

Macrozooplankton communities and environmental variables in the Barents Sea marginal ice zone in late winter and spring

Janne E. Søreide^{1,2,3,*}, Haakon Hop¹, Stig Falk-Petersen¹, Bjørn Gulliksen², Edmond Hansen¹

¹Norwegian Polar Institute, 9296 Tromsø, Norway

²Norwegian College of Fishery Science, University of Tromsø, 9037 Tromsø, Norway

³Present address: Akvaplan-niva, 9296 Tromsø, Norway

ABSTRACT: The horizontal distribution of macrozooplankton (≥ 3 mm) was studied with respect to changes in environmental conditions along 3 transects across the marginal ice zone (MIZ) in the NW Barents Sea during late winter (March 2000) and spring (May 1999). The water masses, which were identified by their salinity and temperature characteristics, largely determined the macrozooplankton composition, but season (late winter vs spring), geographical area (latitude and longitude) and bottom depth were also important. Almost 80% of the total macrozooplankton variability could be explained by changes in these environmental variables. Ice cover and the algal bloom situation had no significant impact on the horizontal macrozooplankton distribution early in the season (March to May). We sampled 3 main water masses: cold and less saline Arctic water (ArW), warm and saline Atlantic water (AtW) and mixtures of these (MIX); 5 distinct macrozooplankton communities were found, 2 in ArW (ArW bank and ArW slope), 2 in MIX (warm, $>1^{\circ}\text{C}$, and cold, $<0^{\circ}\text{C}$, MIX) and 1 in AtW. These communities were characterised by differences in species abundance rather than differences in taxonomic composition. Numerically important macrozooplankton were *Calanus glacialis*, *C. hyperboreus*, *Thysanoessa inermis* and *Aglantha digitale*. These were also important in terms of wet biomass together with *Beröe cucumis*, *Clione limacina* and *Sagitta elegans*. Good indicator species for ArW were *C. glacialis*, *C. limacina*, *Mertensia ovum* and *Parathemisto libellula*, and for AtW *Thysanoessa* spp. (*T. inermis*, *T. longicaudata* and *T. raschii*). Characteristic for MIX, i.e. the Polar Front region, was low macrozooplankton abundance, biomass and species richness compared to AtW and ArW. Seasonal variability (late winter vs spring) accounted for 21% of the total macrozooplankton variability. Particularly the herbivores showed large seasonal variability in abundance and biomass, most probably due to their seasonal migration patterns.

KEY WORDS: Macrozooplankton · Barents Sea · Marginal ice zone · Multivariate community analyses · Ordination

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INTRODUCTION

The Barents Sea is an Arctic shelf sea, located between 70 to 80° N and 20 to 60° E, with an average depth of 230 m (Zenckevitch 1963). It is a productive, high-latitude marine ecosystem that supports one of the world's richest fisheries (Zenckevitch 1963, Hamre 1994, Sakshaug et al. 1994). Most zooplankton studies in the

Barents Sea have been limited to the numerically important copepods, particularly of the genus *Calanus*, which may constitute up to 90% of the total zooplankton biomass during summer (e.g. Eilertsen et al. 1989, Hassel 1995, Pedersen et al. 1995, Falk-Petersen et al. 1999). Distribution and quantitative information on large zooplankton organisms (≥ 3 mm), i.e. hydromedusas, siphonophores, ctenophores, chaetognaths, amphipods

*Email: jes@akvaplan.niva.no

and euphausiids, are still limited. Although their contribution to the zooplankton in terms of abundance can be negligible, their role in trophodynamic processes might be very important due to their large predation impact (Falkenhaus 1991, Swanberg & Båmstedt 1991, Dalpadado & Skjoldal 1996, Dalpadado et al. 2001). Large variations in zooplankton abundance, biomass and structure have been recorded in the Barents Sea on seasonal, interannual and geographical scales (Hassel 1986, Skjoldal et al. 1987, Skjoldal & Rey 1989, Arashkevich et al. 2002). Strong seasonality combined with large intra- and interannual variations in inflowing warm ($>1^{\circ}\text{C}$) and saline (≥ 35 PSU) Atlantic water (AtW) and, thus, ice cover, contributes to these zooplankton fluctuations, but to what extent is unknown.

The Barents Sea is a highly advective ecosystem, being connected to the Arctic Ocean in the north, the Kara Sea in the east and the Norwegian Sea in the southwest. The main inflow of AtW is from the southwest via the deeper trench between Norway and Bear Island (Bjørnøya), but some AtW (derived from the West Spitsbergen Current) also flows in from the north between Nordaustlandet and Franz Josef Land as a near-bottom current (Loeng 1991, Løyning 2000). The latter AtW is often referred to as cold AtW, because it is usually cooled and partly transformed on its way around the western and northern Spitsbergen coasts (Løyning 2000, Kaltin et al. 2002). AtW meets and mixes with the colder ($<0^{\circ}\text{C}$) and less saline (34.3 to 34.8 PSU) Arctic water (ArW) at the Polar Front (see Fig. 1). This topographically steered oceanic front divides the western Barents Sea into a warm, ice-free southern part and a cold, seasonally ice-covered, northern part (Loeng 1991). The maximum sea-ice extent during winter normally coincides with the Polar Front, and during late summer and autumn, the Barents Sea becomes almost ice-free (Vinje & Kvambekk 1991). Melting of sea ice during spring and summer gives rise to strongly stratified surface waters that, in concert with increasing light levels and winter-accumulated nutrients, create conditions for intensive algal blooms (Skjoldal & Rey 1989, Hegseth 1998, Falk-Petersen et al. 2000a). These blooms follow the receding ice edge as it moves northwards, and produce a high zooplankton abundance and biomass that subsequently influence the abundance of fishes as well as marine mammals and sea birds (Hassel et al. 1991, Nilssen et al. 1995, Mehlum et al. 1998). The intense seasonality of primary production at high latitudes means that food for herbivorous zooplankton is severely limited in winter. Many of them thus enter a non-feeding mode and overwinter at depth, utilising lipid reserves synthesised the previous summer (Tande & Henderson 1988, Hagen & Auel 2001). The seasonal resource limitation is one important cause for the generally delayed repro-

ductive maturity and longer life span in high-latitude marine invertebrates compared to those from lower, more temperate latitudes (Clarke 1983, 1988). For instance, the generation time of the large herbivorous copepod *Calanus hyperboreus* ranges from 1 yr in the Norwegian Sea to 3–4 yr in the Greenland Sea and the Arctic Ocean (Wiborg 1954, Østvedt 1955, Dawson 1978, Hirche 1997). Zooplankton populations of different zoogeographical origin (i.e. Arctic vs Atlantic) may therefore have markedly different life histories and size distributions (Mileikovsky 1970, Kwasniewski et al. 2003). Potentially, a total biomass of 660×10^3 t C of the Atlantic copepod *Calanus finmarchicus* can be transported with AtW into the Barents Sea (Pedersen 1995). In comparison, the endemic production of *C. finmarchicus* during the same period is about 100×10^3 t C (Pedersen 1995). The distribution of ArW and AtW, and their mixing (MIX), may therefore have a major influence on zooplankton distribution and abundance in the Barents Sea (Tande et al. 1985, Hassel 1995, Pedersen 1995, Falk-Petersen et al. 1999).

In the present study, the horizontal community pattern of macrozooplankton across the marginal ice zone (MIZ) in the Barents Sea, from dense pack-ice to open water, was determined during late winter (March) and spring (May). Species were divided into developmental stages (copepods) and size-classes (abundant non-copepod species) and subsequently into herbivores, omnivores and carnivores in order to study community structures. Multivariate statistics were used to relate the major community patterns to the environmental variables: ice cover, salinity, temperature, bottom depth, latitude, longitude and stage of the algal bloom.

MATERIALS AND METHODS

Transect description. The data were collected during 2 cruises with the ice-strengthened RV 'Lance' from 1 to 26 May 1999 and 8 to 23 March 2000. Stations were located in areas with different ice conditions (close pack-ice, open drift-ice and open water) within the MIZ. Transects began as far north into the pack ice as ice conditions allowed, and moved southwards into less dense ice (see Table 1, Fig. 1). In May, 2 transects were followed in the MIZ: Transect A (7 to 14 May) in the central Barents Sea started at the southern Great Bank (<200 m) and ended in the deeper Hopen Trench (~ 300 m), and Transect B (16 to 24 May) was further west, starting north of Hopen (~ 200 m) and extending south into the shallower parts of the Spitsbergen Bank (<100 m). The last station on each transect (Stns A5 and B5) was supplemented by an oceanographical transect (including 15 stations) along the ice edge

across the Hopen Trench (5 to 7 May) (Hop & Falk-Petersen 2003). In March, another transect was sampled in the MIZ in the central Barents Sea: Transect C (16 to 20 March), starting from the NW Great Bank (<180 m) and ending up in the Hopen Trench (~300 m). A second transect across MIZ near Hopen in March was cancelled due to bad weather.

Hydrography, ice characteristics and chlorophyll *a*.

Salinity and temperature were recorded at each station, within 1 h before the macrozooplankton sampling, with a Sea-Bird Electronics SBE 911+ CTD sonde. The properties of the water masses (Arctic vs Atlantic) with respect to salinity and temperature were obtained from recent literature (Loeng 1991, Harris et al. 1998). The CTD data were assigned to a regular grid in MATLAB v6.5, and the salinity–temperature field between the individual stations was calculated by linear interpolation.

Ice concentration, ice thickness and floe size were observed and noted every third hour from the ship's bridge by trained personnel, and documented by digital pictures (Hop & Falk-Petersen 2003). Estimation of ice concentration (in tenths) was based on schematic diagrams from the National Oceanic and Atmospheric Administration (NOAA 2001). The chlorophyll *a* biomass (integrated over 0 to 50 m) and the stage of the algal bloom in May 1999 and March 2000 were obtained from Engelsen et al. (2002) and E. N. Hegseth (unpubl.). Recordings from a Sea Tech fluorometer attached to the CTD were used to estimate the approximate algal biomass at stations for which chlorophyll *a* samples were missing (Stns A3, B5, C2 and C3). The algal bloom situation was determined from the vertical distribution of chlorophyll *a* ($\text{mg chl } a \text{ m}^{-3}$).

Zooplankton sampling. Since trawling is risky and often impossible in the MIZ, vertical hauls with a large Nansen closing net (Macrozooplankton net, Hydro-Bios) specially made for this study were used to ensure a sufficient volume of filtered water. The net had a mouth opening of 2.01 m² and a 7.0 m long net bag with 1.55 mm mesh. The sampling depth was calculated from the wire angle and wire length, whereas the volume of filtered water was calculated using a flow meter (digital flow meter, Model 438 110, Hydro-Bios). Comparisons of flowmeter readings and the sampled volume of water calculated from the wire length and mouth opening gave filtration efficiency close to 100% ($100.8 \pm 1.7\%$), and 100% filtration efficiency was assumed. We sampled 3 replicates per station, vertically, from ca. 20 m above the bottom to the surface, at a hauling speed of $\sim 1 \text{ m s}^{-1}$. All sampling was performed during daylight.

In March 2000, 2 depth strata were sampled at Stns C1 and C2: 3 samples below and 3 above the pycnocline, which was determined from the CTD profile before sampling. The depth-stratified samples were subse-

quently combined in the analyses of horizontal macrozooplankton distribution. Zooplankton was preserved in 4% buffered formaldehyde solution immediately after sampling and was analysed within 1 to 3 mo.

Zooplankton smaller than adult *Calanus glacialis* (<3 mm) were poorly sampled (<10%) with the macrozooplankton net compared to the multinet (opening 0.25 m², mesh size 180 μm) used in a complementary project during the May 1999 cruise (Hop & Falk-Petersen 2003). Therefore, only zooplankton $\geq 3 \text{ mm}$ were defined as macrozooplankton in this study (this excluded the copepods *Metridia longa*, and *C. finmarchicus* and smaller copepodites of *C. glacialis* [$< \text{CVI}$], *C. hyperboreus* [$< \text{CVI}$] and *Pareuchaetha* spp. [$< \text{CVI}$]). Half of the numbers ($51.6 \pm 17.1\%$) of adult *C. glacialis*, the smallest copepod defined as macrozooplankton in this study, were caught by the macrozooplankton net, whereas adults of the large *C. hyperboreus* were caught in slightly higher numbers ($119.0 \pm 15.7\%$) than in the multinet.

Zooplankton analysis. All specimens were counted and measured to the nearest millimetre under a stereomicroscope equipped with a calibrated ocular micrometer, and identified to species level when possible. Different stages of *Calanus* species were identified by prosome length (Unstad & Tande 1991). Euphausiids were classified as juvenile or adult by secondary sexual characteristics, the petasma of males and the thelycum of females (Einarsson 1945). Individuals with no visible secondary sexual characteristics were classified as juveniles.

