Papers

Contrasting zooplankton communities (Arctic vs. Atlantic) in the European Arctic Marginal Ice Zone

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Abstract

Relationships between the zooplankton community and various environmental factors (salinity, temperature, sampling depth and bottom depth) were established in the European Arctic Marginal Ice Zone (MIZ) using multivariate statistics. Three main zooplankton communities were identified: an Atlantic Shallow Community (AtSC), an Arctic Shallow Community (ArSC) and a Deep Water Community (DWC). All species belonging to AtSC and ArSC were pooled and their relative abundances in the total zooplankton calculated with respect to a particular layer (surface, mid and deep strata), regions (the Barents Sea, Fram Strait and the waters off northern Svalbard), years (1999 or 2003) and seasons (spring or autumn). Mapping of the proportions of Arctic and Atlantic species led to the conclusion that zooplankton from the MIZs do not exactly follow complementary water masses, although the general pattern of AtSC and ArSC dominance accords with the physical oceanography of the study area (AtW and ArW respectively). The mid layer proved to be a better predictor of mesozooplankton distribution than the unstable conditions near the surface.

1. Introduction

It is widely believed that the effect of global climate change will be perceptible first and foremost in the Polar Regions (ACIA 2005). In this context, seasonally ice-covered shelf seas are of special interest, since they are more productive than the deep Arctic Ocean, which is almost permanently covered by multi-year ice (Hegseth 1998, after Gosselin et al. 1997).

The Marginal Ice Zone (MIZ) is the key productive area of Arctic shelf seas (Slagstad & Stokke 1994, Loeng et al. 1995, Falk-Petersen et al. 2000). As a transitional area, between ice-free and permanently ice-covered sea (Frankenstein et al. 2001), MIZ is influenced by both Atlantic (AtW) and Arctic waters (ArW), and the plankton community comprises associated fauna from both the North Atlantic and the Arctic domains (Strömberg 1989, Walkusz et al. 2003, Daase & Eiane 2007). The ongoing warming of Arctic regions is expected to lead to a northward retreat of the MIZ and, in consequence, to the expansion of the geographical ranges of many temperate marine species associated with the displacement of Arctic species (Drinkwater 2006). The current study integrates substantial mesozooplankton data from the MIZ of the Barents Sea, Fram Strait and northern Svalbard waters.

The Barents Sea is one of the most productive regions in the world and one of two major routes by which Atlantic waters enter the Arctic Ocean. Large variations in zooplankton abundance and biomass structures have been recorded on various temporal and spatial scales (Hassel 1986, Skjoldal et al. 1987, Skjoldal & Rey 1989, Arashkevich et al. 2002, Søreide et al. 2003, Blachowiak-Samolyk et al. 2006). The relationship between physical and biological conditions in the Barents Sea has been addressed in several studies (e.g. Unstad & Tande 1991, Pedersen et al. 1995, Hansen et al. 1996, Falk-Petersen et al. 1999, Søreide et al. 2003, Ellingsen et al. 2008, Blachowiak-Samolyk et al. 2008a,b).

Even though Fram Strait is the most important passage, and the only deep one, between the Arctic Ocean and the Nordic Seas (Morison 1991), information on the structure of the pelagic biota in this region is still limited (e.g. Smith et al. 1985, Smith 1988, Hirche et al. 1991, Blachowiak-Samolyk et al. 2007, Blachowiak-Samolyk et al. 2008b). The pelagic ecosystem of Fram Strait, highly influenced by advection, has recently been reviewed thoroughly by Hop et al. (2006), but knowledge of the north-eastern Svalbard region remains relatively poor. Apart from the studies on lipids in *Clione limacina* and *Limacina helicina* (Falk-Petersen et al. 2001) and on *Calanus* feeding strategies (Søreide et al. 2008), the only results to date on the relationship between hydrodynamics and the zooplankton community structure from the north-eastern Svalbard area have been published by Daase & Eiane (2007).

In recent decades, the influx of AtW to the Arctic Ocean has increased (Morison et al. 2000, Schauer et al. 2004), but it remains unclear how flux variability affects its pelagic ecosystem. The current paper was initiated by the question whether Atlantic Shallow Community (AtSC) and Arctic Shallow Community (ArSC) mesozooplankton follow complementary water masses (AtW and ArW, respectively) in the European Arctic. In this context, the main aim of the investigation was to compare contrasting mesozooplankton communities (Arctic vs. Atlantic) from different MIZ of Fram Strait, the waters off northern Svalbard and the Barents Sea with respect to vertical stratification and different hydrographic regimes.

2. Material and methods

2.1. Description of the study areas

This study was based on a compilation of mesozooplankton data collected during two projects carried out in the Marginal Ice Zones (MIZs) of the Barents Sea, Fram Strait and the waters off northern Svalbard by the Norwegian Polar Institute: 'Spatial and temporal variability of the ice-ocean system in the Marginal Ice Zone of the Barents Sea' (MARINØK) and 'On Thin Ice' (OTI).

The MARINØK survey was conducted in the central Barents Sea in May 1999. The physical conditions of this continental shelf sea (av. depth 230 m) have already been described (Loeng 1991, Rudels et al. 1991, Steele et al. 1995), so only a brief description of the hydrographic features prevailing at the time of the survey is given here. Typically, in the central Barents Sea warm Atlantic water (AtW) from the south encounters cold water from the north over the Hopen Trench, forming the Polar Front, approximately at the 250 m isobath. The warm, saline AtW is advected northwards by the Norwegian Atlantic Current, which splits at the Bear Island Channel. Part of the branch entering the Barents Sea flows northwards along the axis of the Hopen Trench, and then to the west and north of the Central Bank.

'On Thin Ice' (OTI) was carried out in May 2003 in the eastern Fram Strait, the most important gateway between the Atlantic and Arctic oceans, which is influenced by the West Spitsbergen Current (WSC), and is a continuation of the North Atlantic Current (Figure 1) and the major pathway of heat to the interior of the Arctic Ocean (Aagaard et al. 1987, Schauer et al. 2004). Warm, saline and nutrient-rich water of Atlantic origin follows the continental shelf slope of West Spitsbergen (Mosby 1938).

