

Seasonal and spatial changes in biomass, structure, and development progress of the zooplankton community in the Barents Sea

Elena Arashkevich^{a,*}, Paul Wassmann^b, Anna Pasternak^a, Christian Wexels Riser^b

^a*P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences, Nakhimovsky Avenue 36, Moscow 117851, Russia*

^b*Norwegian College of Fishery Science, University of Tromsø, N-9037 Tromsø, Norway*

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Abstract

During three cruises, in March and May 1998 and July 1999, seasonal and regional variations in biomass and vertical distribution of mesozooplankton as well as cohort development in *Calanus* spp. were investigated along a transect across the central Barents Sea and marginal ice zone. There were no considerable changes in zooplankton biomass between the seasons. Throughout the investigation, the average biomass for the entire region approximated to ca. 5 g dry weight (DW) m⁻² while station-to-station variation ranged with an order of magnitude (1–14 g DW m⁻²). Biomass of nauplii and small copepods (200–500 µm in body length) obtained from water bottles samples exceeded that from WP-2 net samples 1.5–6.6 times. The maximum abundance of this group reached 16 × 10⁵ ind. m⁻² in the upper 100-m layer, suggesting a significant grazing pressure on phytoplankton. Spatial distribution of *Calanus* species and some selected species suggests that the zooplankton community composition was primarily affected by water mass circulation and bottom topography. Both the depth distribution of mesozooplankton and cohort progress in *Calanus finmarchicus* and *Calanus glacialis* revealed two waves of spring events. The first started in the southernmost area of the Barents Sea and the second nearby the Polar Front. Both developed towards the north.

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Keywords: Barents Sea; Zooplankton; Depth distribution; Seasonal changes; *Calanus*; Development progress

1. Introduction

The Barents Sea is one of the most productive regions of the World Ocean (Zenkevich, 1963; Bogorov et al., 1968). Zooplankton communities in the basin have been intensively investigated since the

beginning of the last century (Gran, 1902; Linko, 1907; Jashnov, 1939, 1967; Kamshilov, 1952; Zelikman and Kamshilov, 1960; Degtereva, 1973). It has been shown that abundance and structure of the zooplankton community display considerable variations on seasonal, interannual, and regional scales. The seasonal variation in zooplankton is connected with the strong seasonal pulse in environmental conditions that are typical for high-latitude ecosystems (Zelikman and Kamshilov, 1960; Hassel, 1986; Pedersen et al.,

* Corresponding author. Fax: +7-95-1248515.

E-mail address: aelena@sio.rssi.ru (E. Arashkevich).

1995). A short, 2- to 3-month-long vegetative period accompanied by developmental progress in zooplankton gives place to a long period of overwintering accompanied by migration of most forms to depth.

Interannual fluctuations in zooplankton biomass are reported to be as high as an order of magnitude (Zelikman and Kamshilov, 1960; Skjoldal et al., 1987). Different factors and processes contribute to these oscillations: temperature (Degtereva, 1973; Timofeev, 1997), predation (Zelikman and Kamshilov, 1960; Hassel et al., 1991), and advection of zooplank-

ton with the Atlantic water (Skjoldal et al., 1987; Loeng et al., 1997; Helle, 2000). Although links between interannual variations in zooplankton biomass and the variability in the Atlantic inflow have been suggested, endemic processes in the Barents Sea also appear to contribute to zooplankton biomass and productivity (Zelikman and Kamshilov, 1960; Tande, 1991; Tande et al., 2000).

Spatial variation in zooplankton biomass is affected by local feeding conditions (Zelikman and Kamshilov, 1960), and grazing by planktophagous

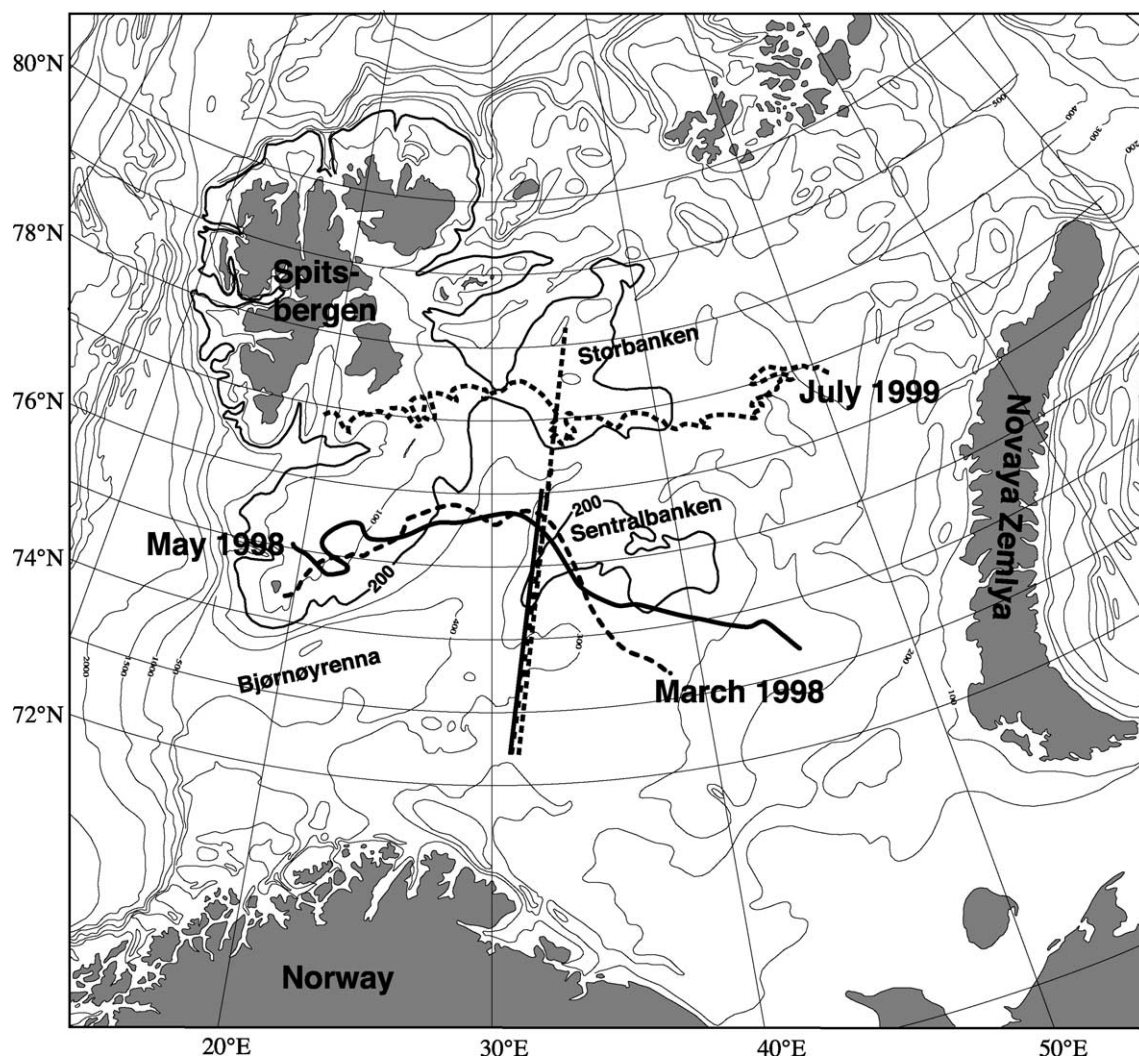


Fig. 1. The study area in the central Barents Sea, position of the transects, and ice edge location during the three cruises in March 1998, May 1998, and July 1999.

fish (Hassel et al., 1991) and ctenophores (Zelikman and Kamshilov, 1960; Swanberg and Båmstedt, 1991). The regional changes in plankton structure are conditioned by latitudinal alteration in climate and complicated by oceanographic conditions in the Barents Sea (Loeng, 1991). Bottom topography is likely to be one of the factors affecting the spatial

heterogeneity in new production (Reigstad et al., 2002) and zooplankton distribution (Pedersen et al., 1995).

Key zooplankton species in the Barents Sea are the copepods *Calanus finmarchicus* and *Calanus glacialis*. The former is of North Atlantic origin and can be used as a tracer of Atlantic water masses; the latter is a

