

Distribution and abundance of euphausiid larvae in the Prydz Bay region, Antarctica

G.W. HOSIE

Australian Antarctic Division, Channel Highway, Kingston, Tasmania 7050, Australia

Abstract: In January 1985 a net sampling survey was carried out on the distribution and abundance of euphausiid larvae in the Prydz Bay region. *Euphausia superba* occurred in low abundance, probably due to sampling preceding the main spawning period. *Thysanoessa macrura* occurred throughout the study area in consistently high abundance. *Euphausia crystallorophias* was marginally more abundant within its restricted range. Distinct north-south variations in larval age and developmental stages of *T. macrura* were observed indicating regional differences in spawning. *Euphausia frigida* was mainly confined to the upper 200 m of the Antarctic Circumpolar Current. *E. superba* larvae produced north of the shelf break, between 70°–83°E, moved north-east into the Antarctic Circumpolar Current. Larvae originating on the shelf moved rapidly west in the East Wind drift. *E. crystallorophias* had the same westward dispersion, but some larvae appeared to return eastward via the Prydz Bay Gyre and remain in the region. The data indicate that most *E. superba* larvae, providing they survive injurious cold temperature and food deprivation, will leave the area, suggests that Prydz Bay krill may not be a self maintaining stock.

Received 31 July 1990, accepted 20 December 1990

Keywords: abundance, *Euphausia*, distribution, developmental stages, krill, *Thysanoessa*.

Introduction

Since the mid-1970s, the Antarctic krill, *Euphausia superba* Dana, has been the principal fishery around Antarctica with catches exceeding the total Antarctic finfish catch. Current statistics ranks the krill fishery thirtieth amongst world fisheries and it is the largest single species crustacean fishery (FAO 1989). While this fishery is still in its infancy, but growing, implementation of management policies as part of the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) is also at an early stage, with much of the data needed to make sound decisions still lacking (Nicol 1989). Fundamental to the successful management and protection of *E. superba* will be a thorough understanding of the population dynamics, especially the responses of the population to changes in the fishery and natural factors influencing abundance. Key components affecting stock size are the number of larvae produced annually, their survival/mortality, dispersion and their subsequent recruitment.

Much emphasis has been placed on studying the ecology of the post-larval and adult krill, and this bias is reflected in the literature. The adults are after all the focus of the krill fishery. Determining the distribution and abundance of krill has been an important part of this work and most of this information has emanated from the Atlantic sector (Miller & Hampton 1989), despite the occurrence of extensive krill fishing in the Indian ocean sector (Lubimova *et al.* 1985, Ichii 1990). As for the adults, most of the information on the ecology of the larvae comes from the Atlantic sector, but by

comparison larval ecology is poorly understood (Hempel 1985, Brinton *et al.* 1986, Miller & Hampton 1989). Few studies have attempted to study the factors controlling the fate of the larvae, e.g. Brinton (1985).

Prior to 1985, Australia's contribution to the international BIOMASS (Biological Investigation Of Marine Antarctic Systems and Stocks) programme centred on establishing the distribution and biomass of adult krill in the Prydz Bay region of the Indian Ocean (Higginbottom *et al.* 1988, Hosie *et al.* 1988). In January 1984, Australia carried out a limited sampling programme to study the distribution and abundance of larvae (Hosie & Kirkwood 1986). Few *E. superba* larvae were collected and low abundances were also observed later in April 1984 north of Enderby and Kemp Land in the western Prydz Bay region (Miller 1986). *Thysanoessa macrura* G.O. Sars and *E. crystallorophias* Holt & Tattersall were the most abundant euphausiid larvae at the time of sampling in January 1984 (Hosie & Kirkwood 1986). *T. macrura* was also the most widely distributed species of euphausiid occurring at all but one sampling site, with more older furciliae in the north and younger calyptopis larvae in the south (Hosie & Kirkwood 1986). North-south differences in developmental stages of *T. macrura* and *E. frigida* Hansen larvae have also been observed in the Atlantic sector by Makarov (1983) and Brinton (1985), respectively.

During SIBEX II (Second International BIOMASS Experiment, Phase II) January 1985, a geographically extensive survey of the biology of the Prydz Bay region was undertaken. One of the prime objectives was to study the distribution and abundance of *E. superba* larvae. A gyre exists in the region

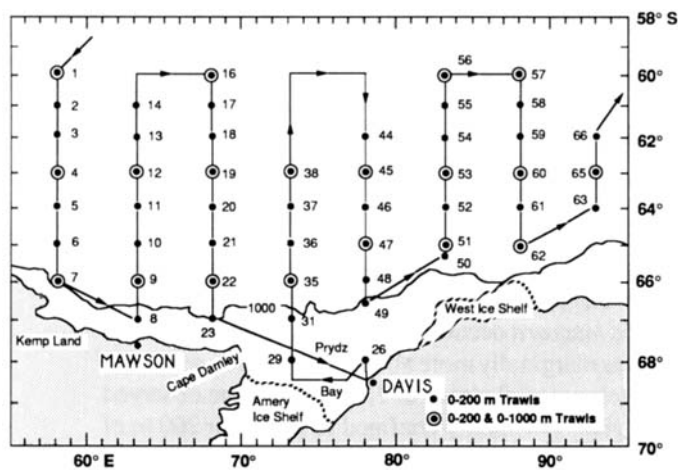


Fig. 1. Cruise track of the M.S. *Nella Dan*, 4–26 January 1985, showing the net sampling sites and 1000 m contour.

which is thought to be permanent (Smith *et al.* 1984), and of particular interest was the influence of water circulation on the distribution of the larvae. The ecology of other common euphausiids in the region was also studied.

Methods

Sampling sites were located along eight longitudinal transects, between 58° and 93° E, at intervals of one degree latitude from 60°S to the coast (Fig. 1). Larvae were collected using a Rectangular Midwater Trawl (RMT 1) net, 300 µm mesh and nominal 1 m² mouth area, as part of an RMT 1+8 system (Baker *et al.* 1973). At each site a shallow 0–200 m double-oblique haul was made, with an additional deep 0–1000 m double-oblique haul at every third station. The main purpose of the deep haul was to collect the early developmental stages of *E. superba* (Marr 1962, Hempel *et al.* 1979). The effective mouth area of the RMT net is a function of the towing speed and trajectory (Roe *et al.* 1980, Pommeranz *et al.* 1982). In this study, the towing speed was predominantly set at 2 knots and the assumption was made that the originally designed mouth area of 1 m² remained constant for the purposes of the double-oblique haul. The RMT 1 was equipped with a flowmeter to determine the volume of water filtered. Complete sampling details, e.g. sampling position, time, depth, conditions, etc., as well as details of the catch composition are provided by Ikeda *et al.* (1986).

After the cruise the euphausiid larvae were identified to species, classified into their various developmental stages under a dissecting microscope, and counted. The larvae of *E. superba* and *E. crystallophias* raised from eggs in the laboratory (Ikeda 1984, 1986) were used as a reference. This facilitated the identification of the early developmental stages of these two species which closely resemble each other.

For the purpose of mapping the distribution of larvae, each

stage was numbered sequentially from youngest to oldest. Thus the labels 1,2,3 were assigned for the three nauplius stages (nauplius I, nauplius II, metanauplius), 4,5,6 for the three calyptopis stages I to III, and 7 to 12 for the furcilia stages I to VI. This scheme replaces the conventional developmental stage nomenclature with a numerical value, hence facilitating comparison of development within and between species. At each sampling site a weighted mean value, mean stage index, was calculated for each species present, by multiplying the assigned number of a developmental stage by its relative abundance. The mean stage index (MSI), however, may have been derived from either a uni- or multi-modal frequency distribution of developmental stages. Cluster analysis was also used to compare the actual frequency distribution of developmental stages between sampling sites. The Bray-Curtis dissimilarity index (Bray & Curtis 1957) was used for this comparison, coupled with unweighted-pairs group average linkage (UPGMA). Analysis was carried out using BIOSTAT II (Pimental & Smith, 1985 Sigma Soft, Placentia, California). Since the purpose of the analysis was to compare patterns in the frequency distribution of stages, data were standardized as percentage frequency of abundance within the site. Cluster analysis was only used on *T. macrura* data, as the low number of site occurrences or the general paucity of specimens made this analysis unrealistic for the other species.

Results

The larvae of five euphausiid species were collected — *Euphausia superba*, *E. crystallophias*, *E. frigida*, *E. triacantha* Holt & Tattersall and *Thysanoessa macrura*. The distribution of abundances and MSI are shown in Figs. 2 & 3, respectively, and frequency distributions of developmental stages in Fig. 4. Estimates of mean abundances are provided in Table I for 0–200 and 0–1000 m depth ranges for all species. Only sites where a species was collected were used for estimating the mean, i.e. stations where a species was absent were not included. Although this may result in a positive bias, the alternative of including “absent” sampling sites in the mean estimate would result in a negative bias if such sites are not within a species distribution range. *E. triacantha* occurred at only five 0–200 m sites (Stations 14, 16, 55, 57, 58) in very low abundance ranging from 3.14 to 9.43 individuals 1000 m⁻³ and larvae were found in only one deep trawl at Station 57. The infrequent occurrence and low abundance of this species mean it will not be considered further here.

