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Distribution and abundance of post-larval krill (*Euphausia superba* Dana) near Prydz Bay in summer with reference to environmental conditions

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Abstract: Data on the distribution, abundance and population structure of krill in the Prydz Bay area during January–February 1985 are considered in relation to hydrography and phytoplankton standing stocks. Stratified mean density and biomass estimated for the whole surveyed area from RMT-8 hauls were among the lowest recorded (3.3 individuals 1000 m^{-3} and 3.1 g 1000 m^{-3}) confirming Prydz Bay as a low krill abundance area in the Southern Ocean. Age cohorts 1+ to 4+ were present, the size of the animals increased from south to north and juveniles were mostly found in surface waters near the pack-ice. Adults were in an active reproductive phase: 98% of the females were mated and 35% were ready to spawn whereas 86% of the males carried spermatophores. Breeding was taking place in oceanic waters over deep zones with the spawning season limited to January–April. Phytoplankton biomass was also very low in the area (mean of 29 mg Chl *a* m^{-2} in the upper 200 m) and currents speed low, never reaching 10 cm s^{-1}. Krill distribution was strongly related to water circulation pattern but not related to phytoplankton distribution.

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Introduction

It is well accepted that krill *Euphausia superba*, is a key species in the Southern Ocean even though the classic Antarctic food chain diatoms-krill-higher predators is increasingly questioned (Siegfried *et al.* 1985) and may constitute only a part of the energy flow within the Antarctic marine ecosystem's food web.

Since the Discovery Committee studies (1926 onwards), research has focused intensively on this pelagic crustacean, most recently in the framework of the international "Biological Investigations of Marine Antarctic Systems and Stocks" (BIOMASS) programme. Concentration on western Antarctic waters along the Antarctic Peninsula and the Weddell Sea has meant far less attention to the Indian sector which was, prior to BIOMASS, the least known biologically (El-Sayed *et al.* 1979). Based on reports of high biological productivity and abundance of krill (Everson 1977, BIOMASS 1981) however, interest was recently focussed on the Prydz Bay area (BIOMASS 1982). During SIBEX (Second International BIOMASS Experiment, 1984–85) four countries (South Africa, Japan, Australia and France) surveyed krill populations by means of hydroacoustic and net sampling in this area. The French survey took place on both sides of the Antarctic Divergence that is encountered at variable latitude between 63° and 65°S (Deacon 1937). This frontal zone, characterized by the abundance of small cyclonic structures (Tchernia & Jeannin 1980) separating the west-going coastal current and the east-going ocean current offshore, is considered to be of primary importance for krill (Amos 1984).

During the survey research focused on krill biology, its trophic environment and potential predators (Anonymous 1990). This paper presents results on the distribution, abundance, and population structure of *E. superba* north of Prydz Bay, in relation to hydrography and phytoplankton standing stocks during the austral summer of 1985. It is part of the French contribution to SIBEX II and aims to improve understanding of krill populations in the Indian sector of the Southern Ocean.

Methodology

Sampling

Net samples were taken on board R.V. *Marion Dufresne* during the French MD42/SIBEX cruise to the Indian sector of the Southern Ocean from 12 January to 7 February 1985. The cruise track and sampling stations are shown in Fig. 1. A Rectangular Midwater Trawl (RMT-8) (Baker *et al.* 1973) with 4.5 mm mesh size at the entrance and 2 mm at the cod-end was used. Wire speed while paying out and towing in and the ship's speed were: 0.6 m s^{-1}, 0.3 m s^{-1} and 2–2.5 knots respectively, as recommended by BIOMASS (Pommeranz *et al.* 1982).

Three types of hauls were carried out: deep (D), mid (M) and surface (S) waters hauls at stations 10 to 34 (Fig. 1)

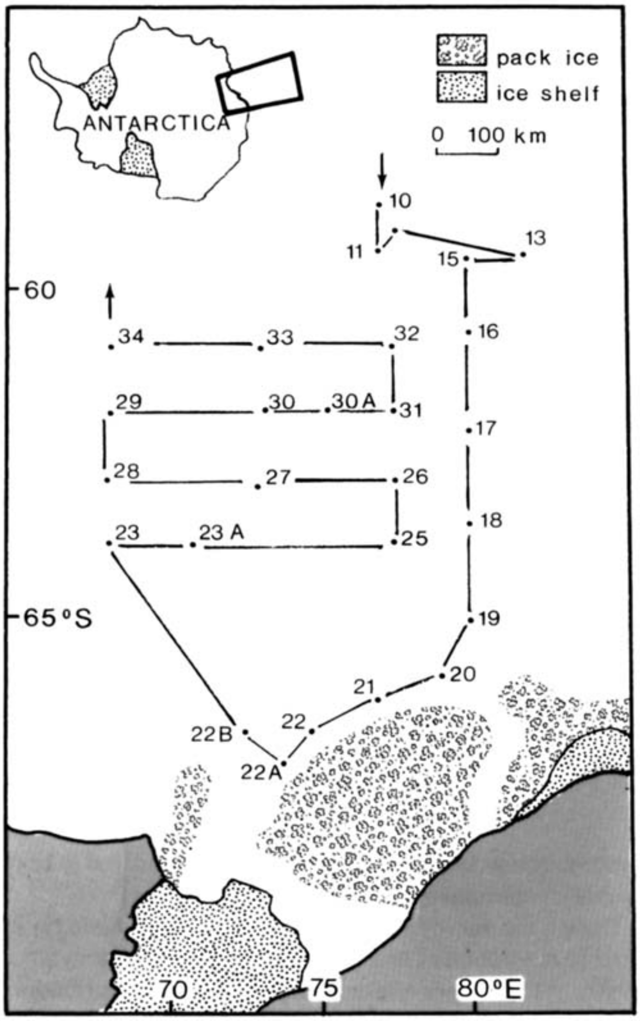

Fig. 1. Map of the area showing survey grid, ice position and station numbers where RMT-8 hauls were done during the cruise MD42/SIBEX of R.V. *Marion Dufresne*. Pack-ice and ice-shelf information from Navy-NOAA sea ice chart for January 31, 1985.

making a total of 59 hauls. They were done at fixed stations (see Anonymous 1990, p. 19–24 for geographic coordinates). From station 10 to 20 only the deep hauls were done. Surface water hauls (upper 50 meters) aimed at obtaining healthy individuals for experiments on board. The net was brought in by steps (2 to 4) of 5 to 10 minutes at 50 to 30 m depth. These catches are considered only qualitatively. Mid water hauls, for biomass estimations, were double oblique hauls between the surface and 150 m depth according to the BIOMASS protocol (Pommeranz *et al.* 1982). Deep water hauls (designed to catch myctophid fishes), were double oblique from the surface down to 400–600 m. Since krill normally inhabits the upper 100 to 150 m of the water column (Miller & Hampton 1989) these hauls were considered similar to the "mid" water hauls for this krill study.

Total settled volumes and total fresh weight of the net collection were measured directly after capture. Krill specimens were sorted out and the remaining sample, or subsample was preserved in a 4 % buffered formaldehyde seawater solution. Krill were counted and the length, sex and maturity stage were determined for at least 50 individuals on board. The remaining specimens were preserved for later laboratory analysis. Krill length was measured to 0.1 mm from the tip of the rostrum to the posterior edge of uropods (standard measurement 1; Mauchline 1980). Damaged specimens were measured only to the posterior end of the abdomen (standard measurement 2) or of the cephalothorax (standard measurement 4) and the lengths transformed to standard length 1 by the equations:

$$SL1 = 1.15\ SL2 + 0.68$$

(correlation coefficient $r = 0.98$) 120 pairs of observations for 33.1 to 56.3 mm SL1

$$SL1 = 2.86\ SL4 + 2.63$$

(R. Williams, Antarctic Division, Australia; personal *communication*)

Sex and maturity stages of post-larval krill (juveniles, subadults and adults) were classified according to Makarov & Denys' (1982). The three subadult stages of the males were distinguished but, due to their scarcity, are grouped.

