Climate variations and the state of zooplankton in the barents sea

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Abstract

We present data on zooplankton biomass distribution in August-September 2005-2006 obtained in the integrated ecosystem system survey for the Barents Sea performed by Russian and Norwegian vessels. In order to establish the general regularities of plankton biomass, data collected in the central latitudinal zone of the Barents Sea in individual years (cold 1987, moderate warm 1989, anomalous warm 2002, 2004, 2005) were analysed. Considerable annual differences in the species and age structure of plankton community in water masses of different origin depending on dynamics of the ice cover in that part of the sea were found.

In 2002, owing to the northerly position of the ice edge in summer, the plankton community was characterized by its mixed composition (Atlantic and Arctic species) and high abundance. In 2005 when the advective processes were weak and the eastern areas became free from ice later, a considerable reduction in the abundance of warm-water species was observed. When the position of the ice edge was most southerly in 2004, the bulk of the plankton community was made up of Arctic species and a lack of warm-water species was recorded. In 1987 and 1989, high horizontal gradients of water temperature in the areas of Atlantic and interactions of Arctic water masses were, together with anomalous ice distribution, the main factors influencing the state of zooplankton.

Key-words: ice edge, plankton, *C. finmarchicus, C. glacialis,* distribution, biomass

Introduction

The central Barents Sea is an important feeding area for many commercial fish species and zooplankton form the basis food during most of their life cycle.The state of the food supply of commercial fishes is of great importance for the ability to attain peak physiological condition and form strong year-classes.

Most plankton investigations in the north of the Barents Sea are restricted to the central part of the sea and to the spring/summer season, when copepod reproduction and development occur (Skjoldal, Hassel, Ray et al., 1987; Melle, Skjoldal, 1998; Arashkevich et al., 2002). These studies paid most attention to the life cycles of two dominant copepods, *Calanus finmarchicus* and *Calanus glacialis*. The latter species is most dominant in the Arctic water masses in the north (Jaschnov, 1970; Hassel et al.; 1991; Tande, 1991), and may comprise up to 80-90% of the total mass of copepods in some areas. A number of papers written between 1980 and 2000 cover the data on biomass, age composition and reproduction of dominant copepods (Koptev, Nesterova, 1983; Degtereva, Nesterova, Panasenko, 1990; Skjoldal, Gjøsæter, Loeng, 1992; Orlova, Boitsov, Ushakov, 2004). Other studies provide information on copepod seasonal reproduction and growth features and on the impact of climate

145

variations on biological processes in the central and north-eastern part of the sea (Orlova et al., 2002, 2005, 2007).

In this paper we discuss the inter-annual variability in the structure of plankton community and biomass in different water masses. The influence of heat-related sea-ice dynamics on zooplankton during summer in different years was also investigated.

Materials and Methods

Regular plankton investigations by PINRO in the north of the Barents Sea have been carried out in 1982-1993 and 2002 to the present, and by IMR since 1990 to the present (Table 1). The catches are taken using several plankton gears, including Juday (PINRO), WP2 and MOCNESS (IMR). The materials for cold (1987), moderate (1989) and warm (2002, 2004, 2005) years were analysed. A total of 437 zooplankton samples were processed by PINRO during this period. Most attention was paid to two biomass-forming species, the North Atlantic *C. finmarchicus* and the Arctic *C. glacialis*. The maps of the ice edge position in July were made using the data from the Norwegian Meteorological Institute in Tromsø.

Table 1. Plankton studies in the North Barents Sea were carried out by PINRO and IMR.

| | IMR | | PINRO | |
| | WP2 | MOCNESS | WP2 | JUDAY |
year	N stations			
1982				52
1983				78
1984				79
1985				260
1986				88
1987				91
1988				169
1989				42
1990	107	27		143
1991	129	25		
1992	123	28		138
1993	112	30		156
1994	141	33		
1995	117	42		
1996	113	54		
1997	129	44		
1998	201	44		
1999	169	39		
2000	139	56		
2001	142	50		
2002	129	43		62
2003	88	37	86	
2004	157	34	35	37
2005	134	48	51	41
2006	150	43		133

Results
Oceanographic conditions

 The central Barents Sea is occupied by waters of three basic types: Atlantic, Arctic and waters of the Barents Sea (Loeng, 1991; Ozhigin, Ivshin, 1999). Since the central latitudinal zone is very extended, the regime of its individual parts is formed under the influence of both general and local hydrographical and meteorological factors (Boitsov, Tereshchenko, 1998; Tereshchenko, 1999).

In 1987, a weakened seasonal heating in the surface layer in the spring-summer period caused a warmth deficit. Even in July the ice edge was located along parallel 76° N in the west, between 76-77 °N in the centre, and 60-100 miles southward of the mean annual condition in the east (Fig. 1). In September, the pack ice was between 79 and 80° N, and was close to normal. In 1989, in June-August, waters in the branches of warm currents in the Barents Sea in the upper 200-metre layer had an abnormally high temperature. The ice coverage in the sea in June corresponded to the norm, although in July-August, in the central part of the sea, the ice edge was 60-80 miles south of its usual position, owing to the intensive ice transport from the north east.
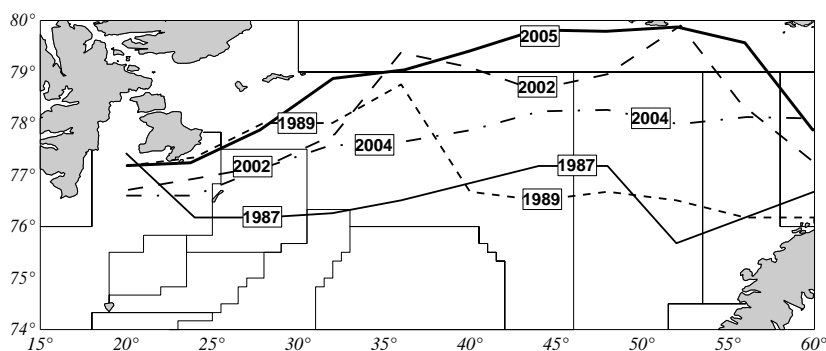

Figure 1. Location of ice edge in July 1987, 1989, 2002, 2004, 2005.

On the whole, the hydrological regime in August 1989 was formed under the influence of the intensified inflow of both Arctic and Atlantic waters.

A warm period in 2000, after a series of cold years, was characterized by inter-annual differences in oceanographic conditions, including the ice coverage of the sea. Although the mean annual values of this parameter in 2002, 2004 and 2005 were below the mean annual level, it was observed that in the summer the sea became free of ice at different rates (Borovkov et al., 2004; Pedchenko et al., 2005).

A specific feature of the oceanographic regime in the Barents Sea in 2002 was the intensification of the warm advection by a system of the North Cape and Murmansk Currents in the spring-summer period. At that time, the total ice coverage of the sea was 8-15% less than normal. In July, in the north-east of the Sea, the ice edge was located to the north of its mean annual position, while on the meridian 50° E, it was close to Franz Josef Land (FJL), which was approximately 100 miles north of the normal position.

In the spring-summer period 2004, intensive heating of the surface layers was observed, reaching a peak in July. The ice edge in July 2004 was at the mean annual level. In September, the edge was at 82° N, and the pack ice was represented by a small "tongue" along the eastern coast of FJL.

In summer 2005 there was intensive ice melting and pack ice destruction in the Barents Sea. Ice coverage in July was only 13%, which was almost half of its normal extent. In the north-east of the sea the ice edge was observed to the north of the mean annual position and of the position in July 2002 and 2004. In August – September, the Barents Sea water area was ice-free. The pack ice was located generally to the north of 81° N.