Thysanoessa macrura

T. macrura was the second most abundant species overall, but was the most widespread abundant species throughout the region. This species was collected at all sampling sites, shallow and deep. At sites of paired sampling, the number

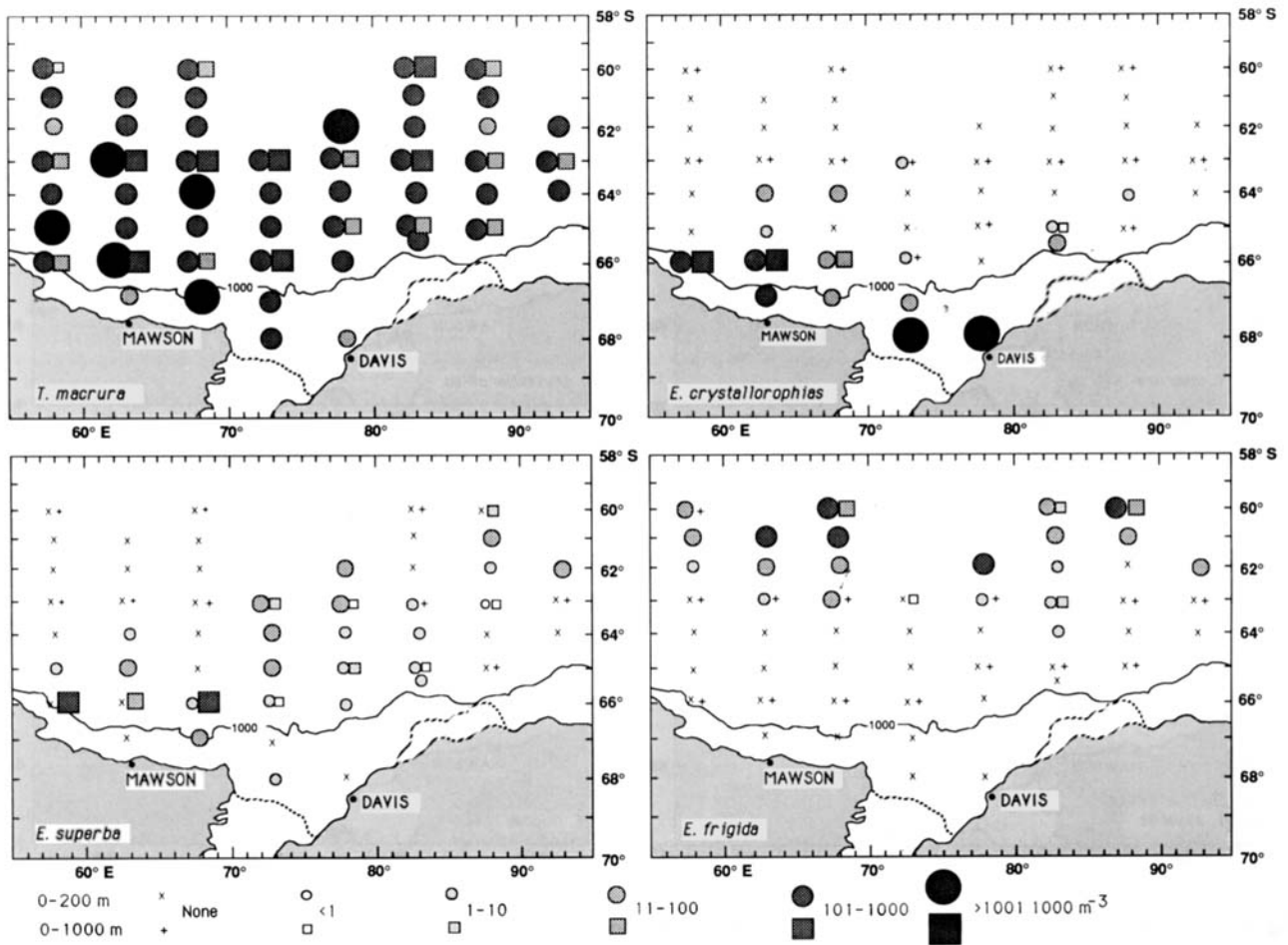


Fig. 2. Distribution and abundances of the euphausiid larvae for shallow (0–200 m, circles) and deep (0–1000 m, squares) trawls. Abundances are expressed as individuals 1000 m^{-3} .

of larvae collected in shallow and deep hauls were compared to determine if larvae were more abundant in a particular layer. Overall, more larvae were collected in the shallow hauls at these sites, 7134 in total compared with 6428 in deep hauls, but statistically, shallow and deep abundances were not significantly different [Mann-Whitney U -test (Zar 1984); $U = 209.5$, $n = 19$, $P > 0.2$]. All developmental stages from calyptopis I to furcilia VI were well represented in both deep and shallow hauls. Although not clearly shown in Fig. 4, a few specimens of nauplius I and metanauplius were collected (Station 19, 0–200 m; Stations 7 and 38, 0–1000 m). No nauplii II were collected.

Analysis of geographic distribution of the MSI shows a clear trend of stage development in the upper 200 m proceeding from south to north, and to a lesser extent from west to east in the lower latitudes (Fig. 3). At the 19 sites of joint shallow and deep hauls, there was no significant difference in the MSI between the two depths ($t = -0.200$, $df = 36$). Six groups of MSI were chosen, from 5 (calyptopis II) to 10+ (furcilia IV +), and consequently six groups were also selected from the dendrogram (Fig. 5), at 32% dissimilarity, in order to

determine if there was correspondence between the geographic distribution patterns for the modal frequencies and that of the MSI's. Comparison of Figs. 3 & 6 shows considerable similarity in the two distribution patterns, e.g. the close fit of the group 2 and larvae less than MSI 6.

The six cluster groups, ranging in size from 1 to 17 stations showed distinct frequency distributions of developmental stages (Fig. 7). Early developmental calyptopis stages were observed in group 1 just north of Mawson. Group 2 occupied most of the inshore region, except for two sites in the north west, and comprised calyptopis stages with many early furcilia stages. Group 3, further to the north, comprised more furcilia stages with the furcilia I stage most abundant. Group 4 of the outer middle region of Prydz Bay comprised sites with increasing amounts of later furcilia stages. Group 5 comprised only three sites in the north-east, but are distinct in having fewer calyptopis stages and two modal peaks, one of early furcilia stages, the second peak of later stages. Group 6 composed of one station in the north-east, had an exceptionally high abundance of the last developmental stage furcilia VI.

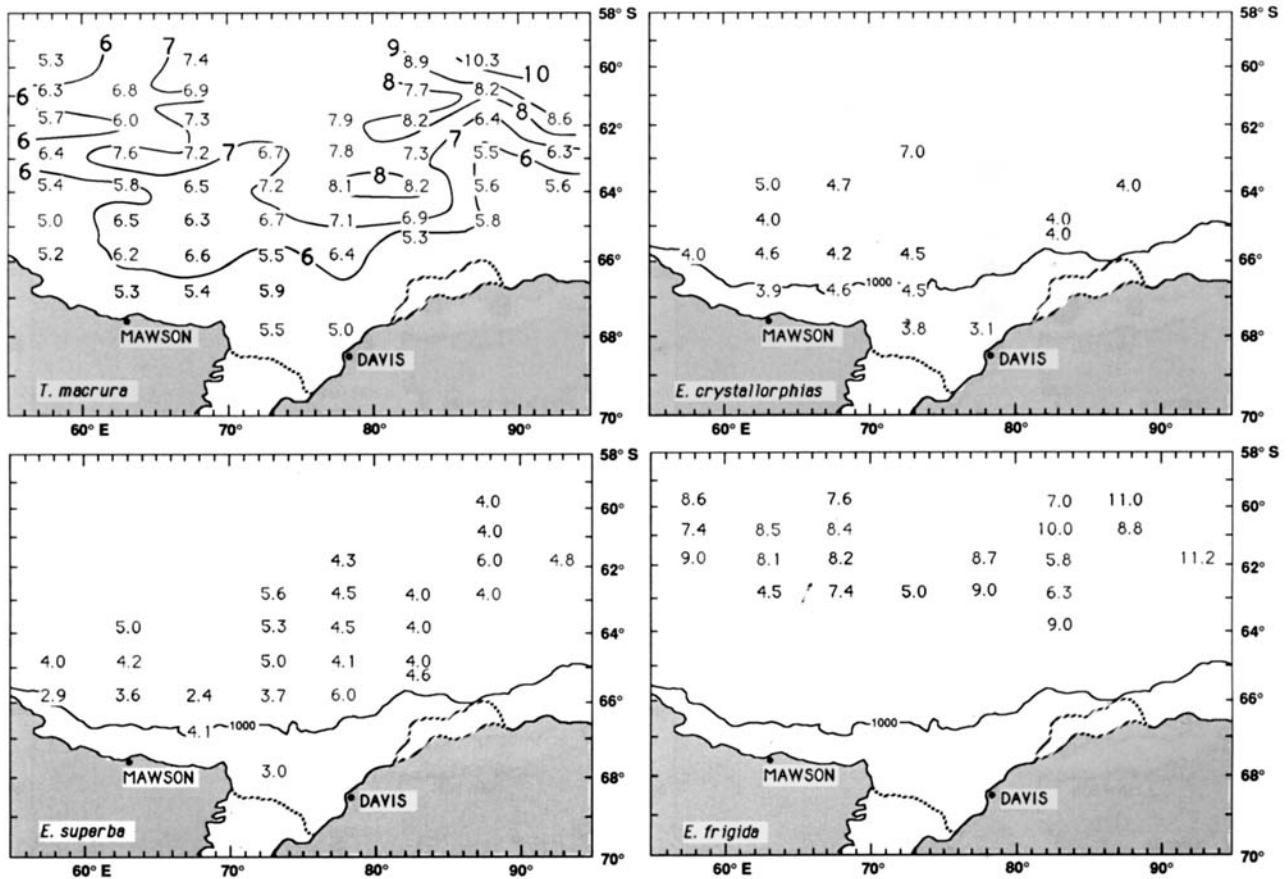


Fig. 3. Distribution of the mean stage index for euphausiid larvae in the upper 200 m. Contour lines of the mean stage index are presented for *T. macrura* only, as no other species had both high site occurrence and abundance for contour line construction. Contour lines were calculated and drawn by hand. Decimal points approximate sample site. For clarity, sites where larvae were not collected are not shown. 5,6 = calyptopis II, III respectively, 7 to 12 = furcilia I to VI.

