SEASONAL POPULATION DYNAMICS OF DOMINANT COPEPOD SPECIES IN THE CANADA BASIN OF THE ARCTIC OCEAN

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ABSTRACT - This paper deals with the round-year observations made on population dynamics of dominant species of the Arctic zooplankton – *Calanus hyperboreus, C. glacialis*, and *Metridia longa.* Material is based upon a yearlong zooplankton catches carried out during the SHEBA (Surface Heat Budget in the Arctic Ocean) Ice Camp drift in the Canada Basin of the Arctic Ocean from October 1997 (75°N and 142°W) to October 1998 (80°N and 166°W). We found that the contribution of these species to the total copepods biomass makes up 78% in winter and 85% in summer. Substantial variations of zooplankton biomass were observed in the upper 0-150 m in a range of 10 mg/m^3 in winter and 300 mg/m^3 in summer. In the area of the SHEBA drift the spawning of these copepods began approximately a month earlier than it was previously known for these species in the central Arctic Ocean. Life cycle of *C. hyperboreus* is expected no less than three years and two-years long life cycle of *C. glacialis*, that is similar to the literature data, however, we can suggest that one hemipopulation of *M. longa* has one-year long life cycle. We speculate that recent warming in the Arctic could increase the vegetation period that is, in turn, could impact on the population dynamics of the Arctic Ocean zooplankton.

KEY WORDS: Arctic Ocean; Canada Basin; zooplankton; dominant species; age composition; population dynamic; environmental changes

INTRODUCTION

During the last two decades in the Arctic Ocean there were recognized changes in the climate (Flato, 1996; Schindell *et al.*, 1999), in the sea ice retreat (Johanessen *et al.*, 1995; Cavaliere *et al.*, 1997; Parkinson *et al.*., 1999; Rothrock *et al.*, 1999), in atmospheric pressure fields (Proshutinsky and Johnson, 1997; Johnson *et al.*, 1999), in ocean circulation (McLaughlin *et al.*, 1996), in expansion of Atlantic and Pacific waters (Alekseev *et al.*, 1998; Maslowski *et al.*, 1999), in ice drift patterns (Kolatschek *et al.*., 1996) and in the freshwater content of the upper ocean (McPhee *et al.*, 1998; Macdonald *et al.*, 1999a; Ekwurzel *et al.*, 2001). As a result of these environmental changes in the air-ice-water system, it expects changes in the composition, structure and dynamic of sea ice and upper ocean biological communities.

During the SHEBA expedition (**S**urface **HE**at **B**udget of the **A**rctic Ocean) in the Beaufort Sea, 1997-1998, the round-year multi-disciplinary biological observations have been conducted (Melnikov *et al.*, 1998; Welch, 1998). The noticeable changes were observed in species composition of zooplankton (Melnikov and Kolosova, 2001). In this region we found new invertebrate animals originally from the North Pacific zooplankton: copepods *Calanus marshallae, Eucalanus bungii, Metridia pacifica, Lucicutia ovaliformis, Heterorhabdus pacificus*, amphipod *Scina pusilla*, hydromedusas *Atolla tenera* and *Pantachogon haeckeli*. These species were never been indicated in the Canada Basin zooplankton collected here in a period of the 1950-1980: “Cancolim II” in 1951 and “Salvelinus” in 1960-1962 (Grainger, 1965), T-3 in 1958-1965 (Grainger, 1965; Harding, 1966; Hughes, 1968), North Pole-22 in 1975-1976 and in 1979-1980 (Kosobokova, 1981; 1982).

This paper deals with the round-year observations made on population dynamics of dominant species of the Arctic zooplankton – *Calanus hyperboreus, C. glacialis*, and *Metridia longa.* Life cycles of these species have been studied beginning from the 1950-1980th expeditions (Grainger, 1959, 1965; Harding, 1966; Hopkins, 1969; Brodsky and Pavshtiks, 1976; Pavshtiks, 1977; 1980; Heinrich *et al.*, 1980; Kosobokova, 1982; Diel, 1991). However, till now, little is known about the round-year age composition and seasonal vertical dynamics of these species due to well-known problems in collecting of materials in the ice-covered polar region and, especially, during the winter period. Our goal in this paper is to show the age composition and vertical dynamics of *Calanus hyperboreus, C. glacialis*, and *Metridia longa* in the Canada Basin of the Arctic Ocean.