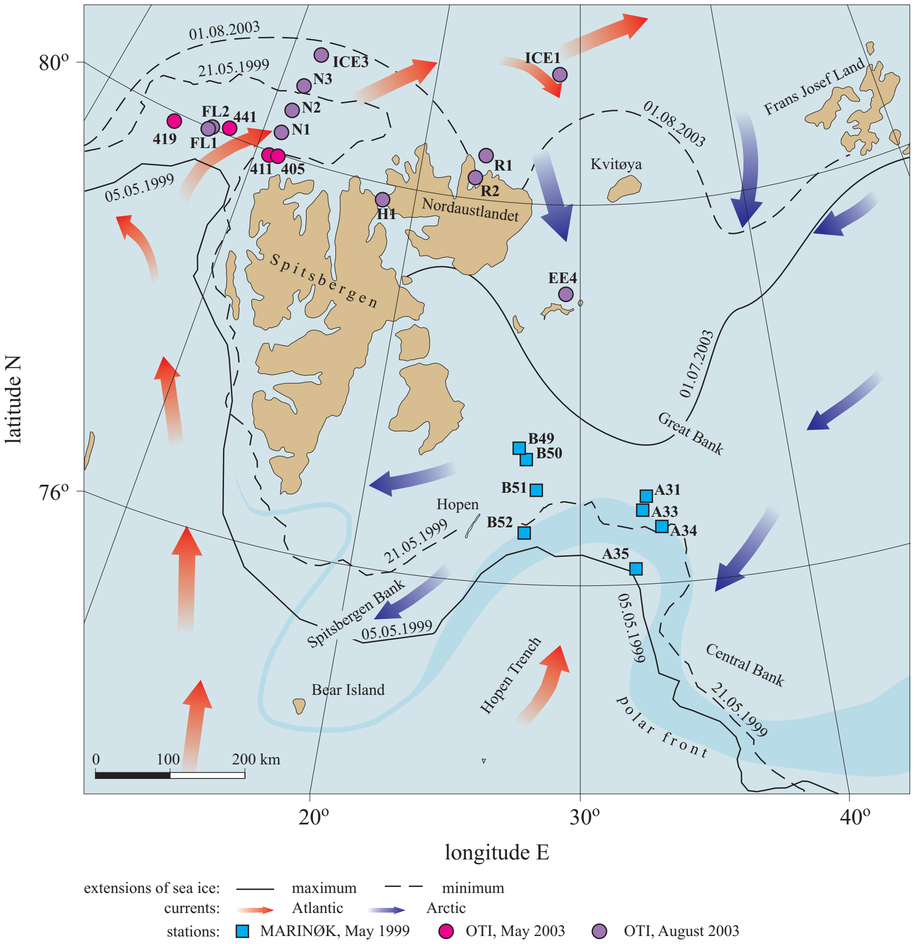

Figure 1. Sampling area in the Arctic Marginal Ice Zone (MIZ) of the Barents Sea (May 1999), Fram Strait (May 2003 and August 2003) and off northern Svalbard waters (August 2003)

During the autumn OTI cruise (August 2003) the study area covered Fram Strait dominated by AtW and the area north of Svalbard, where Arctic waters (ArW) of low temperature and moderate salinity prevail. North of Svalbard, the AtW mass submerges below the Arctic water (ArW) and forms a relatively warm and saline intermediate layer that is detectable throughout the Arctic Ocean (Rudels et al. 1991). During the summer ice melt, a third water mass is formed in the surface layer. This surface mix water (MW) is characterised by low salinity (typically < 34.3 PSU) (Loeng 1991, Harris et al. 1998).

In the northern Barents Sea and over the Great Bank, the upper 150 m of the water column is colder and less saline; it is also defined as ArW (Loeng 1991). This cold ArW layer is initially formed by the freshening of Atlantic water as a result of ice melt, by net precipitation, and perhaps also by mixing with less saline water advected from the Kara Sea (Rudels et al. 1991, Steele et al. 1995); it is subsequently homogenised during winter by haline convection in the area of origin, the northern Barents Sea. Then, mainly as a result of the northerly winds prevailing in winter and spring, it is transported southwards, forming the northern component of the Polar Front (Vinje & Kvambekk 1991).

The area investigated during the MARINØK project comprised the inner part of the Hopen Trench surrounded by the Barents Sea banks between 76°03′N–77°31′N and 26°53′E–33°08′E (Table 1, Figure 1). Zooplankton and oceanographic parameters were collected with the ice-strengthened r/v 'Lance' from 9 to 22 May 1999. Two transects (A – eastern at 33°E, and B – western at 27°E near Hopen), each consisting of four stations, were sampled from north to south across the MIZ. During two OTI cruises zooplankton was collected from the waters north of Svalbard (Figure 1). The spring cruise with r/v 'Jan Mayen' was carried out in May 2003, whereas the autumn cruise (August 2003) took place on board r/v 'Lance'.

For the present work, a set of zooplankton samples from four May stations and eleven August stations was selected (Table 1). In spring, sampling was carried out on the shelf (station 405), on the continental slope (stations 411 and 441) of Fram Strait and over deep water in Sofiadjupet (station 419). In autumn, a transect from the shelf waters over Norskebanken (station N1) to deep waters (stations N2, N3 and Ice3) was sampled together with two stations on the slope of Flaket (stations FL1 and FL2). Additionally, zooplankton from a few stations situated in north-eastern Svalbard waters was sampled: on the slope of Hinlopen (station H1), as well as in the shallow areas of Erik Eriksen Strait (station EE4), Rijpfjorden (stations Outer-R1 and Inner-R2) and northern Kvitøyrenna (station Ice1).

2.2. Oceanographic conditions and sea ice

During the MARINØK cruise, ice concentration, ice thickness and floe size were measured and recorded every three hours (Hop & Falk-Petersen 2003). Estimates of ice concentration were based on schematic diagrams from the National Oceanic and Atmospheric Administration (NOAA 2001).

During OTI cruises, sea ice concentrations were derived from satellite data on two spatial scales: the 25 km grid from the Special Sensor Microwave Imager (SSM/I), and the 1.1 km grid from the Advanced Very High Resolution Radiometer (AVHRR), provided by the National Snow and Ice Data Centre (NISDC) and NOAA respectively.

Table 1. Stations, sample (replication) ID, dates, water mass classification, bottom depth, position and ice concentration in the Barents Sea, Fram Strait and off northern Svalbard waters

Project/Area	Station ID	Date	Latitude [°N]	Longitude [°E]	Bottom depth [m]	Water mass	Ice [%]
MARINØK – May							
Barents Sea	**A31**–01	09.05.1999	76.92	32.92	162	ArW	100
Barents Sea	A31–03	09.05.1999	76.96	33.00	169	ArW	100
Barents Sea	A31–05	09.05.1999	76.99	33.03	158	ArW	100
Barents Sea	A31–07	10.05.1999	77.01	33.08	150	ArW	100
Barents Sea	A31–09	10.05.1999	77.01	33.07	141	ArW	100
Barents Sea	**A33**–01	11.05.1999	76.82	32.82	191	ArW	50
Barents Sea	A33–02	11.05.1999	76.80	33.53	186	ArW	50
Barents Sea	A33–03	12.05.1999	76.79	32.97	170	ArW	50
Barents Sea	A33–04	12.05.1999	76.75	33.07	151	ArW	50
Barents Sea	A33–05	12.05.1999	76.75	33.13	147	ArW	50
Barents Sea	**A34**–01	12.05.1999	76.64	32.89	182	ArW	10
Barents Sea	A34–03	13.05.1999	76.64	33.09	186	ArW	10
Barents Sea	A34–05	13.05.1999	76.63	33.12	187	ArW	10
Barents Sea	A34–07	13.05.1999	76.65	33.31	162	ArW	10
Barents Sea	A34–09	13.05.1999	76.64	33.30	166	ArW	10
Barents Sea	**A35**–01	14.05.1999	76.09	32.65	317	ArW	0
Barents Sea	A35–03	14.05.1999	76.11	32.39	319	ArW	0
Barents Sea	A35–05	14.05.1999	76.08	32.67	312	ArW	0
Barents Sea	A35–06	14.05.1999	76.05	32.37	312	ArW	0
Barents Sea	A35–07	15.05.1999	76.09	32.69	316	ArW	0
Barents Sea	**B49**–01	17.05.1999	77.43	27.03	188	ArW	100
Barents Sea	B49–03	17.05.1999	77.43	27.07	187	ArW	100
Barents Sea	B49–05	17.05.1999	77.45	27.00	196	ArW	100
Barents Sea	B49–07	17.05.1999	77.48	27.00	188	ArW	100
Barents Sea	B49–09	17.05.1999	77.52	26.88	172	ArW	100
Barents Sea	**B50**–01	18.05.1999	77.30	27.28	180	ArW	50
Barents Sea	B50–02	18.05.1999	77.37	27.17	171	ArW	50
Barents Sea	B50–04	19.05.1999	77.37	27.16	173	ArW	50
Barents Sea	B50–05	19.05.1999	77.38	27.42	188	ArW	50
Barents Sea	B50–06	19.05.1999	77.37	27.49	199	ArW	50
Barents Sea	**B51**–01	20.05.1999	77.14	27.90	180	AtW/ArW	10
Barents Sea	B51–03	20.05.1999	77.13	28.13	177	AtW/ArW	10
Barents Sea	B51–05	20.05.1999	77.07	28.19	181	AtW/ArW	10
Barents Sea	B51–07	20.05.1999	77.00	28.13	148	AtW/ArW	10
Barents Sea	B51–09	20.05.1999	76.93	28.09	111	AtW/ArW	10
Barents Sea	**B52**–01	21.05.1999	76.52	27.80	128	AtW/ArW	0
Barents Sea	B52–02	21.05.1999	76.49	27.71	133	AtW/ArW	0
Barents Sea	B52–04	21.05.1999	76.47	27.68	129	AtW/ArW	0
Barents Sea	B52–07	21.05.1999	76.49	27.76	129	AtW/ArW	0
Barents Sea	B52–08	21.05.1999	76.35	27.67	135	AtW/ArW	0
‘On Thin Ice’ – May							
Norskenbanken	405	16.05.2003	79.29	10.13	258	AtW	70

