

RESULTS FROM BIOLOGICAL INVESTIGATIONS OF KRILL
(*EUPHAUSIA SUPERBA*) IN THE SOUTHERN INDIAN
OCEAN DURING SIBEX I

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Abstract: During March/April 1984 South Africa studied the hydrology of an area of the South Indian Ocean (52–64°E) as part of the first phase of the Second International BIOMASS Experiment (SIBEX). Both Bongo and neuston nets were deployed at each of 45 oceanographic stations and krill (*Euphausia superba* DANA) were collected. Net sample analyses showed post-larval krill to be unevenly distributed throughout the survey area and concentrated in the East Wind Drift south of the 0°C surface temperature isotherm. The mean areal biomass of post-larval krill was 5.5×10^6 t ($\pm 45\%$). Only late stage larvae were encountered and the mean numerical abundance (32.5 per 1000 m³) of larvae was low. Larvae were more or less evenly distributed throughout the survey area. The inter-relationship between krill distribution patterns and water circulation in the region is discussed.

1. Introduction

The south-east Indian Ocean is one of the least well studied biogeographical regions of the Southern Ocean (EL-SAYED *et al.*, 1979). This is surprising since both Prydz Bay and the Enderby Peninsula (50–70°E) environs have long been implicated as areas of high biological productivity (MARR, 1962; MACKINTOSH, 1972; EVERSON, 1977; LUBIMOVA *et al.*, 1980). In particular, the presence of relatively large, localised concentrations of krill (*Euphausia superba* DANA) in the region (MACKINTOSH, 1973; HAMPTON, 1983) has been thought to result from circulatory effects induced by a persistent and large anti-cyclonic gyre between 50 and 85°E (ZVEREV, 1963; LUBIMOVA *et al.*, 1980; SMITH *et al.*, 1984).

During the First International BIOMASS Experiment (FIBEX) in 1981, hydro-acoustic results provided direct evidence of high krill abundances near Prydz Bay (ANONYMOUS, 1981). Estimates put the absolute krill biomass at 5.4×10^7 t or some 5 times greater than a similar area surveyed in the Western Atlantic (HAMPTON, 1983); hitherto considered one of the areas in which krill abundance is highest (MARR, 1962; EVERSON, 1977; LUBIMOVA *et al.*, 1980).

Following FIBEX, the BIOMASS Technical Group on Programme Implementation and Co-ordination recommended that the Second International BIOMASS Experiment (SIBEX) should focus on process-orientated studies of krill tropho-dynamics during the summers of 1983–84 and 1984–85 (ANONYMOUS, 1982). Given the meagre knowledge of hydrology in the Prydz Bay region, it was decided that initial emphasis should be placed on describing prevailing physical and biological oceanography in the first

season (1983–84). Not only would this be important to understanding the possible effects of water circulation on krill distribution, it would also constitute an essential prerequisite for the determination of areas of biological interest to be studied during the second phase of the experiment (ANONYMOUS, 1982).

The southern Indian Ocean area surveyed during SIBEX I was divided into three sectors. Japan (twice), Australia and South Africa were each responsible for a separate sector. This paper reports results from studies of krill biology undertaken as part of the South African contribution.

2. Materials and Methods

An area of the south-east Indian Ocean ($62\text{--}66^\circ\text{S}$; $52\text{--}64^\circ\text{E}$) was surveyed between 26 March and 20 April, 1984 by the South African Antarctic research and supply vessel, MV S. A. AGULHAS. Forty-five oceanographic stations (CTD and Niskin bottle casts) were occupied in a grid of 7 legs; each leg extended from the pack-ice edge to approximately 200 nautical miles north (Fig. 1).

Paired B57 (Bongo) nets were deployed at each station and hauled obliquely from 250 m to the surface. Each net had a mouth diameter of approximately 60 cm and

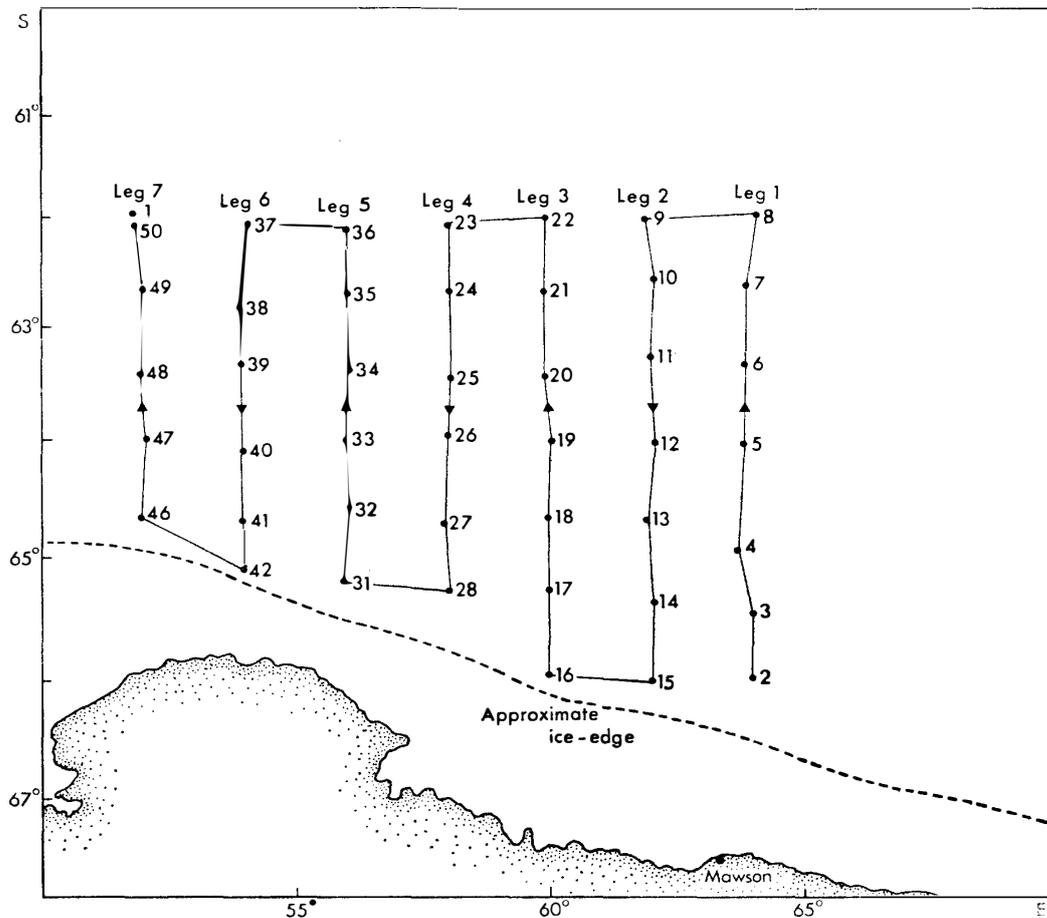


Fig. 1. South African SIBEX I survey grid showing positions of net stations.

nets were fitted with 500 and 300 μm mesh respectively. Net filtering rates were measured by a flowmeter mounted in the mouth of each net. Both water temperature and net depth were monitored continuously during fishing with a submersible, electronic bathythermograph. This gave a real-time display of both parameters on deck. Data were logged directly to digital computer tape and printed out at 5 m intervals.

A neuston net (mouth area; 0.98 m², 950 μm mesh), weighted with a 10 kg lead-filled pipe attached to the lower mouth bar, was deployed at each station from a boom on the ship's forward port quarter. It was hauled for 10–15 min over a distance of approximately one kilometer and the volume of water filtered was calculated from the net's dimensions and speed through the water. During all fishing operations ship's speed was maintained as close as possible to 2.5 kn (1.25 m/s).

Net samples were sorted aboard, both total and krill catch displacement volumes being measured. Larval and post-larval krill were extracted and counted. Prescribed techniques were used to assess body length (MAUCHLINE, 1981a), sexual maturity (MAKAROV and DENYS, 1981), larval development (FRASER, 1936; MAKAROV, 1981) and state of feeding (RAKUSA-SUSZCZEWSKI, 1982). Samples were preserved in buffered formalin (4%) and wet/dry weight determinations carried out on representative sample aliquots ashore. Catch data were standardised per 1000 m water volume filtered.

3. Results

3.1. Post-larval krill

Post-larval krill were collected in 10 neuston net catches and at 35 Bongo stations. The biomass of each catch was calculated from the number of krill in each length class (1 mm classes) following the procedure outlined by NAST (1982) and POMMERANZ *et al.* (1982). The wet weight of 708 animals was measured (277 juveniles/subadults, 219 males and 181 females). The following length (l) to weight conversion (W) was obtained for animals at all stages of sexual maturity and was used in the biomass calculations:

$$W = 0.0017 l^{3.4237}, \quad (1)$$

where W is in mg (wet weight) and l in mm. Values obtained for the exponential standard error of the regression slope and intercept were 0.0313 and 0.00014, respectively. The regression coefficient (r) was 0.983 for the log-log plot of weight on length (Fig. 2). A comparison of the above relationship with similar expressions derived by SAHRHAGE (1977/78) and JAZDZEWSKI *et al.* (1978) indicated only slight differences for the post-larval size ranges sampled (Fig. 2).

Bongo krill catch biomass varied between 0 and 491.4 g/1000 m³ and for the neuston net between 0 and 74528.6 g/1000 m³. In the absence of significant differences between the two mesh sizes used (level of significance $P = 0.01$), Bongo catches were pooled and a mean krill biomass calculated for each station. From the station distribution it is apparent that the largest catches of krill were taken in the south of the survey grid (Figs. 3 and 4), particularly at Stns. 16 and 31. Both these stations lay within an area of relatively cold surface water ($< -0.05^\circ\text{C}$) and were situated close to the ice-edge (Fig. 5).

