Proc. NIPR Symp. Polar Biol., 5, 44–54, 1992

DISTRIBUTION OF EUPHAUSIID LARVAE IN THE WEDDELL GYRE IN SEPTEMBER–OCTOBER 1989

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Abstract: Distribution of Euphausiid larvae in the Weddell Gyre of late winter was examined. There were only some eggs of *Thysanoessa* near the ice margin in September, and the eggs and larvae (from nauplius to calyptopis I) were collected under the ice in October. The furcilia VI of *Euphausia superba* was found under the ice in the north of the eastern part of the Maud Rise region. A single calyptopis I of *E. frigida* was recorded over the region (in the WWCC waters) and the furcilia of *Stylocherion maximum* was found in the WWCC waters in the west of the region. The furciliae IV to VI of *E. superba*, larvae (from metanauplius to furcilia I) of *Thysanoessa* and larvae (from calyptopis I to furcilia I) of *E. frigida* were abundant in the ice-free waters of the Scotia Sea in September. The calyptopis I of *E. triacantha* was found at the northernmost station.

Spawning of *Thysanoessa* in the ice-free waters started in early August, and under the ice it started in late September or in early October. *E. frigida* initiated the spawning in the ice-free waters in July, while the spawning of *E. superba* has not begun yet.

1. Introduction

Weddell Gyre (WG), the greatest circulation system inside the Antarctic area, demonstrates distinct changes in phenological state of plankton and species composition at the boundary of different waters (secondary frontal zone (SFZ)) (BRINTON, 1985; MAKAROV, 1982; VLADYMIRSKAYA, 1982; SUSHIN *et al.*, 1985 and others). These changes in the western part of the Gyre have the latitudinal direction while in the eastern part the zonation is destroyed in accordance with drift of the Antarctic Circumpolar Current (ACC) waters to the south and then to the west as Warm Weddell Countercurrent (WWCC) (BAGRYANTZEV and GURETZKY, 1986) and even may be quite the opposite. Plankton inhabiting the WWCC waters may have more distinct features of lower latitudes than in the Weddell Sea waters which are situated in the north of them (MAKAROV *et al.*, in press). These differences were shown for the summer period (MAKAROV, 1979; MAKAROV *et al.*, 1990). In the northern part of the Scotia Sea, near South Georgia Island, these discrepances were traced during various seasons (MAKAROV *et al.*, 1982; MAKAROV *et al.*, 1984; MENSHENINA, 1990b; MENSHENINA, in press). There is only one paper which reported the state of plankton (in particular the euphausiid larvae) in the early spring in the Weddell Gyre (DALY and MACAULEY, 1988).