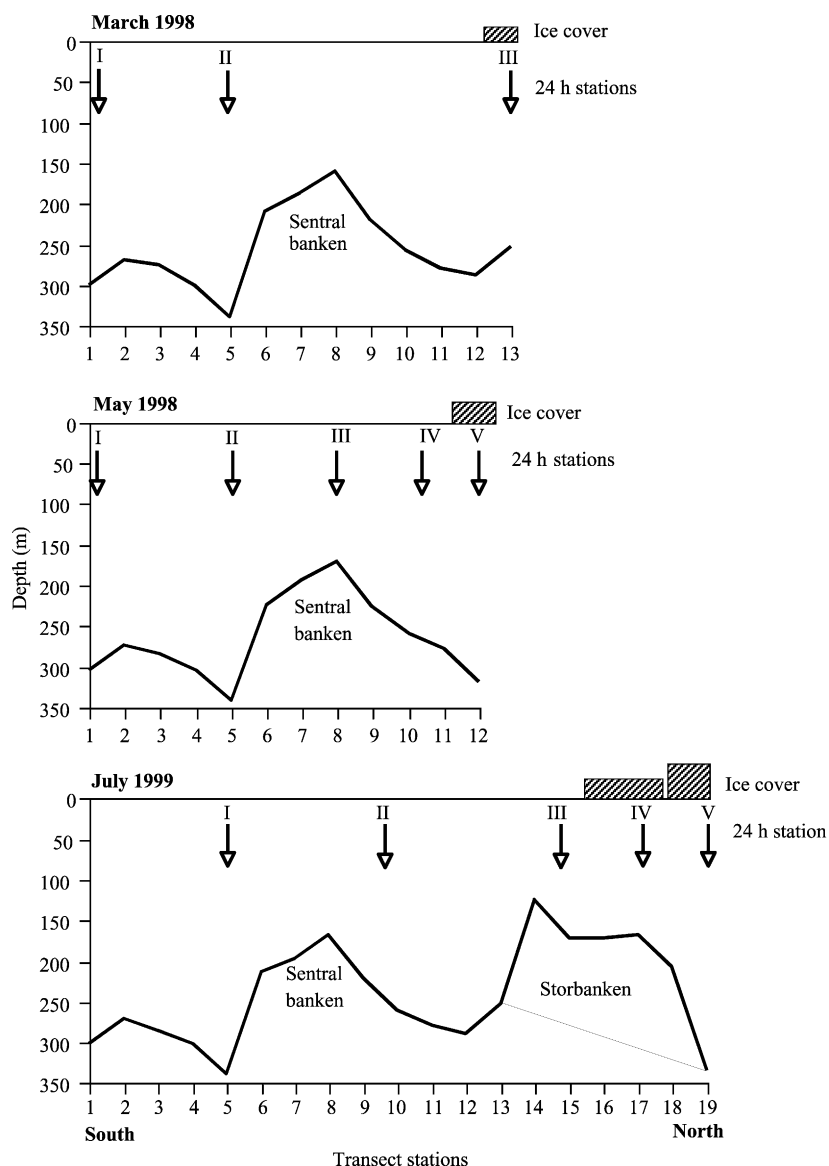


Fig. 2. Topography and ice index along the transects in the central Barents Sea in March and May 1998 and July 1999. Also shown are the transect stations (x-axis) and the 24-h station (roman numerals).

Table 1

Summary of biological sampling during three cruises in the Barents Sea in March (ALV-I), May (ALV-II) 1998, and June/July 1999 (ALV-III) with the percentage of ice cover

	Date	Time	Latitude	Longitude	Ice (%)	Sampling depths (m)
<i>ALV-I</i>						
<i>Transect stations</i>						
1	17/03	22:00	72°30.0'	30°59.7'	0	WP-2, 290–0
3	18/03	04:10	73°09.2'	31°23.1'	0	WP-2, 266–0
5	18/03	08:00	73°48.7'	31°44.5'	0	WP-2, 330–0
7	18/03	14:45	74°28.2'	32°12.0'	0	WP-2, 180–0
9	18/03	18:00	75°07.5'	32°33.2'	0	WP-2, 210–0
11	18/03	22:30	75°49.0'	32°59.5'	0	WP-2, 270–0
13	19/03	02:30	76°23.9'	33°20.9'	50–70	WP-2, 246–0
<i>24-h stations</i>						
I	23/03	11:00	72°32.9'	30°58.9'	0	NWB, 10, 30, 50, 75, 90
	23/03	12:30				WP-2, 280–100, 100–50, 50–0
	23/03	23:00				NWB, 10, 30, 50, 75, 90
	24/03	01:00				WP-2, 290–100, 100–50, 50–0
II	21/03	11:00	73°46.0'	31°52.6'		NWB, 10, 30, 50, 75, 90
	21/03	12:30				WP-2, 340–100, 100–50, 50–0
	21/03	23:00				NWB, 10, 30, 50, 75, 90
	22/03	00:30				WP-2, 325–100, 100–50, 50–0
III	19/03	10:00	76°23.2'	33°12.5'	50–70	NWB, 10, 30, 50, 75, 90
	19/03	15:00				WP-2, 250–100, 100–50, 50–0
	19/03	22:00				NWB, 10, 30, 50, 75, 90
	20/03	00:30				WP-2, 340–100, 100–50, 50–0
<i>ALV-II</i>						
<i>Transect stations</i>						
1	19/05	01:00	72°30.1'	30°59.6'	0	WP-2, 280–0
11	19/05	23:55	75°27.2'	32°45.3'	0	WP-2, 271–0
<i>24-h stations</i>						
I	28/05	10:30	72°29.7'	30°56.8'	0	WP-2, 100–50, 50–0
	28/05	12:00				NWB, 10, 30, 50, 100, 150
	28/05	23:00				WP-2, 290–100, 100–50, 50–0
	29/05	00:00				NWB, 10, 30, 50, 100, 150
II	26/05	12:00	73°47.3'	31°38.6'	0	NWB, 10, 30, 50, 100, 150
	27/05	00:00				NWB, 10, 30, 50, 100, 150
III	24/05	11:00	74°48.1'	32°27.5'	0	WP-2, 168–100, 100–50, 50–0
	24/05	12:00				NWB, 10, 30, 50, 100, 150
	24/05	23:00				WP-2, 165–100, 100–50, 50–0
IV	22/05	11:30	75°36.7'	33°03.7'	0	WP-2, 230–100, 100–50, 50–0
	22/05	12:30				NWB, 10, 30, 50, 100, 150
	22/05	23:00				WP-2, 240–100, 100–50, 50–0
	23/05	00:00				NWB, 10, 30, 50, 100, 150
V	20/05	10:00	76°01.2'	32°59.4'	50–80	WP-2, 100–50, 50–0
	20/05	12:00				NWB, 10, 30, 50, 100, 150
	20/05	23:00				WP-2, 315–100, 100–50, 50–0
	21/05	00:00				NWB, 10, 30, 50, 100, 150
<i>ALV-III</i>						
<i>Transect stations</i>						
1	29/06	21:00	72°29.9'	30°59.8'	0	WP-2, 260–0
3	30/06	02:15	73°08.7'	31°22.8'	0	WP-2, 280–0

Table 1 (continued)

	Date	Time	Latitude	Longitude	Ice (%)	Sampling depths (m)
<i>ALV-III</i>						
<i>Transect stations</i>						
5	30/06	07:30	73°48.7'	31°44.6'	0	WP-2, 310–0
7	30/06	12:45	74°28.0'	32°11.6'	0	WP-2, 190–0
9	30/06	16:45	75°07.5'	32°33.1'	0	WP-2, 210–0
11	30/06	21:35	75°48.9'	32°58.1'	0	WP-2, 270–0
13	01/07	01:45	76°23.9'	33°21.4'	0	WP-2, 240–0
15	01/07	06:45	77°03.5'	33°46.5'	0	WP-2, 160–0
17	01/07	13:45	77°41.1'	34°12.4'	20–50	WP-2, 160–0
19	01/07	21:30	78°12.0'	34°31.2'	50–80	WP-2, 220–0
<i>24-h stations</i>						
I	09/07	10:00	73°49.9'	31°46.5'	0	NWB, 10, 30, 50, 100, 150
	09/07	11:00				WP-2, 330–100, 100–50, 50–0
	09/07	22:00				NWB, 10, 30, 50, 100, 150
	09/07	23:00				WP-2, 325–100, 100–50, 50–0
II	07/07	22:00	75°08.3'	32°21.8'	0	NWB, 10, 30, 50, 100, 150
	07/07	23:30				WP-2, 230–100, 100–50, 50–0
	08/07	10:00				NWB, 10, 30, 50, 100, 150
	08/07	12:00				WP-2, 230–100, 100–50, 50–0
III	05/07	22:00	77°03.5'	33°48.0'	0	NWB, 10, 30, 50, 100, 150
	05/07	23:00				WP-2, 160–100, 100–50, 50–0
	06/07	10:00				NWB, 10, 30, 50, 100, 150
	06/07	11:30				WP-2, 160–100, 100–50, 50–0
IV	04/07	10:00	77°38.8'	34°17.5'	20–50	NWB, 10, 30, 50, 100, 150
	04/07	11:00				WP-2, 186–100, 100–50, 50–0
	04/07	22:00				NWB, 10, 30, 50, 100, 150
	04/07	23:00				WP-2, 185–100, 100–50, 50–0
V	02/07	10:00	78°14.6'	34°13.8'	50–80	NWB, 10, 30, 50, 100, 150
	02/07	12:00				WP-2, 180–100, 100–50, 50–0
	02/07	22:00				NWB, 10, 30, 50, 100, 150
	02/07	23:30				WP-2, 180–100, 100–50, 50–0

Samples were collected with a standard plankton net (WP-2) and Niskin water bottles (NWB).

typical Arctic species (Jashnov, 1967). These species contribute up to 90% of the total zooplankton biomass during the summer period (Jashnov, 1939). Recently, more detailed studies of the ecology of *Calanus* spp. have been performed (Tande et al., 1985; Tande, 1991; Unstad and Tande, 1991; Pedersen et al., 1995; Melle and Skjoldal, 1998). While many studies are devoted to the ecology of large-sized species of *Calanus*, *Metridia*, and *Pseudocalanus* (Hansen et al., 1996; Falk-Petersen et al., 1999 and citations therein), information on smaller copepods is still limited. As their contribution to zooplankton biomass can be significant (Pasternak et al., 2000), their trophodynamic role remains to be illuminated.