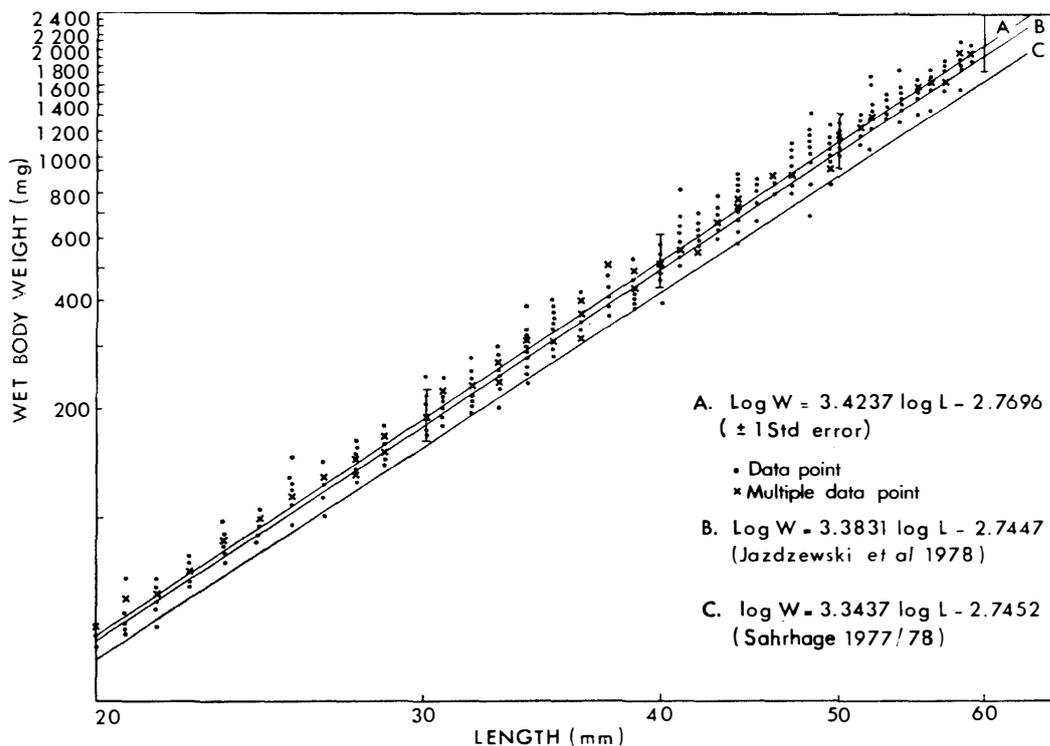


Fig. 2. A comparison of length-weight relationships derived from expressions obtained during the present survey (A) with those obtained by, (B) JAZDZEWSKI et al. (1978) and (C) SAHRHAGE (1977/78).

As a result of observed trends in catch distributions, and to improve precision of the catch results overall, the survey area was stratified according to the procedure set out by SAVILLE (1977) and modified by NAST (1982). Two strata were arbitrarily identified north and south of the 0°C isotherm. The isotherm coincided with an area of apparent midwater upwelling and appeared to represent the boundary between the presence of winter water to the north and its absence in the south (*i.e.* the “Antarctic Divergence”) (BRUNDRIT, 1985).

Stratified mean areal krill biomass and associated variance (NAST, 1982) were calculated from both neuston and Bongo catch results (Tables 1 and 2). The proportionate standard error of the mean Bongo catch biomass (Table 1) was directly comparable with similar results reported by NAST (1982) for RMT-8 catches in the Western Atlantic. Assuming that post-larval krill are confined to approximately the top 150m of the water column gives a survey total areal biomass of 5.5×10^5 t ($\pm 45\%$) at the 80% confidence level. It is noticeable that both Bongo mean catch and variance were significantly greater in the south than in the northern stratum. This was confirmed by a statistical comparison of the mean biomass/haul for the two areal strata using an independent sample analysis (SNEDECOR and COCHRAN, 1978). The significant difference ($P=0.05$) between the two strata can be attributed to an incidence of large catches at Stns. 16, 31 and 28, in addition to an associated increase in stratal variance in the south (Fig. 3).

Neuston net catches exhibited high variance (Table 2), partly as a result of an ex-

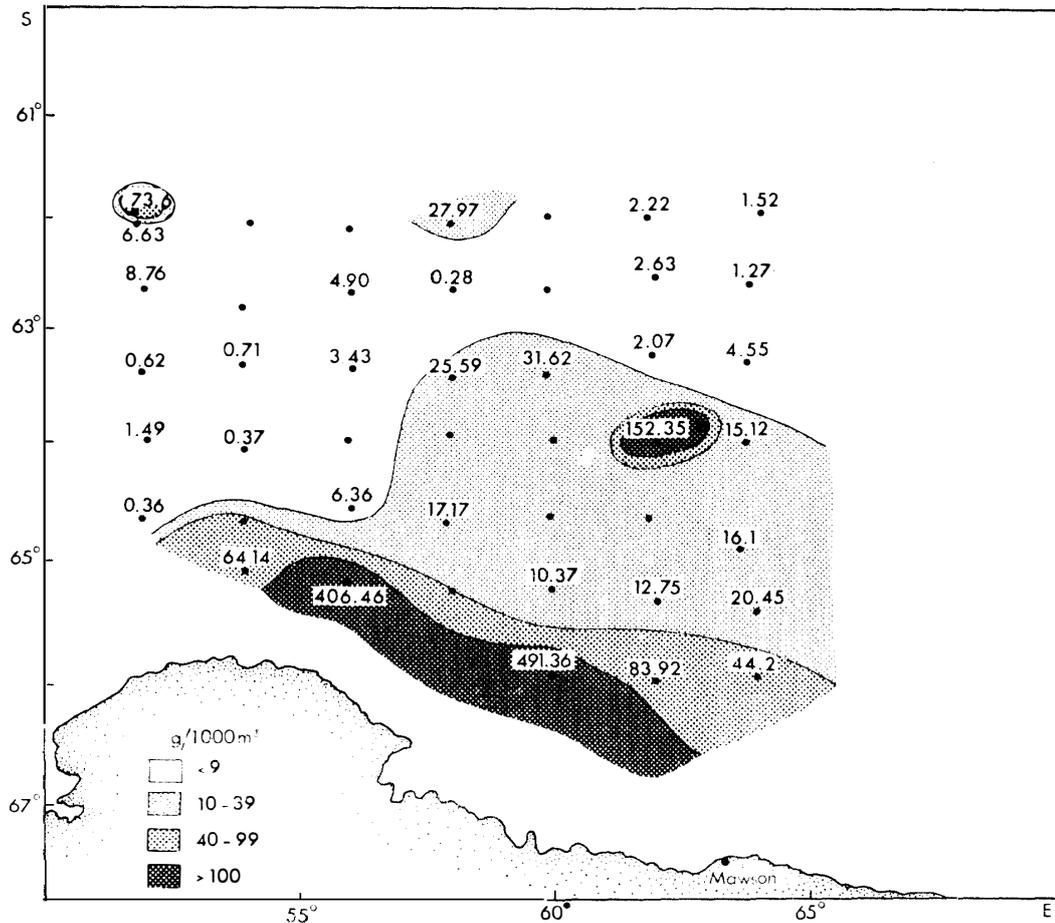


Fig. 3. Biomass of adult krill caught at each Bongo net station in g/1000 m³.

Table 1. 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 ind. hauls	267.9	139.5
Mean biomass/haul \bar{x} (g/10³m³)	8.6	77.5
Variance (\bar{x})	10.7	972.8
Size of area (nm²)	41286	25221
Stratified mean biomass/10³m³	$\bar{X}_{st} = 34.8$	
Variance stratified mean	var (\bar{X}_{st}) = 144.0	
Standard deviation stratified mean	= 12.0	
90% confidence limits	= 34.76 ± 57% (g/10³m³)	
80% confidence limits	= 34.76 ± 45% (g/10³m³)	
Size of area × 150 m depth	1.59 × 10¹³ m³	
Biomass of krill in whole area	5.5 × 10¹¹ g krill	
	5.5 × 10⁵ t (± 45%)	

