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Zooplankton life under the perennial Antarctic Sea ice

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Abstract. Zooplankton was collected during the drift on the USA-Russia Ice Station Weddell 1 in the western Weddell Sea. Stratified tows up to 1,000 m depths were performed under perennial ice at a distance of ca. 300 km from the marginal ice zone from March to May 1992. Seasonal abundance, developmental stage composition and vertical distribution in populations of large dominant calanoid copepod species were studied. The abundance of *Calanoides acutus* changed inconspicuously and averaged 1,260 ind. m^{-2}; its developmental stage composition was characterised by the dominance of copepodites V (CV) and hardly changed in the course of observations. *Calanus propinquus* was at most stations in fairly low abundance and was represented by CV and adults; at the latest stations, it was not found. *Rhincalanus gigas* was also scarce; III-IV stages were present, but the first of them only at the southernmost stations. In contrast to this species, in the relatively abundant population of *Metridia gerlachei* (1,370 ind. m^{-2} on average), a new generation was observed. There was a clear deepening of the median depth of occurrence of the above three species from March to early May, while in late May a shifting to upper layers was observed which remained unexplained. The data obtained were compared to the data collected in the ice-open eastern part of the Weddell Sea in the corresponding season. It can be seen that the differences in populations dynamics of the four species under the perennial ice depends on their trophic mode, i.e. capability to store lipid reserves in summer and/or to feed in winter, and with food spectra.

Introduction

Sea ice is of paramount importance for the Antarctic pelagic ecosystem. Its coverage is immense: from ca. 4 million km^2 in summer, it increases to nearly 20 million km^2 in winter, deeply impacting the pattern and timing of the production processes. The under-ice studies of zooplankton were conducted either in pack ice (Stepien *1982*; Hopkins and Torres *1988*) or under fast ice near coastal stations

(Fukuchi et al. *1985*; Foster *1987*, *1989*; Knox et al. *1996*). On the basis of these data, a list of zooplankton species occurring under ice was presented (Hopkins and Torres *1988*) and seasonal dynamics of abundance of particular taxa near the stations Syowa (Fukuchi et al. *1985*; Tanimura and Otsuka 1985; Tanimura et al. *1986*) and McMurdo (Foster *1987, 1989*; Knox et al. *1996*) described. Little is known, however, about the processes in zooplankton taking place under perennial ice far distant from both the coastal ice and the seasonal ice edge.

Zooplankton samples collected under the ice at Ice Station Weddell 1 (ISW, 1) which drifted in the vast ice mass in the western Weddell Sea, demonstrated that similar to Antarctic open waters, in this part of the pelagial, copepods are a dominant group, composing 62% of numerical abundance and 63% of biomass of mesozooplankton. The proportion of dominant species appears, however, to be different in these two biotopes (Voronina and Kolosova, *in press*). The present paper deals in detail with the dynamics of abundance, developmental stage composition and vertical distribution in four species which usually dominate in the pelagic community in the Antarctic, i.e. *Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas* and *Metridia gerlachei*.

Materials and methods

Zooplankton was collected at Ice Station Weddell 1 from March to May 1992 at a distance of ca. 300 km from the ice edge at eight stations (sts. 1, 2, 4-9) in the 0- to 1,000-m layer. Positions of stations are shown in Fig. 1. Vertical catches by Juday net (mouth opening 37 cm, filtering part opening 50 cm, 176 µm mesh size) were performed through the hole in the ice field with a hauling speed of 0.5 m s^{-1} in the following layers: 0-50, 50-250, 250-450 and 450-1,000 m. The first two layers are referred to as to Antarctic Surface Water; the third one corresponds to the thermo- and pycnocline layer, while the fourth layer lies within the upper Deep Water mass. The ice drift velocity during towing was less than 100 m h^{-1}. Ice thickness amounted to ca. 2 m; the thickness of snow on ice was ca. 0.5 m.

