UNDER-ICE ZOOPLANKTON OF THE WESTERN WEDDELL SEA

Larisa L. Menshenina¹ and Igor A. Melnikov²

¹All-Russian Institute of Marine Fishery and Oceanography, Krasnoselskaya 17a, Moscow 107140, Russia ²P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences, Krasikova 23, Moscow 117857, Russia

Abstract: Species composition, abundance, and seasonal dynamics of the under-ice zooplankton collected during the USA-Russia ISW-1 Expedition, from the end of February to the middle of May in 1992, in the western rim of the Weddell Sea Gyre are presented. Zooplankton were collected by a diver with plankton landing net directly from the under-ice surface (0 m layer) and at 5-m depth.

Larvae and postlarvae of Euphausia superba (Euphausiidae), Oithona similis, Stephos longipes, Paralabidocera antarctica, Pseudocyclopina belgicae, Microcalanus pigmaeus and Ctenocalanus citer (Copepoda) were most abundant in both layers. Differences in the stage composition and abundance of these species between two layers (0 and 5 m) were found. E. superba, S. longipes, P. antarctica and P. belgicae were numerous near the under-ice surface and scarce at 5 m. O. similis density was greater at 5 m than at 0 m. M. pigmaeus and C. citer were comparatively greater in number at 5 m. Seasonal changes in abundance and stage structure of euphausiids and copepods are discussed. A delay in seasonal development of E. superba, S. longipes, P. antarctica and P. belgicae comparing is shown.

1. Introduction

The primary production of sea ice flora is now believed to be one of the first trophic levels in both the Arctic and Antarctic marine ecosystems (Bunt, 1963; MEGURO et al., 1967; HORNER, 1976; SULLIVAN and PALMISANO, 1981; HOSHIAI et al., 1989; MELNIKOV, 1989a, b; IRWIN, 1990). The consumers of the sea ice flora, cryopelagic fauna, or fauna associated with the bottom ice surface (Andrijashev, 1967), represent the second trophic level of the food chain in the sea ice ecosystem and have been mainly studied in the Arctic (Melnikov and Kulikov, 1980; Gulliksen, 1984; Runge and Ingram, 1988). Cryopelagic organisms constitute links in transport of energy from the sea ice flora to sea birds and mammals living in high latitudes and to deep-sea plankton in the open ocean. Our knowledge of this important trophic level in the Antarctic sea ice ecosystem is based mainly on observations in coastal regions, e.g., Lützow-Holm Bay (Fukuchi and Tanimura, 1981; Tanimura et al., 1984; Fukuchi et al., 1985a, b; Tanimura et al., 1986); McMurdo Sound (Foster, 1987, 1989; Waghorn and Knox, 1988); Prydz Bay near Davis Station (Tucker and Burton, 1988, 1990) and in the Weddell Sea

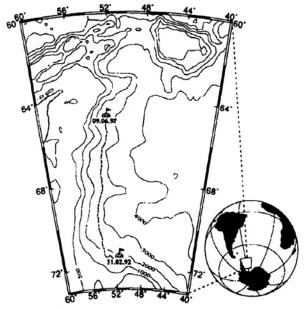
near Halley Bay, where some stations have been located rather far from the shore (KURBJEWEIT et al., 1993). Zooplankton of the Antarctic sea ice zone have also been studied (DALY and MACAULEY, 1988; HOPKINS and TORRES, 1988; MENSHENINA, 1992; BATHMANN et al., 1993; KUBJEWEIT, 1993). These studies were conducted from vessels, and materials collected mainly during a short period of observations. These materials are of great biological interest for understanding the function of the Antarctic sea ice zone.

The purpose of the present study was to examine species composition and seasonal dynamics of the under-ice zooplankton in the western Weddell Sea.

2. Materials and Methods

Investigations were carried out in the perennial ice area of the western rim of the Weddell Sea Gyre where the USA-Russia Ice Station Weddell (ISW-1) drifted between 72 and 65°S latitude and 51 and 53°W longitude from February 11 to June 9, 1992 (GORDON and LUKIN, 1992) (Fig. 1).

Cryopelagic fauna were caught by a SCUBA-diver under the perennial drifting ice at midday. Dives were carried out through a separate hydrohole made in the ice floe. Some observations were carried out under the newly formed ice in leads. In all cases, samples were collected by scraping a plankton net (mesh size $180\,\mu\text{m}$) with a 40×20 -cm-wide flat top at the opening frame for 30 m along the under-ice surface. After the tow the plankton net was closed in the water in order to avoid sampling



Flg. 1. Drifting course of the USA-Russia Ice Station Weddell-1 (ISW-1) from February 11 to June 9, 1992.

planktonic fauna. Planktonic fauna were also collected with horizontal tows at 5-m depth by the same plankton net. Other than the SCUBA sampling, animals were also collected in the hydrohole.