In 1987 and 2004, the ice edge dynamics were maximal compared to 2002 and 2005. This was caused by extreme positive anomalies in the air temperature and stable southerly winds, which greatly influenced the processes of ice melting and disintegration. The character of the ice edge dynamics in the different parts of the sea was heterogeneous, so it was provisionally divided into western (30-32° E), centre (32-45° E) and eastern (46-60° E) sectors.

Zooplankton

The data for recent years shows that plankton biomass has grown from 7.3 to 9.2 g/m^2 (Fig. 2.) One of the major factors behind this growth was a decrease in the stock of the basic plankton consumer; capelin (Fig. 3). However, the plankton biomass is also influenced by other predators such as young cod, haddock and herring in particular, as their abundance has increased in the recent years. Besides these, during the past few years, an increase in abundance and expansion to the western part of the Barents Sea of blue whiting and polar cod in the east have been observed. These may increase the total pressure on zooplankton. The intensification of advective plankton drift with the Atlantic waters is also an important factor.
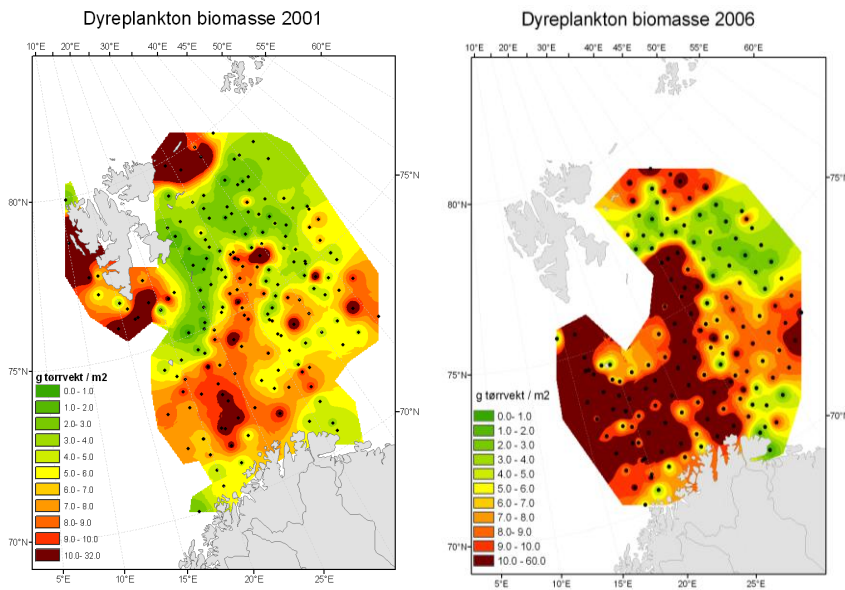

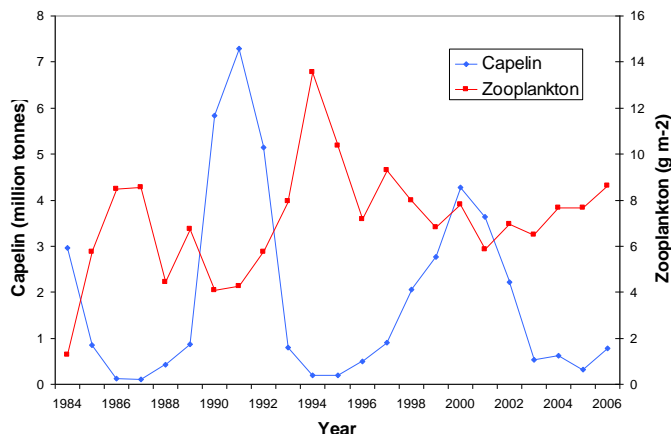**Figure 2**. Distribution of zooplankton biomass in 2001 and 2006.

Figure 3. Annual fluctuations in zooplankton biomass (WP2) and size of capelin stock in the Barents Sea.

148

In 1987, the Arctic water masses occupied practically all of the central and eastern parts of the latitudinal zone from the surface to the bottom. Meanwhile, in northern waters, there were some areas where the water temperature was below -1° C. In the west a thermal front zone was formed. A characteristic of that year was a relative low abundance of plankton in August, which was related to the greater ice cover of the Barents Sea in July, which prevented copepod transportation. The abundance of the North Atlantic species *C. finmarchicus* was characterized by the greatest variability. In the beginning of August, in the east (50-56° E), and in the second part of the month, in the centre (36-42° E), its abundance in the Arctic water masses was very low (Fig. 4). Although on the Novaya Zemlya Bank (46-48° E), where the rates of destruction of the ice edge and the shift of the edge northwards were at their greatest, a sudden increase in abundance of this species was observed. In the mixed waters, the concentrations of *C. finmarchicus* in the centre were also low, and only incertain areas in the west (the South Cape Deep) did they increase with an abrupt retreat of the ice edge.
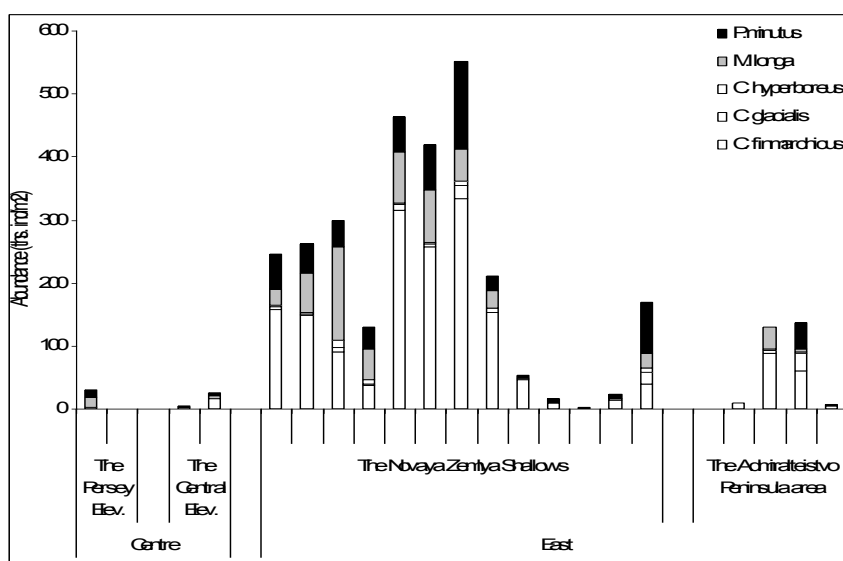

Figure 4. Abundance of zooplankton in Arctic waters in August 1987.

Arctic species were mostly found in the central and eastern areas. *C. glacialis* was unevenly distributed, mostly in the north of the eastern areas. We should note that a specific feature of 1987 was a correspondence between dominant concentrations and areas with increased horizontal water temperature gradients.

More complete information on the ways of forming aggregations and copepod biomass is provided by their age structure. At the beginning of August, in Arctic waters, in the north of the eastern areas, the reproduction of the local *C. finmarchicus* stock was observed. The spawning progress was judged by the presence of females (in some cases together with males), by the number of nauplii at IV-V stages, and rarely by the presence of Calanoid eggs.