Total body length (TL) of fully extended krill and amphipods were measured along the dorsal line from the tip of the rostrum (from the front of the head in amphipods) to the end of the telson. The TL of chaetognaths was measured from the top of the head to the end of the tail (excluding the tail fin) and the TL of the pteropod *Clione limacina* was measured from the top of the head (excluding anterior antenna) to the end of the body. In the ctenophores *Beröe cucumis* and *Mertensia ovum*, the TL and oral–aboral length were measured, respectively. Live lengths of ctenophores and *C. limacina* were preferred, since their body lengths shrank considerably after preservation. In May 1999, live length of *C. limacina* <10 mm and ctenophores was not measured, only body length after preservation. Live lengths (TL_{live}) of these individuals were therefore calculated from formaldehyde-preserved (TL_{formalin})—live length regressions obtained from individuals collected in March 2000: *M. ovum*: $\text{TL}_{\text{live}} = 2.104 \text{ TL}_{\text{formalin}} + 3.897$ ($n = 7$, TL_{live} range = 13–40 mm, $r^2 = 0.70$, $F_{1,5} = 11.7$, $p = 0.018$); *B. cucumis*: $\text{TL}_{\text{live}} = 2.509 \text{ TL}_{\text{formalin}}$ ($n = 12$, TL_{live} range = 10–58 mm, $r^2 = 0.87$, $F_{1,10} = 69.9$, $p < 0.001$); *C. limacina*: $\text{TL}_{\text{live}} = 1.732 \text{ TL}_{\text{formalin}} - 1.484$ ($n = 29$, TL_{live} range = 10–60 mm, $r^2 = 0.73$, $F_{1,27} = 74.1$, $p < 0.001$).

The total bell height of *Aglantha digitale* was measured from the tip of the manubrium to its rim (Fig. 2 in Matthews & Hestad 1977). This dimension does not shrink by fixation in formaldehyde (Rasmussen 1971).

Wet weights (± 0.1 mg) were obtained from formaldehyde-preserved individuals. The specimens were blotted quickly on filter paper to remove water adhering to the body surface prior to weighing. Taxa with small-sized individuals (copepods, *Sarsia* spp. and *Aeginopsis laurentii*) were pooled before weighing. Depth-integrated (bottom-to-surface) species abundance and biomass were analysed and calculated independently for each replicate.

Data analyses. In terms of abundance (individuals m^{-2}), the commonly occurring macrozooplankton species were divided into small, medium and large individuals, but in terms of wet biomass ($g\ m^{-2}$) they were not. Replicate variability in species abundance and biomass was examined by the similarity analysis program SIMPER and non-metrical multi-dimensional scaling (MDS) in PRIMER v5.0 (Clarke & Warwick 1994, Clarke & Gorley 2001). The analyses were based on Bray-Curtis similarities between sample pairs (Bray & Curtis 1957) on log ($x + 1$)-transformed abundance and biomass data.

To study the effect of several environmental variables simultaneously on a multitude of species, indirect (correspondence analysis, CA) and direct (canonical correspondence analysis, CCA) gradient analyses were performed using CANOCO for Windows v4.0 (ter Braak & Smilauer 1998). CA and CCA are based on the assumption of a non-linear species-environment response, and are applied to relative, not absolute, species data (ter Braak & Smilauer 1998). Our species data contained 50% zeros and showed a moderate unimodal response (gradient length ~ 2 SD). Principal correspondence analysis, which assumes a linear species-environment response, was tested, but the non-linear methods fitted our data slightly better. Species data with many zeros are often best analysed with unimodal methods (ter Braak & Verdonschot 1995, ter Braak & Smilauer 1998). The mean species data per station were used in the CA and CCA. The species data were log ($x + 1$)-transformed, and rarely occurring taxa were made redundant (i.e. passive) to prevent them from greatly influencing the analyses (ter Braak & Smilauer 1998). CA was used to determine the major macrozooplankton distribution patterns, whereas CCA was used to rank the environmental variables according to their relative importance by applying a stepwise procedure called 'forward selection' (ter Braak & Verdonschot 1995). Only those environmental variables that significantly explained the species patterns in the CCA (Monte Carlo test run with 999 unrestricted permutations, $p < 0.05$) were used in

the CA analyses. The statistical significance of the relationship between species and the whole set of environmental variables, given the covariables (when present), was tested by a Monte Carlo permutation test using 'the global permutation test' in the CANOCO-package (ter Braak & Smilauer 1998). Seasonal macrozooplankton variability was removed by identifying season as covariable (partial correspondence analysis) (ter Braak & Verdonschot 1995). The environmental variables salinity and temperature were determined from the mean salinity and temperature of the ArW, AtW or MIX, depending on which of these 3 water masses dominated at a station. At Stns C1 and C2, the mean salinity and temperature of the upper and lower depth strata were chosen. Ordination techniques and rules of interpretation of the ordination diagram have been reviewed by Jongman et al. (1995) and ter Braak & Verdonschot (1995). In short, because of the relatively short gradient (~ 2 SD) in our species data, the position of species and samples can be determined using the biplot rule. The closer the species or samples cluster together, the more similar environmental preferences and species composition they have, respectively. Projection of species and samples perpendicular to the environmental variables (shown as arrows in Figs. 5 & 6) reveals their optima on these environmental gradients. Quantitative environmental variables are standardized and centred, and indicate the direction of maximum change. The angle between environmental arrows indicates their correlation, i.e. they are uncorrelated if they are perpendicular to each other and highly correlated (positive or negative) if the angle is small. Long arrows indicate higher correlation to the species patterns than shorter arrows.

Based on the results of CA and MDS, stations with similar species composition were grouped and total species abundance, biomass and richness were compared using non-parametric tests (Mann-Whitney *U*-test and Kruskal-Wallis median test; STATISCA 6.0).

RESULTS

Ice conditions

In May 1999, the ice edge followed the Polar Front in the study area (Fig. 1). The thaw had set in, and the ice receded markedly northwards during May. The ice was < 1.5 m thick and characterised as first-year ice. Transects A and B began in close pack-ice (7 to 9/10), continued through open pack ice (3 to 6/10) and ended in open water (1/10) along the ice edge (Table 1). In March 2000, the ice edge in the central Barents Sea was located much further north of the Polar Front than in May 1999 (Fig. 1). Strong southerly winds pushed

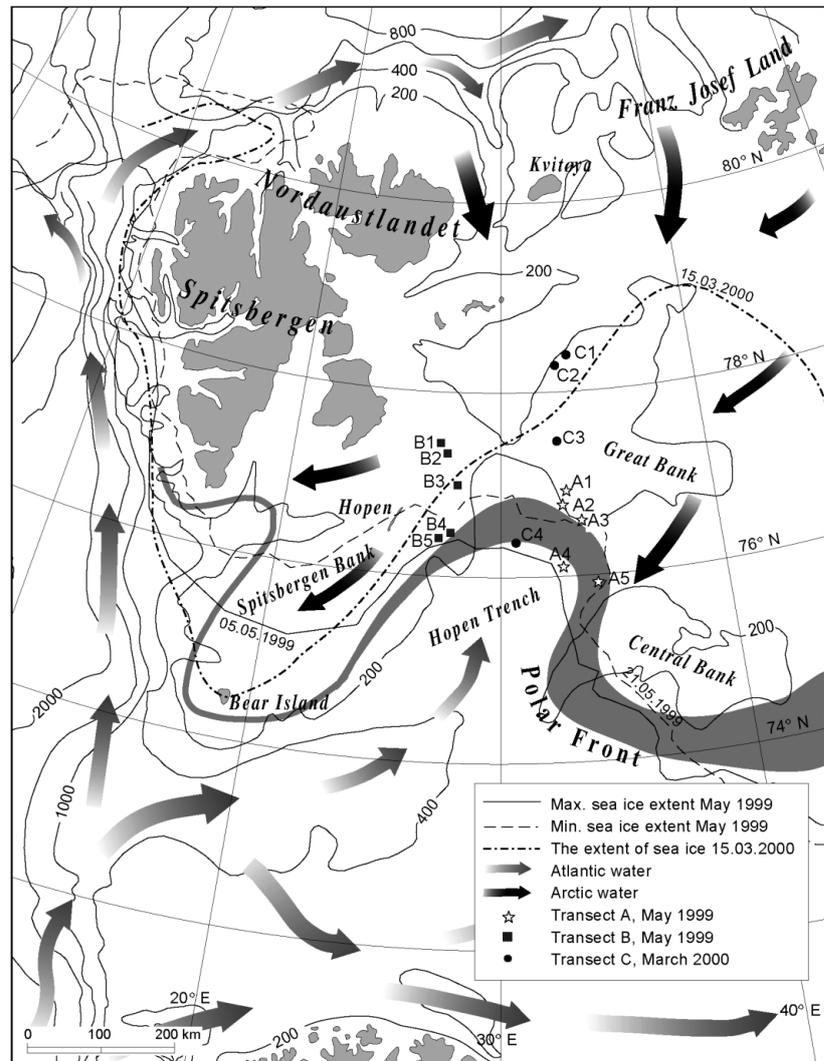


Fig. 1. Sampling stations and ice extent in the investigated area during May 1999 and March 2000. The Polar Front is shaded grey and is drawn thicker in areas where it is usually less defined (Loeng 1991). Atlantic and Arctic currents indicated by arrows

Table 1. Stations, cruise identity (ID) nos., dates, positions, bottom depths, volumes of filtered water (w.filt.) (mean \pm SE of 3 replicates), mean salinity and temperature of dominant water masses (Waterm.), ice concentrations (in tenths, NOAA 2001), ice ranking (1: open water, 2: open drift-ice, 3: close pack-ice), integrated (0 to 50 m) chlorophyll a biomass and stage of algal bloom (0: non-bloom, 1: pre-bloom, 1.5 to 2.5: bloom, 3: late-bloom). ArW, AtW, MIX: Arctic, Atlantic and mixture of these water masses, respectively; nd: no data

Transect station	Cruise ID	Date (d. mo. yr)	Position	Depth (m)	w.filt. (m)	Waterm.	S (PSU)	T (°C)	Ice conc.	Ice rank	Chl a (mg m ⁻²)	bloom
A1	A31	09.05.99	76° 55' N, 32° 56' E	160	302 \pm 2	ArW	34.77	-1.62	9/10	3	162.1	1.5
A2	A33	11.05.99	76° 48' N, 32° 32' E	186	344 \pm 2	ArW	34.79	-1.19	4-6/10	2	286.6	2
A3	A34	13.05.99	76° 38' N, 33° 07' E	159	323 \pm 2	ArW	34.80	-1.47	4-6/10	2	nd	3
A4	A35	14.05.99	76° 07' N, 32° 20' E	312	722 \pm 5	AtW	35.01	1.56	1/10	1	293.9	3
A5	T15	07.05.99	75° 52' N, 34° 25' E	224	431 \pm 7	MIX	34.98	1.03	1/10	1	195.2	2.5
B1	B49	17.05.99	77° 27' N, 27° 00' E	186	321 \pm 13	ArW	34.44	-1.41	7-9/10	3	30.4	1
B2	B50	18.05.99	77° 22' N, 27° 10' E	173	274 \pm 5	ArW	34.44	-1.37	7-9/10	3	68.2	1
B3	B51	20.05.99	77° 08' N, 27° 57' E	175	335 \pm 2	ArW	34.57	-1.22	4-6/10	2	158.2	2.5
B4	B52	21.05.99	76° 30' N, 27° 43' E	128	226 \pm 11	MIX	34.92	-0.05	1/10	1	280.4	3
B5	T3	05.05.99	76° 25' N, 27° 07' E	97	167 \pm 5	MIX	34.87	-0.82	1/10	1	nd	2
C1	C33	17.03.00	78° 21' N, 33° 20' E	179	304 \pm 2	ArW	34.59	-0.54	4-5/10	2	0.1	0
C2	C32	16.03.00	78° 16' N, 33° 00' E	156	326 \pm 38	ArW	34.55	-0.84	4/10	2	nd	0
C3	C35	18.03.00	77° 29' N, 32° 51' E	158	431 \pm 2	ArW	34.61	-1.55	4/10	2	nd	0
C4	C49	20.03.00	76° 30' N, 31° 26' E	317	832 \pm 57	AtW	35.01	1.95	0	1	0.1	0

the MIZ northwards, and large swells broke the ice into smaller floes (<10 m in diameter). The ice was <0.7 m thick, characterised as first-year ice. The first 3 stations (Stns C1 to C3) were in open pack-ice, whereas the last station (Stn C4) was in open water (0/10) (Table 1).

