

The South African SIBEX I Cruise to the Prydz Bay region, 1984: IX. Krill (*Euphausia superba* Dana)

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Although emphasis during SIBEX I was on investigations of physical and biological oceanography, some work was directed to investigations of the distribution, abundance, and biology of krill in the survey area. This paper presents a preliminary synopsis of the results from the krill biology research component of the cruise. It is concluded that krill did not appear to be concentrated in this survey area by the pattern of water circulation operative at the time of the survey.

Hoewel die klem tydens SIBEX I op fisiese en biologiese oseaanografiese waarnemings geval het, is daar ook aandag geskenk aan ondersoek oor die verspreiding, voorkoms en biologie van kril in die opnamegebied. In hierdie artikel word 'n voorlopige samevatting gegee van die navorsingskomponent tydens die vaart wat oor krilbiologie gehandel het. Daar is tot die gevolgtrekking gekom dat kril skynbaar nie tydens die ondersoekperiode deur die watersirkulasiepatroon in die waarnemingsgebied gekonsentreer is nie.

Introduction

The Indian sector of the Antarctic Ocean is one of the least well studied biological regions of the Southern Ocean (El-Sayed *et al.* 1979). In particular, the oceanic environs of Prydz Bay and the Enderby Peninsula (50 – 70°E) have long been considered regions of high biological productivity (Marr 1962, Mackintosh 1972, Everson 1977, Lubimova *et al.* 1980 and many others) which supposedly contain large concentrations of krill (*Euphausia superba* Dana) (Mackintosh 1972, Hampton 1983). It is hypothesised that an anti-cyclonic gyral system provides the hydrological conditions necessary for the maintenance of a regionally localised krill stock (Lubimova *et al.* 1980, Smith *et al.* 1984).

It was not until the First International BIOMASS Experiment (FIBEX) in 1981 that hydroacoustic surveys provided direct evidence for high krill abundances near Prydz Bay (Anon. 1981). Mean estimates of krill abundance put the absolute biomass at some 19 times higher than for the Scotia Sea region of the western Atlantic (Hampton 1983); hitherto thought to be one of the richest krill areas in the whole Antarctic (Marr 1962, Everson 1977, Lubimova *et al.* 1980).

Following FIBEX, the BIOMASS (Biological Investigations of Marine Antarctic Systems and Stocks) Technical Group on Programme Implementation and Co-ordination recommended that part of the Second International BIOMASS Experiment (SIBEX) should be devoted to a survey of the southern Indian Ocean during the summer seasons of 1983/4 and 1984/5 (Anon. 1982). Considering our meagre knowledge of water circulation in the Prydz Bay region and in view of its proposed effect on krill distribution, it was decided that emphasis should be placed on investigations of physical and biological oceanography in the first season (1983/4). This was seen as constituting an essential prerequisite for the determination of areas of biological interest

to be studied during the second phase of the experiment in 1984/85 (Anon. 1982).

The SIBEX I survey area was divided into three sectors which were surveyed by Japan (twice), Australia and South Africa respectively. This report is a preliminary synopsis of krill biological results obtained as part of the South African contribution.

Material and methods

An area of the southern Indian Ocean (62 – 66°S; 52 – 64°E) was surveyed during the 35th voyage of the SA *Agulhas* between 26 March and 20 April 1984. Forty-five oceanographic stations (CTD and bottle casts) occupied a grid of seven legs, each leg extending from the pack-ice edge to approximately 200 nautical miles north (Fig. 1).

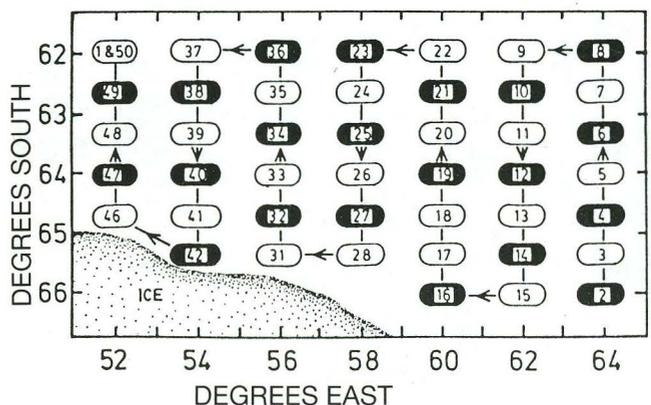


Fig. 1. South Africa SIBEX I survey grid showing positions of net stations. This grid differs from Figure 1 (Section 2).

Paired B57 (Bongo) nets were deployed at each station and a double oblique tow made from the surface to between 250 and 300 m depth. Net mouth diameter was approximately 60 cms and nets were fitted with 500 μ m and 300 μ m mesh respectively. Filtering rates were measured by a flowmeter mounted in the mouth of each net. Both water temperature and fishing depth were monitored continuously by a submersible monitoring unit and information was relayed via multi-core conductor cable to give a real-time display of both parameters on deck. Data were also logged directly onto computer tape and printed out at 5 m intervals.

A weighted neuston net (mouth area – 0,98 m²; 950 μ m mesh) was also towed at each station from a boom on the ship's forward port quarter. It was hauled for 10 – 15 mins over a distance of approximately one kilometre and the volume of water filtered was calculated based on net-mouth area and speed through the water. During all fishing operations ship's speed was maintained as close to 2,5 knots (1,25 m/sec) as possible.

Preliminary sorting of net samples was carried out on board. Both total and krill catch displacement volumes were measured. Adult and larval krill were extracted. Prescribed techniques were used to assess body length (Mauchline 1981a), sexual maturity (Makarov & Denys 1981), larval development (Fraser 1936, Makarov 1981) and feeding state (Rakusa-Suszczewski 1982). All krill samples were preserved in buffered formalin (4 %) and wet/dry weight determinations were carried out on representative sample aliquots ashore. Catch data were standardised per 1000 m³ water volume filtered. Zooplankton other than krill were preserved separately for specialist analysis ashore.