Calculation of filtered volumes

Volumes filtered depend on the real distance towed and on the opening area of the RMT-8, which varies according to the hauling speed (Roe *et al.* 1980). The length of the net tow was calculated from the depth reached by the net (read on a Tsurumi bathykimograph) and the distance hauled. The latter was derived from the geographic position at the beginning and at the end of each phase of the hauls, and from the speed of the ship and the duration of paying-out and hauling-in. Calculations of the towing distance by both methods differed only by 6%. The opening area of the net at work was derived from the effective mouth angle during an oblique haul (Pommeranz *et al.* 1983) and the opening size of the net at rest (12 m^2). Volumes filtered were estimated for the 0–150 m depth range in both mid and deep hauls. Computations were done separately for the paying-out and hauling-in phases and the contribution of these two phases to the volume filtered were respectively 38% and 62% for M-hauls and 34% and 66% for D-hauls.

Biomass and density estimation

Krill biomass was calculated from the abundance of individuals in each 1 mm size class. To increase the precision of the biomass estimation krill was divided into three groups: "adult males", "gravid females" and "standard krill (others)", and biomasses were predicted using the model B presented by Morris *et al.* (1988; table VII and appendix I).

An attempt was made to estimate krill density and biomass for the area delimited by parallels 58°S and 67°S and meridians 68°E and 82°E, excluding the waters north of 60°S and west of 76°E where no hauls were done (total area of 6.2 x 10^5 km^2). To reduce the effect of the uneven distribution of krill (Everson 1977), the area was divided into four sub-areas (strata) for density and biomass respectively (Saville 1977). Contour lines (stratum boundaries) were determined by inverse distance interpolation between stations. Mean and variance were estimated for each stratum separately and then combined into estimates for the area as a whole. The stratified mean for the surveyed area is:

$$\bar{x}_{st} = \sum \frac{\bar{x}_n \cdot \text{area(N)}}{\text{total area}}$$

and the variance of the stratified mean:

$$\text{var}\ (\bar{x}_{st}) = \sum \text{var}\ (\bar{x}_n) \left[\frac{\text{area(N)}}{\text{total area}}\right]^2$$

in which $\bar{x}_n$ is the mean for the stratum N and var $(\bar{x}_n)$ its variance.

The surface area of each stratum was obtained by integration of the areas in each degree of latitude in order to take into account mercator geographic projection (Nast 1982).

Comparisons of net hauls

When two or more hauls were done at the same station, differences between them in size and maturity stage of individuals were tested with the null hypothesis that there was homogeneity among hauls. Statistics comparison were made using the non-parametric Kruskal-Wallis test for stations with three hauls and Wilcoxon-Mann-Whitney test (Sokhal & Rohlf 1981) for stations with only two hauls, or for paired hauls in stations having three hauls. Information from the population sampled in the standard 150–0 m haul (M-haul) was combined with data from the D- and S- hauls presenting a high similarity in size structure and maturity stage composition (Tables I and II).

Environmental conditions

Physical oceanography

Temperature-salinity diagram for surface waters (Bedo 1987) shows a discontinuity as stations 19 to 22 had lower surface temperatures, close to 0°C. T-S diagrams for the whole water column (Fig. 2) clearly show the position of the Antarctic divergence between 63°46'S and 63°58'S during the cruise. Lower surface salinity at stations 19 to 21 indicates significant ice melting at these stations whereas at stations 22 high salinity was noted. South-north vertical transects of temperature and salinity along the longitudes 77-78°E and 79-80°E (Fig. 3) show a stratified water structure and locate the krill population in waters in the range of $-1.5<T<+2.0$°C for temperature (extremes found in stations 21 and 32) and of $33.5<S<34.5$ for salinity (extremes in stations 19 and 17, 25, 26), i.e. open ocean Antarctic surface waters.

The geostrophic circulation was calculated by Gamberoni (unpublished) from the conductivity-temperature-depth data referenced to 500 m depth. Middleton & Humphries (1989) did the same calculations from a finer station grid for the same period. Surface water flow in summer 1985 based on both works, which closely agree, is presented in Fig. 4. The only differences noticed during our survey were:

a) between stations 21 and 25 there was a weak component to the south-west (less than 0.2 cm s^{-1}) that may indicate that the gyre around 67°S,79°E was more important

b) along 61°S the east to north-east current was observed further east, between 75°E and 80°E and more strongly northward oriented. This northward meridional flow across the Crozet and Kerguelen-Gaussberg Plateaus is induced topographically (Gordon *et al.* 1978). Further north, westward oriented surface flow reaching 1.5 cm s^{-1} was detected (Fig. 4). The more important northward flow along 61°S and the westward flow indicate some important changes in surface water currents; these changes in direction seem to be centred around 59–60°S and 78–79°E.

The pattern in surface water flow observed in summer

Table I. Statistics on body length of *E. superba* for homogeneity of hauls from positive multi-hauls stations.

Station No.	Type of Hauls[a]	Kruskal-Wallis test		Wilcoxon-Mann-Whitney test					
				D/M		D/S		M/S	
		H	*P*	t_s	*P*	t_s	*P*	t_s	*P*
21	D,M	-	-	1.376	0.1688	-	-	-	-
22	D,M,S	17.879	0.0001***	3.679	0.0002***	2.777	0.0054*	2.238	0.0252*
23A	D,M,S	0.152	0.9268	0.124	0.9007	0.384	0.7005	0.001	0.9995
25	M,S	-	-	-	-	-	-	0.933	0.3506
26	D,M,S	20.717	0.0000***	2.301	0.0214*	2.252	0.0243*	3.781	0.0001***
27	D,M,S	16.931	0.0002***	1.049	0.2938	2.008	0.0446*	3.964	0.0001***
32	D,M,S	22.140	0.0000***	1.263	0.2063	2.103	0.0354*	4.653	0.0000***

[a] Type of hauls: D, deep; M, mid; S, surface waters

H and t_s, test statistic; *P*, significance level for accepting the null assumption of homogeneity among hauls;

* < 0.05 , ** < 0.005 , *** < 0.0005

Table II. Statistics on sexual maturity stages of *E. superba* for homogeneity of hauls from positive multi-hauls stations.

Station No.	Type of Hauls[a]	Kruskal-Wallis test		Wilcoxon-Mann-Whitney test					
				D/M		D/S		M/S	
		H	P	t_s	P	t_s	P	t_s	P
21	D,M	-	-	0.471	0.6373	-	-	-	-
22	D,M,S	31.869	0.0000***	5.592	0.0000***	3.298	0.0010**	0.770	0.4411
23A	D,M,S	3.156	0.2063	0.384	0.7009	1.745	0.0808	0.826	0.4086
25	M,S	-	-	-	-	-	-	0.601	0.5481
26	D,M,S	11.829	0.0027**	0.396	0.6919	2.838	0.0045**	3.475	0.0005**
27	D,M,S	13.876	0.0009**	2.129	0.0332	3.571	0.0003***	2.459	0.0153*
32	D,M,S	28.284	0.0000***	3.566	0.0003***	0.524	0.5999	5.099	0.0000***

[a] Type of hauls: D, deep; M, mid; S, surface waters

H and t_s, test statistic; P, significance level for accepting the null assumption of homogeneity among hauls;

* < 0.05 , ** < 0.005 , *** < 0.0005

1985 agrees with the known hydrography of the Prydz Bay area (Smith *et al.* 1984): the main characteristic is the occurrence of a large cyclonic gyre centred on the divergence zone. Bedo (1987) suspected such a hydrological feature from spectral size analysis of seston which suggested some mixing processes taking place in the central surveyed area. Surface waters are generally highly variable in and about the bay and the coastal regions show strong variability with occasional east flowing currents in addition to the wind-driven west flowing currents. Further north, the geostrophic lines were consistent with the eastward flowing Antarctic Circumpolar Current and the north-east flow between 62°S and 60°S has also been reported by Naganobu & Nasu (1986).

