum interannual difference obtained from standardized hydroacoustic surveys was 71.27 tonnes/n miles^2 (1983/84) and 7.95 tonnes/n miles^2, which is a factor of 8.9 times.

In general it can be concluded that the seasonal fluctuation in abundance and biomass of the krill stock off the Antarctic Peninsula is several times higher than the interannual variability. The situation might be different in areas like South Georgia, where krill is living close to its northern distribution limits and large-scale ocean atmosphere processes may lead to a dramatic decline in the krill stock of this region from year to year (Bonner *et al.*,1978; Morris and

Priddle, 1984; Heywood *et al.*, 1985; Priddle *et al.*, 1988). The extremely low krill abundance off South Georgia does not necessarily mean a decrease in total abundance in the Atlantic sector, because at the same time abundance may increase further south in the Scotia Sea.

The interannual variation in krill abundance might be explained by oceanographic circumstances besides at least one known biological factor. Recruitment shows a general alternation of good and bad year classes (Siegel, 1989). Data indicated that during the last years several year-classes had been poor or almost missing, e.g. year-class 1983/84 as well as 1986/87 and 1988/89 (present data). This led to variation in the total abundance and biomass of the krill stock. Since mean length-per-age of gravid female indicate that krill becomes mature during 3^+ age group and krill live at least as long as 5^+ age group, several age groups contribute to the spawning success. Therefore a breakdown of the entire spawning stock like for the South Georgia region was never observed.

Information on post-larval krill mortality are rare in the published literature. Estimates obtained by different methods were summarized by Miller and Hampton (1989). In determining natural mortality of krill a critical review of methods and assumptions is required.

Kawakami and Doi (1979) analysed krill mortality by applying Edmondson's method, which considers several parameters like duration of egg development, number of offspring, hatching rates, larval survival and length-at-age (see Miller and Hampton, 1989). For most parameters assumptions had to be made. The natural mortality rate of krill at one year after hatch was estimated as M = 5.5. Calculations based on length-at-age data with a two to three year life cycle will, however, strongly affect the results by increasing the mortality rate. Meanwhile studies on longevity suggest a longer life span of krill and 6 to 8 age groups seem to be more realistic, so that the value of Kawakami and Doi (1979) seems to be too high at least for the postlarval age groups (see below).

Brinton and Townsend (1984) tried to avoid the assumption of a constant mortality rate over several years and supported figures for single age groups. They derived estimates for the 1980/81 season of M = 2.31 for 1 to 2 year old krill and M = 0.6 for 2 to 3 year old animals. The problem arises that Brinton and Townsend (1984) based their calculations on a three year life span of krill. Their age group 1 (20 to 43 mm) included the two age groups 1^+ and 2^+. Age group 2^+ was represented at that time by the poor 1978/79 year class (Witek *et al.*, 1980), which disappeared in the chosen log-transformed length frequency distribution given by these authors. Furthermore the spawning season 1980/81 was extremely successful (Rakusa-Suszczewski, 1984; Hempel, 1985) so that larval age group 0 was abundant above average. From this it has to be assumed the first mortality rate of M = 2.31 is too high. Age group 3 (44 to 58 mm) of Brinton and Townsend (1984) also included more than one age group, which would lead to an overestimation of the abundance in this group and consequently underestimate the annual mortality rate.

Siegel (1986) estimated total mortality rates by regression analysis based on age composition data from various years (linearized catch curve method). Results varied from Z = M = 0.78 to 1.17. One disadvantage was the fact that calculations were based on data from limited areas. Abundance data from the Bransfield Strait might be problematic, because the concept on spatial succession of krill stages/age groups (Siegel, 1988 and present data) showed that older stages are under-represented inside Bransfield Strait. Other data were available from one transect off Anvers Island which covered the distribution range from juvenile to adult krill and thus included all age groups, but abundance data from a single transect might be arbitrary and not representative for the composition of the whole stock along the Peninsula.