In the laboratory the samples were washed on nylon gauze (mesh size $180 \,\mu\text{m}$). The organisms were immediately fixed with 5% formaldehyde. Plankters were identified in a plankton counting tray. Depending on the abundance of organisms, all or 1/10, sparated by stemple pipette, were enumerated. The numbers were not standardized per volume of water but reflected the catch per sample (per set length, i.e. $30 \, \text{m}$).

3. Results

3.1. Occurrence of zooplankton under the ice

A total of 31 samples were analyzed, 15 from the under surface of the ice (0 m layer) and 5 from 5 m below it, and 11 from the water surface through the hydrohole in the ice (the hole).

The occurrence of 7 most numerous species from the 0 and 5 m layers and the hole are given in Table 1 (1 species of euphausiid and 6 of copepods). High abundances of *E. superba* were observed at 0 m and in the hole. At 5 m this species was distinctly less abundant. Abundance of copepods as a whole group at 0 and 5 m were roughly equal. Markedly lower numbers of copepods were caught in the hole. Among copepods at 0 m S. longipes predominated. At 0 m S. longipes appeared to be an order of magnitude greater than at 5 m and in the hole. But difference in number with a subdominant species (O. similis) was more marked at 0 m than in the hole. O. similis was a subdominant species at 0 m and in the hole. The number of O. similis was 4 times greater at 0 m than in the hole. At 5 m O. similis showed the highest abundance (5 times greater than at 0 m) and was the dominant species. P. belgicae was obviously present at 0 m. It was scarce at 5 m and absent in the hole. P. antarctica decreased in abundance at 5 m, compare with 0 m, and was almost absent in the hole. M. pigmaeus and C. citer were scarce in the sampling sites but M. pigmaeus showed a slight increase in abundance at 5 m.

A number of plankters were caught but they were not included in Table 1

Table 1. Mean numbers (per sample) of abundant plankton species under the ice-floe in the western Weddell Sea from late February to May 1992.

Species	Hauls from		The hole
	0 m	5 m	The noie
Euphausia superba	28.80	6.60	49.27
Stephos longipes	47.40	4.80	6.36
Paralabidocera antarctica	9.07	4.40	.73
Microcalanus pigmaeus	1.87	5.80	1.73
Ctenocalanus citer	1.93	2.20	.64
Oithona similis	23.13	96.20	5.36
Pseudocyclopina belgica	13.60	2	0

because of their low abundance or because of uncertainties about identification. A large polychaeta, Tomopteris carpenteri was caught three times at 0 m and once at 5 m. Chaethognaths, Eukrohnia hamata, Sagitta gazellae and S. marri, were usually observed at 0 m. Euphausia crystallorophias (up to 8 specimens per sample) was registered 5 times only at 0 m. Siphonophores were caught three times at 0 m and three times in the hole. Juvenile gammarid amphipods were mainly observed from 5 m, there were less than 5 specimens. In a single sample from 0 m 4 ostracods were found. Two specimens of appendicularia (Oicopleuridae) were registered at 0 m. Nine species of copepods never reached more than 10 specimens and never caught at 0 m. Among them Calanus propinquus was occurred from one to five times at all sites. Metridia gerlachei and Calanoides acutus was absent in the hole; Spinocalanus sp. (copepodites), Euchaeta sp. (copepodites), Oithona frigida and Oncaea notopus were caught only at 0 m; O. curvata was found everywhere but only once at each site; O. conifera was found in a single sample in the hole. Harpacticoids were caught mainly at 0 m in a few samples. Copepod nauplii were rare, possibly because they were small enough to pass through the mesh.

3.2. Age composition of dominant species

Age composition E. superba, S. longipes, P. antarctica, C. citer and M. pigmaeus distinctly differed among the catches from 0 m, 5 m layer and the hole (Fig. 2). The age composition of P. belgicae differed slightly between 0 and 5 m (in the hole P. belgicae was absent). Age composition of O. similis showed no differences.

E. superba was represented by furcilia V, VI and postlarvae. Furcilia V was observed only in the hole in very small number. Furcilia VI and postlarvae were numerous at all three sites. At 0 m postlarvae predominated. At 5 m the percent age of furcilia VI and postlarvae were roughly equal. In the hole furcilia VI predominated.