The present study was carried out within the framework of the project “Climatic variability and vertical

carbon flux in the marginal ice zone in the central Barents Sea” under the Norwegian Research Council ALV program. The study was conducted along a transect between the Atlantic water, crossing the Polar Front and the Arctic water and the MIZ in the central Barents Sea. This transect has been investigated repeatedly throughout the last two decades (Rey and Loeng, 1985; Skjoldal et al., 1987; Norrbin, 1991; Wassmann and Slagstad, 1993; Hansen et al., 1996; Wassmann et al., 1999). The multidisciplinary approach of the project implies that the seasonal distribution, composition, and biomass of plankton species should be at hand. The main objectives of our study are:

1. to provide data on seasonal changes of zooplankton biomass in different hydrophysical regimes;

2. to evaluate the contribution of small (less than 500 μm) copepods and nauplii; and
3. to describe seasonal and regional variations in the zooplankton depth distribution.

2. Materials and methods

2.1. Study area

The Barents Sea is a shallow continental shelf sea with an average depth of 230 m. The maximum depth of 500 m is found in the Bjørnøyrænna Channel that connects to the Norwegian Sea. The shallower areas are found over banks, where depths are less than 100–150 m (Loeng, 1991). The physical conditions are determined by three main water masses: Coastal water, Atlantic water, and Arctic water. At the Polar Front, Atlantic and Arctic water masses meet and mix. The water masses are linked to corresponding current systems. The Norwegian Coastal Current (NCC) flows eastwards along the northern coast of Norway and Russia. The Norwegian Atlantic Current (NAC) flows into the Barents Sea along the Bjørnøyrænna Channel and continues as two branches in different directions: eastward parallel to the coast and northward along the Hopen Trench. The Arctic water flows southwestwards through the opening between Frans Josef Land and Novaja Zemlja and southwards along the eastern coast of Spitsbergen. Seasonal variation in sea ice is similar from year to year in the west and centre with maximum in March–May and minimum coverage in September. During the winter and early spring, the position of the ice edge follows the Polar Front (Loeng, 1991).

2.2. Sampling

Studies were performed during different seasons: late winter (March 17–23, 1998), late spring (May 18–28, 1998), and early summer (June 30–July 9, 1999). The transect stations were investigated at regular spatial intervals from south to north (Fig. 1). In all cruises, the southernmost station was located at 72°30'N (Atlantic water), at least one station was visited in the marginal ice zone (MIZ), and the northernmost station was located in densely ice-covered

water (Fig. 2). In addition to the transect stations, three 24-h Lagrangian drift stations in March and five in May and July were conducted. They were investigated chronologically from north to south, but numbered from south to north to keep the sequence order of transect stations (Fig. 2).

Samples for the spatial distribution of zooplankton were collected at 7 transect stations in March, 2 stations (Stations 1 and 11) in May, and 10 stations in July (Fig. 2 and Table 1). Clogging of nets by the mucilaginous algae *Phaeocystis pouchetii* caused the low number of zooplankton stations in May. For the May cruise, regional changes in zooplankton composition and biomass along the transect were compiled from depth-stratified samples taken at the 24-h stations.

The vertical distribution of zooplankton during day and night was studied at the 24-h stations. The position, time, and ice conditions of the stations as well as depth strata sampled are shown in Table 1. At the transect stations, mesozooplankton were obtained with WP-2 nets (mesh size 180 μm) towed vertically at a speed of 40 m min^{-1} from ca. 10 m above the bottom to the surface. Stratified sampling of zooplankton was carried out with the same net, equipped with a closing device (0–50 m, 50–100 m, and 100 m–bottom; Table 1).

The net was not equipped with a flowmeter and the filtered water volume was calculated from the wire length and the net mouth area assuming 100% filtration efficiency. The samples were preserved with borax-buffered formaldehyde (4% final concentration) and 1,2-propanediol solution (5% by volume).

To study the abundance and distribution of small copepods (less than 500 μm in body length), zooplankton samples were collected with 10-l Niskin water bottles at the 24-h stations (10, 30, 75, and 90 m in March; 10, 30, 50, 100, and 150 m in May and July; Table 1). Samples were obtained twice a day (day/night), concentrated in containers with permeable walls (20 μm mesh size), and preserved with glutaraldehyde (4% final concentration).

2.3. Laboratory treatment

Identification, measurement, and enumeration were carried out under a dissecting microscope. All

large organisms (more than 4 mm in body length) in a sample were quantified. Subsamples for the smaller species (one fifth or one tenth of sample volume, depending on zooplankton abundance) were placed in a Bogorov chamber and analysed at $\times 32$ magnification. Two sibling species, *C. glacialis* (Jashnov) and *C. finmarchicus* (Gunnerus), were distinguished by the characters of the fifth legs (Jashnov, 1955; Frost, 1974) at adult and fifth copepodite stages, and by the prosome length of younger copepodite stages (Unstad and Tande, 1991). About 40 species were identified in the region. By including sexes and developmental stages, 80 categories were enumerated and measured.

Calculations of biomass were based on published individual dry weight data and specific weight–length relationships. The dry weight of the older copepodite stages (CIV–CVI) of *Calanus*, *Metridia*, *Pseudocalanus*, *Microcalanus*, *Oithona*, and *Oncea* species were taken from Richter (1994). The dry weight of these copepods' younger stages, as well as the weight of Euchaetidae and Aetidaedae species, were calculated from the individual wet weights given by Kanaeva (1962), applying a conversion factor of 0.16 (Vinogradov and Shushkina, 1987). The dry weight for copepod nauplii and *Thysanoessa* spp. were calculated from specific weight–length relationships presented by Hygum et al. (2000) and

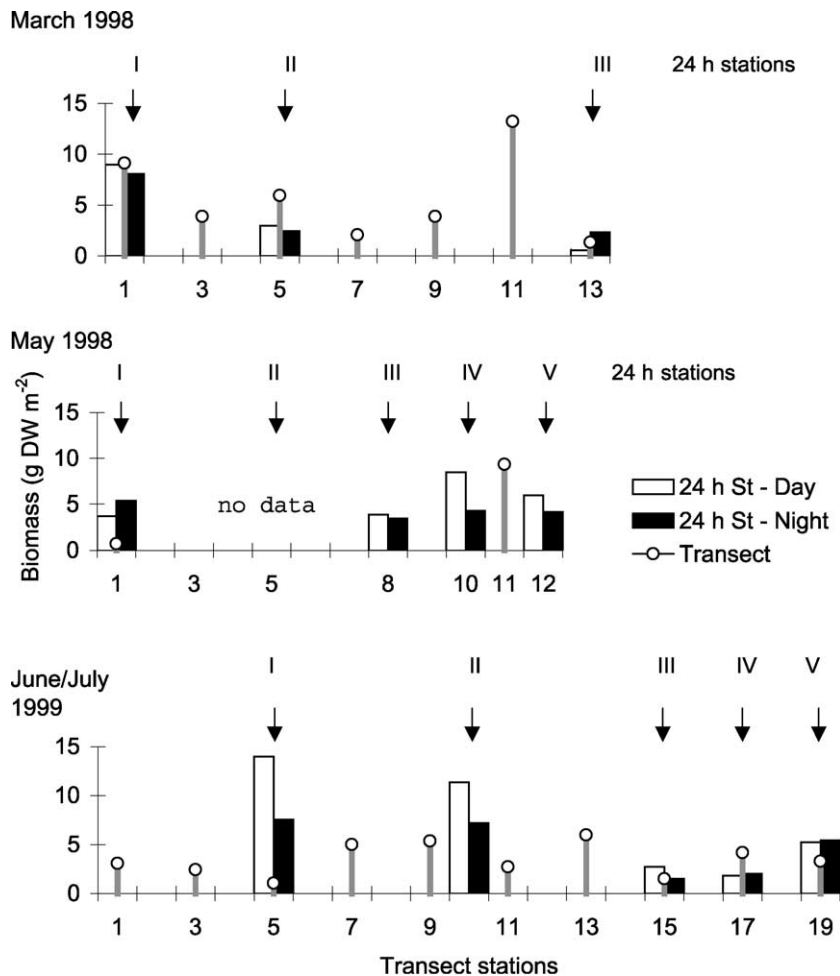


Fig. 3. Seasonal and spatial changes in zooplankton biomass (g DW m^{-2}).

Dalpadado and Skjoldal (1996), respectively. The weight of the other species was calculated using nomograms (three-dimensional forms vs. biomass) of Chislenko (1968) and conversion factors of 0.16 for crustaceans and meroplankton, 0.03 for Chaetognatha and Appendicularia, and 0.01 for Medusa (Vinogradov and Shushkina, 1987).

3. Results

3.1. Hydrography

Atlantic waters dominated the southern part of the transect with the Polar Front region located in the trench between Sentralbanken and Storbanken. In the north, the water masses had Arctic characteristics. In July 1999, the Polar Front meander was observed south of Sentralbanken. For details, see Reigstad et al. (2002).

3.2. Seasonal and regional variations in mesozooplankton biomass

Strong regional variations in depth integrated (0 m–bottom) biomass were observed at all seasons (Fig. 3). The biomass concentrations ranged between 0.6 and 13.2, 0.8 and 9.3, and 1.1 and 14.0 g dry weight (DW) m^{-2} in March, May, and July, respectively.