Results

Krill adults

Post-larval krill were collected in 10 neuston net catches and at 35 Bongo stations. The biomass of each catch was estimated using the methods prescribed by Nast (1982) and Pommeranz *et al.* (1982). Krill biomass in the Bongo catches was between 0 and 491 g/1000 m³ and in the neuston net between 0 and 74529 g/1000 m³. From the station distribution it was apparent that the largest catches of krill were taken in the south of the survey grid (Figs. 2 and 3).

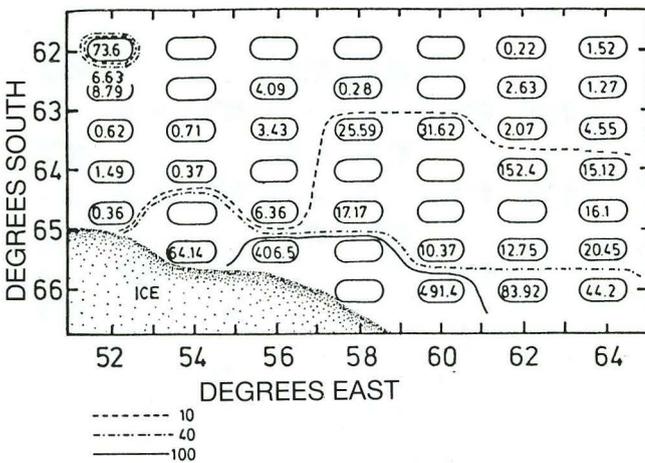


Fig. 2. Biomass of adult krill caught at each Bongo net station in g/1000 m³.

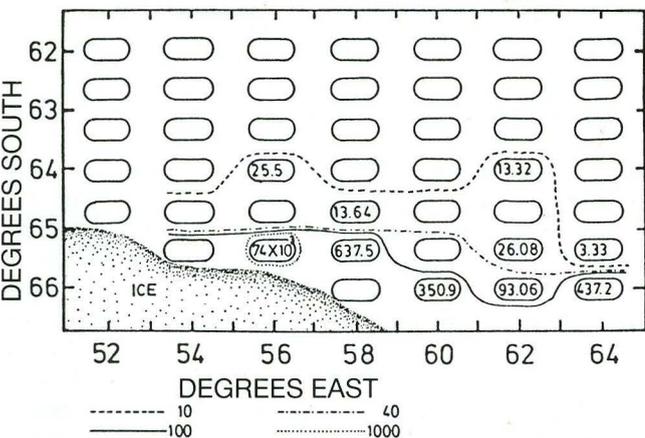


Fig. 3. Biomass of adult krill caught at each neuston net station in g/1000 m³.

Stations 16 and 31 gave clear indication of this trend and both these stations were observed to lie within an area of relatively cold surface water (<-0.05 C) close to the ice-edge (Fig. 4). As a result of this trend and to improve precision of the catch results, the sampling area was stratified according to criteria set out in Saville (1977) and modified by Nast (1982). Two strata were arbitrarily selected north and south of the 0 °C isotherm. This coincided with an area of apparent midwater upwelling and represented the boundary between the presence of Winter Water to the north and its absence in the south (ie. the "Antarctic Divergence").

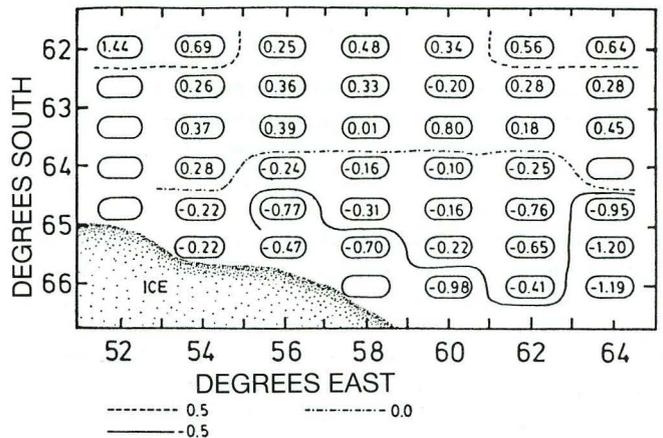


Fig. 4. Surface water temperature distribution in the SIBEX I area surveyed by South Africa.

Stratified mean areal krill biomass and associated variance (Nast 1982) were calculated from both neuston and Bongo catches (Tables 1 and 2). The proportionate standard error of the Bongo mean catch (Table 2) was directly comparable with similar results reported by Nast (1982) at both the 80 and 90 per cent confidence levels. Taking that krill are confined to approximately the top 150 m of the water column gave a total areal biomass of 5.5 × 10⁶ t (±45 %) at the 80 per cent confidence level. Bongo mean catch variance was significantly greater in the south than in the north. This was confirmed by a statistical comparison of the two areal strata (P=0.05, Snedecor & Cochran 1978). The difference was attributed to the incidence of large catches at stations 16, 31 and 28 as well as to a general occurrence of larger catches in the south (Fig. 2).

Table 1

Biomass of post-larval krill collected in two arbitrary strata with the neuston net.

	Biomass strata	
	>0 °C	<0 °C
Number of hauls	25	20
Variance between individual hauls	—	16647,5
Mean biomass/haul \bar{x} (g/10 ³ m ³)	—	3805,2
Variance (\bar{x})	—	13856988
Size of area (nm ²)	41286	25221
Stratified mean biomass/10 ³ m ³ \bar{x}_{st}	1443,0	*{35,8}
Variance stratified mean var (\bar{x}_{st})	1992634,9	*{356,2}
Standard deviation stratified mean	1411,6	*{18,87}
90 % confidence limits	= 1443,0 ± 164 % (g/10 ³ m ³)	*{35,8 ± 89 % (g/10 ³ m ³)}
80 % confidence limits	= 1443,0 ± 127 % (g/10 ³ m ³)	*{35,8 ± 68 % (g/10 ³ m ³)}

*{ } - Excluding station 31

Table 2
Biomass of post-larval krill collected in two arbitrary strata with the Bongo net.

