Korean Journal of Polar Research
Volume 4(2): 51-59, 1993

Distribution, Abundance and Reproductive Ecology of *Thysanoessa macrura* G.O. Sars in the Prydz Bay Region, Antarctica

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During the austral summer of 1989/1990 and 1990/1991 net sampling surveys were carried out to delineate the distribution, abundance, larval development stage composition, rate of larval development and reproductive ecology of *Thysanoessa macrura* in the Prydz Bay region. Larvae occurred throughout the sampling areas with comparatively high abundance. They were more abundant in open ocean area than in slope and shelf areas. Latitudinal difference in larval development stage composition or Mean Stage Index (MSI) could be clearly found, i.e. the closer to the shelf the younger the larvae. The average duration of larval development through a single stage obtained from field data were 13-19 days in 1989/1990 and 11 days in 1990/1991. The breeding season of *T. macrura* in Prydz Bay area seemed to start in early October and end in early January. Adults and juveniles were widely dispersed, but swarms were found mostly close to the Antarctic Divergence. Inter-annual variations in abundance and rate of larval development were evident.

Key words: *Thysanoessa macrura*, Prydz Bay region, Antarctica

INTRODUCTION

The present investigations and knowledges on the biology and ecology of Antarctic euphausiids are focused on the most abundant species, *Euphausia superba*. But the other euphausiid species, *Thysanoessa macrura*, is a very common and widespread circumpolar species. It is found in all Antarctic waters from pack ice to the open oceans (Mauchline and Fisher, 1969; Kirkwood, 1982). *Thysanoessa* macrura sometimes exceeds *E. superba* in total numbers (Hempel, 1981; Kirkwood, 1982; Kittel and Stepnik, 1983; Pires, 1986). In the areas of low *E. superba* abundance, *T. macrura* possibly replaces the former species as the major source of predation of higher trophic levels (Kirkwood, 1982). Because *T. macrura* occupies practically the same latitudinal position with *E. superba* (Rustad, 1934; Nemoto and Nasu, 1958; Lomatina, 1964), there must be some reciprocal adaptations to the environment, for example the difference in spawning times, distribution, and the changes of inter-annual abundance between the two species. *Thysanoessa macrura* may play an important role in the Southern Ocean ecosystem together with *E. superba*. This paper presents the results on the distribution, abundance, developmental stage composition, larval developmental rate and spawning period of *T. macrura* in the Prydz Bay region based on the data collected during two austral summers, 1989/1990 and 1990/1991.

MATERIALS AND METHODS

The cruise tracks and sampling stations of the two surveys are shown in Fig. 1. From January 7 to March 3, 1990, 28 sampling sites along four transects between 65°30′ E and 80° E, at intervals of one degree latitude from 62° S to the coast and other 6 sites in Prydz Bay were sampled. From December 28, 1990 to January 11, 1991, 37 sites were sampled along nine longitudinal transects, between 68° E and 108° E, at intervals of one degree latitude from 62° S to the coast. During the cruise from Prydz Bay to Australia in early January, 1991, surface zooplankton samples were col-