In March 1998, there was a marked increase in biomass at the trench stations (Stations 1, 5, and 11) as compared with the bank stations (Stations 7 and 13). The same tendency was detected for zooplankton distribution in terms of biomass per cubic meter. High concentrations were observed at the deeper stations 1 and 11 (37.9 and 52.6 mg DW m^{-3} , respectively), and the lower–shallower stations 7 and 13 (11.4 and 5.4 mg DW m^{-3} , respectively). The day and night biomass at the 24-h Stations I and II differed by less than 20%. In contrast, the nighttime biomass at 24-h

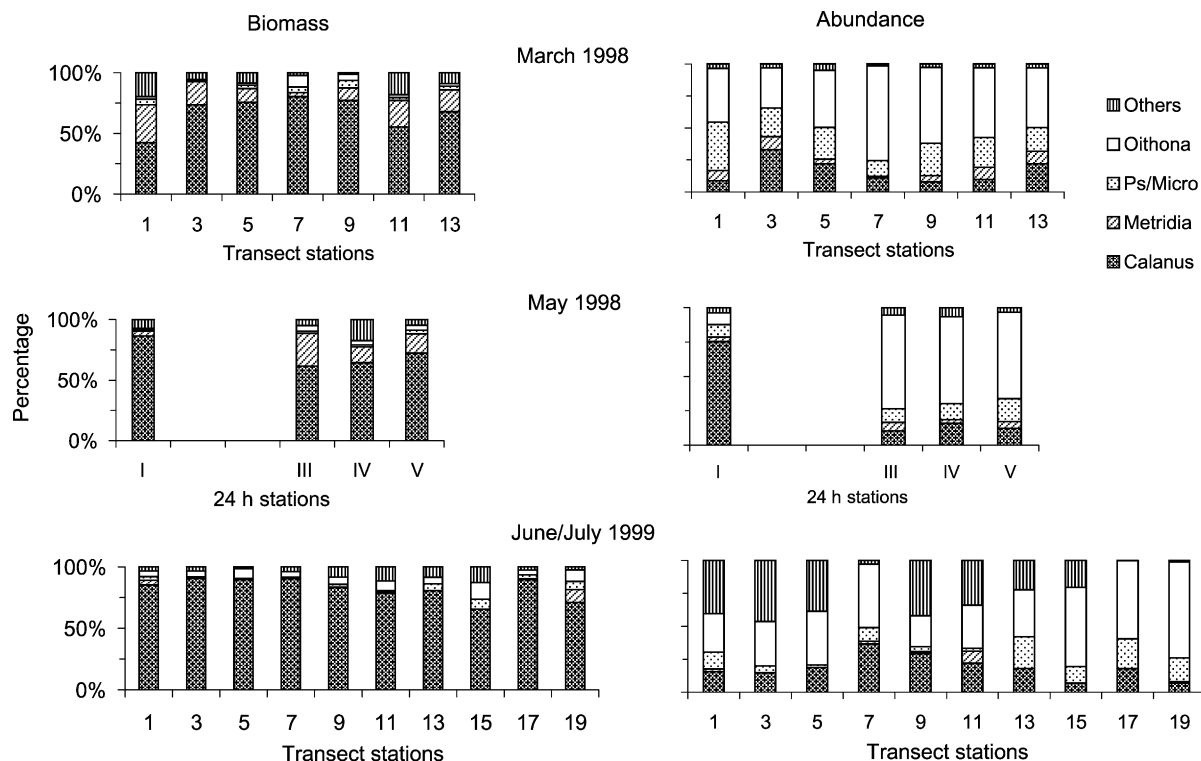


Fig. 4. Seasonal and regional variations in zooplankton composition. Contribution of different groups of zooplankton to total biomass (left panel) and total numbers (right panel). Nauplii are not included.

Table 2

Biomass (mg dry weight m^{-3}) of different size groups of zooplankton collected with water bottles and WP-2 nets in the upper 100-m layer as average from day and night samples at 24-h stations

	WBSZ	Max WBSZ	NSZ	NTZ
<i>March 1998</i>				
Station I	1.2	2.5 (30 m)	0.8	12.1
Station II	2.9	5.4 (50 m)	1.3	3.8
Station III	7.1	14.7 (50 m)	2.1	4.7
<i>May 1998</i>				
Station I	13.9	32.5 (50 m)	2.3	41.2
Station II	14.4	31.4 (30 m)	No data	No data
Station III	6.3	15.2 (30 m)	3.8	34.1
Station IV	13.6	36.9 (30 m)	6.0	48.4
Station V	12.6	45.5 (30 m)	4.9	49.2
<i>July 1999</i>				
Station I	22.5	73.5 (10 m)	3.4	11.4
Station II	14.5	29.1 (10 m)	3.1	34.0
Station III	9.9	34.6 (10 m)	3.2	19.4
Station IV	10.6	23.7 (10 m)	3.6	12.9
Station V	7.7	17.2 (10 m)	2.7	45.1

WBSZ—biomass of small zooplankton ($<500 \mu\text{m}$ in body length) sampled with water bottles; max WBSZ—maximum biomass of small zooplankton (the depth of maximum is shown in brackets); NSZ—biomass of small zooplankton sampled with nets; NTZ—biomass of total mesozooplankton sampled with nets.

Station III was nearly four times greater than at daytime. At this station, due to ice drift, the vessel moved into deeper locations. The hauls were thus performed from 250 m in the daytime and 340 m at night. However, not only the total biomass, but also the concentration of zooplankton per cubic meter increased at night (6.9 vs. 2.2 mg DW m^{-3} at daytime).

In May 1998, because of net clogging by *P. pouchetii*, the zooplankton samples from four transect stations in the Atlantic water had to be discarded. The biomass from Station 1 (0.8 mg DW m^{-2}) is shown in Fig. 3, though it hardly represents the true quantity. Station I was sampled 10 days later when the *P. pouchetii* colonies had disintegrated and single cells predominated (Ratkova and Wassmann, 2002). Then, the zooplankton biomass was 5.4 mg DW m^{-2} . In May, maximum biomass was observed in the MIZ at Stations 11 and IV (9.3 and 8.5 g DW m^{-2} and 34 and 37 mg DW m^{-3} , respectively).

In July 1999, two noticeable zooplankton maxima were found in the Atlantic water at Station I (the southern branch of NAC) located at the deepest part of the transect (ca. 340 m), and Station II (the northern branch of NAC) located over the northern slope of Sentralbanken (14.0 and 11.4 g DW m^{-2} and 42.4 and 49.4 mg DW m^{-3} , respectively). In the Arctic water (Stations 13–19 and III–V), zooplankton biomass ranged from 1.5 to 5.4 g DW m^{-2} or from 10 to 30 mg DW m^{-3} . A nearly twofold difference between the day and night biomass was observed at the southernmost 24-h station very likely reflects small-scale heterogeneity in zooplankton distribution.

Whereas there were appreciable biomass variations on a regional scale, the seasonal difference in biomass was insignificant. On average, for the entire investigated region, zooplankton biomass made up 5.1 ± 3.9 , 5.4 ± 2.1 , and $4.7 \pm 3.4 \text{ g DW m}^{-2}$ in March and May 1998 and July 1999, respectively. In July, the biomass in the Atlantic and Arctic water differed

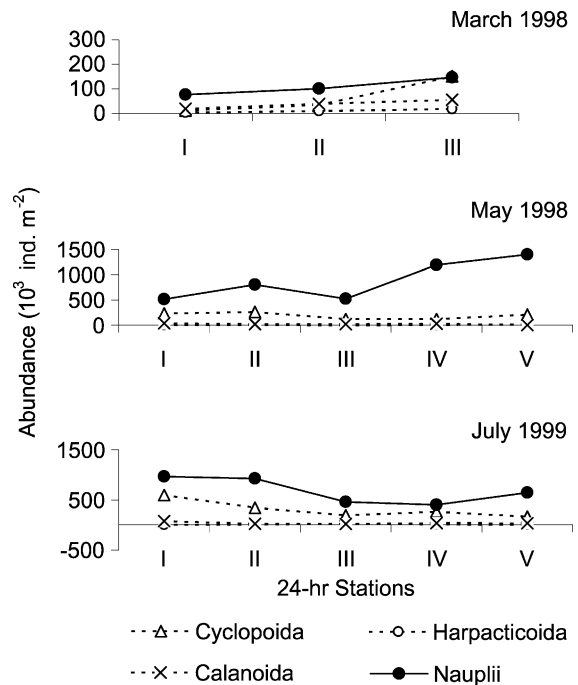


Fig. 5. Seasonal and regional changes in abundance of nauplii and small copepods ($<500 \mu\text{m}$ in body length) collected with Niskin bottles in the upper 100-m layer.

noticeably, on average 6.0 ± 3.9 and 3.1 ± 1.6 g DW m^{-2} , respectively (t test, $p=0.05$). However, in terms of biomass per cubic meter, there was no significant difference between these regions— 23.3 ± 14.3 and 17.4 ± 8.3 mg DW m^{-3} , respectively (t test, $p=0.29$).

3.3. Zooplankton community composition

In terms of dry weight, *Calanus* spp. were the most important group in the region throughout the investigation (Fig. 4, left panel). They contributed up to 90% of the total mesozooplankton biomass. The contribution of *Metridia longa* varied between the years. Whereas it reached 35% of the total biomass in March and May 1998, its share was negligible in July 1999. Small calanoid copepods, *Pseudocalanus* spp. and *Microcalanus* spp., and cyclopoids (mainly *Oithona similis*) contributed <10% to the total mesozooplankton biomass, usually 2–4%. Among the

other groups, the most important were euphausiids (March, Stations 1 and 11), chaetognaths (May, Station IV), and euphausiids and chaetognaths (July, Stations 9–15).