Euphausia crystallorophias

E. crystallorophias was found only in the south of the area surveyed, mainly on the continental shelf (Fig. 2). In the region north of Mawson a number of specimens were found well north beyond the continental shelf. In the limited area where this species occurred, it was the most abundant species, slightly more so than *T. macrura*. More larvae were caught in deep trawls at the paired sampling sites, 798 total in shallow and 1568 in deep hauls, but differences in the numbers of larvae between shallow and deep hauls were not significant ($U=18.5, n=6, P>0.2$). All naupliar and calyptopis stages were collected, but no furciliae. The main components in the upper 200 m were metanauplius and calyptopis I, and in 0–1000 m calyptopis I and calyptopis II. Most of the youngest naupliar stages (nauplius I) were found at Stations 26 and 29 in the Amery Basin, and it was at these stations that the highest abundances were observed, 2786 and 4688 individuals 1000 m^{-3} , respectively. Much lower abundances of nauplius II and metanauplius were caught at Stations 7, 8, 9, 23 and 31. There was a tendency for later stages to occur more in the north, particularly at the three most northerly

sites off Mawson (Fig. 3), although caution is required since the MSI estimates at these sites are based on only a few specimens.

Euphausia superba

E. superba had a distinct diagonal south-west to north-east distribution (Fig. 2). Calyptopis I larvae were dominant in the upper 200 m, with fewer calyptopis II, calyptopis III, and furcilia I also present (Fig 4). However, collectively they had a very low abundance, only marginally more than *E. triacantha*. The greater part of the larval abundance was observed in the 0–1000 m trawls at Stations 7, 9 and 22 just north of the shelf break near Mawson. Station 7 in particular returned the highest abundance of 749 individuals 1000 m^{-3} , with no larvae in the shallow trawl. Similarly, no larvae were collected in the upper 200 m at Station 9. Deep trawls in the middle of the region and in the north-east caught very few specimens. Overall, there was significantly more larvae caught in the deep hauls at paired sampling sites, 44 in shallow and 3430 total in deep hauls ($U=92, n=11, 0.02<P<0.05$).

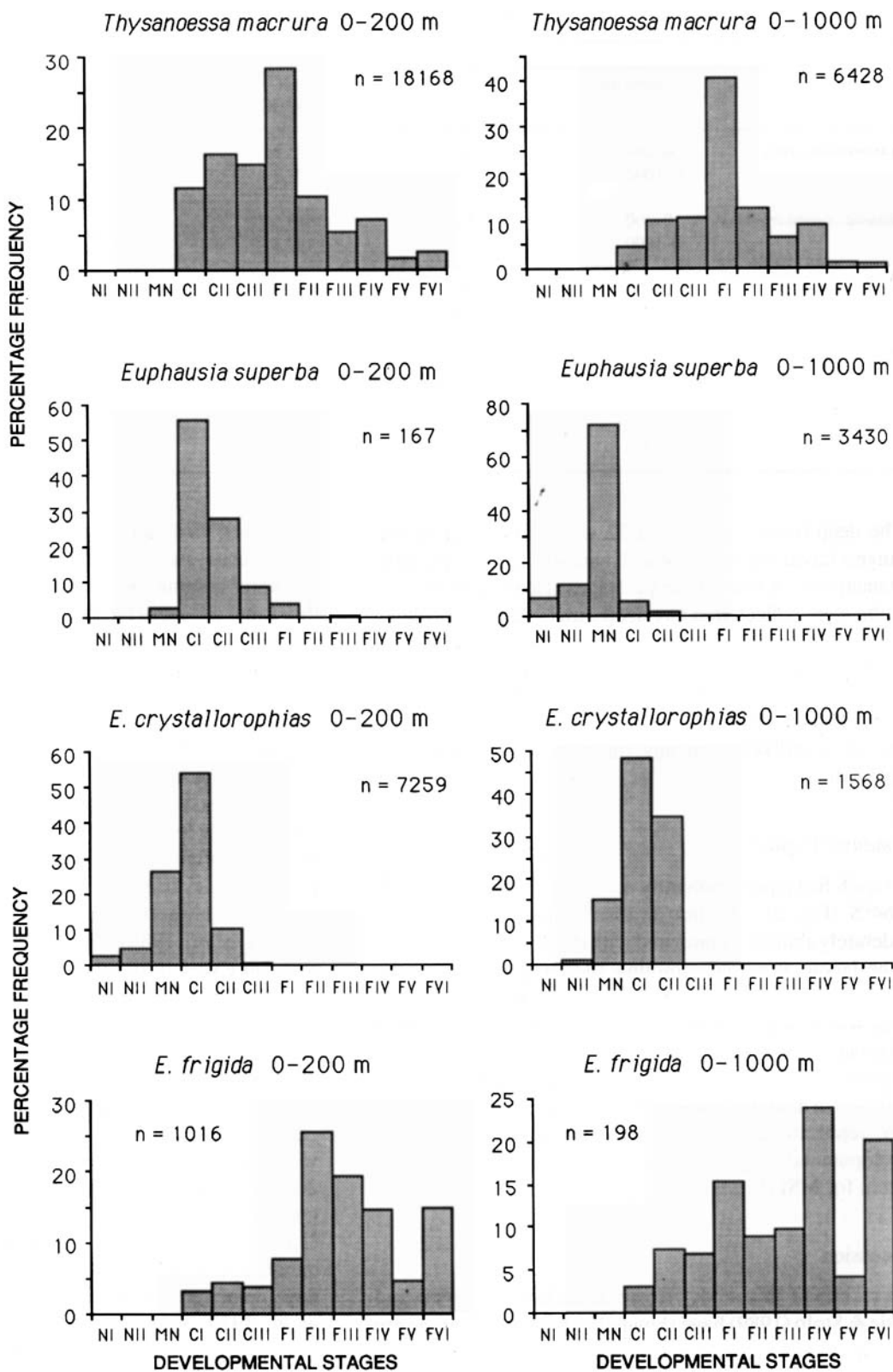


Fig. 4. Percentage frequency distribution of developmental stages within each species for shallow (0-200 m) and deep (0-1000 m) trawls. NI, NII = nauplius I and II; MN = metanauplius; CI, CII, CIII = calyptopis I, II, III; FI to FVI = furcilia I to VI; n = total number of individuals identified.

Table I. Estimated mean densities for larvae of all species observed, for shallow (0–200 m) and deep (0–1000 m) trawls. Only sites where a particular species was collected were used for estimating the mean. *n* = number of sampling sites.

Species	Depth (m)	<i>n</i>	Mean no. 1000 m ³	sd	Range
<i>Thysanoessa macrura</i>	0–200	50	471.8	361.8	27.7–1488.6
	0–1000	19	121.3	138.0	1.4–507.4
<i>Euphausia crystallorophias</i>	0–200	16	564.3	1302.9	1.9–4687.9
	0–1000	4	127.8	151.7	0.9–324.4
<i>Euphausia superba</i>	0–200	23	9.8	12.0	1.0–56.9
	0–1000	10	97.3	235.1	0.4–748.6
<i>Euphausia frigida</i>	0–200	20	74.3	96.9	1.7–339.6
	0–1000	7	10.2	15.4	0.7–40.9
<i>Euphausia triacantha</i>	0–200	5	5.7	3.0	3.1–9.4
	0–1000	1	4.7	-	

The deep trawls at 7, 9 and 22 were dominated by the youngest larval stages, nauplius I, nauplius II and especially metanauplius. A few calytopis stages also occurred but no furcilia were collected in any deep trawl. Along meridians 63° and 73°E (Fig. 3) there was a trend of later stages occurring further off-shore as seen in *T. macrura*. However, there was no clear distribution pattern of MSI overall. Many of the off-shore MSI are based on very low abundances, hence it is unlikely that any inherent pattern would be displayed.

Euphausia frigida

E. frigida had a predominantly northerly distribution, north of 64°S (Fig. 2). Within its distributional range it was moderately abundant compared with the other species. Most of the larvae at paired sampling sites were caught in the upper 200 m, 462 in total compared with 198 in deep hauls, but as with *T. macrura* and *E. crystallorophias*, the number of larvae collected in shallow hauls was not significantly different from the number caught in deep hauls ($U=55$, $n=9$, $P>0.2$). No naupliar stages were collected. All other stages were represented with furciliae prominent, mainly late developmental stages. There was no clear distribution pattern for MSI (Fig. 3).

Discussion

The results of this study, Hosie & Kirkwood (1986) and Hosie & Stolp (1989) have shown that *T. macrura* larvae are consistently the most abundant euphausiid larvae in the Prydz Bay region from September to January. Comparable abundance estimates of *T. macrura* have been reported from the Atlantic sector (Makarov 1979, Brinton 1985, Kittel *et al.* 1985), sometimes numerically dominating the other euphausiid larvae (Hempel 1981, Pires 1986). Yet, very

little is known about this species and its role in the Antarctic marine ecosystem, especially since it is well established in the water column, with advanced developmental stages, at the time *E. superba* commences spawning. Equally, *E. crystallorophias* is also very abundant within the confines of its distributional range in Prydz Bay, which overlaps those of *E. superba* and *T. macrura*.