The present analysis circumvents the problem by considering weighted data from the entire survey area. Average mortality rates were obtained by deleting age groups which were known to be under-represented in the stock. Results varied between Z = 0.88 and 0.96 for data from two different years.

Natural mortality and the growth constant **K** of the von Bertalanffy growth curve are closely related. Priddle *et al.* (1988) estimated the instantaneous rate of natural mortality from growth parameters obtained by Rosenberg *et al.* (1986) for a six to seven year life-span of krill. Under the assumption that **M** is about two times greater than **K**, the values would range from M = 0.8 to 1.35. Siegel (1986) also calculated natural mortality rates from Bertalanffy growth curve parameters which was based on six age groups and resulted M = 0.94 to 0.99. This method is of course highly dependent on the validity of the age determination. The conversion factor 2 for **K** to **M** used by Priddle *et al.* (1988) was taken from clupeoid fish. Beverton and Holt (1959) found values of the ratio **M/K** mainly ranging between 1.5 and 2.5. Siegel (1986) determined the growth parameter **K** for krill by different methods and his results ranged from K = 0.4018 to 0.4728 which would result a factor of M/K = 1.86 to 2.39. Therefore results obtained by this method have to be considered as rough estimates of the natural mortality rate.

Basson and Beddington (1989) estimated krill mortality by different approaches. They considered the length specific aspect of mortality and transformed *Discovery* data to cumulative length frequency distribution and from this modelled curve they derived a relatively low average mortality rate of M = 0.5. This value is almost identical with the growth rate (K = 0.52) estimated from the same data. Basson and Beddington (1989) further tried to estimate krill mortality including length specific aspects of predation with the assumption that predators mainly feed on larger krill. They established a simple length dependent predation curve and estimated average mortality rates for simulated and observed length frequency data. Total mortality was Z = 0.65 for the time before and Z = 0.45 for the period after the reduction of the whale stock. The authors stated, however, that there was no indication of a continued trend for the decrease in krill mortality rate.

Naturally small specimens are exposed to a larger predation than larger ones, simply because small animals have more predators (Sparre *et al.*, 1989). Peters (1955), for example, supported data on length frequencies from whale stomachs and found high abundances of 20 to 30 mm juvenile krill. These size groups represented age class 1^+ and indicate that these length classes are also heavily exploited by whales when they are most abundant in early summer. Furthermore, other carnivorous zooplankton seem to feed heavily on younger krill life stages (Hosie, 1988). In general the simple predation model is a valid alternative method, but the hypothetical curve of length-specific predation rates possibly needs further improvement, because data on krill predation are still insufficient or even missing for many components of the related food web.

In principal longevity is more closely related to mortality than to **K** and $\mathbf{L}_\infty$ (Sparre *et al.*, 1989). Following Alagaraja (1984) the life span of a species is the age at which 99% of a cohort had died and it had been exposed to natural mortality only:

$$M_{1\%} = -\ln(0.01)/Tm \qquad \text{(Tm as longevity in years)}$$

Recently published results on number of krill age groups range from six groups including larval 0 group which means a life span of at least five years (Siegel, 1987) up to six to seven year life span (Rosenberg *et al.*, 1986) or eight age groups and a maximum longevity of seven years (Ettershank, 1984 and 1985). Based on this maximum range krill mortality rate then would be expected as M = 0.92 for a five year life span or M = 0.66 for a seven year life span. This general approach once again demonstrates that some of the results mentioned above deviate considerably from the expected level.

Total production can be calculated from the standing stock over a given time and the growth rate of the species. In the season 1987/88 total abundance, biomass and production were higher than in 1989/90, although two age groups (1^+ and 3^+) were almost missing in this season instead of only one (1^+) in 1989/90. The amount of krill listed in Table 4 support estimates of instantaneous biomass and abundance. Since the area off the Antarctic Peninsula is not static but highly dynamic, the potential or effective total biomass within one season will be higher than reflected by the present results.