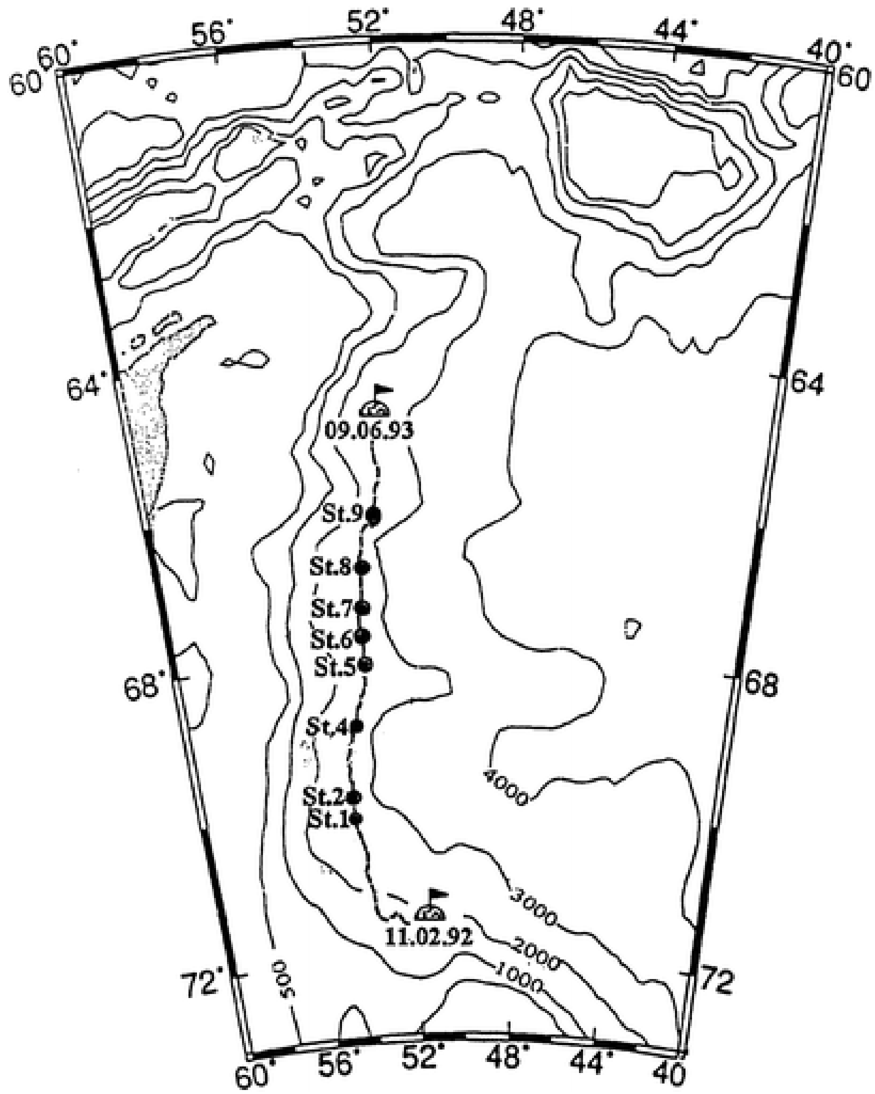

Fig. 1. Stations investigated during Ice Station Weddell 1

Plankton samples were preserved in 5% formalin. All copepodite stages of *Calanoides acutus, Calanus propinquus, R. gigas* and *M. gerlachei* were identified and counted, and the total length of these copepods was measured in entire samples. For comparison, zooplankton samples from three stations collected during the cruise of R/V *Dmitry Mendeleev* in the ice-open Weddell Sea waters at 62°S, 15°W between 20 February and 2 April 1989 were used (Voronina and Kolosova 1993). This material was collected by the same net model but down to 1,250 or 1,500 m depth. In the present study, only the data from the upper 1,000 m were used.

Results

Calanoides acutus

Total abundance of this species showed little variation during the period of observation and ranged between 890 and 1,660 ind. m^{-2}, 1,260 ind. m^{-2} on average. The maximum abundance recorded on 10 April only slightly exceeded the average value (Fig. 2). At all stations, the developmental stage composition was characterised by the dominance of copepodite V (CV), amounting to 66-88% of the population. Next in abundance were adult females (12-18%). The maximum abundance of copepodite I (CI) observed in March was only 6% of the population; copepodites II-IV (CII-CIV) were more scanty. The increase of the CII-CIII fraction, which could correspond to the decrease of the CI fraction, was not observed later in the season.