Table 1. (*continued*)

Project/Area	Station ID	Date	Latitude [°N]	Longitude [°E]	Bottom depth [m]	Water mass	Ice [%]
Norskenbanken	411	17.05.2003	79.28	9.28	406	AtW	70
Fram Strait	419	19.05.2003	79.20	4.32	> 2700	AtW	60
Flaket	441	21.05.2003	80.04	8.31	508	AtW	70
'On Thin Ice' – August							
Flaket	FL1	13.08.2003	80.04	8.28	520	AtW	0
Flaket	FL2	13.08.2003	80.04	8.28	516	AtW	0
Norskebanken	N1	13.08.2003	80.11	12.01	203	AtW	0
Norskebanken	N2	14.08.2003	80.19	12.00	793	AtW	0
Norskebanken	N3	14.08.2003	80.25	12.01	1139	AtW	50
Hinlopen	H1	17.08.2003	79.26	18.12	425	ArW	0
Erik Eriksen Strait	EE4	20.08.2003	79.14	29.02	286	ArW	0
N Kvitoyrenna	ICE1	23.08.2003	80.32	28.19	208	ArW	70
Outer Rijpjorden	R1	27.08.2003	80.20	22.07	250	ArW	10
Inner Rijpfjorden	R2	28.08.2003	80.03	22.08	205	ArW	10
Sofiadjupet	ICE3	01.09.2003	80.31	12.29	1683	AtW	70

During both projects, water mass properties (salinity, temperature and density) were measured at each station with a Sea-Bird Electronics SBE 911+ CTD sonde deployed vertically to just above the bottom. For the purpose of the statistical analyses, the dominant water masses were defined as AtW ($S > 34.9$ PSU; $T > 1°C$) vs. ArW ($S < 34.8$ PSU; $T < 0°C$) (based on Loeng 1991, Pfirman et al. 1994, Saloranta & Svendsen 2001).

2.3. Zooplankton sampling

Stratified vertical hauls were carried out with a multiple plankton sampler (MPS; Hydro-Bios, Kiel) consisting of five closing nets each with a 0.25 m^2 square opening and a 0.180 mm mesh. At each MARINØK station, 5 replicates of vertical net hauls were taken at 6 h intervals during the 24 hours of the Polar Day from the following layers: 0–10 m, 10–30 m, 30–50 m, 50–100 m and 100 m-bottom. 40 stations were investigated in the central Barents Sea with this sampling regime (see Table 1 for details). Because of the considerable similarities among replications from the same station (Blachowiak-Samolyk et al. 2008a) and for reasons of clarity (limited space on maps), the mean water mass properties, as well as the mean mesozooplankton abundances from five replicates of each MARINØK station, were combined; as a result, only 8 stations are displayed on the maps (Figures 1–2 (see p. 366, 372) and 5–7 (see p. 376, 377, 378)). The statistical analysis, however, takes all replicates (all 40 stations) into consideration.

At OTI stations with depths less than 600 m, five depth strata were sampled: 0–20 m, 20–50 m, 50–100 m, 100–200 m and 200 m-bottom; at deep-water stations (where the bottom depth > 600 m), the strata sampled were: 0–20 m, 20–50 m, 50–200 m, 200–600 m and 600 m-bottom.

The volume of filtered water was calculated from the flow meter records for each sample. All samples were fixed in 4% borax-buffered formaldehyde immediately after collection. Organisms were identified and counted under a stereomicroscope equipped with an ocular micrometer, according to the standard procedure (e.g. Falk-Petersen et al. 1999, Harris et al. 2000, Blachowiak-Samolyk et al. 2008b). Approximately 500 individuals of small zooplankters (most Copepoda, Cirripedia, juvenile stages of Pteropoda, Euphausiacea, Amphipoda and Chaetognatha) were identified and counted in sub-samples (volumes) taken from the sample by automatic pipette. Large zooplankters (large Copepoda, Pteropoda, Euphausiacea, Amphipoda, Decapoda, Appendicularia, Chaetognatha and Pisces) were sorted and identified from the whole sample. Representatives of *Calanus* were identified to species level on the basis of morphology and prosome lengths of the individual copepodid stages, according to the identification methods applied in other studies (e.g. Tande 1991, Kwasniewski et al. 2003).

2.4. Statistical analysis

In order to reveal similarities in the mesozooplankton community among stations, multivariate cluster analysis was performed on a data matrix of species abundances integrated for the whole water column (indiv. m^{-2}). The cluster analysis was performed on the Bray-Curtis similarity index calculated for double-root transformed data, and samples were grouped using the group-average linkage procedure in PRIMER v.5 (Clarke & Warwick 1994).

To study the relationship between abiotic environmental variables (depth stratum, bottom depth, water temperature, salinity) and the multiple species assemblage, redundancy analysis (RDA) in the CANOCO for Windows v4.5 package was used (ter Braak & Smilauer 2002). The vertical gradients in the mesozooplankton distribution were investigated by RDA performed on depth-integrated abundances (indiv. m^{-3}) for three depth categories: surface (0–50 m), middle (50–100 m for shallower stations, and 50–200 m for deep stations) and deep (100-bottom for shallow stations, and 200-bottom for deep stations). Mean temperatures and salinities from each depth stratum were used in the statistical analysis.

For CANOCO, zooplankton abundance (indiv. m^{-3}) data were log transformed ($x' = \log x + 0.1$) prior to analysis so as to allow also the less important taxa to influence the species patterns (Krebs 1989). Those environmental variables that significantly ($p < 0.05$) explained the species variability were included in the final analysis. The environmental variables were ranked according to their quantitative importance by forward selection using a Monte Carlo permutation test (ter Braak & Smilauer 2002).

The ordination techniques and the rules for interpreting the ordination diagram have been reviewed by ter Braak & Verdonschot (1995) and ter Braak & Smilauer (2002). In short, the closer the species and samples are clustered together, the greater the similarity of their environmental preferences and species compositions. The angle between the arrows representing species and environmental variables indicates their correlation: they are uncorrelated if they are perpendicular to each other and highly correlated (negatively or positively) if the angle is small. Long arrows indicate a higher correlation to the species pattern than shorter ones.

3. Results

3.1. Hydrography and sea ice

For the purpose of the present paper, the water masses of the entire study area were simplified and categorised into the following types: Atlantic water (AtW), Arctic water (ArW) and mix water (MW) (Figure 2).