Several basic parameters are available in the literature to come at least to a rough idea of the krill fluxes through the area. It is known that krill occurrence is extremely low in the entire area during the whole winter season and that the increase in abundance and biomass is commencing not before late October, while the stock declines rapidly during March (Stepnik, 1982; Siegel, 1988). This gives a maximum time span of 150 days while krill is immigrating in considerable numbers to maintain the high level of the summer stock. The main currents run from the southwest to the northeast. Current speed measurements for the upper 400 m water column show a maximum range between 6.5 and 32 cm/sec (Stein, 1979; Wittstock and Zenk, 1983; Nowlin and Zenk, 1988). An average velocity of 20 cm/sec for the near-surface layer obtained from tracking the drift of FGGE buoys seems to be more realistic to follow the drift of krill, because this layer is more strongly influenced by wind than the deeper layers where current meter measurements had been carried out.

The survey area extended over approximately 650 nautical miles. Let us assume that krill is continually drifting in from the southwest and transported with the mean current speed and no retention occurs by meanders or eddies. Under these circumstances a minimum time interval of 70 days is necessary for a complete exchange of the water masses and the krill standing stock along the Peninsula. This means that during an entire summer season the krill stock could be exchanged about two times at a maximum. The instantaneous biomass was estimated as 1.65×10^6 tonnes (for all age groups) in 1987/88 and 1.16×10^6 tonnes in 1989/90. The biomass including the krill production would amount to 2.52×10^6 tonnes and 2.13×10^6 tonnes, respectively. Considering an exchange rate of 2.0 a maximum effective total stock size of 5.0×10^6 and 4.3×10^6 tonnes, respectively, would have passed the survey area during the seasons under consideration. Taking into account the meandering of the current system and the occurrence of eddies with accumulating and retention of krill this is included in the estimation of the instantaneous biomass - then the exchange rate is obviously too high and the potential or effective total biomass and production represent the extreme upper limit of the krill stock passing the survey area within one season.

Several attempts had been made to estimate the ratio of production to biomass (P/B) and were discussed by Miller and Hampton (1989). Allen (1971) was the first to calculate a ratio of P/B = 1.8 to 2.3 and stated the lower end of the range being more likely. Yamanaka (1983) estimated a ratio of P/B = 1.19, which was at least partly based on the assumptions made by Kawakami and Doi (1979) for the calculation of the natural mortality rate as described above. Miller *et al.* (1985) obtained different values ranging from P/B = 1.19 to 2.77. Siegel (1986) calculated production from age group composition analysis and found smaller P/B ratios ranging from 0.8 to 1.1. Almost identical results (P/B = 0.83 to 0.94) were obtained in the present study applying the same method for different and more comprehensive survey data sets. A more theoretical value of 1.1 was derived from the same analysis by substituting some data of strongly under-represented age groups with expected abundances.

The P/B estimations of Allen (1971) were carried out for various growth and mortality models and showed that longevity and mortality rates as well as growth rates are fundamentally important to obtain reasonable estimates of the P/B ratio.

REFERENCES

ALAGARAJA, K. 1984. Simple methods for estimation of parameters for assessing exploited fish stocks. *Indian J. Fish. 31:* 177-208.

ALLEN, K.R. 1971. Relation between production and biomass. *J. Fish. Res. Bd. Canada 28:* 1573-1581.

BASSON, M. and J.R. BEDDINGTON. 1989. Preliminary analysis of growth and mortality rates of Antarctic krill *(Euphausia superba)* from length frequency samples. In: HEYWOOD, R.B. (Ed.). *University Research in Antarctica, Antarctic Special Topic*: 51-55.

BEVERTON, R.J.H. and S.J. HOLT. 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. In: WOLSTENHOLME, G.E.W. and M. O'CONNOR (Eds.). *The Lifespan of Animals*, Vol. 5: 142-180.

BONNER, W.N., I. EVERSON, P.A. PRINCE. 1978. A shortage of krill, *Euphausia superba,* around South Georgia. *ICES Biol. Oceanogr. Cttee. C.M. 1978 L24:* 1-3.