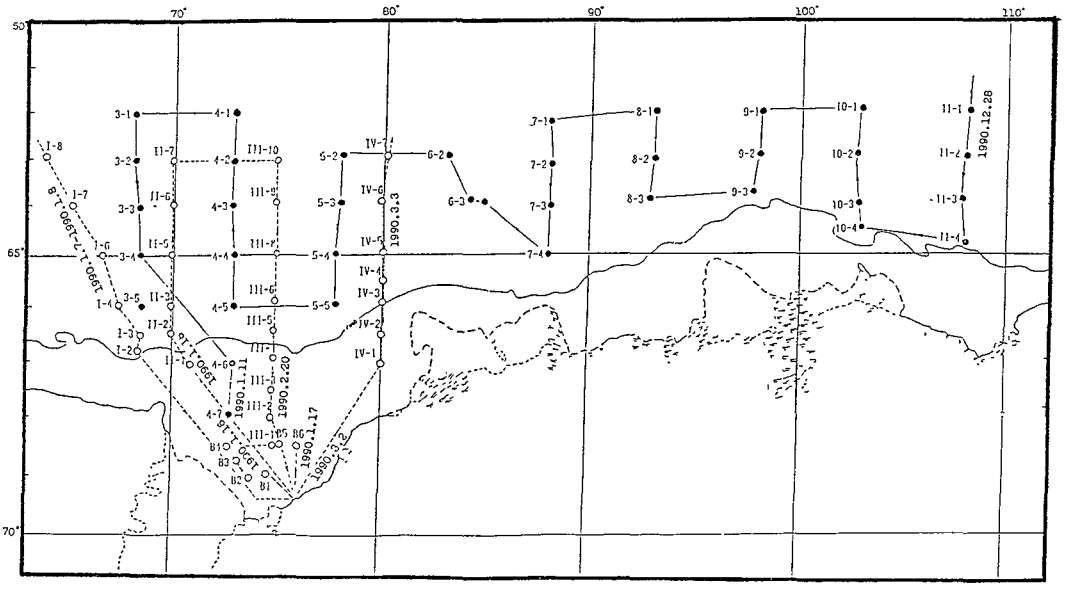

Fig. 1. Cruise tracks and sampling sites of the cruises 1989/1990 (dashed line, open circle) and 1990/1991 (solid line, closed circle).

lected using High-Speed Zooplankton Collector (HSZC).

At each of these stations, vertical hauls were made from 200 m depth to the surface using 80 cm diameter plankton net with 0.333 mm mesh size. The volume of water filtered was measured with General Oceanic Flowmeter. Oblique tows were made from 100 m depth to the surface using IKMT net. Between each of two stations, and during the cruise from Prydz Bay to Australia, 6 cm diameter HSZC with 0.333 mm mesh was used to collect zooplankton samples at about 0-20 m surface water layer during 1990/1991 survey. Samples were preserved in formalin for laboratory analysis.

In the laboratory, *Thysanoessa macrura* were sorted out, enumerated and classified to maturity stage (i.e., nauplii, metanauplii, calyptopis 1-3 (C_1-C_3), furcilia 1-6 (F_1-F_6) and postlarvae).

For the purpose of mapping the distribution of larvae and developmental stage composition at different sampling times, the Mean Stage Index (MSI) was used

$$MSI = (C_1*1+C_2*2+....+F_6*9)/N$$

where MSI is the mean stage index at each sampling sites or at each sampling times and C_1····F_6 are abundance of larval stages from calyptopis through furcilia 6, and N is the sum of the abundance of all stages.

RESULTS

Distribution of Larval Abundance and Developmental Stage Composition

Thysanoessa macrura was found at almost all stations with the depth from 120 m to 4300 m during the two sampling surveys except for two stations (Figs 2, 3).

Larvae of *Thysanoessa macrura* were consistently more abundant in the north than that in the south of the sampling region, i.e. they were more abundant in oceanic areas than in slope and shelf areas. The mean densities were 74 ind.·1000 m^{-3} south of 1000 m depth contour line and 310 ind.·1000 m^{-3} north of that in 1989/1990 season, and 166 and 1241 ind.·1000 m^{-3}, respectively, south and north of 1000 m depth contour line in 1990/1991.

Analysis of developmental stage composition and geographic distribution of the MSI showed a distinct latitudinal trend of stage development. Older furciliae larvae were found in the north and younger calyptopis in the south (Figs 4, 5).