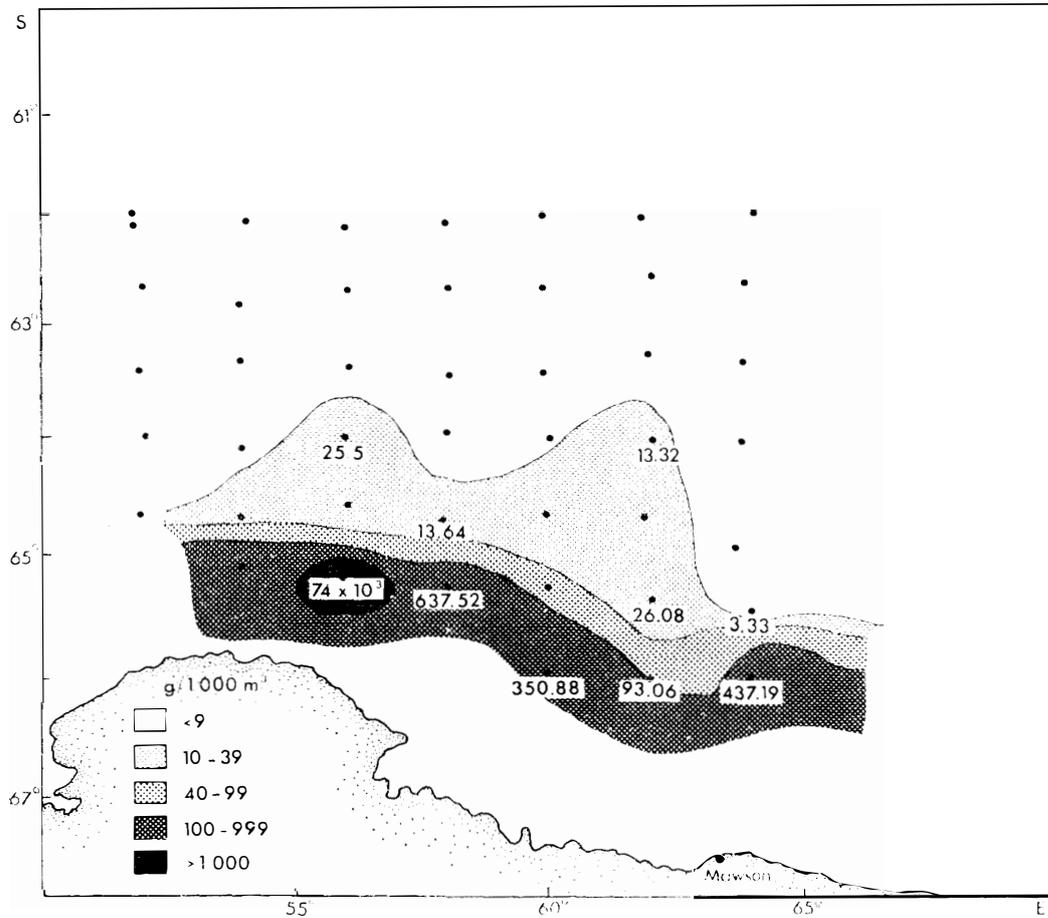


Fig. 4. Biomass of adult krill caught at each neuston net station in g/1000 m³.

Table 2. 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 ind. 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	$\text{var}(\bar{X}_{st})=1992634.9$	* [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 Stn. 31.

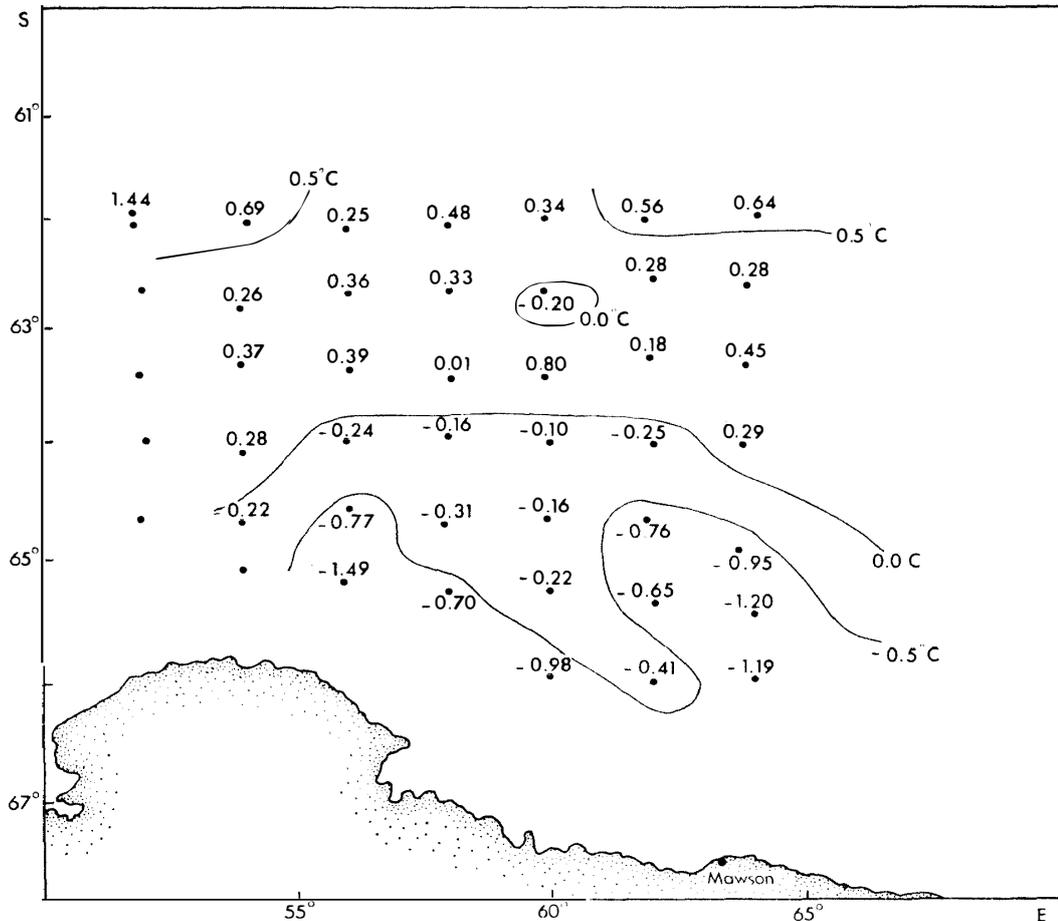


Fig. 5. Surface water temperature distribution in the SIBEX I area surveyed by South Africa.

ceptionally large catch at Stn. 31 and partly due to an absence of catches in the northern stratum (Fig. 4). The relatively short time (± 2 min) required to fill the net at Stn. 31 indicated that it probably encountered a dense krill swarm on the surface. Excluding Stn. 31 from the stratal analysis resulted in a marked decrease in the overall catch variance and a significant improvement in confidence limits (Table 2)—reasons for this are discussed later in the paper. Although the absence of neuston net catches in the northern stratum tends to validate Bongo catch stratal differences, a lack of data precludes a similar statistical evaluation to that undertaken for the Bongo catches in the two strata.

No significant differences ($P=0.05$) were observed between night (1600–0800 local time) and day (0800–1600) Bongo catch biomass. Conversely, daylight neuston catches ($P=0.05$) were significantly larger than those taken at night. Again, this could be attributed to undefined bias caused by an exceptionally large catch at Stn. 31 during the day. Exclusion of Stn. 31 data from the analyses resulted in no significant difference between day and night neuston net catches ($P=0.05$).

A total of 3952 krill were measured and accumulated length frequency promilles for the respective nets are shown (Fig. 6). Weighted-mean body lengths were calculated for the neuston (33.5 mm), for the 300 μ m (42.2 mm) and for the 500 μ m (42.3 mm)

Bongo net catches respectively. No significant differences were apparent between either the mean lengths or length frequency distributions obtained for the two Bongo net meshes used ($P=0.05$). Animals caught with the neuston net were significantly smaller than those collected with either Bongo ($P=0.05$) (Fig. 6), except at Stn. 31 (Fig. 7).

Most adult and sub-adult maturity stages were present in the Bongo net catches (Figs. 8 and 9). Of the 804 male krill staged (Fig. 8), mature but reproductively inactive animals (Stage 3A—MAKAROV and DENYS, 1981) were predominant. Conversely, the majority of females ($n=758$) were sub-adult (Stage 2B) (Fig. 9). Juvenile animals (Stage 1) comprised approximately 20% of all Bongo catches. Maturity stage distributions were not significantly different for either Bongo net mesh ($P=0.05$).

Body length and sexual maturity were clearly associated in both sexes (Fig. 10). At Stn. 12, however, Stage 2B females 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. 11). A statistical comparison of the body length/maturity stage regression (after SNEDECOR and COCHRAN, 1978) for female krill at all the stations with that for all females excluding Stn. 12 (Fig. 11) indicated a significant difference ($P=0.05$) between the two regression coefficients. This suggests a body length/maturity stage disassociation for female krill at Stn. 12.