BRINTON, E. and A.W. TOWNSEND. 1984. Regional relationships between development and growth in larvae of Antarctic krill, *Euphausia superba,* from field samples. *J. Crust. Biol. 4* (Spec.1): 224-246.

DIMMLER, W. and T.H. KLINDT. 1990. A new electronic system for the rectangular midwater trawl (RMT). *Mar. Biol. 107*: 345-348.

ETTERSHANK, G. 1984. A new approach to the assessment of longevity in Antarctic krill *Euphausia superba. J. Crust. Biol. 4* (Spec.1): 295-305.

ETTERSHANK, G. 1985. Population age structure in males and juveniles of the Antarctic krill, *Euphausia superba* Dana. *Polar Biol. 4:* 199-201.

EVERSON, I. 1977. The Southern Ocean. The living resources of the Southern Ocean. *FAO GLO/SO/77/1*: 1-156.

GODLEWSKA, M. and S. RAKUSA-SUSZCZEWSKI. 1988. Variability of krill, *Euphausia superba,* Dana 1852 (Crustacea, Euphausiacea), distribution and biomass in the Western Antarctic (Bransfield Strait, Drake Passage, Elephant Island) during 1976-1987. *Inv. Pesq. 52:* 575-586.

HEMPEL, I. 1985. Variation in geographical distribution of larvae of Antarctic krill, *Euphausia superba,* in the Southern Atlantic Ocean. In: SIEGFRIED, W.R., P.R. CONDY and R.M. LAWS (Eds). *Antarctic Nutrient Cycles and Food Webs.* Berlin, Heidelberg, New York: Springer. pp 304-307.

HEYWOOD, R.B., I. EVERSON and J. PRIDDLE. 1985. The absence of krill from the South Georgia zone, winter 1983. *Deep-Sea Res. 32:* 369-378.

HOSIE, G. 1988. In: Workshop on Antarctic Phytoplankton/Zooplankton Relationships (II). *BIOMASS Rep. Ser. 56:* 1-13.

HOSIE, G.W., T. IKEDA, and M. STOLP. 1988. Distribution, abundance and population structure of the Antarctic krill (*Euphausia superba* Dana) in the Prydz Bay region, Antarctica. *Polar Biol. 8:* 213-224.

KAWAKAMI, T. and T. DOI. 1979. Natural mortality of krill and density in swarms. In: DOI, T. (Ed.). *Comprehensive report on the population of krill, Euphausia superba, in the Antarctic.* Tokai Regional Fisheries Research Laboratory. pp 19-21.

MACDONALD, P.D.M. and T.I. PITCHER. 1979. Age-groups from size-frequency data: A versatile and efficient method of analysing distribution mixtures. J. *Fish. Res. Bd. Canada 36:* 987-1001.

MILLER, D.G.M. and I. HAMPTON,. 1989. Biology and Ecology of the Antarctic krill *(Euphausia superba* Dana): A review. *BIOMASS Scient. Ser. 9*: *1-1*66.

MILLER, D.G.M., I. HAMPTON, J. HENRY, R.W. ABRAMS and J. COOPER. 1985. The relationship between krill food requirements and phytoplankton production in a sector of the southern Indian Ocean. In: SIEGFRIED, W.R., P.R. CONDY and R.M. LAWS (Eds.): *Antarctic Nutrient Cycles and Food Webs.* Berlin, Heidelberg, New York: Springer. pp 362-371.

MORRIS, D.J. and J. PRIDDLE. 1984. Observations on the feeding and moulting of the Antarctic krill, *Euphausia superba* Dana, in winter. *Br. Antarct. Surv. Bull. 65:* 57-63.

NOWLIN, W.D. and W. ZENK. 1988. Westward bottom currents along the margin of the South Shetland Island Arc. *Deep-Sea Res. 35:* 269-301.

PETERS, H. 1955. Uber das Vorkommen des Walkrebschens *Euphausia superba* Dana und seine Bedeutung fur die Ernahrung der sudlichen Bartenwale. *Arch. Fisch Wiss. 6:* 288-304.