	Biomass strata	
	>0 °C	<0 °C
Number of hauls	25	20
Variance between individual hauls	267,9	139,5
Mean biomass/haul \bar{x} (g/10 ³ m ³)	8,6	77,5
Variance (\bar{x})	10,7	972,8
Size of area (nm ²)	41286	25221
Stratified mean biomass/10 ³ m ³ (\bar{x}_{st}) =	34,8	
Variance stratified mean var (\bar{x}_{st}) =	144,0	
Standard deviation stratified mean =	12,0	
90 % confidence limits =	34,76 ± 57 % (g/10 ³ m ³)	
80 % confidence limits =	34,76 ± 45 % (g/10 ³ m ³)	
Size of area + 150 m depth		
1,59 × 10 ¹³ m ³	5,5 × 10 ¹¹ g krill	
Biomass of krill in whole area	5,5 × 10 ⁶ tonnes (± 45 %)	

Neuston net catches exhibited extremely high variance (Table 1) partly as a result of an exceptionally large catch at station 31 and partly due to an absence of catches in the northern stratum (Fig. 3). The relatively short time (± 2 mins) required to fill the net at station 31 indicated that it fished directly on a very dense surface swarm. Exclusion of station 31 resulted in a marked decrease in the overall catch variance and significant increase in the confidence limits (Table 1). Although the lack of neuston net catches in the north validates the Bongo stratal comparison, lack of data precluded a similar statistical evaluation of the two neuston catch strata.

No significant differences ($P=0,05$) were observed between night (16h00 – 08h00 local time) and day (08h00 – 16h00) Bongo net catches. Conversely, daylight neuston catches ($P=0,05$) were significantly larger than those taken at night. Again, this was attributable to bias introduced by the large catch at station 31 taken during the day. Exclusion of this station resulted in no significant difference between day and night neuston net catches ($P=0,05$).

A total of 3 952 animals were measured and accumulated length frequency promilles for the respective nets are shown in Figure 5. Weighted-mean body lengths were calculated for the neuston (33,5 mm), for the 300 μ m (42,3 mm) and for the 500 μ m (42,2 mm) Bongo nets respectively. Mean length and length frequency distributions showed no significant differences for the two Bongo net meshes used ($P=0,05$). Animals caught in the neuston net were significantly smaller than those collected with either Bongo ($P=0,05$) (Fig. 5).

At station 31, however, Bongo and neuston net length frequency distributions were found to be similar (Fig. 6).

A wide range of adult and sub-adult maturity stages were present in the Bongo net catches (Figs. 7 and 8). Of the 804 male krill stages (Fig. 7), mature but reproductively inactive animals (Stage 3A – Makarov & Denys 1981) were predominant. Conversely, the majority of females ($N=758$) were in the sub-adult (Stage 2B) developmental phase (Fig. 8). Juvenile animals (Stage 1) comprised approximately 20 per cent of all Bongo catches. There were no significant differences between maturity stage distributions for either Bongo net mesh ($P=0,05$). A clear association between body length and maturity stage was evident for both sexes (Fig. 9). At station 12, however, the majority of females in the sub-adult

phase (Stage 2B) were significantly larger (mean body length – 48,5 mm) than sub-adults (mean body length – 34,2 mm) from any of the other stations (Fig. 10a). Comparison of the body length/maturity stage regression line for all female krill with that for all females excluding station 12 (Fig. 10b) indicated a significant difference ($P=0,05$) between the two regression coefficients (Snedecor & Cochran 1978). This suggests a body length/maturity stage disassociation for female krill at station 12.

In keeping with catch and length frequency distributions reported above, sub-adult (Stage 2A and B) animals dominated the neuston net catches (Fig. 11). This was particularly evident at Station 31.

Ovigerous or spent females (Stages 3D and 3E) were only encountered in significant numbers at station 1. Both sexually active male and female animals (Stages 3B and 3C), with spermatophores attached, were present at only 9 stations and no discernible distributional pattern was evident.

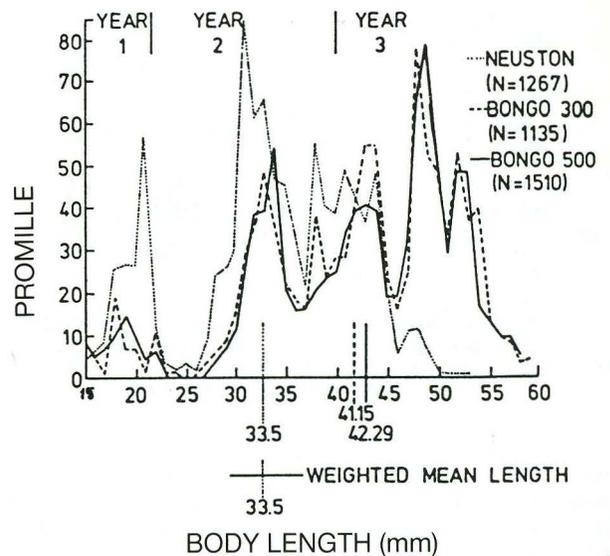


Fig. 5. Accumulated length frequency promilles for the neuston, Bongo 300 μ m and 500 μ m catches. Also shown are krill year-class divisions (after Mauchline & Fisher 1969).