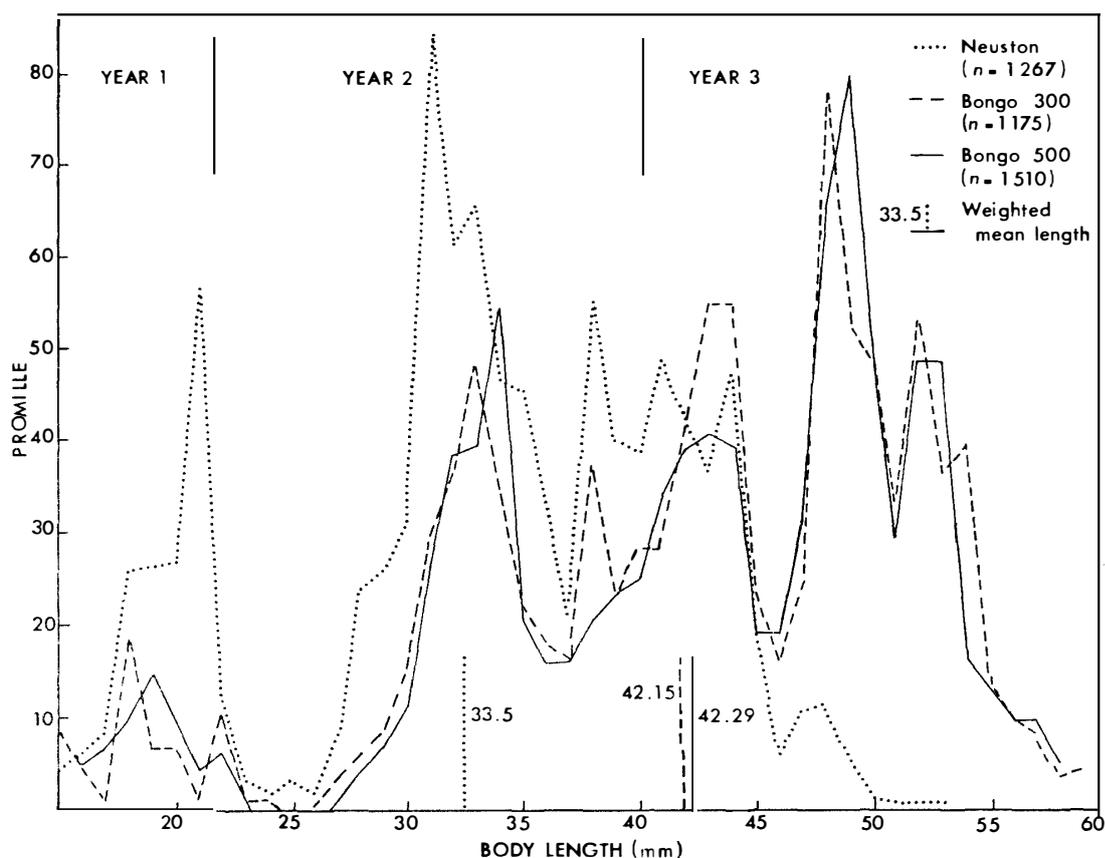


Fig. 6. Accumulated length frequency promilles for the neuston, Bongo 300 and 500 μm catches. Also shown are krill year-class divisions (after MAUCLINE and FISHER, 1969).

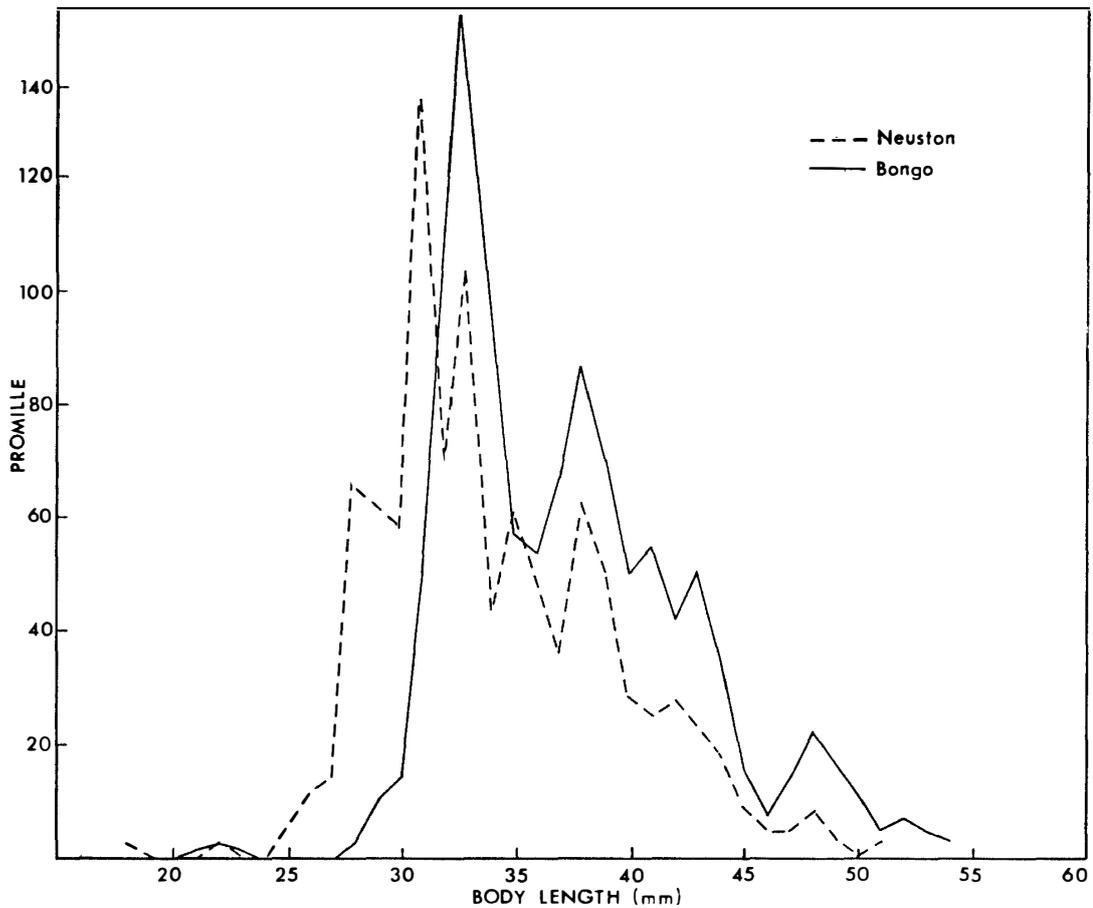


Fig. 7. Length frequency promille of animals collected at Stn. 31 by both Bongo and neuston nets.

In keeping with the length frequency distributions reported above, sub-adult (Stages 2A and B) animals dominated the neuston net catches (Fig. 12). This was particularly evident at Stn. 31.

Ovigerous or spent females (Stages 3D and 3E) were only encountered in significant numbers at Stn. 1. Both sexually active male and female animals (Stages 3B and 3C), with spermatophores attached, were collected at only 5 stations and no discernible distributional pattern was evident.

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

$$Y_{ij} = \log(X_{ij} + 1) \tag{2}$$

where X_{ij} = proportionate frequency of the i th maturity stage in the j th sample; Y_{ij} = corresponding transformed score (CLIFFORD and STEPHENSON, 1975). The subsequent dendrogram was divided at 60 and 73% similarity to provide 3 broad station affinity groupings for the various maturity stage affiliations (Fig. 13). The resultant similarity

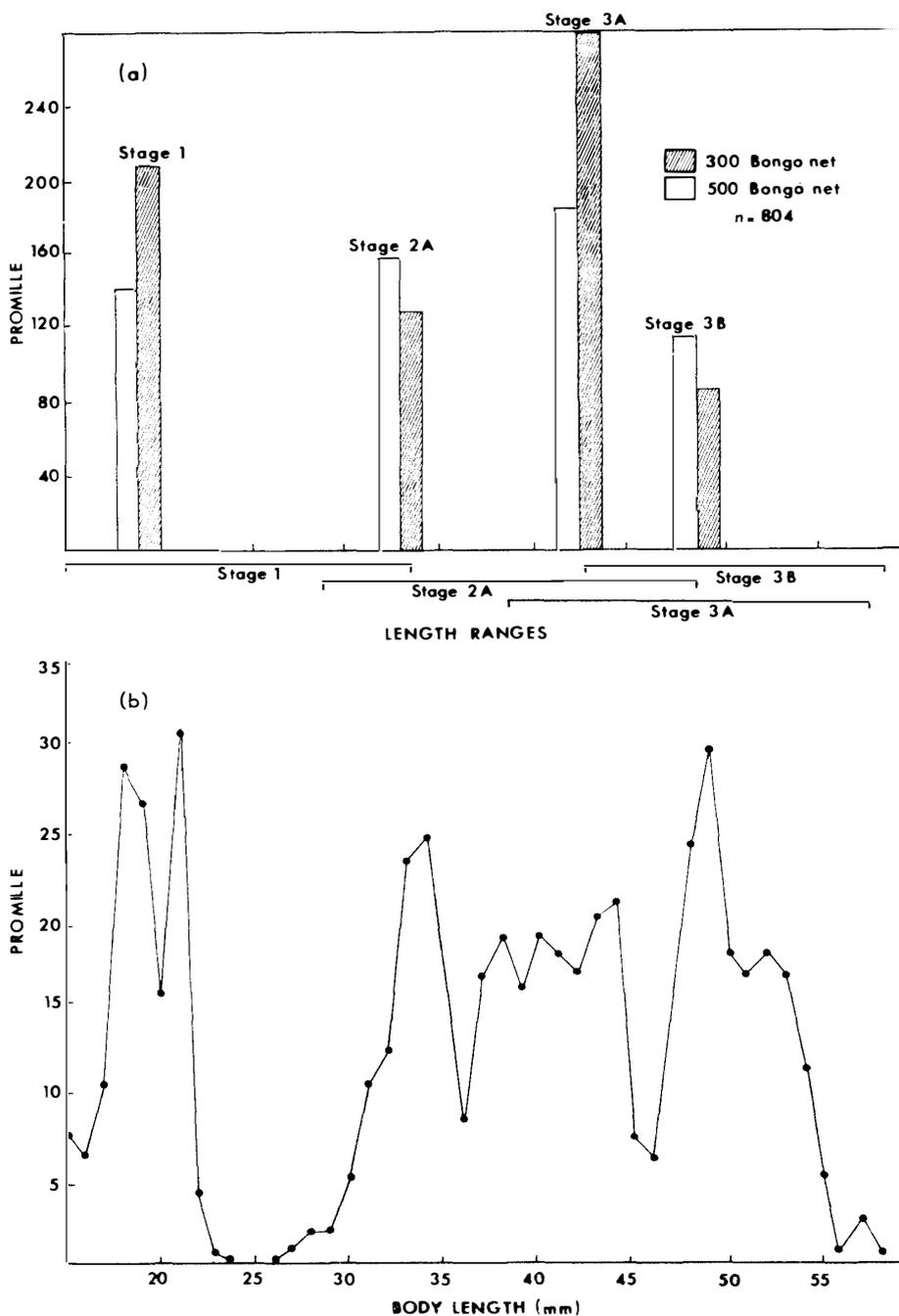


Fig. 8. Maturity stage and length frequency distributions of male krill in Bongo net catches. The accumulated maturity stage (a) and length frequency (b) promilles are shown together with body length ranges for each maturity stage.