During the MARINØK sampling period, the ice edge was located near the Polar Front by the inner part of the Hopen Trench. Cold ArW (< -1.2°C) with salinities close to 34.8 PSU was prevalent over the slopes of the Great Bank on transect A (stations A31, A33, A34), whereas relatively warm (> 1°C), saline (> 35.0 PSU) AtW prevailed further south in the deeper Hopen Trench (station A35). Cold ArW was dominant over the Spitsbergen Bank (stations B49, B50, B51). In the shallowest area, south-east of Hopen (station B52), cold mix water (< 0°C) prevailed (Figures 1 and 2). A more detailed classification of the hydrographic situation during MARINØK will be found in Blachowiak-Samolyk et al. (2006).

During OTI, AtW was found at stations along and near the shelf slope of Fram Strait, while ArW was predominant on the shelf and fjord stations of the northern Barents Sea (stations H1, R1, R2, EE4) (Hegseth & Sundfjord 2007, A. Sundfjord, unpublished data).

The ice conditions at each MARINØK station changed continuously, depending on winds and tides. Thus, stations A31 and B49 were in compact pack ice (100%), there was c. 50% ice cover at stations A33 and B50, and c. 10% ice cover at stations A34 and B51 near the ice-edge; stations A35 and B52 were located in the 'open water' (Table 1, Figure 1). The ice was generally < 2 m thick and described as first-year ice.

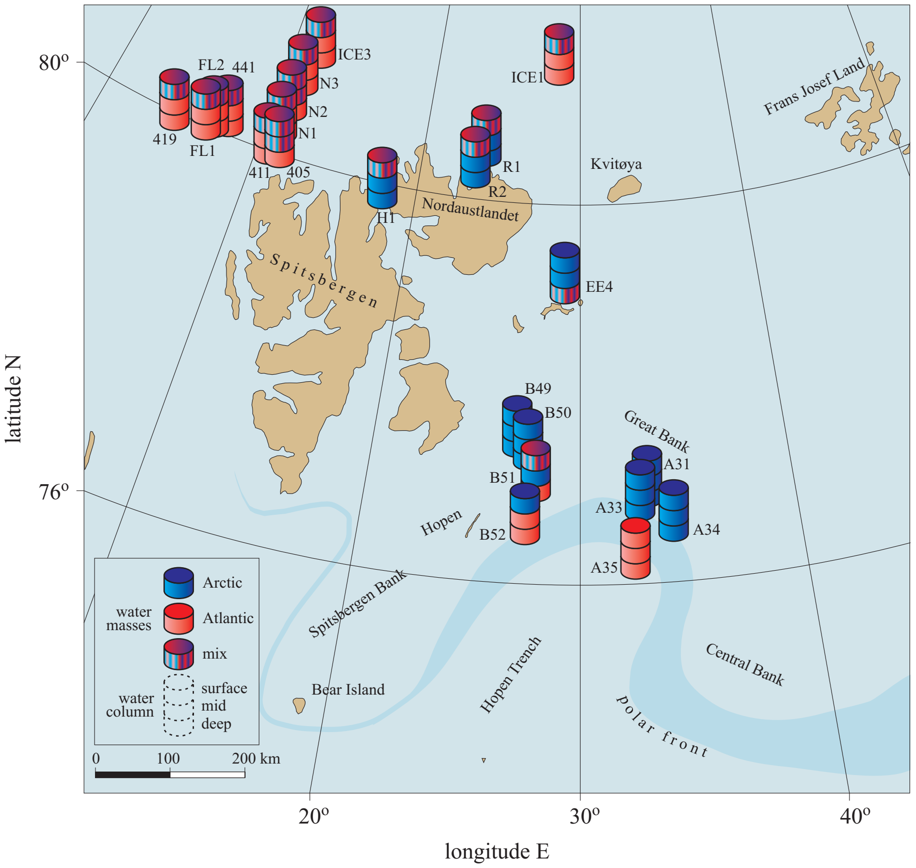

Figure 2. Water masses determined from CTD casts simplified for the purposes of this paper in the Barents Sea (May 1999) and the waters off northern Svalbard (May and August 2003). AtW: Atlantic water (> 1°C, > 35.0 PSU); ArW: Arctic water (< 0°C, 34.3–34.8 PSU); MW: mix water with characteristics different in the Atlantic Fram Strait (S < 34.7 PSU, T > 1.5°C) from those in the waters off northern Svalbard and in the central Barents Sea (S < 34.0 PSU; T < 0°C). Three depth categories were applied: surface (0–50 m), middle (50–100 m at shallow stations, and 50–200 m at deep stations) and deep (100 m to bottom at shallow stations, and 200 m to bottom at deep stations)

In May 2003, OTI sampling took place in consolidated pack ice (50 –90%) near the ice edge north-west of Spitsbergen, whereas stations in both open water and c. 70–90% ice cover were sampled in August 2003 (Table 1). In May 2003, the sea ice had recently opened up (< 14 days) (Table 1). In August, little sea ice was present, except in northern Kvitøyrenna (station Ice1), in Sofiadjupet (station Ice3) and Norskebanken (station N3) (Hegseth & Sundfjord 2007).

3.2. Mesozooplankton

A detailed description of the dominant mesozooplankton species/taxa in the MIZ of the central Barents Sea (MARINØK) has been published as a diel vertical migration (DVM) issue (Blachowiak-Samolyk et al. 2006) and also in response to the question, how representative the single zooplankton sample is in comparison with replicates (Blachowiak-Samolyk et al. 2008a). Zooplankton data from Fram Strait and the northern Svalbard area (OTI) have been described recently in the context of their trophic structure (Blachowiak-Samolyk et al. 2007) and their relations with the hydrology of the relevant water masses (Blachowiak-Samolyk et al. 2008b).

3.2.1. Cluster analysis

Cluster analysis based on the abundances of all mesozooplankton species/taxa (indiv. m^{-2}) revealed two main groups of stations in the study area (Figure 3). One large group linked all the stations located in the Barents Sea area influenced mainly by ArW (both projects and seasons). The second group connected all AtW-influenced stations situated in Fram Strait (both seasons). Within the Barents Sea group, the August OTI samples taken from the northern Svalbard/Barents Sea region (stations H4, R1, R2 and EE4) constituted a subgroup separate from all the other central Barents Sea samples. In terms of the last mentioned subgroup, the clear separation of

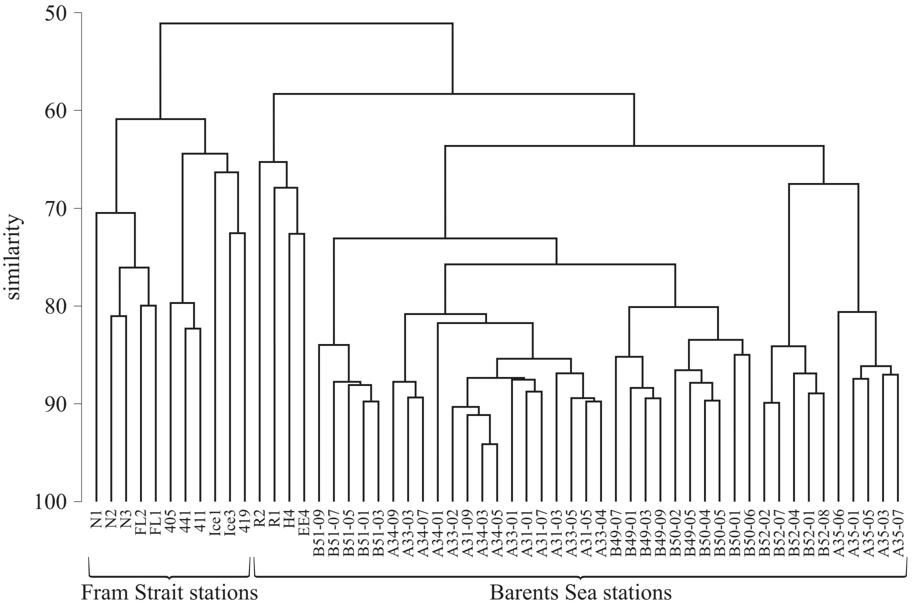

Figure 3. Cluster of stations for total mesozooplankton abundance (indiv. m^{-2})

'ice' stations (A31, A33, A34, B49, B50 and B51) and open-water stations (A35 and B52) was confirmed.