Hydrography

In May 1999, sampling was performed in the vicinity of the Polar Front and MIX was recorded at all stations (Figs. 1 & 2). Cold ArW (<−1.2°C) with salinities close to 34.8 PSU dominated over the slopes of the SW Great Bank (Stns A1 to A3), whereas warm, saline AtW (Stn A4) and less saline, but warm (>1°C) MIX (Stn A5) prevailed further south in the deeper Hopen Trench (Table 1). Cold ArW (<−1.2°C) with salinities close to

core ArW (34.3 to 34.5 PSU; Loeng 1991), covered by a surface melt-water layer (MW), dominated over the Spitsbergen Bank north of Hopen (Stns B1 to B3). In shallower areas, southeast of Hopen (Stns B4 and B5), cold MIX (<0°C) prevailed. In March 2000, ArW dominated over the NW (Stns C1 and C2) and central Great Bank (Stn C3), whereas increased temperatures (0 to 0.5°C) and salinities (34.6 to 34.8 PSU) occurred over the slopes of the NW Great Bank below 80 to 150 m depth (shown as an undefined water mass in Fig. 2). AtW dominated in the Hopen Trench (Stn C4).

Pelagic algae

In May 1999, the chlorophyll *a* biomass (0 to 50 m integrated) increased along both across-ice transects (A and B) from north to south, ranging from 162.1 to

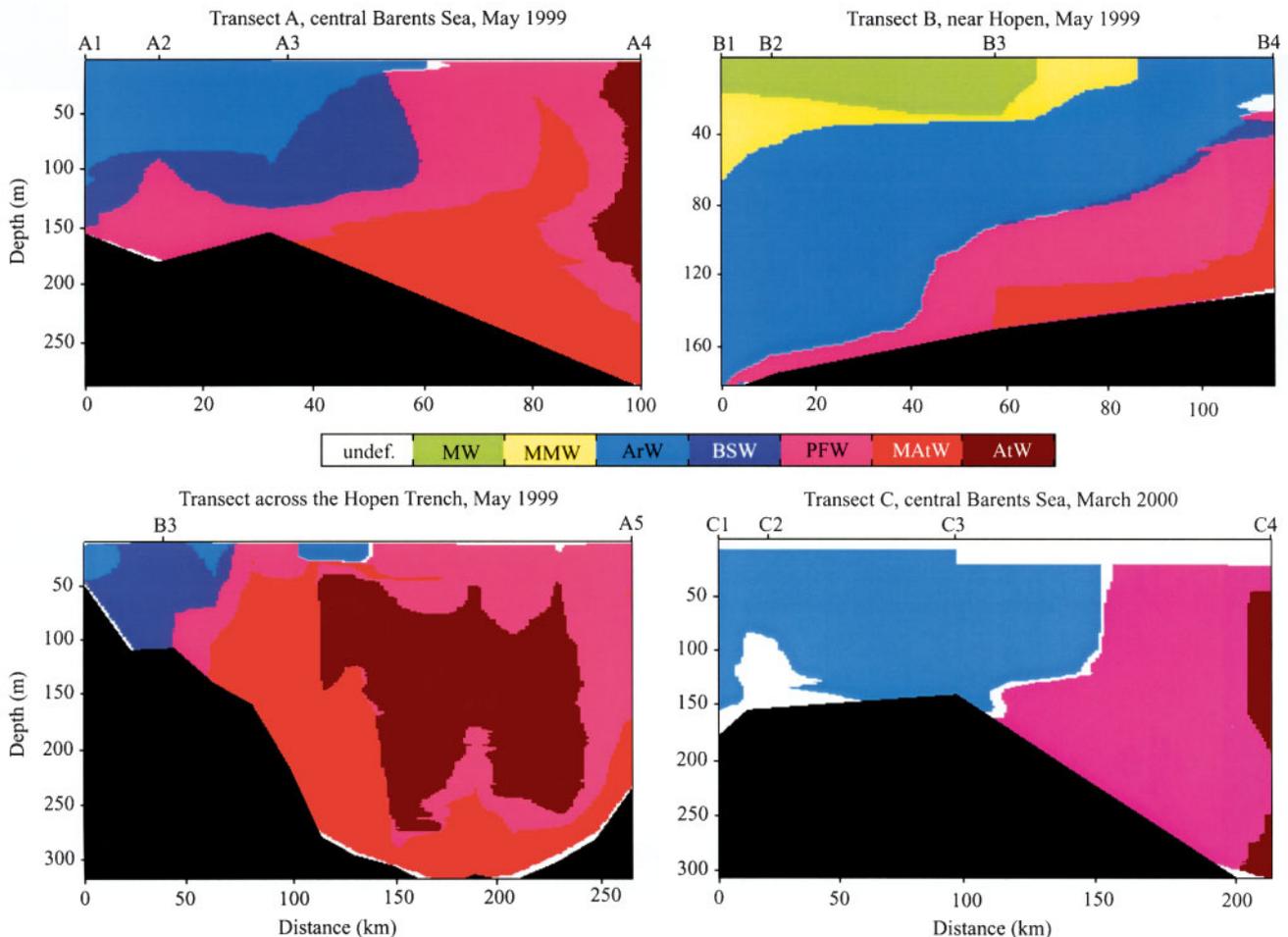


Fig. 2. Water masses along different sampling transects in May 1999 (Transects A and B) and March 2000 (Transect C). ArW: Arctic water (34.3 to 34.8 PSU, <0°C); AtW: Atlantic water (>35.0 PSU, >1°C); MAtW: modified Atlantic water (>34.95 PSU, −1.0 to 1.0°C); PFW, BSW: warm and cold mixtures of AtW and ArW, i.e. Polar Front water (34.8 to 35.0 PSU, 1.0 to 3.0°C; or 34.8 to 34.95 PSU, −0.5 to 1.0°C) and Barents Sea water (34.8 to 34.95 PSU, <−0.5°C), respectively; MW, MMW: melt water (<34.2 PSU) and mixed melt water (34.2 to 34.3 PSU, <0°C) introduced through melting of sea ice, respectively; undef.: undefined water masses. Note differences in ordinate and abscissa scales

293.9 mg m⁻² and 30.4 to 280.4 mg m⁻² at Transects A and B, respectively (Table 1). Algae in bloom and late-bloom phase prevailed along Transect A, whereas the algal bloom had barely started (pre-bloom) at the 2 northernmost stations (B1 and B2) of Transect B (Table 1). However, in less dense ice further south on Transect B (Stns B3 and B4), the algal bloom had progressed for some time and had reached late-bloom phase (deep chlorophyll *a* maximum). In March 2000, the phytoplankton biomass (0 to 50 m integrated) showed typically low winter values (<0.1 mg chl *a* m⁻²) and no algal blooms were recorded (Table 1) (E. N. Hegseth pers. comm.).

Macrozooplankton

A total of 27 macrozooplankton taxa, including 20 taxa at species level, were recorded during May 1999 and March 2000, of which 18 species and 2 taxa were found on both cruises (Table 2). The only additional species sampled in March was the pteropod *Limacina helicina*, but its abundance was very low (<0.2 individuals [ind.] m⁻²). Half the recorded species were found at >70% of the stations, but their abundance at the different stations varied (Table 2); 15 species and 1 taxon were mainly carnivorous, 2 species were mainly omnivorous, and 3 species were mainly herbivorous (Table 2). The feeding category of the remaining 6 taxa (which were rarely found) was undetermined.

Hydromedusae (*Aglantha digitale*), ctenophores (*Berøe cucumis* and *Mertensia ovum*), pteropods (*Clione limacina*), euphausiids (*Thysanoessa longicaudata* and *T. inermis*) and chaetognaths (*Eukrohnia hamata* and *Sagitta elegans*) were relatively abundant and divided into small (S), medium (M) and large (L) individuals (Table 2, Fig. 3). Other relatively abundant species were the hydromedusae *Aeginopsis laurentii* and *Sarsia* spp. (sizes not measured) and the siphonophore *Dimophyes arctica*. The hyperiid amphipods *Parathemisto abyssorum* (median TL = 10 mm), *P. libellula* (median TL = 22 mm), and *Hyperia galba* (median TL = 6 mm) and the remaining non-copepod taxa were found in too low abundances to be divided into size classes. The abundant copepods *Calanus glacialis* and *C. hyperboreus* and the less abundant *Pareuchaeta* spp. were divided into developmental stages.

The life histories of *Aglantha digitale*, *Berøe cucumis*, *Mertensia ovum*, *Clione limacina*, *Eukrohnia hamata* and *Sagitta elegans* in the Barents Sea are largely unknown. Since the smallest individuals were poorly sampled (Fig. 3), possible cohorts could not be estimated from their size distributions alone. They were therefore divided into size groups (small, medium and large) of regular lengths (Table 2).

The size distribution of *Thysanoessa longicaudata* and *T. inermis* in the present study consisted of at least 3 cohorts (year classes), determined according to Dalpadado & Skjoldal (1996) (Fig. 3). Small *T. inermis* (<16 mm) (juveniles only) represented the 0 and 1st cohorts, whereas medium (16 to 22 mm) and large specimens (>22 mm) (all mature) represented the 2nd and the 3rd cohort. Small *T. longicaudata* (<12 mm) (mix of juvenile and mature) made up the 0 and 1st cohorts, whereas medium (12 to 15 mm) and large (>15 mm) *T. longicaudata* (all mature) constituted the 2nd and the 3rd cohorts.

Sample replicability

The 3 replicates at each station showed high similarity in species abundance (60 to 80% similarity, SIMPER), except for the 3 replicates at Stn C4, sampled in AtW in March 2000 (Fig. 4a). These 3 replicates varied greatly in total abundance (8.1, 19.9 and 99.4 ind. m⁻²), and showed only 38% similarity in species abundance (SIMPER). The sample variability within stations was less than between stations (except for Stn C4), and stations located close to each other, with similar hydrographical characteristics (i.e. samples obtained from Stns A1–A3, B1–B3 and C1–C2), showed high similarity in species abundance (80, 69 and 66% similarity, respectively). A gradual change in the macrozooplankton composition from AtW to ArW existed, in terms of both species abundance and biomass (Fig. 4). Stations dominated by MIX (Stns A5, B4 and B5) differed from stations dominated by either ArW or AtW, mainly because of their low total abundance (<35 ind. m⁻²) and biomass (<1.2 g m⁻²). A gradual change in species abundance and biomass was also found from warm (Stn A5) to cold MIX (Stns B4 and B5) stations.

In terms of species biomass, the replicates were 48 to 73% similar, except at Stn C4, where the 3 replicates were only 13% similar in species biomass (SIMPER).