MATERIALS AND METHODS

This research is based upon a year-long zooplankton catches made during the SHEBA ice camp drift from October 1997 (75°N and 142°W) to October 1998 (80°N and 166°W). From October 1997 to February 1998, SHEBA drifted westward over the Canada Abyssal Plain along 75°N, bottom depth of 3800 m. During February-September 1998, the ice camp crossed the Chukchi Plateau over depths of 300-1000 m in a northwest direc-

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tion, and then again drifted northward to the Canada Abyssal Plain over the 3300 m depth in September-October 1998. Locations of plankton stations are shown in Fig. 1.

Vertical tows were taken with a Juday net with a 37 cm wide flat top and 150 µm mesh-size filtering cone. Date and positions of samplings are presented in Table. Five depth layers were sampled: 0-35, 35-50, 50-150, 150-300 and 300-1000 m in connection with the CTD characteristics of water masses in the region of the ice camp drift. Plankton samples were concentrated on nylon gauze (mesh size 150 µm) and the organisms were immediately fixed with 5% formaldehyde. Plankters were identified and enumerated on a plankton counting tray using light microscope at 300x. The biomass was calculated using the animal-body-size measurements under laboratory conditions as follows: each animal body size was measured and biomass was calculated by formula: $W = K \times L^3$, where W is animal weight in mg, L is length in mm, and K is coefficient (Vinogradov and Shushkina, 1987).

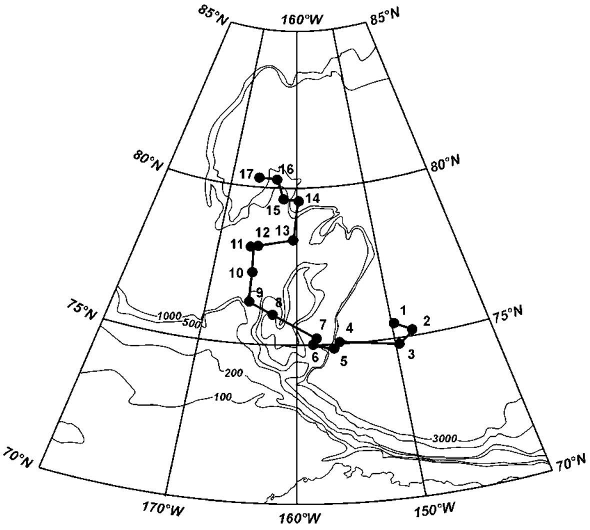

Fig. 1. SHEBA Ice Camp track in the Canada Basin of the Arctic Ocean from October 1997 to October 1998. Numbers indicate the location of plankton stations. Positions and date of samplings are shown in Table 1

RESULTS

Environmental conditions. The ice field, where the ice camp was established in October 1997, was a consolidated multi-year ice floe, 1.7 to 2.1 m thick (J. Bitters, pers. comm.), marked with many shelves, hummocks, caverns, and cracks. Averaged over the year (October 1997-October 1998), the 2 m air temperature was 0.6°C less than the climatological 2 m air temperature derived from data from 1979 to 1996 (Perovich *et al.*, 1999). The melt season was long, lasting nearly 80 days. In comparison, melt seasons observed at ice stations of the former Soviet Union from 1960-1990 averaged 55 days, and ranged from 20 to 83 days (Lindsay, 1998).

The hydrological conditions we discussed in (Melnikov and Kolosova, 2001). Here, we note that the most important feature of the hydrological regime in the SHEBA area was an existence of steady-stable pycnocline of 2-3 m thick at the depth between 30-35 m during the winter period up to April (McPhee *et al.*, 1998),

Table. Station list and sampling protocol (SHEBA Ice Camp, 1997-1998, the Canada Basin of the Arctic Ocean)

№ Sts.	Date	Position		Sampling strata, m				
		N	W					
1	19.12.97	75 32.6	150 17.1	0-35	33-45	48-150	146-300	298-1000
2	30.12.98	75 15.2	149 59.8	0-35	33-50	48-150	146-300	290-1000
3	12.01.98	74 51.6	150 25.2	0-35	33-50	50-150	148-300	289-1000
4	30.01.98	75 05.8	156 21.0	0-35	35-50	48-150	147-300	285-1000
5	11.02.98	74 54.7	157 47.6	0-35	33-50	49-150	143-300	289-1000
6	26.02.98	75 03.0	159 39.6	0-35	33-50	51-150	142-300	287-1000
7	06.03.98	75 13.8	159 57.8	0-35	34-50	51-150	150-300	295-1000
8	03.05.98	76 00.5	165 30.4	0-35	35-50	50-150	150-300	300-440
9	22.05.98	76 20.8	166 35.2	0-35	35-50	50-150	150-300	-
10	17.06.98	77 17.4	166 28.6	0-35	36-50	50-150	150-300	300-600
11	02.07.98	78 07.9	166 48.5	0-35	35-50	50-150	150-280	-
12	15.07.98	78 05.6	166 08.4	0-35	35-50	50-150	150-300	300-420
13	01.08.98	78 19.3	161 25.2	0-35	35-50	50-150	150-300	300-740
14	27.08.98	79 34.8	160 01.0	0-35	35-50	50-150	150-300	300-1000
15	10.09.98	79 38.2	162 00.9	0-35	34-50	46-150	144-300	285-1000
16	21.09.98	80 14.5	164 42.7	0-35	35-50	50-150	150-300	300-1000
17	01.10.98	80 14.8	166 00.7	0-35	34-50	49-150	148-300	300-1000