Current speed at any depth between two stations was derived from the dynamic calculations. Table III lists the maximum speed in the upper 200 m water layer along four south-north and three west-east transects. The maximum current speed estimated is 4.3 cm s^{-1} using 500 m as reference. As expected, using a greater depth as reference the maximum current speed is higher (6.1 cm s^{-1}). This difference could be quantified for the deeper profiles at 3.1–3.3 cm s^{-1} and thus it is possible to conclude that water currents in the upper

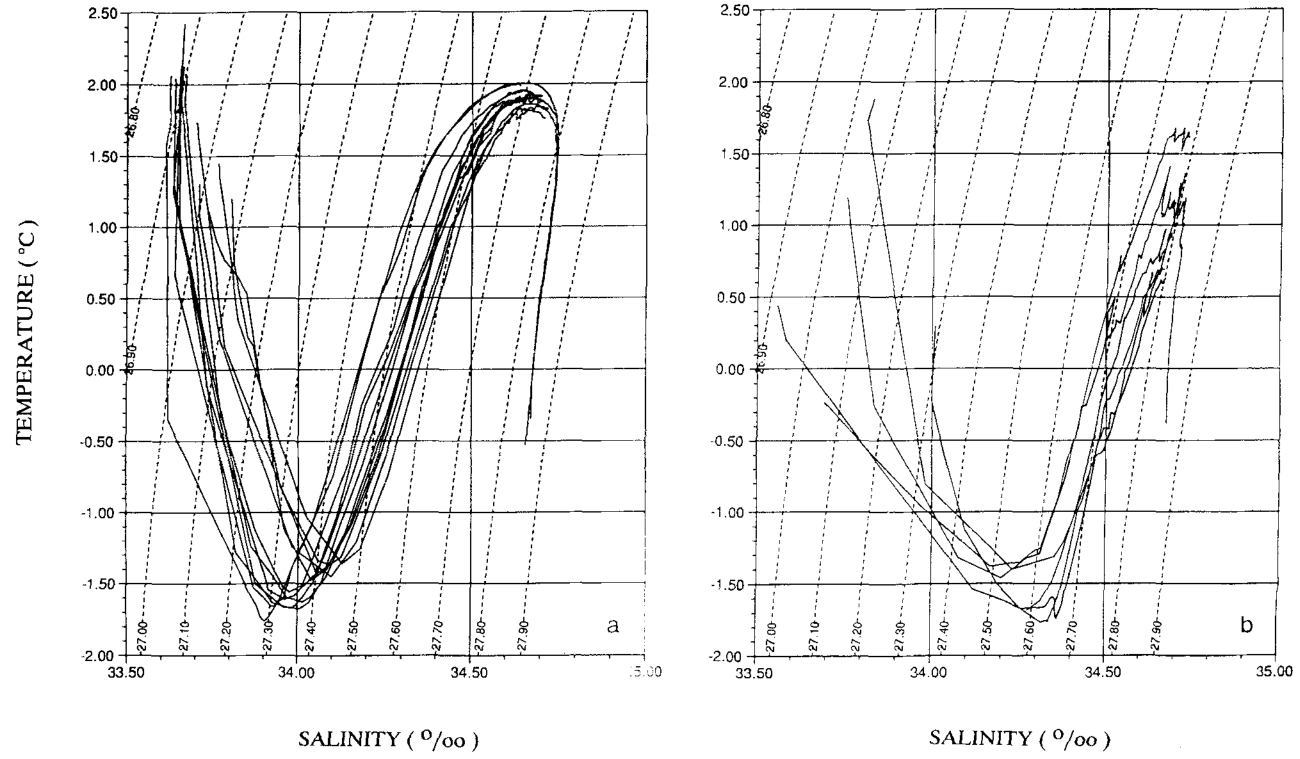

Fig. 2. Temperature-salinity diagrams for the whole water column during MD42/SIBEX. **a.** stations north of 63°46'S, **b.** stations south of 63°58'S (courtesy of L. Gamberoni).

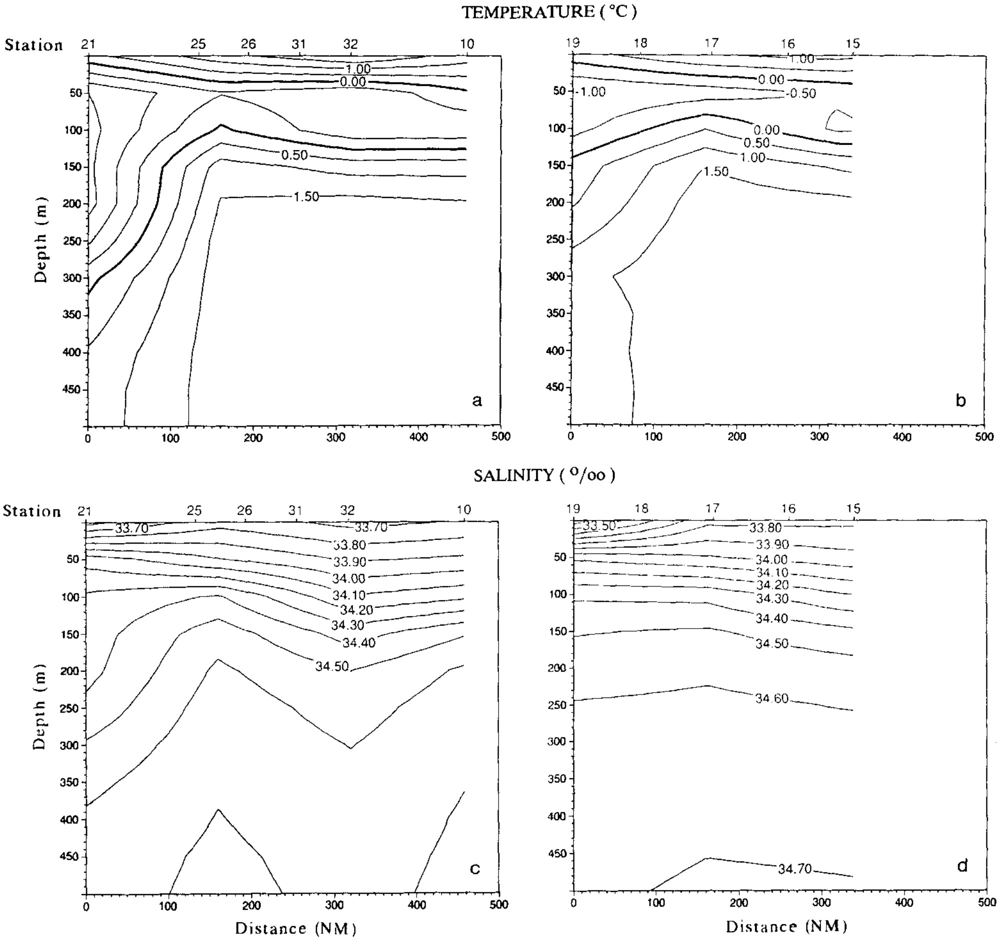

Fig. 3. South-North vertical transects of temperature (**a,b**) and salinity (**c,d**) along longitudes 77–78°E (**a,c**) and 79–80°E (**b,d**) during MD42/SIBEX (courtesy of L. Gamberoni).

200 m did not reach 10 cm s^{-1} in absolute values. Lowest speeds of water current were found in the southern stations (21–25) and along the eastern stations (15–18). By contrast, highest speeds were measured in the north-west stations (23–28, 29–34, 30–33), alternating with low flows (28–29, 33–34) while central stations had flows comprised between 1 and 2 cm s^{-1} (relative to 500 m).