matrix and multi-dimensional scaling (MDS) (FIELD *et al.*, 1982) were used to ordinate net stations in a two dimensional matrix (Fig. 14). Subsequent MDS clusters confirmed dendrogram groupings. Most noticeable was the strong similarity (>80%) between stations falling within the dendrogram grouping 1A and these were confined to the southern extremities of survey Legs 1-6 (Fig. 15). An information statistic test (FIELD, 1969; FIELD *et al.*, 1982) was used to assess the maturity stage attributes contributing

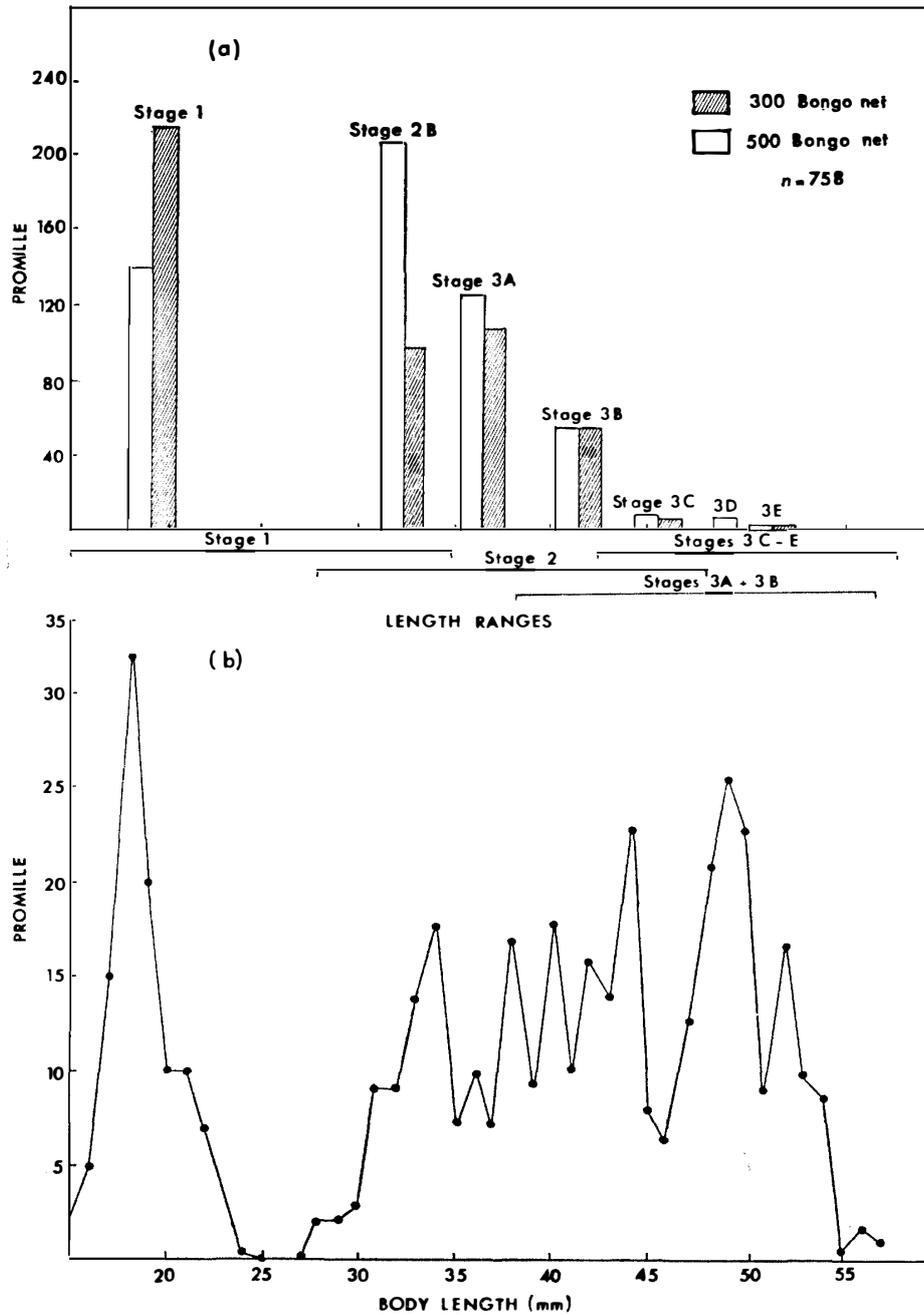


Fig. 9. Maturity stage and length frequency distribution of female krill in Bongo net catches. The accumulated maturity stage (a) and length frequency (b) promilles are shown together with body length ranges for each maturity stage.

most to station affinity weightings. From the results (Table 3) it is apparent that a high incidence of juvenile and sub-adult krill (Stages 1 and 2) characterized the southern-most stations, separating them from those to the north.

3.2. Larvae

Late stage larvae (Furcilia stages 5 and 6) were numerically predominant in the

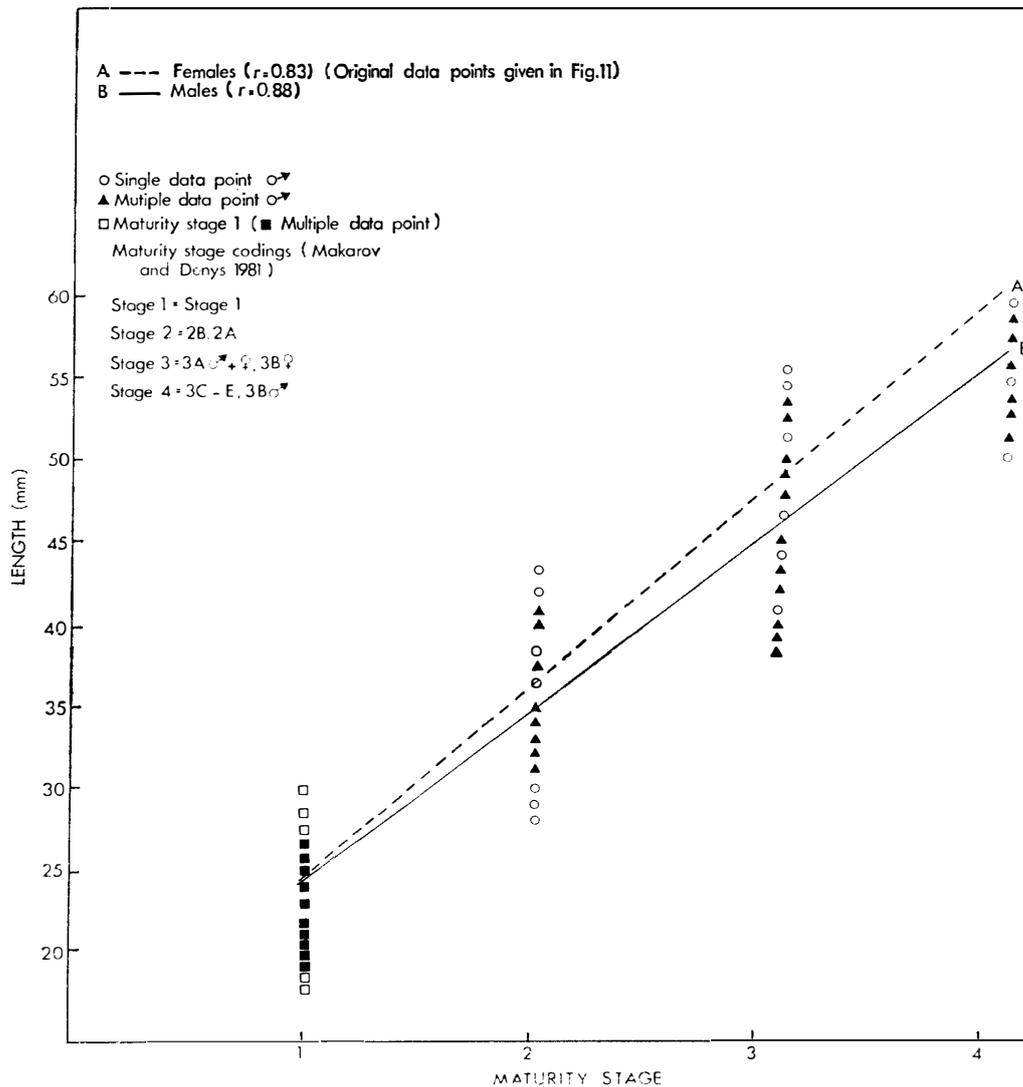


Fig. 10. Maturity stage/body length regressions of both female and male krill collected with the Bongo nets. Regression coefficients (r) are significant at $P=0.01$.

Bongo catches (Fig. 16). The size ranges of 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 shown for the two net meshes used ($P=0.05$). Larvae were relatively evenly distributed throughout the survey area (Fig. 17) and the mean numerical abundance of all larval stages was low (Table 4). Compared to post-larval animals, the variance of the mean larval catch was significantly less and no significant differences were observed between the two areal strata ($P=0.05$) (Table 4). All attempts to elucidate larval developmental stage station affinities were unsuccessful using both the Bray-Curtis analysis and MDS. Calyptopis (Stages 1–3) and early furcilia (Stages 1–2) stages were encountered at only 10 stations, 6 of which were situated south of 64°S .