S. longipes was represented by all copepodite stages and adults at 0 m layer. Copepodites II, III, IV (CII, CIII, CIV) and adults were numerous while CI and CV were scarce. At 0 m and at 5 m CIII predominated and CII was subdominant. At 5 m the percent of CII was more than at 0 m. In the hole adults were numerous while all copepodite stages were scarce.

In P. antarctica, CIV predominated at 0 m, at 5 m CV predominated and in the hole adults were dominant. The percent age of non-dominant stages was low everywhere.

M. pigmaeus CV and adults were represent at 0 m. CV slightly predominated. At 5 m CIV, CV and adults were caught. In the hole CIII and CV, roughly equal in numbers, were present.

C. citer showed increase of share of later copepodite stages (CIV was dominant) at 5 m compared with 0 m and in the hole. At 0 m and 5 m layer CII—CV were caught while in the hole only CII and CIII were present. Adults were absent in all samples.

Age composition of *P. belgicae* was similar between 0 and 5 m. The population consisted of CIV, CV and adults. Juveniles prevailed in both layers but increased at

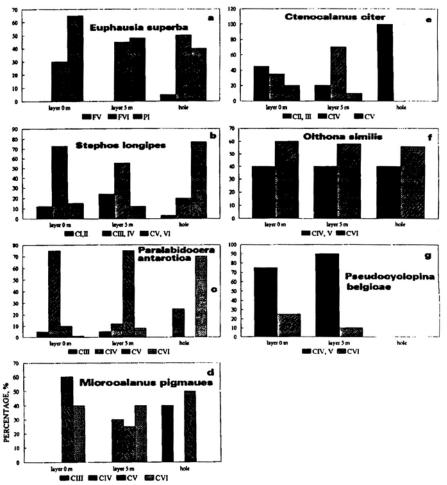


Fig. 2. Stage composition of most abundant plankton species under-surface of the ice, at 5-m depth from the bottom of the ice and in the hole in the ice.

5 m compared with 0 m.

Age composition of O. similis (CIV, CV and adults were caught and adults predominated) was identical at 0 and 5 m and in the hole.

3.3. Seasonal dynamics of dominant species

3.3.1. Seasonal changes of abundance

Samples collected at 0 m were used for seasonal dynamics studies mainly. At 5 m and in the hole O. similis (at 5 m) and E. superba (in the hole) were the only species to yield adequate numbers for enumeration and analysis. Despite the increase in abundance of M. pigmaeus and C. citer at 5 m compared to 0 m, their

absence in three (M. pigmaeus) or four (C. citer) samples at 5 m made it impossible to estimate temporal changes of these species there.

The abundance of *E. superba* at 0 m was highest at the end of February and the beginning of May (Fig. 3). From the middle of May to the middle of April it was comparatively low. At the end of April a rapid increase of *E. superba* abundance was registered. In the hole the greatest abundance took place at the end of May (May 19) and beginning of April (April 9) (Fig. 4). For *E. superba* distribution (even for larvae) patchiness is very characteristic (MARR, 1962). The presence of four maxima (two in the hole and two at 0 m) at different times revealed that

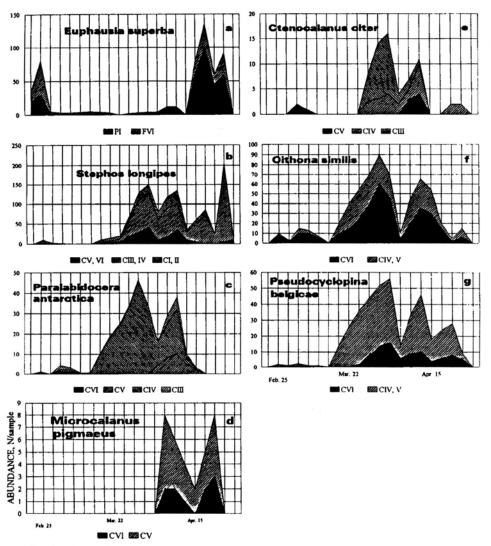


Fig. 3. Seasonal changes in abundances and stage compositions of most abundant plankton species under-surface (0 m layer) of the ice (number per sample).