Environmental influence on species patterns (CA and CCA)

The macrozooplankton distribution in the MIZ in the Barents Sea was significantly correlated to the measured environmental variables latitude, longitude, salinity, temperature, bottom depth and season (Table 1), which together explained almost 80% of the total macrozooplankton variability during May 1999 and March 2000 (Table 3, Fig. 5). The ice concentration and algal bloom stage (Table 1) had no additional impact ($p = 0.1$ and 0.8 , respectively) on the

Table 2. Macrozooplankton species in the Barents Sea marginal ice zone in May 1999 (spring) and March 2000 (late winter), showing frequency of occurrence (Freq.) and mean (\pm SE), minimum and maximum abundance at the 14 stations (total of 42 samples) sampled (f: female; m: male; indet.: indeterminate). Station with maximum abundance (Stn max.) is listed for each taxon. For correspondence analysis (CA) the percentage of species variability explained by environmental variables in 2-dimensional ordination plots (Expl. 2-dim.) is listed together with taxon abbreviations (Abbr.) used in Figs. 5 & 6. Taxa grouped by feeding mode (h: herbivore; o: omnivore; c: carnivore; u: unknown) and zoogeographical (zoogeo.) distribution (a: Arctic; ab: Arctic-boreal; ba: boreal-Arctic; c: cosmopolitan; u: unknown) from data derived from literature (sources)

Taxon (feeding mode)	Abbr.	Freq. (%)	Abundance (ind. m ⁻²) Mean \pm SE	min.–max.	Stn max.	Expl. 2-dim. (%) Fig. 5 Fig. 6	Zoogeo.	Source
Hydromedusa								
<i>Aglantha digitale</i> (O.F. Müller)	(c)	93 ⁺	7.3 \pm 0.7	0.1–31.2	C1		ab	Rasmussen (1971), Zelikman (1972)
<i>A. digitale</i> <10 mm	(c) Ad S	71 ⁺	2.0 \pm 0.7	0.2–7.9	A3	7.3 74.1	ab	
<i>A. digitale</i> 10–15 mm	(c) Ad M	86 ⁺	3.8 \pm 1.1	0.2–13.3	C1	55.2 73.1	ab	
<i>A. digitale</i> >15 mm	(c) Ad L	79 ⁺	1.4 \pm 0.4	0.2–3.8	A4	51.4 72.6	ab	
<i>Aeginopsis laurentii</i> Brandt	(c) Alau	71 ⁺	2.1 \pm 1.4	0.2–18.4	C1	64.1 36.4	ab	Zelikman (1972), Madin (1988)
<i>Sarsia</i> spp.	(c) Sar	71 ⁺	0.8 \pm 0.3	0.1–4.4	A3	41.5 30.3	u	Madin (1988)
Siphonophora								
<i>Dimophyes arctica</i> (Chun)	(c) Darc	57 ⁺	3.6 \pm 2.5	0.1–34.0	C1	75.6 15.4	c	Zelikman (1972), Madin (1988)
Siphonophora indet.	(u) Siph*	7	0.1 \pm 0.1	1.4	A4	26.5 27.2	u	
Ctenophora								
<i>Berøe cucumis</i> Fabricius	(c)	100 ⁺	5.1 \pm 0.8	0.9–11.5	B1		ab	Zelikman (1972), Falk-Petersen et al. (2002)
<i>B. cucumis</i> <20 mm	(c) Bcu S	100 ⁺	3.8 \pm 0.8	0.7–11.0	B1	51.7 6.7	ab	
<i>B. cucumis</i> 20–39 mm	(c) /	93 ⁺	1.1 \pm 0.3	0.1–3.6	C1	0.5 3.6	ab	
<i>B. cucumis</i> >39 mm	(c) Bcu L	86 ⁺	0.3 \pm 0.1	0.1–0.7	A1	26.3 6.7	ab	
<i>Mertensia ovum</i> (Fabricius)	(c)	64 ⁺	1.0 \pm 0.4	0.3–4.2	B1		a	Ekman (1953), Falk-Petersen et al. (2002)
<i>M. ovum</i> <20 mm	(c) Mo S	50 ⁺	0.4 \pm 0.2	0.2–2.5	B2	69.6 57.4	a	
<i>M. ovum</i> 20–39 mm	(c) Mo M	64 ⁺	0.4 \pm 0.2	0.1–1.5	B2	78.8 67.8	a	
<i>M. ovum</i> >39 mm	(c) Mo L	36 ⁺	0.2 \pm 0.1	0.2–0.8	B2	71.7 66.8	a	
Sipuncula								
Sipuncula indet.	(u) Sipun*	7	0.0 \pm 0.0	0.1	A4	26.5 27.2	u	
Pteropoda								
<i>Clione limacina</i> Phipps	(c)	93 ⁺	1.3 \pm 0.4	0.2–4.4	B2		ab	Colin & Satterlie (1992)
<i>C. limacina</i> <20 mm	(c) Cli S	71 ⁺	0.7 \pm 0.2	0.2–3.0	B2	76.6 60.8	ab	
<i>C. limacina</i> 20–39 mm	(c) Cli M	86 ⁺	0.4 \pm 0.1	0.1–1.2	B2	74 72.6	ab	
<i>C. limacina</i> >39 mm	(c) Cli L	57 ⁺	0.2 \pm 0.0	0.1–0.5	C2	33.8 48.2	ab	
<i>Limacina helicina</i> Phipps	(o) Lhe*	7	0.0 \pm 0.0	0.2	C1	42.3 8.6	ab	Colin & Satterlie (1992)
Copepoda								
<i>Calanus glacialis</i> Jaschnov CVI	(h)	100 ⁺	64.5 \pm 22.5	1.2–292.3	B2		a	Eilertsen et al. (1989)
<i>C. glacialis</i> CVI f	(h) CgVIf	100 ⁺	63.8 \pm 22.3	1.2–290.6	B2	72. 70.4	a	
<i>C. glacialis</i> CVI m	(h) CgVIm	64 ⁺	0.7 \pm 0.3	0.2–3.7	C1	50.1 43.4	a	
<i>Calanus hyperboreus</i> Krøyer CV–CVI	(h)	100 ⁺	21.2 \pm 4.0	2.9–48.1	A4		a	Eilertsen et al. (1989)
<i>C. hyperboreus</i> CVI f	(h) /	100 ⁺	9.6 \pm 2.0	1.3–27.0	C2	7.4 7.4	a	
<i>C. hyperboreus</i> CVI m	(h) ChVIm	34 ⁺	0.7 \pm 0.5	0.1–5.5	C1	79.8 3	a	
<i>C. hyperboreus</i> CV	(h) ChV	100 ⁺	8.8 \pm 2.6	0.4–35.0	A4	61 2.2	a	
<i>C. hyperboreus</i> CIV	(h) ChIV	71 ⁺	2.1 \pm 1.0	0.3–10.3	A2	6.9 46	a	
<i>Pareuchaeta</i> spp. CIV–CVI	(c)	93 ⁺	3.6 \pm 1.3	0.2–15.9	C1		a	
<i>P. norvegica</i> (Boeck) CVI f	(c) PnVIf	79 ⁺	0.7 \pm 0.3	0.1–2.7	C1	51.3 32.7	ab	Harding (1974), Klekowski & Weslawski (1991)
<i>P. glacialis</i> (Hansen) CVI f	(c) PgVIf	21 ⁺	0.1 \pm 0.0	0.2–0.5	A1	11.4 30.8	a	Longhurst (1976), Klekowski & Weslawski (1991)
<i>Pareuchaeta</i> spp. CVI m	(c) ParVIm	29 ⁺	0.1 \pm 0.1	0.4–0.8	C1	80.1 20.8	a	
<i>Pareuchaeta</i> spp. CV	(c) ParV	86 ⁺	2.5 \pm 1.0	0.2–11.2	C1	32.1 13	a	
<i>Pareuchaeta</i> spp. CIV	(c) ParIV	21 ⁺	0.1 \pm 0.1	0.2–1.0	C1	79.1 4.4	a	
Mysidacea								
Mysidacea indet.	(u) Mys*	7	0.0 \pm 0.0	0.7	A5	29.7 32.7	u	

Table 2 (continued)

Taxon (feeding mode)	Abbr.	Freq. (%)	Abundance (ind. m ⁻²) Mean ± SE	min.–max.	Stn max.	Expl. 2-dim. (%) Fig. 5	Zoogeo. Fig. 6	Source
Amphipoda								
<i>Parathemisto abyssorum</i> Boeck	(c) Pab	21 ⁺	0.1 ± 0.0	0.2–0.4	B3	15.0	15.8	ab Dunbar (1954), Klekowski & Weslawski (1991)
<i>Parathemisto libellula</i> (Boeck)	(c) Pli	57 ⁺	0.4 ± 0.1	0.2–2.1	B2	56.8	60.2	a Dunbar (1964), Klekowski & Weslawski (1991)
<i>Hyperia galba</i> (Montagu)	(c) Hga	43 ⁺	0.6 ± 0.3	0.3–3.3	C1	75.4	8.8	ab Klekowski & Weslawski (1991), Dittrich (1992)
<i>Onisimus</i> spp.	(u) Oni	14 ⁺	0.0 ± 0.0	0.1–0.2	C2	23.1	11	u
Euphausiacea								
<i>Thysanoessa longicaudata</i> (Krøyer)	(c)	93 ⁺	1.8 ± 0.5	0.2–7.3	A4			ba Klekowski & Weslawski (1991), Falk-Petersen et al. (2000b)
<i>T. longicaudata</i> <12 mm	(c) Tlo S	71 ⁺	1.3 ± 0.5	0.2–6.3	A4	70.2	71.7	ba
<i>T. longicaudata</i> 12–15 mm	(c) Tlo M	86 ⁺	0.5 ± 0.2	0.2–2.2	C2	18.9	29.9	ba
<i>T. longicaudata</i> >15 mm	(c) Tlo L	14	0.0 ± 0.0	0.1–0.4	C2	24.6	4.9	ba
<i>Thysanoessa inermis</i> (Krøyer)	(h)	93 ⁺	6.0 ± 2.2	0.6–30.0	A4			ba Klekowski & Weslawski (1991), Falk-Petersen et al. (2000b)
<i>T. inermis</i> <16 mm	(h) Ti S	86 ⁺	3.9 ± 1.3	0.2–16.8	A4	85.4	72.8	ba
<i>T. inermis</i> 16–22 mm	(h) Ti M	79 ⁺	1.3 ± 0.6	0.5–9.0	A4	38.6	53.6	ba
<i>T. inermis</i> >22 mm	(h) Ti L	29.0	0.7 ± 0.4	0.2–4.7	A5	59.2	64.4	ba
<i>Thysanoessa raschii</i> (M. Sars)	(o) Tra	64 ⁺	0.3 ± 0.1	0.2–0.9	C2	41.7	49.7	ba Klekowski & Weslawski (1991), Falk-Petersen et al. (2000b)
<i>Meganyctiphanes norvegica</i> (M. Sars)	(c) */	7	0.0 ± 0.0	0.5	B3	9.3	12.1	b Klekowski & Weslawski (1991), Falk-Petersen et al. (2000b)
Decapoda								
Decapoda larvae	(u) Deca	50	0.3 ± 0.1	0.1–1.4	A5	28.1	11.1	u
Chaetognatha								
<i>Eukrohnia hamata</i> (Möbius)	(c)	79 ⁺	2.9 ± 1.2	0.1–14.9	C1			c Pierrot-Bults & Chidgey (1988)
<i>E. hamata</i> <19 mm	(c) Eha S	43 ⁺	0.4 ± 0.2	0.2–2.1	C2	64.9	7.3	c
<i>E. hamata</i> 20–28 mm	(c) Eha M	71 ⁺	1.7 ± 0.6	0.2–7.5	C1	65.1	58.7	c
<i>E. hamata</i> >28 mm	(c) Eha L	64 ⁺	0.4 ± 0.2	0.1–3.5	C1	51.3	21.9	c
<i>Sagitta elegans arctica</i> Aurivillius	(c)	93 ⁺	3.3 ± 2.2	0.5–10.0	C1			ab Pierrot-Bults & Chidgey (1988)
<i>S. elegans</i> <29 mm	(c) Sel S	57 ⁺	0.6 ± 0.2	0.2–2.2	C4	3.5	25.7	ab
<i>S. elegans</i> 29–36 mm	(c) Sel M	93 ⁺	2.3 ± 0.7	0.2–8.0	C1	17.1	30.8	ab
<i>S. elegans</i> >36 mm	(c) Sel L	57 ⁺	0.4 ± 0.2	0.2–1.4	C3	34.7	51	ab
Vertebrata								
Pisces larvae	(u) Pisces	29	0.1 ± 0.0	0.2–0.4	B2	78	52.1	u

* Taxa made supplementary in correspondence analysis (CA) and canonical correspondence analysis (CCA)

/ Taxon not in Figs. 5 or 6 since these two 2-dimensional plots explained <15% of its variability

+ Taxa recorded in both May 1999 and March 2000

macrozooplankton patterns after salinity and temperature (which were highly correlated with the fraction of ice concentration; $r > -0.83$) and season (which was highly correlated to bloom stage; $r = 0.84$) were taken into account. There was a high degree of faunal similarity among the samples, which was reflected by the relatively low eigenvalues (<0.22) and low total inertia (<0.8) (Table 4). Normally, eigenvalues of 0.3 to 0.5 indicate good separation of species or samples, i.e. that stations have few species in common (ter Braak & Verdonschot 1995).

There were 2 main macrozooplankton gradients, one along the salinity and temperature gradients and one along the seasonal (March to May) gradient, which was not correlated with the salinity ($r = 0.22$) or temperature ($r = -0.16$) gradients (Fig. 5). Geographical position was correlated to salinity, temperature and season, and latitude was more highly correlated with these 3 environmental variables ($r = -0.80$, -0.47 and -0.67 , respectively) than longitude ($r = 0.38$, 0.20 and -0.42 , respectively). Geographical position (latitude and longitude), which explained a significant

additional part of species variability, explained a slightly higher percentage (33%) of the macrozooplankton variability than did water masses (31%) (Table 3). However, after subtracting seasonal variability, which accounted for 21% of total macrozooplankton variability, the water masses explained almost twice as much of the species variability than geographical position (40 vs 25%). The macrozooplankton composition over the slopes of the NW (Stns C1 and C2) and SW (Stns A1 to A3) Great Bank displayed high similarity after adjusting for seasonal

macrozooplankton variability; thus, 1 strong macrozooplankton gradient, highly correlated with salinity gradient, appeared (Table 3, Fig. 6).

