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DISTRIBUTIONAL ECOLOGY OF EUPHAUSIID LARVAE IN THE ANTARCTIC PENINSULA REGION AND ADJACENT WATERS

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Abstract: The distribution of euphausiid larvae was investigated in the Antarctic Peninsula region and adjacent waters in the summers of 1976–79 and in the autumns of 1981–82. Larvae of *Euphausia frigida* and *E. triacantha* (particularly) were restricted to the northern, oceanic part of the region. Larvae of *E. superba* were most abundant and were found at the shelf and slope areas, where waters of high-latitude origin and waters of the frontal zone were distributed. Larvae of *Thysanoessa macrura* were found in all types of waters. Within the intermediate (confluence) zone, these larvae were most scanty and younger than those found anywhere. In distinction from the last two species, larvae of *E. crystallorophias* were abundant only at the southwestern inshore region. There was a notable decrease of the larval abundance of all species and a strong contrast of age composition in the Palmer Archipelago region. Larvae are older to the north-east than to the south-west of this area. In the oceanic zone (ACC), *T. macrura* begins to spawn after *E. frigida*. In the inshore waters the spawning begins in the following order: *T. macrura*, *E. crystallorophias*, and then *E. superba*.

1. Introduction

The regularities of distribution of euphausiid larvae in waters near the Antarctic Peninsula are relatively little understood in spite of the many planktological studies in these waters. Beginning from the "DISCOVERY" expeditions (HART, 1942; MACKINTOSH, 1934, 1937), a number of investigations including FIBEX and SIBEX experiments (EL-SAYED, 1988) were carried out there. Almost half of the recent papers published from these investigations are devoted to euphausiid larvae. Most of them describe the distribution of *Euphausia superba* larvae (see for example HEMPEL, 1983; MUJICA and ASENCIO, 1983; KITTEL and JAZDZEWSKI, 1982; BRINTON and TOWNSEND, 1984). Larvae of *Thysanoessa macrura* also have been a subject of special investigation (MAKAROV and MASLENNIKOV, 1980).

Larvae of *E. superba* are the most abundant in this region (WITEK *et al.*, 1985; HEMPEL and HEMPEL, 1978). The localities of their high abundance were the shelf (WITEK *et al.*, 1980), the deep shelf and the slope (WITEK *et al.*, 1980), beyond the slope (KITTEL and JAZDZEWSKI, 1982), and even the deep oceanic areas (HEMPEL, 1983). The conclusion that the highest abundance of *E. superba* larvae is confined to the shelf water may be erroneous due to less reliable sampling in deep oceanic waters (HEMPEL, 1983).

Only latitudinal differences in the geographic distribution are known on larvae of other species (WITEK and KITTEL, 1985; HEMPEL and MARSCHOFF, 1980). It has been shown that *E. frigida* larvae disappear upon the slope and the shelf. *T. macrura* larvae are common in the shelf region of Joinville Island, where larvae of *E. crystallorophias* are numerous (WITEK and KITTEL, 1985); larvae of the latter species do not reach waters north of the Bransfield Strait.

Geographically almost all the previous papers were restricted to the waters east of the Palmer Archipelago. As exceptions, two papers described the distribution of *T. macrura* larvae in the entire region (MAKAROV and MASLENNIKOV, 1980; MAKAROV *et al.*, 1982). Clearly, an adequate idea of the peculiarity of the fauna and ecology of euphausiid larvae could be gained by the broad examination of samples from eastern and western parts of the region including adjacent waters of the Bellingshausen and Weddell Seas, as done in this study.

2. Materials and Methods

The samples of euphausiid larvae were collected during three expeditions of RV "AKADEMIK KNIPOVICH" (VNIRO, U.S.S.R.) all over the region to be discussed: in the summers of 1975/76 (Dec.–Jan.), 1978 (Jan.–Feb.) and 1978/79 (Dec.–Jan.). Two autumn samplings in the east part of the region (Apr.–May 1981, 1982) are the complements of the summer data.

The samples were collected with a 0.1 m^2 Juday net (4 mesh per mm) from 1000 (500) m depth to the surface. All larvae in a sample were counted. Their developmental stage and species were determined.

3. Results

As it would require too many figures to present the distribution of larvae of each species of all these surveys, only the maps of the most typical situations are presented here. The data on abundance and stage composition of the larvae of four euphausiid species obtained from each survey are presented in Table 1 for three subregions.

While larvae of *E. triacantha* were encountered in the very north of the region, they were not included in the present analyses because of their low abundance of 1–3 larvae per station.

E. frigida larvae exibited a wider to-the-south distribution than *E. triacantha*, with the highest abundance up to 340 individuals per m^2. In summer these larvae were distributed even near the shore (South Shetland Islands) (Fig. 1). Most larvae were encountered in the eastern part. Larvae in the western part were always older than in the eastern part.