which was like an original barrier between mixed surface layer and intermediate water masses.

Zooplankton. A total list of the SHEBA zooplankton collection includes 81 species (Melnikov and Kolosova, 2001). In term of biomass, copepods contributed (depending on time and depth of copepods' habituation) from 30 to 90% of the total zooplankton biomass (Fig. 2a). Chaetognaths, appendicularians, euphausiids and amphipods were subdominant, however, their biomass has never been exceeded copepods' biomass, which was formed mainly by three dominant species: *Calanus hyperboreus, C. glacialis* and *Metridia longa*. Their contribution to a total copepods' biomass makes up 78% in winter and 85% in summer (Fig. 2b). Small size and highest abundant copepods *Oithona similis, Microcalanus pygmaeus, Pseudocalanus minutus, Oncaea borealis* contribute the rest of zooplankton biomass.

Seasonal variations in vertical distribution of zooplankton biomass are determined by the life cycles of the dominant copepod species. Upward migration of copepods from the depth to the surface begins with a phytoplankton bloom in spring but downward migration starts with the end of vegetation period in autumn. Even copepods migrate within the whole water column, however, the substantial variations of zooplankton biomass we observed in the upper 0-150 m in a range of 10 mg/m^3 in winter and 300 mg/m^3 in summer (Fig. 2a). In the deeper water (150-300 m) biomass differed insufficient and in the 300-1000 m strata was not noticeable.

C. hyperboreus (Fig. 3) is a species, whose life cycle is completed within the 0-1000 m water column (Brodsky, 1957; Virketis, 1959; Johnson, 1963; Harding, 1966; Pavshtiks, 1977, 1980; Heinrich *et al.*, 1980; Kosobokova, 1981; *etc.*). In the SHEBA collection, *C. hyperboreus* was presented by all development stages (copepodites I, II, III, IV, V or CI, CII, CIII, CIV, CV) and adults of both sexes. This species was the dominating component, making-up 89% of the total zooplankton biomass in the upper 0-50 m in June-July. The first signal to reproduction of this species we indicated in winter, when we found a smooth increasing of number of males from December through March in the 300-1000 m layer. In this period, females prevailed between the adults in the 50-150 m layer (middle of January) and than in the 150-300 m (up to May). In June-July, animals of both sexes lifted up to the surface and concentrated in the 0-35 m layer increasing zooplankton biomass by a factor of 10 (Melnikov and Kolosova, 2001). In August, number of females was decreased in consequence of their mortality after spawning. New females, which were formed due to molting of CV, have begun descending to the wintering depth (50-150 m) in September. In the late July, a numerous amount of the first CI appeared in the 0-35 m and also in the 35-50 m and 50-150 m layers but in the few numbers. In the late August, CI transformed into CII stage and from this time CI is absent in plankton. In September, one part of the CII hemipopulation transformed into CIII stage but other part of CII descended to deeper layers, where CII was found in a few number up to October. In winter, CII stage was not indicated in our collection. The development of *C. Hyperboreus* from an egg and nauplii to CI stage was lengthened two months but a period from CI to CIII was approximately a month. Duration of the CIII stage was remarkably longer: in September, CIII descended to the 150 m depth, where one part of the CIII population transformed into CIV, however, a second portion of CIII lifted down to wintering layer (300-1000 m). CIV and CV stages were the most numerous in our collection. Duration of these stages may be reached two years and we can suggest that in zooplankton there are presented two generations simultaneously. In winter, the CIV and CV stages habituate deeper than females (in the 300-1000 m layer) and in June, they lift up to the surface, where they reach a maximum biomass in the 0-35 m layer. The CIV and CV biomass (190 mg/m^3) exceeds the females' biomass (76 mg/m^3) by a factor of 2 and that is about 50% of the total biomass during the maximum zooplankton development in summer (300 mg/m^3). In summer, during the grazing and accumulating of storage lipids, the CIV and CV stages grew up to adults and then descended to the depth of 150-300 m in the late September, and then a deeper. Most authors (Ostvedt, 1955; Pavshtiks, 1977; 1980; Dawson, 1978; Diel, 1991; Vinogradov *et al.*, 1996) expect that only a part of populations of CIV and CV lift up to the surface at the second year for a spawning