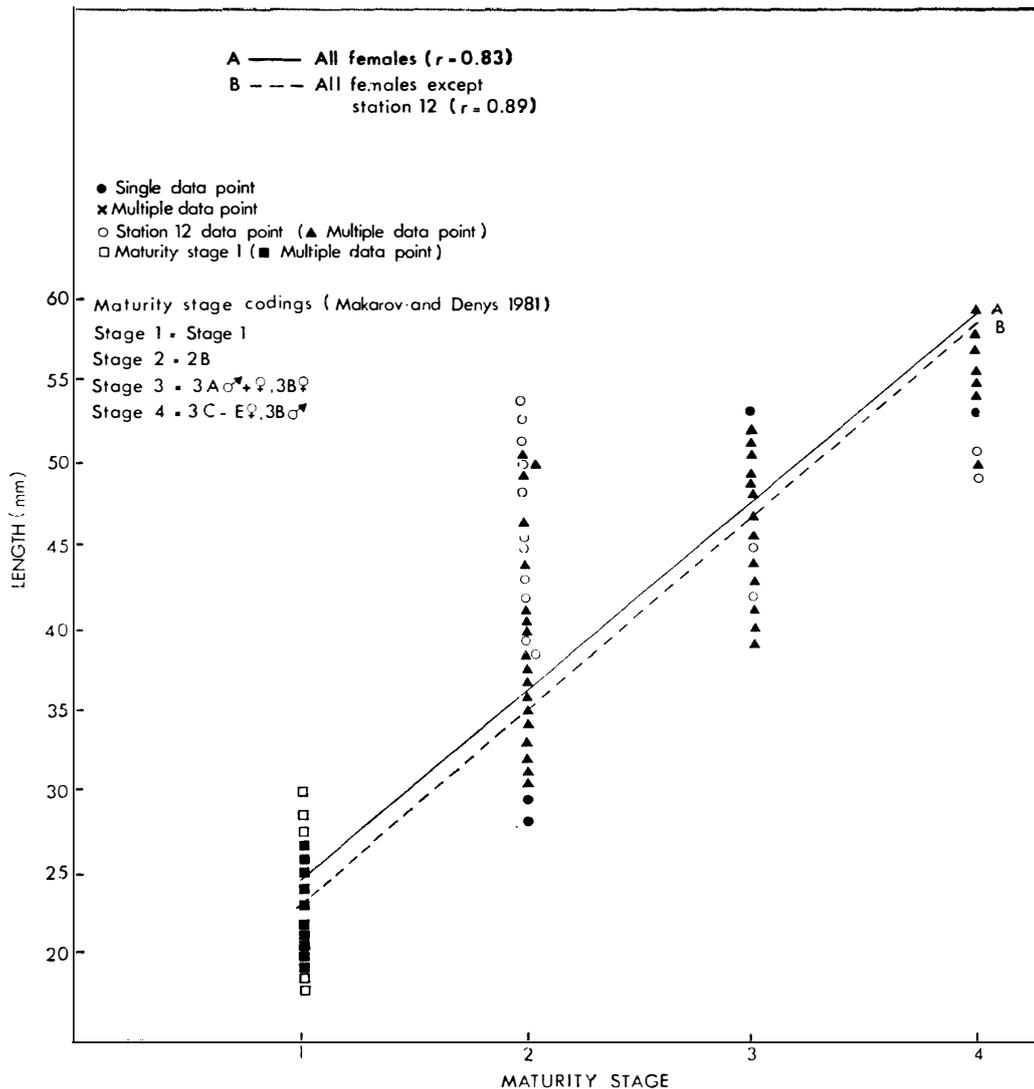


Fig. 11. Maturity stage/body length distribution of female krill collected with the Bongo net at all stations and excluding Stn. 12.

4. Discussion

Despite possible systematic errors induced by such effects as active net avoidance by large krill (ANONYMOUS, 1981; BRINTON and ANTEZANA, 1984) and clogging of nets by dense phytoplankton aggregations (MARUYAMA *et al.*, 1982), Bongo net catch variance was directly comparable with similar values reported from net surveys else-where in the Antarctic (NAST, 1982; MARUYAMA *et al.*, 1982; SIEGEL, 1982). The mean areal biomass 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 (6.2 g/m²) obtained during FIBEX in Indian Ocean Sector A (15–58°E), but is significantly lower than mean density (60.81 g/m²) in Indian Ocean Sector B (61–80°E) (HAMPTON, 1983).

Conversely, neuston net catches exhibited a high variance and therefore it does

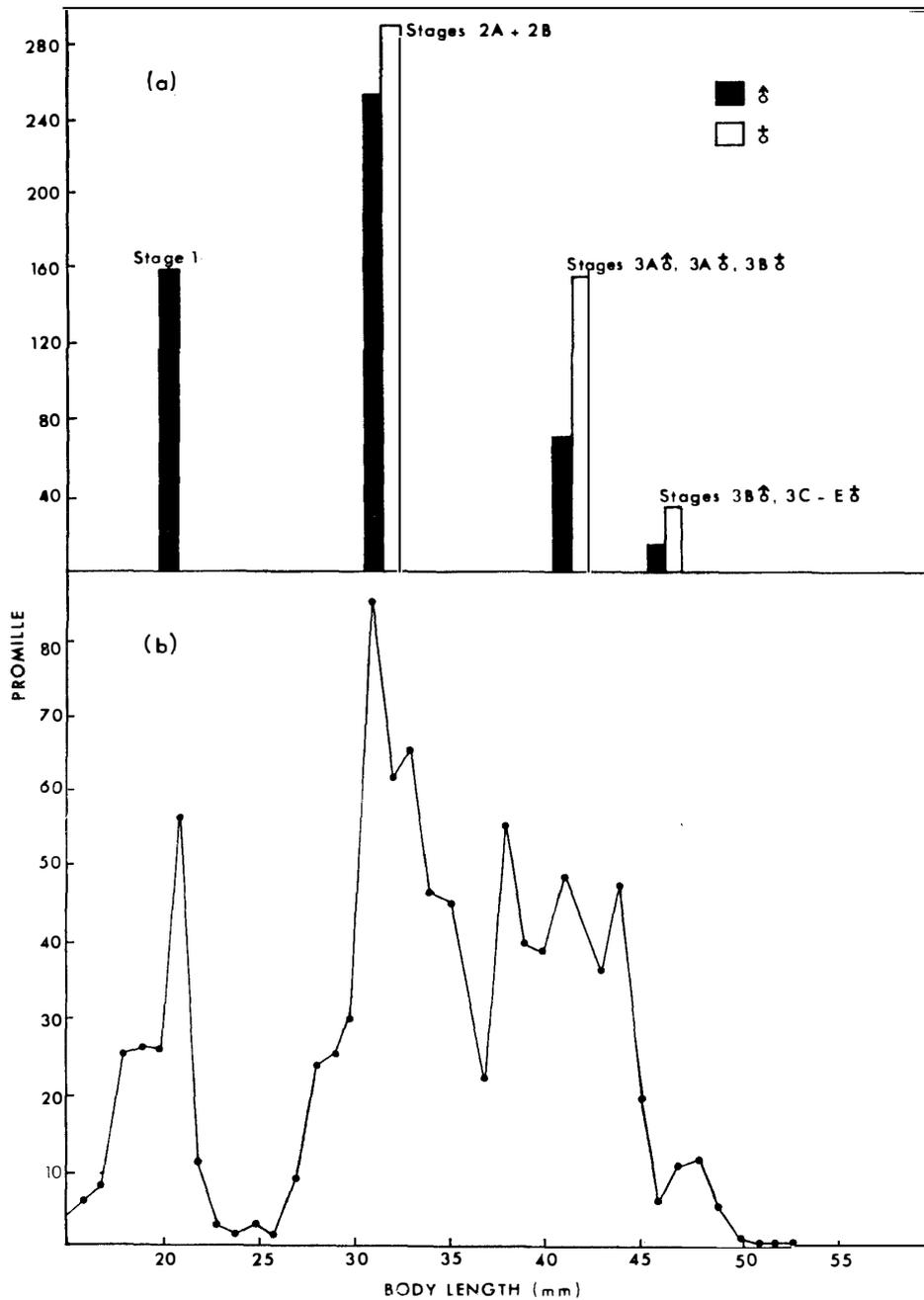


Fig. 12. Maturity stage (a) and body length distributions (b) of female and male krill collected with the neuston net.

not appear valid to use neuston catch data for mean areal biomass estimates. As such, horizontal patchiness could account for the extremely skewed catch distributions observed (SAVILLE, 1977). In particular, Stn. 31 clearly illustrates an extreme effect of patchy distribution which is a characteristic feature of krill's swarming behaviour (MARR, 1962; MAUCLINE, 1981b).

Specific data are insufficient to account for the relatively high abundance of krill at Stn. 31 shown by both neuston and Bongo net catches. Indications are that this

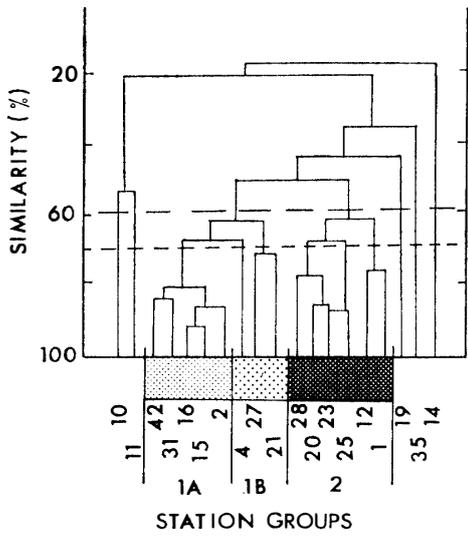


Fig. 13. Dendrogram of maturity stage station affinities obtained using a Bray-Curtis diversity analysis.