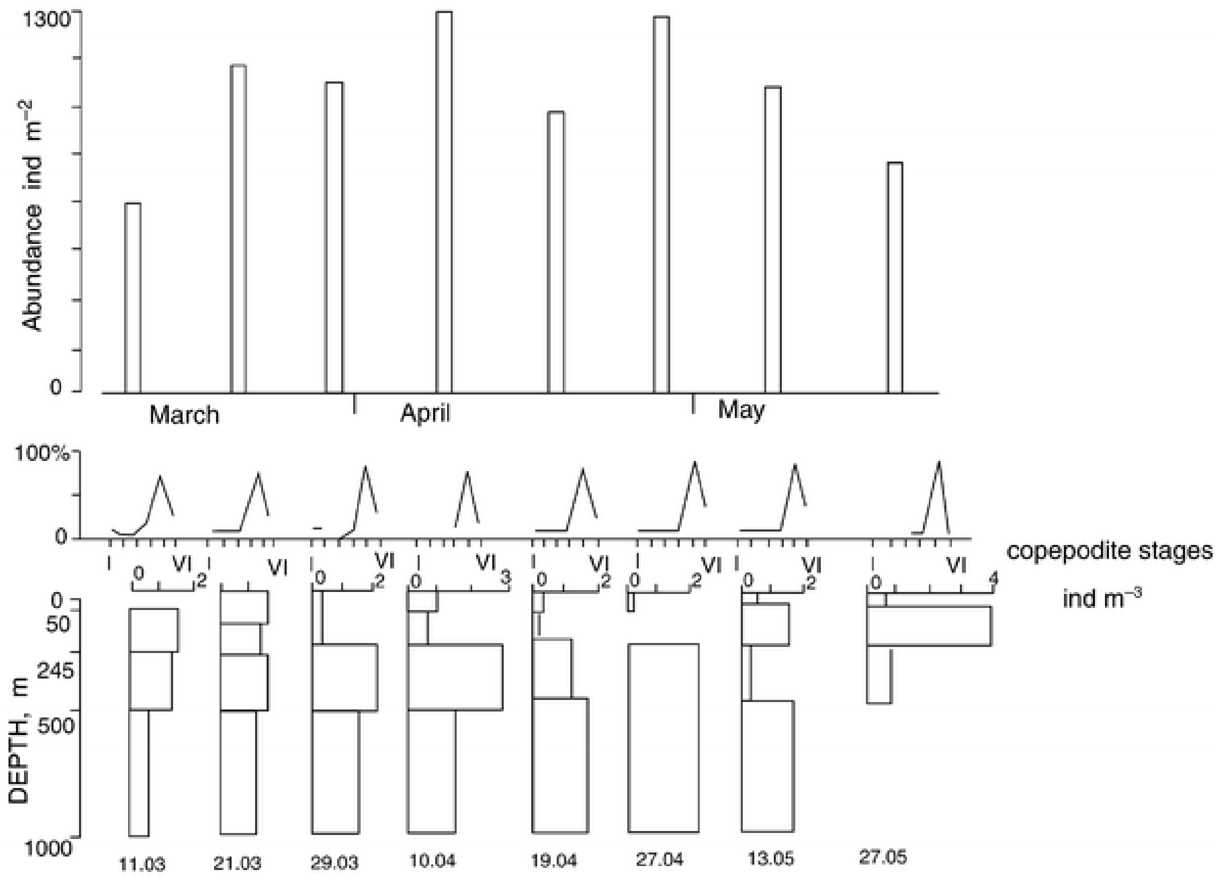

Fig. 2. Dynamics of abundance (ind. m^{-2} in 0- to 1,000-m layer), developmental stage composition (%) and vertical distribution (ind. m^{-3}) of *Calanoides acutus* under perennial ice

The changes of the vertical distribution from March to the first ten days of April were characterised by a shift in the maximum abundance from the surface water to the pycnocline layer, and later to greater depth. However in May, the concentration of copepods in the surface layers increased, again showing the vertical distribution pattern typical for summer.

Calanus propinquus

The population of *Calanus propinquus* was very scarce under ice with the exception of st. 1, where the total abundance exceeded 300 ind. m^{-2} while the concentration in the upper layer was 3 ind. m^{-3} (Fig. 3). At other stations, the abundance of this copepod was ca. 10 ind. m^{-2}; adult females and, in some cases, CV dominated the population. In April the population occurs at maximum depth, while in May *Calanus propinquus* was found only in the surface layers. The median depth of occurrence changed from 25 m at st. 1 to 725 m at st. 6 and back to 25 m at st.8.