Phytoplankton biomass

In nearly all the stations the vertical profiles of chlorophyll showed a sub-surface maximum, usually at 30–50 m, with maximum values averaging only 0.46 µg Chl *a* l^{-1} (minimum: 0.06 at stations 19 and 20; maximum: 1.40 at station 27). Phytoplankton biomass in the upper 200 m of the water column was very low, emphasizing the very low level of chlorophyll in the entire area with a mean of 29 mg Chl *a* m^{-2} south of 59°S latitude (Panouse 1990). The minimum value observed was 2 mg Chl *a* m^{-2} at station 20 and the maximum was 57 mg Chl *a* m^{-2} at station 22. The horizontal distribution of integrated phytoplankton biomasses (Fig. 5) indicates a decreasing

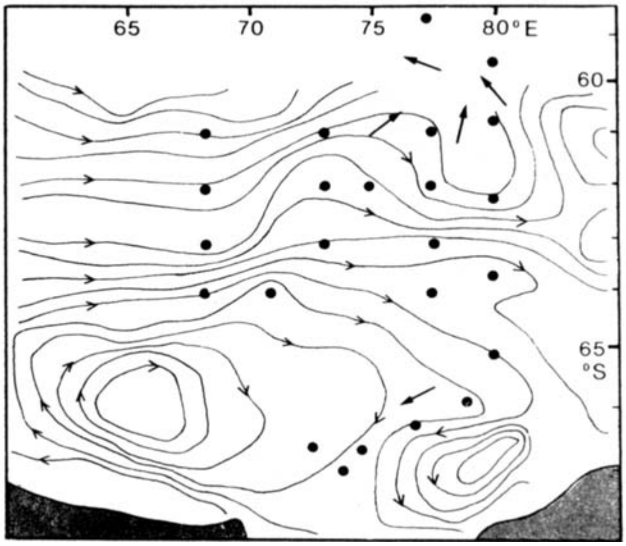

Fig. 4. Direction of surface water flow and boundaries of gyre during January 1985 based on the contours of geopotential anomaly drawn relative to 600 m by Middleton & Humphries (1989) and present study. Arrows indicate differing observations. Dots indicate the position of the stations during French MD42/SIBEX.

Table III. Maximum speed of water flow in the upper 200 m of the water column along four south-north and three west-east transects during MD42/SIBEX.

Stations	Depth of reference (m)	Max. speed (cm s^{-1})	Stations	Depth of reference (m)	Max. speed (cm s^{-1})
23–28	500	4.3	19–18	500	1.1
28–29	500	0.3	19–18	3500	4.2
29–34	500	2.8	18–17	500	0.7
29–34	4300	6.1	17–16	500	0.3
			16–15	500	0.2
22–27	500	0.5			
27–30	500	1.4	34–33	500	0.2
30–33	500	4.0	33–32	500	1.0
			32–16	500	1.7
21–25	500	0.2			
25–26	500	1.4	23A–25	500	0.2
26–31	500	1.8			
31–32	500	1.3	22–21	500	0.6
32–10	500	1.5			

concentration of chlorophyll *a* from southwest to east and north.

Krill population

Effect of daylight on catches

To ascertain whether the time of trawling influenced catches, comparisons were made between krill densities obtained at different hours of the day, and with different irradiance at the sea surface at the moment of fishing. Very low catches (d≤1 individuals 1000 m^{-3}) were obtained at all times of the day and mean densities for periods of 4 hours were not significantly different throughout the daytime. The relation between abundance and irradiances tested by regression analysis was not significant (t= -1.082; P= 0.286) and only 3 % of the variability in densities could be explained by light intensity at the surface while trawling. Thus, no significant day/night effect on the catches could be noticed. A similar conclusion was reached by miller (1985), while Everson & Bone (1986) noticed an important avoidance of the RMT-8 by krill swarms only during daytime. Different reactions of krill to the net may be related to clustering of the animals and avoidance thus decreases with lower densities.

Distribution and abundance

Krill were collected at 22 out of the 27 stations located south of 58°S . The density of krill in the area ranged from 0 to 20 individuals 1000 m^{-3} (Fig. 6). The highest densities were recorded south of 66°S and in the central part of the area, particularly along meridians 77–78°E; a high density was also recorded at station 13, in the north-east part of the area. The stratified mean density in the whole area was 3.3 individuals 1000 m^{-3} ± 36% (Table IV). Although, the variance usually increases with population density, it

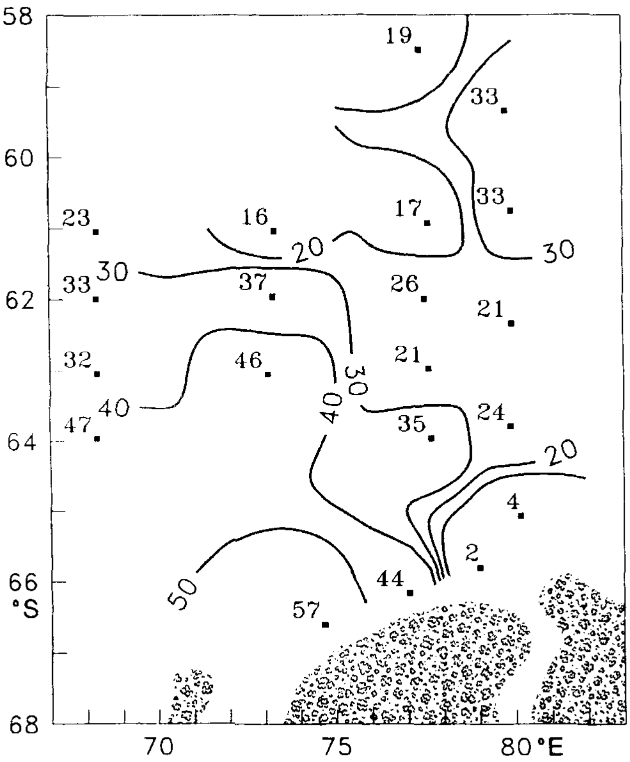

Fig. 5. Integrated phytoplankton biomass (in mg Chl *a* m^{-2}) in the upper 200 m of the water column during mD42/SIBEX. Shading shows pack-ice (courtesy of M. Panouse).

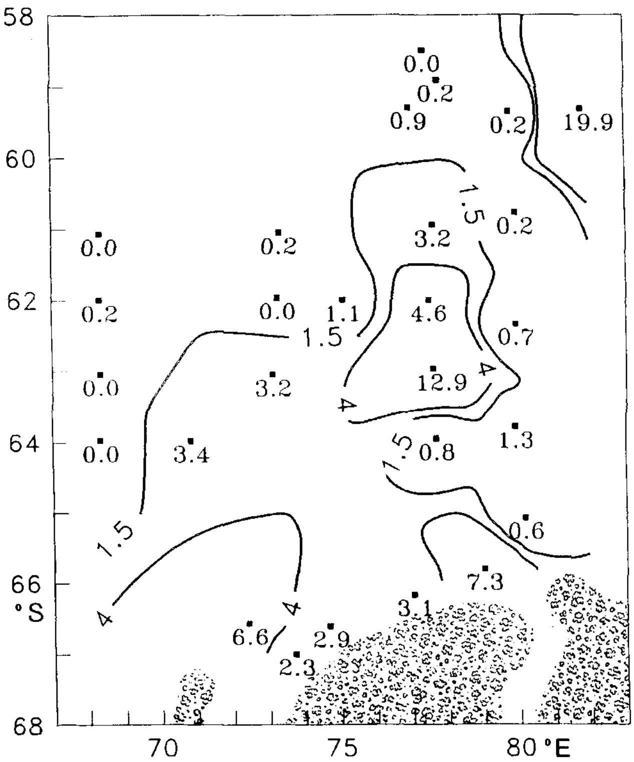

Fig. 6. Krill abundance and strata of similar density (individuals 1000 m^{-3}) during MD42/SIBEX. Shading shows pack-ice.

Table IV. Krill abundance in four-density stratified zones and estimation of the number of krill in the surveyed area during MD42/SIBEX.

	Density sub-areas			
	<0.5	0.5–1.5	1.5–4	>4
Number of hauls	10	6	6	5
Variance between individual hauls	0.011	0.068	0.150	38.523
Mean density (individuals 1000 m^{-3})	0.10	0.90	3.02	10.26
Variance mean density	0.001	0.011	0.025	7.705
Size of area (x 10^{10} m^2)	13.45	16.53	19.12	12.77
Stratified mean density (individuals 1000 m^{-3})	3.31			
Variance stratified mean	0.332			
Standard deviation stratified mean	0.576			
90% Confidence limits (individuals 1000 m^{-3})	3.3 ± 0.98 = 3.3 ± 29%			
95% Confidence limits (individuals 1000 m^{-3})	3.3 ± 1.18 = 3.3 ± 36%			
Volume of area to 150 m depth	9280.13 x 10^{10} m^3			
Number of krill in the total area	30.741 x 10^{10} (±36%) animals			

remained rather low even for the highest density-stratum. Thus, the stratified standard deviation was small and the precision in the estimation of the mean density is satisfactory, even at 95% confidence limit. Considering the upper 150 m of the water column as the habitat of *E. superba*, the estimated number of adult and juvenile krill in the area derived from the stratified mean density would be 30.7 x 10^{10} individuals.