In the east and in the centre, we observed areas where all these features appeared almost simultaneously, which indicated mass reproduction. The population was recruited also from young fry (CI-II), brought from the other areas; the number of crustaceans CIII was smaller (Fig. 5). In the second part of the month, in the western areas, the relative number of *C. finmarchicus* CIII-IV was high. The *C. glacialis* population in most cases was made up of hibernates CIII-V. At the same time, during the first ten-day period of August, in the north of the Novaya Zemlya Bank area (76-77° N), a large number of females was observed, (sometimes together with males) while large eggs of those species were also found.
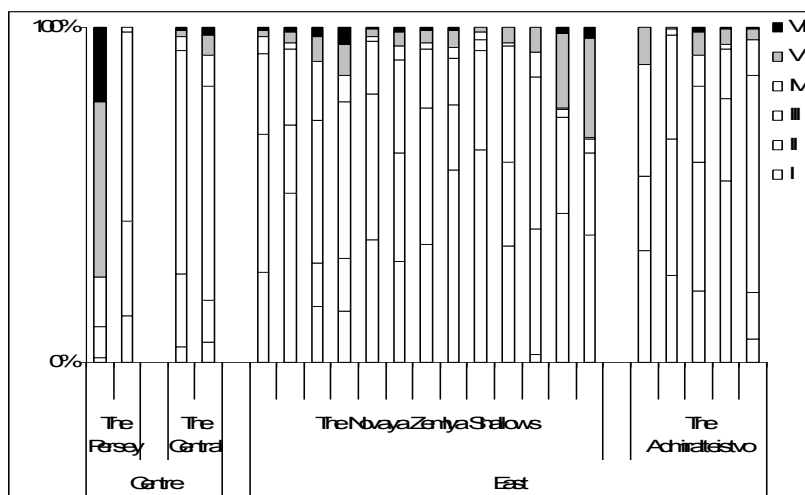
Figure 5. Stage composition of *Calanus finmarchicus* in Arctic waters in August 1987.

The formation of aggregations and the reproduction of the most dominant copepods, observed in August in the northern water areas, corresponded to heavy (3-4 points) blooms of diatoms and golden-brown algae. This was most evident in the first ten-day period of the month, on the Novaya Zemlya Bank, and, in the area of Admiralty Peninsula, where *C. glacialis* was observed in great quantities. In the centre, the bloom finished earlier, due to a more rapid ice retreat, and the number of copepods was thus lower than usual. The exception was the north-west of the Persey Elevation, where in mid-August, in Arctic and mixed waters, intense blooms of diatoms remained, and larger numbers of *C. finmarchicus* concentrations were found. In the west, at the end of August, in the northern waters(mixed waters) the uneven blooming of diatoms and golden-brown algae (Chaetoceros, Phaeocystis) remained, the spawning of *C. finmarchicus* was also observed, but, in most cases, the bulk of its population was made up by copepodite stages (CI-III). The percentage of older *C. finmarchicus* copepodite stages increased in the southern direction, a relative part of *C. glacialis* decreased simultaneously .

As well as the distribution of copepods, there were some differences in their vertical distribution, which influenced biomass values. In the upper layer (0-50 m), they were estimated by a correlation between copepodite stages, maturing and mature individuals. Similarly, in the Arctic and mixed waters of the Novaya Zemlya Bank and the Admiralty Peninsula, where *C. finmarchicus* and *C. glacialis* young were predominant, biomasses were low (2-5 g/m^2). In the center, where high abundance of *C. finmarchicus* CI-IV and *C. glacialis* CIII-V only remained in the north-west of the Persey Elevation, the biomass reached 11-12 g/m^2; in the west, biomasses varied considerably (Fig. 6). In 50-100 m layer, the plankton species composition was close to that one in 0-50 m layer. The areas with relatively close aggregations of *C. glacialis* CV in the north-west and *C. hyperboreus* CIV in the centre and in the east and their joint aggregations were found.

Thus, it should be noticed that copepods had basic migrations within the feeding ground within the depth range of 0-100 m. Meanwhile in some cases our data allow us to support their quite flexible food strategy, which consisted in the shift of food migration time depending on food supply. This peculiarity appeared locally and differentially in different species and age of crustaceans, which conditioned great variations in biomass rates in different layers. On the whole, in the cold 1987, a distinctive feature is low copepod abundance of adults and younger stages, in early August,. The total biomass, mainly consisting of two copepod species, *C. finmarchicus* and *C. glacialis* was low, 1-4 g/m^2. The percentage of *C. glacialis* in Arctic waters was 42-68%, in the mixed waters - 21-75%.
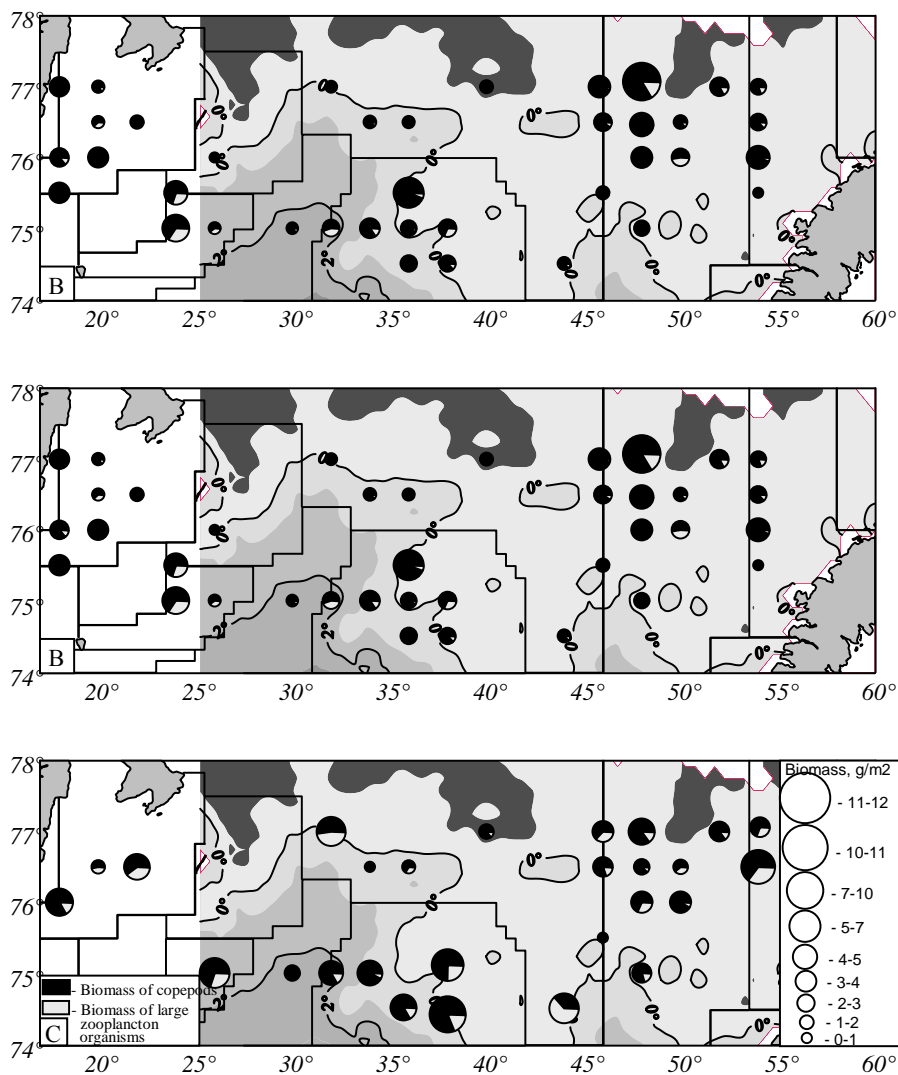
Figure 6. Zooplankton biomass distribution in the 0-50 m layer (A), 50-100 m layer (B) and 100 m-bottom layer (C) in August 1987.

In 1989, the ice conditions in July influenced configuration of boundaries of the Arctic water mass distribution in August-September.