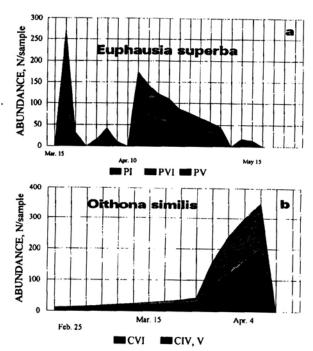


Fig. 4. Seasonal changes in abundances and stage compositions of Euphausia superba in the hole in the ice and Oithona similis at 5-m depth from the bottom of the ice.

changes in abundance of this species were accidental. Age composition of E, superba changed both at 0 m under the ice and in on hole. The percent composition of postlarvae increased with time. At 0 m the increasing was more noticeable (Figs. 3 and 4).

Seasonal dynamics in all the copepod species abundance was seems to be similar. All the species were absent (M. pigmaeus) or scarce (C. citer, P. belgicae, S. longipes, P. antarctica and O. similis) from the end of February to the end of March or beginning of April. At the end of March (P. antarctica, O. similis, P. belgicae) or beginning of April (S. longipes, M. pigmaeus, C. citer) a rapid increase of abundance took place (Fig. 2). P. antarctica, C. citer, O. similis and P. belgicae showed distinct decreases in abundance in late April. S. longipes and M. pigmaeus reached their highest densities at the end of April.

Temporal dynamics of O. similis at 5 m was seems to be similar to that at 0 m (Figs. 2 and 4). Appearance of S. longipes in the hole (from 18 of March to 9 of April) and at 5 m (April 6) coincided with a period of greater abundance at 0 m (Fig. 3). At 5 m (March 24 and April 6) and in the hole (March 18, 19 and 25, April 2) several specimens of P. antarctica were caught when the abundance of this species at the under surface of ice was the greatest (Fig. 3). The presence of C. citer and M. pigmaeus at 5 m (April 6) and in the hole (April 9) took place simultaneously with increase of these species numbers at 0 m (Fig. 3).

3.3.2. Seasonal changes of stage composition

Stage composition temporal changes were noted in all the species. They were not distinct in *M. pigmaeus*. This species was represented at 0 m by CV and adults. The percent of adults increased during April from 25% to 50% (Fig. 3). *P. belgicae* was characterized by absence of adults toward the beginning of April. Then their percentage increased and reached 67% at the end of April (Fig. 3). In *O. similis* copepodites were scarce from the end February to the middle of May. After the middle of May they reached roughly 50% and did not change their percentage. During April, *C. citer* developed gradually from earlier stage of CIII to later stages of CIV and CV. No adults of *C. citer* appeared even in the latest samples (Fig. 3).

Only early (CI and CII) copepodites of S. longipes were observed toward the end of March when this species was scarce. Then adults and all the other copepodite stages (CIII, CIV and a few specimens of CV) appeared at the beginning of April. CIII predominated during April. The percentage composition of adults and CI and CII gradually decreased toward the end of April. At the end of April almost all specimens of S. longipes were CIII.

P. antarctica was represented by CIII, CIV and adults from the end of February to the middle of May, while their abundances were low. CIII predominated. When abundance increased, adults disappeared and CIV became the dominant stage. At the beginning of April CV appeared and then CIV and CV became dominant during April.

4. Discussion

Calanoides acutus, Calanus propinquus, Metridia gerlachei, Oithona similis, Oncaea curvata, Microcalanus pigmaeus can be considered as oceanic (TUCKER and BURTON, 1990; KURBJEWEIT, 1993). Paralabidocera antarctica can be classified as an inshore resident (TUCKER and BURTON, 1990) as well as Pseudocyclopina belgicae (WAGHORN and KNOX, 1988). Stephos longipes can be considered as both inshore (TUCKER and BURTON, 1990) and typical oceanic species (KURBJEWEIT, 1993). Euphausia superba is an ice-neritic species (BECKLEMISHEV, 1958) and E. crystallorophias is a typical neritic species (VORONINA, 1984).

E. superba does not or poorly breeds in high-latitude waters (MAKAROV and MENSHENINA, 1989) in the region of the present investigation. Early larvae of E. crystallorophias were always found in the shelf waters not far from the coast (MAKAROV and MENSHENINA, 1989).

Furcilia VI and postlarvae of E. superba and E. crystallorophias obviously hatched during the previous summer according to the spawning period (MENSHENINA, 1990) and developmental rate of larvae (IKEDA, 1984; MENSHENINA and SPIRIDONOV, 1991). Hence these specimens must have been hatched not far from the coast of Queen Maud Land from where the ice-floe drifted (A. PROVORKIN, personal communication) (both species breed off Queen Maud Land (MAKAROV and MENSHENINA, 1992)). As in the water column under the ice-floe, no euphausiid larvae were caught (E. KOLOSOVA, personal communication). It may be concluded

that the present data confirm that these two species do not breed there.