Abundance and Developmental Stage Composition at Difference Sampling Times

In early January 1990, the larval stages from C_1

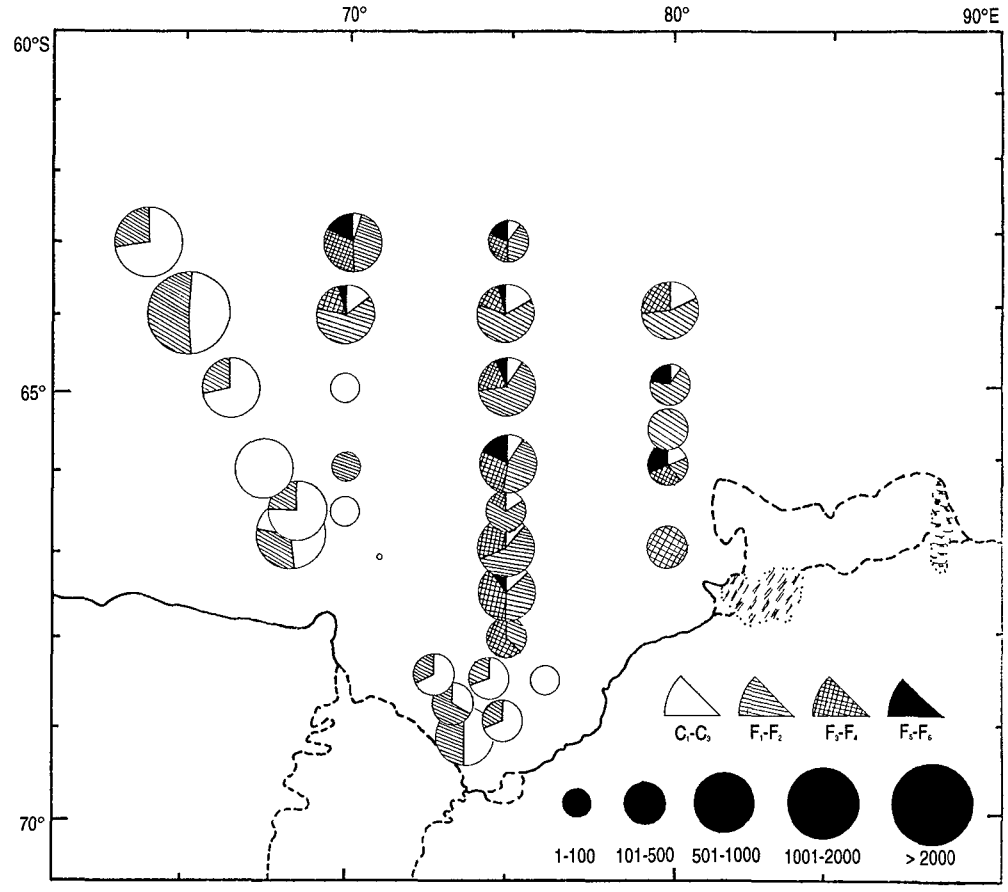

Fig. 2. Larval abundance and developmental stage composition of *Thysanoessa macrura*, 1989/1990 (ind.·1000 m).

to F_2 were found in transect I, with the MSI = 2.78 (Figs 2, 6A). Calyptopis and Furcilia 1 stage were more abundant. Larval abundance ranged from 126 to 2249 ind.·1000 m^{-3}, with the average density of 744 ind.·1000 m^{-3}. In mid-February, 1990, the stage composition was C_2-F_5, with MSI = 4.89. The abundance ranged from 6 to 482 ind.·1000 m^{-3} with the average density of 130 ind.·1000 m^{-3} in transect II and III (Figs 2, 6B). Transect IV was surveyed in early March, 1990. The average density dropped to 87 ind.·1000 m^{-3}. C_3-F_6 stages were found and the MSI was 5.00 (Figs 2, 6B).

In summer 1990/1991, sampling was conducted from December 28, 1990 to January 11, 1991. Stages C_1-F_3 were captured with the MSI = 3.75. The average density was 1155 ind.·1000 m^{-3}. Even though larvae were found at all stations, the abundance varied over three orders of magnitude, with highest numbers of up to 4354 ind.·1000 m^{-3} in station 91 and lowest abundance 27 ind.·1000 m^{-3} in station 104 (Figs 3, 6D). In early March, 1990, samples collected by HSZC contained only furcilia larvae. F_6 and juveniles were dominant, and the MSI was 8.70 (Fig. 6e).