Species and their environmental optima

The environmental preferences for macrozooplankton, defined as Arctic and boreal-Arctic taxa in the literature (Table 2), corresponded well with the environmental variables in the ordination plots (Figs. 5b &

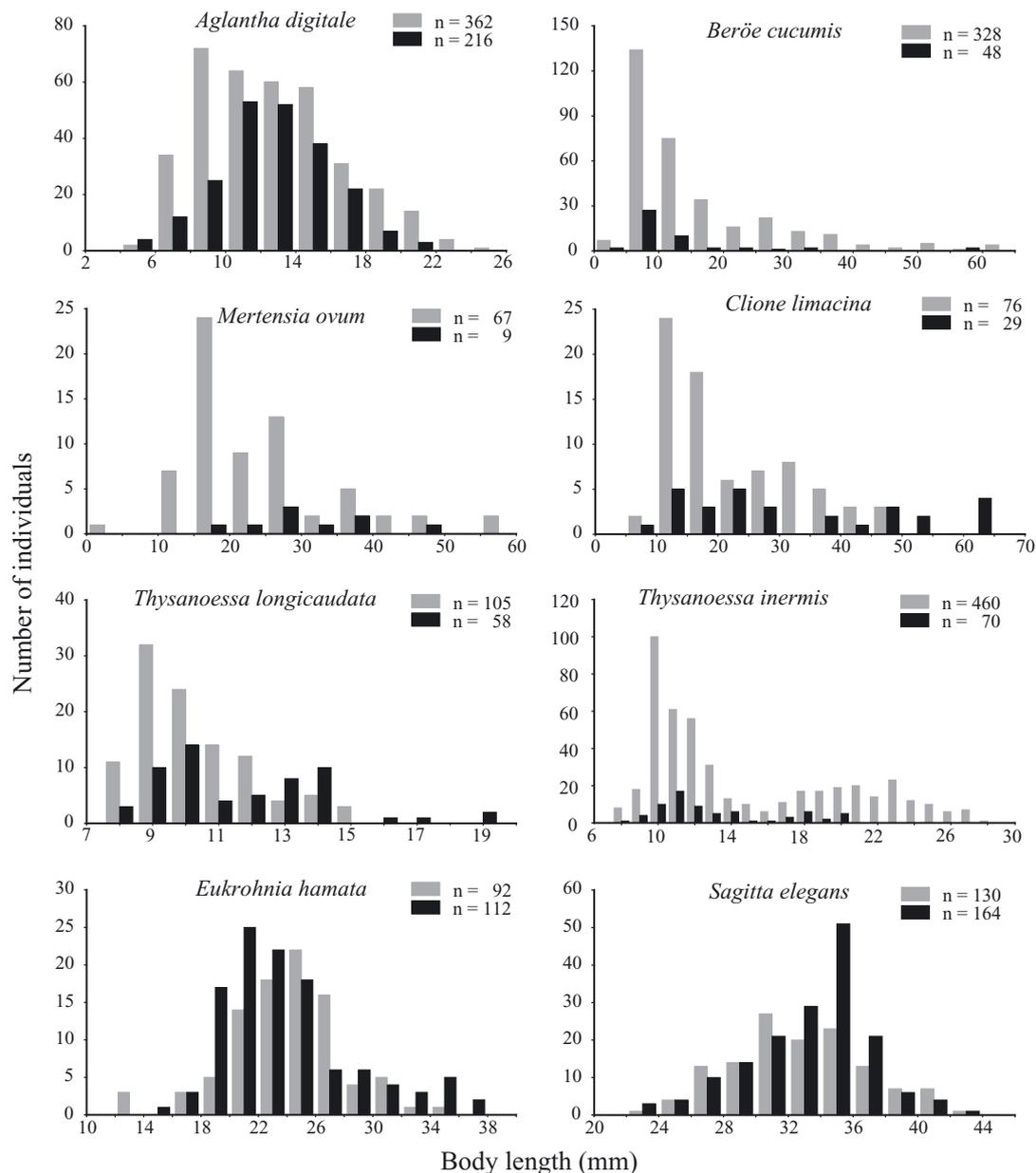


Fig. 3. Length–frequency histograms of selected macrozooplankton during May 1999 (grey columns) and March 2000 (black columns) in the Barents Sea marginal ice zone. Note differences in ordinate and abscissa scales

6b). Arctic taxa were concentrated in cold and less saline waters over the banks (Stns B1 to B3 and C3), whereas boreal-Arctic taxa were concentrated in warm and saline waters in the deeper Hopen Trench (Stns A4, A5 and C4). Arctic-boreal taxa were scattered, but after seasonal variability was removed they were confined to ArW either over the banks (ArW bank, Stns B1 to B3 and Stn C3) or over the slopes (ArW slope, Stns A1 to A3 and Stns C1 and C2). The cosmopolitan species *Dimophyes arctica* and *Eukrohnia hamata* showed high seasonality in their abundance, which peaked during March on the ArW slope (Stns C1 and C2).

After seasonal variability has been removed, small, medium and large individuals of various species displayed relatively similar environmental preferences (except for *Sagitta elegans*), although medium-sized specimens were generally more widely distributed than the small and large specimens (Figs. 5b & 6b). Prior to dividing species into developmental stages (copepods) and size classes (abundant non-copepod species), seasonal macrozooplankton variability was non-significant ($p = 0.07$). Even though there was less heterogeneity in species data prior to division into developmental stages and size classes, a higher percentage of the data was explained by environmental

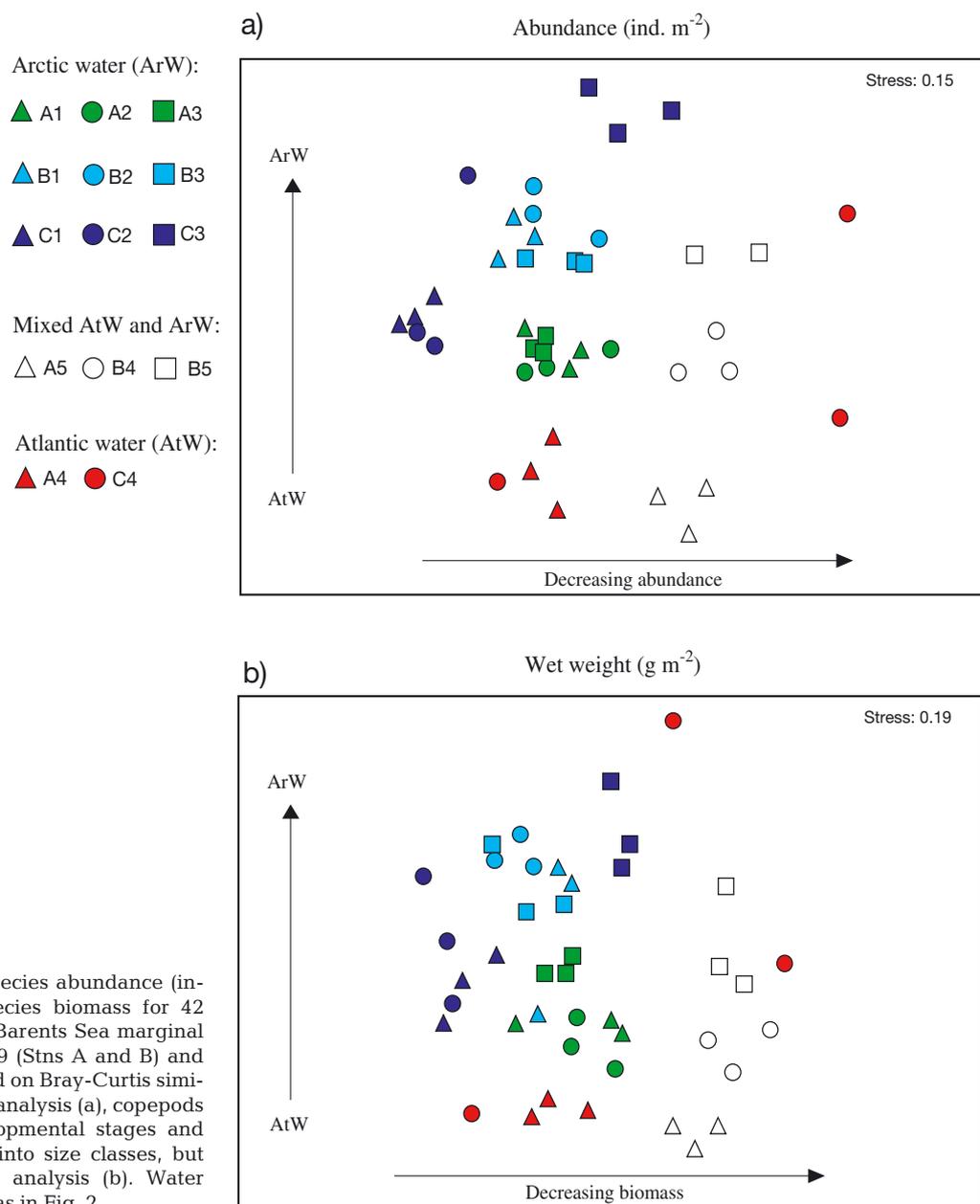


Fig. 4. MDS-plot of (a) species abundance (individuals m⁻²) and (b) species biomass for 42 samples collected in the Barents Sea marginal ice zone during May 1999 (Stns A and B) and March 2000 (Stn C), based on Bray-Curtis similarity. For the abundance analysis (a), copepods were divided into developmental stages and abundant non-copepods into size classes, but not for the wet biomass analysis (b). Water abbreviations as in Fig. 2

Table 3. Ranking of environmental variables that significantly (Monte Carlo permutation test in CCA, $p < 0.05$) influenced distribution of macrozooplankton in the Barents Sea marginal ice zone in May 1999 (spring) and March 2000 (late winter). Environmental variable that best explains macrozooplankton distribution is ranked first, remaining variables are ranked on basis of additional fit. (A) Seasonal variability included; (B) seasonal variability removed

Environmental variable	p-value	F-value	Explained Inertia		Correlation	
			%	%	Axis 1	Axis 2
(A) Season incl.						
Latitude (°N)	0.001	4.33	0.20	26.1	-0.96	-0.11
Salinity (PSU)	0.001	4.46	0.17	22.2	0.81	-0.46
Temperature (°C)	0.004	2.45	0.07	9.1	0.55	-0.58
Depth (m)	0.035	1.85	0.06	7.8	0.46	-0.40
Longitude (°E)	0.018	2.12	0.05	6.5	0.02	-0.76
Season (March/May)	0.030	2.34	0.06	7.8	0.63	0.57
Total	0.001	4.49	0.61	79.6		
(B) Season excl.						
Salinity (PSU)	0.001	4.53	0.18	29.8	0.92	0.02
Latitude (°N)	0.003	2.79	0.09	14.9	-0.81	-0.37
Temperature (°C)	0.016	2.12	0.06	9.9	0.84	0.32
Depth (m)	0.034	2.02	0.06	9.9	0.63	0.22
Longitude (°E)	0.032	2.57	0.06	9.9	0.61	-0.40
Total	0.001	3.95	0.45	74.5		

variables after such division (74.4 vs 79.4%). In addition, more information on the macrozooplankton community structure was gained.

After subtracting seasonal macrozooplankton variability, the species–environment correlations of macrozooplankton concentrated along the seasonal gradient (i.e. *Dimophyes arctica*, small and large *Beröe cucumis*, *Calanus hyperboreus* CV, *Pareuchaeta* spp. CV–CVI [male] and small and large *Eukrohnia hamata*) were

markedly reduced (Table 2, Figs. 5b & 6b). After adjusting for seasonal variability, 3 major centres of macrozooplankton distribution were found: (1) in cold and less saline waters over the banks (*Aeginopsis laurentii*, *Sarsia* spp., *Mertensia ovum*, *Clione limacina*, *Calanus glacialis*, *Parathemisto libellula* and *Sagitta elegans* >29 mm); (2) in cold, but relatively saline waters over the slopes (*Aglantha digitale*, *D. arctica*, *Pareuchaeta* spp. CVI and *E. hamata* ≥20 mm); and (3) in warm and saline waters in the deeper Hopen Trench (*Thysanoessa longicaudata* ≤15 mm, *T. inermis* and *T. raschii* and the rarely occurring taxa Siphonophora indet., Sipuncula indet. and Mysidacea indet.). Medium-sized *B. cucumis* and females of *C. hyperboreus* showed no consistent gradient in species abundance, and had a poor fit (<10% variability explained) in the CA (Table 2).