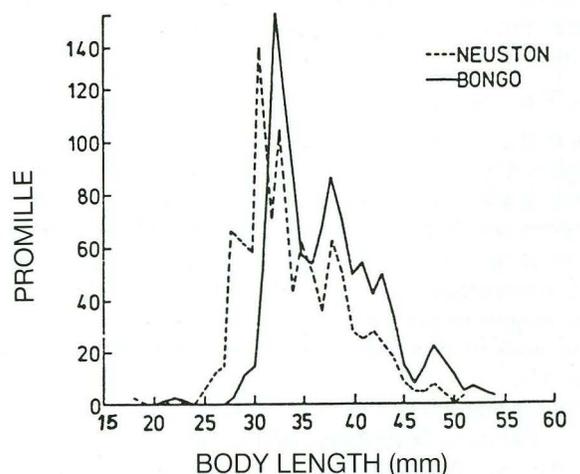


Fig. 6. Length frequency promille of animals collected at station 31 by both Bongo and neuston nets.

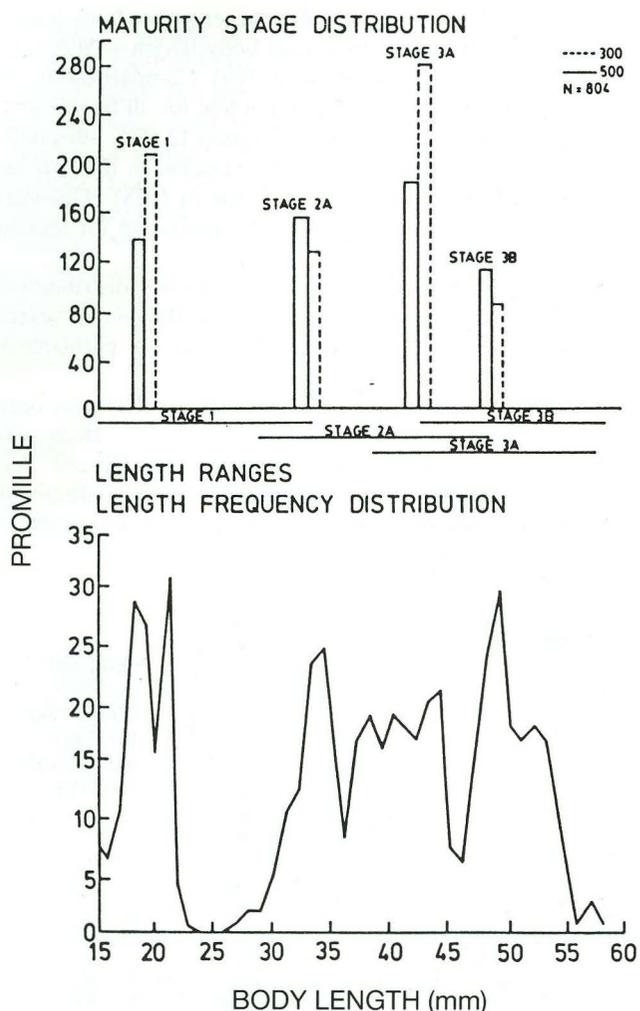


Fig. 7. Maturity stage distribution of male krill in Bongo net catches. The accumulated length frequency promille is also shown for all male animals measured along with body length ranges for each maturity stage.

Stations were grouped according to their respective maturity stage affinities as follows. A Bray-Curtis diversity analysis was used (Field *et al.* 1982, Miller 1985) to classify the proportionate maturity stage distributions of each Bongo net catch (both nets). Catch data were logarithmically transformed as:

$$Y_{ij} = \log(X_{ij} + 1) \quad (1)$$

where X_{ij} = proportionate frequency of the "i"th maturity stage in the "j"th sample; Y_{ij} = corresponding transformed score (Clifford & Stephenson 1975). The subsequent dendrogram was divided at 60 and 73 % similarity. Station affinities of the various maturity stage distributions fell into 3 broad groupings (Fig. 12). The resultant similarity matrix and multi-dimensional scaling (MDS) (Field *et al.* 1982) were used to ordinate the net stations in two dimensions (Fig. 13).

Subsequent MDS clusters confirmed dendrogram groupings, exhibited a horizontal configuration similar to the catch distributions illustrated in Figure 2 (Fig. 14) and confirmed stratification differences in catch distributions. Most noticeable was the high degree of similarity (>80 %) found between stations (Group 1A) in the extreme south of Legs 1 -

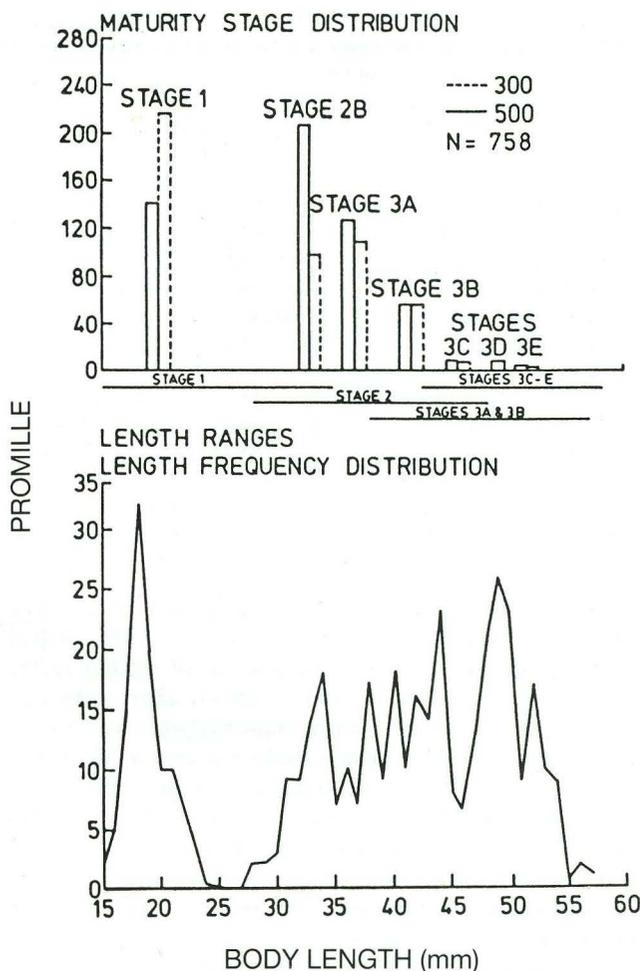


Fig. 8. Maturity stage and length frequency distribution of female krill in Bongo net catches. The accumulated length frequency and maturity stage promilles are shown together with body length ranges for each maturity stage.