POMMERANZ, T., C. HERRMANN and A. KUHN. 1982. Mouth angles of the Rectangular Midwater Trawl RMT 1+8 during paying out and hauling. *Meeresforsch. 29:* 267-274, 1982.

PRIDDLE, J., J.P. CROXALL, I. EVERSON, R.B. HEYWOOD, E.J. MURPHY, P.A. PRINCE and C.B. SEAR. 1988. Large-scale fluctuations in distribution and abundance of krill - A discussion of possible causes. In: SAHRHAGE, D. (Ed.). *Antarctic Ocean and Resources Variability.* Berlin: Springer-Verlag. pp 169-182.

S. RAKUSA-SUSZCZEWSKI. 1984. Krill larvae in the Atlantic sector of the Southern Ocean during FIBEX, 1981. *Polar Biol. 3:* 141-147.

ROE, H.S.J. and D.M. SHALE. 1979. A new multiple Rectangular Midwater Trawl (RMT 1+8) and some modifications to the Institute of Oceanographic Science's RMT 1+8. *Mar. Biol. 50:* 283-288.

ROSENBERG, A.A., J.R. BEDDINGTON and M. BASSON. 1986. Growth and longevity of krill during the first decade of pelagic whaling. *Nature 324:* 152154.

SAVILLE, A. 1977. Survey methods of appraising fishery resources. *FAO Fish. Tech. Pap. 171:* 1-76.

SIEGEL, V. 1986. Untersuchungen zur Biologie des antarktischen Krill, *Euphausia superba,* im Bereich der Bransfield Straße und angrenzender Gebiete. *Mitt. Inst. Seefisch., Hamburg 38:* 1-244.

SIEGEL, V. 1987. Age and growth of Antarctic Euphausiacea (Crustacea) under natural conditions. *Mar. Biol. 96:* 483-495.

SIEGEL, V. 1988. A concept of seasonal variation of krill (*Euphausia superba)* distribution and abundance west of the Antarctic Peninsula. In: SAHRHAGE, D. (Ed.). *Antarctic Ocean and Resources Variability*. Berlin: Springer-Verlag. pp 219-230.

SIEGEL, V. 1989. Winter and spring distribution and status of the krill stock in Antarctic Peninsula waters. *Arch. Fisch Wiss. 39* (Beih.1): 4572 .

SPARRE, P., E. URSIN, and S.C. VENEMA. 1989. Introduction to tropical fish stock assessment. *FAO Fisheries Tech. Paper 306:* 1-317.

STEIN, M. 1979. Stratification and currents off Elephant Island in early February 1976. *Meeresforsch. 27:* 75-87.

STEPNIK, J.C. 1982. All-year populational studies of Euphausiacea (Crustacea) in the Admiralty Bay (King George Island, South Shetland Islands, Antarctic). *Pol. Polar Res. 3:* 49-68.

WATKINS, J.L ., D.J. MORRIS and C. RICKETTS . 1985. Nocturnal changes in the mean length of a euphausiid population: vertical migration, net avoidance, or experimental error? *Mar. Biol. 86:* 123-127.

WINBERG, G.G. 1971. *Methods for the Estimation of Production of Aquatic Animals.* London: Academic Press. pp 175.

WITEK, Z., A. KORONKIEWICZ and G.J. SOSZKA. 1980. Certain aspects of the early life history of krill, *Euphausia superba* Dana (Crustacea). *Pol. Polar Res. 1:* 97-115.

WITTSTOCK, R.R. and W. ZENK. 1983. Some current observations and surface T/S distribution from the Scotia Sea and Bransfield Strait during early austral summer 1980/81. *Meteor Forsch.-Ergeb. Reihe A/B 24:* 77-86 .

YAMANAKA, I. 1983. Interaction among krill, whales and other animals in the Antarctic ecosystem. *Nem. Natl Inst. Polar Res. 27:* 220-232.