Abundance, biomass and species richness

Stations with similar relative macrozooplankton composition were grouped, although March and May samples were separated since season had a significant impact on the macrozooplankton patterns. Because of the low total abundance and biomass in MIX, these communities were treated separately, and divided into warm (>1°C) and cold (<0°C) MIX.

In terms of species richness, significantly fewer species were caught per replicate in MIX (warm and cold) and AtW in March than in ArW (bank and slope) and

Table 4. Summary of CA and CCA of macrozooplankton data from the Barents Sea marginal ice zone in May 1999 (spring) and March 2000 (late winter). (A) Seasonal variability included; (B) seasonal variability removed. Season accounted for 21% of the total macrozooplankton variability ($0.162/0.766 \times 100 = 21.1\%$)

Analysis	Axis				Total inertia
	1	2	3	4	
(A) Season incl.					
Eigenvalue (CA)	0.212	0.185	0.099	0.067	0.766
Eigenvalue (CCA)	0.210	0.176	0.082	0.065	0.766
Species–environment correlation (CA)	0.993	0.971	0.869	0.975	
Cumulative % variance of species data (CA)	27.7	51.9	64.9	73.7	
Cumulative % of species–environment relation (CA)	34.5	63.2	75.5	86	
(B) Season excl.					
Eigenvalue (CA)	0.198	0.117	0.073	0.054	0.604
Eigenvalue (CCA)	0.193	0.099	0.070	0.051	0.604
Species–environment correlation (CA)	0.985	0.900	0.969	0.958	
Cumulative % variance of species data (CA)	32.8	52.1	64.2	73.2	
Cumulative % of species–environment relation (CA)	43.4	64.3	79.7	90.8	
Seasonal variability					0.162

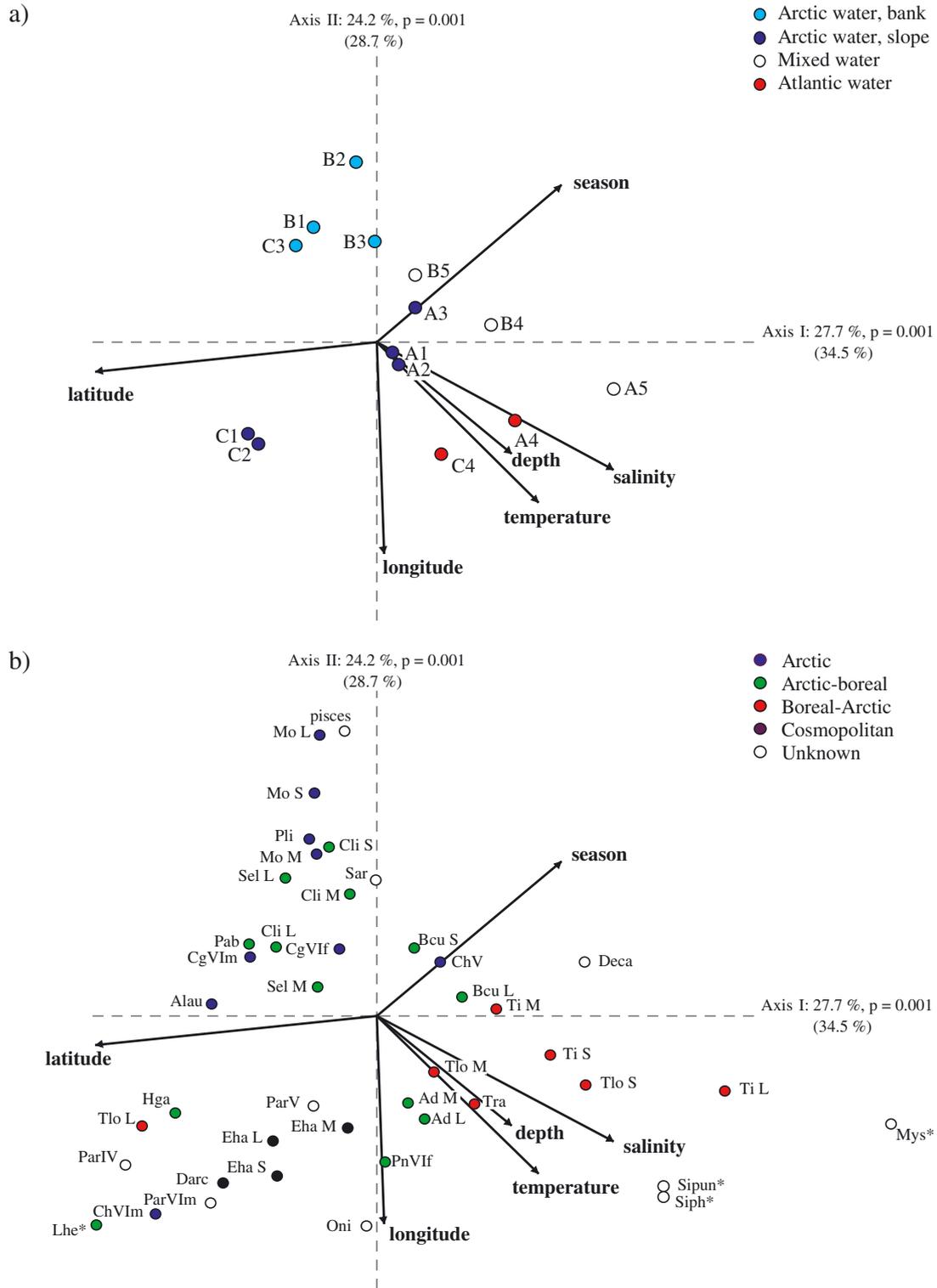


Fig. 5. Correspondence analysis (CA) (Axes I and II) of macrozooplankton abundance data describing their relationship to selected environmental variables (arrows) in the Barents Sea marginal ice zone during May 1999 (spring) and March 2000 (late winter). Plots explain 51.9% of total species variation and 63.2% of species–environment relationship (values in parentheses). Ordination of (a) stations and (b) taxa are displayed separately for clarity. Stations were classified according to dominating water mass, taxa were classified according to zoogeographical distribution. Abbreviations and literature sources as in Table 2. Taxa with distribution patterns <15% explained by 2-dimensional CA are not shown

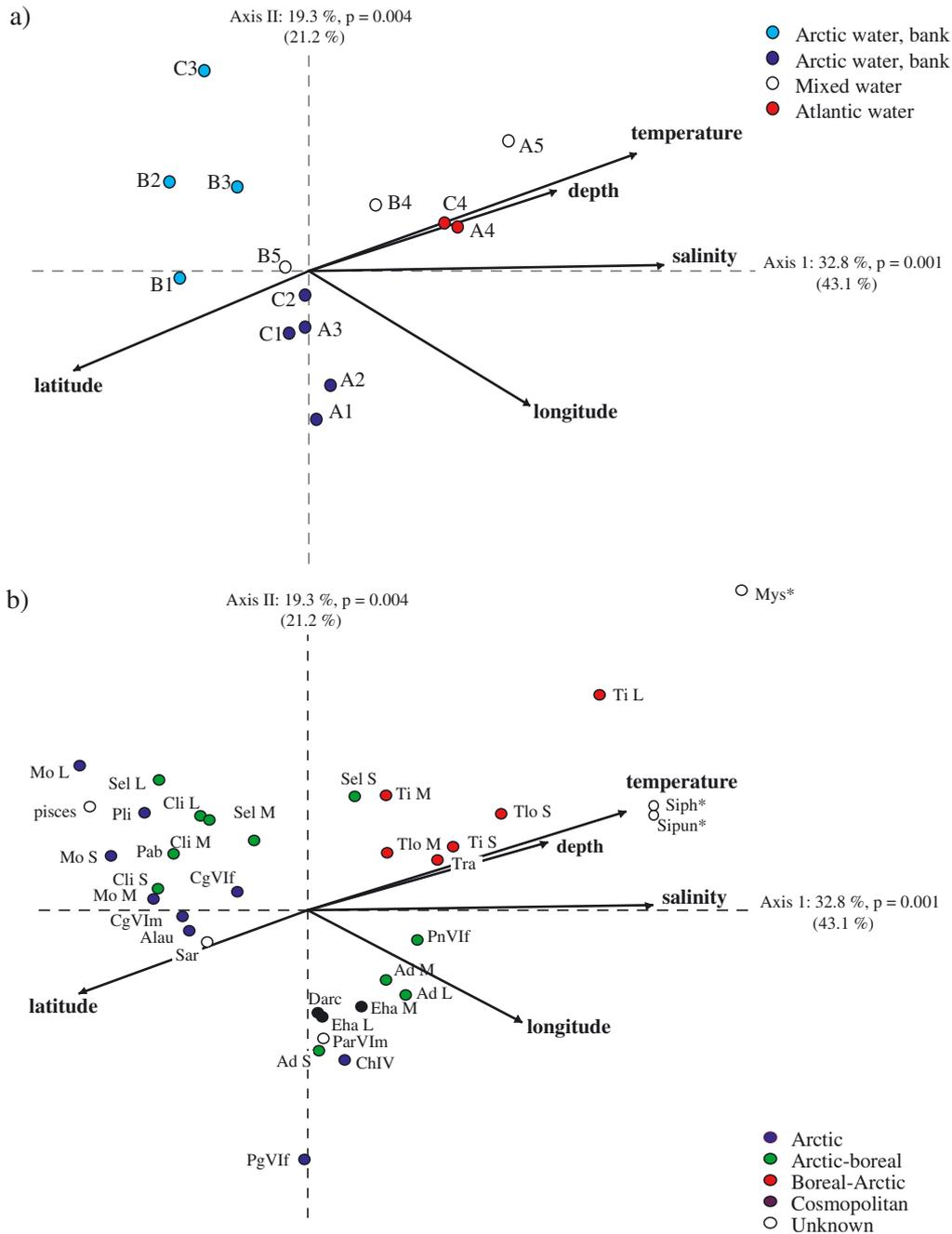


Fig. 6. Data from Fig. 5, with covariable month of sampling ('season') removed. Plots explain 52.1% of total species variation and 64.3% of species–environment relationship (in parentheses). Abbreviations as in Table 2

AtW in May (Fig. 7). A similar pattern was found for the total number of species: 12 to 14 species were found in MIX (warm and cold) and AtW in March, whereas 15 to 20 were found in ArW (bank and slope) and AtW in May.

Numerically, *Calanus glacialis* was most important north of the Polar Front (ArW), followed by *C. hyperboreus* (Fig. 8a). In AtW, *C. hyperboreus* was also

important numerically, together with *Thysanoessa inermis*, but only in May. In March, the abundance of *C. hyperboreus* was low in AtW (<2.5 ind. m^{-2} in all 3 replicates), whereas *T. inermis* was still relatively numerous, although its abundance varied greatly among the 3 replicates (0.3, 1.5 and 19 ind. m^{-2}). The most abundant carnivorous species in the NW Barents Sea was *Aglantha digitale* (up to 31.2 ind. m^{-2}), but

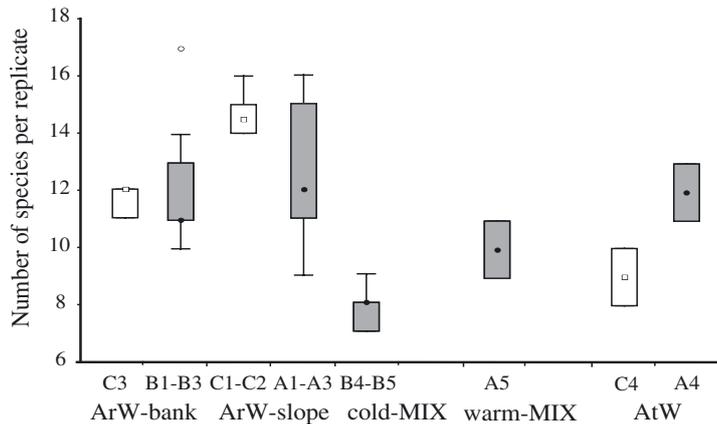


Fig. 7. Box plots of number of species sampled per replicate in macrozooplankton communities in the Barents Sea marginal ice zone during May 1999 (spring; grey boxes) and March 2000 (late winter; white boxes). Whiskers represent the non-outlier range and empty circles (°) outliers. Water abbreviations as in Fig. 2