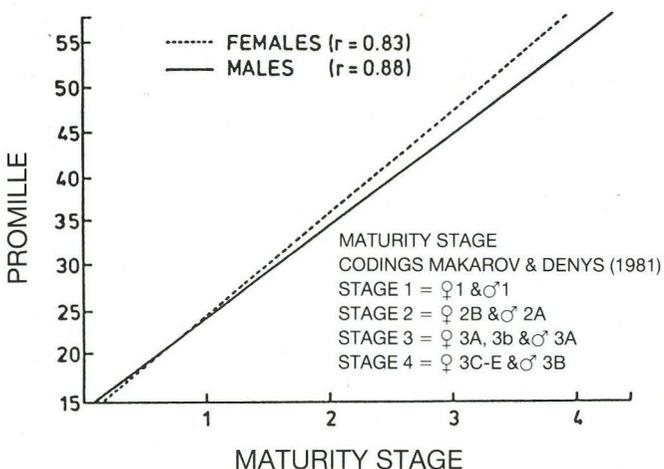


Fig. 9. Maturity stage/body length regressions of both female and male krill collected with the Bongo nets. Regression coefficients (r) are significant at $P=0,01$

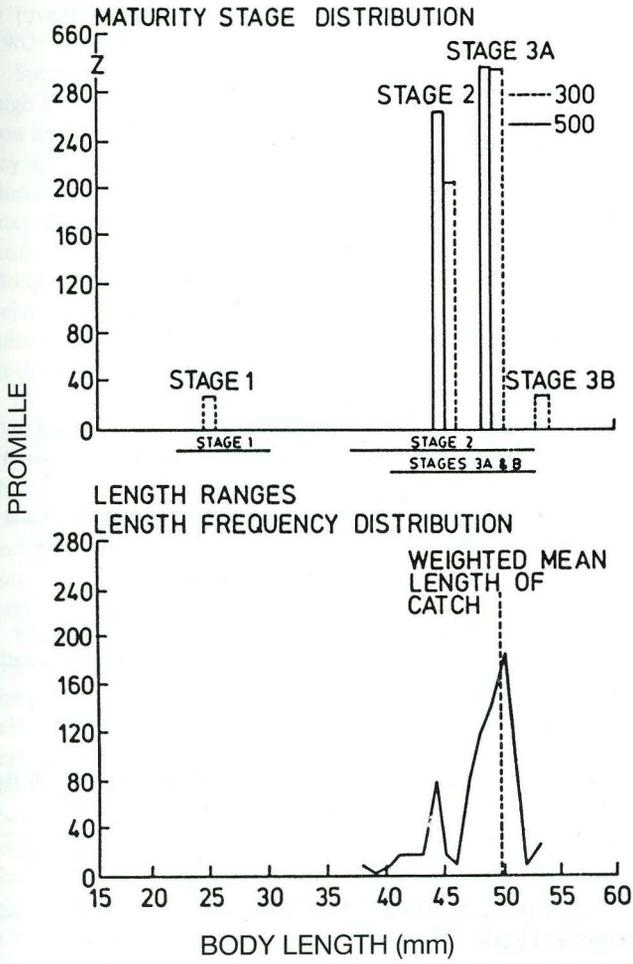


Fig. 10a. Maturity stage/body length distribution of female krill collected with the Bongo net at Station 12.

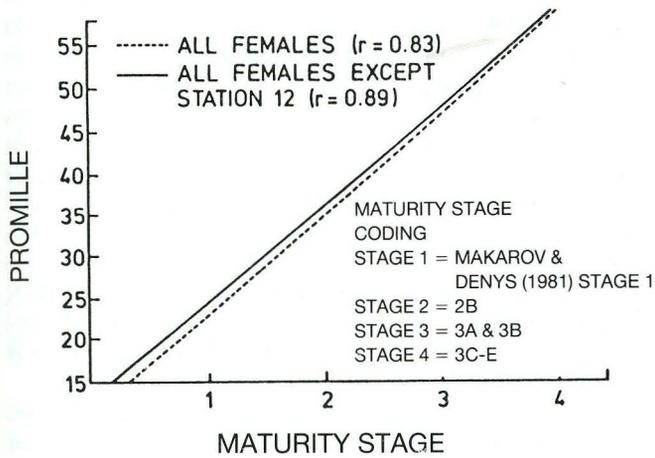


Fig. 10b. Maturity stage/body length regression lines for female krill at all stations and at all stations excluding station 12.