Miller & Hampton (1989) suggested that the Prydz Bay region was an area of generally low abundances of *E. superba* larvae. The abundance estimates from Prydz Bay for the present study and Hosie & Kirkwood (1986) are considerably lower than the 10⁴ to 10⁶ individuals 1000 m⁻³ estimates often reported from the Atlantic sector for the period January to March (Kittel & Jazdzewski 1982, Mujica & Asencio 1983, Brinton & Townsend 1984, Hempel 1985, Brinton *et al.* 1986). Very low estimates of adult krill abundance were recorded during January 1985 and represented only 3.4 % of the total zooplankton biomass in Prydz Bay (Hosie *et al.* 1988). However, due to the recent onset of spawning observed in Prydz Bay (see below), realistic estimates and comparison of abundance are not possible until after the main peak of spawning.

Despite the inability to sample the shallow and deep waters discretely, due to both methods sampling the upper 200 m, *E. superba* was the only species observed with the greater proportion of larvae in the deep 0–1000 m trawls. This deep distribution of larvae, notably nauplius and metanauplius, was expected due to this species' deep water developmental ascent of early stages (Marr 1962, Hempel *et al.* 1979, Hempel & Hempel 1986). *E. frigida* and *T. macrura* also exhibit deep water developmental ascent (Makarov 1979, 1983), but no naupliar stages of *E. frigida* were observed in this study and only 26 *T. macrura* nauplii, despite numerous deep hauls within their respective geographic ranges. Spawning may have ceased at the time of sampling, or the 300 µm mesh of the RMT 1 might have been too large

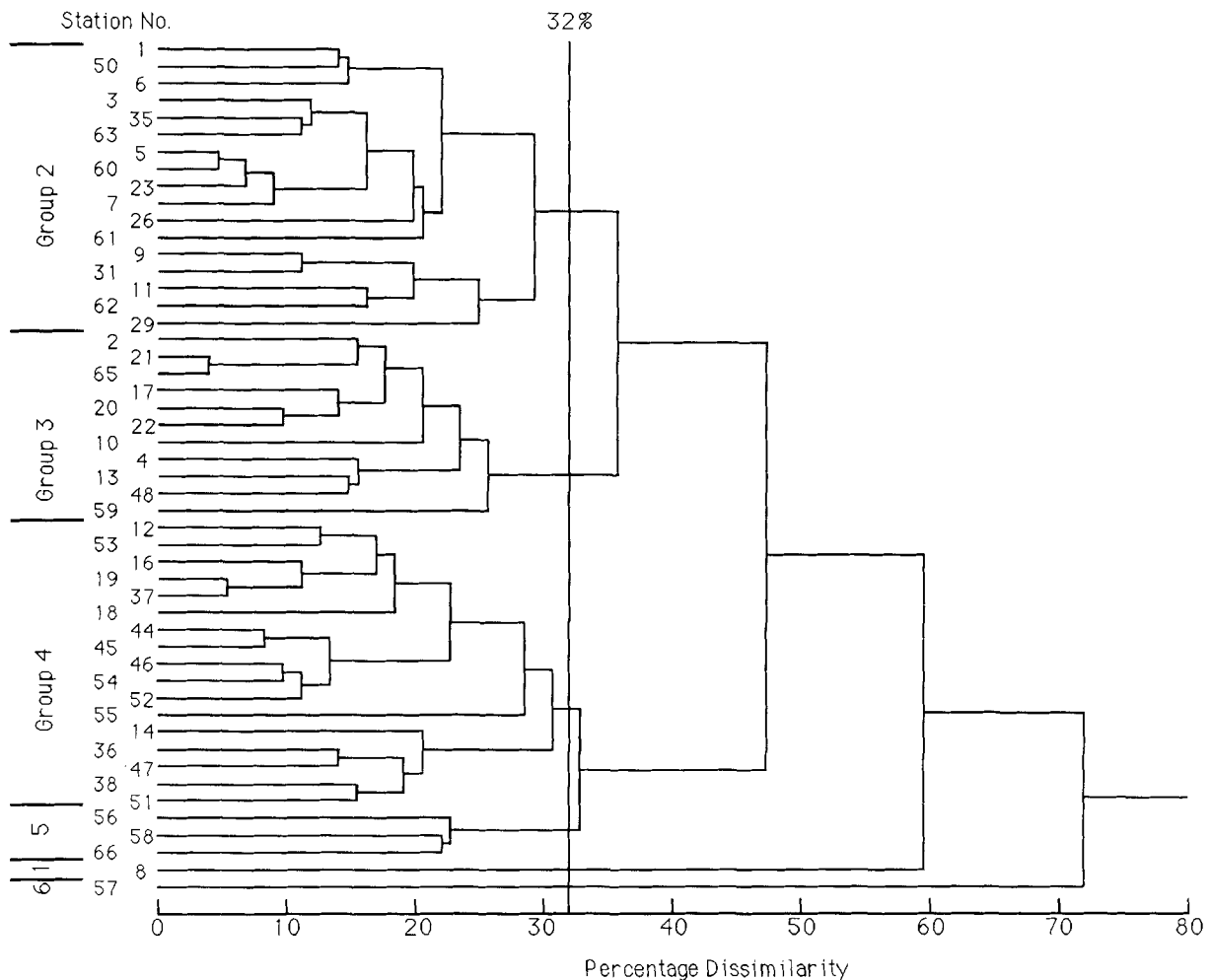


Fig. 5. Dendrogram of cluster analysis comparing the frequency distribution of *T. macrura* developmental stages at each sampling site. The Bray-Curtis dissimilarity index was used for the comparison coupled with UPGMA linkage, after transformation to % frequency of abundance. Six groups were selected at 32% dissimilarity level.

to sample nauplii. Hosie & Stolp (1989) sampling in October 1985 in the western Prydz Bay region also failed to collect naupliar stages using the same net. Marschall and Hirsche (1984) reported that *E. superba* eggs are easily damaged and lost during the sampling process. It is possible that the smaller nauplii of *E. frigida* and *T. macrura* could be lost for the same reason.

In addition to the developmental ascent, the results of Pires (1986) and Montú *et al.* (1990) have shown that calyptopis and furcilia larvae of both *E. superba* and *T. macrura* can occur in significant numbers below 200 m. On the other hand, *E. crystallorophias* may exhibit sinking during larval development (Makarov 1983). This would suggest that the standard 0–200 m double oblique hauls were perhaps not deep enough for efficient sampling of calyptopis and furcilia larvae at all sites. In this study, *E. superba* did have a large number of larvae below 200 m but were predominantly nauplii and metanauplii. For the other three

species, there were no significant differences in the number of larvae collected in the 0–200 m hauls compared with the number from the 0–1000 m hauls at the sites of paired sampling. Hence, one can conclude that almost all of the larvae were in fact in the upper 200 m water layer and that the 0–200 m oblique hauls were adequate. This being the case, then the abundance of *T. macrura*, *E. frigida* and *E. crystallorophias* larvae in the deeper water layers below 200 m will be considerably less than indicated by the 0–1000 m hauls in Table I. Also the differences in the developmental stage composition between shallow and deep hauls (Fig. 4) are more likely a result of geographical variation between all shallow sampling sites rather than genuine vertical differences. For example, considerable spatial variation in the developmental stages of *T. macrura* was observed in the shallow hauls (Figs. 6 & 7).

Some *E. superba* females are capable of spawning as early as the end of November, as indicated by the presence of a few

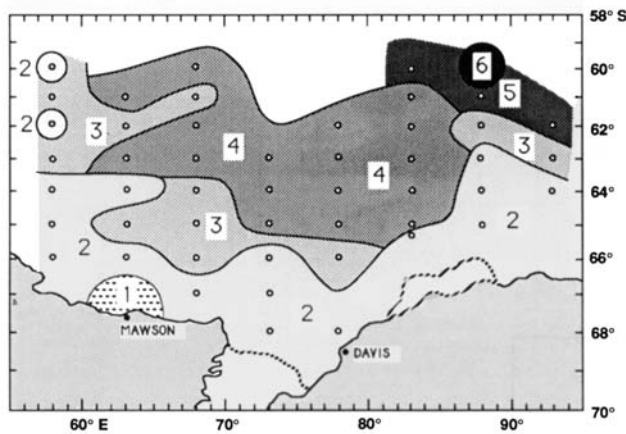


Fig. 6. Distribution of the six groups of *T. macrura* developmental stages identified by the cluster analysis shown in Fig. 5.

advanced developmental stages in the samples, e.g. calyptopis III. The very high proportion of metanauplii suggests the commencement of the main period of spawning was more towards the end of December, based on a comparison with the known laboratory development times for Prydz Bay larvae (Ikeda 1984). This sequence of events is similar to the pattern observed in krill from west of the Antarctic Peninsula (Ross & Quetin 1986). Hosie *et al.* (1988) noted a high proportion of enlarged gravid females in Prydz Bay in March 1981 indicating that spawning extends to at least March. *E. crystallophias* has similar laboratory development times to *E. superba* (Ikeda 1984, 1986) and the higher number of calyptopis larvae suggests that spawning in *E. crystallophias* commenced earlier in November. Spawning females have previously been collected off Enderby Land in November (Harrington & Thomas 1987). This sequence of spawning of these two species follows previous observations by Fevolden (1979, 1980) and Hempel & Hempel (1982). On the other hand *E. frigida* and *T. macrura* start spawning as early as the beginning of September in the Prydz Bay region (Hosie & Stolp 1989), with an associated protracted spawning season (Makarov 1979).