Overwintering stages of E. superba are furciliae V and VI (DALY and MACAULAY, 1988) or even furcilia IV (MENSHENINA, 1992). Further development of overwintered larvae was observed in 1989 in the eastern part of the Weddell Sea. In October the earliest stage was furcilia VI (MENSHENINA, 1992). Supposing a common developmental rate of larvae, one could expect to find only postlarvae of E. superba from the end of February to the middle of May. Nevertheless, even in the middle of May furcilia VI was almost as abundant as postlarvae. Hence the notable delay of spring, a start of development of overwintered stages or slowing of development of E. superba larvae took place.

E. crystallorophias was represented by the same stages, but sparse information on later furciliae of this species (MAKAROV et al., 1990) does not permit numerical estimates.

S. longipes, M. pigmaeus, M. gerlachei and C. propinquus are considered to be dominant copepod species in the Weddell Sea (Kurjeweit, 1993), as well as O. similis, C. citer and Oncaea curvata (Fransz, 1988). Among them only S. longipes and O. similis were numerous at 0 m; M. pigmaeus and C. citer were characterized with low dense and O. curvata and M. gerlachei were almost absent at 0 m. At 5 m abundances of all these species except S. longipes were higher than at 0 m. Among these species only S. longipes inhabits sea ice during its life cycle (Kurjeweit, 1993; Schnack-Schiel and Mizdalski, 1994; Schnack et al., 1985).

Comparing periods of maximum abundance and changes of stage composition of S. longipes with the privious studies (KURBJEWEIT, 1993; KURBJEWEIT et al., 1993: TUCKER and BURTON, 1990) some distinctive features may be found. Highest abundances of S. longipes near Davis station (the Prydz Bay) were observed from February to April. Increase of abundance started in January and was rapid (TUCKER and BURTON, 1990). Rapid increase of abundance at ISW was observed at the beginning of April. At the end of April there were no signs of any decrease of S. longipes abundance. A preliminary picture of the life cycle of S. longipes was drawn by Kurbjwewit et al. (1993) using data collected off the east coast of the Weddell Sea. They described the life cycle as "at the end of December or beginning of January, young copepodite stages leave the brine channels inside the ice floes to feed in the upper under-ice water layer". Rapid increase in number of copepodites of this species in January described by TUCKER and BURTON (1990) agreed with their scheme. At ISW-1 appearance of numerous early copepodite stages (CII-CIII), however, took place at the beginning of April. Then, early copepodite stages develop to CIV and CV by the end of March and then migrate to greater depth as observed by Kurbjeweit et al. (1993). At ISW-1 at the end of March S. longipes in the upper water column (5 m) was still absent, appearing from the beginning of April at CII and CIII. At 0 m up to the end of April CIII distinctly predominated. Hence, the phenological state of the S. longipes population at ISW-1 was earlier than that presented by KURBJEWEIT et al. (1993) for March. Differences between data on seasonal changes in number of S. longipes in Prydz Bay, the scheme of S. longipes life cycle observed at ISW-1, showed that a delay of two to three months took place

in seasonal development of S. longipes at ISW-1 compared with other localities.

O. similis, M. pigmaeus and C. citer abundances and stage composition changed during the period. But all of them mainly inhabit the water column (SCHNACK et al., 1985; SCHNACK-SCHIEL and MIZDALSKI, 1994). Hence the sampling method used was insufficient to estimate abundances and stage compositions of these species. So it is impossible to compare the seasonal dynamics of these species with those in other localities.

P. antarctica is a species whose life cycle is completed within ice (KUBJEWEIT et al., 1993). It is typically observed in inshore regions and is considered to be endemic to coastal species (FUKUCHI et al., 1985). It was collected under a drifting ice-floe far from a coast, but its abundance appeared to be three orders of magnitude less than in inshore regions. In Lützow-Holm Bay P. antarctica occurred in the highest concentration between December and February and disappeared in March (TANIMURA et al., 1984). In catches of ISW-1 its highest abundance was observed from the middle of May to the middle of April. Then P. antarctica disappeared from catches. Similar stage composition was observed in Lützow-Holm Bay in the middle of December (TANIMURA et al., 1984) and at ISW-1 in late March and early April (CIV predominated). Thus it may be suggested that a delay in seasonal development of P. antarctica under the ice-floes in the western part of the Weddell Sea compared with the inshore region. Seasonal changes of P. belgicae, typical inshore species (WAGHORN and KNOX, 1988) from November to January were described in McMurdo Sound (WAGHORN and KNOX, 1988). It was most numerous there from late November to the middle of December. In late November CII predominated. In the middle of December CIV became dominant. At ISW-1 this species was most abundant from the end of March to the middle of April. Early copepodite stages (CI-CIII) were absent. Adults were less abundant than CIV and CV up to the middle of April. Then adults prevailed. If this species really has a short spawning period and overwintering stages were late copepodites or adults (WAGHORN and KNOX, 1988), the phase of seasonal development observed in March at ISW-1 may be compared with that observed in the middle of December in McMurdo Sound. Thus the possible delay in seasonal development of this species is about three months.