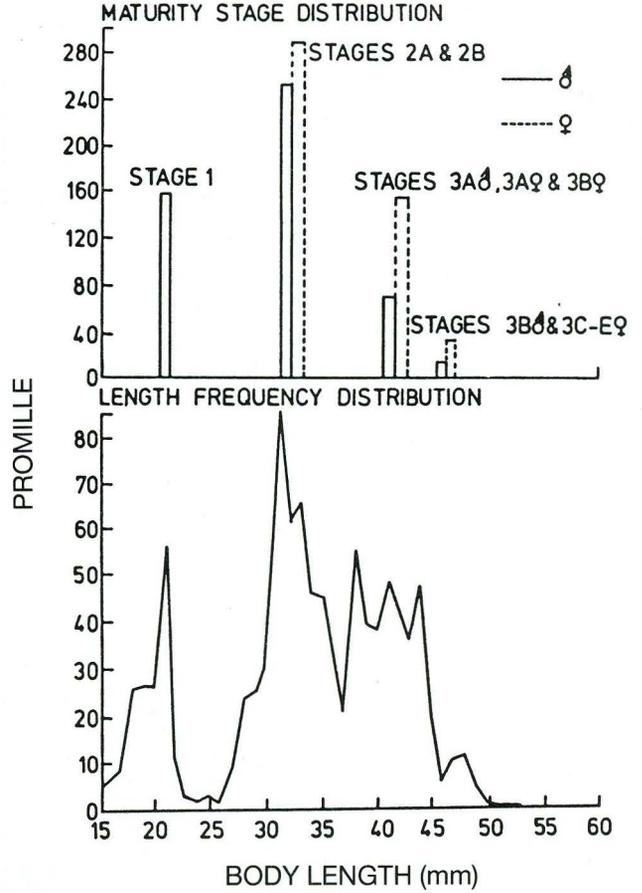


Fig. 11. Maturity stage and body length distributions of both female and male krill collected with the neuston net.

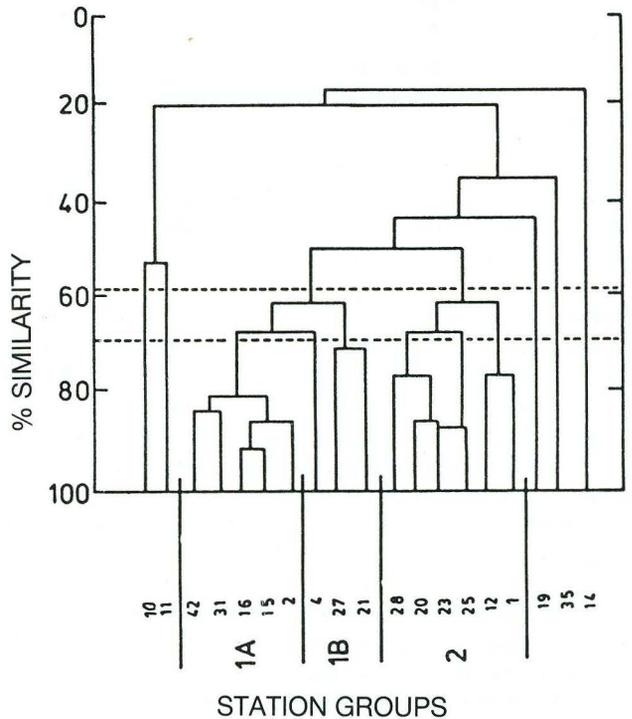


Fig. 12. Dendrogram of maturity stage station affinities obtained using a Bray-Curtis diversity analysis.

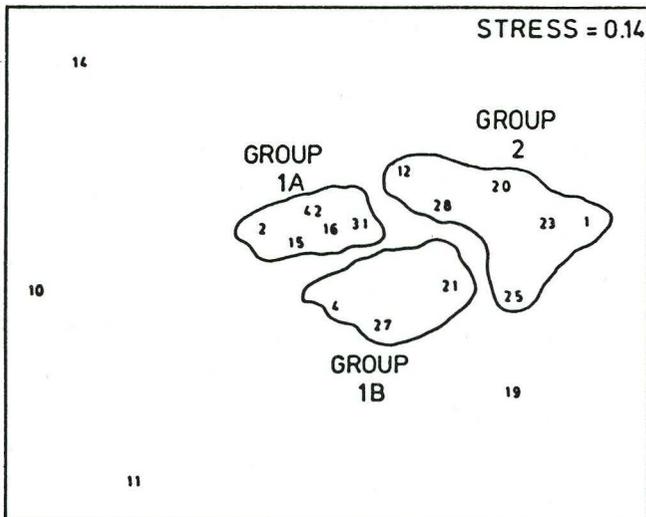


Fig. 13. Two dimensional configuration of maturity stage station affinities obtained by multi-dimensional scaling.

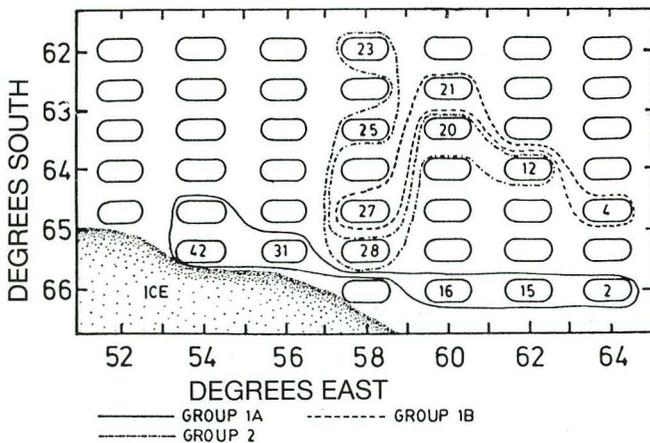


Fig. 14. Horizontal distribution of maturity stage station affinity groupings obtained from a Bray-Curtis analysis and multi-dimensional scaling.

6. The maturity stage attributes of these particular stations were heavily weighted by a preponderance of immature, sub-adult animals (Stage 2).

Larvae

Late stage larvae (furcilia Stages 5 and 6) were numerically predominant in the Bongo catches (Fig. 15). The size ranges of the respective larval developmental stages agreed closely with literature values (Fraser 1936, Makarov 1981). No significant differences in either catch levels or length/developmental stage distributions could be demonstrated for the two net meshes used ($P=0,05$). Larval numerical abundance was relatively even throughout the survey grid (Fig. 16) and the mean value was low (Table 3). The variance of the mean larval catch was significantly smaller than that obtained for adult animals and no significant difference could be demonstrated between the two areal strata ($P=0,05$) (Table 3). Attempts to elucidate larval developmental stage station affinities were unsuccessful using both the Bray-Curtis analysis and MDS. Early calyptopis (Stages 1 – 3) and furcilia (Stages 1 – 2) stages were encountered at 10 stations, 6 of which were south of 64°S.