The differences in the observed age structure of *T. macrura* can be attributed to a southward progression of spawning as evidenced by the different frequency distributions of *T. macrura* developmental stages identified by the cluster analysis (Figs. 6 & 7). Large numbers of calyptopis I, and some calyptopis II, have been collected in October north of Mawson, circa 59° to 62°S and 55° to 64°E (Hosie *et al.* 1987), and were considered to be the result of an early September spawning in this area (Hosie & Stolp 1989). A few calyptopis I were also caught a little further south towards 63° 30'S. At the same time, gravid and spent *T. macrura* females were only collected north of 63°S, i.e. in the same area as the larvae, although net sampling had extended to the coast (Australian Antarctic Division, unpublished records). Thus, the distribution of Groups 4, 5

and 6 in the northern waters are a result of this early September spawning, coupled with a protracted spawning season (Makarov 1979) producing a wide range of developmental stages from calyptopis I to furcilia VI. The onset of spawning then progressed southward with time. Group 1 larvae would then be the most recently spawned and consequently only calyptopis stages were observed. No detailed data on larval development times are presently available for *T. macrura*, but comparison with times for *E. superba* and *E. crystallophias* larvae (Ikeda 1984, 1986) would suggest that Group 1 were a result of a late November to early December spawning.

The observed north-south distribution patterns of *T. macrura* developmental stages and MSI could also result from spawning being restricted to coastal waters, with larvae then being transported northward, extending their distribution with growth. Off-shore currents are evident in the Prydz Bay region, as discussed below, and undoubtedly have an effect on the distribution of *T. macrura* larvae. It is unlikely that these currents would account for the observed distribution patterns *in toto*. As mentioned above, gravid and spent females have been found in the north of the Prydz Bay region, while adult *T. macrura*, in general, occur throughout the region, and in particular they were found at all sampling sites during the present study (Williams *et al.* 1983, 1986, Ikeda *et al.* 1986, Hosie & Stolp 1989). Further, *T. macrura* has a widespread circumpolar distribution extending south from 50°S (Mauchline & Fisher 1969). There is no evidence as yet to suggest that *T. macrura* is capable of migrating long distances to inshore waters in order to spawn. Hence, it is more plausible that the observed distribution patterns of developmental stages are primarily a result of spawning progressing southward with time.

North-south "phenological waves" in the onset of spawning and larval development have previously been described for Antarctic euphausiids (Makarov 1979, 1983, Brinton 1985) and also for phytoplankton development (Hart 1942). Brinton (1985) observed north-south distribution of old to young larvae of *E. frigida* in the Atlantic sector. No clear pattern was observed in this study for *E. frigida*, although young larvae were observed along the southern edge of this species range (Fig. 3) and the oldest larvae in the far north-east, as seen in *T. macrura*, where there is a southward flow of water (Fig. 8). The lack of a clear pattern is primarily due to this study only sampling a small part of the southern limit of *E. frigida*.

The factors controlling the onset of spawning are yet to be properly defined, although, as with Hart's (1942) "wave" for phytoplankton blooms, it has been proposed that the southward progress of spawning follows the receding ice edge (Daly & Macaulay 1988). The MSI contours and cluster groups of *T. macrura* observed in this study closely parallel the southward receding ice edge observed annually between 1973 and 1982 in the Prydz Bay region (Zwally *et al.* 1982 figs. 4.2–4.7, 5.1–5.12, Jacka 1983 figs. 4.1–4.12).

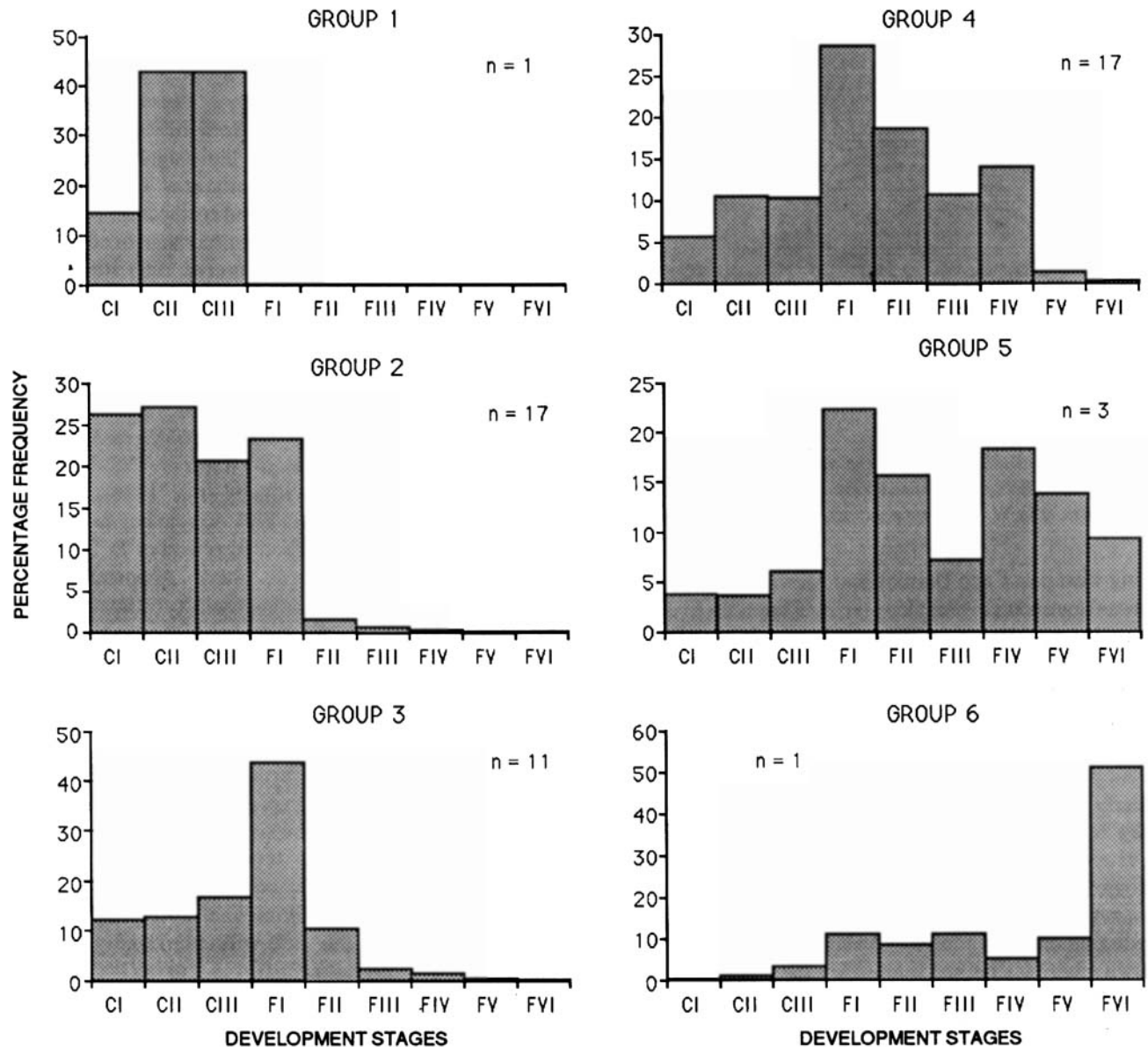


Fig. 7. Percentage frequency distribution of developmental stages of *T. macrura*, for each of the six cluster groups identified (Fig. 5). n = number of sample sites; CI, CII, CIII = calytopis I, II, III; FI to FVI = furcilia I to VI.

In contrast, substantial numbers of early calytopis larvae of *T. macrura* and *E. frigida*, as well as gravid *T. macrura* females, have been collected from under the pack ice up to 220 nautical miles from the ice edge located along 59° 30'S (Hosie & Stolp 1989). This indicates that spawning by *T. macrura* and *E. frigida* can occur well south into the pack ice zone. Nonetheless, the fact remains that different groups of development stages exist within the region. Therefore, attempts to estimate mortality or growth by following cohorts is difficult, unless consideration is given to the spawning and developmental history of the group of larvae studied.

While sampling was apparently too close to the start of spawning of *E. superba* to obtain a true estimate of abundance

of larvae, there were sufficient numbers in the water column along with the more abundant *E. crystallorophias* larvae to see the influence of water circulation on the distribution of the larvae. The water circulation pattern and general physical oceanography of the Prydz Bay region has been described by Khimitsa (1976), Smith *et al.* (1984), Middleton & Humphries (1989). The horizontal circulation as determined for Prydz Bay during January 1985 is shown in Fig. 8 (R.A. Nunes Vaz & G.W. Lennon, personal communication 1990). The Prydz Bay gyre is located in the vicinity of 63° to 80°E and south of 63°S. The geostrophic water flow of the gyre is shown to move south onto the continental shelf between 72° and 76°E, before moving cyclonically past the Amery Ice Shelf then

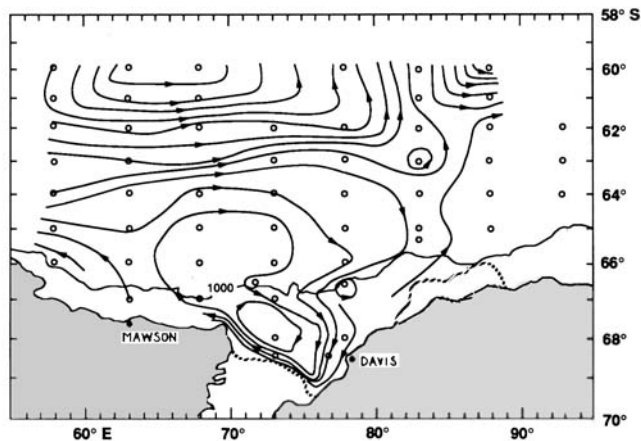


Fig. 8. The geostrophic water flow in the Prydz Bay region, redrawn from the geopotential anomaly contours of R. A. Nunes Vaz & G.W. Lennon (personal communication 1990).

exiting west past Cape Darnley and Mawson Station. The westward transport of water along the shelf has been confirmed by satellite tracking of icebergs (Tchernia & Jeanin 1983) and sea-ice (ICEX) buoys (Allison 1989), as well as by current meter moorings (Hodgkinson *et al.* 1988).