Larvae of *T. macrura* inhabited deep oceanic as well as shelf areas (Figs. 2–4). Summer sampling data of different years showed the constant presence of *T. macrura* larvae in the oceanic zone. The individual density varied from 1 to more than 500 individuals per m^2. The oceanic zone of high abundance of *T. macrura* larvae extends from west to east, a pattern similar to that seen in *E. frigida.*

In the inshore zone (above the shelf and slope), distribution of *T. macrura* larvae varied considerably. Their abundance in the shelf zone was found to be comparable to

Table 1. The stage composition (%) of euphausiid larvae for three subregions (see text for details) in the Antarctic Peninsula area.

Time of collection	Subregion	*E. frigida*				*T. macrura*				*E. superba*				*E. crystallorophias*				Stations (*n*)
		n	c	f	*N*	n	c	f	*N*	n	c	f	*N*	n	c	f	*N*	
January 1976	ocean	19	41	40	59	0	22	78	1583	1	99	0	277	0	0	0	0	28
	inshore, NE	0	0	0	0	0	32	68	177	0	99	0	6939	0	16	84	64	29
	inshore, SW	0	0	0	0	5	67	28	239	0	100	0	425	13	87	0	1285	39
January, February 1978	ocean	57	39	4	67	5	43	52	1569	44	56	0	9	0	0	0	0	18
	inshore, NE	0	0	0	0	9	91	0	65	47	53	0	19	0	100	0	1	24
	inshore, SW	0	0	0	0	2	96	2	152	0	0	0	0	100	0	0	1	34
December, 1978–January, 1979	ocean	11	87	2	157	1	50	49	595	0	0	0	0	0	0	0	0	31
	inshore, NE	0	0	0	0	6	84	10	1105	31	69	0	32	42	58	0	130	16
	inshore, SW	0	0	0	0	4	96	0	117	73	27	0	15	0	0	0	0	21
April–May, 1980	ocean	0	0	0	0	0	0	100	6	0	0	100	701	0	0	0	0	24
	inshore, NE	0	0	0	0	0	0	0	0	0	0	100	824	0	0	0	0	44
April, 1981	ocean	0	0	0	0	0	0	100	9	0	54	46	4065	0	0	0	0	17
	inshore, NE	0	0	0	0	0	0	100	11	0	6	94	245	0	0	0	0	23

n—nauplius; c—calyptopis; f—furcilia; *N*—number of larvae.