Temporal changes of abundance and stage composition of *E. superba*, *S. longipes*, *P. antarctica* and *P. belgicae* were compared with those in other regions. For all the species seasonal development was delayed from two to three months. It seems that the reasons for the delay for *E. superba* may differ from that for three copepod species. Seasonal changes of *S. longipes*, *P. antarctica* and *P. belgicae* were studied earlier in the inshore regions (Tanimura *et al.*, 1984; Waghorn and Knox, 1988; Tucker and Burton, 1990; Kurbjeweit *et al.*, 1993). In the inshore region the so-called "oasis effect" was found. In regions near a coast seasonal development of plankton community is more rapid compared with the oceanic region to the north (Makarov *et al.*, 1982; Vladimirskaya *et al.*, 1985; Vladymirskaya *et al.*, 1988). The ice-floe with the ISW-1 drifted during field deployment in the oceanic region. The delays in seasonal development of three

copepod species may mark slow rate of seasonal development of the whole zooplankton community in the ocean region compared with inshore regions as supposed in the "oasis effect" conception. An earlier "oasis effect" was shown for epipelagic species (MAKAROV et al., 1982; VLADMIRSKAYA et al., 1988). It obviously influences species closely associated with sea ice.

The beginning of development of overwintered *E. superba* larvae was studied in lower latitude regions (the northern part of the Weddell Sea) or in the eastern part of the Weddell Sea (DALY and MACAULEY, 1988; MENSHENINA, 1992) where modified waters of the Antarctic Circumpolar Current may intrude (BAGRYANTZEV and GURETZKY, 1986). In these warmer regions biological spring must begin earlier. So the delay in the development of overwintered stages of *E. superba* may mark a difficult to achieve general seasonal developmental rate in the cold waters in the western part of the Weddell Sea.

Acknowledgments

This work was supported by the Grant #94-5-16707 of the Russian Foundation for Basic Research.

References

- ANDRIJASHEV, A. P. (1967): Mikroflora i fauna associirovannaja s Antarkticheskim pripaem (Microflora and fauna associated with the Antarctic fast ice). Zool. Zh. (Zool. J.), 44, 1585-1594.
- BAGRYANTZEV, N. V. and GURETZKY, V. V. (1986): O perenose tepla v antarcticheskoy zone Jujnogo okeana (On warm transport in the Antarctic Zone of the Southern Ocean). Meteorol. Gidrol. (Meteorol. Hydrol.), 1, 62-69.
- BATHMANN, U. V., MAKAROV, R. R., SPIRIDONOV, V. A. and ROHARDT, G. (1993): Winter distribution and overwintering strategies of the Antarctic copepod species Calanoides acutus, Rhincalanus gigas and Calanus propinquus (Crustacea, alanoida) in the Weddell Sea. Polar Biol., 13, 333-346.
- BECKLEMISHEV, K. V. (1958): Biogeographicheskaya priroda nekotoryh vidov antarkticheskogo zooplanktona (Biogeographic nature of some species of Antarctic zooplankton). Dokl. Akad. Nauk SSSR (Rep. Acad. Sci. USSR), 120, 507-509.
- BUNT, J. S. (1963): Diatoms of Antarctic sea ice as agents of primary production. Nature, 199, 1255-1257.
- DALY, K. L. and MACAULEY, M. C. (1988): Abundance and distribution of krill in the ice edge zone of the Weddell Sea, austral spring 1983. Deep-Sea Res., 35, 21-41.
- FOSTER, B. A. (1987): Composition and abundance of zooplankton under the spring sea-ice of McMurdo Sound, Antarctica. Polar Biol., 8, 41-48.
- FOSTER, B. A. (1989): Time and depth comparisons of sub-ice zooplankton in McMurdo Sound, Antarctica. Polar Biol., 9, 431-435.
- Fransz, H. G. (1988): Vernal abundance, structure and development of epipelagic copepod populations of the eastern Weddell Sea (Antarctica). Polar Biol., 9, 107-114.
- FUKUCHI, M. and TANIMURA A. (1981): A preliminary note on the occurrence of copepods under sea ice near Syowa Station, Antarctica. Mem. Natl Inst. Polar Res., Ser. E (Biol. Med. Sci), 34, 37-43.
- FUKUCHI, M., TANIMURA, A. and OHTSUKA H. (1985a): Marine biological and oceanographical investigatopns in Lützow-Holm Bay, Antarctica. Antarctic Nutrient Cycles and Food Webs,