As for the densities, highest biomasses were observed in the central and north-eastern parts of the surveyed area (Fig. 7). Smaller biomasses, however, were observed in the central southern part, suggesting the occurrence of smaller size animals closer to the pack-ice. Isolines 1.5 and 4.0 g 1000 m^{-3} follow the same contours as the density-lines except for the stations south of 66°S. The mean biomasses showed small (Table V) variances for all strata giving a satisfactory precision in the estimation of the biomass for the whole area. The stratified mean biomass was 3.1 g (wet weight) 1000 m^{-3} ± 33% at 95% confidence limit and the estimated total biomass for the surveyed area (6.2 x 10^5 km^2) was 2.9 x 10^5 tons.

Results indicate that the abundance of *E. superba* was low in the area during January–February 1985 and that its geographic boundary to the north was at the vicinity of 59°S. Apparently, there was no influence of the Antarctic Divergence on the krill distribution. Particularly noticeable was the near absence of krill in the western/north-western part of the surveyed area (west of 70°E and, north of 62°S, west of 74°E). Even so, catches were more important than during the first French leg of SIBEX (Antiprod III, 16 January to 22 February 1984) done in the same geographic area. In 1984, *E. superba* was fished in only three stations out of 15 stations situated south of 58°S.

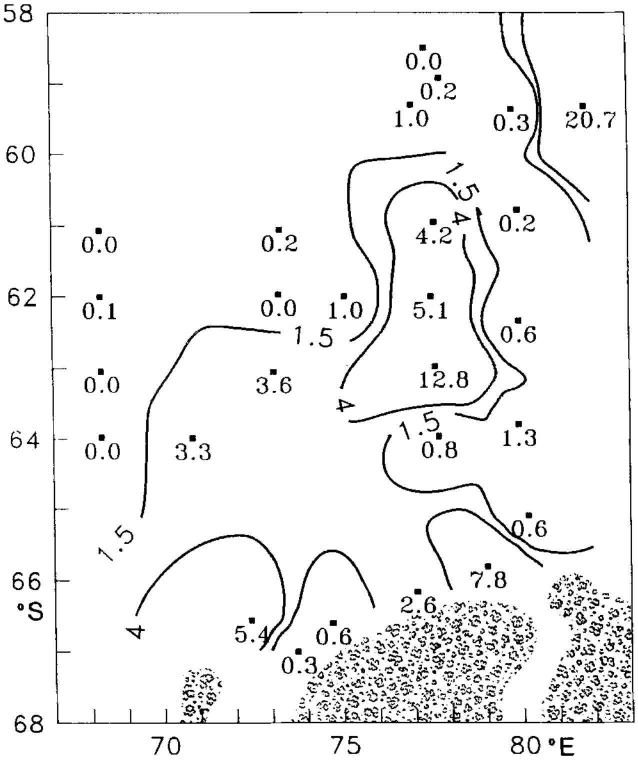

Fig. 7. Krill biomass and strata of similar biomass (g 1000 m^{-3}) during MD42/SIBEX. Shading shows pack-ice.

Vertical distribution

Samples from multi-haul stations showed some differences with depth in size and maturity stage except for station 23A (Tables I and II). Deep and mid water catches were often comparable for size whereas surface catches had different size structure. Sexual maturity stages were similar only in surface and mid waters south of 63°S.

Although the hauls were unsuitable for an accurate vertical analysis some general information can be obtained from

Table V. Krill biomass in four stratified zones and estimation of the biomass of krill in the surveyed area during MD42/SIBEX.

	Biomass sub-areas			
	<0.5	0.5–1.5	1.5–4	>4
Number of hauls	11	7	3	6
Variance between individual hauls	0.013	0.064	0.208	33.710
Mean biomass (g 1000 m^{-3})	0.12	0.84	3.18	9.34
Variance mean biomass	0.001	0.009	0.069	5.618
Size of area (x 10^{10} m^2)	15.11	15.69	18.24	12.83
Stratified mean biomass (g 1000 m^{-3})	3.12			
Variance stratified mean	0.248			
Standard deviation stratified mean	0.498			
90% Confidence limits (g 1000 m^{-3})	3.1 ± 0.85 = 3.1 ± 27%			
95% Confidence limits (g 1000 m^{-3})	3.1 ± 1.02 = 3.1 ± 33%			
Volume of area to 150 m depth	9280.13 x 10^{10} m^3			
Biomass of krill in the total area	2.892 x 10^5 (±33%) tons			

stations with heterogeneous data: juveniles, when present, were always in waters close to the surface and were never fished in deep hauls; females were usually larger in deep hauls and spent females (maturity stage 3E) were mostly found in the deep hauls, appearing closer to the surface only in stations 27 and 32; males were more evenly distributed and no clear depth pattern was noticed in their distribution. The krill composition (size and sexual maturity) for each individual haul is in Miquel (1990).

Size and age-groups composition

The length-frequency distribution by station (Fig. 8) shows a trend of increasing size from south to north along meridians 77–78°E (station 21 northward to station 32) and southwest to northeast from stations 23A, 27 to station 32 where the largest specimens of krill were caught.

In the surveyed area the sampled population was largely composed of individuals longer than 40 mm (Fig. 9). Age-group analysis from size-frequency data (MacDonald & Pitcher 1979) applied to krill from the Prydz Bay region (Hosie *et al.* 1988) indicates the presence of 4 year classes. Age class 1+, juveniles with a mean body length of 20 mm; age class 3+, the most abundant in both sexes, with a mean length of 48 mm and age classes 2+ and 4+ present only in females with a mean body length of 42 and 54 mm. The presence of males age class 4+ is not clear from the modal length-frequencies because of the smaller number of large size males caught.

Possible shrinkage of body length of adult krill during winter (Ikeda & Dixon 1982) affects modal length-frequency analysis for larger animals and may obscure several year classes in a single mode. Ettershank (1983, 1985) determined age structure of krill from Prydz Bay from lipofuscins age pigments and concluded the existence of six year-classes including juveniles. A similar conclusion was reached by Siegel (1987) from length-frequency data for the Antarctic Peninsula while Aseyev (1984) concluded that five year-classes existed (including juveniles) in the Indian sector. These results and Rosenberg *et al.* (1986) analysis of a 10 year time series of length composition of krill taken by the R.R.S. *Discovery* indicate that in the Prydz Bay area krill