In the east (54-56° E), where the ice edge occupied the most southern area in July, an intensive bloom of diatoms was observed. However, there were few copepods (*C. finmarchicus*, in particular) in that period (Fig. 7). The copepods in minimal numbers were found at the ice edge correspondingly (76°06' N 52°00' E). A stable increase in copepod concentrations, including *C. finmarchicus*, was observed on early August in the northern water areas, in the centre and in the east, along 44-48° E, where the rates of the ice edge retreat rose, followed by an intensive bloom of diatoms. Besides *C. finmarchicus*, the density of *C. glacialis* aggregations also increased there. During the second ten-day period of August, in the centre along 40° E, where the ice edge suddenly retreated to the north, the situation was almost the same, but with the diatom bloom fading. There, in a small territory occupied by Arctic water, at the end of the second ten-day period in August, the bloom was weak and there were few copepods.
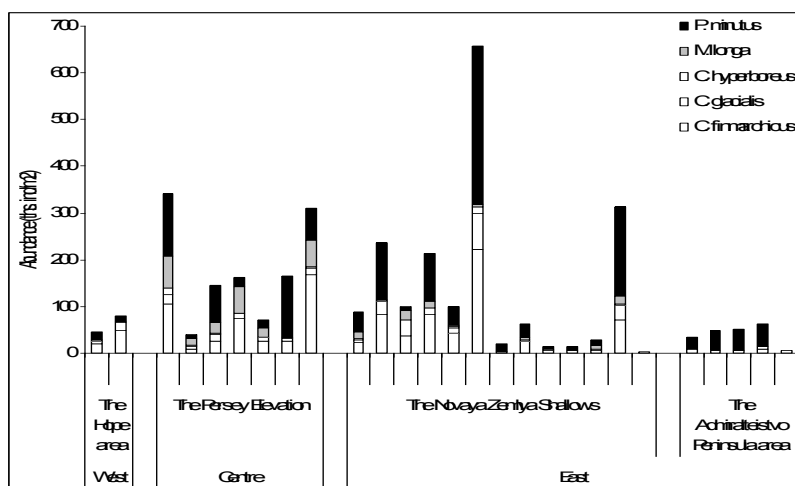
Figure 7. Abundance of zooplankton in Arctic waters in August 1989..

In the areas with mixed waters, the copepods formed denser aggregations, although their numbers were higher in the west. The distribution of *C. finmarchicus* was uneven, with its greatest aggregations mostly in areas with temperatures of 0-1° C. Besides that species, *C. glacialis* was characterized by a wide distribution with a higher density of aggregations mostly in the west and in the centre.

The rates of the ice retreat also influenced the age composition of copepod populations. Along with hibernates overwintering adrift, young fry CI-II and, to a less degree, CIII appeared in the Arctic water masses, at the beginning of August, in areas that had recently became free of ice, where *C. finmarchicus* aggregations were very low (Fig. 8). Although *C. finmarchicus* started their process of reproduction, number of Calanoid nauplii were still low. In the northern water areas, where the temperature was 0-1° C and the intense phytoplankton bloom was observed, the wintered females started the reproduction process, which had a mass character in the east and the centre, after which they accumulated and probably matured. This year, a peculiarity of the *C. glacialis* population structure in the Arctic waters was the abundance of crustaceans CI-III, brought there by the Arctic water masses after the ice-melt in some areas (alongside with wintered individuals CIV-V). The percentage of fry was highest in the east.
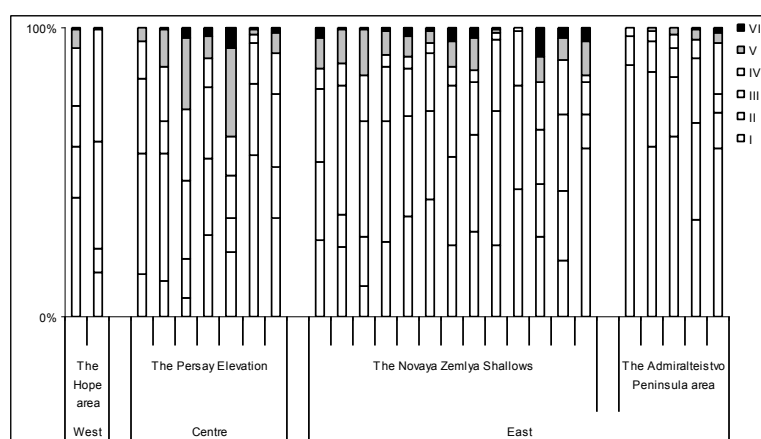

Figure 8. Stage composition of *Calanus finmarchicus* in Arctic waters in August 1989.

In the mixed waters, with their wide spread in the centre and east, the structure of *C. finmarchicus* population was close to that in the Arctic waters. The age composition of populations of *C. glacialis* was generally influenced by the isotherm position at 0° C, which in the west (40° N) passed mostly through northern waters, while in the east, through southern

waters. As a result, in the west, where the ice melting was faster, the percentage of drifting fry (mostly CII-III) was higher (on average 65%, as against 40% in the east). There was an inverse correlation between numbers of individuals in the prespawning stock (CIV-V) and mature females.

On the whole, in 1989, when a increased inflow of Atlantic water occurred simultaneously with wider distribution of Arctic water, plankton biomass was greater than in1987, especially in the mixed waters, where older stages of *C. glacialis* were prevalent. Biomasses were thus also higher., at 3-8 g/m^2 (Fig. 9). In the Arctic water masses,biomasses did not exceed 3-4 $g/m^{2.}$, with a range of of *C. glacialis* of bewteen 44-85%.

In early September 2002, copepod abundance was high, particularly in waters north of 78° N and 40 – 44° E (Fig. 10). *C. glacialis* abundance varied somewhat less. In the toal area, in the centre, occupied by mixed waters, the number of *C. finmarchicus* increased. The exception was the area of the Admiralty Peninsula, where, just as in Arctic waters, the abundance of *C. glacialis* was high. The densest aggregations of that species were in the north-east (77°50’ N 57°50’ E), where ice remained for a long time, and, in mid-September, a bloom of Ceratium (1-3 points) was recorded.
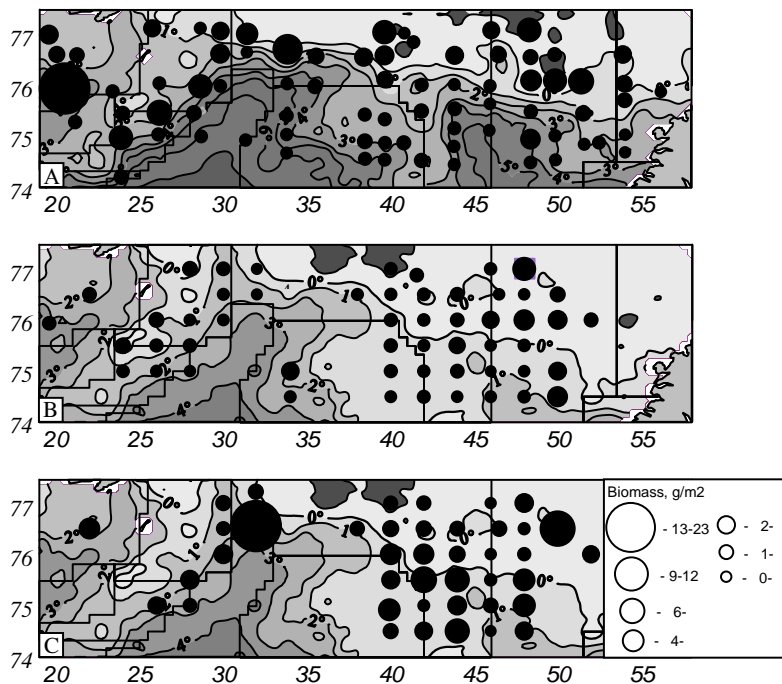

Figure 9. Zooplankton biomass distribution in the 0-50 m layer (A), 50-100 m layer (B) and 100 m-bottom layer (C) in August 1989.