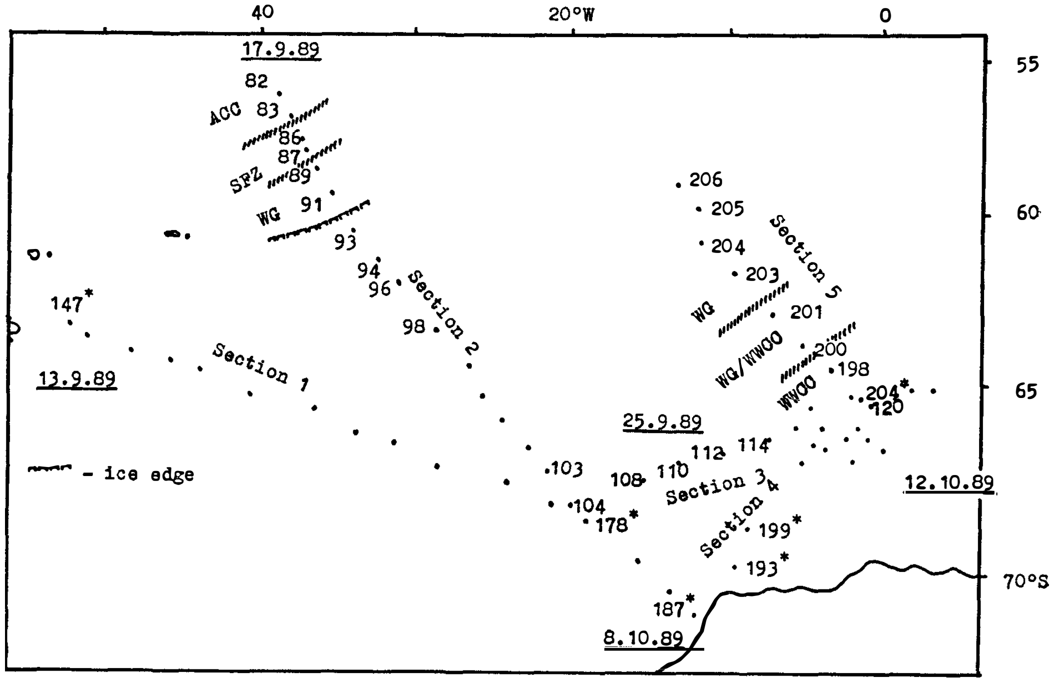

Fig. 1. *Number of stations, number of sections and period of sampling on each section, boundaries between waters of different origin. ACC, Antarctic Circumpolar Current; SFZ, Secondary frontal zone of the Scotia Sea; WG, waters of the Weddell Gyre; WWCC, Warm Weddell Countercurrent. * stations of R. V. "Polarstern".*

2. Materials and Methods

Plankton samples were collected along five transects in the Weddell Sea during the expedition "Winter Weddell Gyre Study" in September–October 1989. Several samples were taken in the Scotia Sea. Figure 1 shows position of sections and periods of sampling. Sections 1 and 5 were surveyed on board R.V. "Polarstern", the others (section 2 to 4) on board R.V. "Akademik Fedorov". Several additional stations were investigated by R.V. "Akademik Fedorov" over the Maud Rise. Samples on R.V. "Polarstern" were gathered with Multinet (mouth area 0.25 m^2, mesh size 100 μm), on R.V. "Akademik Fedorov"—with Bongo net (mouth area 0.5 m^2, mesh size 300 μm) except the last eight stations on section 4 (Stns. 196–206) where Judey net was used (mouth area 0.1 m^2, mesh size 100 μm). Almost all stations were located in the water covered with ice except Stns. 82–91 of section 2 which were in the open water. In general the fishing depth ranged from the surface down to 1000 m. A few hauls were carried out from the surface to 500 m (Table 1). The time of spawning was estimated on the basis of larval stage composition in accordance with duration of developmental stages (MENSHENINA and SPIRIDONOV, in press).

3. Results

Larvae of *Thysanoessa* spp., *Euphausia frigida*, *E. superba*, *E. triacantha* and *Stylocheiron maximum* were registered.

Table 1. Abundance of euphausiid larvae (ind/m²) captured on board "Akademik Fedorov".

Station	Depth of haul (m)	*Euphausia superba* stages				*Thysanoessa* stages							*E. frigida* stages				
		FIV	FV	VI	Pl	O	N	M	CI	CII	CIII	FO	M	CI	CII	CIII	FI
82	0–500								4610	2590	340	50	290	3220	860	140	50
83	0–500								860	900	100		100	3550	3840	900	290
86	0–500							20	2400	860	30		210	300	160	50	30
87	0–500	80	260	380	4	4			20	4				10	4		
89	0–500								4					4			
93	0–500	10				70	10		3								
94	0–1000					40		4									
114	0–500			4													
162	0–500						4	10									
204*	0–1000					198	1280	500	4								
193*	0–1000							4									
196	0–1000				10												
198	0–1000					540	370	210	20					10			
200	0–1000					1110	120	40									
201	0–1000					700	90	140	10								
204	0–1000			20	160	500	120	240	210								
205	0–1000			10		210	100	160	110								
206	0–500			110	40	130		90	80								

O, ova; N, nauplii; M, metanauplii; C, calyptopis; F, furcilia; Pl, postlarva.
Besides, there were calyptopes of *Euphausia triacantha* from Stn. 82 (240 ind/m²) and a single furcilia I of *Stylicheiron maximum* from Stn. 120 (*i.e.* 4 ind/m²). Stns. 204* and 193* were investigated on board R. V. "Polarstern".