3.2.2. Environmental influence on the vertical species distribution pattern (RDA)

Evident regularities were revealed in RDA based on vertical mesozooplankton abundances (indiv. m^{-3}) when all the investigated stations and the three depth categories were considered (Figure 4). The environmental variables depth layer, temperature, salinity and bottom depth together

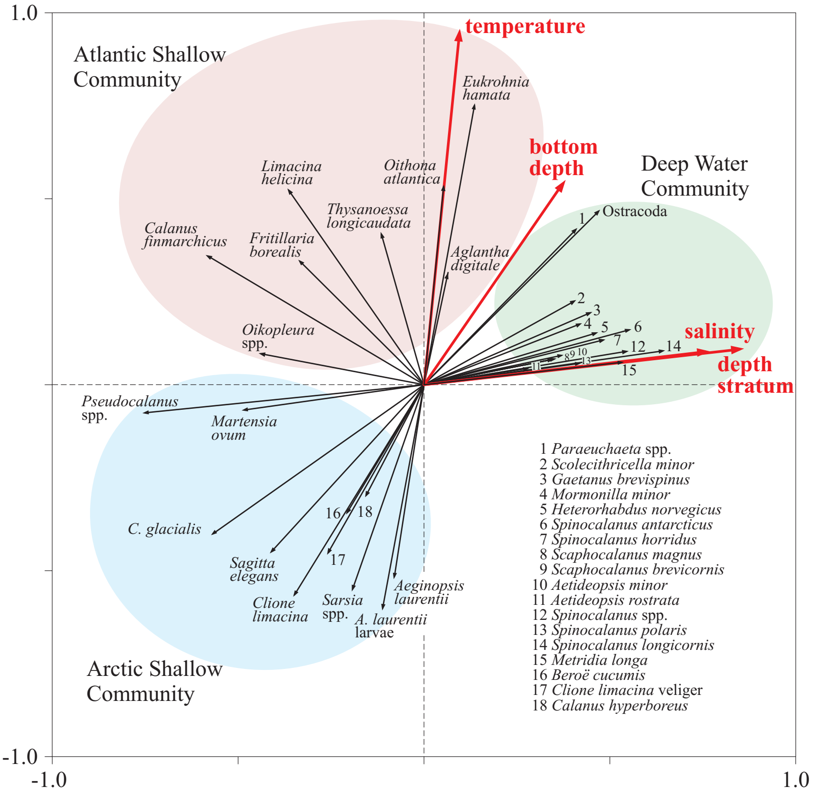

Figure 4. Redundancy analysis (RDA) of depth-integrated mesozooplankton abundance (indiv. m^{-3}) in the Barents Sea, Fram Strait and off northern Svalbard waters. Three depth categories were applied: surface (0–50 m), middle (50–100 m at shallow stations, and 50–200 m at deep stations) and deep (100 m to bottom at shallow stations, and 200 m to bottom at deep stations). The first canonical axis (RDA-1) explains 46.4% of the species-environmental relationship, and the second axis (RDA-2) explains 36%. Variance of species data accounts for 14% and 10.9%, with regard to axes 1 and 2 respectively

explained 37% of the total variability in mesozooplankton abundance within the study area (Table 2).

Table 2. Ranking of environmental variables in the Barents Sea, Fram Strait and off northern Svalbard waters with a significant influence on mesozooplankton distribution (Monte Carlo permutation test in RDA, $p < 0.05$), with significant values in bold. Note: the eigenvalue (λ) for each variable indicates the portion of the total variance explained by the model

Explanatory variables	Explained variability [%]	p-value	F-value
depth stratum	17	**0.002**	13.47
salinity	10	**0.002**	9.67
tempterature	9	**0.002**	8.52
bottom depth	1	0.348	1.05
Total	**37**		

Depth stratum was the strongest contributor to the RDA model, explaining 17% of the overall mesozooplankton variability. A close relationship between this parameter and increasing abundances of all the deeper water inhabitants (Table 2, Figure 4) was established. Salinity explained 10% and temperature an additional 9% of the total mesozooplankton heterogeneity. Bottom depth was the weakest contributor to the model, explaining only 1% of the overall variability and having no significant impact on the mesozooplankton patterns.

A clear relationship in the mesozooplankton community composition was manifested in RDA (Figure 4); as a result, three key zooplankton communities were identified. Abundances of representatives of the first group, including *Eukrohnia hamata*, *Oithona atlantica*, *Aglantha digitale*, *Fritillaria borealis*, *Calanus finmarchicus*, *Thysanoessa longicaudata*, *Oikopleura* spp. and *Limacina helicina*, were closely correlated with increasing temperature and constituted the Atlantic Shallow Community (AtSC). The second group represented the Arctic Shallow Community (ArSC) and included *Aeginopsis laurentii*, *Sarsia* sp., *Clione limacina*, *Beroë cucumis*, *C. hyperboreus*, *C. glacialis*, *Sagitta elegans*, *Pseudocalanus* spp. and *Mertensia ovum*; it was negatively correlated with the temperature gradient. The third group, the Deep Water Community (DWC), consisted of typical meso- and bathypelagic inhabitants – *Spinocalanus elongatus*, *S. antarcticus*, *S. horridus*, *S. longicornis*, *Aetideopsis rostrata*, *A. minor*, *Mormonilla minor*, *Heterorhabdus norvegicus*, *Scaphocalanus brevicornis*, *S. magnus*, *Metridia longa*, *Scolecithricella minor*, *Paraeuchaeta* spp. and

Ostracoda – and was clearly associated with increasing bottom depth, salinity and depth stratum (Figure 4).

3.2.3. Mapping indices of Arctic and Atlantic mesozooplankton communities

All species belonging to the Atlantic Shallow Community (AtSC) and Arctic Shallow Community (ArSC) were pooled and their relative abundances in the total zooplankton calculated with respect to a given layer (surface, mid and deep strata), regions (the Barents Sea, Fram Strait and the waters off northern Svalbard), years (1999 or 2003) and seasons (spring or autumn). Depending on the prevailing AtSC or ArSC, the proportion Atl/Ar or Ar/Atl groups yielded an 'Atlantic' or an 'Arctic'