- ed. by W. R. SIEGFRIED et al. Berlin, Springer, 52-59.
- FUKUCHI, M., TANIMURA, A. and OHTSUKA, H. (1985b): Zooplankton community condition under sea ice near Syowa Station, Antarctica. Bull. Mar. Sci., 37, 518-528.
- GORDON, A. L. and LUKIN, V. V. (1992): Ice Station Weddell #1. Antarct. J. U. S., 27, 97-99.
- GULLIKSEN, B. (1984): Under-ice fauna from Svalbard waters. Sarsia, 69, 17-23.
- HORNER, R. A. (1976): Sea ice organisms. Oceanogr. Mar. Biol. Annu. Rev., 14, 167-182.
- HOSHIAI, T., TANIMURA, A. and WATANABE, K. (1989): Ice algae as a food of an Antarctic ice-associated copepod, *Paralabidocera antarctica*. Proc. NIRP Symp. Polar. Biol., 2, 61-64.
- HOPKINS, T. L. and TORRES, J. J. (1988): The zooplankton community in the vicinity of the ice edge, Western Weddell Sea, March 1986. Polar Biol., 9, 79-87.
- IKEDA, T. (1984): Development of the larvae of Antarctic krill (Euphausia superba Dana) observed in the laboratory. J. Exped. Mar. Biol. Ecol., 75, 107-117.
- IRWIN, B. D. (1990): Primary production of ice algae on a seasonally-ice-covered, continental shelf. Polar Biol., 11, 179-184.
- KURBJEWEIT, F. (1993): Reproduktion und lebenszyklen dominanter copepodenarten aus dem Weddellmeer, Antarktis. Ber. Polarforsch., 129, 35-61.
- KURBJEWEIT, F., GRADINGER, R. and WEISSENBERGER, J. (1993): The life cycle of Stephos longipes—an example for cryopelagic coupling in the Weddell Sea (Antarctica). Mar. Ecol. Prog. Ser., 98, 255-262.
- MAKAROV R. R. and MENSHENINA, L. L. (1989): Obshie cherti raspredelenia lichinok evphausiid v vodah Antarctiki (On the investigation of euphausiid larvae in the Antarctic waters). Okeanologia (Oceanology), 29, 825-831.
- MAKAROV, R. R. and MENSHENINA, L. L. (1992): Larvae of euphausiids off Queen Maud Land. Polar Biol., 11, 515-523.
- MAKAROV, R. R., MASLENNIKOV, V. V., MOVCHAN, O. A. and SOLYANKIN, E. V. (1982): Okeanographicheskie uslovia i regionalnie osobennosti sezonnih sukczessij v planktone pribrezjgnih vod Antarcticheskogo poluostrova (Oceanography conditions and regional peculiarities of seasonal succession on plankton of coastal waters off the Antarctic Peninsula). Antarctica (Antarctic), 21, 101-107.
- MAKAROV, R. R., MENSHENINA, L. L., TIMONIN, V. P. and SHURUNOV, N. A. (1990): Ekologya lichinok i razmnojenie evphausiid v more Rossa (Larval ecology and spawning of euphausiids in the Ross Sea). Biol. Mor. (Mar. Biol.), 1990(3), 38-45.
- MARR, J. W. S. (1962): The natural history and geography of the Antarctic krill (Euphausia superba Dana). Discovery Rep., 32, 33-464.
- MEGURO, H., ITO, K. and FUKUSHIMA, H. (1967): Ice flora (bottom type): A mechanisms of primary production in polar seas and the growth of diatoms in sea ice. Arctic, 20, 114-133.
- MELNIKOV, I. A. (1989a): Ecology of Arctic ocean Cryopelagic fauna. The Arctic Seas: Climatology, Oceanography, Geology, and Biology, ed. by Y. HERMAN. New York, Van Nostrand Reinhold, 235–255.
- MELNIKOV, I. A. (1989b): Ecosystema Arkticheskogo Morskogo Lda (Arctic Sea Ice Ecosystem).