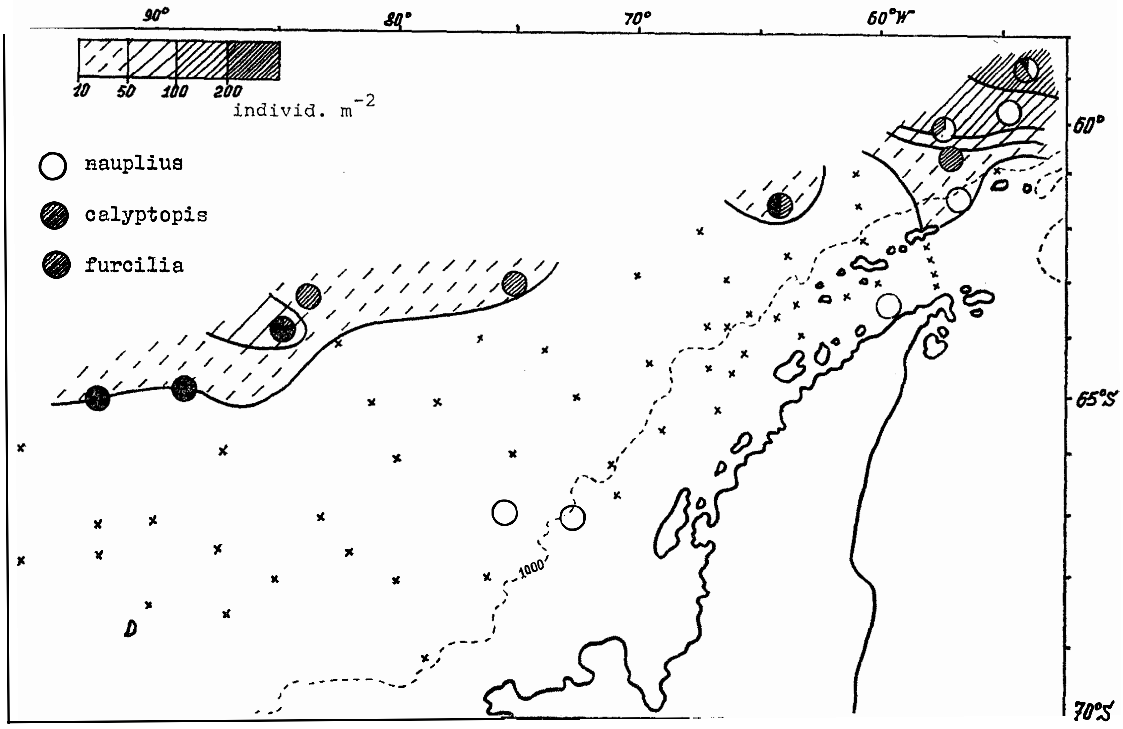

Fig. 1. Distribution of larval stages of Euphausia frigida *in the Antarctic Peninsula region in January–February 1978.*

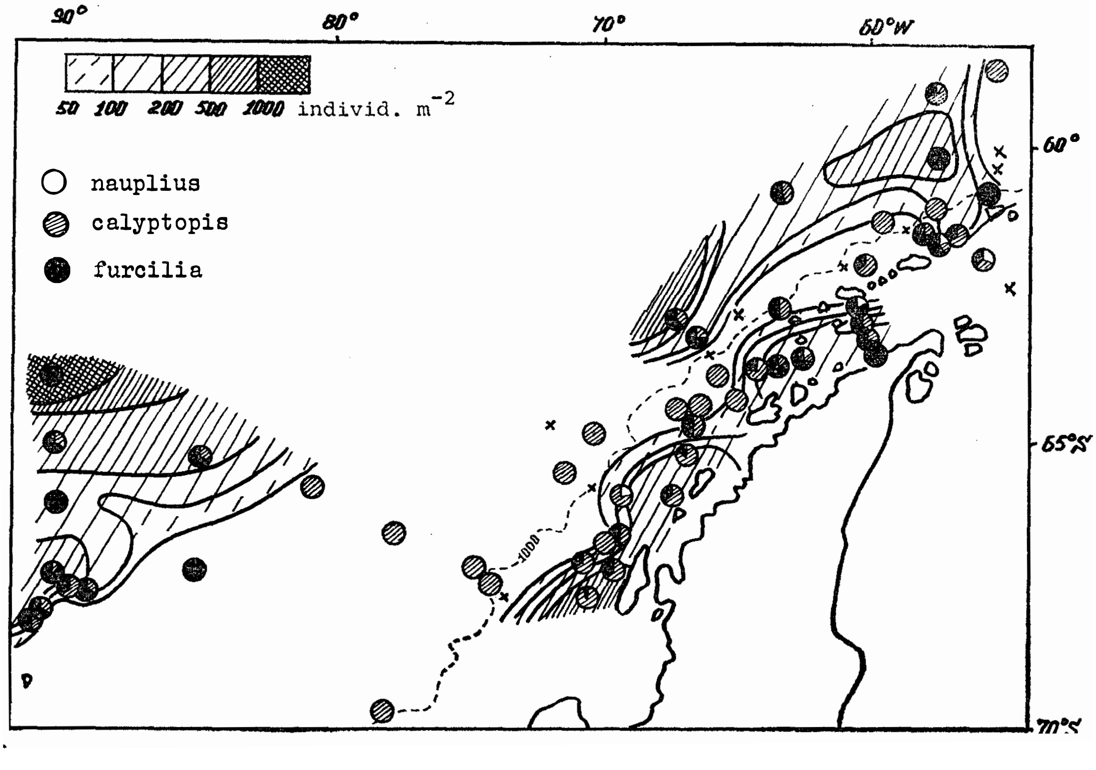

Fig. 2. Distritution of larval stages of Thysanoessa macrura *in the Antarctic Peninsula region in January 1976.*

that in the oceanic zone in two surveys (1976 and 1978/79) (Figs. 2 and 4). In 1977/78, most larvae were encountered only in the oceanic area and their number decreased from the north to the south (Fig. 3). In the other two years the oceanic and shelf zones of