surface layer

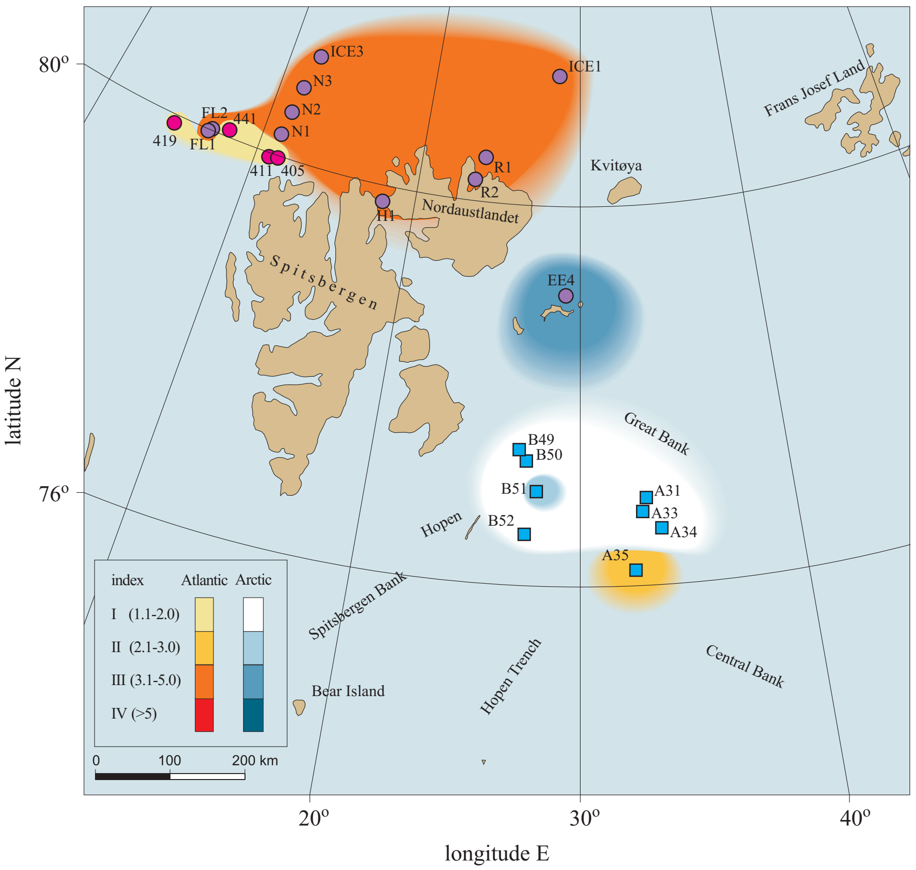

Figure 5. Atlantic and Arctic mesozooplankton indices in the surface water layer of the Barents Sea, Fram Strait and off northern Svalbard waters

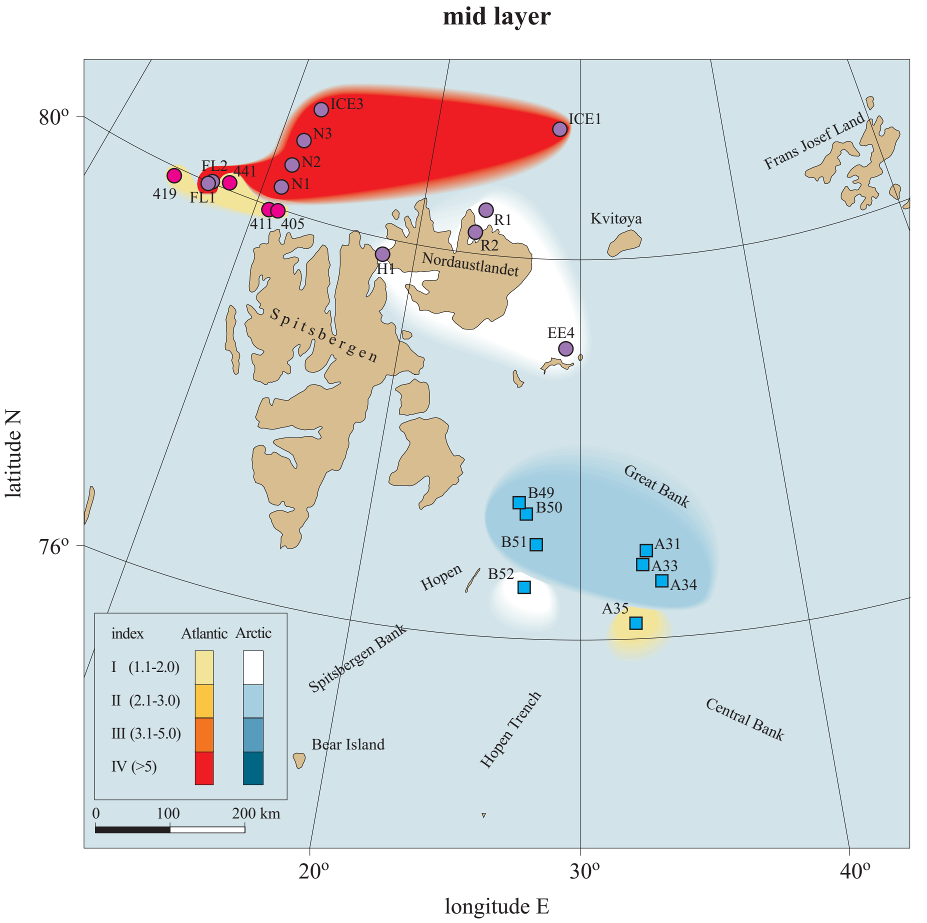

Figure 6. Atlantic and Arctic mesozooplankton indices in the mid water layer of the Barents Sea, Fram Strait and off northern Svalbard waters

Index respectively. Generally, the Index has four categories and visualises, separately for each depth stratum, the extent to which the Atlantic community prevails over the Arctic one (different shades of red on the maps) or vice versa (different shades of blue) (Figures 5–7).

The surface layer (0–50 m) in Fram Strait and the waters off northern Svalbard influenced by mix waters (MW) (Figure 2) were occupied by the Atlantic community (Figure 5). The Atlantic Index reached higher values in autumn than in spring 2003 (3.1 and 1.9 respectively). The upper layers of the Barents Sea were influenced by ArW, except for one area of Atlantic character, represented by station A35. The Arctic Index reached its highest value (4.8) in the northern part of the Barents Sea (station EE4), then decreased southwards to 3 at the MW-dominated station B51,

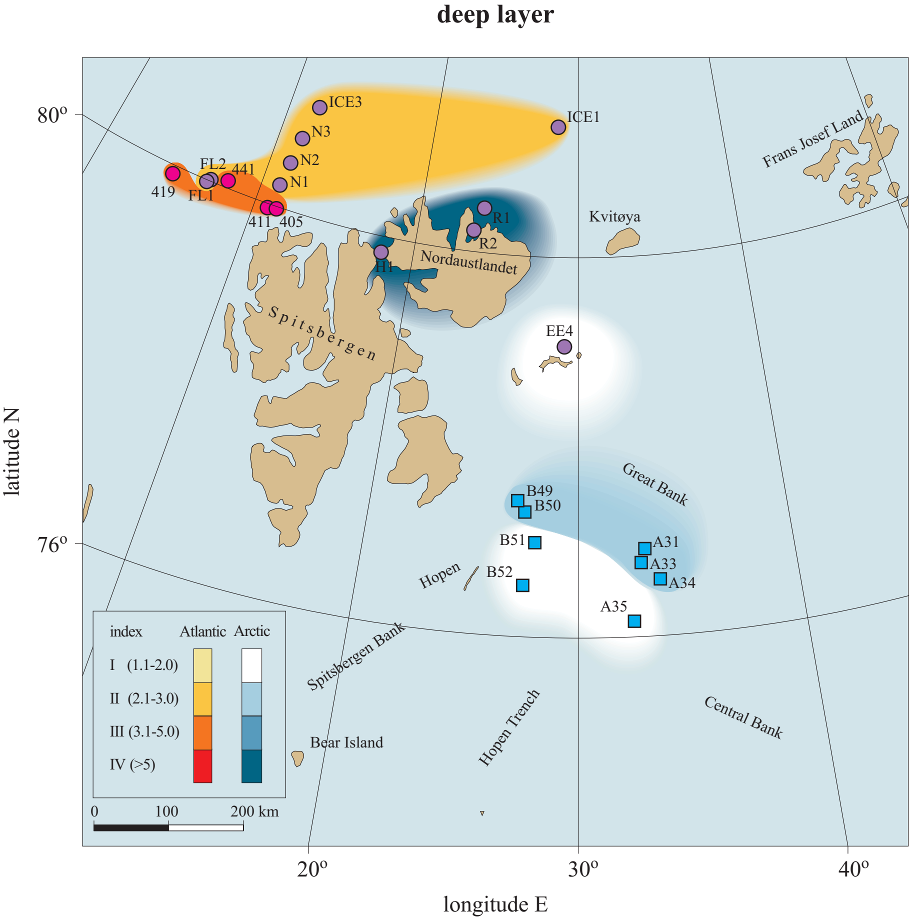

Figure 7. Atlantic and Arctic mesozooplankton indices in the deep water layer of the Barents Sea, Fram Strait and off northern Svalbard waters