In terms of numbers, *Oithona* spp. were the most abundant copepod contributing to half or more of total copepod numbers at most stations (Fig. 4, right panel) with the exception of Station I in May 1998, where the zooplankton community was dominated by the youngest stages of *C. finmarchicus*. The contribution of *Pseudocalanus* spp. and *Microcalanus* spp. to zooplankton abundance was substantial in March over the entire studied region (15–40%) and in May and July in the northern part of the transect (10–20% of the total zooplankton numbers). In July, a “bloom” of appendicularians (mainly *Fritillaria borealis*) was observed in the Atlantic and mixed waters. They contributed to about half of total zooplankton numbers (Fig. 4, group “Others”).

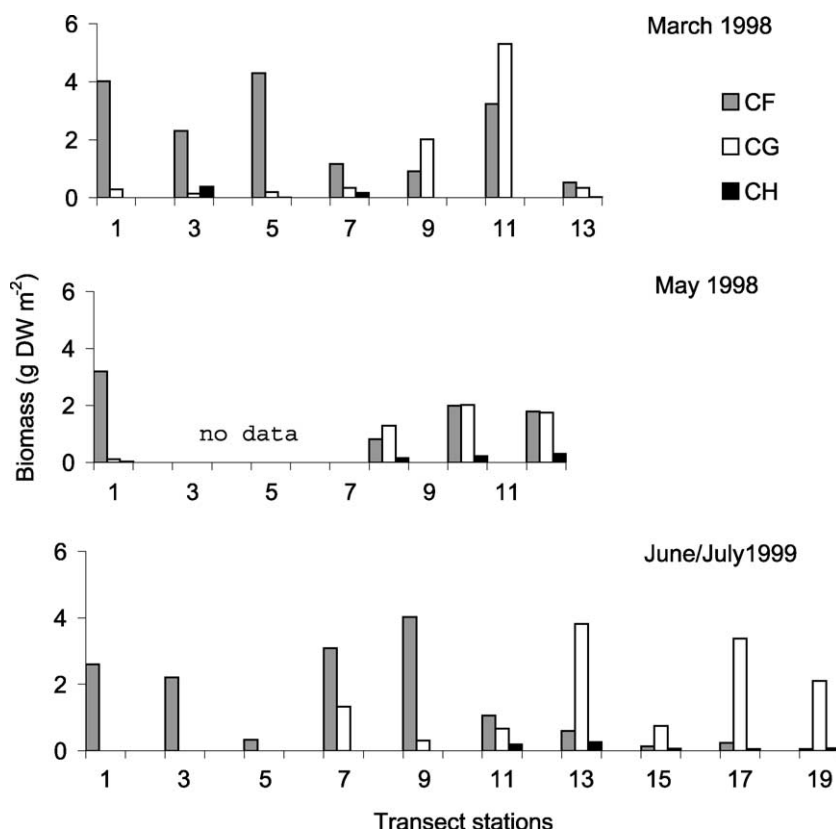


Fig. 6. Spatial distribution of *Calanus* spp. in different seasons.

3.4. Contribution of small copepods and nauplii

The contribution of small zooplankton forms can be underestimated when zooplankton is sampled with 180- μm mesh size nets. The biomass of zooplankton 200–500 μm in body length (nauplii, the youngest copepodite stages of calanoids, Cyclopoida and Harpacticoida) obtained with WP-2 net and Niskin water bottles in the upper 100 m is shown in Table 2. When sampled with water bottles, the biomass of the small zooplankton was two to six times higher than the biomass of small copepods collected with the net. Maximum concentrations of the small forms were observed at the depth of 30–50 m in March, 30 m in May, and 10 m in July. Maximum biomass of small zooplankton sampled with bottles was often equal and sometimes even higher than the total “net” zooplankton biomass.

Copepod nauplii were the most abundant microzooplankton group (Fig. 5). In March, there was a slight increase of abundance in the south–north direction from 8×10^4 to 15×10^4 ind. m^{-2} in the upper 100 m. In May, maximum numbers were observed in the MIZ and under the ice, reaching $12\text{--}14 \times 10^5$ ind. m^{-2} . In July, the number of nauplii varied from 4×10^5 to 10×10^5 ind. m^{-2} with maximum abundance in Atlantic water. Cyclopoid copepods were numerous at all seasons and peaked in July ($3.5\text{--}6 \times 10^5$ ind. m^{-2}) in Atlantic water. The youngest stages of small calanoid copepods were found in about equal number throughout the seasons ($20\text{--}50 \times 10^3$, $10\text{--}40 \times 10^3$, and $20\text{--}60 \times 10^3$ ind. m^{-2} in March, May, and July, respectively). Harpacticoids were less abundant and made up $3\text{--}10 \times 10^3$ ind. m^{-2} .

3.5. Spatial distribution of selected species

3.5.1. *Calanus spp.*

C. finmarchicus was abundant along the transect from $72^\circ 30'$ up to $76^\circ 30'$ N. In this region, its biomass ranged between 0.9 and 4.3, 0.8 and 3.2, and 0.4 and 4.0 g DW m^{-2} in March, May, and July, respectively (Fig. 6). North of the Polar Front, the maximum biomass of *C. glacialis* was similar to that of *C. finmarchicus*—5.3, 2.0, and 3.8 g DW m^{-2} in March, May, and July, respectively. The population of *C. hyperboreus* was scarce throughout all studied sea-

sons (<0.3 g DW m^{-2}). In May and July, this species was located mainly at the Polar Front region and north of it.

3.5.2. Distribution of some nondominant species

In July 1999, Appendicularia were represented by two species: *Oikopleura vanhoeffeni* and *F. borealis*. The latter contributed $>90\%$ to total numbers of larvaceans at most locations (Fig. 7). The exception was the ice-covered water (Stations 17–19) where only *O. vanhoeffeni* was collected. Thus, the distribution of *F. borealis* along the transect is considered to reflect the NAC. Maximum number of *F. borealis* (13×10^4 m^{-2}) was observed over the northern slope of Sentralbanken (Station 9).

Medusa, mainly *Aglantha digitale*, was abundant over Sentralbanken and in the trench between Sen-

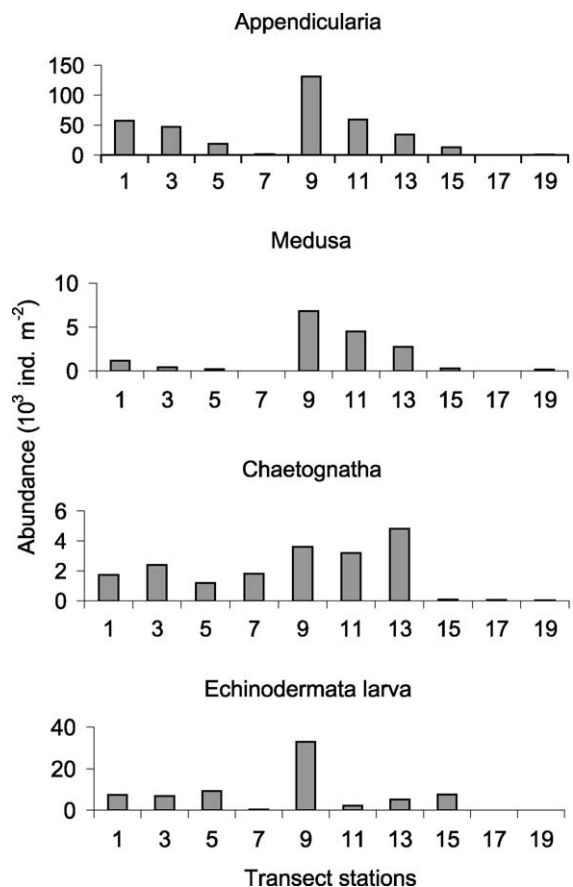


Fig. 7. Spatial distribution of selected species in July 1999.

tralbanken and Storbanken ($3\text{--}7 \times 10^3 \text{ m}^{-2}$). Along the remaining transect, their numbers were negligible.

Meroplankton was absolutely dominated by ophiuroid larvae (plutei). As expected, their maximum was located over the banks. The presence of these larvae at other locations suggests transport with the currents. This is supported by the pattern of larvae stage composition (result is not shown). In the direction from the southernmost station to north and from Sentralbanken area to north, the stage composition changed from the domination of early to fully developed plutei and free-swimming juvenile ophiuroids.

3.6. Vertical distribution of mesozooplankton

In March, most zooplankton occupied the depths below 100 m (Fig. 8). Maximum biomass ($37.6 \text{ mg DW m}^{-3}$) was found at the southernmost stations in the 100- to 280-m layer.

In May, zooplankton inhabited mainly the upper 100 m. The maximum concentration of zooplankton was encountered in the 50- to 100-m layer during daytime and varied from 38 (Station III) to 107 mg DW m^{-3} (Station V). There was a significant difference in day/night vertical distribution of zooplankton at the northernmost stations (Fig. 8). The average concentration of zooplankton in the upper 100 m layer between stations ranged from 34.1 to $49.2 \text{ mg DW m}^{-3}$.