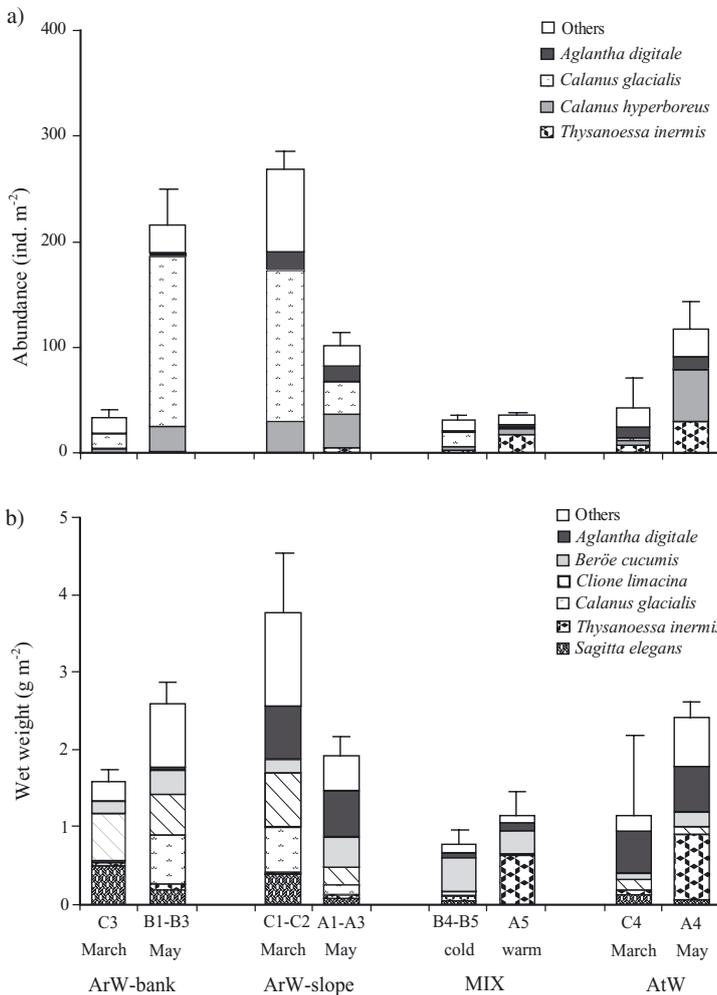


Fig. 8. (a) Abundance and (b) biomass of most important macrozooplankton species in sampling area in the Barents Sea marginal ice zone during May 1999 (spring) and March 2000 (late-winter). Error bars = SE of total. Water abbreviations as in Fig. 2

its abundance in MIX (cold and warm) and ArW bank waters was low (<2.0 ind. m^{-2}) (Table 2).

In terms of wet biomass, *Berøe cucumis* was important in all water masses sampled (Fig. 8b). *Clione limacina* contributed much to the total biomass north of the Polar Front, whereas *Aglantha digitale* and *Thysanoessa inermis* made up most of the biomass in AtW, except for *T. inermis* in March since only small juvenile individuals (<16 mm) were sampled at that time of the year in AtW. In May, a relatively high proportion of large and mature *T. inermis* (>22 mm) was sampled in warm-MIX compared to AtW, and the biomass of *T. inermis* was slightly higher in warm-MIX than in AtW. In May, the main biomass of *Calanus glacialis* was in the ArW bank waters, whereas in March the main biomass of this species was in ArW slope waters. The biomass of the carnivorous *Sagitta elegans* was 2 to 3 times larger in March than in May in ArW (bank and slope).

Trophic composition and seasonal trends

Herbivorous macrozooplankton dominated numerically in the northern Barents Sea, whereas the carnivores dominated in terms of wet biomass (Fig. 9). The abundance and biomass of herbivores increased from March to May in the ArW bank and AtW ($p < 0.049$), whereas no differences were found for the carnivores ($p > 0.052$). In ArW slope waters, the opposite was found. Here, the herbivores decreased in abundance and biomass from March to May ($p < 0.003$) as did the carnivores ($p = 0.018$), except in terms of biomass ($p = 0.157$).

In May, lower abundance of herbivores and carnivores were found in MIX (warm and cold) than in AtW and ArW (bank and slope) ($p < 0.049$) (Fig. 9). In biomass, the same was true, except for no differences in herbivorous biomass in the warm-MIX and ArW slope waters ($p = 0.052$). In March, herbivores and carnivores were found in similar low abundance and small biomass in the ArW bank and AtW ($p > 0.513$), whereas markedly higher abundance and larger biomass of herbivores ($p < 0.01$) and carnivores ($p < 0.049$) were found in the ArW slope (except for the carnivores in terms of biomass: $p > 0.51$).

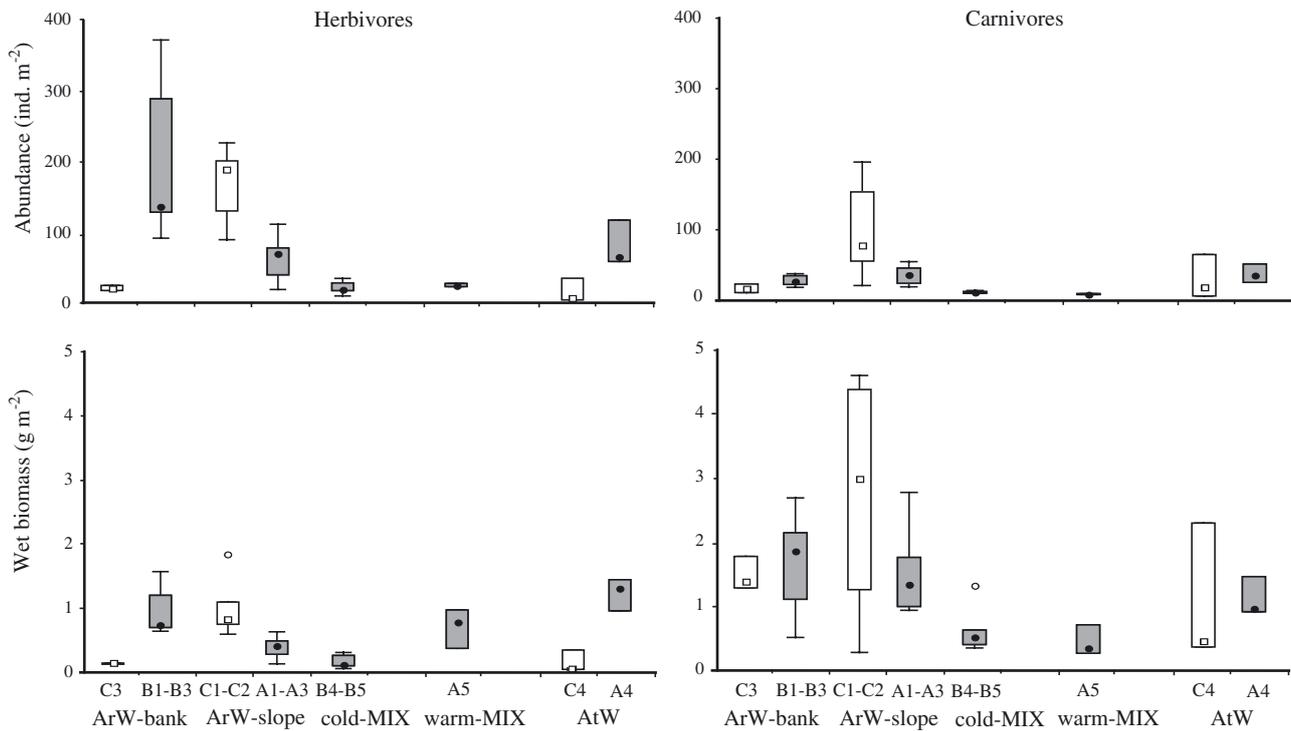


Fig. 9. Box plots of abundance and biomass of herbivores and carnivores in macrozooplankton communities sampled in the Barents Sea marginal ice zone during May 1999 (spring; grey boxes) and March 2000 (late-winter; white boxes). Whiskers represent the non-outlier range and empty circles (○) outliers. Water abbreviations as in Fig. 2

DISCUSSION

Macrozooplankton variability

A central question associated with plankton ecology is: How representative is the sampling in space and time? Replicate samples are the best way to address this question. In the present study, the variability in macrozooplankton abundance and biomass within stations was relatively low and did not exceed that between stations (Fig. 4). The spatial resolution was therefore sufficient to detect differences in horizontal macrozooplankton composition that were larger than those expected by chance. However, an exception was the highly variable macrozooplankton abundance and biomass in the 3 replicates in AtW in March. The reason for this variability is not known, since depth and sampled volume of water were similar and the same sampling procedure was followed in the 3 hauls. However, in March the AtW station (Stn C4) was located close to the Polar Front (Fig. 2) and, thus, hydrographical conditions could have changed during sampling, as the ship was adrift. But this variability could also be a result of patchiness, since there was no consistent decline or increase in total abundance during sampling of these 3 replicates (Hamner 1988). In particular, the

number of krill (*Thysanoessa* spp.), which is known to form aggregations (Zelikman et al. 1978), varied largely among the 3 replicates.

Of special concern in regard to the estimates of macrozooplankton abundance and biomass was the error induced by net-selectivity. The macrozooplankton includes highly mobile organisms such as krill and amphipods, and visual avoidance of the net may have led to an underestimate of macrozooplankton abundance and biomass (Dalpadado & Skjoldal 1991, Samoeto et al. 2000). Trawling is preferable for sampling the larger zooplankton fraction (Samoeto et al. 2000), but in dense pack-ice trawling is risky and often impossible. However, the large mouth opening (2.01 m²), the high filtration efficiency (~100%) and the relatively large volume of water filtered per station (500 to 2000 m³) probably minimised the sampling error arising from net avoidance (UNESCO 1968, Samoeto et al. 2000). However, the extrusion of smaller animals, may have been extensive (Samoeto et al. 2000). The abundance estimates of *Calanus glacialis* females may be 50% too low (see 'Materials and methods'); nevertheless, female *C. glacialis* were included in the analyses because their abundances were within the range of previously reported abundances in the MIZ in the Barents Sea (204 to 1557 ind.

m^{-2} ; Falk-Petersen et al. 1999). However, the total abundance and biomass data for adult *C. glacialis* and CVI of *C. hyperboreus* and *Pareuchaeta* spp. and for the other species in this study should be interpreted with caution because the total population was most probably not sampled (Fig. 3). The estimates of total abundance and biomass do not, however, affect the analyses of community- and species-environment relationships, since these were based on relative data.

Environmental influences

Only ~20% of the total macrozooplankton variability was unexplained by the environmental variables latitude, longitude, salinity, temperature, bottom depth and season, indicating that these environmental variables are of great importance, or are possibly highly correlated with other important variables in determining the horizontal macrozooplankton distribution in the Barents Sea MIZ. Of greatest importance was water-mass distribution, followed by geographical position, season (late-winter vs spring) and bottom depth (Table 3). In spite of spatial and temporal limitations in the sampling design, our results are in good agreement with previous zooplankton studies in the Barents Sea, which indicate that water-mass distribution is of major importance in structuring the plankton communities in this region (Hassel 1986, Loeng 1989, Arashkevich et al. 2002). Gradients in zooplankton community and population structure from close pack-ice to open water have been recorded in the MIZ in the Barents Sea (Falk-Petersen et al. 1999), but whether this is a direct affect of the ice cover is not known. Quantitative studies of how several environmental factors affect, simultaneously, the zooplankton communities in the MIZ in the Arctic are lacking. In our study, ice-cover (close pack-ice, open drift-ice and open water) and the stage of the associated spring bloom (Skjoldal & Rey 1989, Hegseth 1998, Falk-Petersen et al. 2000a, Engelsen et al. 2002) had no influence on horizontal macrozooplankton structure. However, the sampling time period was limited and offspring were poorly sampled due to the selective sampling method. In addition, carnivorous taxa dominated the macrozooplankton communities, and these are generally less subject to seasonal food shortage than herbivorous zooplankton (Falkenhaus 1997, Hagen 1999). The Arctic herbivorous copepods *Calanus glacialis* and *C. hyperboreus* have also developed a variety of energetic adaptations and reproductive strategies that make them robust to seasonal variation in food availability. For instance, *C. hyperboreus* stores lipids, enabling this species to spawn during the dark season, and *C. glacialis* may utilise ice algae, which begin to grow as early as March in the Barents

Sea (Runge & Ingram 1988, Conover & Huntley 1991, Hegseth 1992). However, the stage of algal bloom (surface vs deep chlorophyll *a* maximum) may be important in determining the vertical distribution of macrozooplankton (e.g. Eilertsen et al. 1989, Unstad & Tande 1991, Falkenhaus 1997).