Current meter moorings deployed along the edge of the continental shelf recorded a generally south-west to westerly current near Station 31, and a consistent very strong north-westerly water flow north of Mawson (Hodgkinson *et al.* 1988). Mean speeds to the end of March 1985 were 14.2–17.3 cm s^{-1} and 39.4–75.1 cm s^{-1} , respectively, for four depths through the water column. The much higher speeds off Mawson were attributed to the East Wind Drift (EWD) converging onto the continental shelf somewhere between the two mooring sites and reinforcing the water flow along the shelf (Hodgkinson *et al.* 1988). ICES buoys released on the shelf in Prydz Bay moved west and out of the region past Enderby Land proceeding past 30°E while remaining in the EWD (Allison 1989, figs. 1, 6). Icebergs also entrained by the EWD in this region, indicated an averaged water flow of 20.5–23.7 cm s^{-1} (Kumagori & Yanagawa 1958, Tchernia & Jeanin 1983, plates 1, 2).

The influence of the EWD on the dispersal of larvae can be seen in the westward distribution, along the continental shelf and slope, of *E. superba* and especially *E. crystallorophias* larvae. The youngest and most abundant larvae of *E. crystallorophias* are found in the southern part of Prydz Bay, at Stations 26 and 29, an area of the highest concentration of adults within the region (Williams *et al.* 1986). Slightly older larvae occur to the west, as would be expected with most larvae originating in Prydz Bay and then carried west by the EWD. Accepting this as the case, current speeds can be calculated by using the development times of *E. crystallorophias* larvae reported by Ikeda (1986), e.g. of 34 days to the metanauplius stage and 54 days to calyptopis

I at -1°C , against the estimated MSI at sampling sites. If $68^\circ30'\text{S}$ by 74°E is taken as the arbitrary starting point then estimates of 27.1, 19.5 and 15.3 cm s^{-1} are obtained to Stations 7, 8, and 9 respectively. These values are not inconsistent with those estimates from the icebergs (Tchernia & Jeanin 1983) and are within the ranges obtained from current meter moorings (Hodgkinson *et al.* 1988). The fewer but older larvae observed north and northeast of Mawson are well outside the observed distribution range of adults which are confined to the shelf (Williams *et al.* 1983, 1986, Ikeda *et al.* 1986). The distribution of these larvae tends to follow the western part of the Prydz Bay gyre. This suggests that some larvae in the upper 200 m may be returned to Prydz Bay, rather than being carried west past Enderby Land and out of the region as indicated by the ICES buoys and icebergs.

The adults of *E. superba* generally are widespread throughout the region, although infrequently north of 62°S (Hosie *et al.* 1988) or south of 68°S (Williams *et al.* 1986). However, higher concentrations of adult krill, especially gravid females, are usually found along the shelf edge west of 78°E (Williams *et al.* 1983, 1986, Ikeda *et al.* 1986). Abundances in this region far exceed the mean annual density estimates reported by Hosie *et al.* (1988). Further, the shelf edge between 55° and 70°E has been the focus of Japanese krill fishing activities in the Prydz Bay region (Ichii 1990). Marr (1962) had postulated that spawning in *E. superba* was a phenomenon associated with the shelf and slope water of the high latitudes. Kanda *et al.* (1982) went further, providing evidence that adult krill in the Prydz Bay region migrate south towards the shelf in order to spawn. The site at which spawning occurs in relation to the shelf will determine by which of the two apparent major dispersal routes the larvae will be carried (Fig. 9). It may also determine the survival of the larvae. Larvae produced on the shelf will undoubtedly follow the same route as *E. crystallorophias* in moving west along the shelf edge. For example, the large numbers of metanauplii at the western Station 7 can be traced back to a likely release site between $67^\circ30'\text{E}$ and 69°E on or near the shelf, assuming a 24 day development time to the metanauplius stage at -1°C (Ross *et al.* 1988) and EWD current speeds of 20.5–23.7 cm s^{-1} . The other larvae observed on longitudes 58° , 63° and 68°E most likely originated further east in Prydz Bay. Unlike the eggs of *E. crystallorophias* which remain in surface waters (Makarov 1983, Ikeda 1986), embryos of *E. superba* sink during development (Hempel & Hempel 1986). To complete development, larvae must reach the surface and commence feeding within 10–14 days of becoming a calyptopis I (Ross & Quetin 1989). Where the larvae reach the surface waters will govern whether the larvae continue west past Enderby land or return to Prydz bay as indicated by *E. crystallorophias* larvae. It is not clear, from the observed distribution of *E. superba*, whether they follow the northern route of *E. crystallorophias*.

Regardless of whether the larvae move west or not, it is quite likely that many of these larvae will perish. Ross *et al.*

(1988) reported that larvae, produced by females in the Atlantic sector, will not survive if they encounter -1°C during a cold sensitive period of early development. They found that three out of four batches of larvae died within three days of becoming calyptopis I if reared at -1°C . The water temperatures on the shelf of Prydz Bay and to the west are -1° to $<-1.5^{\circ}\text{C}$ throughout most of the water column, which is consistent between years (Kerry & Woehler 1987, Kerry *et al.* 1987a 1987b, Woehler & Williams 1988). Unless Prydz Bay larvae have a higher tolerance of cold temperatures than that of the more northerly distributed Atlantic larvae, then the $<-1.5^{\circ}\text{C}$ temperatures along the shelf are likely to cause a substantial drop in larval recruitment, despite the high phytoplankton abundance in this area (Fig. 10). Such a loss would explain the low abundances of larvae observed by Miller (1986) off Enderby and Kemp Land in April 1984. Eggs released on the shelf east of about 72°E should be swept south as part of the cyclonic flow of water in Prydz Bay and past the Amery Ice Shelf (Fig. 9). Consequently, these larvae will experience colder water ($<-1.8^{\circ}\text{C}$, Kerry *et al.* 1987a) for a longer period, than larvae released west of Cape Darnley.

The second major dispersal route is to the north-east, confirmed again by iceberg and ICEX buoy trajectories (Fig. 9). North of the Prydz Bay shelf, *c.* $63^{\circ}30'$ to $65^{\circ}30'$ S by $76^{\circ}30'$ to 83°E , icebergs drifted north-east reaching approximately 61°S before moving east in the Antarctic Circumpolar Current (ACC), indicating a water flow of $18.5\text{--}24.9\text{ cm s}^{-1}$ (Kumagori & Yanagawa 1958, Tchernia & Jeanin 1983, plates 4–7). Three ICEX buoys released in an area just off the Prydz Bay shelf, *i.e.* $65^{\circ}30'$ to 66°S by 70° to $77^{\circ}30'\text{E}$, also had a similar north-easterly trajectory (Allison 1989, figs. 1, 6). The *E. superba* larvae in the eastern part of the Prydz Bay region had a distinct north-eastern distribution, consistent with this water flow. Using the speeds of $18.5\text{--}24.9\text{ cm s}^{-1}$ and the development times from Ikeda (1984) for 0°C , then the larvae can be tracked back to an approximate area of 63° to 66°S by 70° to 83°E . Most of these larvae are distributed in warmer waters, *e.g.* up to $+1.8^{\circ}\text{C}$ (Kerry *et al.* 1987a), than the larvae along the shelf, and therefore a higher temperature related survival rate would be expected as well as faster growth (Ross *et al.* 1988). The survival of these larvae is still doubtful in relation to food availability. At the time of sampling in January 1985 the concentrations of chlorophyll *a* east of Prydz Bay (Wright 1987) were much lower than the minimum food concentration of $0.5\text{ }\mu\text{g Chl } a\text{ l}^{-1}$ necessary for the continued development of larvae through the calyptopis I stage (Ross & Quetin 1989). At the chlorophyll *a* concentrations shown in Fig. 10, the north-east larvae would have suffered partial starvation, eventually depleting their lipid reserves. According to Ross & Quetin (1989) calyptopis I larvae that exhaust their lipid reserves will have passed the point-of-no-return and will die even if sufficient food is then encountered. In addition, the salp *Salpa thompsoni* Foxton was exceptionally

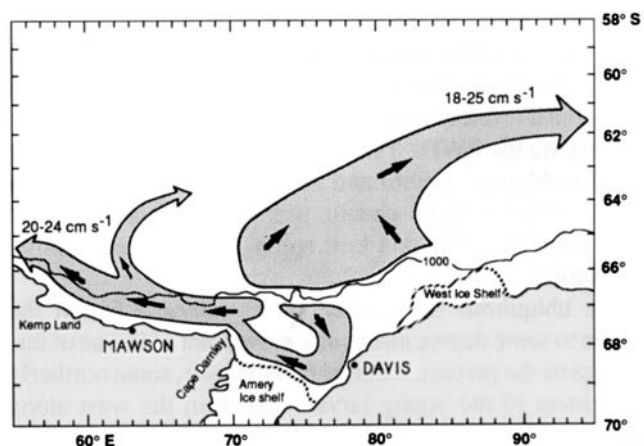


Fig. 9. The apparent dispersal routes of larvae, particularly for *E. superba* and *E. crystallophias* (mainly to the west), determined from sea-ice buoy and iceberg trajectories, current meters and geostrophic flow. Current speeds shown are determined from iceberg trajectories.