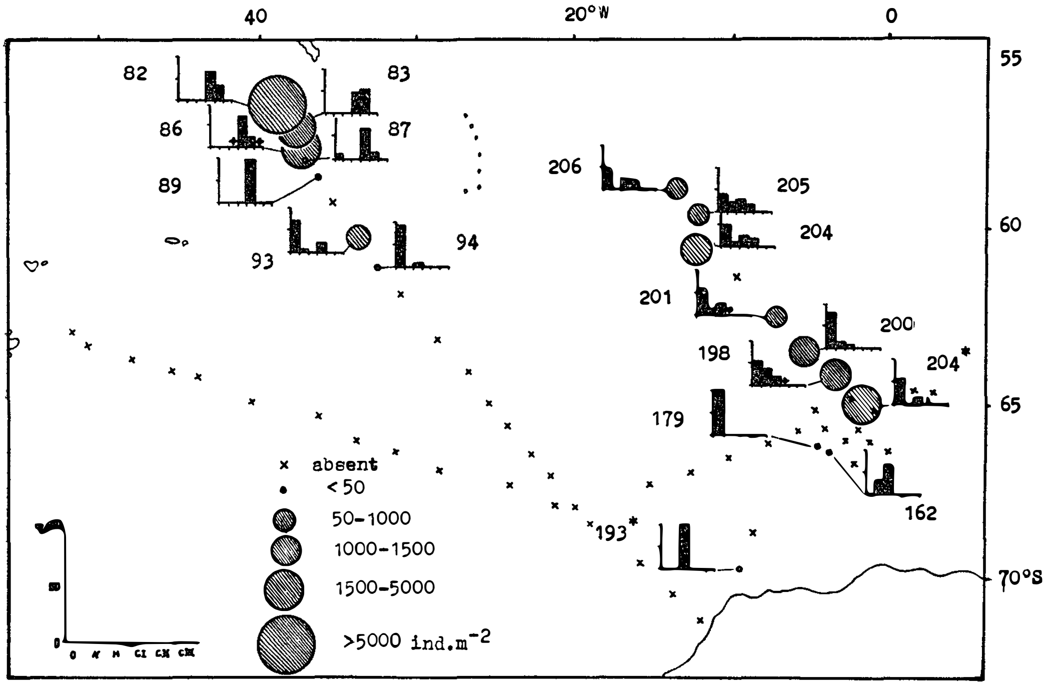

Fig. 2. Distribution and stage composition (% of specimens on each stage) of Thysanoessa *larvae in the Weddell Gyre (September 13–October 23, 1989). O, ovae, N, nauplii; M, metanauplii; C, calyptopis. +— less then 1.0%.*

3.1. Thysanoessa *spp.* (*Fig. 2*)

Eggs were numerous (up to 1980 ind/m^2) on section 4, northwest of the Maud Rise (October). Along section 2 (September) only a few eggs near the very ice margin were recorded (Stns. 93 and 94; Fig. 2).

Nauplii and metanauplii were captured mainly in the same region and at the same time with eggs (near the Maud Rise, in October). The highest abundance of nauplii (1280 ind/m^2) was over the Maud Rise while metanauplii were distributed along the same section (4) more or less homogeneously (the highest abundance was 500 ind/m^2). Some of them were met in September on section 2 near the ice margin (Stns. 93 and 94). A single nauplius was obtained near the shore (Stn. 193 of section 5).

Occurrence of calyptopis in September (section 2) was restricted to the open water with maximum of 7540 ind/m^2 at the northernmost station. Their abundance strongly decreased southward. Almost everywhere calyptopis I was dominant (Table 1). The abundance of calyptopis II and III decreased more abruptly southward than that of calyptopis I.

In October (section 4) calyptopes were sparse and they were captured only in the north of section 4. Only calyptopis I was recorded.