In our study, salinity was the most important environmental variable determining the horizontal macrozooplankton distribution in the Barents Sea MIZ. However, salinity is more properly an indication of important advective processes. Experimental evidence suggests that a small salinity difference of 2.5 PSU, which exceeds the salinity difference between ArW and AtW, has no measurable effect on the physiology of zooplankters (McLaren et al. 1968, Kinne 1971). However, small changes in temperature may limit zooplankton distribution through altered growth, reproduction and/or mortality rates (McLaren 1969, Kinne 1970). The Barents Sea is a highly advective ecosystem, and many species, particularly those with centres of distribution in more temperate areas, may not successfully reproduce there. These expatriate populations will eventually become depleted, unless they are continually supplied by advected individuals (Pedersen 1995). In the northern Barents Sea, salinity is a better measure of AtW influence than temperature, because the temperature of a water mass is not only altered by water mixing, but also by atmospheric cooling during transport (Loeng 1991). Since our study used mean salinity and temperature of the dominant water mass at each station, the advective processes were not addressed properly. Latitude, longitude and bottom depth most probably identified some of the advective processes that our salinity and temperature variables did not describe. The latitudinal gradient was generally in good agreement with the salinity and temperature gradients, but exceptions were found because of the deep inflow of AtW between Nordaustlandet and Franz Josef Land and the strong impact of the bottom topography (Loeng 1991, Løyning 2000). Generally, ArW occurs in the bank areas in the northern Barents Sea, but over the shelf breaks (slopes) strong tidal currents force the heavier AtW up and onto the banks (Loeng 1991, Kowalik & Proshutinsky 1995). This transport is particularly apparent over shallow banks (Kowalik & Proshutinsky 1995), which explains the dominance of MIX over the shallow Spitsbergen Bank (Stns B4 and B5), relatively far from the shelf break (Fig. 2). A circular eddy that is topographically trapped may exist around the Great Bank (Løyning 2000), similar to the anticyclonic vortex around the Central Bank in the Barents Sea (Loeng 1989, Quadfasel et al. 1992). If this is so, the concentrating effect of this eddy, in addition to the inflow of Atlantic-derived waters from the north, would explain the relatively high faunal

similarity over the northern and southern slopes of the Great Bank (Fig. 6). However, a relatively large seasonal difference in macrozooplankton composition was found within the ArW slope community (Fig. 5). The reasons for this difference may be cooling and/or, partly, the transformation of AtW on its way around Spitsbergen, and also the latitudinal distance between the northern and southern Great Banks (Fig. 1). At high latitudes, the solar angle, and thus the onset of spring, changes markedly over short latitudinal distances, especially in ice-covered waters (Sakshaug & Slagstad 1991, Falk-Petersen et al. 2000a, Engelsen et al. 2002). In the Barents Sea MIZ, the spring bloom begins in mid-April to early May at the southernmost fringes of the first-year ice, and as late as August/September close to the multiyear ice (Zenckevitch 1963, Sakshaug & Slagstad 1991, Hegseth 1997). Latitudinal difference, as well as seasonal variability, was much less pronounced in the ArW bank and AtW macrozooplankton communities. It should be mentioned, however, that because season and latitude were moderately correlated, some of the latitudinal macrozooplankton variability might have been removed when adjusting for seasonal variability (ter Braak & Smilauer 1998).

Species–environment relationships

In ArW bank, the most 'Arctic' environment, maximum abundances of the ctenophore *Mertensia ovum* (all sizes), the copepod *Calanus glacialis* (adults) and the amphipod *Parathemisto libellula* were found as expected (Figs. 5 & 6) (Unstad & Tande 1991, Hassel 1995, Dalpadado et al. 2001). The species that were most restricted to ArW were *M. ovum* and *P. libellula*, which were not recorded in warm-MIX or AtW during May 1999 and March 2000. However, relatively high abundances of small *M. ovum* (<15 mm) have been found south of the Polar Front in May (Swanberg & Båmstedt 1991). In our study, mainly *M. ovum* >15 mm were caught (Fig. 3). The second ctenophore, the Arctic-boreal *Berøe cucumis*, was widely distributed in the northern Barents Sea, but increased in abundance during spring (Fig. 8a). A possible predator–prey interaction has been suggested between *B. cucumis* and *M. ovum* (Greve 1981, Falk-Petersen et al. 2002). Above the Spitsbergen Bank, maximum numbers of small *B. cucumis* (<20 mm) coincided with maximum numbers of *M. ovum* (Table 2), which may indicate favourable feeding conditions for *B. cucumis* in that region (Hagen 1999). The abundance of *P. libellula* was very low in our study. High abundances of *P. libellula* (430 ind. m⁻²) have been found in May to June close to the Polar Front (Dalpadado et al. 2001), but most of

these specimens (40 to 93%) were 2 to 8 mm. In our study, individuals <2.5 mm were found in female brood-pouches, but were not counted. A southern (boreal) and a northern (Arctic) population of the pteropod *Clione limacina* co-exist in the Barents Sea (Mileikovsky 1970). In our study, small, medium and large individuals of *C. limacina* were confined to ArW bank, indicating that mainly individuals of the Arctic population occur in the Barents Sea MIZ. The chaetognath *Sagitta elegans* may also be comprised of 2 populations in the NW Barents Sea. *S. elegans* originating from more temperate regions have smaller maximum lengths than Arctic populations (McLaren 1969), which may explain the different environmental preferences of small- and large-sized *S. elegans* in this study.

In May, the Arctic copepod *Calanus hyperboreus* was found in high numbers both in ArW (bank and slope) and AtW. Seasonal migration and advective transport may explain the high abundance of *C. hyperboreus* in AtW in May and its low abundance there in March. In the Norwegian Sea, *C. hyperboreus* migrates to deep water (500 to 1500 m) in autumn, i.e. to depths below those of the Barents Sea (Loeng 1991). However, in spring (April), it migrates upwards to feed, and is thus subjected to the North Atlantic current and transportation to the Barents Sea (Loeng 1991, Pedersen 1995, Hirche 1997).

In the relatively cold and saline waters of the ArW slope, the cosmopolitan species *Dimophyes arctica* and *Eukrohnia hamata* peaked in abundance together with the Arctic-boreal species *Aglantha digitale* and the cold-water species *Pareuchaeta* spp. These species are all widely distributed deep-water species (Bakke 1977, Sands 1980, Kirkpatrick & Pugh 1984). They may not thrive in shallow bank areas or are less subject to advective transport into bank areas in the Barents Sea (Loeng 1991). *A. digitale* is considered to be a good indicator species of AtW (Mumm 1991, Hassel 1995). The similarly high abundance of this species in ArW slope and AtW can be a result of advection. However, the population of *A. digitale* in the Barents Sea may be of Arctic origin (Zelikman 1972). The ordination (Fig. 6b) showed that small *A. digitale* (≤9 mm) were less restricted to warm and saline waters than larger individuals (>9 mm), which might support the idea that *A. digitale* is reproductively cold-adaptive. It is also possible that *A. digitale* reproduces later in ArW than in AtW. The siphonophore *D. arctica* was found in very low abundance in the NW Barents Sea, except for its particularly high abundance over the slopes of the NW Great Bank in March, where the hydromedusa *Aeginopsis laurentii* was also found in high abundance. Population bursts of *A. laurentii* and *D. arctica* can occur during warm years in the Barents Sea (Zelikman 1972). The year 1999 was characterised as

warm, and the temperature continued to increase in 2000 (ICES 2000). The warmer temperatures may have had a positive impact on the populations of *D. arctica* and *A. laurentii*, since the previous years (1996 to 1998) were relatively cold (Ingvaldsen et al. 2002). The higher abundance of *Pareuchaeta* spp. and *E. hamata*, and also of *Sagitta elegans* in March compared to May might be explained by their life history. In Malangen, northern Norway, these 3 carnivores reach maximum abundances in October to February, and minimum abundances during summer (Falken-
haug 1997).

The boreal-Arctic *Thysanoessa* spp. showed, as expected, peak abundances in AtW (Dalpadado & Skjoldal 1991). The distribution patterns of small, medium and large *Thysanoessa* spp. differed, particularly for *T. longicaudata*, but the differences were less extensive after seasonal variability had been removed. The largest individuals of *T. longicaudata* (>15 mm) were found in ArW, corresponding to the findings of Dalpadado & Skjoldal (1991). *T. longicaudata* probably grows to a larger size and reaches an older age in cold ArW than in warmer AtW (Dalpadado & Skjoldal 1996). Large *T. inermis* (>22 mm) were only found in May in the Hopen Trench. However, large *T. inermis* could also have been present there in March, as they may live close to the bottom during the winter months (Kulka & Corey 1978, Lindley 1980, Dalpadado & Skjoldal 1995) and would therefore not have been sampled during our study. Only 2 individuals of the euphausiid *Meganyctiphanes norvegica* were found during May 1999 and March 2000, confirming the more boreal distribution of this species compared to *Thysanoessa* spp. Rarely occurring taxa were mainly restricted to AtW and were probably expatriate species transported into the Barents Sea.

Macrozooplankton species diversity, abundance and biomass

The abundance of macrozooplankton in the MIZ in the Barents Sea was low, approximately 40 times lower than the recorded abundance of meso-zooplankton (>180 μm) in the same area in May 1999 (S. Kwasniewski et al. unpubl.). Oceanic fronts are generally connected with enhanced biological production (Mann & Lazier 1996), and this has also been suggested for the Polar Front in the Barents Sea (Loeng 1989, Mehlum et al. 1998). However, in May 1999, the abundance, biomass and number of macrozooplankton species were particularly low in the frontal areas (MIX) compared to those in AtW and ArW (except for in AtW in March). The low values suggest that the Polar Front is not only a physical border but also a biological border for many

macrozooplankton species. However, most studies from the Barents Sea report a high biomass of macrozooplankton in summer and late autumn, but a low biomass in spring (Zelikman & Kamshilov 1960, Hassel 1986, Loeng 1989). The macrozooplankton abundance and biomass in MIX might therefore increase during summer. Usually, AtW is connected with higher abundance and biomass than ArW (Mumm et al. 1998). However, in this study the stations dominated by AtW were located at the extreme northern end of the AtW influence. AtW normally maintains a temperature of 3 to 6°C close to Bear Island, but cools on its way north (Loeng 1991). During May 1999 and March 2000, the AtW was 1 to 1.5°C in the inner Hopen Trench. This gradual cooling along with the increasing distance from the Norwegian Sea result in rare occurrences of boreal species in the northern Barents Sea (Loeng 1989).

Some differences in macrozooplankton abundance and biomass were not readily explained by water-mass distribution alone, such as the particularly low abundance and biomass of herbivores in the ArW bank in March compared to May (Fig. 9). Seasonal adaptations are closely related to the trophic level of zooplankters, and the life-cycle strategies of the herbivorous *Calanus glacialis* and *C. hyperboreus* include seasonal vertical migrations and diapause (Conover & Huntley 1991, Hagen 1999). *Calanus* spp. that descend for overwintering, 'stream' down to deeper parts of the shelf and into trenches, where they concentrate close to the bottom (Kashkin 1962). Seasonal migration patterns most probably explain the variability in species abundance and biomass within the ArW slope and ArW bank communities. Carnivorous macrozooplankton also increased in abundance in ArW slope in winter, although their biomass did not significantly increase. However, carnivores usually feed year-round, and may therefore follow the seasonal migrations of their copepod prey (Øresland 1990, Falken-
haug 1997, Hagen & Auel 2001). The much lower abundance of herbivores in AtW in March than in AtW in May can be explained by seasonal migrations and advective transport (as for *C. hyperboreus* described above). However, the particularly small biomass of herbivores, was also a result of the absence of large *Thysanoessa inermis* (≥ 16 mm) in AtW in March.

Large-scale water-mixing in the NW Barents Sea leads to communities characterised by differences in species abundance and biomass rather than differences in taxonomic composition. Both the physical and biological environment alter a species survival, growth and generation time. It is therefore important in future studies to compare developmental stages and/or size classes rather than species as one unit when studying community–environment relationships. Increased

knowledge of species' ecology, i.e. their trophic levels, population dynamics and limiting physical and biological factors (e.g. temperature, competition and predation pressure) is essential in order to better understand the spatial and temporal variations in zooplankton abundance and biomass.

Acknowledgements. We thank J. Wiktor and E. N. Hegseth for the chlorophyll *a* data, and the captain and crew of RV 'Lance' for ship logistics and assistance in the field. We further thank the Norwegian Polar Institute, Tromsø, the Institute of Oceanology, Sopot and the partners of the Barents Sea Production Licenses 182, 225 and 228 (Norsk Hydro, Statoil, Agip, Chevron, Fortum, Petero and Enterprise—contract no. 900000465) for financial and technical support.

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Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

*Submitted: October 4, 2002; Accepted: August 7, 2003
Proofs received from author(s): November 14, 2003*