Table 1: Stratified mean and total abundance of krill for different years and site clusters (cluster numbers of earlier years refer to results given by Siegel (1987 and 1989)).

Year/Cluster	Str. Mean (n x 1 000 m^{-3})	Approx. Cluster Size (n $miles^2$)	Absoulte Abundance (n x 10^9)
85/1	225.30	1 300	205
85/2	165.59	30 000	3 450
85/3	6.25	31 000	141
86/1	9.51	7 800	51
86/2	5.55	19 400	74
87/1	93.71	2 100	140
87/2	118.99	30 000	2 553
87/3	49.76	49 000	1 735
90/1	217.13	6 900	1 021
90/2	77.46	9 900	527
90/3	36.51	40 000	1 028
90/4	9.84	20 000	140

Table 2: Statistical table of krill biomass calculations for different surveys in the region of the Antarctic Peninsula (the stratified mean is calculated for the area of krill occurrence).

	February 1982	March 1985	May/June 1986	Nov/Dec 1987	Dec/Jan 1989/90
Number of Stations	21	59	59	74	69
Strat. Mean (g/m^2)	4.90	4.23	0.55	6.13	4.50
90% Confidence Limits (%)	± 79	± 102	± 85	± 108	± 60
Tonnes/n $miles^2$	16.8	14.5	1.9	21.0	15.43
Size of Survey Area (n $miles^2$)	14 300	97 200	78 940	88 230	93 800
Size of Krill Area (%)		64	35	89	80
Total Biomass (10^6 tonnes)		0.905	0.053	1.651	1.160

Table 3: Results of distribution mixture analysis for age group composition of the krill stock during summer 1987/88 and 1989/90.

	Age Groups				
	1^+	2^+	3^+	4^+	5^+
1987/88					
Proportion %	1.5	78.4	4.4	11.3	4.3
Mean Length	15.4	29.6	44.7	51.6	55.3
σ	1.4	3.7	2.5	2.6	1.1
1989/90					
Proportion %	2.34	51.20	27.97	15.18	3.31
Mean Length	26.5	35.9	44.3	50.8	55.4
σ	1.3	3.3	2.7	2.8	1.9

Table 4: Estimated total abundance of krill age groups, biomass and production from 1987/88 and 1989/90 survey data (* indicate theoretical values obtained from regression analysis in Figure 11.

		Season			
		1987/88		1989/90	
ln N	1+	24.92	(29.84)*	24.88	(29.02)*
	2+	28.87		27.96	
	3+	23.42	(27.92)*	27.36	
	4+	26.94		26.75	
	≥ 5+	25.97		25.22	
$N \times 10^9$	1+	66.4	(9 106)*	63.7	(4 011)*
	2+	3472.1		1391.8	
	3+	194.9	(1 362)*	760.4	
	4+	500.5		412.6	
	≥ 5+	190.4		90.1	
W (10^3tonnes)	1+	1.4	(192)	5.3	(335)
	2+	543		339	
	3+	109	(764)	384	
	4+	439		336	
	≥ 5+	209		100	
E (10^3tonnes/year)					
	2+	500		429	
	3+	(757)		236	
	4+	619		229	
	≥ 5+	306		308	
P (10^3tonnes/year)					
	2+	851		434	
	3+	(978)		281	
	4+	293		181	
	≥ 5+	77		71	
$B = \Sigma W_{(2-5)}$ (10^3tonnes) (instantaneous biomass)		1300	(1 956)	1159	
$\Sigma P_{(2-5)}$ (10^3tonnes)		1221	(2199)	967	
$P+B_{(1-5)}$ (10^3tonnes)		2522		2131	
P/B		0.94	(1.1)	0.83	