3.2. E. frigida (*Fig. 3*)

Metanauplii were gathered in September (on section 2) at the two northernmost stations in the open water (Stns. 82 and 83). Their abundance was equel to 290 ind/m^2. Calyptopes occurred at five northern stations of section 2 in the open water (Stns. 82–89) in September. At two northernmost stations their abundance was higher than

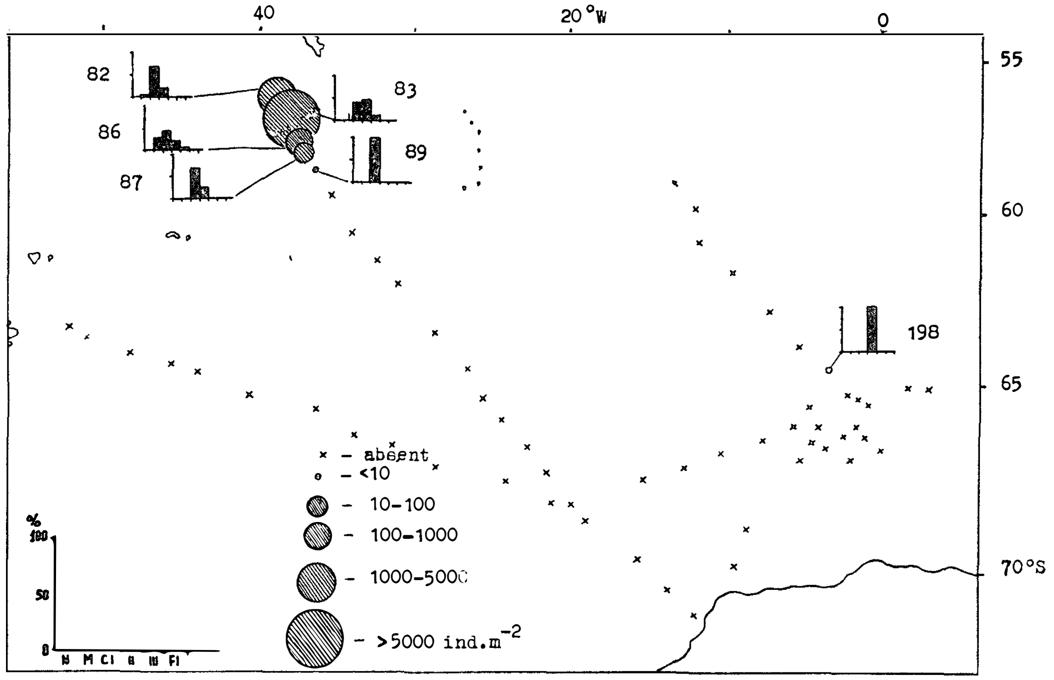

Fig. 3. Distribution and stage composition (% of specimens on each stage) of Euphausia frigida *larvae in the Weddell Gyre (September 13–October 23, 1989). N, nauplii; M, metanauplii; C, calyptopes; F, furciliae.*

1000 ind/m^2 (Stns. 82 and 83), at the third station (Stn. 86) it was ten times less, and at the last two stations (Stns. 87 and 89) only several specimens were captured. In total main the first stage was dominant (Table 1). One specimen of the first calyptopis was captured over the Maud Rise in October.

Furciliae (only the first stage) were collected only in the open water (Stns. 82, 83 and 86 of section 2, September). The highest abundance was 290 ind/m^2.

3.3. E. triacantha

240 ind/m^2 of calyptopis I were collected at the northernmost station (Stn. 82) of section 2 (September, in the open water).

3.4. E. superba (*Fig. 4*)

Only furciliae IV to VI and postlarvae were collected. The highest abundance (720 ind/m^2) was recorded in the open water near the ice margin (section 2, September). Furcilia VI was dominant. On section 4 northwest of the Maud Rise near the ice margin (at three northernmost stations), furcilia VI and postlarvae up to 180 ind/m^2 (Stn. 204) were collected. The postlarvae were dominant (Table 1).

3.5. Stylocheiron maximum

A single larva (furcilia with one pair of non-setose pleopods) was captured over the Maud Rise (Stn. 120 of section 3, October).