In July, the vertical distribution of zooplankton in the Arctic water (Stations III–V) resembled that in May, but there was no day/night difference. The maximum concentration of $62.6 \text{ mg DW m}^{-3}$ was observed in the 50- to 100-m layer at the northernmost station. In the Atlantic water, the vertical distribution suggests descent to depth. At Stations I and II, maximum concentration below 100 m was about 64 mg DW m^{-3} . In the upper 50 m

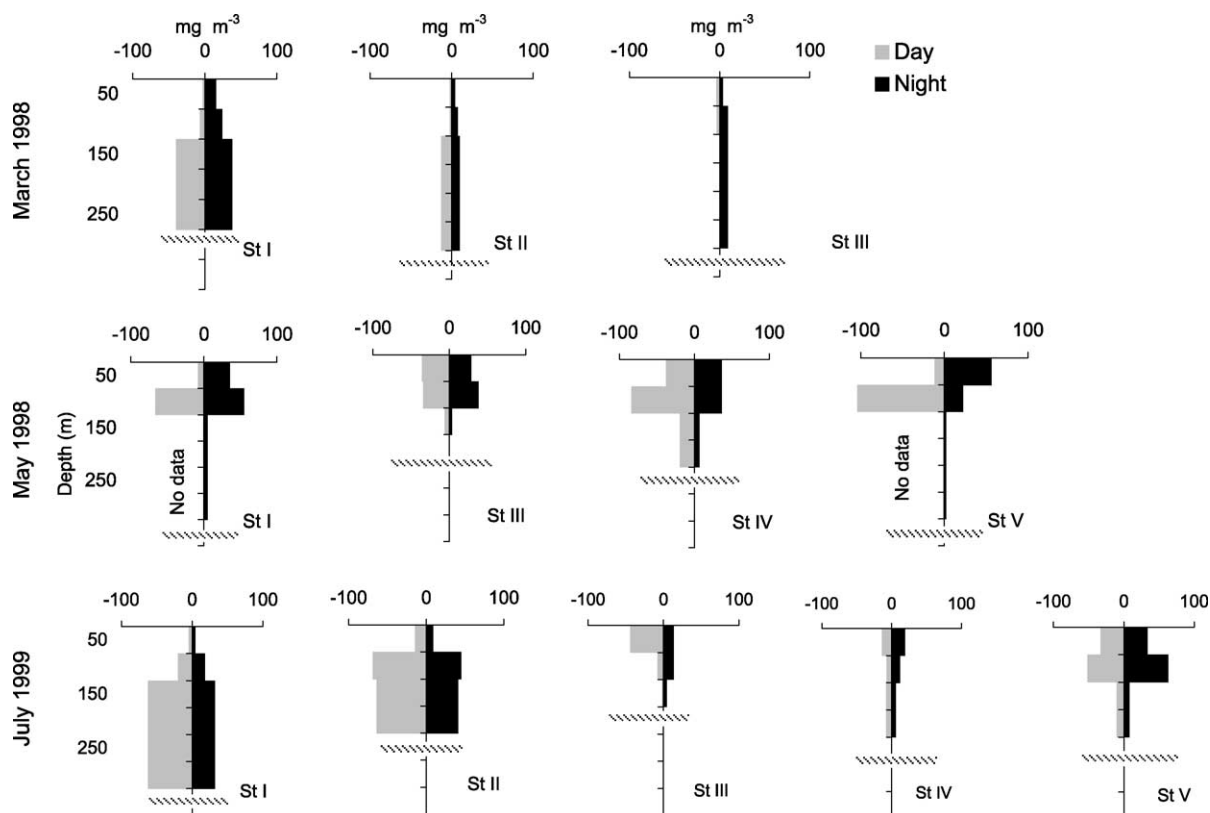


Fig. 8. Seasonal and regional changes in day/night vertical distribution of zooplankton.

layer, zooplankton biomass decreased by a factor of 10 as compared to maximum concentrations in May.

3.7. Seasonal and regional changes in the development of calanoids

In March, only the oldest copepodite stages (CIV–CVI) of *C. finmarchicus* were found and there was a large variation in relative proportion of different stages along the transect (Fig. 9). While the under ice-dwelling part of the population (Station 13) consisted mainly of CIV–CV, the southernmost *C. finmarchicus* population (Station 1) was dominated by adults ready to spawn. The population of *C. glacialis* consisted of CIII, CIV, and CVI. CVs were absent or extremely scarce. The more mature part of the population with the predominance of adults was found in the MIZ (Station 11). We did not consider samples from Stations 1 and 2 because of low abundance (<70 specimens).

In May, the northern population of *C. finmarchicus* was in an early state of development with a small proportion of CI–CII. The oldest stages (CV–CVI) of G_0 were still predominant. In Atlantic water, the population was mainly represented by the young copepodite stages (CI–CIV) belonging to a new generation. In Arctic water, the development of *C. glacialis* was more advanced as compared to that of *C. finmarchicus*. The oldest stages of G_0 (CIV–CVI) comprised <40% to the total number of the *C. glacialis* population. Under the ice, CI dominated the population. In the ice-free water of the MIZ, the proportion of CII and CIII increased.

In July, changes of stage composition mimicked the seasonal pattern of cohort development in both populations. The northernmost populations started to create a new generation. The population was dominated by the oldest stages of G_0 with a small proportion of CIs. Towards the south, both populations became more developed with a systematic domination of CI, CII, CIII, and CIV.

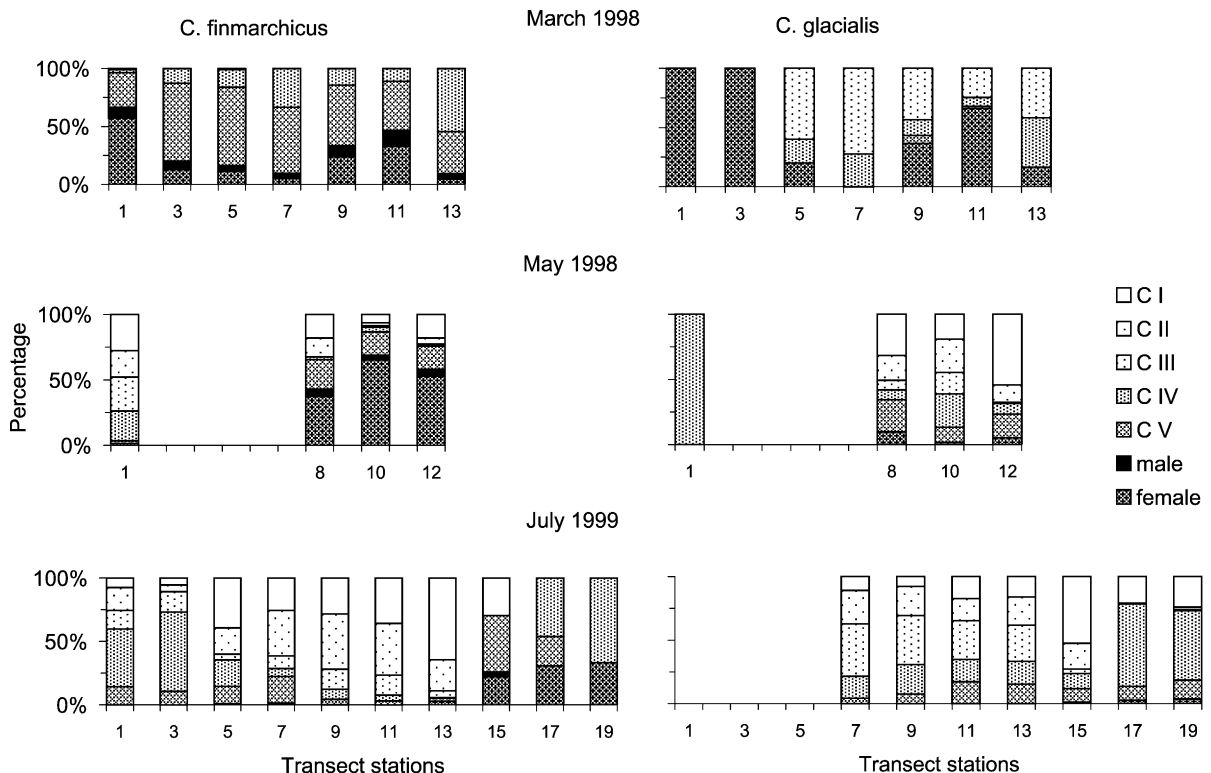


Fig. 9. Seasonal and spatial changes in the stage composition of *C. finmarchicus* and *C. glacialis*.

4. Discussion

4.1. Biomass: spatial variations

The investigation covered the central part of the Barents Sea influenced by NAC, the Polar Front and its meanders, and the ice-covered Arctic water, covering 4–6° of latitude. Strong spatial variation in zooplankton biomass with amplitude up to one order of magnitude was observed during all studied seasons. Both oceanographic conditions and bottom topography can affect the total zooplankton biomass. Nevertheless, no clear regularity in the biomass variability has been found along the transect, which would directly reflect oceanography or topography. This applies both to the integrated biomass and the biomass per cubic meter. Only a slight tendency for increased biomass over the northern slope of Sentralbanken could be detected throughout all seasons. The bottom topography in the Sentralbanken region creates a persistent anticyclonic eddy (Loeng, 1991) and hydrological processes in the convergent zone appear to be the cause for a steady zooplankton aggregation. However, also the new production in this region is the highest along the transect (Reigstad et al., 2002) that would enrich the feeding grounds for zooplankton.