Rate of Larval Development and Spawning Time

The sampling periods of about 3 months during 1989/1990 and 1990/1991 made it possible to investigate the larval development rate of *Thysanoessa macrura*. We used two methods to estimate the development rates: 1) the occurrence of the youngest or oldest stage between two sampling times, 2) the increase of MSI between two sampling times. Based on these two methods (Fig. 6), we got the results that the mean larval development rate from C_1 to F_6 were 13-19 days per stage in 1989/1990 and 11 days per stage in 1990/1991, i.e.

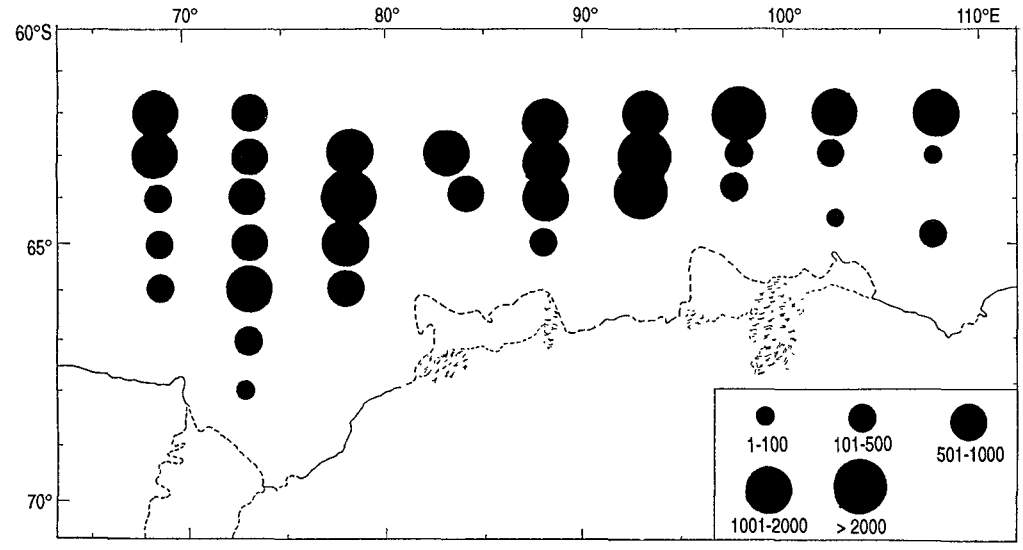

Fig. 3. Larval distribution and abundance of *Thysanoessa macrura*, 1990/1991 (ind.·1000 m^{-3}).