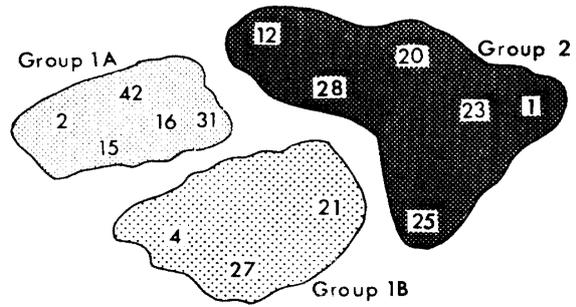


Fig. 14. Two dimensional configuration of maturity stage station affinities obtained by multi-dimensional scaling.

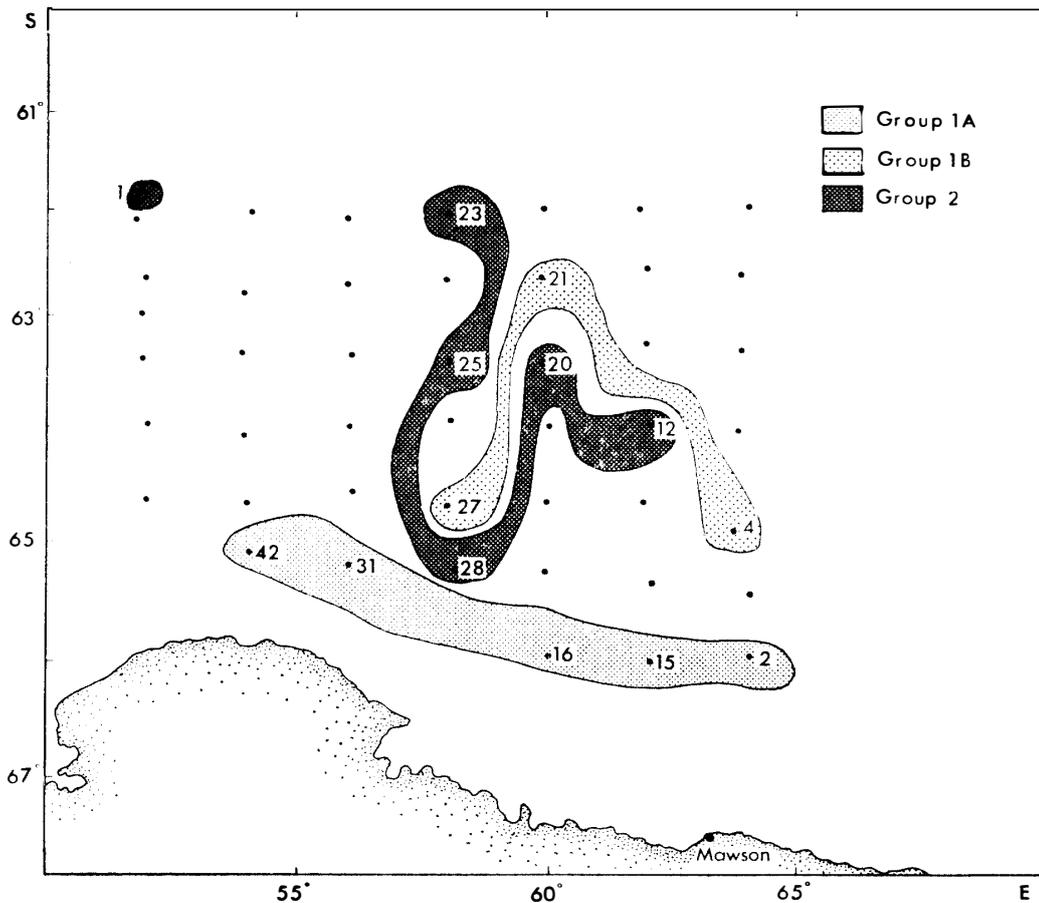


Fig. 15. Horizontal distribution of maturity stage station affinity groupings obtained from a Bray-Curtis analysis and multi-dimensional scaling.

Table 3. Frequencies of occurrence of post-larval maturity stages, which best characterize Group 1A catches and separate them from Groups 1B and 2. Maturity stage classifications after MAKAROV and DENYS (1981).

Maturity stage	Group 1A	Groups 1B and 2
2A	10	5
1	10	8
2B	10	10
3B (Male)	2	13
3B (Female)	3	14
3E (Female)	0	4
3A (Female)	9	18
3C (Female)	1	5
3D (Female)	0	1
3A (Male)	9	15

Species above the upper broken line have an information content > 6.63 ($P=0.01$); those above the lower line score > 3.84 ($P=0.05$). Maximum possible occurrences are Group 1A=10, Groups 1B and 2=18.

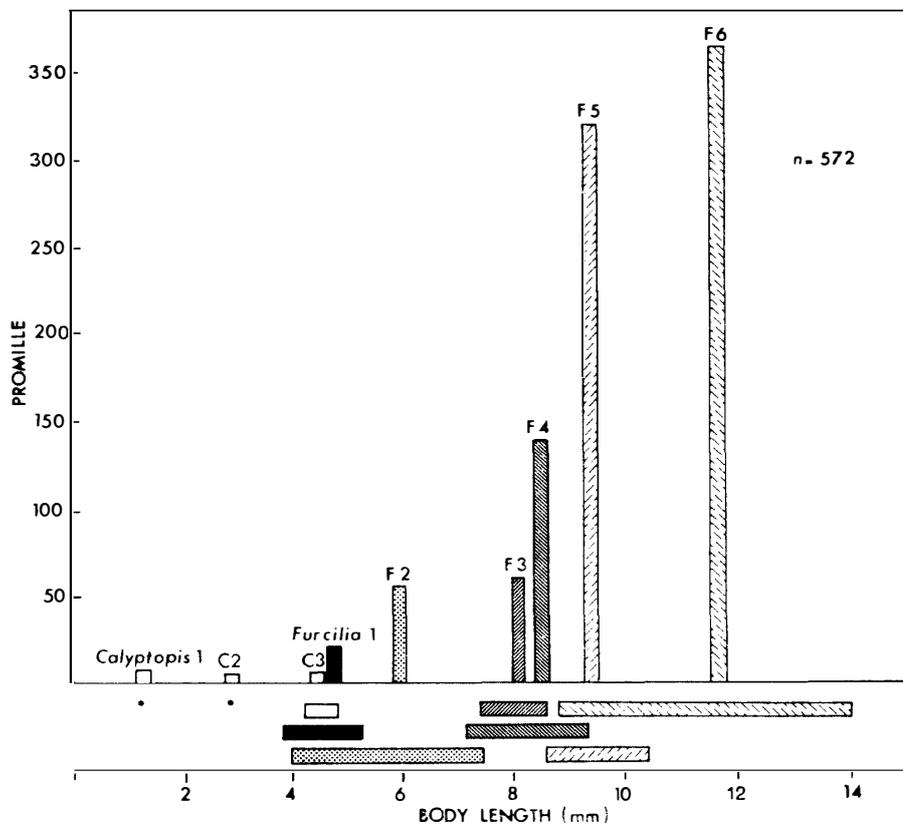


Fig. 16. Krill larval developmental stage distributions and length ranges of Bongo net catches.

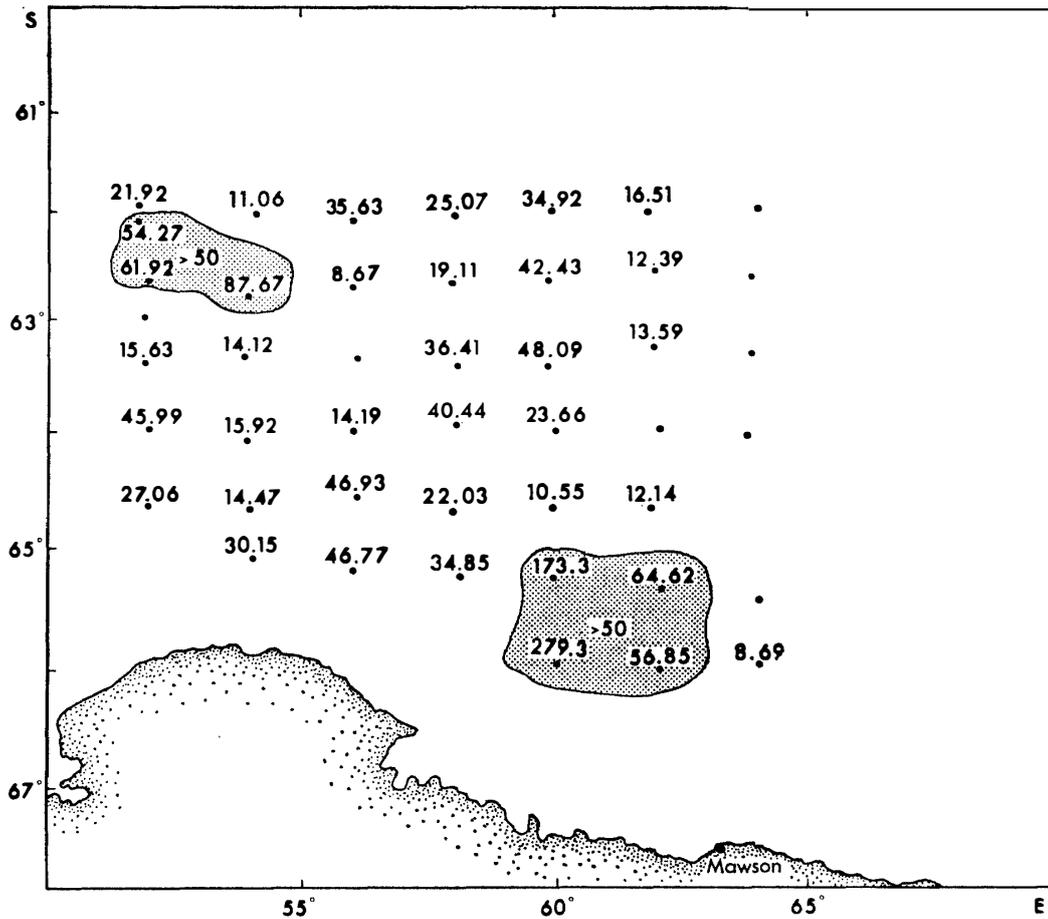


Fig. 17. Horizontal distribution of krill larvae in number of larvae/1000 m³.