and finally declined to 1.6 at the remaining ArW stations (A31, A33, A34, B49 and B50) in the central Barents Sea. The Atlantic community was predominant (Atlantic Index = 2.7) at the surface of the only MARINØK station influenced by Atlantic waters – A35 (Figure 5).

In the mid layer (50–100 m in shallow waters and 50–200 m in deeper areas) of Fram Strait and the waters off northern Svalbard, the Atlantic community was predominant (Figure 6). As in the surface layer, the Atlantic Index was much higher in August than in May 2003 (6.3 and 2.0 respectively). The Arctic Index of the zooplankton from off northern Svalbard (stations R1, R2, H4 and EE4) was relatively low (2.0), whereas that of the zooplankton from the central, ice-covered Barents Sea (stations A31, A33, A34, B49, B50 and B51) was higher (2.8). In the mid layer of the Atlantic-influenced area of the Barents Sea (stations A35 and B52), the Atlantic community was marginally dominant at station A35 (Atlantic Index = 1.1), whereas the Arctic community was moderately dominant at station B52 (Arctic Index = 1.1; Figure 6).

In the deep layer (100 m-bottom in shallow waters and 200 m-bottom at deeper stations) of the Atlantic Fram Strait stations, the Atlantic community was prevalent. In contrast to the two upper depth strata analysed above, the Atlantic Index was higher in May than in August 2003 (3.7 and 2.3 respectively) (Figure 7). The Arctic Index reached a value of 6.2 (the highest recorded in the whole study area) in the deepest layer of the Arctic stations in the waters off northern Svalbard (R1, R2 and H4). At Arctic station EE4 in the northern Barents Sea, the Arctic Index diminished to 1.8, but increased to 2.5 at Arctic stations in the central Barents Sea (A31, A33, A34, B49 and B50). Surprisingly, the deep layer zooplankton from AtW-influenced stations A35, B51 and B52 had an Arctic Index of 1.9.

4. Discussion

The geographical integrity of the horizontal mesozooplankton distribution structure was clear-cut throughout the cluster analysis. Its location in the study area corresponded well with the hydrography because stations from both the central Barents Sea and the waters off northern Svalbard were influenced mainly by ArW (apart from one typically AtW station – A35), whereas the Fram Strait stations were strongly impacted by AtW (Figure 3). A similar geographical-hydrological integrity was recently reported from the northern Svalbard waters by Daase & Eiane (2007).

Zooplankton communities are often found to form assemblages with a close relationship to specific water masses (e.g. Pedersen et al. 1995, Dalpadado et al. 2003, Søreide et al. 2003, Blachowiak-Samolyk et al. 2008b). To obtain detailed information on the quality and scale of the interactions between the various environmental factors and zooplankton abundance, a correspondence analysis was performed using the RDA ordination model (CANOCO).

The following environmental variables – depth layer, salinity, temperature, bottom depth – together accounted for 37% of the overall mesozooplankton variability in the investigated area. The total variability explained here was not very high, especially in comparison with previous studies (Søreide et al. 2003, Blachowiak-Samolyk et al. 2008a). However, the fact that the higher explanation rates obtained in the latter papers must have been strongly influenced by the very much smaller study areas (central Barents Sea and northern Svalbard waters respectively) should be taken into consideration.

Depth layer can be a very important variable structuring the vertical mesozooplankton distribution (Thor et al. 2005), and the present study revealed quite a clear separation of samples from different depths, with deep samples associated with the depth gradient and surface-to-mid samples with increasing temperature. Depth stratum was the most important contributor to the RDA model, describing 17% of the variation in species. Many authors have indicated consistent vertical distribution patterns of the main zooplankton taxa specific to each region (e.g. Søreide et al. 2003) and depth (e.g. Pedersen et al. 1995). Temperature and salinity had very similar influences (about 10% each) on the overall mesozooplankton pattern. An earlier study on species-environment relationships in the Barents Sea from March–May 1989 (Pedersen et al. 1995) showed that the zooplankton community could not be grouped according to temperature and/or salinity. Recently, Søreide et al. (2003) and also the present authors (Blachowiak-Samolyk et al. 2008a) pointed out the quite high, respective impacts of salinity and temperature on macro- and mesozooplankton distribution in the Barents Sea.

Bottom depth has been reported as having a great influence on mesozooplankton distribution in the Barents Sea (Arashkevich et al. 2002, Søreide et al. 2003) and in the waters off northern Svalbard (Daase & Eiane 2007, Blachowiak-Samolyk et al. 2008b), but this was not confirmed in the current study. Very probably, sea depth had no significant impact on mesozooplankton variability in the area analysed owing to the rather extensive depth ranges of the stations investigated (from about 200 –300 m in the central Barents Sea to max. 2700 m in Fram Strait).

Ice concentration was also tested, but it was subsequently excluded from RDA as it did not contribute significantly to the overall mesozooplankton variability. Similar results were also indicated by earlier investigations in the Barents Sea (Falk-Petersen et al. 1999, Søreide et al. 2003). The influence of sea ice concentration on zooplankton is complex, because the ice conditions differ regionally and seasonally, and may affect species differently. One of the reasons why it is very difficult to assess the influence of ice concentration on the zooplankton community in the entire water column is the fact that the effect of ice on pelagic biota most likely diminishes with increasing depth.

Both descriptive and multivariate methods identified three distinct assemblages with regard to the vertical distribution of mesozooplankton abundance: an Atlantic Shallow Community (AtSC), an Arctic Shallow Community (ArSC) and a Deep Water Community (DWC).

Atlantic-associated species such as *Eukrohnia hamata*, *Oithona atlantica*, *Aglantha digitale*, *Fritillaria borealis*, *Calanus finmarchicus*, *Thysanoessa longicaudata*, *Oikopleura* spp. and *Limacina helicina* increased in abundance with increasing temperature. The preferences of *C. finmarchicus* and *O. atlantica* for AtW have been comprehensively described by many authors (e.g. Kielhorn 1952, Brodsky 1967), as have those of *A. digitale* (Zelikman 1972). Although *L. helicina* is known to be an Arctic-boreal species (Kielhorn 1952, Hermans & Satterlie 1992), the abundance of the species scaled positively with increasing temperature. Unlike the above-mentioned taxa, *E. hamata* is a cosmopolitan species (Pierrot-Bults & Chidgey 1988), which has been found to dominate the zooplankton in deep regions of the Laptev Sea (Kosobokova et al. 1998). The noticeable preference of *F. borealis* for AtW accorded with previous observations by Arashkevich et al. (2002). The abundance of *T. longicaudata* correlated with surface samples from the Fram Strait (AtW) stations, which confirmed the previously observed vertical distribution pattern of the species in the Barents Sea (Dalpadado & Skjoldal 1991).

