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Magnitude of mesozooplankton variability: a case study from the Marginal Ice Zone of the Barents Sea in spring

KATARZYNA BLACHOWIAK-SAMOLYK[1]*, SLAWEK KWASNIEWSKI[1], HAAKON HOP[2] AND STIG FALK-PETERSEN[2]
[1]INSTITUTE OF OCEANOLOGY, POLISH ACADEMY OF SCIENCES, POWSTANCOW WARSZAWY ST. 55, 81-712 SOPOT, POLAND
AND [2]NORWEGIAN POLAR INSTITUTE, N-9296 TROMSØ, NORWAY

*CORRESPONDING AUTHOR: kasiab@iopan.gda.pl

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Zooplankton was studied on eight stations in the marginal ice zone (MIZ) of the Barents Sea, in May 1999, along two transects across the ice edge. On each station, physical background measurements and zooplankton samples were taken every 6 h over a 24 h period at five discrete depth intervals. Cluster analysis revealed separation of open water stations from all ice stations as well as high similarity level among replicates belonging to particular station. Based on five replicates per station, analysis of variance (ANOVA) confirmed significant differences ($P < 0.05$) in abundances of the main mesozooplankton taxa among stations. Relations between the zooplankton community and environmental parameters were established using redundancy analysis (CANOCO). In total, 55% of mesozooplankton variability within studied area was explained by eight variables with significant conditional effects: depth stratum, fluorescence, temperature, salinity, bottom depth, latitude, bloom situation, and ice concentration. GLM models supported supposition about clear and negative relationship between concentration of Oithona similis, *and overall mesozooplankton diversity. The analyses showed a dynamic relationship between mesozooplankton distribution and hydrological conditions on short-term scale. Furthermore, our study demonstrated that variability in the physical environment of dynamic MIZ of the Barents Sea has measurable effect on the Arctic pelagic ecosystem.*

INTRODUCTION

The dynamics of the ocean climate can be important in structuring the biodiversity and the energy flow of Arctic ecosystems (Richardson and Schoeman, 2004; Falk-Petersen *et al.*, 2006). The Marginal Ice Zone (MIZ) of the Barents Sea is the transitional area between ice free and permanently ice covered sea (Frankenstein *et al.*, 2001), and is one of the most dynamic and productive regions in the world's oceans (Slagstad and Stokke, 1994; Loeng *et al.*, 1995; Falk-Petersen *et al.*, 2000). Zooplankton play a vital role in the Barents Sea ecosystem (e.g. Hegseth, 1992, Dayton *et al.*, 1994). The production of pelagic zooplankton supports, directly and indirectly, among others large stocks of commercially important fishes, such as polar cod (*Boreogadus saida*), capelin (*Mallotus villosus*) and herring (*Clupea harengus*) (Dragesund and Gjøsæter, 1988). In the Barents Sea, large variations in zooplankton structure, abundance and biomass have been recorded on various temporal as well as spatial scales

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(Hassel, 1986; Skjoldal *et al*., 1987; Skjoldal and Rey, 1989; Arashkevich *et al*., 2002; Søreide *et al*., 2003; Blachowiak-Samolyk *et al*., 2006). In the ice-covered waters of the Barents Sea, however, the biological variability in the pelagic zone and its relationship with abiotic environmental parameters (e.g. water masses or ice cover) has been proved using statistical analysis only in a few studies (Unstad and Tande, 1991; Pedersen *et al*., 1995; Hansen *et al*., 1996; Dalpadado *et al*., 2003; Søreide *et al*., 2003; Daase and Eiane, 2007). Thus, our intensive investigation in this dynamic part of the Barents Sea gave a unique opportunity for a comprehensive study of the variability in mesozooplankton distribution.

This study was initiated by the research question: How representative a single zooplankton sample is, compared to five "replicates"? The attempt to answer this question was based on replicate samples from eight stations in two parallel transects situated across the MIZ. The variability in abundance of mesozooplankton was analysed in relation to biotic and abiotic parameters by means of redundancy analyses (RDAs). Therefore, the main task was to asses the magnitude of short-term variability in mesozooplankton in the MIZ of the Barents Sea as well as to establish existing regularities and to examine their relationships with different environmental parameters.

METHOD

Description of the study area

This study was a part of a programme "Spatial and temporal variability of the ice-ocean system in the Marginal Ice Zone of the Barents Sea" carried out by the Norwegian Polar Institute (Hop and Falk-Petersen, 2003). The investigated area was at the inner part of the Hopen Trench and surrounding banks of the Barents Sea, between 76°03′N–77°31′N and 26°53′E–33°08′E (Table I, Fig. 1). Zooplankton and oceanographic parameters were collected during a cruise with the ice-strengthened research vessel *Lance* between 9 and 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. Thus, stations A31 and B49 were in compact pack ice (100%), stations A33 and B50 were in about 50% ice cover, stations A34 and B51 were near the ice-edge in about 10% ice cover and stations A35 and B52 were located in the "open water" (Fig. 1, Table I). Further details with regard to the ice conditions are described in Engelsen *et al*. (Engelsen *et al*., 2002).

Environmental background sampling

Ice concentration, ice thickness and floe size were observed and documented every third hour (Hop and Falk-Petersen, 2003). Estimation of ice concentration was based on schematic diagrams from the National Oceanic and Atmospheric Administration (NOAA, 2001). Water mass properties (salinity, temperature, and fluorescence) were measured at each station with a Sea-Bird Electronics SBE 911+ CTD deployed vertically to near the bottom. Algal bloom conditions were obtained from Engelsen *et al*. (Engelsen *et al*., 2002) and Søreide *et al*. (Søreide *et al*., 2003).