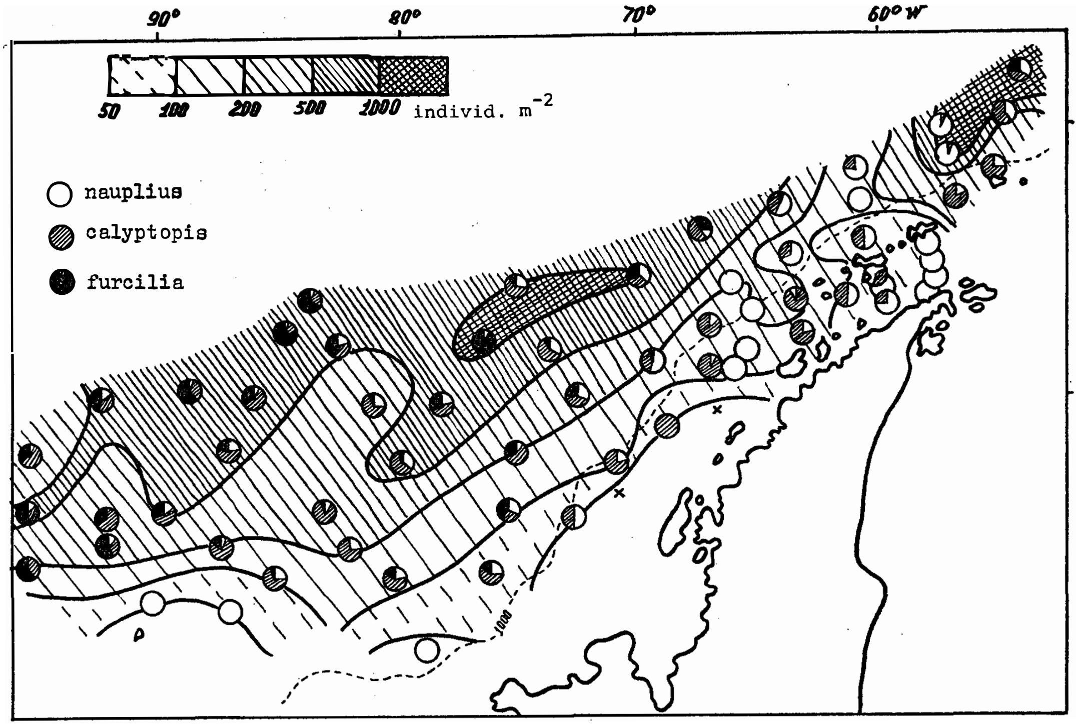

Fig. 3. Distribution of larval stages of Thysanoessa macrura *in the Antarctic Peninsula region in January–February 1978.*

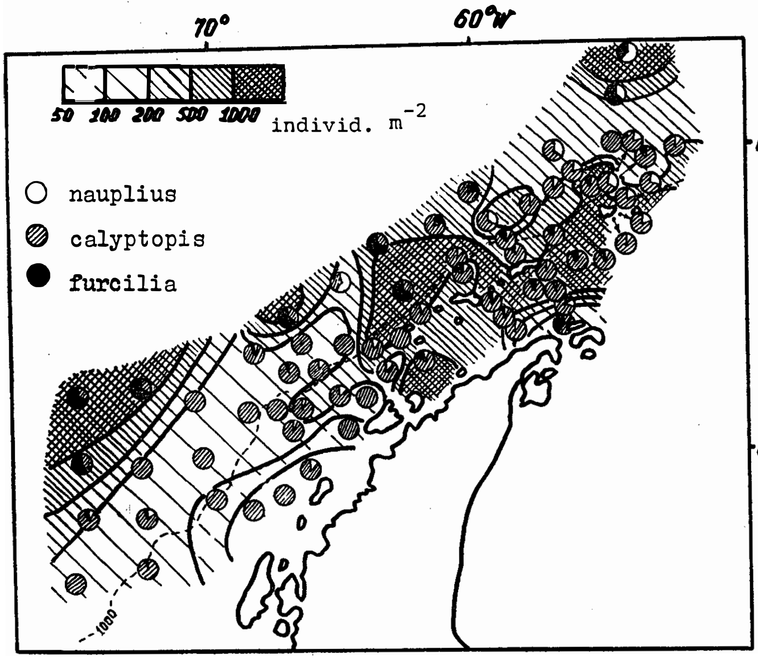

Fig. 4. Distribution of larval stages of Thysanoessa macrura *in the Antarctic Peninsula region in December 1978–January 1979.*