The Arctic Surface Community (ArSC), with *Aeginopsis laurentii*, *Sarsia* sp., *Clione limacina*, *Beroë cucumis*, *Calanus hyperboreus*, *C. glacialis*, *Sagitta elegans*, *Pseudocalanus* spp. and *Mertensia ovum*, exhibited increasing abundances with decreasing temperature. The preferences of *A. laurentii* and *B. cucumis* for ArW have recently been described by Willis et al. (2006) and Zelikman (1972) respectively. Unstad & Tande (1991) demonstrated that the distribution of *C. glacialis* in the Barents Sea was closely related to that of ArW; the present investigation confirmed these observations. The sparse occurrence of *C. hyperboreus* in northern Svalbard waters accords with earlier results from the Barents Sea (Hassel 1986, Eilertsen et al. 1989, Tande 1991) and points to the fact that in addition to being an Arctic species, this is a deep-water species inhabiting primarily the Greenland Sea and the Arctic Ocean (Hirche 1997). *Mertensia ovum* was distributed in ArW, as previously described in the Barents Sea by Søreide et al. (2003). The present study also confirmed the extensive occurrence of *C. limacina* in ArW (Mileikovsky 1970, Søreide et al. 2003), as well as the preference of *S. elegans* for colder waters indicated by Wiborg (1955). The results of the present study concur with those of other investigations characterising representatives of *Pseudocalanus* as neritic species in both the Barents Sea and the Canadian Arctic (Conover & Huntley 1991).

The Deep Water Community (DWC) clearly associated with Fram Strait, the only deep area in the survey area (stations 419, N2, N3 and Ice3), included widely occurring meso- and bathypelagic species. The present study also confirmed the distinct increase in abundance of DWC towards deeper waters. This group was associated with increasing bottom depth, salinity and depth stratum. Many of these deep-water zooplankters are cosmopolitan species commonly found elsewhere in the Atlantic Ocean (e.g.

Kosobokova & Hirche 2000). Thus, the distribution of these animals reflects the circulation of Atlantic water, which enters the Arctic Ocean north of Svalbard and extends to the east as a cyclonic boundary current along the Eurasian continental rise (Aagaard et al. 1987, Mumm et al. 1998).

Recent ocean warming has extended the geographical range of many temperate marine species, and many cold-adapted species have declined (Beaugrand et al. 2002). There are indications that the Arctic is warming up at a rate faster than the global mean trend (ACIA 2004). This is due in part to the more intensive inflow of relatively warm and saline Atlantic water masses into the Arctic in recent decades; nevertheless, it remains unclear how an increase in temperature and salinity (Morison et al. 2000, Schauer et al. 2004) will affect Arctic marine ecosystems.

The Marginal Ice Zone (MIZ) is one of the most important and dynamic features in the Arctic, and even small changes in the global climate will noticeably affect its position. The Barents Sea MIZ is closely associated with the Polar Front at maximum ice extent, whereas the boundary between the onshore shelf waters of Fram Strait and the West Spitsbergen Current (WSC) forms the shelf Arctic Front. The composition, numbers and relative abundances of zooplankton species vary across the fronts, because they create a kind of barrier to many marine organisms (Arctic vs. Atlantic) (e.g. Dragesund & Gjøsæter 1988).

In the present paper the relative abundances of Atlantic and Arctic mesozooplankton communities were compared in order to test the hypothesis whether ArW and AtW determine the corresponding zooplankton assemblages. This discussion is taking on a new dimension, especially in the light of the model of Ellingsen et al. (2008), according to which in the coming years the simulated production of Atlantic zooplankton species will increase by approximately 20% and become more abundant in the eastern Barents Sea. On the other hand, the model also predicts that the Arctic zooplankton biomass will decrease significantly (50%) in the sea, causing the total simulated production to decrease.

As observed in this study, variability in the physical conditions of the surface layer (mix water) directly affected the mesozooplankton of Fram Strait and the waters off northern Svalbard, and in consequence AtSC was clearly dominant in these areas. According to Saloranta & Svendsen (2001) the Arctic Front at the surface of Fram Strait is a density coastal front associated with less saline surface water, often resembling a wedge that thickens towards the shore and most probably affecting the zooplankton composition there. The bulk of this fresh water originates from glaciers and rivers, especially via the major fjords of Spitsbergen (Saloranta & Svendsen 2001). This is in agreement with Cottier & Venables (2007), who stated that this front separates the warm, saline Atlantic water in the West Spitsbergen Current from the cooler, fresher water over the West Spitsbergen Shelf. The surface layer of the only typically ArW station – EE4 in the northern Barents Sea – had a high Arctic Index, which suggests that this is a kind of transitional area between the central Barents Sea and the waters off northern Svalbard. The indices of the mesozooplankton from the upper depth stratum of the central Barents Sea were in good agreement with complementary hydrographic characteristics (ArW = Arctic Index and AtW = Atlantic Index).

The Atlantic and Arctic Indices from the mid layer, which is more stable than the surface waters, reflected the closest association of zooplankton with hydrology. The only exception was station B52, where a slight prevalence of the Arctic community was detected in the AtW layer. The ambiguous situation there could be explained by the proximity of this station to the Polar Front (Figure 1). According to Daase et al. (2007), the subsurface hydrography between 50–150 m is a better predictor of *Calanus* spp. abundance than the near-surface conditions in the Atlantic transition zone around Svalbard during early autumn.

The deep layer of Fram Strait was inhabited predominantly by the Atlantic community, which is in accordance with the region's hydrology. North of Svalbard, ArW stations (R1, R2 and H1) registered the highest Arctic Index owing to the extremely high abundance of *C. glacialis* (Blachowiak-Samolyk et al. 2008b). The lowest Arctic Index in the mix deep layer at station EE4 may have been due to the inflow of some AtW (from WSC) from the north between Nordaustlandet and Franz Josef Land as a near-bottom current (Loeng 1991). In the central Barents Sea, the Arctic community was prevalent in the deep layer of ArW-influenced stations (A31, A33, A34, B49 and B50), whereas the deep layer of AtW-dominated stations had a lower Arctic Index. The different hydrology of the two open water stations offers a partial explanation for this situation. Station A35 on the eastern Transect A was located south of the Polar Front, and therefore, both 'across-ice-edge' and 'across-Polar-Front' conditions were sampled. Transect B (and station B52) on the other hand was located entirely in Arctic water north of the Polar Front. It is also characteristic that in the regions where Arctic and Atlantic water masses meet, boreal taxa co-occur with typical Arctic species (Conover 1988, Hirche & Mumm 1992). The conclusion from this study is that the considerable variability in mesozooplankton abundance in the investigated MIZs is governed primarily by environmental conditions, water masses and bottom depth. Much of the variation can be explained by the depth layer, but it is also strongly modified by biological factors (not analysed here) like growth, life cycle, diel vertical migration and ontogenetic seasonal migration (Mackas & Tsuda 1999, Blachowiak-Samolyk et al. 2006, Cottier et al. 2006, Willis et al. 2006).

Mapping of Atlantic and Arctic Indices shows that, in most cases, the mesozooplankton match the hydrology of the complementary depth stratum and region. The most probable explanation for the observed exceptions is the substantial advective transport of pelagic organisms between areas and populations (Irigoien et al. 2004, Torgersen & Huse 2005). The mid layer proved to be a better predictor of mesozooplankton distribution than the relatively unstable, near surface conditions.

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