3.6. Overview

Thus, euphausiid larvae were captured in two areas of investigation: the northern

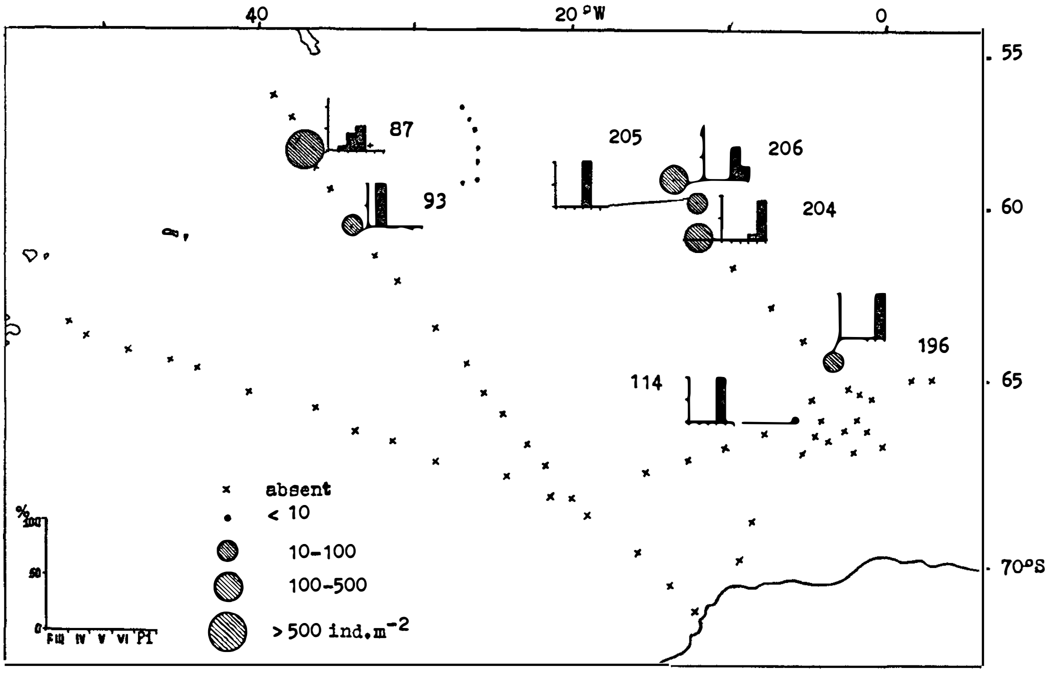

Fig. 4. Distribution and stage composition (% of specimens on each stage) of Euphausia superba *larvae in the Weddell Gyre (September 13–October 23, 1989). F, furciliae; Pl, postlarvae.*

part of section 2 and section 4 with Stn. 204 of section 5. On other sections there were no larvae but a single nauplius of *Thysanoessa* was collected at Stn. 193 (southernmost of section 5).

In the western region larvae of four species of antarctic euphausiids were abundant while in the eastern region only those of *Thysanoessa* were numerous.

The samplings in the former area were made a month earlier than in the latter. Section 2 crossed waters of the Antarctic Circumpolar Current (ACC) (two northernmost Stns. 82 and 83), the secondary frontal zone (SFZ) of the Scotia Sea (three stations to the south of previous, Stns. 86–89) and the Weddell Sea waters (all of the rest stations). The last station of section 2 as well as all stations of section 3 lay in the WWCC waters. On section 4 the WWCC waters were distributed wider (Stns. 194 to 198, southernmost stations of the section and Stn. 204 of section 5 which coincided with Stn. 194), while the Weddell Sea waters were located in the north of the section (Stns. 203 to 206) and mixed waters of WWCC and Weddell Sea were recognized in the middle of the section (Stns. 200 and 201) (BATHMANN *et al.*, in press).

Stations 82 to 91 were located in the ice-free water. All the other stations were in the water covered with ice.

4. Discussion

Differences in distribution and abundance of euphausiid larvae arose from the difference in sampling period in the west and the east areas and different features of water distribution. The most distinct changes were usually seen when crossing the boundary between different waters. In the region of this investigation two fronts were usually recognized—the SFZ of the Scotia Sea and the front between the WWCC and Weddell Sea waters (BAGRYANTZEV and GURETZKY, 1986).