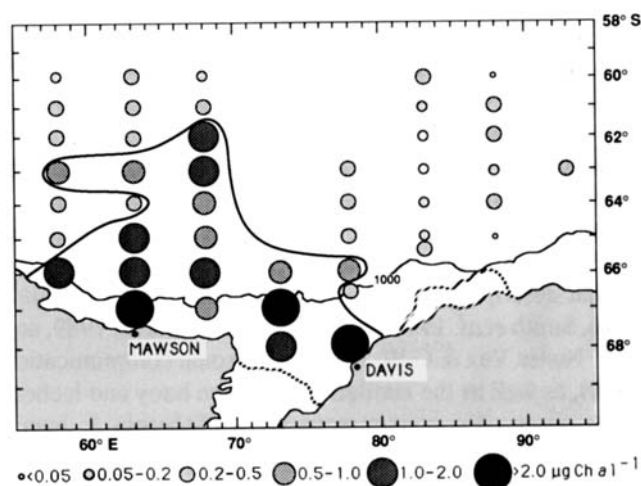


Fig. 10. Distribution of chlorophyll *a* concentration as $\mu\text{g l}^{-1}$, integrated for the upper 100 m water layer (data from Wright 1987). The heavy line surrounds those sites with $>0.50\text{ }\mu\text{g Chl } a\text{ l}^{-1}$, necessary for the successful development of larvae through the calyptopis I stage (Ross & Quetin 1989).

abundant in January 1985, representing 39.4% of the total zooplankton biomass by wet weight throughout the Prydz Bay region, 73.3% north of 63°S and 89.6% north of 62°S (Ikeda *et al.* 1986). *S. thompsoni* is not only capable of competing with *E. superba* larvae for food resources but is also capable of eating large numbers of krill larvae (Huntley *et al.* 1989).

The combined evidence of larval distribution and water movement indicates that most larvae, providing they survive

the <-1°C water temperatures and food deprivation, will leave the Prydz Bay region to the west or via the north-east. Hence, the Prydz Bay krill may not be a self maintaining group but a result of recruitment from other areas, e.g. from the east via the EWD. This is consistent with the results of Macdonald *et al.* (1986) and Fevolden & Schneppenheim (1989) who found no genetic separation in the Antarctic krill, thus indicating that krill belong to one interbreeding population.

The ubiquitous distribution of *T. macrura* within the region to some degree masks any movement of larvae of this species by the perceived currents. However, some northerly movement of the young larvae is seen in the west along longitude 58°E and over to 63°E at Station 11, a possible result of the gyre. A more distinct northerly movement is seen in the east along longitude 88°E, commensurate with the north-easterly movement of the icebergs. As discussed above, the observed distribution patterns of *T. macrura* developmental stages are most likely the result of a north-south difference in the commencement of spawning, rather than due totally to off-shore transport of larvae from localized spawning sites along the coast. Nevertheless, the currents do have an apparent effect on the distribution patterns of *T. macrura* larvae, but secondary to the southward progression of spawning. The distribution of *E. frigida* was consistent with previous studies (John 1936, Hempel & Hempel 1982, Makarov 1983) in being confined to the waters of the ACC.

The great similarity in oceanographic patterns between January and March (Kerry *et al.* 1987a, 1987b, Woehler & Williams 1988) indicates a remarkable consistency in the oceanography of the Prydz Bay region when *E. superba* larvae are in the water column. This is supported by the similar description of the gyre for various years (Khimitsa 1976, Smith *et al.* 1984, Middleton & Humphries 1989, and R.A. Nunes Vaz & G.W. Lennon, personal communication 1990), as well as the similarity in sea-ice buoy and iceberg drifts observed over numerous years (Tchernia & Jeanin 1983, Allison 1989). The environmental factors affecting the larval distributions observed in this study in 1985 could therefore be expected to have similar effects in subsequent years. Hence, the Prydz Bay region would seem to be an ideal locality for studying the ecology of larvae in relation to hydrography, e.g. spawning, development, distribution and mortality, as compared to the Atlantic sector where the hydrographic patterns are most complex (Amos 1984) but where most research has so far been conducted.

Acknowledgements

I am extremely grateful to Drs R.A. Nunes Vaz and G.W. Lennon for their discussions on the oceanography of Prydz Bay, and for providing their unpublished results on horizontal circulation. I am also grateful to Drs S. Nicol, J. Watkins, R.M. Ross and L.B. Quetin for advice and comments on the manuscript. I also thank R. Burbury, R. Kirkwood,

S. Harrington, Dr D. O'Brien and Dr T. Ikeda for their help in sampling throughout the cruise. A special acknowledgement goes to M. Stolp for his assistance, both on ship and later in the laboratory, in the processing of samples.

References

- ALLISON, I. 1989. Pack-ice drift off East Antarctica and some implications. *Annals of Glaciology*, **12**, 1-8.
- AMOS, A.F. 1984. Distribution of krill (*Euphausia superba*) and the hydrography of the Southern Ocean: Large scale processes. *Journal of Crustacean Biology*, **4** (Spec. No. 1), 306-329.
- BAKER, A. de C., CLARKE M.R., & HARRIS, M.J. 1973. The NIO combination net (RMT 1+8) and further developments of rectangular midwater trawls. *Journal of the Marine Biological Association of the United Kingdom*, **53**, 167-184.
- BRAY, J.R. & CURTIS, J.T. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, **27**, 325-349.
- BRINTON, E. 1985. The oceanographic structure of the eastern Scotia Sea. - III. Distributions of the euphausiid species and their developmental stages in 1981 in relation to hydrography. *Deep-Sea Research*, **32**, 1153-1180.
- BRINTON, E. & TOWNSEND, A.W. 1984. Regional relationships between the development and growth in larvae of Antarctic krill, *Euphausia superba*, from field samples. *Journal of Crustacean Biology*, **4** (Spec. No. 1), 224-246.
- BRINTON, E., HUNTLEY, M. & TOWNSEND, A.W. 1986. Larvae of *Euphausia superba* in the Scotia Sea and Bransfield Strait in March 1984- Development and abundance compared with 1981 larvae. *Polar Biology*, **5**, 221-234.
- DALY, K.L. & MACAULAY, M.C. 1988. Abundance and distribution of krill in the ice edge zone of the Weddell Sea, austral spring 1983. *Deep-Sea Research*, **35**, 21-41.
- FAO 1989. *FAO Year Book 1987. Fisheries statistics. Catches and landings. Vol. 64.* Rome: Food and Agriculture Organization of the United Nations, 490 pp.
- FEVOLDEN, S.E. 1979. Investigations on krill (Euphausiacea) sampled during the Norwegian Antarctic research Expedition 1976/77. *Sarsia*, **64**, 189-198.
- FEVOLDEN, S.E. 1980. Krill off Bouvetöya and in the southern Weddell Sea with a description of larval stages of *Euphausia crystallorophias*. *Sarsia*, **65**, 149-162.
- FEVOLDEN, S.E. & SCHNEPPENHEIM, R. 1989. Genetic homogeneity (*Euphausia superba* Dana) in the Southern Ocean. *Polar Biology*, **9**, 533-539.
- HARRINGTON, S.A. & THOMAS, P.G. 1987. Observations on spawning by *Euphausia crystallorophias* from the waters adjacent to Enderby Land (East Antarctica) and speculations on the early ontogenetic ecology of neritic euphausiids. *Polar Biology*, **7**, 93-95.
- HART, T.J. 1942. Phytoplankton periodicity in Antarctic surface waters. *Discovery Reports*, **21**, 261-356.
- HEMPEL, G. 1985. Variations in geographical distribution and abundance of larvae of Antarctic krill, *Euphausia superba*, in the Southern Ocean. In SIEGFRIED, W.R., CONDY, P.R. & LAWS, R.M. eds. *Antarctic Nutrient Cycles and Food Webs. Proceeding of the 4th Symposium on Antarctic Biology.* Berlin: Springer-Verlag, 304-307.
- HEMPEL, I. 1981. Euphausiid larvae in the Scotia Sea and adjacent waters in summer 1977/78. *Meeresforschung*, **29**, 53-59.
- HEMPEL, I. & HEMPEL, G. 1982. Distribution of euphausiid larvae in the southern Weddell Sea. *Meeresforschung*, **29**, 253-266.
- HEMPEL, I. & HEMPEL, G. 1986. Field observations on the developmental ascent of larval *Euphausia superba* (Crustacea). *Polar Biology*, **6**, 121-126.
- HEMPEL, I., HEMPEL, G. & BAKER, A. de C. 1979. Early life history stages of