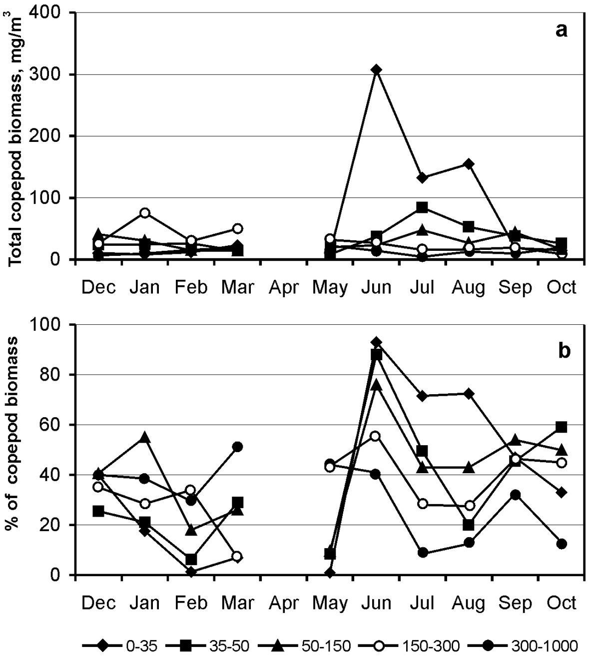

Fig. 2. *Total copepod biomass (a) and percentage of dominant species* ***Calanus hyperboreus, C. glacialis*** *and* ***Metridia longa*** *in the total copepod biomass (b) in the 0-1000 m water column (SHEBA, December 1997-October 1998, the Canada Basin of the Arctic Ocean). No data for April*