On section 2 the contrast in the seasonal condition of plankton was obvious between the ACC waters where the succession had begun according to phytoplankton bloom (BATHMANN *et al.*, in press) and the Weddell Sea waters where the winter still lasted. According to stage composition of *Thysanoessa* larvae (Table 1) this species seems to have begun spawning in the ACC waters in the middle of August. The same period of spawning was indicated earlier (MENSHENINA, 1990a).

The SFZ in this season (early spring) is a very distinct boundary as in the summer (MAKAROV, 1982; MAKAROV and MENSHENINA, 1988). So it is obvious that the southward decrease of larval abundance and of late calyptopis portion of *Thysanoessa* (Table 1) is connected with crossing the SFZ, *i.e.* phenological differences between low-latitudinal waters and high-latitudinal ones. However, the distinct phenological boundary may be caused by ice melting (factors controlling the phenological condition must be different between ice-covered and open waters).

Spawning of *E. frigida* seems to have begun earlier than *Thysanoessa*, in the middle of July, because of younger stage composition (Table 1) and longer duration of larval development (MENSHENINA and SPIRIDONOV, in press). Similar results were given by MENSHENINA (1990a) by examing larval stage composition in the same region. Decrease in number of *E. frigida* along section 2 is not similar to that of *Thysanoessa*, because in the case of *Thysanoessa* larvae the later the stages the faster disappearance, while in *E. frigida* larvae of both the later and earlier stages disappear with constant occurrence of dominant stage, calyptopis I, in the southern direction (Table 1). It may testify that difference between the ACC and Weddell Sea waters in the case of *E. frigida* is not phenological but faunistical nature, because such stage composition means that the difference is connected with drift of larvae rather than with time difference in spawning (MENSHENINA and FEDOTOV, 1990).

The SFZ of the Scotia Sea is usually very distinct. Its distinction is connected with phenological contrasts as well as with high abundance of *E. superba* larvae as was reported earlier (MAKAROV, 1972; RAKUSA-SUSZCZEWSKI, 1984; MAKAROV and MENSHENINA, 1988). Besides, in the ACC waters were captured *E. triacantha* larvae which were absent in the south.

The difference in euphausiid larval composition between north and south of the SFZ may be strengthened by the ice margin. Existence of the ice may be one of the factors which hinder *Thysanoessa* from spawning in the Weddell Sea waters. On section 4 (October) it is obvious that the spawning of *Thysanoessa* began not earlier than the middle of September according to larval stage composition. Rather high abundance of larvae under the ice is worth noting. According to stage composition of *Thysanoessa* larvae (up to furcilia III) near the ice margin (DALY and MACAULEY, 1988) it is possible to suppose that *Thysanoessa* can spawn under the ice. However, these authors supported hypothesis that recruitment for *Thysanoessa* follows the receding ice edge. Presence of eggs and the earliest larval stages under the ice in the WWGS materials as well as advanced stage composition near the ice margin in DALY and MACAULEY (1988) make clear that spawning under the ice is a characteristic feature of this spring-spawning antarctic euphausiid. Other species of antarctic euphausiid normally do not spawn under the ice. *E. superba* larvae (furciliae IV–VI) collected under the ice had hatched during the previous summer. Occurrence of furcilia I of *Stylocheiron maximum* may be explained by drift of ovigerous female in the WWCC waters. Hatched larvae could develop during a restricted period of time without nourishment and then feed in the WWCC waters. Anyhow it is a rare case of expatriation. A similar case was the occurrence of a calyptopis I of *E. frigida* in the same place.

On section 4 *Thysanoessa* larvae were very abundant in the WWCC waters, where this species is reported to breed more intensively than in the Weddell Sea waters (MAKAROV and MENSHENINA, 1989). In the northern part of the section these larvae were more advanced than at the southern stations (Table 1) in accordance with HART's "phenological wave" which moves from north to south (HART, 1942; VORONINA, 1984).