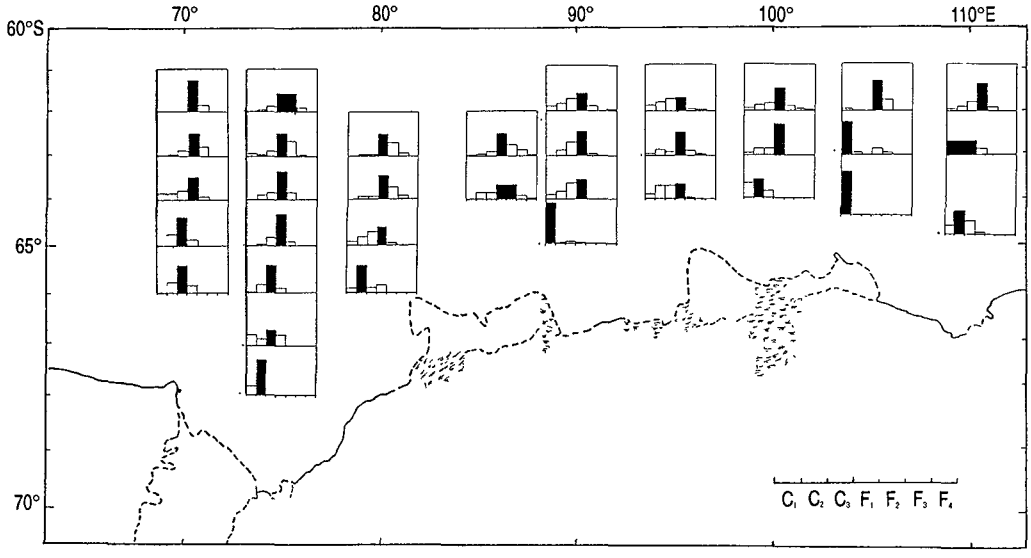

Fig. 4. Larval developmental stage composition of *Thysanoessa macrura*, 1990/1991.

T. macrura developed from C_1 to F_6 in about 104-152 days in 1989/1990 and about 88 days in 1990/1991.

Using the data of the larval development rate and the data on the occurrence of oldest and youngest larval stage at some sampling times, we could estimate the onset and ending of spawning. Because there were no data on larval development time from egg to C_1 stage of *Thysanoessa macrura*, analogous data on other euphausiids was used to estimate the spawning season. The development time data from C_1 through F_6 were obtained from this study. Cultivation experiments conducted on the larvae of *Euphausia superba* and *E. crystallorphias* have revealed that development time from egg to stage C_1 takes about 30 days (Ikeda, 1984, 1986; Ross *et al.*,1988). Therefore, we used the average 30 days from egg to stage C_1 and about 15 days per stage in 1989/1990 and 11 days per stage in 1990/1991 from C_1 to F_6 stage to estimate the

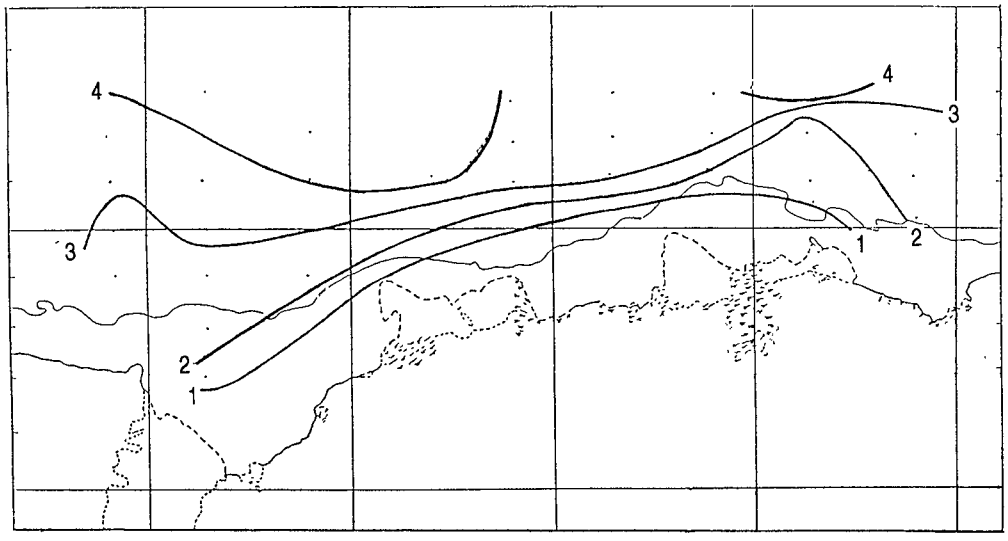

Fig. 5. Distribution of contours of larval developmental Mean Stage Index for *Thysanoessa macrura*, 1990/1991.