In the areas dominated by *C. finmarchicus*, in the Arctic water masses, its population was mainly represented by fry, but the abundance of young fry (CI-II) was higher in the most northern water areas (FJL), which became free from ice later (Fig. 11). The structure of *C. glacialis* population was also characterized by the fry predominance, but in the area of FJL, the percentage of young fry was low, while the percentage of CIV-V (VI) notably increased.
The predominance of *C. finmarchicus* in the population structure in the north (78-81° N) of the recruitment area, in particular, caused biomass variations. In the mixed waters, their biomass rates reached a maximum level (4.4-12.5 g/m^2) in the north of FJL area and in the east with *C. glacialis, a* value of 75-90% (Fig. 12).
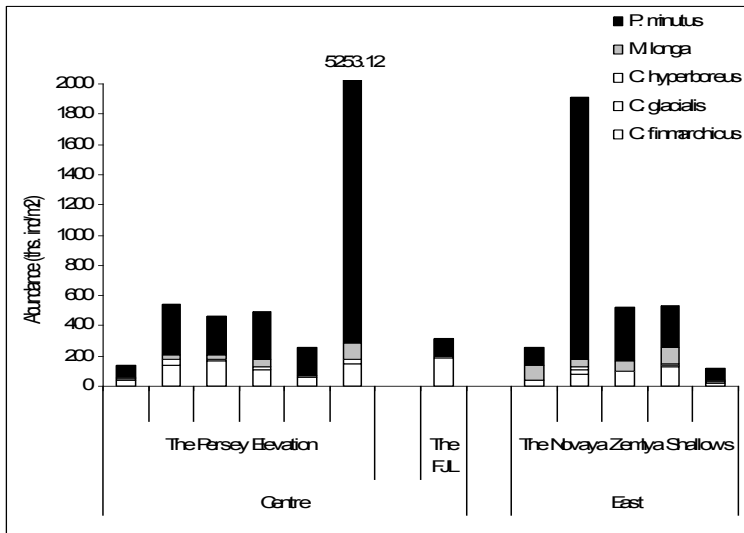
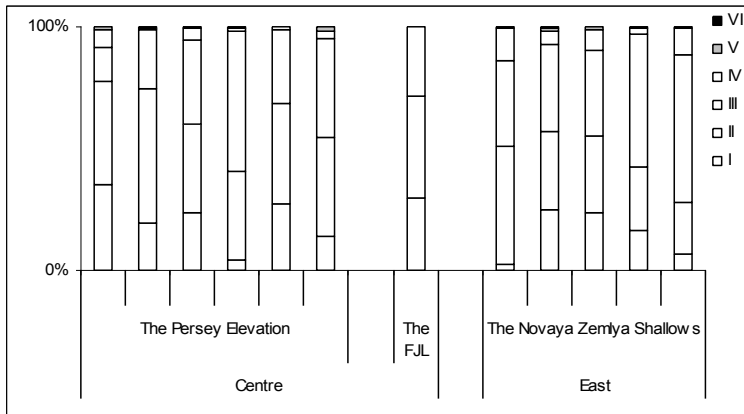**Figure 10**. Abundance of zooplankton in Arctic waters in August-September 2002**.**

Figure 11. Stage composition of *Calanus finmarchicus* in Arctic waters in August 2002.
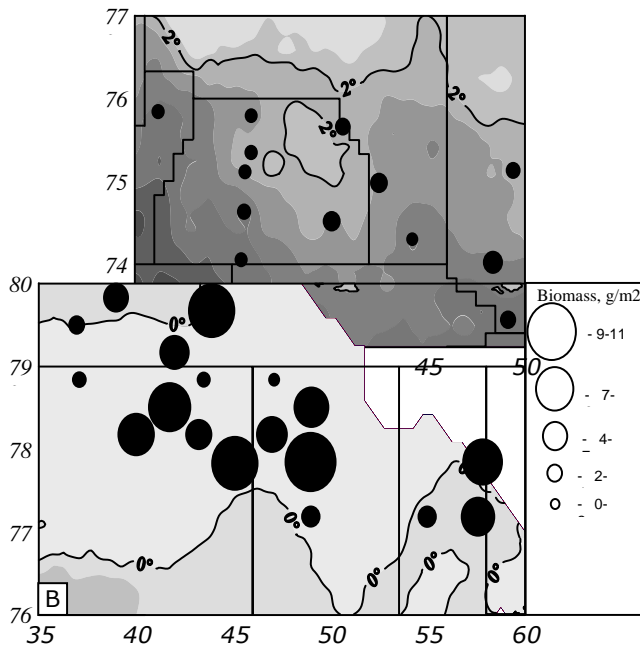

Figure 12. Zooplankton biomass distribution in the 0-50 m layer (A) and 100 m-bottom layer (B) in August-September 2002.

In 2004 the Arctic waters were widespread only in the north-east (FJL, the Novaya Zemlya Bank), while the mixed waters occupied a large area from eastern to north-western areas, with a southern boundary around 76-77° N.

154

In Arctic waters between September 4 and 19, a bloom of Peridinea algae was observed, reaching its greatest intensity (3 points) in the east. Among the plankton, Arctic species were observed in equal ratios (Fig. 13). On the Novaya Zemlya Bank, the percentage of *C. finmarchicus* was also high. Both speciues of Calanus were generally represented by fry. In areas with mixed waters (between 76-77° and 81° N), the basic differences in plankton were a result of the abundance and age composition of *C. finmarchicus* and *C. glacialis*, which predominated in different sea areas. A predominance of *C. finmarchicus* was clearly observed to the west of FJL (81°25' N 31°33' E), but its abundance decreased eastwards, while the abundance of *C. glacialis* rose in the eastern area. In the areas of *C. glacialis* predominance, that species was obviously reproducing, as its large eggs were regularly found here.
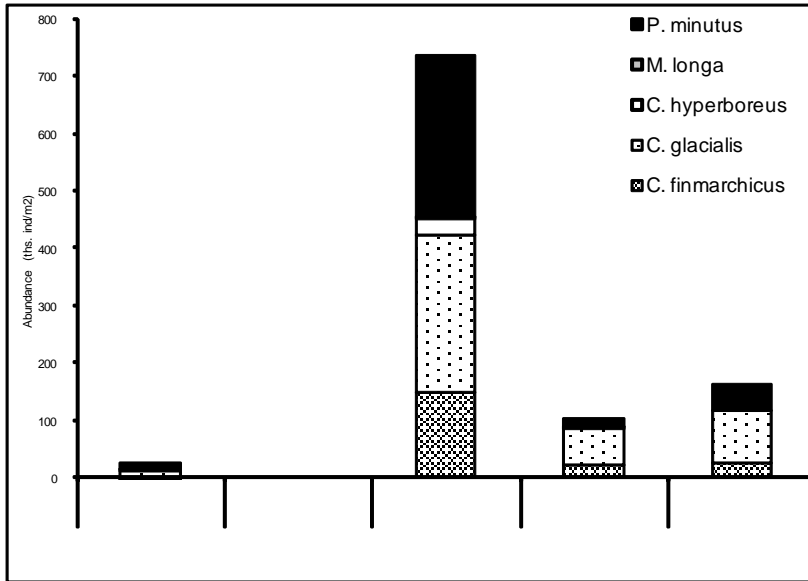

Figur 13. Abundance of zooplankton in Arctic waters in August-September 2004.