In the summer, on the contrary, more advanced larvae occurred in the southern part than in the northern part of the same region (MAKAROV *et al.*, in press). This phenomenon was named "phenological inversion" and is connected with inversion of waters of low-latitude origin (WWCC) lying to the south and waters of high-latitude origin (the Weddell Sea waters) to the north (BAGRYANTZEV and GURETZKY, 1986).

It is noteworthy that the inversion was distinct in the summer but absent in early spring, thus showing seasonal changes. Similar seasonal changes were demonstrated and discussed near South Georgia Island (MENSHENINA, 1990b, in press). In the spring the euphausiid larval stage composition near the island did not differ in the ACC from the Weddell Sea waters. In the summer the difference was distinct. During late summer it increased and reached maximum in autumn. So, it was supposed that the leading factor at the very beginning of spawning was latitude while later the water type became more important.

The same regularities may take place in the region of this study. The presence of *E. frigida* and *S. maximum* larvae over the Maud Rise demonstrates that water currents brought plankters from low-latitude areas with the WWCC waters. So, the absence of the phenological inversion when the inversion of waters is present means that features of the plankton community are determined by latitude in early spring. In this season they are affected by water type to the least extent. Later in consequence with more distinct mixing inside a water type then between water types, the differences of plankton communities on the boundary between waters are formed (MAKAROV *et al.*, 1990).

Another situation is registered in larvae of *E. superba*. The larvae (later furciliae) obviously hatched during the previous summer. Spawning period of this species has not begun yet, but development of overwintered larvae has started: in October (section 4) the youngest larvae were furcilia VI, in September (section 2) furciliae IV, and so development after September was taking place at a common rate (IKEDA, 1984; MENSHENINA and SPIRIDONOV, in press). These larvae are associated with the SFZ waters of the Scotia Sea (section 2), as in the other seasons. It means that drift from the spawning zone (SFZ) of these larvae was rather restricted.

Thus the suggestion on summer-autumn forming of phenological differences between waters (MENSHENINA, 1990b, in press) may be considered supportable. But it is true only when parts of area with different waters are both free or both covered with ice. The margin of ice in phenological regard is rather stronger factor. The thawing of ice does not induce spawning of all spring-spawning species (*Thysanoessa* begins to spawn before ice melting). But thickeness of ice may be related with the induction of *Thysanoessa* spawning. For instance, on section 4, especially upon the Maud Rise, ice cover was weaker than on sections 1–3 (BATHMANN *et al.*, in press). Distinct difference in spawning timing in open and ice-covered areas may testify that different factors induce spawning.

In general, *Thysanoessa* begins to spawn a month and a half later under the ice than in the open water (in our case in the ACC waters), as demonstrated on section 2 which crossed the SFZ of the Scotia Sea. The ice margin usually coincides in this region with the SFZ for a long time. Seasonal melting of the ice moves there not in the south but rather in the west direction (ZWALLI *et al.*, 1983). This fact increases phenological contrast between the ACC and Weddell Sea waters at least for *Thysanoessa* larvae.

Thus in the period of investigation spawning of all euphausiids (except *E. superba*) began in the open water. *Thysanoessa* was the only species that spawned also under the ice. Phenological wave takes place under the ice as well as in the open water (according to stage composition of *Thysanoessa* larvae on section 4). Later spawning of *Thysanoessa* in the southern parts of sections 2 and 5 and on the whole sections 1 and 3 is connected with both ice cover and southern position of these localities. The WWCC waters promote in some way beginning of seasonal succession but in winter and early spring their influence is not strong enough to form phenological inversion. Phenological contrast between different waters in September was distinct only near the ice margin and may be connected with influence of the ice. According to previous investigations made in late summer after ice melting contrasts are formed in every locality where waters of different types contact with each other.

Acknowledgments

I am glad to thank Drs. U. BATHMANN (Alfred Wegener Institution, Germany), R. R. MAKAROV, V. A. SPIRIDONOV and V. V. MASLENNIKOV (VNIRO, U.S.S.R.) for collection of material and Dr. R. R. MAKAROV for discussion.

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(Received March 19, 1991; Revised manuscript received September 13, 1991)