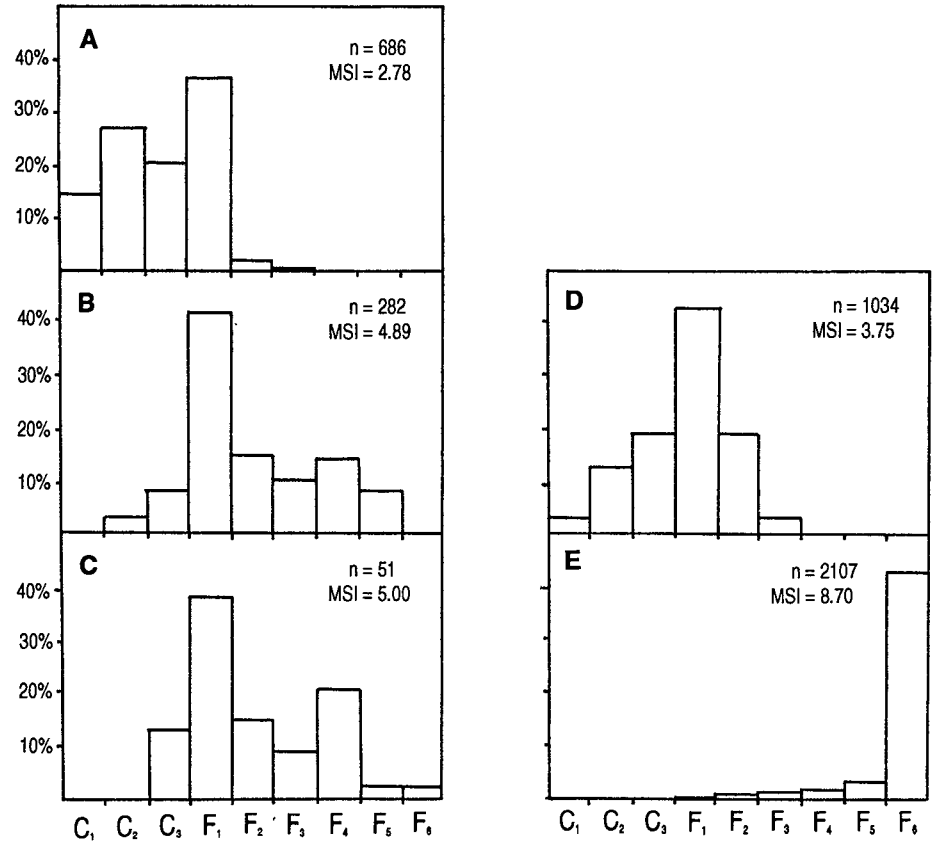

Fig. 6. Larval developmental stage composition and MSI at different sampling periods for *Thysanoessa macrura*. A, 7-8 Jan.,1990; B, 16-20 Feb., 1990; C, 2-3 Mar.,1990; D, 5-8 Jan.,1991; E, 3-4 Mar.,1991; n, total number of larvae.