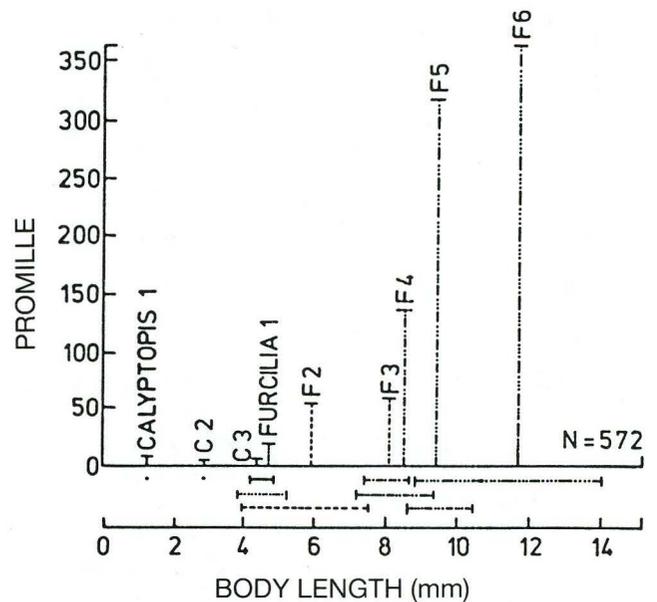


Fig. 15. Krill larval developmental stage distributions and length ranges of Bongo net catches.

Table 3
Numbers of krill larvae collected in two arbitrary strata with the Bongo net.

	Biomass strata	
	>0 °C	<0 °C
Number of hauls	25	20
Variance between individual hauls	488,9	4460,1
Mean number/haul \bar{x} (no/10 ³ m ³)	24,2	46,1
Variance (\bar{x})	19,6	223,0
Size of area (nm ²)	41286	25221
Stratified mean number /10 ³ m ³ \bar{x}_{st}	= 32,5	
Variance stratified mean var (\bar{x}_{st})	= 39,6	
Standard deviation stratified mean	= 6,3	
90 % confidence limits	= 32,5 ± 33 % (no/10 ³ m ³)	
80 % confidence limits	= 32,5 ± 25 % (no/10 ³ m ³)	

Discussion

Despite the possible effects of systematic errors such as active net avoidance by large krill (Anon 1981; Brinton and Antezana 1984) and clogging of the nets by dense phytoplankton aggregations (Maruyama *et al.* 1982), Bongo net catch variances were directly comparable with similar values reported from net surveys elsewhere in the Antarctic (Nast 1982; Maruyama *et al.* 1982; Siegel 1982). The mean density calculated from net catch data (5,21 g/m²) compares favourably with Marr's (1962) lower density estimate for krill in the Weddell Gyre (4,65 g/m²). It is also directly comparable with mean krill density (6,20 g/m²) obtained during FIBEX in Indian Ocean Sector A (15 – 58°E), but is significantly lower than the density (60,81 g/m²) in Indian Ocean Sector B (61 – 80°E) (Hampton 1983).

Conversely, neuston net catches exhibited high variance and it does not appear valid to use neuston catch data for mean areal density estimates. As such, horizontal patchiness would account for the extremely skewed catch distribution obtained (Saville 1977). In particular, station 31 clearly illustrated the effects of patchy distribution, an effect considered

a prominent feature of krill's swarming behaviour (Marr 1962; Mauchline 1981b).

Specific data are insufficient to account for the relatively high abundance of krill at station 31 shown by both the neuston and Bongo net catches. Indications are that this station lay within an area of comparatively high phytoplankton productivity (see Fig. 4 in Allanson, this volume) and therefore may have provided a suitable feeding ground for foraging krill. Full fore-guts in most of the animals collected with the Bongo net tends to confirm this hypothesis. However, the relatively empty stomachs of the neuston catch suggest that animals on the surface were not actively engaged in feeding at the time of capture.

In accordance with the ideas proposed by Hamner *et al.* (1983), these animals could well have represented a migrating swarm and therefore would not be expected to feed. Although Hamner *et al.* (1983) do show that krill feed on the surface, the biomass (74528,6 g/1000 m³) of krill at station 31 and the relatively short fishing time required for their capture provides further support for the presence of a densely packed, migrating aggregation.

The significantly higher abundances of krill in the southern stratum indicated a close association between krill and the pack-ice edge. Although the near-ice zone is an area of relatively cold water, there are indications that it is characterised by enhanced productivity (El-Sayed & Taguchi 1981, Smith & Nelson 1985). Higher incidence of krill would therefore be expected near to the ice and this has often been reported (Everson 1977). Comparatively high primary productivity (Allanson, this volume) near the continental margin and a clear separation between the krill-poor north strata and the krill-rich south strata confirms that the productive near-ice zone is attractive to krill.

Oceanographic observations showed a gentle north-south shoaling of density isopycnals towards 64°40'S (Brundrit, this volume); a position relatively close to the 0 °C isotherm. On most legs, this feature coincided with the disappearance of Winter Water from the north and the appearance of a deep mixed layer to the south. As such, this zone of apparent midwater upwelling would represent the "Antarctic Divergence" which is well developed in the region 55 – 85°E (Khimitsa 1976). It would also appear to provide a boundary to the higher krill abundances observed in the south. Voronina (1968) hypothesises that the Antarctic Divergence limits the northern extremity of high zooplankton abundance close to the Antarctic continent and this is supported by the distribution of Japanese commercial krill catches in the present survey region (Nasu 1983). In combination with the above observations and with those reported by Marr (1962), the current survey results clearly demonstrate a concentration of krill in the productive East Wind Drift zone. For this reason, it is imperative that future work seriously considers the effects of bio-oceanographic variability on krill to the north and to the south of the Antarctic Divergence; particularly as the Divergence is a well developed and prominent frontal feature in the particular region under discussion (Khimitsa 1976, Nasu 1983).