Table 4. 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 ind. 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)	

station lay within an area of comparatively high phytoplankton production (ALLANSON, 1985) and therefore could have constituted a suitable feeding ground for foraging krill. Full fore-guts in animals collected with the Bongo net confirmed this hypothesis and

demonstrates that krill were actively feeding at the station. Conversely, the relatively empty stomachs of the neuston catch indicates that animals on the surface were not feeding at the time of capture. In accordance with ideas proposed by HAMNER *et al.* (1983) and HAMPTON (1985), these animals may have represented a densely-packed migrating swarm and therefore would not be expected to feed. Although HAMNER *et al.* (1983) have shown that krill do indeed feed on the surface, the high density (74528.6 g/1000 m³) of animals at Stn. 31 provides further support for the presence of a densely packed, migrating aggregation. Similarly the predominance of sub-adult animals in the neuston net catch would be in direct accordance with ontogenic differences in krill schooling behaviour proposed by HAMNER (1984). Such differences are supposedly most manifest in juvenile/sub-adult animals which migrate for large horizontal distances in search of food in both shallow and deep waters.

Significantly higher abundances of krill in the southern stratum suggests 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 characterized by enhanced productivity (EL-SAYED and TAGUCHI, 1981; SMITH and NELSON, 1985). A 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, 1985) near the continental margin and a clear separation between the krill-poor north strata and the krill-rich south strata confirms the more widespread affiliation of krill to the near-ice zone during the present survey.

Oceanographic observations showed a gentle north-south shoaling of density isopycnals towards 64°40'S (BRUNDRIT, 1985); 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. This zone of apparent midwater upwelling was indicative of the "Antarctic Divergence", which is well developed in the region 55–85°E (KHIMITSA, 1976). It may also provide a marginal boundary to higher krill abundances observed in the south. VORONINA (1968) has hypothesised that the Antarctic Divergence limits the northern extremity of high zooplankton abundances 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 results support a concentration of krill in the productive East Wind Drift zone. For this reason, it is imperative that future work should seriously consider the effects of bio-oceanographic variability on krill caused by the presence of well developed frontal features like the Divergence. This would seem to be particularly important in the region 52–65°E where, as already mentioned, the Divergence is well developed (KHIMITSA, 1976; NASU, 1983).

Catch length frequency distributions indicate three year classes. These comprised a Year-1 class (MAUCLINE and FISHER, 1969) smaller than 22 mm which, according to MARR (1962), would result from an early summer spawning. If animals were confined to the East Wind Drift then it seems logical to assume that recruitment to the present survey area originates in the east. Similarly, the presence of a sub-adult (Year-2) year class (*ca.* 23–40 mm) would also be indicative of immigration from farther east (*i.e.* upstream). If, as MACKINTOSH (1973) and LUBIMOVA *et al.* (1980) propose, hy-

drological mechanisms concentrate krill in the Enderby-Kerguelen basin, then Year-2 animals would provide the following summer's spawning stock for a greater part of the area 50–85°E.

The presence of sexually mature animals (Year-3; >40 mm) provides evidence for krill spawning in the region, although a low incidence of reproductively active animals (male stage 3B and female stages 3C–3E) indicates that it may occur at relatively low levels. Regional spawning activity is confirmed to some extent by the apparent body length/maturity stage disassociation observed at Stn. 12. Recent work (POLECK and DENYS, 1982; ETTERS HANK, 1983) has shown that female krill may revert to an immature sub-adult phase (Stage 2B) on cessation of spawning activity. The presence of large, immature females could therefore indicate that spawning had in fact taken place shortly before commencement of the survey.

Knowledge of larval development times (ROSS and QUETIN, 1983) and the presence of early larval stages (calyptopis and early furcilia) indicate that spawning activity occurred in the survey area during late January or early February. Published results show that krill may spawn any time between November and April depending on hydrological conditions (*e.g.* 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 and JAZDZEWSKI, 1982; HEMPEL, 1983; RAKUSA-SUSZCZEWSKI, 1984) the absolute abundance of krill larvae was low. Despite widespread temporal variations in maximal spawning activity reported above, the relative late seasonal cover (March–April) of the present survey seems the most logical explanation for low larval abundances encountered. Also compared with similar surveys elsewhere (HEMPEL *et al.*, 1979; HEMPEL and HEMPEL, 1982; KITTEL and JAZDZEWSKI, 1982; RAKUSA-SUSZCZEWSKI, 1984), the inter-station variability of larval catches was low. Two explanations can be offered for this observation.

MACKINTOSH (1972) and others (*e.g.* VORONINA, 1974; EVERSON, 1977; MAKAROV, 1983) have suggested that spawning probably occurs throughout most of the adult distributional range. In the present survey area, widespread spawning would have the ultimate effect of evenly distributing larvae over a wide area and in the low abundances observed.

The second explanation presupposes a strong interaction between water circulation and larval dispersal. RAKUSA-SUSZCZEWSKI (1984) has shown that krill larvae are more widely distributed than adults, the latter being primarily confined to nearshore waters. Similarly, BRINTON and TOWNSEND (1984) have shown that krill larvae are more susceptible to effects of oceanic circulation than adults. Assuming circulation in the survey area not to be conducive to concentration of larvae then the observed lack of stratal differences in larval catches would substantiate widespread larval dispersion. Taking this argument further, BOGDANOV *et al.* (1980) maintain that, in some areas, early stage krill larvae are carried northward away from the continental edge by deep-water currents and tend to be most heavily concentrated near the Divergence. In the Prydz Bay region, water circulation north of the Divergence is characterized by a predominantly eastward flow, while between the Divergence and the continental rise it

comprises a series of broken eddies flowing westward (SMITH *et al.*, 1984). Young larvae, originally concentrated near the Divergence, would thus be dispersed to the east, north of the Divergence, and to the west in the south. Consequently later larval stages would be quite widely dispersed (as observed); the extent of horizontal dispersion depending on topographical interactions, dynamic topography and wind induced effects. Rather than being confined to high latitudes, larvae could therefore be dispersed far to the north (AMOS, 1984) and would be effectively removed from the system if unable to return to the productive East Wind Drift.

Both the above explanations account for an absence of localized larval concentrations. An additional factor, however, must also be considered. At present there is no way of ascertaining to what extent predation (either by other groups and/or by adult krill) may affect late-stage larval distribution and abundance. An absence of concentrated spawning activity in any one locality would not only serve to disperse larvae but may also preclude any significant benefits offered against elective predation by concentration of larvae in high numbers (ANTEZANA and RAY, 1983) or by transport away from areas of high adult abundances (MAKAROV, 1983). This may constitute an additional factor affecting both the proportion of larvae ultimately attaining recruitment age as well as their horizontal distribution.

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 appear more capable of overcoming circulatory effects than larvae so congregating in areas of enhanced food availability (*e.g.* in the East Wind Drift or near-ice zone). Adult krill would also therefore be expected to exhibit rather more patchy distribution than larvae; particularly if water circulation favoured dispersion of the latter. Unfortunately, a lack of suitable data precludes further discussion. However, since most krill larval studies have been confined to the western Atlantic, the present results should provide a useful basis for comparison.

Other than the apparent boundary effect of the Antarctic Divergence to the northerly distribution of post-larvae, the survey provided little direct oceanographic evidence to suggest that local water circulation patterns concentrate krill in the survey region. This was confirmed by the relatively low abundances of adult animals encountered. Furthermore, low larval abundances and a hydrological regime that favours larval dispersion would effectively preclude substantial regional recruitment. This would not favour the existence of a persistently localized krill stock; an observation supported by IKEDA (personal communication). Similarly, an Australian survey undertaken earlier in the summer of 1984 also encountered low abundances of krill larvae in the area 58–73°E (HOSIE and KIRKWOOD, 1986).

It seems probable, therefore, that both 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 region as a whole may be rather more ephemeral and localized than hitherto thought. Resynthesis of FIBEX acoustic results has revealed that areal estimates of high krill abundance may in fact be biased by extremely patchy distribution and by artifacts induced through survey stratal selection procedures (ANONYMOUS, 1985). By inference therefore, it would appear that both krill distribution and hydrological effects exhibit a far greater geographical and seasonal variation

in the area 52–64°E than previously appreciated. Consequently considerably more data are required before the effects of water dynamics on krill distribution in the Prydz Bay region can be confidently outlined.

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