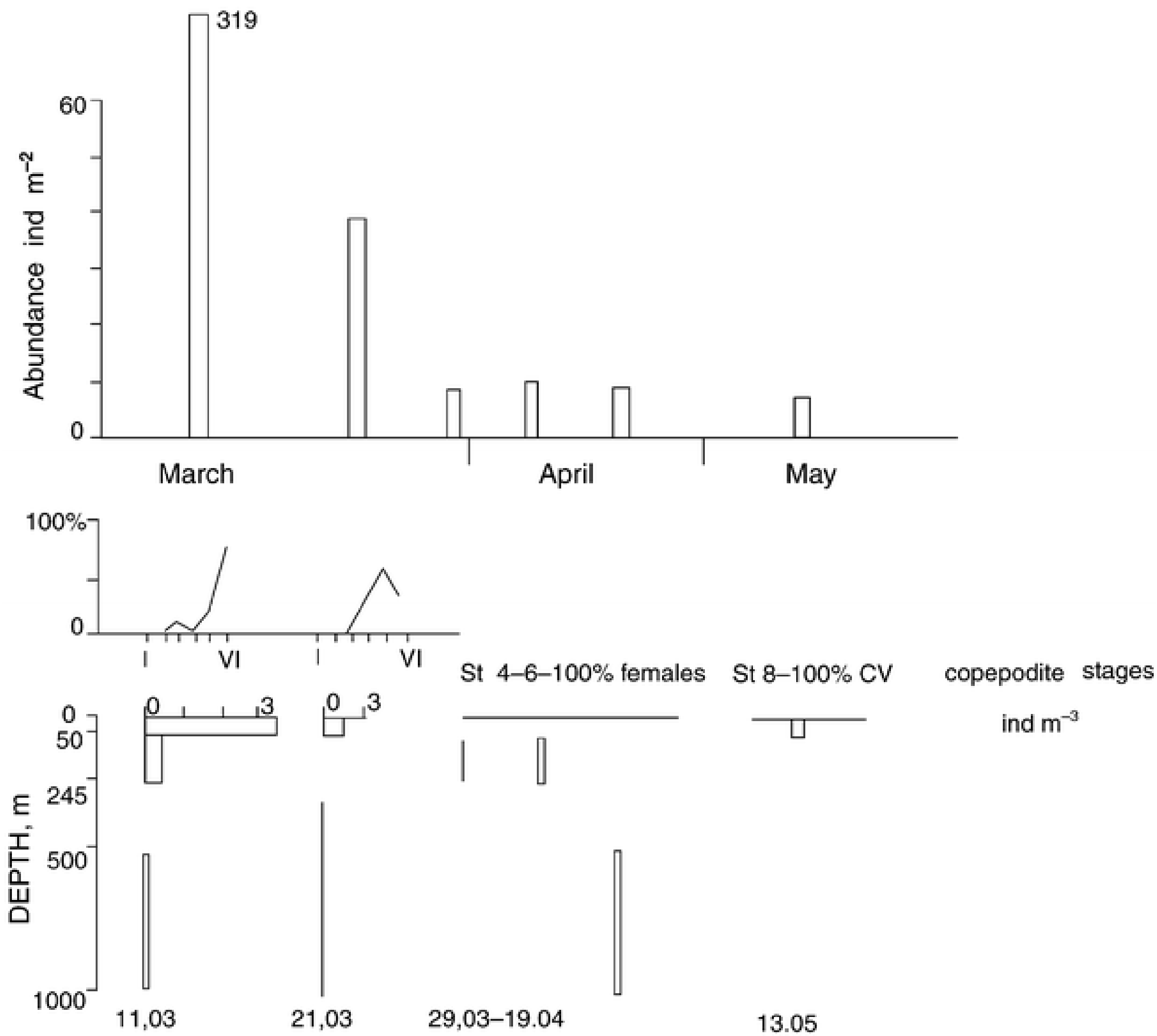

Fig. 3. Dynamics of abundance (ind. m^{-2} in 0- to 1,000-m layer), developmental stage composition (%) and vertical distribution (ind. m^{-3}) of *Calanus propinquus* under perennial ice

Rhincalanus gigas

The abundance of *R. gigas* was low and exceeded 100 ind. m^{-2} at only two stations. The population was usually dominated by either CV or CVI; young copepodites were found only at two stations (Fig. 4). In vertical distribution, increased concentration of this species was observed above 450 m, but as a rule it did not reach the surface layers; at st. 6 *R. gigas* was found only in the lowermost towed horizon, while later it occurred in the pycnocline and again in the surface water mass. The median depth of species occurrence changed from 275-400 m at the beginning of observations to 725-542 m, and finally back to 300-400 m (Fig. 4).