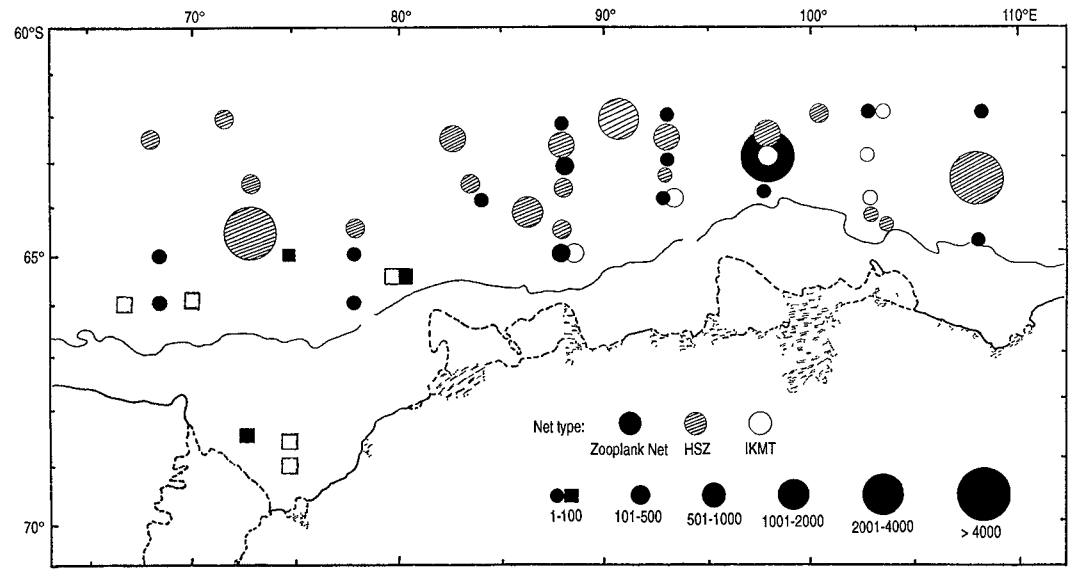

Fig. 7. Distribution and abundance of postlarvae of *Thysanoessa macrura*. squares, 1989/1990; circles, 1990/1991 (ind.·1000 m^{-3}).

Table 1. Abundance of postlarvae obtained from different sampling methods (ind.·1000 m^{-3})

	1989/1990		1990/1991		
Net type	Captured frequency	Avarage density	Captured frequency	Abundance	Average density
IKMT	5/28	6	8/37	2-443	100
Zooplank.net	3/28	8	16/37	6-4408	315
High-speed	no sample	–	19/33	52-11190	1391

Table 2. Surface temperature, chlorophll-a concentation, net phytoplankton cells, larval abundance of *Thysanoessa macrura*, MSI in comparetive season of 1989/1990 and 1990/1991, summerized by data of closedly located stations of the two cruises

Latitude	January 7-8,1990					January 9-10, 1991				
	T (°C)	chl-a ($\mu g/dm^3$)	cells ($10^3/dm^3$)	larvae ($No/10^3m^3$)	MSI	T (°C)	chl-a ($\mu g/dm^3$)	cells ($10^3/dm^3$)	larvae ($No/10^3m^3$)	MSI
63° S	-0.25	0.063	714	816	2.43	0.99	0.289	9728	1874	4.06
64° S	-0.03	0.154	5145	2282	3.23	0.40	0.310	4428	134	3.82
65° S	0.10	0.243	2350	366	2.39	0.15	0.282	8125	488	3.85
66° S	-0.61	0.216	2652	126	1.78	-0.35	0.324	6944	366	2.85
Average density	-0.20	0.169	2715	898	2.45	0.301	0.301	7306	716	3.65

spawning season. In early January, 1990 larval development had only attained the F_2 stage, and in early March, 1990, the youngest larval development stage captured was C_3 stage. In early January, 1991, the oldest stage was F_3 and in early March the youngest stage was F_2. According to these data, it was estimated that the main breeding season of *T. macrura* in Prydz Bay region seemed to start in early October and end in early January in 1989/1990 and 1990/1991.

Abundance Distribution of Postlarvae

Postlarvae of *Thysanoessa macrura* were widely dispersed over the sampling regions, but swarms were found mostly close to the Antarctic Divergence (Fig. 7). The results of abundance obtained from different sampling methods varied very much, this may be due to the different sampling efficiency by different types of nets used. The abundance of postlarvae obtained from each net type were shown in Table 1.

DISCUSSION

Like *Euphausia superba*, *Thysanoessa macrura* also exhibit deep water developmental ascent (Marr, 1962; Makarou, 1979, 1983). Calyptopis 1 larvae are the first stage to appear in the photic zone to get food (Makarou, 1982). This might be the main reason that we could not capture the nauplii and metanauplii larvae by trawling upper to 200 m depth. In addition to the developmental ascent, the result of Pires (1986) had shown that calyptopis and furcilia larvae of *T. macrura* could occur in significant numbers below 200 m depth. This would suggest that the standard 0-200 m hauls were perhaps not deep enough for efficient sampling of calyptopis and furcilia larvae. But the result of Hosie (1991) had shown that there was no significant difference in the number of larvae collected in the 0-200 m hauls compared with the number from the 0-1000 m hauls of *T. macrura* in Prydz Bay region, and he thought that the 0-200 m hauls were adequate.