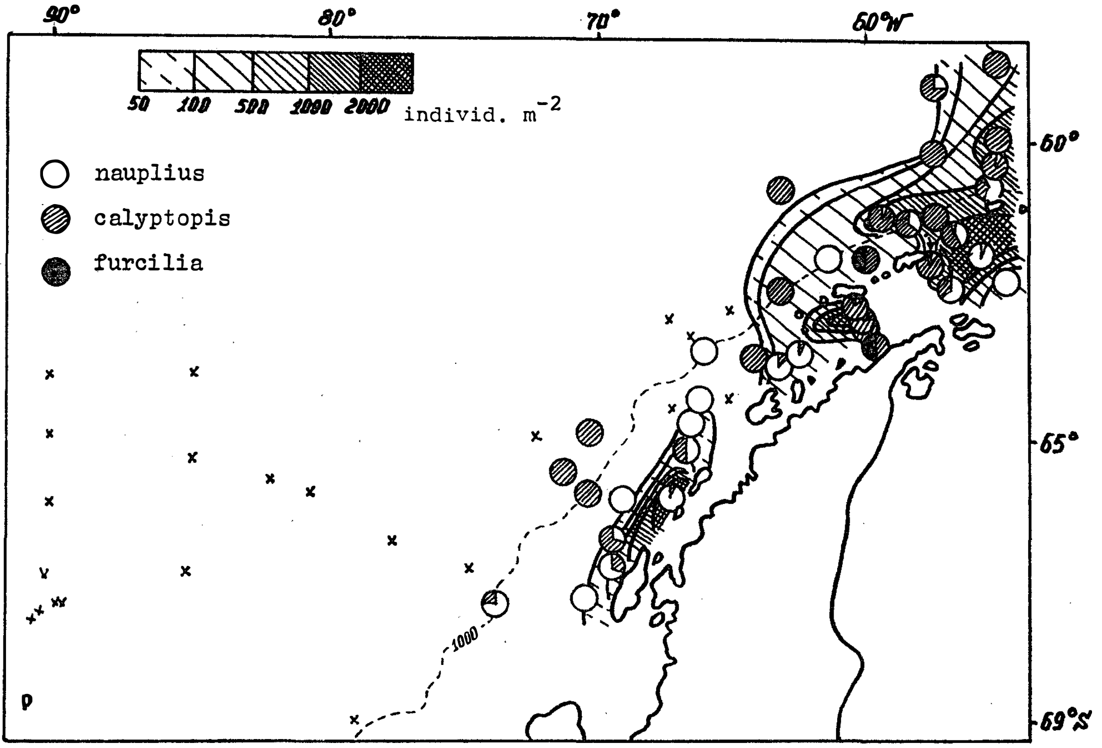

Fig. 5. Distribution of larval stages of Euphausia superba *in the Antarctic Peninsula region in January 1976.*

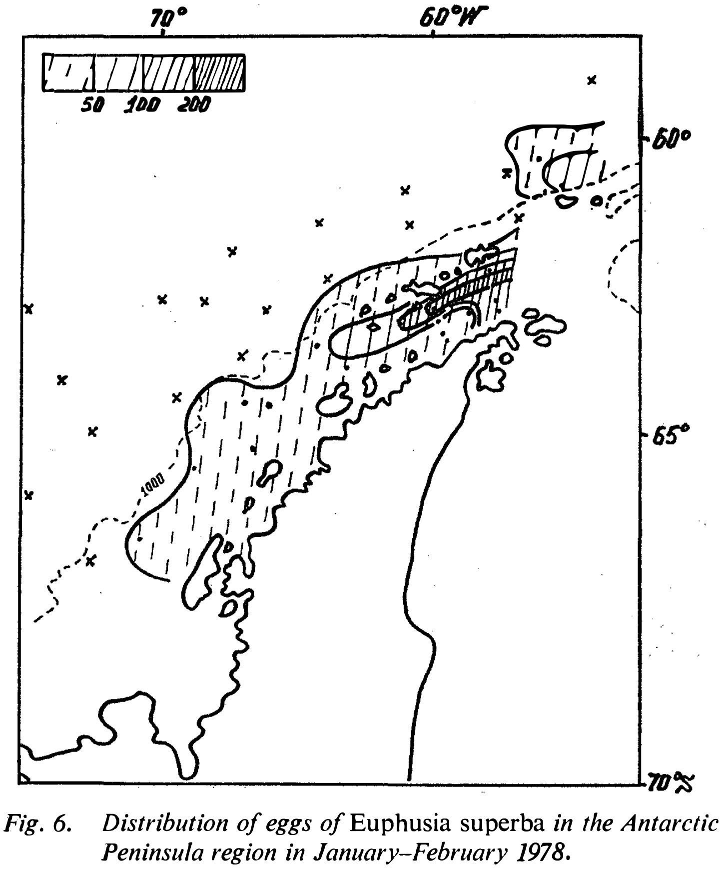

Fig. 6. Distribution of eggs of Euphusia superba *in the Antarctic Peninsula region in January–February 1978.*

high abundance of the larvae were divided by an extremely low abundance zone (Fig. 2). In 1978/79, this zone was formed by several spots (Fig. 4).