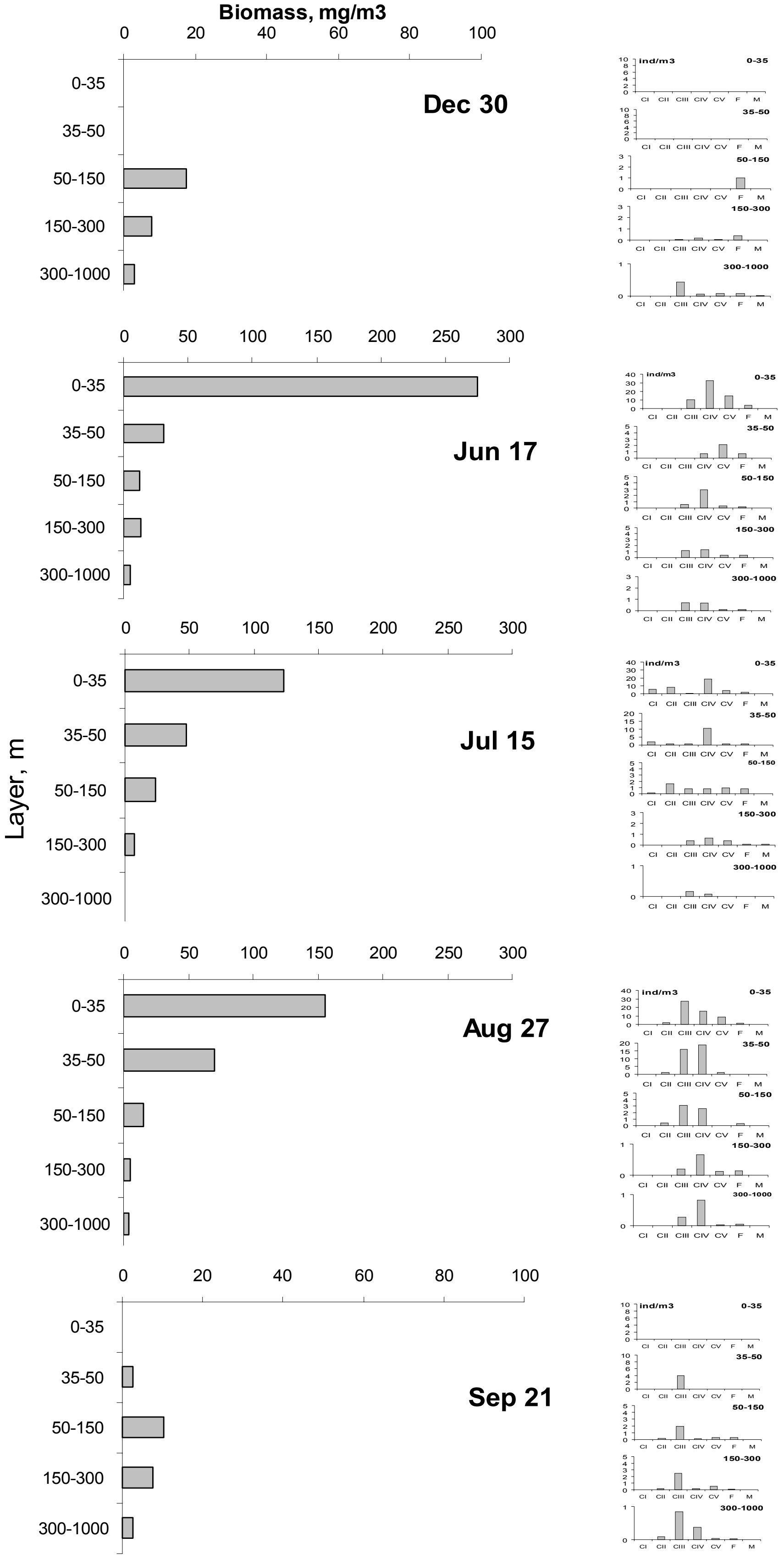

Fig. 3. ***Calanus hyperboreus.*** *Vertical distribution of biomass (mg/m*^{3}*) and abundance (ind/m*^{3}*) of copepodites and adults (females and males) within the 0-1000 m water column from December 30, 1997, to September 21, 1998, at selected plankton stations (SHEBA, the Canada Basin of the Arctic Ocean)*