On average, the concentration of zooplankton in terms of biomass per cubic meter in the Atlantic and Arctic or mixed waters differed insignificantly. The MIZ in the Barents Sea has often been classified as a highly productive area (e.g., Dayton et al., 1994). However, this classification refers usually to production or phytoplankton biomass in the upper layers. For the entire water column, the MIZ of the Barents Sea has a clearly decreased new production compared to Atlantic water (Wassmann et al., 1999; Reigstad et al., 2002). We found indeed lower zooplankton biomass in the MIZ in March and July (0.5–2 and 1.5–2.7 g DW m⁻², respectively). In the Atlantic waters, the lowest biomass was observed at Stations 1 (May) and 5 (July), but 10 days later at the 24-h station located nearby these positions, the biomass was higher by a factor of 10 (Fig. 3). This suggests that zooplankton variability on small time and space scales is in the same range as that of the seasonal and regional variations. This fully coincides with recent data on *C. finmarchicus* variability in the

southern and central Barents Sea by Tande et al. (2000) and Helle (2000).

In March, a tendency for an increase of integrated biomass with increasing bottom depth was encountered. As *C. finmarchicus* and *C. glacialis* comprise the bulk zooplankton biomass, they determined the pattern of zooplankton distribution. After seasonal descent to depth (see 4.5), diapausing *Calanus* can “stream” down to the deeper parts of the shelf into trenches and concentrate there close to the bottom. Based on seasonal changes in the copepod cross-shelf and slope distribution, a similar type of overwintering strategy for *C. finmarchicus* has been hypothesised by Kashkin (1962). Plankton can hardly be collected in a 10-m layer above the bottom when sampled with nets, but when winter zooplankton was collected with a pump, a high density aggregation of *C. finmarchicus* was found close to the bottom in the central Barents Sea (Pedersen, 1995). Nets thus significantly underestimate *Calanus* in autumn–winter, especially in shallow regions.

4.2. Biomass: seasonal and interannual variations

In spite of large regional and short-term variations, the average zooplankton biomass was surprisingly similar in all seasons (about 5 g DW m⁻²). This result appears to be in conflict with the considerable seasonal order-of-magnitude changes in zooplankton biomass, with minimum in late winter and maximum in summer (Jashnov, 1939; Zelikman and Kamshilov, 1960). However, the stage composition of the two dominant species of *Calanus* suggests that both populations were still in development progress in July. Hence, their biomass did not culminate during the May and July cruises.

How does the biomass estimated for the productive seasons in 1998/1999 fit into a long-term biomass variation in the Barents Sea? Regular zooplankton sampling was performed by PINRO (Russia) along two transects, from the North Cape to Bear Island and at the Kola meridian (33°30'E) in 1959–1992. The long-term, summer–autumn data have shown interannual variations in biomass density in the range of 16–160 mg DW m⁻³ along North Cape–Bear Island transect and in the range of 5–96 mg DW m⁻³ along the Kola meridian transect in the upper 50 m (recalculated from Timofeev, 1997). At the Dalnezelenetsky

transect (running from the Kola Peninsula to Novaja Zemlja), interannual variations in biomass, inferred from ca. 5000 samples, were in the range of 1.3–9.6 g DW m⁻² in the 1953–1958 productive seasons (recalculated from Zelikman and Kamshilov, 1960). During the same period, variations in the average annual biomass in the southern part of the Barents Sea (south of 72°30'N) were smaller, fluctuating in the range of 0.9–4.2 g DW m⁻² (Zelikman and Kamshilov, 1960). For the central Barents Sea and the major part of the present transect, Skjoldal et al. (1987) reported interannual zooplankton biomass variations in the range of 2–20 g DW m⁻² during late spring/early summer in 1979–1984.

Most data on interannual variation were obtained in terms of displacement volume that complicates direct comparison with our data. The spatial variations in zooplankton biomass in the present study (from 1 to 15 g DW m⁻²) are in the same order of magnitude as reported interannual variation. The station-to-station variations in zooplankton biomass in the upper 100 m layer, ranging from 4 to 100 mg DW m⁻³ in spring 1998/summer 1999, are also comparable with a range of interannual variations.

The question arises if internal factors (regional climate, circulation features, feeding conditions, predation) or external factors (global climate variability, Atlantic water advection) regulate the zooplankton standing stock in the Barents Sea. Debates about this issue have persisted for a long time (Zelikman and Kamshilov, 1960; Skjoldal et al., 1987; Loeng et al., 1997; Tande, 1991; Tande et al., 2000; Helle, 2000). The climatologically driven interannual variability of advection of Atlantic water into the Barents Sea is significant and varies between cold and warm years (Ådlandsvik and Loeng, 1991). According to Skjoldal et al. (1992), the timing and the size of the inflow influence zooplankton advection from the Norwegian Sea onto the Barents Sea shelf. Thus, warm periods where the major inflows of Atlantic water take place during late autumn and winter, and cold years with low inflow would result in low zooplankton advection. Increased zooplankton advection would be expected if large inflow takes place during spring after the ascent of overwintering *C. finmarchicus* in the Norwegian Sea. However, these signals are strongly modified by the local food conditions or predation by planktivores such as capelin and herring

(Sakshaug and Skjoldal, 1989) or ctenophores (Swanberg and Båmstedt, 1991). There exist also arguments suggesting an independence of zooplankton biomass from Atlantic water advection. Zelikman and Kamshilov (1960) observed maximum zooplankton biomass produced by a minor initial female's abundance in cold year under favourable feeding conditions and low predator pressure.

An example of the predominance of internal over external factors in forcing the zooplankton standing stock, based on the long-term plankton observations, has been shown for the Black Sea. This basin is practically closed and the biological processes are not affected by Mediterranean inflow. Nevertheless, the interannual variation in the average annual zooplankton biomass during five decades varied with an order of magnitude (Kovalev et al., 1998). This suggests that local, rather than external, factors regulate the year-to-year variations in zooplankton community here. In the Barents Sea, a differentiation between internal and external factors is impossible unless the significance of advection is quantified and predictable. We suggest that internal factors may play a role in the zooplankton stocks of the Barents Sea. That zooplankton biomass variation on a regional scale in the Barents Sea is in the same range than those reported for the interannual biomass variation supports this suggestion.

4.3. Role of small copepods in the plankton community

The boundary between micro- and mesoplankton was established at 200 µm (UNESCO, 1968). An evaluation of trophodynamic processes in the pelagic demands knowledge about the abundance of all zooplankton size categories. While microheterotrophic organisms (<200 µm) are sampled quite adequately with water bottles, small zooplankters (<500 µm in body length and <180 µm in width) cannot be properly retained with 180-µm mesh nets (Nickols and Thompson, 1991). The smaller organisms, in particular those with <200 µm body length, have so far not been adequately investigated in the Barents Sea.

The role of microzooplankton (bacteria, heterotrophic flagellates, and ciliates) for recycling of organic matter in the Barents Sea has been emphasised by

Sakshaug et al. (1994), Hansen et al. (1996), and Verity et al. (2002). A comparative evaluation of the biological processes revealed that microzooplankton plays a more important role in utilisation and transformation of primary production than mesozooplankton (Hansen et al., 1996). Biomass of mesozooplankton (copepods *Metridia* and *Calanus* spp.) was found to be insignificant (10–20%) in comparison to that of microzooplankton. A total of 64–97% of the daily chlorophyll production were due to grazing losses in July 1999, predominantly caused by microzooplankton (Verity et al., 2002). The results are in contrast to the traditional role given to “classical” phytoplankton grazers in trophodynamics evaluations.

The present study revealed a significant underestimation of small organisms sampled with WP-2 net. In the upper 100-m layer, a difference between biomass of small zooplankton sampled with nets and that sampled with water bottles occasionally exceeded six times. This is in accordance with evaluations of biomass of small copepods sampled with bottles and nets in a north Norwegian fjord (Pasternak et al., 2000). The biomass of small zooplankton in the upper 10- to 30-m layer was similar or higher than total mesozooplankton biomass. A comparison with data on distribution of heterotrophic flagellates and ciliates along the transect in July 1999 (Verity et al., 2002) showed no significant difference in biomass of “microbial” organisms and small crustacean in the surface layer. In summary, the present data suggest that small copepods, copepodites, and nauplii play a significant role in trophodynamic processes in the pelagic, also in the Arctic.

4.4. Seasonal and regional variations in zooplankton community structure

Calanus species are important not only in terms of their contribution to zooplankton biomass (80%) and more to total zooplankton biomass. Their distribution can be used to trace different water masses in the Barents Sea (Jashnov, 1967). Three regions could be distinguished along the transect: one dominated by *C. finmarchicus*, one dominated by *C. glacialis*, and one where both species were found in almost equal proportions (Fig. 6). This pattern coincides with a dominance of Atlantic, Arctic, and mixed water. In the latter region, the total biomass of these species was

usually higher than in the two others. The occurrence of *C. finmarchicus* at the northernmost locations reflects advection of the Atlantic water below Arctic surface water north of the Polar Front. The abundance of both *C. glacialis* and *C. finmarchicus* at the southern part of Sentralbanken in July (Station 7) reflects the location of the Polar Front meander.

A contribution of krill to total zooplankton biomass was noticeable only in March (20%), but high abundance of their nauplii in May and juveniles in July suggests that krill plays an important role. Although krill avoids small, slowly moving nets, the biomass estimated from WP-2 nets from the Barents Sea was of the same order of magnitude than the average biomass obtained with a MOCNESS of 1 m diameter (Dalpadado and Skjoldal, 1996). The spatial distribution of euphausiids and their juveniles indicates that dense aggregations were located in the same regions, e.g., the slope of banks. This suggests that a local population persisted in these regions.