Water temperature and food concentration might be the most important environmental factors that influence the geographic distribution of larvae abundance and development. In this study, it is apparent that the larval distribution and abundance had a positive relationship with the phytoplankton concentration, but had no direct relationship with the water temperature. The larval development was mainly influenced by water temperature. In the middle area of the sampling region of 1990/1991, the larval abundance was higher than in the east and west of the region. This might be because there was a comparatively higher chlorophyll-a concentration in the middle of the region (Dr. Ning, pers. comm.). The highest MSI value in the northwest of the region (Fig. 5) corresponded with the highest water temperature in this area (Dr. Shi, personal communication), but this area had the lowest chlorophyll-a concentration of the sampling region (Dr. Ning, personal communication).

Water temperature and phytoplankton concentration might influence the year to year variation of larval abundance and development also. As the sampling season and region of the two cruises were not the same, only the data of stations which are closely located and sampled at the nearly same season of the two years were collected to compare the year to year changes of larval abundance and development, and compared with the surface temperature, chlorophyll-a concentration and net phytoplankton cells at each station (Table 2). The most obvious difference of the environmental factors of the two cruises was that the temperature in 1990/1991 was much higher than that in 1989/1990. More advanced larval stages and higher MSI value in 1990/1991 might be attributed to the warmer water as compared with 1989/1990. The positive relationship between larval abundance and chlorophyll-a concentration and net phytoplankton cells at each station of the two cruises is shown in Table 2 also.

The north-south distribution of older to younger larvae might also be caused by the temperature. Temperature difference from north to south may be indicative of different spawning times, e.g. the colder water may have delayed the onset of spawning at inshore region, and the growth rate of larvae in the warmer north region is probably faster than that in the colder south region. The phenomenon of earlier spawning in northern latitudes is well known for the Southern Ocean zooplankton (Makarov, 1979, 1983; Brinton *et al.*, 1985; Makarov *et al.*, 1990; Hosie, 1991; Makarov and Menshenina, 1992). This phenomenon may be in accordance

with Hart's "phenological wave" which moves from north to south (Hart, 1942), and it has been proposed that the southward progress of spawning follows the receding ice edge (Daly and Macaulay, 1988). Hosie (1991) found that the MSI contours of *Thysanoessa macrura* in 1985 closely parallel the southward receding ice edge observed annually between 1973 and 1982 in the Prydz Bay region.

Miller and Hampton (1989) suggested that the Prydz Bay region was an area of generally low abundance of *Euphausia superba* larvae, and 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 region (Hosie *et al.*, 1988). The result of this study, Hosie and Kirkwood (1986), Hosie and Stolp (1989) and Hosie (1991) have shown that *Thysanoessa macrura* larvae are consistently the most abundant euphausiid larvae in the Prydz Bay region from September to January. The larval abundance in Prydz Bay region was almost the same as that in the Atlantic Sector (Makarov, 1979; Brinton *et al.*, 1985; Makarov *et al.*, 1990; Nordhausen and Huntley, 1990). There were still few data on postlarval abundance of *T. macrura* both in Prydz Bay region and Atlantic Sector. In summer 1992/1993, we captured almost the same of postlarvae of *T. macrura* as *E. superba* in biomass by IKMT net and HSZC in Prydz Bay region (not published). We can propose that *T. macrura* may play an important role in the marine ecosystem of Prydz Bay region together with *E. superba*. *Thysanoessa macrura* occupies the same latitudinal position with *E. superba* (Rustad, 1934; Nemoto and Nasu, 1959; Lomakina, 1964), but the spawning season of *T. macrura* is earlier than that of *E. superba* (Makarov, 1979; Hosie and Kirkwood, 1986; Hosie, 1991). Our study about *E. superba* on the same sampling programmes showed that the main breeding season of *E. superba* in Prydz Bay region was from late January to late February, when *T. macrura* had ceased breeding. It is important to study the reciprocal adaptation, i.e. the spawning seasons, geographic and vertical distributions, food collected, etc. The annual variability of abundance of *E. superba* may be related to the annual variability of *T. macrura*.

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