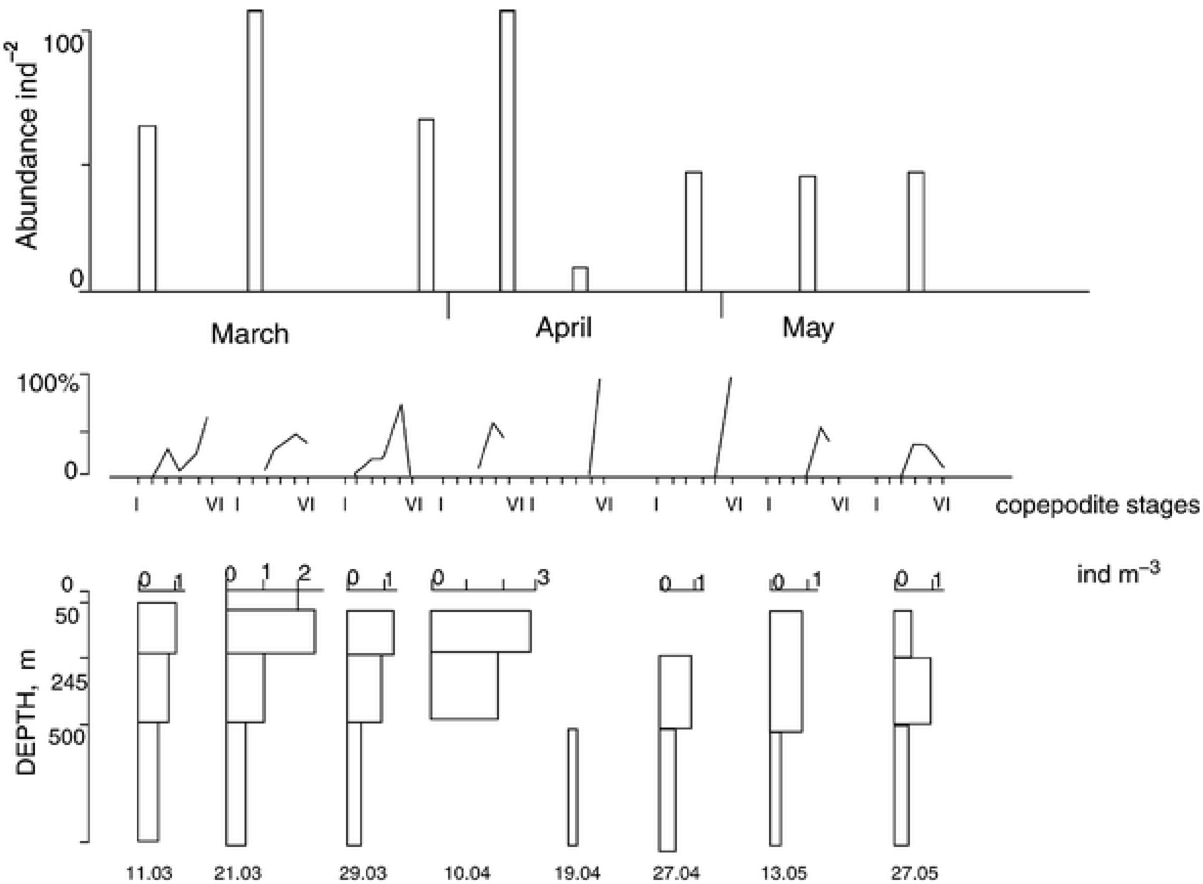

Fig. 4. Dynamics of abundance (ind. m^{-2} in 0- to 1,000-m layer), developmental stage composition (%) and vertical distribution (ind. m^{-3}) of *Rhincalanus gigas* under perennial ice

Metridia gerlachei

In *M. gerlachei*, the under-ice abundance varied from 500 ind. m^{-2} to 4,100 ind. m^{-2}. The maximum abundance was at st. 1; at the other stations irregular variation occurred. The copepodite stage composition was characterised by a succession from the CIII-CIV dominance in early March to the dominance of younger copepodites and adults in late March and April, then to increasing stages and proportion of the former cohort and decreasing fraction of the latter (Fig. 5). The development of a new generation is, therefore, obvious. Vertical distribution was characterised by the maximum in Antarctic Surface water, which was most clearly expressed in the upper layer at stations where the youngest copepodites dominated (sts. 6-8); at sts. 8 and (especially) 9 at the end of the observation period, the concentration of *M. gerlachei* in the deep layers increased. The median depth of occurrence, which lay above 250 m at most stations, was as deep as 614 m at the last station.