Mass development of appendicularians was observed in the Atlantic water in July 1999, where appendicularians comprised up to 45% of total mesozooplankton abundance. Because of their high filtration rate (Alldredge, 1981), appendicularians can be important food competitors for herbivorous plankton. Medusae and chaetognaths are important planktivorous predators. Due to low dry weight, their contribution to biomass was insignificant (less than 2–5%). Nevertheless, their total predatory impact on the zooplankton community is probably important. These carnivores have high grazing rates (Matsakis and Conover, 1991; Falkenhaus, 1991). When numerous, they affect significantly plankton abundance and size composition, but in July 1999, medusas and chaetognaths were practically absent in the Arctic waters.

4.5. Vertical distribution

The zooplankton vertical distribution reflected both seasonal changes in the productive cycle and a latitudinal shift in the onset of events. Because *C. finmarchicus* and *C. glacialis* dominated total biomass, we assume that the seasonal and regional dynamics in zooplankton depth distribution reflects vertical migration by these two species.

In late winter (March 1998), there was a clear tendency of increased zooplankton biomass at the

southernmost station as compared with the northern ones. Part of the stock had raised to the uppermost layer. *Calanus* species are known to descend to 1000 m depth or more for overwintering in oceanic regions (e.g., Conover, 1988; Hirche, 1991). However, if they encounter an obstacle (e.g., the bottom), they form thin (5–10 m), but dense, aggregations close to this obstacle (Alldredge et al., 1984; Sameoto and Herman, 1990; Vinogradov et al., 1992). This is most likely to be the case in the Barents Sea. In the Arctic, seasonal vertical migrations concur with ontogenetic ones (Hirche, 1991). Indeed, at the southernmost stations, females dominated the population of *C. finmarchicus* and male adults were ready to reproduce. The onset of spawning was also reflected in the appearance of eggs and nauplii at this location (Pasternak et al., 2002).

Over the entire region in May and at the locations north of the Polar Front in July, the pattern of vertical distribution was characterised by zooplankton aggregation in the uppermost layers. The obvious difference in the day/night depth distribution of zooplankton at the northern stations in May suggests diel vertical migration. However, also other explanations are possible. In the Barents Sea, *Calanus* spp. form narrow aggregation layers where up to 80% of the total abundance can be encountered in a 10-m-thick band close to the 50-m isobath (Unstad and Tande, 1991). At this depth where frequently also the maximum concentrations of small zooplankton can be encountered (Table 2), the greatest vertical export attenuation of biogenic matter was observed (Olli et al., 2002). This suggests that zooplankton grazes heavily on the export production leaving the euphotic zone. Water oscillations induced by internal waves could result in vertical dislocation of zooplankton and thereby simulate vertical migration.

In July, most of the zooplankton in the Atlantic water accumulated in the deep layers. Two possible reasons can be suggested: firstly, the descent coincides with the start of the diapause CIV and CV of *C. finmarchicus* that dominated zooplankton here; secondly, the presence of carnivores could impose a downward migration of zooplankton. In the North Atlantic, *C. finmarchicus* usually overwinters as CIV–CV stages (Hirche, 1991) and the ontogenetic downwards migration takes place in June–July. This supports the first argument. Planktivorous fish predation, in particular capelin and herring, influences zooplankton vertical distribution (Hassel et al., 1991) and could have caused the early migration of *Calanus* to depth (Kaartvedt, 1996). We have no data on fish abundance, but dense aggregations of the planktivorous ctenophores were observed at the southernmost stations in July (result not shown). Thus, both ontogenetic migration and predator avoidance appeared to regulate the vertical distribution of zooplankton in summer.

4.6. Seasonal development of *Calanus* spp.

In contrast to the strong station-to-station variability in *C. finmarchicus* and *C. glacialis* abundance, a gradual development of these species was evident from the stage composition data. The changes in the development of *Calanus* stages in the north–south direction mimic the seasonal development (e.g., Falk-Petersen et al., 1999). Since the study was performed at different seasons and covered 4–6° of latitude, we have an opportunity to follow, step-by-step, the entire productive cycle of *Calanus*, from the deep hibernation in ice-covered waters in March to the formation of the new overwintering stock. The latter was observed near the southern boundary of the habitat of *C. glacialis* and at the southernmost locations for *C. finmarchicus*.

The life cycle of *Calanus* spp. in the Barents Sea has been thoroughly described (Skjoldal et al., 1987; Tande, 1991; Melle and Skjoldal, 1998; Falk-Petersen et al., 1999). Most descriptions are reconstructions from scattered data obtained in the productive season (but see Hassel, 1986), covering a smaller latitudinal gradient. Briefly summarising these discussions, the population of *C. finmarchicus* in the Barents Sea has a 1-year life cycle and that of *C. glacialis* a 1- to 2-year life cycle, depending on environmental conditions.

The appearance of the youngest stages of *C. finmarchicus* at the southernmost location in July appears to reflect the development of a second generation or late spawning of G₀. An appraisal of the generation cycle of *C. finmarchicus* based on the stage composition dynamics in the Norwegian Sea (Pedersen et al., 2001; Arashkevich et al., submitted) revealed that the offspring of the second generation appeared at the end of July at 63°N and in the middle of August at 69°N. It appears unlikely that juveniles

of *C. finmarchicus* in the southern Barents Sea (72°30'N) belonged to a new generation. Consequently, they must belong to late spawning G_0 .

In March, the stage composition of *C. glacialis* north of the Polar Front was bimodal, i.e., CIII, CIV, and CVI females dominated it. This finding suggests a 2-year life cycle of *C. glacialis* in the Barents Sea. This corresponds to observations by Tande et al. (1985), Hassel (1986), and Skjoldal et al. (1987), but is in contrast to the 1-year life cycle suggested by Falk-Petersen et al. (1999).

No evidence for any development of a new generation of *C. finmarchicus* was found in the ice-covered water north of 77°N. *Calanus* eggs and nauplii recorded in this region (Pasternak et al., 2002) belonged apparently to *C. glacialis*. The development of a new cohort of *C. glacialis* could be deduced from the appearance of CI at the northernmost stations in July, suggesting early spawning under dense ice cover far ahead of the MIZ bloom. Smith (1990) described the spawning of *C. glacialis* before the spring bloom in Fram Strait. In July 1999, the ice-covered waters were still in prebloom condition with phytoplankton biomass $< 50 \mu\text{g C l}^{-1}$ (Ratkova and Wassmann, 2002) and chlorophyll *a* $< 0.5 \mu\text{g l}^{-1}$ while nutrient concentrations were high (Reigstad et al., 2002). Freshly collected *C. glacialis* females in this region had practically empty guts. At phytoplankton concentrations $< 60\text{--}70 \mu\text{g C l}^{-1}$, *C. glacialis* practically stops feeding on 20- to 36- μm -sized algae (Arashkevich and Drits, 1984).

A key processes influencing the fate of primary production and success of zooplankton growth is the developmental match of zoo- and phytoplankton (Diel and Tande, 1991; Wassmann, 1998). The present study revealed that the onset of developmental progress of the two *Calanus* species was synchronised in time, but separated in space. From the cohort composition, the spawning of *C. finmarchicus* at 72.5°N started at the same period as that of *C. glacialis* at 75.5°N, at the end of March until beginning of April. This is in accordance with conclusions of Tande (1991) and Pedersen et al. (1995). A comparison of the stage composition in these two populations in the mixed water where both species coexisted revealed a significant delay in the cohort development of *C. finmarchicus* in comparison with that of *C. glacialis*. Two waves of offspring—the first by *C. finmarchicus*

in the southern Atlantic water, the second by *C. glacialis* close to the Polar Front—started concurrently and developed northwards. In the southern Barents Sea, vertical mixing ceases slowly because solar warming is gradual. In the north, ice melt gives rise to strong and rapidly developing stratification. According to Wassmann et al. (1999), two waves of phytoplankton bloom development take place in the central Barents Sea in spring to early summer. The first starts in the southern part of the Atlantic water, the second near the Polar Front. Both waves move northwards. Support for this scenario was also found in 1998–1999 (Ratkova and Wassmann, 2002). The onset of spawning by *C. finmarchicus* in the Atlantic water and in *C. glacialis* north of the Polar Front matches the spring phytoplankton bloom and adds to the success of *Calanus* spp. in the Barents Sea.

5. Conclusions

The average mesozooplankton biomass in the central Barents Sea and MIZ was ca. 5 g DW m^{-2} in all investigated seasons. Significant variations in zooplankton biomass ($1\text{--}14 \text{ g DW m}^{-2}$) both on spatial and short-term scales suggest the importance of local factors in zooplankton stock formation.

The abundance of nauplii and small copepods sampled with water bottles in the upper 100-m layer was of the same order of magnitude than the biomass of the total “net” mesozooplankton. A significant underestimation of smaller forms when applying standard nets results in an inadequate evaluation of the role of total zooplankton in the pelagic carbon flow.

Both hydrographic conditions and bottom topography influenced the variation in zooplankton community structure. Species composition in Atlantic and Arctic waters differed significantly.

The life cycle of *Calanus* spp. was observed from deep hibernation (March), through different phases of reproductive activity in the upper layers (May) to accumulation of a new overwintering stock at depth (July). A comparison of the spatial distribution and cohort progress in *C. finmarchicus* and *C. glacialis* revealed two waves of spring events that match the phytoplankton spring bloom. The first started in the southernmost location of the Barents Sea, the second

near the Polar Front, and both developed towards the north.

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