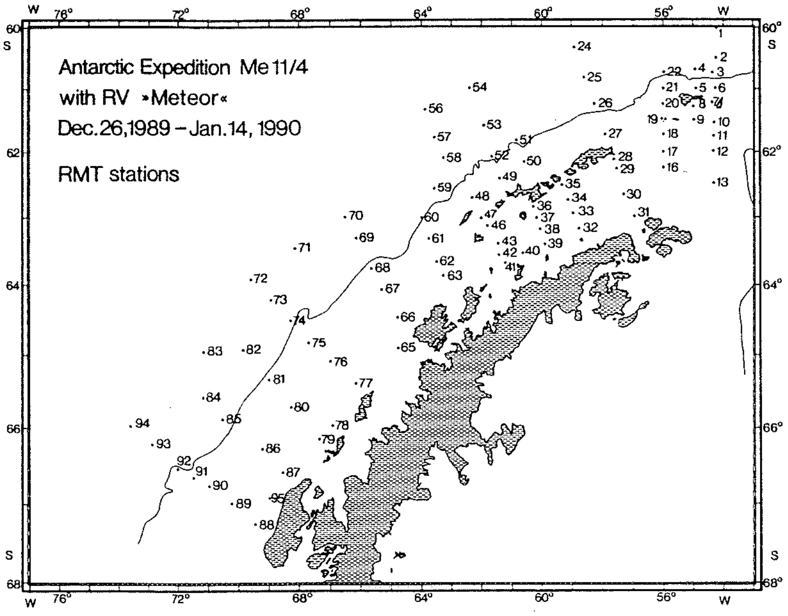

Figure 1: Station grid for RMT net sampling survey during *Meteor* cruise ME11/4, 26 December 1989 to 13 January 1990.