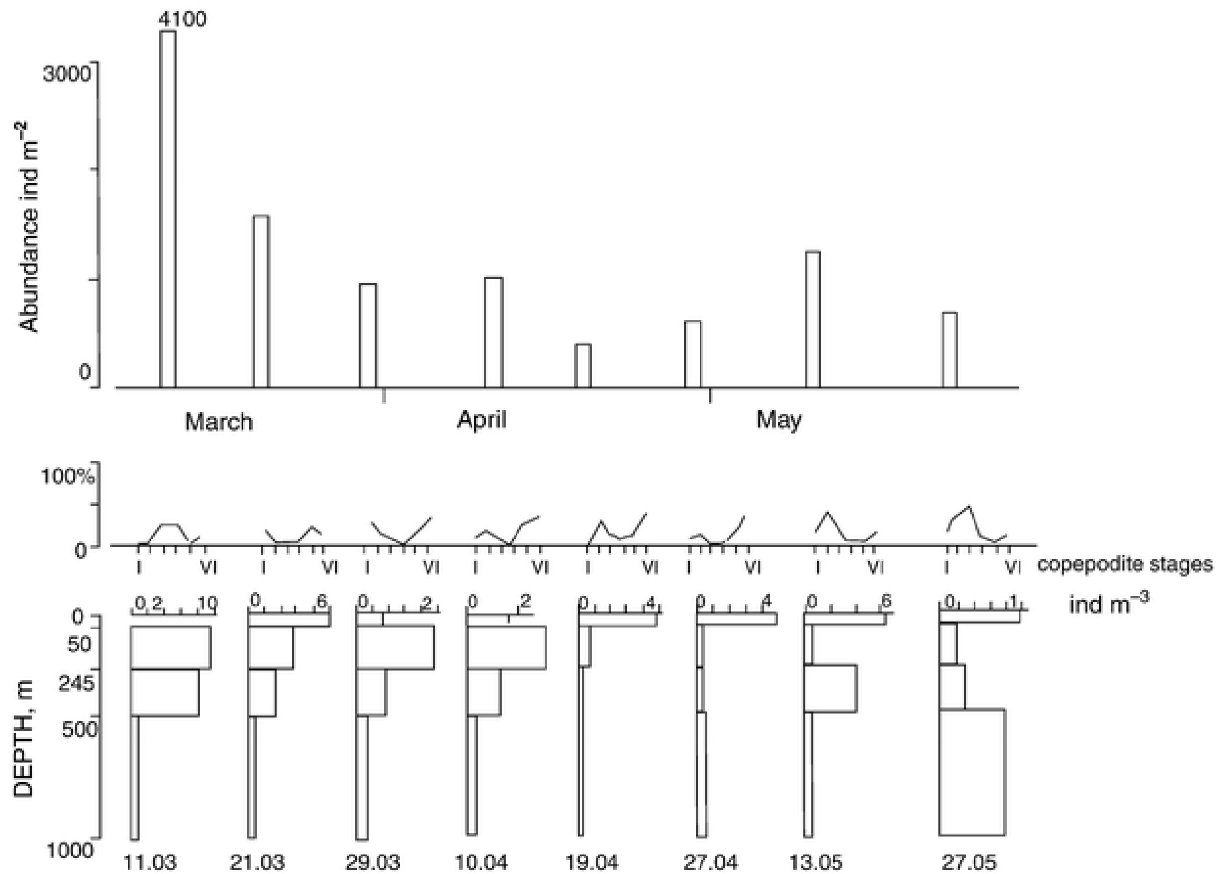

Fig. 5. Dynamics of abundance (ind. m^{-2} in 0- to 1,000-m layer), developmental stage composition (%) and vertical distribution (ind. m^{-3}) of *Metridia gerlachei* under perennial ice. Note that in *lower panel* the scales of abundance for particular stations are different

Discussion

The main characteristics of mass plankton populations - their abundance, developmental stage composition and vertical distribution - under the perennial ice showed significant differences from those in the open ocean. For example, in *Calanoides acutus* on the transect along 20°E at about 70°S, i.e. close to the latitude of the first under-ice station in late February 1957, the dominance of CI of the new generation was clearly observed (Voronina *1984*). In the northeastern Weddell Sea station (62°S, 15°W), selected in order to compare population changes from February to April, an important part of the annual cycle of *Calanoides acutus* was completed during this time. The abundance of this species, which exceeded 4,000 ind. m^{-2} at the beginning of observations, had a nearly fivefold decrease at the end of the study. The dominance of CII in February was followed by the dominance of CIV and CV in April. Vertical distribution showed the surface maximum in February, which changed to the advanced downward migration pattern in March and April. During the course of the observation period, the median depth of population occurrence increased from 35 m to 730 m; this indicates that some fraction of the population migrated below the studied depth and explains the decrease of abundance in the upper 1,000-m layer.