In 2004, the tendency to high biomass formation in the areas of *C. glacialis* mass distribution remained (Fig. 14). This year, with its maximal percentage both in the Arctic and mixed waters, biomasses rose to 2.8-12.6 and 4.6-8.6 g/m^2 correspondingly.
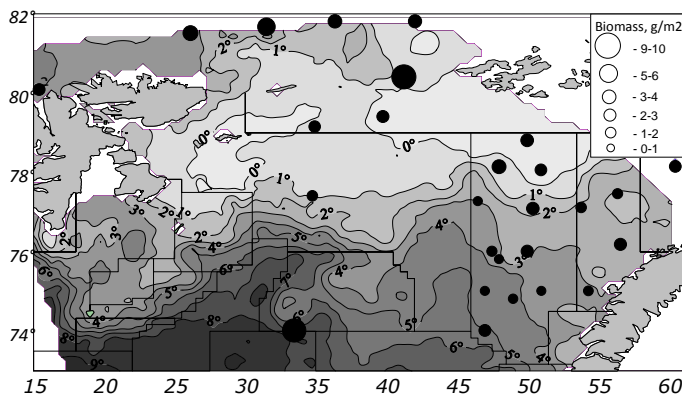
Figure 14. Zooplankton biomass distribution in the 0-50 m layer in August-September 2004.

In 2005 the distribution of the Arctic water masses in September was delimited by the north-western and north-eastern areas. *C. finmarchicus* and *C. glacialis* were predominantin the plankton. Total copepod concentrations were low. In the large area occupied by mixed waters, plankton aggregations reached high values in the western areas of FJL and the Persey Elevation. Their species composition was close to that of the Arctic waters (Fig. 15).
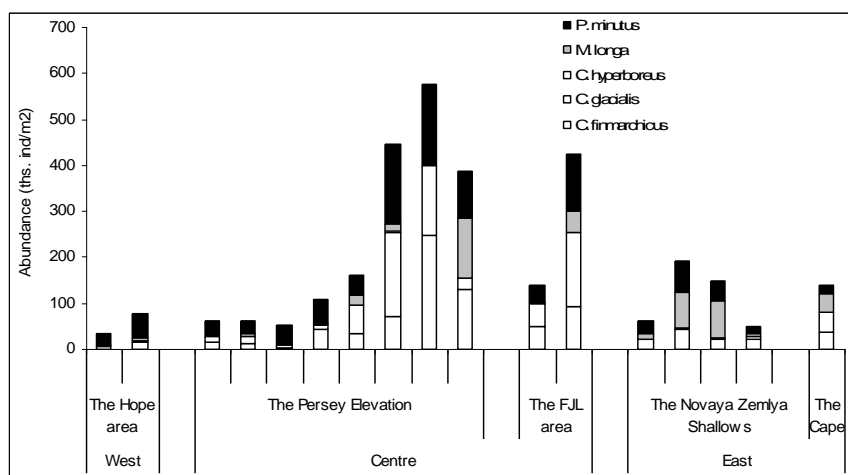
Figure 15. Abundance of zooplankton in the mixed waters in August-September 2005.

In September, individuals of all stages were observed in the Arctic waters, and their relationships were characterized by a large variability. In the north-west between 13 and 24 September, a weak bloom of peridinea algae was observed.

In the *C. finmarchicus* population CI-II fry predominated, and nauplii Calanoida were observed in large quantities, though eggs were rarely found. At the same time, in the centre and east (77°50'-80°45' N 32-59°30' E), phytoplankton development was not homogeneous, presenting a series of isolated patches, where intensive blooms of peridinea and diatom algae were observed along with an absence of algae. The dominating groups of *C. finmarchicus* were CI-III, while CIV individualswere in abundance.

At the same time, in this area, intensive reproduction of *C. glacialis* and *C. hyperboreus* was observed in the east. A similar situation was noticed in the mixed waters, with the difference that in the west (76-78° N 25-30° E), in the second half of September, an intense diatom bloom (1-3 points), and a weak bloom of Peridinea algae were recorded.

The early stage of plankton development took place in the east (78-80° N 33-35° E) as was indicated by a high abundance of *C. finmarchicus* fry (CI-II), the regular occurrence of Calanoid eggs, and large quantities of nauplii and females. Moreover, as the abundance of *C. glacialis* was high, mass reproduction of that species was observed there along with one of *C. hyperborus*. Meanwhile, a sudden replacement of diatoms by Peridinea algae occurred with a high-intensity bloom (2-3 points).

More significant variations in plankton development were observed in the centre and east, where the ice edge reached 80° N in July. The most characteristic features in *C. finmarchicus* population were CIII predominance in the first ten-day period of September. The only exception was the most northerly and easterly areas, where the essential part was occupied by young fry of *C. finmarchicus* and CIII-IV groups and large quantities of nauplii, while in the east, large eggs, probably of *C. glacialis,* were observed. That species reproduced at that time in the vicinity of FJL , where it was characterized by a high abundance. The ratio of males and females was almost equal (3:2; 4:4; 9:8); in the other areas females prevailed.

In 2005, the most significant differences in biomass values were found at the expense of copepods (0.7-6 g/m^2 in the Arctic waters and 0.4-27 g/m^2 in the mixed waters) (Fig. 16). As in 2002-2004, in most cases, the maximal biomasses appeared in northern watersthanks to *C. glacialis*, which came to 60-100% in the Arctic water masses (biomasses 4.7-7.7 g/m^2) and to

156

30-95% in the mixed ones (biomasses 5.6-27 g/m^2). Sometimes, mostly in the mixed waters, the leading role in biomass formation was played by *C. finmarchicus* (biomass 1.8-12 g/m^2).

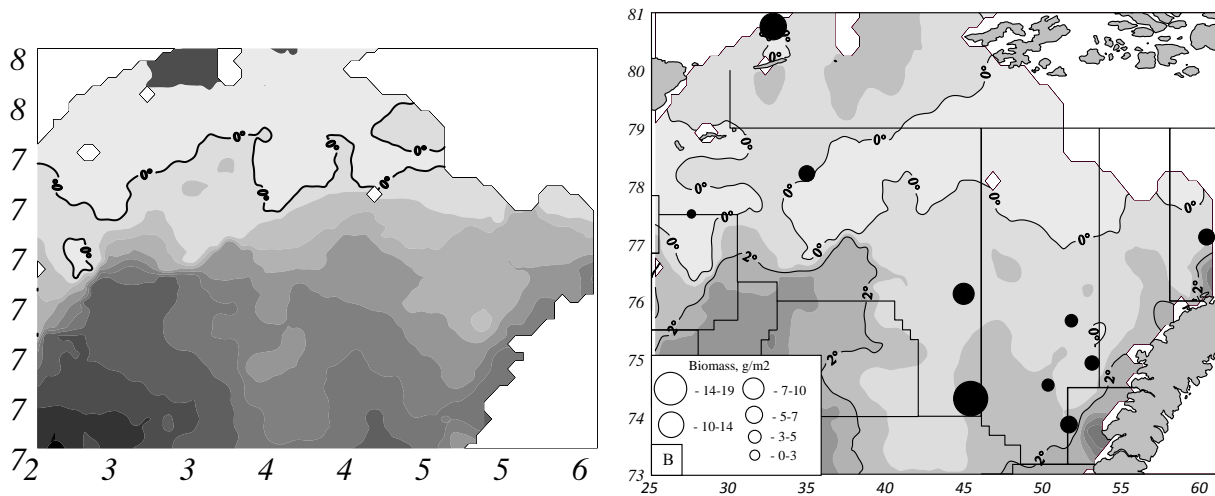**Figure 16**. Zooplankton biomass distribution in the 0-50 m layer (A) and 100 m-bottom layer (B) in August-September 2005.