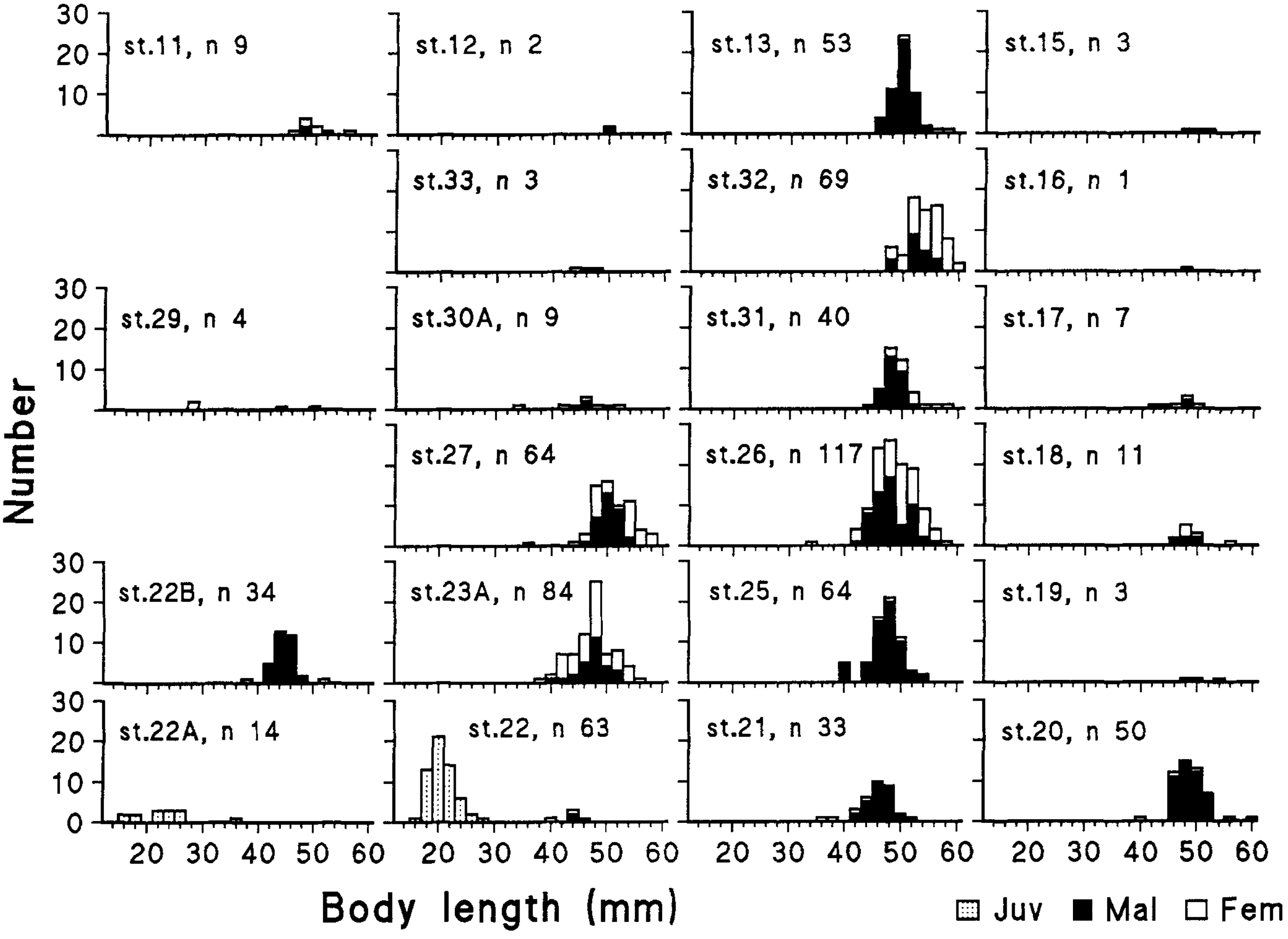

Fig. 8. Size composition of krill at the different stations. Disposition of histograms follow approximately the relative geographic position of the stations. Stations with no catch are not figured; *n*= number of specimens observed.

older than 4 years may occur although these were not seen in the present study because of the scarcity of animals.

Based on the size and age of krill, three major geographic zones can be defined:

a) stations in which krill population was largely dominated by small size specimens, <28 mm length (juveniles and a few specimens of year 2+ and 3+). These stations were located in the southernmost part of the surveyed area (22 and 22A)
b) stations with at least some animals in the range 30–40 mm length although most of the population was of larger size (krill of year cohorts 2+, 3+ and 4+ with 3 years old animals most abundant). These stations formed a ring northward of the first group (21, 22B, 23A, 25 to 27, and 30A)
c) stations composed almost exclusively of animals of large size, >46 mm length (animals of 3+ and 4+ years with cohort 3+ still dominating). These stations were situated further north and east (11 to 20, and 31 to 33).

Maturity stages and reproduction

The juvenile stage was the most geographically limited one (Fig. 10) mostly confined to the southern stations closer to the pack-ice (station 22 and 22A) where they constituted all or nearly all the catch. Isolated single specimens were also caught in surface waters along 63°S while immature subadults of both sexes were rarely present and it happened only in stations situated between 62° and 63°S. Conversely, mature males with spermatophores present in the ejaculatory ducts (stage 3B) were widely distributed and occurred in all but one station. They were most abundant east of 77°E and in the southern stations (21, 22B) in the vicinity of juvenile occurrence. Mature females in pre-spawn and ready to spawn phase (stages 3C and 3D) as well as females with less developed ovary (stages 3A and 3B) and males without spermatophores (stage 3A) also had a wide and scattered distribution. They were present in two thirds of the stations and showed a clear dominance in the central area of the survey. Recent post-spawned females (stage 3E) only appeared to be important in some of the central stations, particularly at station 32 where they contributed half of the individuals. In the north-west stations where krill was nearly absent, the very few females observed were either immature (stage 2) or newly mature but not yet mated (stage 3A). On the contrary, males were already mature and some had spermatophores in the ducts.

Gonads of krill caught during the cruise were histologically studied for gonadal development and maturation (Cuzin-Roudy 1987a). First sexual differences in the gonads appeared among young krill of 28 mm indicating the passing from juvenile to immature subadult. The ovary became fully mature and first spawning occurred in young females of 39 mm while the smallest mature male was 42 mm SL1 body length.

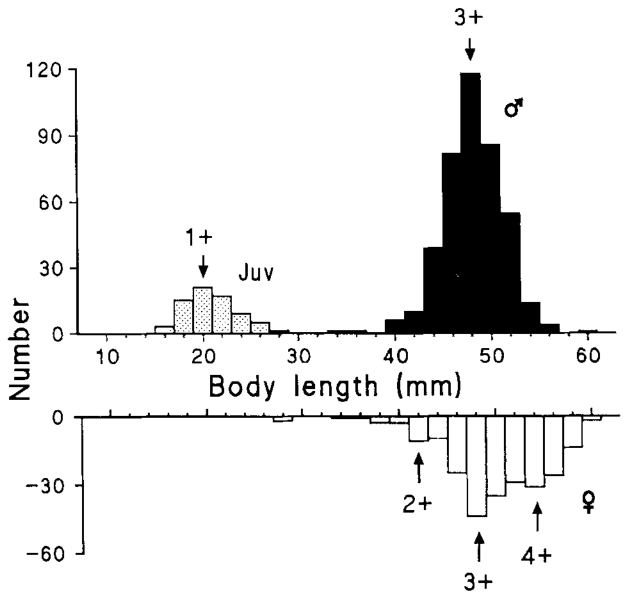

Fig. 9. Size frequency distribution and age-classes of postlarval *E. superba* during MD42/SIBEX. Observations based on 737 specimens.

The histochemical observations indicated that the female krill could successively mature at least three batches of eggs in the season (Cuzin-Roudy 1987b). The abundance of mature oocytes decreases during successive spawning episodes and, as a consequence, some sexual mature females classified as 3C or even 3B were actually ready to spawn. The highest proportion of females had an enlarged ovary and were in spawning phase (stage 3D) (35%, Fig. 11). Most of the females (98%) were mated, i.e. had spermatophores attached to the thelycum and 80% had spermatozoa in their thelyca for fertilization of the eggs. Simultaneously, mature males appeared to be continuously producing sperm and males with spermatophores in the ejaculatory ducts (stage 3B) were by far the most abundant (86%, Fig. 11).

Breeding season and sites

The geographic distribution of krill, with smaller individuals closer to the Antarctic continent and larger animals further offshore, is a well defined mid-summer distribution pattern already observed off some other Antarctic sectors (Nemoto 1983b, Aseyev 1984, Siegel 1989). Daly & Macaulay (1988) found juveniles in abundant quantities close to the pack-ice and indicate that the pack-ice serves as a giant nursery area for krill. In Prydz Bay juveniles were found abundantly only in the two southernmost stations, closest to the pack-ice during January–February 1985. In summer 1984, juveniles were mostly collected in almost the same region (Ikeda *et al.* 1984).