Most *E. superba* larvae in summer were encountered above the shelf and the slope including the Bransfield Strait and even the region of the Adelaide Island (Figs. 5 and 6). The density of larvae varied notably and it reached as high as more than 1000 individuals per m^2 in 1976. They were few in number in the oceanic zone, where they were mainly brought from the shelf. They were captured very rarely far away from the coast (the northernmost finding record was at 63°05′S, 84°15′W, in February, 1978). Larvae were always numerous near the South Shetland Islands. The abundance of larvae was lower near the Palmer Archipelago. In the late summer season, when the larvae were oldest, they were numerous near the Adelaide Island as well as near the South Shetland Islands (Fig. 5). On the other hand, in the early summer, when they hardly reached the first calyptopis stage, they were abundant only in the Bransfield Strait, as in the case of eggs (Fig. 6).

The autumn samplings demonstrated another situation. One can note an increase of the larval abundance above the slope and a decrease above the shelf (Fig. 7). The April sampling in 1981 also showed an increase of larval number to the north of the South Shetland Islands. The larvae were notably advanced in autumn (Table 1). They were numerous there in autumn (up to 9500 individuals per m^2).

In autumn the larvae of the other species were few in number while the postlarvae

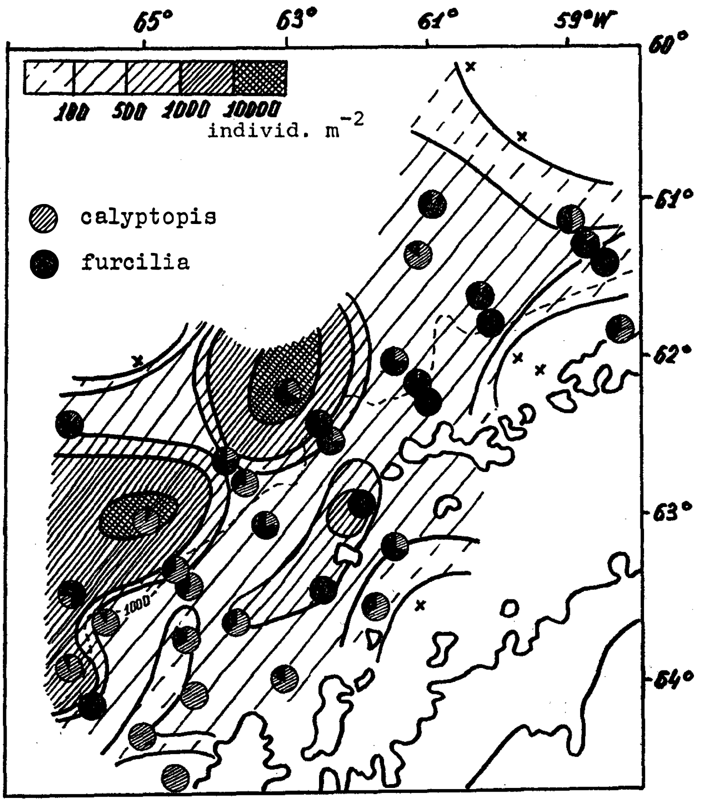

Fig. 7. Distribution of larval stages of Euphausia superba *in the Antarctic Peninsula region in April–May, 1980.*

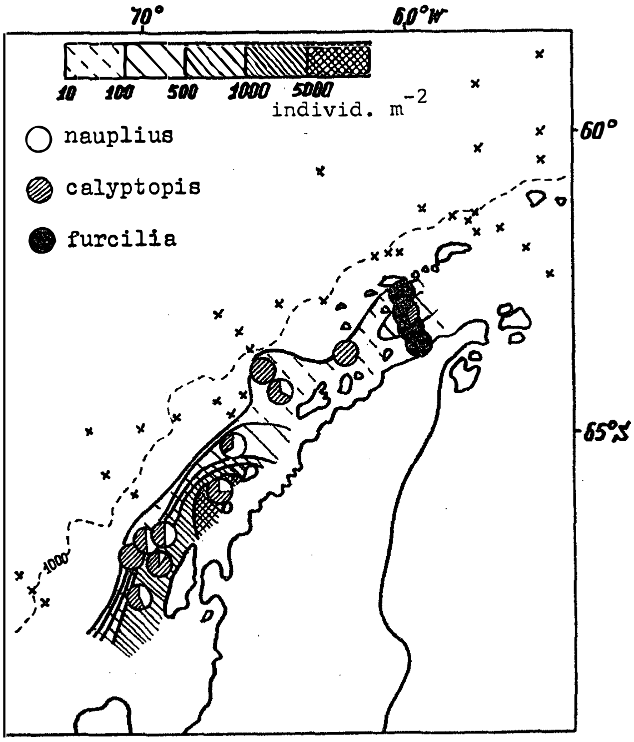

Fig. 8. Distribution of larval stages of Euphausia crystallorophias *in the Antarctic Peninsula region in January 1976.*

were numerous. Only several individuals of later furcilia stages of *T. macrura* were captured. But the absence of *E. superba* and *E. crystallorophias* larvae in the inshore zone could not be ascertained because of ice covering.