DISCUSSION

The data available from the Barents Sea allowed the major pattern of plankton community structure formation in different parts of the Barents Sea to be traced. The sea ice dynamics is the main factor for this process, which influences the distribution of water masses of different origin. This factor was thus crucial in forming the populations of the dominant copepod species, *C. finmarchicus* and *C. glacialis*. The link between plankton and hydrological factors along with the specific character of different climatic periods, had common features in a number of cases.

In August 1987 and 1989, in spite of the differences in the areas occupied by Arctic water (large in 1987 and limited in 1989), the character of the biological processes that took place there was quite similar. In both years, in the Arctic water with its northern boundary along 77° N, intensive reproduction of *C. finmarchicus* was taking place. At the same time its population recruited young fry transported from southern spawning sites. However, due to the late retreat of the ice, the density of *C. finmarchicus* aggregations, as well as those of other species, was not high. At the same time, one can assume that there was an accumulation of transported plankton along the ice edge and during its sudden retreat .

In some places with higher horizontal gradient of water temperature (in 1987 along 44-50° E, in 1989 along 44-48° E) "outbreaks" of *C. finmarchicus* population's growth were observed. They were also found in other locations but with lower intensities. On that background in the mixed waters occupying small areas (in 1987), aggregations of *C. finmarchicus* were small. Its reproduction here in the second half of August was in its final stages, except for northern areas in the west and centre; the distribution of nauplii was wider. In 1989, in the mixed waters, the aggregations of *C. finmarchicus* were larger; its intensive reproduction was only observed in the first ten days of August in the southern areas in the centre and east.

The differences in *C. glacialis* in those years were more prominent. In 1987, in the Arctic water mostly stage V hibernates were found in small numbers, some of which began

157

reproduction throughout the whole area after the ice retreat. In the mixed waters a similar situation was observed. At the same time sparse aggregations of its fry were found, mostly in Arctic waters in the east. In 1989, large numbers of *C. glacialis* were typical, due to large amounts of ice arriving and melting. In the Arctic water (east and centre) large aggregations of hibernating stages IV-V were found, but reproduction of *C. glacialis* was extremely rare. Distribution of the fry was widespread but patchy. In the mixed waters (centre and west) the number of fry was greatest.

The data for 2002, 2004 and 2005 reflected not only the specific character of the warm period but also the specific features of year-to-year dynamics of copepod distribution in September in relation to rates of ice retreat. In 2002, when the ice edge lay to the north of its multi-year average position and Arctic water masses occupied a vast area from 78 to 81° N, the population of *C. finmarchicus* was larger than in other years. This species was also numerous in the northern areas of mixed waters, with a distribution that was significantly greater than that of *C. glacialis*. In 2004, when the ice edge in July was more dynamic the area of distribution of *C. finmarchicus* in Arctic waters was small, as was its population. At the same time dramatic increases in the population of the Arctic *C. glacialis* and in its large habitat were observed, especially in the east. In 2005, in spite of the most northerly position of the ice edge occurring in July, the population of *C. finmarchicus* in Arctic waters was lower than in 2002 and 2004, due to weaker heat advection and the later ice retreat in the east. Its major component was found in the mixed waters; in the centre the aggregations were denser than in the east and sometimes even exceeded those in 2002.

In spite of these differences large numbers of transported fry were characteristic of the populations of both species in both Arctic and mixed waters. In some years (2002, 2005) in northerly areas, *C. finmarchicus* were still reproducing at the same time. In the mixed waters this happened mostly in the north and east (2002), and in 2005 the reproduction period was extended due to the large area occupied by these waters. Reproduction of *C. glacialis* was also more active and prolonged in 2005 in the mixed waters in the centre and east. Along with fry and mature individuals in the populations of *C. finmarchicus* and *C. glacialis,*stage IV-V hibernates were also found locally (2002, 2005).

Development rates also varied. By mid-August in 1987 and 1989, in Arctic waters around the Persey Elevation, a large proportion of *C. finmarchicus* and *C. glacialis* fry had reached stage III; in the west the development was even more rapid. Obviously,particular features of the hydrological regime in those years played the main role: the intensive retreat of the ice to the north due to its faster erosion caused by steady southern winds and thus abnormally higher air temperatures. We may therefore assume that the copepods transported in August were developing in warmer waters further to the south. In September 2002 and 2005 in Arctic waters which were expanding far northwards, C. finmarchicus was mostly represented by CI-II with a transition into CIII, while *C. glacialis* was represented by CII-III. In the mixed waters their reproduction took place more rapidly, and in consequence, stages II-III and III were dominant. In 2005, due to the extended reproduction period of *C. finmarchicus,* a larger proportion of young fry was observed in the north than in the south, where CIII prevailed. In general the crustaceans' development directly depended on their latitude, and at the southern stations they often reached stages IV-V, while in the north, in contrast, in a number of cases their reproduction was still being observed.

The research data illustrate the time difference in seasonal changes in copepod development in different parts of the latitude zone of the Barents Sea, asis confirmed by the condition of

the plant community. Thus, intensive blooms of diatomic algae (often simultaneously with yellow-green algae and peridineans) were usually observed in Arctic waters in the first half of August in the east and centre after the ice edge retreat and in the Arctic and mixed waters in the west; by the end of the month this had slackened (1987, 1989). In September in abnormally warm years the ice edge retreat reached 78-80º N and was accompanied by intensive bloom, though diatomaceous algae were replaced by peridineans (2002, 2004) and only in individual cases in the centre and east (80º N) were blooms simultaneous of diatom and peridinean algae observed (2005).

Thus, while in cold years spring processes in the pelagic zone were already taking place in August, in warmer years the northern ice edge position in July effectively caused these processes to shift to September. This becomes quite obvious when we compare our data for August-September and early July (Arashkevich et al., 2002). The stage structures in the populations of *C. finmarchicus* and *C. glacialis* (August 1987 and 1989) in the ice-free area close to the Persey Elevation thus match quite well those of July (considering the time-related changes in the crustaceans' development). Large numbers of both species' stage CI-III fry were a common feature in these years in the area 76-77º N. The cold year of 1987 was an exception, when *C. glacialis* was represented only by older copepodites (CIII-V). However, further north our data showed an obvious discrepancy with those of the the above-mentioned authors, especially with respect to *C. finmarchicus*. In July 1999 at the northern stations (77-78º N) the latter species was only represented by older, mature individuals (CIV-VI) while in the *C. glacialis* population fry just began to appear. In September of the abnormally warm years (2004-2005) the areas around 78-79º N were free of ice. As a result, in both species, fry were the dominant stage, just as in August 1987 and 1989.

The biomass depended on the numbers of the dominant species; *C. finmarchicus* and *C. glacialis*, their reproduction scale, ratio between younger and older copepodites and growth rates. In this study the maximum biomasses were found in the northern areas in Arctic and mixed waters, where there was a large proportion of older copepodites and mature individuals of both species; the role of *C. glacialis* was becoming more important. This species alone helped the biomasses reach 10-25 g/m^2. In most other cases they varied considerably.