The marked dominance of males carrying spermatophores

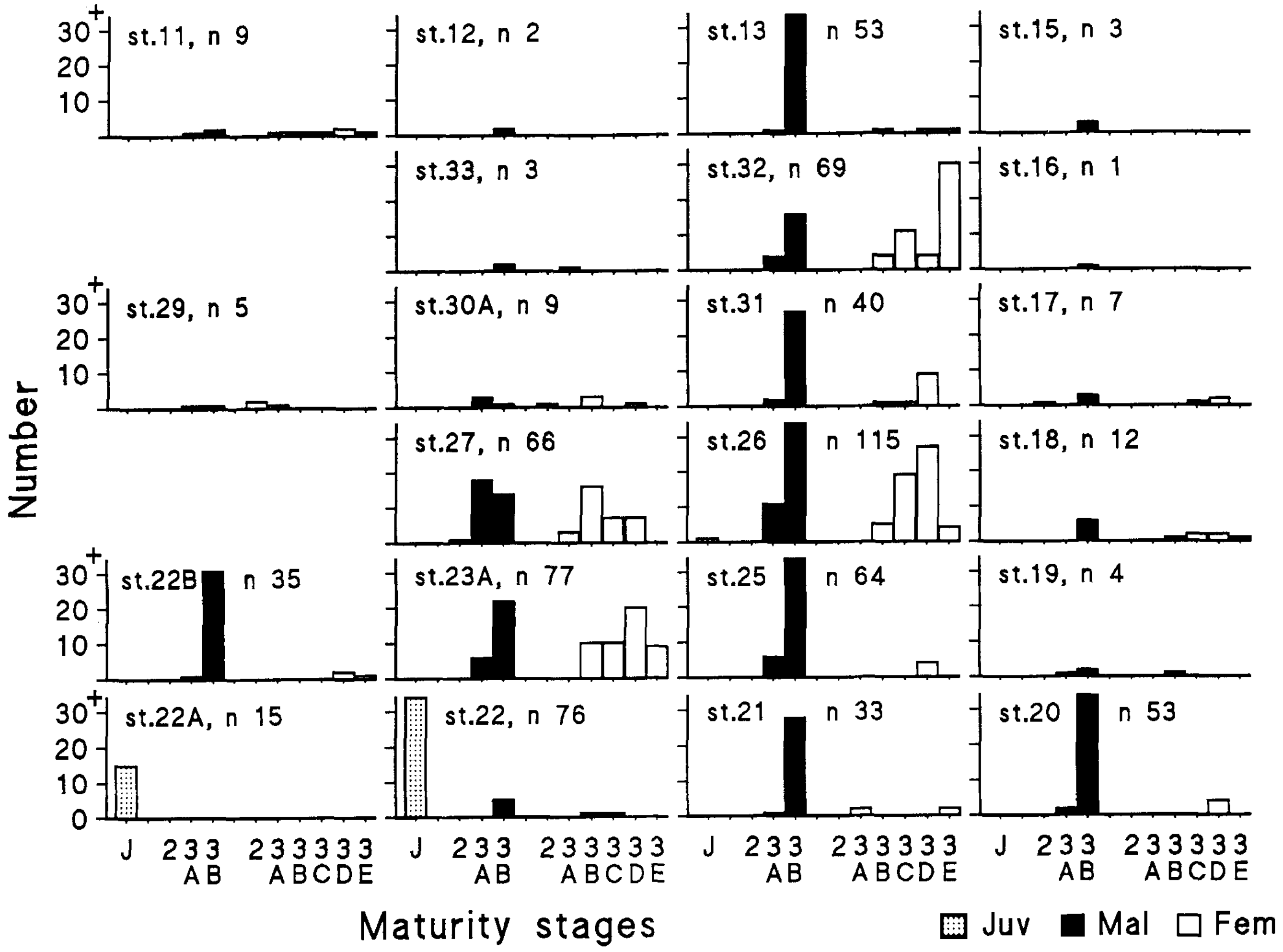

Fig. 10. Sexual maturity stages of krill at the different stations. Disposition of histograms follow approximately the relative geographic position of the stations. Numbers exceeding 35 are plotted with +. See Fig. 11 for description of the maturity stages.

and of females ready to spawn with spermatozoa in the thelycum for fertilization of the eggs clearly indicates that *E. superba* population was in an active reproductive phase by the end of January. Breeding was taking place in oceanic waters over deep zones (stations 17 to 21, 23A to 27 and 30A to 32). The closest point to the Antarctic shore where adults of both sexes were in the reproductive stage was station 22B; at that point the depth was about 2000 m. Breeding took place all the way north up to 59°17'S, the northernmost latitude were krill was caught. Earlier in the month, Hosie *et al.* (1988) had found a much higher proportion of immature subadults, males without spermatophores and females unmated or not ready to spawn, and concluded that spawning started in January. Later in the year (March-April 1984) the population of krill sampled further west, from 52°E to 64°E, was dominated by males without spermatophores (stage 3A) and female subadults (reverted after completion of spawning) while juveniles constituted 20% of the population (Miller 1985) indicating that *E. superba* was at the very end of the reproducing period at this time. Rakusa-Suszczewski (1984) also noted the end of krill spawning in April. Therefore, the krill spawning time in Prydz Bay area seems limited to the January to April period.

Although adults were found breeding well offshore from the Antarctic continent, they are unlikely to be part of the main breeding group producing the bulk of larvae since most of the adults in Prydz Bay region are found near the continental shelf edge (Williams *et al.* 1983, 1986, Ikeda *et al.* 1986, Ichii 1990) i.e., south of the present study area. Consequently, there are at least two major breeding sites in the Prydz Bay area, one along the continental shelf edge and another further off the continent over deep waters.

Despite the low abundance estimates, larval distribution in January 1985 (Ikeda *et al.* 1986) showed concentrations at 62–65°S, 72–83°E and, mainly, at 66–67°S, 58–70°E. Considering the maximum speed of water flow (Table III) and a return to surface waters of larvae at the end of ontogenic migration in less than a month after spawning (Ross & Quetin 1982), it is possible to conclude that calyptopes larvae arrived in surface waters in less than 75 to 90 km from the original spawning site. Although this simple calculation does not consider eventual up- or downstream currents that may modify the descending/ascending pattern, it shows clearly that feeding larvae develop not far from the parental population's location at the time of breeding. Thus, larval distribution also indicates two breeding sites in the area, one around 62–65°S, 72–83°E offshore and another around 66–67°S, 58–70°E near the continental margin. The population sampled by Miller (1985) may originate from this second breeding stock, when the larvae had been transported by the East Wind Drift after their ontogenic migration.

Stock assessment and variability

Various techniques have been used to estimate krill stock populations with net sampling (e.g. Marr 1962, Gulland 1970, Nast 1982) and acoustic estimates (e.g. Hirayama *et al.* 1979, Hampton 1985, Anonymous 1986) being the most widely used. Other techniques have included visual estimates (Marr 1962, Shust 1969) and analysis of stomach content of whales (Nemoto 1970, MackIntosh 1974). This variety of methods may explain contradictory estimates of krill abundance (Everson 1977). Swarming ability of krill and its highly contiguous distribution limits the value of net sampling as it causes excessively high variances (Nast 1982). Nemoto (1983a) considered the midwater trawl efficient only for average densities but Siegel (1986) in Hosie *et al.* (1988) claims that the RMT-8 does not sample juveniles well and Everson & Bone (1986) observed large scale avoidance of the RMT-8 by krill swarms. Thus, the net probably underestimates density but sets at least a lower limit on abundance (Miller & Hampton 1989). Significant, net estimates may be conservative compared to acoustic records of krill stock but Holm-Hansen & Huntley (1984) argued that only netted biomass could be supported by the ambient primary productivity.

The present results for density (3.3 individuals 1000 m^{-3}) and biomass (3.1 g 1000 m^{-3}) based on net catches are very low and very similar results were obtained one month earlier in the same area, using a similar gear (Australian SIBEX programme). Hosie *et al.* (1988) found a mean abundance of *E. superba* of six individuals 1000 m^{-3} or 2 g 1000 m^{-3} integrated in the upper 200 m of the water column with a majority of stations having a density of 0 or <1 individuals 1000 m^{-3}. The acoustic survey during our cruise also indicated the very limited occurrence of sparsely distributed krill (J. Sevellec, unpublished). Both surveys of krill in the Prydz Bay area during the summer 1985 thus indicate one of the lowest biomasses recorded for *E. superba* for an area in Antarctic waters.