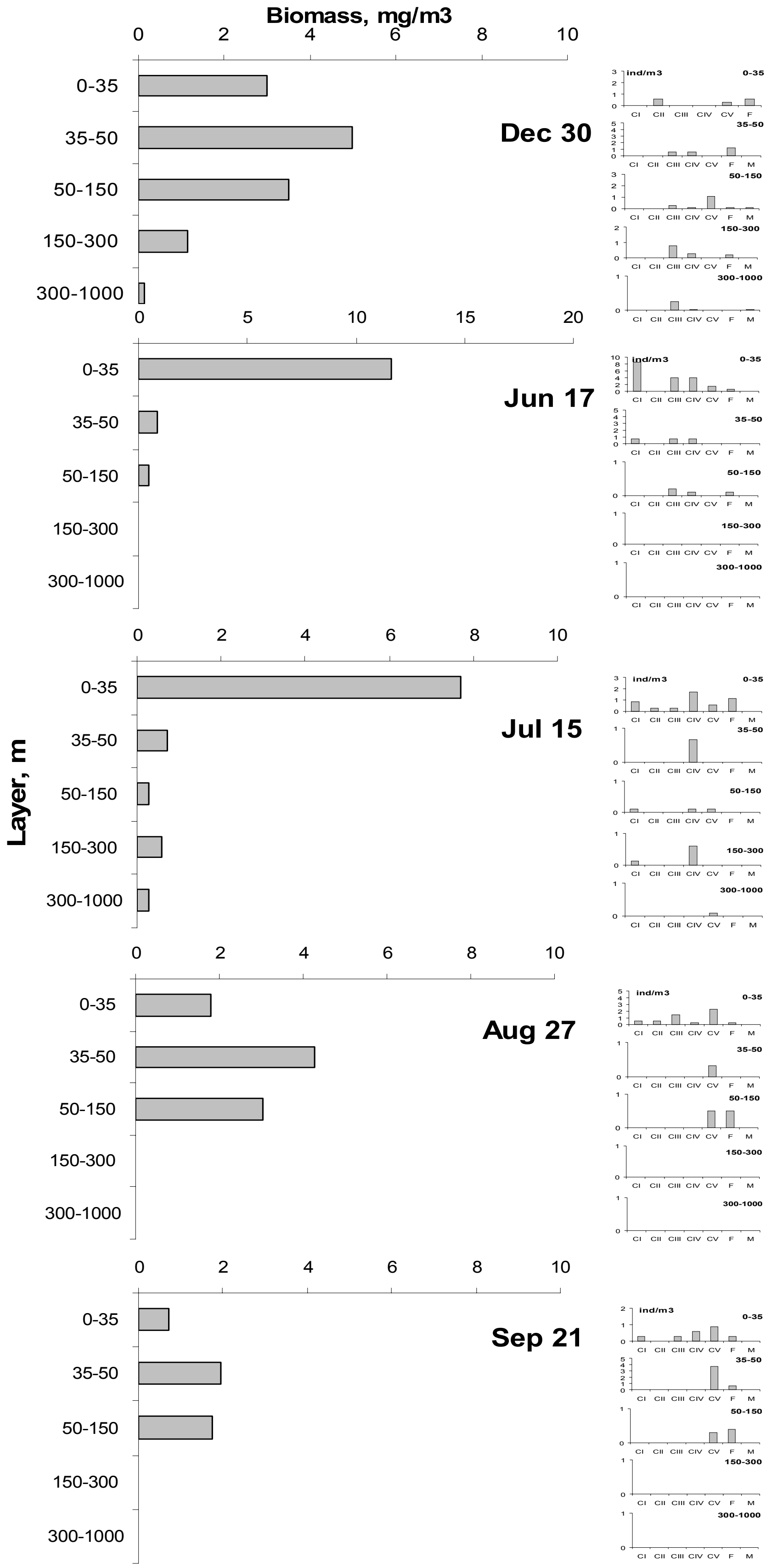

Fig. 4. ***Calanus glacialis.*** *Vertical distribution of biomass (mg/m^3) and abundance (ind/m^3) of copepodites and adults (females and males) within the 0-1000 m water column from December 30, 1997, to September 21, 1998, at selected plankton stations (SHEBA, the Canada Basin of the Arctic Ocean)*