The above comparison demonstrates that the principal difference in population characteristics of *Calanoides acutus* in the ice-open and in the ice-covered environment consists of an almost complete stability of developmental stage composition in the latter habitat. In general, this copepod species accumulates lipids and proteins during summer (Drits et al. *1993*), while in winter it does not feed (Hopkins *1985*; Marin and Schnack-Schiel *1993*). In the western Weddell Sea, the under-ice conditions with the chlorophyll concentration in the water column of 0.3 mg l^{-3} (Melnikov *1995*) are analogous to those in winter in the open ocean. As a result, the copepods advected by currents to this biotope probably have sufficient energetic resources for maintaining a low metabolism but not for moulting and reproduction. Therefore, the population maintained the abundance which corresponded to the normal abundance of overwintering stock in the ice-open or the seasonally ice-covered pelagic zone.

The interpretation of changes in the vertical distribution of *Calanoides acutus* under ice remains unclear. Until mid-April, they may be considered as a population descent in autumn, while the presence of its bulk in the upper layer at the last station in May is very difficult to explain.

In the open-water area, the abundance of *Calanus propinquus* exceeded 4,000 ind. m^{-2} in February and decreased to 710 ind. m^{-2} in early April. The dominance of CIII at the beginning of this period changed to the dominance of CV at the end. The maximum abundance simultaneously changed from the upper layer to the thermocline layer while the median depth changed from 40 to 103 m.

In conclusion, the differences between populations of *Calanus propinquus* in the ice-open and the perennial ice-covered waters were even greater than in *Calanoides acutus*. Not only did the population development of *Calanus propinquus* cease, but the abundance drastically decreased along the direction of the perennial ice drift, while in the southern station it was comparable to the high-latitude population in the seasonal ice waters.

This may be explained by differences in life histories of the two species. Older copepodite stages of *Calanus propinquus* which have accumulated sufficient lipid and protein depots do not undergo a migration to the depths but can stay in upper layers and continue to feed in winter (Schnack-Schiel et al. *1991*; Kosobokova et al. *1993*). However, the range of their food items is rather narrow (Pasternak *1995*) and the absence of sufficient food under ice probably leads to their elimination. In these circumstances, the occurrence of scarce older copepodites of *Calanus propinquus* near the surface at st. 9 in May is surprising.

In the ice-open part of the Weddell Sea, the abundance of *R. gigas* was also not high but some increase (from 100 ind. m^{-2} to 180 ind. m^{-2}) was observed between February and April. During this period, drastic changes in stage composition took place: the dominance of CV and CVI changed to the dominance of CI-CII of the new generation. In the vertical, a rather dispersed distribution in April was observed instead of the maximum abundance in the thermocline in February; between these months, the median depth of occurrence increased from 86 m to 578 m, which indicated autumnal migration.

In this species, a greater diversity of developmental stages under ice and a longer trace of new generation represented by CII (up to st. 4 in late March), as compared to *Calanus propinquus*, are observed. However, in conditions of food scarcity, young copepodites did not moult and were not able to survive. This was indicated by the absence of CIII-CIV from early April to late May while older stages found at sts. 5-8 apparently belonged to the generation of the previous year. But, in general, it is obvious that *R. gigas* has somewhat better capabilities to survive under perennial ice than the two other species. Dr. Pasternak found food in the guts of *Rhincalanus* in our under-ice samples. This fact is in accordance with the idea that it can feed throughout the year and has a wide range of food items (Marin and Schnack-Schiel *1993*; Pasternak *1995*). Nevertheless, under perennial ice, a new generation of these species was not able to develop further than the CII stage, while in free waters developmental rates were sufficiently high (Voronina and Kolosova *1993*).

In the ice-free waters of the Weddell Sea, the abundance of *M. gerlachei* showed a twofold increase between February and March when dominance shifted from CV-CVI to CI; this indicated the rise of the new generation. Vertical distribution was characterised by a maximum in the mid-layers; in April, part of the population showed some descent, and the median depth of occurrence was between 200 and 290 m.

These observations indicate that *M. gerlachei* is the only one of the studied species that basically follows the same pattern of seasonal development in the perennial ice zone and in the ice-free waters, though with some delay in the former habitat. Indeed, in the perennial ice waters, the young generation developed nearly 1 month later than in the ice-open waters, and its partial migration to depth occurred later. Another difference was relatively low abundance of the new generation, which did not show a distinct peak. However, the ability of the population to survive in the extreme conditions of the perennial ice zone is in no doubt. The major precondition for this seems to be the feeding mode of the species. *M. gerlachei* is capable of most active feeding in ice-covered habitats (45% of the population with food in the alimentary tract), having the broadest range of food items, which includes radiolarians, small crustaceans and detritus, as well as phytoplankton (Pasternak *1995*).