- krill (*Euphausia superba*) in the Bransfield Strait and Weddell Sea. *Meeresforschung*, **27**, 267-281.
- HIGGINBOTTOM, I.R., KERRY, K.R., WAYTE, S.E. 1988. The distribution and abundance of krill in the region of Prydz Bay, Antarctica. A report of the hydroacoustic surveys carried out on the research cruises FIBEX, ADBEX-II, and SIBEX-II. *ANARE Research Notes*, No. 62, 1-46.
- HODGKINSON, R.P., COLMAN, R.S., KERRY, K.R. & ROBB, M.S. 1988. Water currents in Prydz Bay, Antarctica during 1985. *ANARE Research Notes*, No. 59, 1-127.
- HOSIE, G.W. & KIRKWOOD, J. 1986. Euphausiid larvae collected from the Prydz Bay region during the Nella Dan cruise (SIBEX I). *Memoirs of the National Institute of Polar Research*, **40**, 110-116.
- HOSIE, G.W. & STOLP, M. 1989. Krill and zooplankton in the western Prydz Bay region, September-November 1985. *Proceedings NIPR Symposium Polar Biology*, **2**, 34-45.
- HOSIE, G.W., IKEDA, T., STOLP, M. & WILLIAMS, R. 1987. ADBEX III cruise krill/zooplankton sampling data. *ANARE Research Notes*, No. 57, 1-34.
- HOSIE, G.W., IKEDA, T. & STOLP, M. 1988. Distribution, abundance and population structure of the Antarctic krill (*Euphausia superba* Dana) in the Prydz Bay region, Antarctica. *Polar Biology*, **8**, 213-224.
- HUNTLEY, M.E., SYKES, P.F. & MARIN, V. 1989. Biometry and trophodynamics of *Salpa thompsoni* Foxton (Tunicata: Thaliacea) near the Antarctic Peninsula in Austral summer, 1983-1984. *Polar Biology*, **10**, 59-70.
- ICHI, T. 1990. Distribution of Antarctic krill concentrations exploited by Japanese krill trawlers and minke whales. *Proceedings NIPR Symposium Polar Biology*, **3**, 36-56.
- IKEDA, T. 1984. Development of the larvae of the Antarctic krill (*Euphausia superba* Dana) observed in the laboratory. *Journal of Experimental Marine Biology and Ecology*, **75**, 107-117.
- IKEDA, T. 1986. Preliminary observations on the development of the larvae of *Euphausia crystallorophias* Holt & Tattersall in the laboratory. *Memoirs of the National Institute of Polar Research*, **40**, 183-186.
- IKEDA, T., HOSIE, G.W. & STOLP, M. 1986. SIBEX II cruise krill/zooplankton data. *ANARE Research Notes*, No. 32, 1-70.
- JACKA, T.H. 1983. A computer data base for Antarctic sea ice extent. *ANARE Research Notes*, No. 13, 1-54.
- JOHN, D.D. 1936. The southern species of the genus *Euphausia*. *Discovery Reports*, **14**, 193-324.
- KANDA, K., TAKAGI, K., SEKI, Y. 1982. Movement of the larger swarms of Antarctic krill *Euphausia superba* population off Enderby Land during 1976-19s77 season. *Journal of the Tokyo University of Fisheries*, **68**, 25-42.
- KERRY, K.R. & WOEHLE, E.J. 1987. Oceanographic data: Prydz Bay region - Antarctic Division BIOMASS Experiment I, MV *Nella Dan*, November-December 1982. *ANARE Research Notes*, No. 52, 1-166.
- KERRY, K.R., WOEHLE, E.J. & ROBB, M.S. 1987a. Oceanographic data: Prydz Bay region - SIBEX II, MV *Nella Dan*, January 1985. *ANARE Research Notes*, No. 53, 1-122.
- KERRY, K.R., WOEHLE, E.J., WRIGHT, S. & DONG, Z. 1987b. Oceanographic data: Prydz Bay region - FIBEX, MV *Nella Dan*, January-March 1981. *ANARE Research Notes*, No. 49, 1-114.
- KHIMITSA, V.A. 1976. Investigations of geostrophic currents in the Antarctic zone on the Indian Ocean. *Oceanology*, **16**, 131-133.
- KITTEL, W. & JAZDZEWSKI, K. 1982. Studies on the larval stages of *Euphausia superba* Dana (Crustacea, Euphausiacea) in the southern Drake Passage and in the Bransfield Strait in February and March 1981 during the BIOMASS-FIBEX expedition. *Polish Polar Research*, **3**, 273-280.
- KITTEL, W., & WIJEK, Z., & CZYKIETA, H. 1985. Distribution of *Euphausia frigida*, *Euphausia crystallorophias*, *Euphausia triacantha*, and *Thysanoessa macrura* in the southern part of Drake Passage and in the Bransfield Strait during the 1983-1984 austral summer (BIOMASS-SIBEX). *Polish Polar Research*, **6**, 133-149.
- KUMAGORI, T. & YANAGAWA, S. 1958. Icebergs in the Antarctic Ocean. *Journal of the Tokyo University of Fisheries*, (special edition No.3), 285-191.
- LUBIMOVA, T.G., MAKAROV, R.R., MASLENKOV, V.V., SHEVTSOV, V.V. & SHUST, K.V. 1985. The ecological peculiarities, stocks and role of *E. superba* in the trophic structure of the Antarctic ecosystem. *Selected Papers Presented to the Scientific Committee CCAMLR 1982-1984*. Hobart, Australia: CCAMLR, Part II, pp 391-505.
- MACDONALD, C.M., WILLIAMS, R. & ADAMSON, M. 1986. Genetic variation and population structure of krill (*Euphausia superba* Dana) from the Prydz Bay Region of Antarctic waters. *Polar Biology*, **6**, 233-236.
- MAKAROV, R.R. 1979. Larval distribution and reproductive ecology of *Thysanoessa macrura* (Crustacea: Euphausiacea) in the Scotia Sea. *Marine Biology*, **52**, 377-386.
- MAKAROV, R.R. 1983. Some problems in the investigation of larval euphausiids in the Antarctic. *Berichte zur Polarforschung Sonderheft*, **4**, 58-69.
- MARR, J.W.S. 1962. The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). *Discovery Reports*, **32**, 33-464.
- MARSCHALL, H.-P. & HIRSCH, H.-J. 1984. Development of eggs and nauplii of *Euphausia superba*. *Polar Biology*, **2**, 245-250.
- MAUCLINE, J. & FISHER, L.R. 1969. The biology of euphausiids. *Advances in Marine Biology*, **7**, 1-454.
- MIDDLETON, J.H. & HUMPHRIES, S.E. 1989. Thermohaline structure and mixing in the region of Prydz Bay, Antarctica. *Deep-Sea Research*, **36**, 1255-1266.
- MILLER, D.G.M. 1986. Results from biological investigations of krill (*Euphausia superba*) in the Southern Indian Ocean during SIBEX I. *Memoirs of the National Institute of Polar Research*, **40**, 117-139.
- MILLER, D.G.M. & HAMPTON, I. 1989. Biology and ecology of the Antarctic krill. *BIOMASS Scientific Series*, No. 9, 1-166.
- MONTÚ, M., FERNANDES, L.F.L., DE OLIVEIRA, I.R. & CORDEIRO, T.A. 1990. Populações de eufáusidos da região do Estreito de Bransfield e adjacências: 1.ª Expedição Antártica Brasileira, Verão 1982-83 (2.ª fase). *Neritca, Pontal do Sul, PR*, **5**, 65-94.
- MUJICA, A. & ASENSIO, V. 1983. Distribution and abundance of krill larvae (*Euphausia superba* Dana). *Berichte zur Polarforschung Sonderheft*, **4**, 21-29.
- NICOL, S. 1989. Who's counting on krill? *New Scientist*, **124** (1690), 20-23.
- PIRES, A.M.S. 1986. Vertical distribution of euphausiid larvae (Crustacea) in the Bransfield Strait during the First Brazilian Antarctic Expedition. *Anais da Academia brasileira de ciências*, **58** (Suplemento), 43-51.
- POMMERANZ, T., HERRMANN, C. & KÜHN, A. 1982. Mouth angles of the Rectangular Midwater Trawl (RMT 1+8) during paying out and hauling. *Meeresforschung*, **29**, 267-274.
- ROE, H.S.J., BAKER, A. DE C., CARSON, R.M., WILD, R. & SHALE, D.M. 1980. Behaviour of the Institute of Oceanographic Science's rectangular midwater trawls: theoretical aspects and experimental observations. *Marine Biology*, **56**, 247-259.
- ROSS, R.M. & QUETIN, L.B. 1986. How productive are Antarctic krill? *BioScience*, **36**, 264-269.
- ROSS, R.M. & QUETIN, L.B. 1989. Energetic cost to develop the the first feeding stage of *Euphausia superba* Dana and the effect of delays in food availability. *Journal of Experimental Marine Biology and Ecology*, **133**, 103-127.
- ROSS, R.M., QUETIN, L.B. & KIRSCH, E. 1988. Effect of temperature on development times and survival of early stages of *Euphausia superba* Dana. *Journal of Experimental Marine Biology and Ecology*, **121**, 55-71.
- SMITH, N.R., DONG, Z., KERRY, K.R. & WRIGHT, S. 1984. Water masses and circulation in the region of Prydz Bay, Antarctica. *Deep-Sea Research*, **31**, 1121-1147.
- TCHERNIA, P. & JEANIN, P.F. 1983. *Quelques aspects de la circulation océanique Antarctique révélés par l'observation de la dérivé d'icebergs (1972-1983)*. CNRS Paris: Muséum National d'Historie Naturelle, 474 pp.
- WILLIAMS, R., KIRKWOOD, J.M. & O'SULLIVAN, D.B. 1983. FIBEX cruise zooplankton data. *ANARE Research Notes*, No. 7, 1-163.
- WILLIAMS, R., KIRKWOOD, J.M. & O'SULLIVAN, D.B. 1986. ADBEX I cruise

- zooplankton data. *ANARE Research Notes*, No. 31, 1-108.
- WOEHLER, E.J. & WILLIAMS, R. 1988. Oceanographic data: Prydz Bay region - Australian Antarctic Marine Biological Ecosystem Research 86/87 MV *Nella Dan*, February-April 1987. *ANARE Research Notes*, No. 63, 1-136.
- WRIGHT, S.W. 1987. Phytoplankton pigment data: Prydz Bay region - SIBEX II, MV *Nella Dan*, January 1985. *ANARE Research Notes*, No. 58, 1-102.
- ZAR, J.H. 1984. *Biostatistical Analysis*. Englewood Cliffs, NJ: Prentice-Hall, 718 pp.
- ZWALLY, H.J., COMISO, J.C., PARKINSON, C.L., CAMPBELL, W.J., CARSEY, F.D. & GLOERSEN, P. 1983. *Antarctic sea-ice, 1973-1976: satellite passive-microwave observations*. Washington, DC: National Aeronautics and Space Administration (NASA SP-459), 206 pp.