E. crystrallorophias larvae were captured only in summer above the shelf (Fig. 8). In the summer of 1976, larvae were the most numerous in the waters south-west of the Palmer Archipelago (up to 5000 individuals per m^2). In the north-east they were less numerous and less notably advanced than in the south. In the other years they were sparse and were mainly sampled in the waters north-east of the Palmer Archipelago (Table 1).

4. Discussion

4.1. Hydrography

The waters investigated are represented by Antarctic Circumpolar Current (ACC) waters and waters of high-latitude origin. The latter consist of the Antarctic Peninsula shelf (APS) waters, waters of the Bransfield Strait (BS), and waters of the Weddell Sea (WS) (MAKAROV *et al.*, 1988). These water bodies are distributed mainly above the shelf and are limited by the slope. Along the slope they contact with the ACC waters, forming the frontal (intermediate or confluence) zone (BOGDANOV *et al.*, 1980; MAKAROV *et al.*, 1988; STEIN, 1988). They gradually replace one another along the coast, forming the additional frontal zone in the western part of the Bransfield Strait, and the vicinity of the Palmer Archipelago (MARIN *et al.*, 1985).

4.2. *Larval distribution*

In the ACC waters, larvae of *E. frigida* and *T. macrura* are common and the latter are the most numerous. *E. superba* larvae are present only on the south margin while *E. crystallorophias* larvae are absent. The patterns of distribution of *E. frigida* and *T. macrura* larvae in the ACC waters are characterized by decrease of abundance from the north to the south.

In the inshore region, larvae of *E. crystallorophias*, *E. superba*, as well as *T. macrura* are present. There are no *E. triacantha* larvae; the collection of *E. frigida* larvae was only accidental.

There was a distinct horizontal gradient in the occurrence of euphausiid larvae along the coast: the abundance and stage composition of larvae differ between the south-western and the north-eastern parts of the shelf region. The boundary of these parts (subregions) lies near the Palmer Archipelago. In particular, the density of *E. superba* larvae sharply decreased near the Palmer Archipelago (Fig. 5). When the larvae were rather advanced, there were two patches of high abundance on both sides of the Palmer Archipelago along the shore, with very different stage compositions.

In autumn, two patches of high density of *E. superba* larvae were present above the slope. Although observations were limited to a narrow region, the contrast in the stage composition in the north and in the south was distinct. This phenomenon may be explained by the drift of larvae from the shelf to the slope in the north-eastern direction, which formed two high-density areas upon the slope, while in summer they were on the shelf. The northern patch upon the slope in autumn is probably originated from that near the Palmer Archipelago in summer, while the southern patch with younger larvae may be connected with that to the south-west of the Archipelago. So, the transport of larvae from the shelf to the deeper waters area beyond the slope may have occurred (see also SIEGEL, 1988).

E. crystallorophias larvae were numerous in the waters south-west of the Palmer Archipelago while in the Bransfield Strait they were few in number or even absent (Fig. 8). Nevertheless, the subregional discrepancies in the stage composition of larvae mentioned above for *E. superba* are completely the same as those of *E. crystallorophias*. Besides, it is noteworthy that younger larvae of *E. crystallorophias* are always absent in the north subregion. The low density of *E. crystallorophias* population as well as absence of early larvae suggests the drift of *E. crystallorophias* larvae from the north-east to the Bransfield Strait with the WS waters (MAKAROV *et al.*, 1988) while the southern subregion (waters south of the Palmer Archipelago) must be a site of the intensive spawning.

4.3. *Stage composition*

E. frigida larvae did not demonstrate distinct differences in their stage composition, which is likely due to the fact that only the very south of its spawning ground was covered in this study. It can be seen, however, that when one goes further to the west the larvae become more advanced. This is connected with the difference in the time of sampling as well as with the southward transport of the larvae from the central to the southern stream of ACC, especially in the west (for current pattern, see MAKAROV and MASLENNIKOV, 1980). While the common decrease to the south is absent, the larvae are more advanced near the southern margin of ACC (Fig. 1). *E. frigida* hardly spawns in the southern margin of ACC waters in the west of the region investigated. So the collected larvae seem to be hatched in the central stream and developed during transport. In the northern part of the region, *E. frigida* is the first spawner*.

T. macrura larvae demonstrated the usual latitudinal change in the stage composition in the oceanic area (Figs. 2–4) because of latitudinal difference in the spawning season. This is a common phenomenon of the seasonal development (phenological succession) of the whole plankton community in the Antarctic Ocean (HART, 1942; VORONINA, 1971).