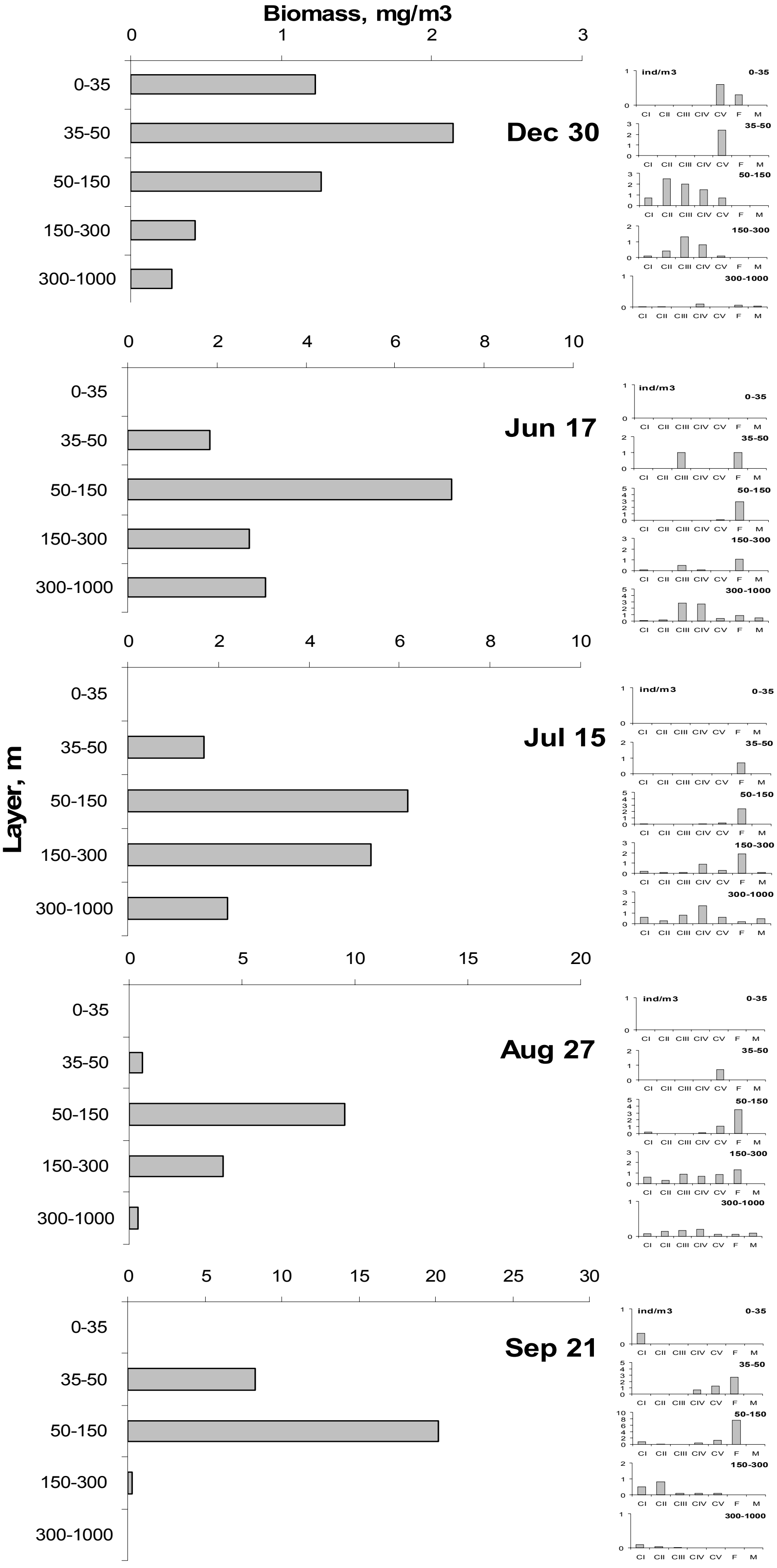

Fig. 5. ***Metridia longa.*** *Vertical distribution of biomass (mg/m^3) and abundance (ind/m^3) of copepodites and adults (females and males) within the 0-1000 m water column from December 30, 1997, to September 21, 1998, at selected plankton stations (SHEBA, the Canada Basin of the Arctic Ocean)*

but other part of these stages continue to stay at the overwintering depth, decreasing of metabolic activity and using high-energetic lipids accumulated during the previous summer period. We found that the life cycle of *C. hyperboreus* is expected no less than three years that is similar to literature data (Ussing, 1938; Dawson, 1975; Pavshtiks, 1980; Diel, 1991).

C. glacialis (Fig. 4) is a subdominant species (after *C. hyperboreus*) by abundance and biomass making-up 30-50% of the total zooplankton biomass in winter (October-January). Males were found in the layer of 50-150 m in December-January and then deeper in 150-300 m layer in February-May. Females occupied the highest layers than males' ones. In December we found a high number of females in the 35-50 m strata (just beneath the pycnoclyne) but during the period from January to May they populated the depth of 50-150 m. From January through May we have not indicated any individuals of *C. glacialis* in waters upper than 50 m, however, beginning from June to September, all hemipopulations of this species migrated to the surface and we indicated only a few of individuals in waters deeper of 35 m. CI appeared in June (a month earlier than *C. hyperboreus* CI); in the middle of July the abundance of CI decreased (a period of *C. hyperboreus* CI domination) but in the end of August, the CI stage increased again forming a second maximum and staying here to the end of October. To this time, CII transformed into CIII and from September, the CIII copepodites descended to the wintering depth, where they developed to the CIV stage. During the period of December-May we indicated single individuals of CI and CII, however, CIII and CIV stages were observed round yearly. In July, just after the lifting-up of *C. glacialis* to the surface, the females' abundance rapidly decreased to the earlier July due to mortality after spawning. In the end of July, females of new generation appeared due to development from the overwintering CV stage and in September-October, they lifted-down to the wintering depth, where they stayed until the next vegetation period. In our case, the domination of the older copepodites in winter and spring before the appearance of young stages is an evidence of two-year long life cycle of *C. glacialis*, that is similar to the literature data (Pavshtiks, 1977; 1980; Heinrich *et al.*, 1980; Kosobokova, 1982; Diel, 1991), though, on opinion of Grainger (1965), a part of *C. glacialis* population can complete the development from an egg to adult during one year.

Metridia longa (Fig. 5) subdominated by biomass after *C. glacialis* during the whole year with the exception of June (a time of reproduction and an active development of *M. longa*). In winter, the contribution of *M. longa* makes-up 35-50% to the total zooplankton biomass in the 0-150 m layer. In spring (March), on the background of scarcity of zooplankton in the upper layer, *M. longa* dominated here making-up 65% of the total zooplankton biomass, and 90% of the total copepod biomass, respectively. Males were distributed within the 50-1000 m water column with a preferable habitation depth of 300-1000 m. We found a smooth increasing of males' number from December through March and a later smooth decreasing to October. Females inhabited the 50-150 m layer, although, as males, they were distributed within the 50-1000 m water column. In March, females' abundance increased, when they lift-up to the surface and redistributed in the 0-150 m water column with a maximum number at the depth of 35-50 m. After a short time descending to the 150-300 m strata in May, they concentrated again in the 50-150 m, where they stayed here to the winter increasing their abundance and forming a second maximum number in September due to development of the CV stage. The CI stage was indicated during the whole year. We found that the most number of CI was in December-January in the layer of 50-150 m and a bit more in February in the uppermost layer (35-50 m). During a period of May-October, they were completely absent in the 0-50 m strata, inhabiting, mainly, in the layer of 150-300 m. In the end of January, CI transformed into CII, and then into CIII stage with a high number of individuals of each stage until May. After the transformation of CIII into CIV, the CIV hemipopulation descended to the depth of 300 m in June-July. Copepodites of the CV stage concentrated within 35-50 m strata. In March, an amount of CV decreased due to molting and transformation of CV to females, the number of which was proportionally increased. In summer, a large part of *M. longa* females populated deeper of 300 m. In August, the number of CV in the 50-150 m strata begun to increase again due to individuals of a new generation. It can be suggested that one hemipopulation of *M. longa* has one-year long life cycle but other hemipopulation of *M. longa* spends the wintertime in the deep water until the next vegetation period.