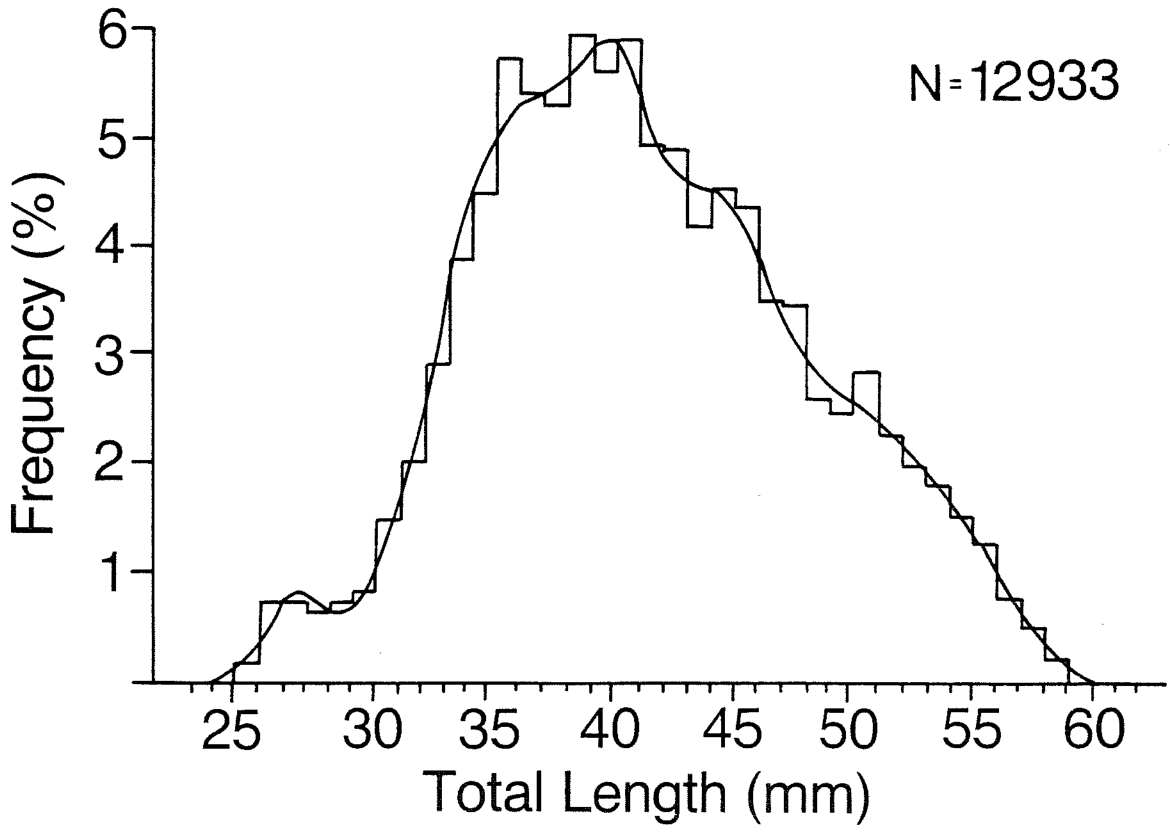

Figure 2: Composite krill length frequency distribution for the survey area in 1989/90 season and fitted line from distribution mixture analysis (see text).

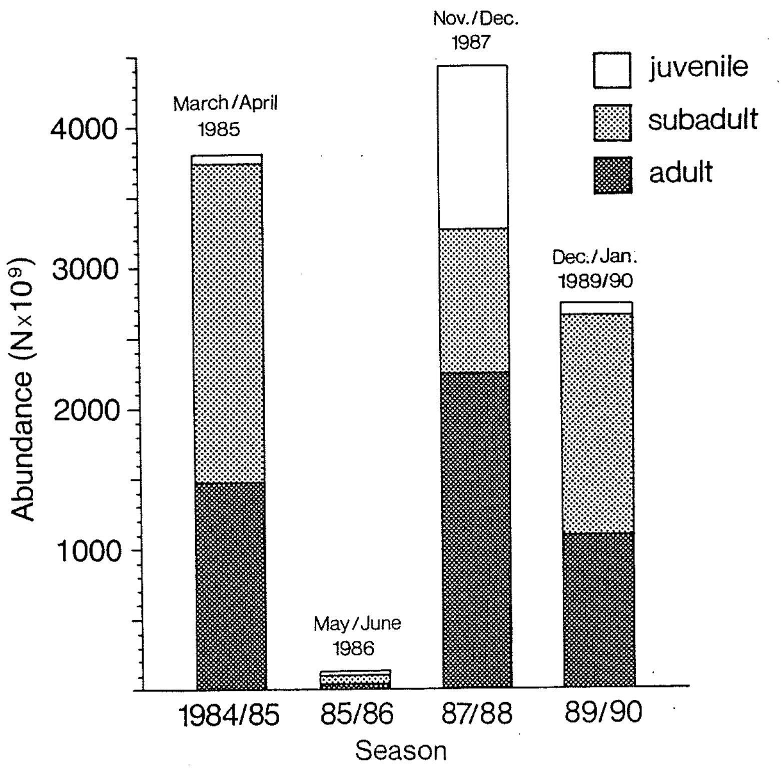

Figure 3: Absolute krill abundance in the Antarctic Peninsula survey area for different years.

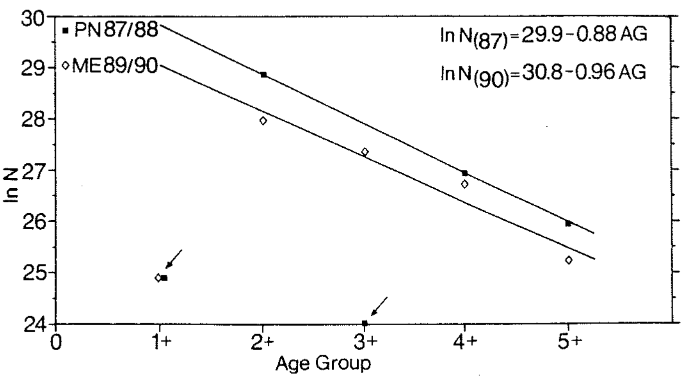

Figure 4: Estimation of krill mortality rate by linearized catch curve analysis for 1987/88 and 1989/90 survey data (data points indicated by arrows were excluded from regression analysis, see text).

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