 Moscow, P.P. Shirshov Institute of Oceanology, 191.
- MELNIKOV, I. A. and KULIKOV, A. S. (1980): Cryopelagicheskaja fauna Centralnogo Arcticheskogo basseina (Cryopelagic fauna of the Central Arctic Ocean). Biologija Centralnogo Arkticheskogo Basseina (Biology of the Central Arctic Ocean), Moscow, Nauka, 97-111.
- MENSHENINA, L. L. (1990): Opredelenie nerestovogo perioda antarkticheskih euphausiid (Determination of antarctic euphausiid spawning period). Okeanologia (Oceanology), 30, 486-491.
- MENSHENINA, L. L. (1992): Distribution of euphausiid larvae in the Weddell Gyre in September October 1989. Proc. NIPR Symp. Polar Biol., 5, 44-54.
- MENSHENINA, L. L. and SPIRIDONOV, V. A. (1991): Sroki razvitia lichinok antarkticheskih evphausiid (po polevim dannim) (The developmental rate of the Antarctic euphausiids (by the field data)). Okeanologia (Oceanology), 31, 621-627.
- RUNGE, J. A. and INGRAM, R. G. (1988): Underice grazing by planktonic, calanoid copepods in

- relation to a bloom of ice microalgae in southeastern Hudson Bay. Limnol. Oceanogr., 33, 280-286.
- SCHNACK, S. B., MARSCHALL, S. and MIZDALSKI, E. (1985): On the distribution of copepods and larvae of Euphausia superba in Antarctic waters during February 1982. Meeresforschung, 30, 251-263.
- SCHNACK-SCHIEL, S. B. and MIZDALSKI, E. (1994): Seasonal variations in distribution and population structure of *Microcalanus pygmaeus* and *Ctenocalanus citer* (Copepoda: Calanoida) in the eastern Weddell Sea, Antarctica. Mar. Biol. (in press).
- Sullivan, C. W. and Palmisano, A. C. (1981): Sea ice microbial communities in McMurdo Sound, Antarctica. Antarct. J. U. S., 16, 126-127.
- TANIMURA, A., FUKUCHI, M. and OHTSUKA, H. (1984): Occurrence and age composition of Paralabidocera antarctica (Calanoida, Copepoda) under the fast ice near Syowa Station, Antarctica. Mem. Natl Inst. Polar Res., Spec. Issue, 32, 81-86.
- TANIMURA, A., FUKUCHI, M. and HOSHIAI, T. (1986): Seasonal change in the abundance of zooplankton and species composition of copepods in the ice-covered sea near Syowa Station, Antarctica. Mem. Natl Inst. Polar Res., Spec. Issue, 40, 212-220.
- Tucker, M. J. and Burton, H. R. (1988): The inshore marine ecosystem off the Vestfold Hills, Antarctica. Hydrobiologia, 165, 129-139.
- Tucker, M. J. and Burton, H. R. (1990): Seasonal and spatial variations in the zooplankton community of an eastern Antarctic coastal location. Polar Biol., 10, 571-579.
- VLADIMIRSKAYA, E. V., POLONSKY V. E., POPKOV V. V. and SPIRIDONOV, V. A. (1985): Raspredelenie i sezonnye osobennosti planktona v sviazi s gidrologicheskimi usloviami v severnoj chasti moria Amundsena oseniu 1982 g. (Distribution and seasonal peculiarities of the plankton in relation to the hydrological conditions in the northern Amundsen Sea (austral autumn 1982). Antarctika (Antarctic), 24, 143-157.
- VLADYMIRSKAYA, E. V., MAKAROV, R. R. and SOLYANKIN E. V. (1988): Ekologia razmnojennia massovyh vidov copepod v vysokoshirotnih rajonah Antarktiki (more Lazareva) (Spawning ecology of dominant copepod species in high-latitude regions of Antarctic (the Lasarev Sea). Antarktica (Antarctic), 27, 142-159.
- VORONINA, N. M. (1984): Pelagicheskije Ecosistemy Uzjnogo Okeana (Pelagic Ecosystems of the Southern Ocean). Moscow, Nauka, 296 p.
- WAGHORN, E. J. and KNOX, G. A. (1988): Summer tide-crack zooplankton at White Island, McMurdo Sound, Antarctica. N. Z. J. Mar. Freshw. Res., 22, 577-582.

(Received April 25, 1994; Revised manuscript received September 20, 1994)