Catch length frequency distributions show the presence of three year classes. These comprised a Year-1 class (Mauchline & Fisher 1969) smaller than 22 mm which, according to Marr (1962), would be the result of an early summer spawning. If these animals were concentrated in the East Wind Drift then it seems logical to assume that recruitment to the present survey area would originate from the east. Similarly,

the existence of a sub-adult (Year-2) year class (23 – 40 mm) would also indicate immigration from farther east. If, as Mackintosh (1972) and Lubimova *et al.* (1980) propose, some hydrological mechanism causes concentration of krill in the area, then Year-2 animals must provide next summer's spawning stock for a greater part of the area between 50 and 85°E.

The presence of sexually mature animals (Year-3; >40 mm) provides evidence for the occurrence of spawning in the region, although the low incidence of reproductively active animals (male stage 3B and female stages 3C-E) indicates it could be at a relatively low level. This is confirmed to some extent by the apparent body length/maturity stage disassociation observed at station 12. Recent work (Ettershank 1983) has shown that female krill probably revert to an immature sub-adult phase (Stage 2B) on cessation of spawning activity. The presence of large, immature females would therefore indicate that spawning had in fact taken place some time shortly before the survey.

Knowledge of larval development times (Ross & Quentin 1983) and the presence of early larval stages (calyptopes and early furcilia) indicate areal spawning activity during late January or early February. Published results show that krill may spawn any time between November and April depending on hydrological conditions (eg. Fraser 1936, Marr 1962, Mackintosh 1972, Hempel 1982). Consequently the time of maximal spawning activity may vary considerably from year to year (Rakusa-Suszczewski 1984). Projected spawning times of krill in the survey area therefore fall well within accepted limits.

Compared with other areas of the Antarctic (Kittel & Jazdzewski 1982, Hempel 1983, Rakusa-Suszczewski 1984) the absolute abundance of krill larvae was low. Despite the widespread temporal variations in maximal spawning activity reported above, the relative late seasonal cover (March – April) of the present survey still seems to offer the most logical explanation for the low larval abundances encountered. An observed low variance in larval catch distributions (Fig. 16), however, is rather more difficult to explain.

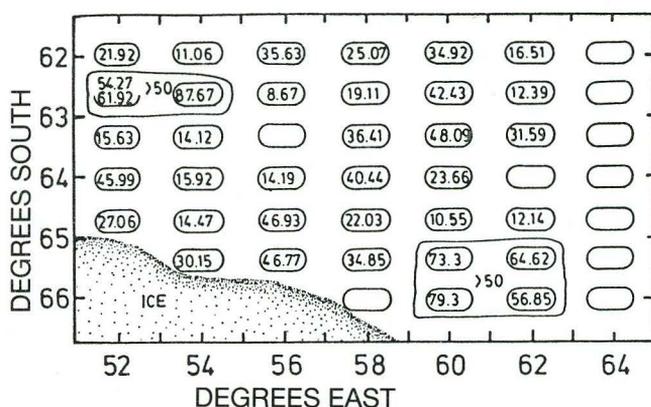


Fig. 16. Horizontal distribution of krill larvae in number of larvae/1000 m³

Rakusa-Suszczewski (1984) has shown that krill larvae are more widely distributed than adults, the latter being confined mainly to nearshore waters. Assuming that larvae are more susceptible to the effects of oceanic circulation (Brinton & Townsend 1984), then a relatively even distribution of larvae would imply that circulation rather favoured larval dispersion. A demonstrated lack of any significant difference between north and south strata in the larval catch distribu-

tions ($P=0,05$) would confirm this. In accordance with the food-searching hypothesis proposed by Hamner *et al.* (1983), and in view of the demonstrated ability of krill to migrate considerable distances (Kanda *et al.* 1982), adult krill would be more capable of overcoming circulatory effects than larvae to congregate in areas of enhanced food availability (i.e. in the East Wind Drift or near-ice zone). Adult krill could thus be expected to exhibit far more skewed distributional patterns than larvae. Unfortunately an absence of data precludes further discussion. Nevertheless, attention must be drawn to the fact that inter-station variability of larval abundances were an order of magnitude less when compared with results of other larval surveys (Hempel *et al.* 1979, Hempel & Hempel 1982, Kittle & Jazdzewski 1982, Rakusa-Suszczewski 1984). In view of the fact that most krill larval studies have been confined to the western Atlantic, the present results should provide a useful basis for future comparison.

Conclusions

Other than the apparent boundary effect of the Antarctic Divergence to the northerly distribution of adults, there is little direct oceanographic evidence to suggest that water circulation patterns were concentrating krill in the survey region. This was confirmed by the relatively low abundances of adult animals encountered, while low larval abundances and a hydrological regime that apparently favours larval dispersion would effectively result in associated low recruitment levels. Low larval abundances and low recruitment do not favour the existence of a persistently localised krill stock; an observation supported by Ikeda (pers comm). As a result, it seems probable that the high krill abundances (Hampton 1983) and water circulation patterns (Lubimova *et al.* 1980, Smith *et al.* 1984) previously described as a feature of the Prydz Bay region may be ephemeral and rather more localised than hitherto appreciated. By inference, it would also appear that both features exhibit far greater geographical and seasonal variation than previously realised. Consequently more data are required before we can confidently outline the effects of water dynamics on krill distribution in the Prydz Bay region.

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