Considering the processes in mass copepod populations (dynamics of abundance, developmental stage composition and changes of vertical distribution) which took place under the perennial ice and in the open ocean, we found that the degree of differences between them in these habitats is different in different species. Differences are most strongly pronounced in *Calanus propinquus*, and are insignificant in *M. gerlachei*, while *R. gigas* and *Calanoides acutus* lie between the two. All these copepods use basically the filtering mode of feeding, and we suppose that the trophic characteristics are the principal factors which determine their ability to survive food deprivation under the perennial ice waters. These are the following: (1) the ability to accumulate lipids and proteins during summer time; (2) the ability to feed in winter; (3) the broad range of potential food items.

Calanoides acutus has a well-developed ability to accumulate reserves, which probably determines its leading position in abundance and biomass of the under-ice zooplankton but does not allow it to produce offspring. *Calanus propinquus* is basically characterised by the ability to feed in winter. But even with this ability, a prolonged resistance of the population to poor feeding conditions under ice was obviously impossible, and it greatly diminished in number during the time of ice drift. *R. gigas* and (especially) *M. gerlachei* possess the second and third characteristics. As a result, the population of *R. gigas* was surviving, while *M. gerlachei* even successfully produced a new generation and became a dominant species.

In the studies of functional structure of pelagic organisms' distributional range (Ekman *1953*; Beklemishev *1963*), a notion of a "sterile zone of expatriation" was developed. This notion suggests the zone where the population is advected out of the more or less closed gyre, which provides conditions for maintaining the population and where recruitment does not balance mortality. According to this terminology, we consider that the environment under the perennial ice appears to be a sterile zone of expatriation for *Calanus propinquus*, *Calanoides acutus* and *R. gigas*, while for *M. gerlachei*, it is a normal part of the distribution range.

It seems that the trophic characteristics of the above species also impact on the vertical structure of the copepod taxocoen (i.e. part of a community consisting of species of a particular high rank taxon - see Beklemishev *1963*). In contrast to the open waters, where the vertical succession of populations is determined by timing of their seasonal migrations (Voronina *1984*), under perennial ice it was probably determined by the trophic activities of particular species. As a result, *M. gerlachei* had the topmost, and *Calanoides acutus* the lowermost core at most stations.

Vertical distribution of all species but *M. gerlachei* showed a tendency for the studied season of deepening of populations, which took place from March to the second half of April. After that, an apparent drastic ascent to the upper layers was observed in May. This observation is difficult to explain. Usually, the upward migration of these species begins in spring with increasing daylight duration. It seems unlikely that these copepods have been advected with the surface water from other areas, either still open or covered by seasonal ice, because throughout both the Scotia and the northern Weddell Sea the populations of *Calanoides acutus*, *Calanus propinquus* and *R. gigas* have been reported to live at depth in May. The observed unusual vertical distribution pattern may be the result of an intensive upwelling, the possibility of which has to be addressed by physical oceanography studies.

Conclusions

The mean characteristics of the zooplankton populations under the perennial ice (their abundance, vertical distribution, stage composition and changes during 3.5 months) were obtained. Comparing these with the same characteristics of open-water plankton, we saw that the degree of differences is not the same among species. Differences are most pronounced in *Calanus propinquus*, and practically smoothed in *M. gerlachei*, *Calanoides acutus* and *R. gigas* being between them. These copepods have in common the filtering mode of feeding. We suppose that trophic peculiarities are the principal factors which determine their ability to survive food deprivation under the perennial ice waters or to succeed there. These are the following: (1) ability to accumulate lipids and proteins during summer time; (2) ability to feed in winter; (3) broad range of potential food items.

R. gigas and *M. gerlachei* possess characteristics 2 and 3. As a result, the population of *R. gigas* was surviving while *M. gerlachei* successfully produced a new generation and became a dominant species.

Calanoides acutus has a well-developed ability to accumulate reserves (Schnack-Schiel et al. *1991*). This probably determines its leading position in abundance in the under-ice zooplankton but does not allow it to produce offspring.

Calanus propinquus is basically characterised by the ability to feed in winter. But even with this ability, a prolonged resistance of the population to poor feeding conditions under ice was impossible and it greatly diminished in numbers during the time of investigation.

In conclusion, the environment under perennial ice can be considered to be a normal part of the distributional range for *M. gerlachei* and a sterile zone of expatriation (Ekman *1953*) for the other three species.

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