Other population estimates for the Indian sector of the Southern Ocean by Miller (1985) for March-April 1984 give a mean biomass of 34.8 g 1000 m^{-3} in the area between 52°E and 64°E, i.e. 15 times higher than the one observed in January–February 1985. He & Huang (1984) reported important catches of *E. superba* in Prydz Bay and adjacent waters but only quantified them as 967 individuals per RMT haul. In the same Prydz Bay region Shirakihara *et al.* (1986) estimated biomasses of 14.3 and 17.5 g m^{-2} (acoustic survey carried in the upper 200 m in December 1983 and January 1984 between 65°E and 75°E). Further east, Terazaki & Wada (1986) caught 0.4 to 16 specimens 1000 m^{-3} in December 1983-January 1984 along 116-150°E and acoustic surveys in the same region gave estimations of 10 to 70 g 1000 m^{-3} (Inagake *et al.* 1985, Inoue *et al.* 1985). Most of these results agree with data given by Marr (1962) and acoustic FIBEX-BIOMASS data (Anonymous 1986) that estimated a krill mean biomass in the Indian sector of 1.97 g m^{-2} with a higher density between 30°E and 60°E and characterized the Prydz Bay as a low abundance region.

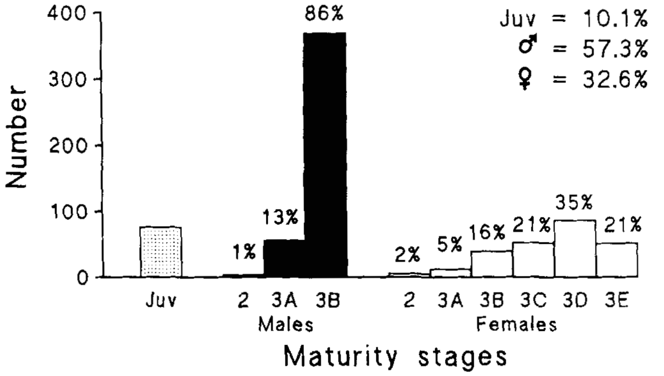

Fig. 11. Frequency distribution of *E. superba* postlarvae maturity stages during MD42/SIBEX. J: juveniles; 2: immature subadults. In males: 3A: mature male without spermatophore in ducts; 3B: mature male with spermatophores, ready to mate. In females: 3A: mature female not mated; 3B: mated mature female, ovary small; 3C: mated mature female, ovaries filling the thorax; 3D: ready to spawn female, carapace and first two abdominal segments swollen with enlarged ovaries; 3E: recently postspawnwed female. Observations based on 751 specimens.

Phytoplankton standing stock in the area was low during SIBEX-1984 (means < 0.5 µg Chl *a* l^{-1} in the euphotic zone, Panouse 1987) and SIBEX-1985 (means < 0.3 µg Chl *a* l^{-1} in the upper 200 m south of 59°S, Panouse 1990). These very low phytoplankton values in the Prydz Bay agree with previous reports for the region and with the low krill biomasses observed during the cruise.

Significant inter-annual variability in krill stocks is well documented (Klindt 1986, Kalinowski 1987, Soliankin & Spiridonov 1987) and the years 1983 through 1985 were of poor catches (Heywood *et al.* 1985, Miller 1985, Nast 1986, Czykieta *et al.* 1986, Hosie *et al.* 1988, present study). Siegel (1989) even considered the strength of year-class 1983-84 extremely poor while year-classes 1980-81 and 1985-86 were estimated extraordinarily strong. These variations may affect simultaneously large parts of the Southern Ocean and may contribute to the differences in krill biomass reported for the Prydz Bay area in the past.

Influence of environmental conditions on krill distribution

Due to the low biomass encountered during the austral summer 1985 the present data do not allow any final conclusion of the impact of hydrographical factors on the concentration of krill. There are indications, however, for a relationship between krill distribution and physical parameters. The lowest biomass of *E. superba* or its complete absence were reported from the north-westerly stations where current speeds were highest and no eddies present (Fig. 7 and Table III). Under such hydrological conditions Samyshev (1985) observed disintegration of krill patches but other studies (Higginbottom & Hosie 1989, Ichii 1990) report the occurrence of high krill abundance in areas with higher current speeds. Conversely, the four regions where krill was most abundant are all associated with changes in surface water circulation (Figs. 4 and 6). In the southernmost part, highest densities (station 20 and 22B) are located at the edges of the gyres at 66°S and 67°S. Higher abundance at the central stations 26 and 31 are associated with the meander deviating waters to the south described by Middleton & Humphries (1989) while the high biomass at the north-eastern station is likely to be associated with the changes in surface flow observed around 59–60°S, 78–79°E. Highest densities in the south and along 63°S were also observed by Ikeda *et al.* (1986) and Naganobu & Komaki (1986).

It is known that krill are strong swimmers able to travel at considerable speeds for extended periods of time. Kils (1983) reported a maximum swimming speed of 60 cm s^{-1} and speeds of 1.5 to 3.5 body lengths s^{-1} through day and night for more than a week in laboratory conditions. Marr (1962) observed a krill swarm swimming against a current at 18 cm s^{-1} for several hours and divers have observed krill swimming at a speed of 20 cm s^{-1} in horizontal direction (Hamner 1984). During our survey current velocity in the upper 200 m did not reach 10 cm s^{-1} and therefore krill can be expected to have been potentially independent of the water masses where it was observed. Naganobu & Hirano (1986) suggested that despite the good correlation between high densities of *E. superba* and geostrophic flows, the water dynamics may not be solely responsible for the krill distribution and that biological factors must be involved as well.

Mesoscale distributions of krill abundance and phytoplankton biomass (Figs. 5 and 6) presented similarities with a main south-west to north-east gradient but were not statistically correlated. The western stations had very few krill despite a wide range of phytoplankton biomass and, it was particularly noteworthy that the extremely low biomass in the south-east waters supported a relatively abundant *E. superba* population. The lack of correlation between these two parameters (which have very different process rates) on the basis of random, discrete samples separated by long distances is not surprising but is at variance with the positive correlation observed at a much smaller scale (El-Sayed 1987).

A close agreement between chlorophyll distribution and the surface water currents (Figs. 4 & 5) was found. In fact, chlorophyll isolines follow approximately the current contours from geostrophic calculations. The straight-through flow region in the northern part and the eddy regions can be distinguished in the phytoplankton biomass chart as well. In a smaller range (4–20 km), Weber *et al.* (1986) suggested that variability in phytoplankton biomass is largely determined by physical processes. In our much larger range (90–150 km), the variability of phytoplankton biomass still seems governed by the same processes. Predator-prey interaction has also been suggested as important in determining phytoplankton distributional patterns (Weber *et al.* 1986). Similarities in pattern distribution of krill and phytoplankton seems more likely to be the consequence of the dependency of both on the hydrographic scheme. McClatchie (1988) reported that krill can often meet their minimum requirements for growth at the low concentrations of phytoplankton characterizing offshore waters in the Southern Ocean, and Morris *et al.* (1984) showed that krill were able to adjust their filtration rate to compensate for the wide range in chlorophyll concentration. These observations lend support to the non-correlated relationship between krill and phytoplankton.

Conclusions

Even if krill estimates based on net survey are conservative compared to acoustic evaluations and estimates based on whale populations, the results of the net surveys carried in summer 1985 (Hosie *et al.* 1988 and present study) clearly indicate a very low krill biomass in Prydz Bay area and confirmed the Bay as a low krill abundance region. The offshore survey we carried indicated that krill was sparsely distributed as far north as 59°17'S, with juveniles most abundant in surface waters near the pack-ice and krill increasing in size/age northwards from the continent. Reproduction was in a very active phase in mid-summer and krill spawning time in Prydz Bay area extends from January to April. Breeding was taking place offshore in oceanic waters over deep zones but it appears that most of the adults are found near the continental shelf edge of the Bay and there is also found the main breeding site. Although currents did not reach 10 cm s^{-1} during the study they influenced krill distribution whereas phytoplankton stocks —which were also very low—was not correlated to krill.

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