DISCUSSION

The main feature of the Arctic zooplankton is a periodical change of maxima of production and biomass of the dominant species in the upper surface water, where the grazing period is very short. In spring, the increasing of the total zooplankton biomass is a result of upward vertical migration of animals from the depth to the surface, and then a result of their further reproduction and growth. At the SHEBA region, in the 0-35 m strata the total zooplankton biomass increased for a short period of time (from May 22 to June 17) by a factor of 20 (14 mg/m^3 and 302 mg/m^3, respectively). To this moment, zooplankton began the downward migration to wintering depths and redistributed within the 50-1000 m water column. It is interesting that different species have a different "schedule" of descending. A short period of the phytoplankton bloom, a high grazing competition, a scarcity of the food resources are of a reason to dissociation of copepodites, adult of both sexes and their hemipopulations in time and space. Populations of *Calanus hyperboreus*, *C. glacialis* and *Metridia longa* have a different time of reproduction and development of copepodites. In turn, it is the good demonstration of species adaptation to the limited food sources in the polar environment.

The most important peculiarity of the life cycle of the high-arctic copepods is a less dependence of their spawning time from the phytoplankton bloom than in the arcto-boreal region (Zelickman, 1977; Heinrich, 1993). So, the spawning of *C. hyperboreus* starts long before the phytoplankton bloom (February-March), since it uses the high-energetic lipids deposited in the previous summer season. This fact is well known for *C. hyperboreus'* nauplii and CI when these stages habituate in deeper layers and, partly, in layers close to the bottom (Ostved, 1955; Diel 1991; Vinogradov *et al*., 1996). It is why we have not found *C. hyperboreus* CI in the water column up to its appearance in the surface layers in the middle July, when the highest biomass values (in term of chlorophyll *a*) were measured (Melnikov *et al*., 2001). *C. glacialis* is more depended on the phytoplankton bloom. On opinion of the most researchers, its nauplii develop faster than *C. hyperboreus* ones (Osvedt, 1955; Dawson, 1975; Pavshtiks, 1977; 1980; Diel, 1991). In spite of the later spawning time (April-May), *C. glacialis* CI reached the highest abundance in June, a month before an appearance of *C. hyperboreus* CI. *M. longa*, as an euryphagous plankter, is less depending species between copepods upon the phytoplankton bloom. It starts to spawn in the earlier winter and finish in March. *M. longa* CI stages are populated in plankton during a year with the exception of April-May when they grew up to the CII and CIII stages. The most number of this species we found in winter (December-February) and the second maximum this species formed in September due to the autumn spawning of females grew up during the summer period.

In the area of the SHEBA drift, we found that the spawning of dominant copepods *Calanus hyperboreus*, *C. glacialis* and *Metridia longa* began approximately a month earlier than it was previously known for these species in the central Arctic Ocean (Virketis, 1957; Grainger, 1959, 1965; Harding, 1966; Pavshtiks, 1977; 1980; Heinrich *et al*., 1980; Kosobokova, 1982; Diel, 1991). It is well remarkable for *M. longa* and *C. glacialis* but less for *C. hyperboreus*. From our point of view, the increasing number of *M. longa* old-stage copepodites in the summer-autumn period is an evidence of the fact that the major part of *M. longa* population has one-year long life cycle. The season of 1997-1998 was anomaly warm (Perovich *et al.*, 1999); the surface water temperature was a several degree higher of the mean integrated temperature for this region; the melt season started at least a month earlier compared to the previous years and was long, lasting nearly 80 days. In comparison, melt seasons observed at ice stations of the former Soviet Union from 1960-1990 averaged 55 days, and ranged from 20 to 83 days (Lindsay, 1998). These environmental conditions were favorable for the earlier and intensive sea ice algae and phytoplankton development (Melnikov *et al*., 2001). It is why that the SHEBA zooplankton dynamic in the surface water looks like "an explosion", when zooplankton biomass increased during a short period of time by a factor of 20. These facts are the base for speculation about the climate impact on the population dynamic of the Arctic Ocean zooplankton.

ACKNOWLEDGEMENTS

We are deeply grateful to Harold (Buster) Welch (Fresh Water Institute, Winnipeg, Canada) for collecting plankton samples along the SHEBA drift during the summer season. Funding supported this work obtained from the Russian Foundation for the Basic Research (grant #99-05-64767).

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