Two parts can be recognized concerning the larval stage composition in the inshore region. Larvae of all the species inhabiting the north-eastern subregion were always more advanced in development than in the south-western one (Table 1). The change of the larval stage composition was most distinct near the Palmer Archipelago. This pattern is less notable in *T. macrura* because of sparse larvae in the waters south-west of Palmer Archipelago.

It is noteworthy that in the zone of the extremely low abundance of *T. macrura* larvae along the slope, they are younger than in the oceanic and inshore zones of high density. The zone of low abundance of *T. macrura* larvae coincides with the confluence zone between the ACC and high-latitude waters, which is contrary to the result of MENSHENINA *et al.* (1990) that the frontal zone is usually an area of high larval density. The abundance of phytoplankton was less in the confluence zone, as compared with the oceanic and shelf zones. Low phytoplankton abundance may stop the development of *T. macrura* larvae beyond calyptopis 1 stage (ROSS and QUETIN, 1986). The low phytoplankton abundance and stage composition of *T. macrura* larvae both demonstrate the backwardness of the phenological succession in the slope water.

The increase in number of *T. macrura* larvae near the shore is connected with a more rapid seasonal succession in the shelf zone where the specific "oasis" conditions develop (MAKAROV *et al.*, 1982). *T. macrura* begins to spawn in the "oasis" and in the oceanic zone simultaneously (Figs. 2 and 4). The disappearance of the ice cover near the shore enhances stratification of water and facilitates growth of phytoplankton, which stimulates the succession of these local ecosystems including euphausiids (MAKAROV *et al.*, 1985). This sort of phenomenon may not appear every year; it was absent in the summer of 1977/78 (Fig. 3), when there was a strong advection of the ACC waters to the shelf. Larvae were scanty and young above the shelf, which means that the regular phenological wave from the north to the south (HART, 1942) reached the shore. "Oasis" conditions were absent, because the shelf gyres, which induces this phenomenon, were destroyed by the advection of ACC waters.

Obviously the development of a near-shore "oasis" seems to enhance the spawning of all species breeding there, particularly *E. crystallorophias* that is inhabiting the shallowest areas of the shelf.

Similar conditions may develop in some other regions near the Antarctic shore.

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* *E. frigida* larvae develop slower than that of *T. macrura* (MENSHENINA and SPIRIDONOV, 1988).

E. crystallorophias can inhabit and successfully spawn under the severe inshore conditions, probably because of regular appearance of the "oasis". Similar situations have been discovered near the Queen Maud Land (VLADIMIRSKAYA *et al.*, 1988), in the inshore region of the Enderby and Wilkes Lands (BUDNICHENKO and KHROMOV, 1988; MENSHENINA *et al.*, 1988). The high abundance of *E. crystallorophias* larvae in the inner Ross Sea (MENSHENINA *et al.*, 1990) and in the inner Weddell Sea (HEMPEL and HEMPEL, 1982) may be due to the same phenomenon.

E. superba larvae demonstrated the largest discrepancies in stage composition between the north-eastern and south-western subregions. The calculation of spawning time in these subregions shows that the differences in spawning time reached at least a month.

The general sequence of spawning of the species investigated was consistent with the previous works (FEVOLDEN, 1979; MAKAROV, 1979) in both subregions. Namely, the first spawner is *T. macrura*, and the last is *E. superba*.

5. Conclusion

According to the density of larvae, the spawning ground of *E. frigida* was estimated to be the ACC waters only; the spawning ground of *T. macrura* the ACC waters as well as the inshore waters; *E. superba* and *E. crystallorophias* the inshore waters only. Along the coast spawning grounds of the latter three species gradually change in respect to each other. The north-eastern subregion is the intensive spawning site of *T. macrura*, and the south-western subregion is an area of *E. crystallorophias* spawning, while *E. superba* successfully spawns in both regions.

The differences in the time of spawning and appearance of euphausiid larvae in plankton as well as discrepancies in their stage composition are explained with differences in the latitudinal position and peculiarities of ice-cover regime in various parts of the region. But the boundaries of the subregions and their locations are determined by the composition of waters which interact inside the region. The possible constant boundary between two subregions lies near the Palmer Archipelago. In the south-western subregion, the shelf waters are under the influence of the Bellingshausen Sea waters (BOGDANOV *et al.*, 1980). North-easterly, these waters move to the north and distribute along the coast of the South Shetland Islands. *E. superba* larvae may drift in this direction and some of them may be brought to the shelf from the spawning area near the Peter I Island. It must impact the stage composition of larvae as the spawning in the Bellingshausen Sea begins later than in the north-eastern region. The north-eastern subregion in the Bransfield Strait area is influenced by the Weddell Sea waters, which may bring there not only *E. crystallorophias*, but also *E. superba* larvae.

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