These data closely match the data of the maximal efficient feeding of capelin at high latitudes in 2002 (Orlova et al., 2006), permitting us to draw a comparison with the cold 1970s, when capelin were abundant and distributed in the north and east (Røttingen and Dommasnes, 1985) and reached high fatness (15-18%) in September because their diet included a high proportion of large copepods (*C. finmarchicus, C. glacialis, C. hyperboreus*) with a higher fat content. Their caloric value in Arctic waters in autumn reaches 2-2.8 Kkal/g (Kosobokova, 1980). Crustaceans, in their turn, have such a high proportion of fat due to their feeding on high-latitude phytoplankton which is characterized by a high lipid content under unstable dietary conditions (Clarke, 1983). This can be explained by the fact that the northern area (78º30′ N) is the richest in the quantitative development of the phytoplankton (Zernova, Shevchenko, Politova, 2002), and because in September large amounts flora typical of the ice zone can still be found south of Franz Josef Land.

References

Anon., 2003.The state of biologic raw material resources in the Barents Sea and the North Atlantic in 2006. PINRO Press, Murmansk (in Russian).

Arashkevich E., Wassmann P., Pasternak A., Riser C.W. 2002. Seasonal and spatial changes in biomass, structure, and development progress of the zooplankton community in the Barents Sea. Journal of Marine Systems 38: 125-145.

Boitsov V.D., Tereshchenko V.V. 1998. Inter-annual variations in characteristics of water masses in the area "Kolsky meridian" during conducted survey of 0 – group fishes in the Barents Sea. In: Materials of the PINRO reporting session on the results of the researches made in 1996-1997. PINRO Press, Murmansk, p. 230-238 (in Russian).

Borovkov V.A., Boitsov V.D., Ozhigin V.K., Guzenko V.V., Nikiforov A.G., Sentaybov E.V., Pedchenko A.P., Lobodenko C.E. 2004. Spatial and temporal variations of abiotic factors and their impact on biological and fishing parameters in the North Basin in 2001-2002. Voprosy promyslovoj okeanologii. VNIRO Press, Moscow, Vyp. 1, pp. 22-39.

Clarke A. 1983. Live in cod water: the physiological ecology of polar marine ecosystems. Oceanography and Mar. Biol. Ann. Rev., No. 21. p. 342-453.

Degtereva, A.A., Nesterova V.N. and L.D.Panasenko. 1990. Forming of feeding zooplankton in the feeding grounds of capelin in the Barents Sea. Kormovye resursy i pishchevye vzaimootnosheniya ryb Severnoj Atlantiki. Selected papers. PINRO – Ichthyological Commission of the Ministry of Fisheries of the USSR. Murmansk, p. 24-33 (in Russian).

Hassel A., Skjoldal H.R., Gjøsæter H. et al. 1991. Impact of grazing by ?? capelin (Mallotus villosus) on zooplankton: a case study in the northern Barents Sea in August 1985. Polar Research 10(2): 371-388.

Koptev A.V., Nesterova V.N. 1983. Latitudinal distribution of summer feeding plankton in the eastern areas of the Barents Sea. Issledovaniya biologii, morphologii and phisiologii gidrobiontov. Apatity, pp 22-28 (in Russian).

Kosobokova K.N. 1980. Caloric value of some zooplankton representatives in the Arctic basin and the White Sea. In : Oceanology. No.1, p. 129-136.

Loeng H. 1991. Features of the physical oceanography of the Barents Sea. Polar Research 10(1): 5-18.

Melle W., Skjoldal H.R. 1998. Reproduction and development of Calanus finmarchicus, C. glacialis and C. hyperboreus in the Barents Sea. Marine Ecology Progress Series: MEPS 169: 211-228.

Orlova E.L., Ushakov N.G., Nesterova V.N., Boitsov V.D. 2002. Food supply and feeding of capelin (Mallotus villosus) of different size in the central latitudinal zone of the Barents Sea during intermediate and warm years. Capelin – What Are They Good For? Biology, Management, and the Ecological Role of Capelin.ICES J. Mar. Sci. 59 (5): 968-975.

Orlova, E.L., Boitsov V.D. and N.G.Ushakov. 2004. Conditions of summer feeding and growth of capelin from the Barents Sea. Murmansk, PINRO Press, 198 pp. (in Russian).

Orlova, E.L., Ushakov N.G., Rudneva G.B., Prozorkevich D.V. et al. 2005. Populational structure, distribution and the long-term dynamics of capelin feeding in the Bear Island-Spitsbergen area. Kompleksnye issledovaniya prirody Shpitsbergena. Apatity, Vyp,5. Proceedings of the 5th International Conference (Murmansk, October 2005), p. 461-480 (in Russian).

Orlova E.L., Boitsov V.D., Rudneva G.B., Nesterova V.N., Konstantinova L.L., Ushakov N.G. 2006. Feeding, conditions, fatness and maturation rates of capelin in the central latitudinal zone of the Barents Sea in 2001-2003. Investigations of interactions between

marine species of the Barents and Norwegian Seas: Selected PINRO papers. PINRO Press, Murmansk, pp. 71-98.

Orlova E.L., Guzenko V.V., Nesterova V.N., Gabova O.V. 2007. Oceanographic peculiarities of plankton community formation in the north- eastern part of the Barents Sea in abnormally warm years. In: Voprosy ribolovstva. Vol. 8, No. 2 (30), p. 195-208 (in Russian).

Ozhigin V.K., Ivshin V.A. 1999. The Barents Sea water masses, PINRO Press, Murmansk, 48 pp (in Russian).

Pedchenko, A.P., Borovkov V.A., Guzenko V.V. et al., Karsakov A.L., Lobodenko S.E. and Sentyabov E. V. 2005. Spatial and temporal variations of abiotic factors and their influence on distribution of main commercial fish species in the North Basin in 2003-2004. Voprosy promyslovoj okeanologii. VNIRO Press, Vyp.2, p. 101-125 (in Russian).

Røttingen I., Dommasnes A. 1985. The acoustic estimation of the Barents Sea capelin stocks in 1974-1984. (review). In : Selected papers of the 2nd Russian- Norwegian symposium. Biology and fishery of the capelin in the Barents Sea.. PINRO Press, Murmansk, p. 49-123.

Skjoldal, H.P., Hassel A., Ray F., Loeng H.. 1987. Spring development of phytoplankton and reproduction of zooplankton in the central part of the Barents Sea in 1979-1984. The effect of hydrographic conditions on distribution and dynamics of commercial fish species populations of the Barents Sea. Selected papers of the 3rd Soviet-Norwegian Symposium. PINRO Press, Murmansk, p. 71-111 (in Russian).

Skjoldal, H.P., Gjøsaeter H. and H.Loeng. 1992. Ecosystem of the Barents sea in the 1980s-1990s: climate variations, plankton and capelin growth. Study of relations of fish populations in the Barents Sea. Selected papers of the 5th Soviet-Norwegian Symposium. PINRO Press, Murmansk, p.310-339 (in Russian).

Tande K.S. (1991) Calanus in north Norwegian fjords and in the Barents Sea. Polar Research (10): 389-407.

Tereshchenko, V.V. 1999. Hydrometeorological conditions in the Barents Sea in 1985-1998. PINRO Press, Murmansk, p. 176 (in Russian).

Yashnov, V.A. 1961. Water masses and plankton. Species of Calanus finmarchicus as indicators of certain water masses. Zool. Zhurnal, vol. 40, No.9, p. 1313-1334 (in Russian).

Zernova V.V, Shevchenko V.P., Politova N.V. 2002. Phytoplankton in the north- eastern part of the Barents sea in the autumn 1997. The Arctic and the Antarctic. Nauka Press, Moscow, p. 193-211 (in Russian).