Zooplankton sampling

During sampling, the ship was drifting together with the ice and the underlying near-surface water masses. Stratified vertical hauls were performed using a multiple plankton sampler (MPS; Hydro-Bios, Kiel) consisting of five closing nets with 0.25 m^2 square opening and 0.180 mm mesh. Generally, five water layers were sampled: 0–10 m, 10–30 m, 30–50 m, 50–100 m and 100 m-bottom, except for two repetitions: one at station A34 (haul A34-03) and one at station B51 (haul B51-09), where only four layers were taken: 0–12 m, 12–50 m, 50–100 m and 100 m-bottom, and 0–10 m, 10–30 m, 30–50 m, and 50 m-bottom, respectively. Vertical net hauls were taken every 6 h (five replicates) at each station during a 24 h daylight period, and a total of 198 zooplankton samples were obtained. The amount of water filtered was calculated based on flow meter measurements for individual samples. Zooplankton samples were preserved in 4% borax-buffered formaldehyde immediately after sampling. Organisms were identified and counted under a stereomicroscope equipped with an ocular micrometer, following standard procedures (e.g. Harris *et al*., 2000).

Statistical analyses

To reveal similarities among different replications as well as among stations, a multivariate cluster analysis was performed on a data matrix of species abundances, integrated for the whole water column (ind. m^{-2}) for each of the five replicates per station. The analyses were based on Bray-Curtis similarities of double-root transformed data using PRIMER v.5 package (Clarke, 1993). The double-root transformation downplays the dominants, but retains the basic quantitative information (Clarke and Warwick, 1994). The resulting dendrogram illustrating similarities among replicates was created using group-average linking procedure.

Table I: Stations; sample (replication) ID; dates; mean: temperature, salinity and fluorescence; bottom depth; position (latitude, longitude); algal bloom condition (0: non-bloom, 1: pre-bloom, 1.5 to 2.5: bloom, 3: late bloom) and ice concentration

Station	Replicate no.	Date (dd mm yy)	Temp. (°C)	Sal. (p.s.u.)	Fluorescence	Bottom depth (m)	Latitude (°N)	Longitude (°E)	Bloom rank	Ice concentration (%)
A31	A31-01	09 May 1999	−1.62	34.76	0.15	162	76.92	32.92	1.5	100
	A31-03	09 May 1999	−1.62	34.76	0.15	169	76.96	33.00	1.5	100
	A31-05	09 May 1999	−1.63	34.76	0.15	158	76.99	33.03	1.5	100
	A31-07	10 May 1999	−1.64	34.74	0.15	150	77.01	33.08	1.5	100
	A31-09	10 May 1999	−1.54	34.75	0.14	141	77.01	33.07	1.5	100
A33	A33-01	11 May 1999	−1.33	34.66	0.22	191	76.82	32.82	2	50
	A33-02	11 May 1999	nd	nd	nd	186	76.80	33.53	2	50
	A33-03	12 May 1999	nd	nd	nd	170	76.79	32.97	2	50
	A33-04	12 May 1999	nd	nd	nd	151	76.75	33.07	2	50
	A33-05	12 May 1999	−1.79	34.74	0.22	147	76.75	33.13	2	50
A34	A34-01	12 May 1999	−0.91	34.79	0.23	182	76.64	32.89	3	10
	A34-03	13 May 1999	−1.20	34.77	0.22	186	76.64	33.09	3	10
	A34-05	13 May 1999	−1.20	34.76	0.20	187	76.63	33.12	3	10
	A34-07	13 May 1999	−1.61	34.75	0.22	162	76.65	33.31	3	10
	A34-09	13 May 1999	−1.69	34.75	0.25	166	76.64	33.30	3	10
A35	A35-01	14 May 1999	1.82	35.02	0.21	317	76.09	32.65	3	0
	A35-03	14 May 1999	1.84	35.00	0.24	319	76.11	32.39	3	0
	A35-05	14 May 1999	1.80	35.02	0.21	312	76.08	32.67	3	0
	A35-06	14 May 1999	1.92	35.01	0.26	312	76.05	32.37	3	0
	A35-07	15 May 1999	1.62	35.01	0.20	316	76.09	32.69	3	0
B49	B49-01	17 May 1999	−1.54	34.32	0.14	188	77.43	27.03	1	100
	B49-03	17 May 1999	−1.55	34.31	0.13	187	77.43	27.07	1	100
	B49-05	17 May 1999	−1.58	34.32	0.13	196	77.45	27.00	1	100
	B49-07	17 May 1999	−1.61	34.31	0.13	188	77.48	27.00	1	100
	B49-09	17 May 1999	−1.64	34.30	0.13	172	77.52	26.88	1	100
B50	B50-01	18 May 1999	−1.39	34.39	0.14	180	77.30	27.28	1	50
	B50-02	18 May 1999	−1.55	34.33	0.13	171	77.37	27.17	1	50
	B50-04	19 May 1999	−1.54	34.32	0.13	173	77.37	27.16	1	50
	B50-05	19 May 1999	−1.46	34.34	0.13	188	77.38	27.42	1	50
	B50-06	19 May 1999	−1.50	34.33	0.13	199	77.37	27.49	1	50
B51	B51-01	20 May 1999	−1.13	34.46	0.19	180	77.14	27.90	2.5	10
	B51-03	20 May 1999	−1.17	34.48	0.18	177	77.13	28.13	2.5	10
	B51-05	20 May 1999	−1.17	34.49	0.15	181	77.07	28.19	2.5	10
	B51-07	20 May 1999	−1.22	34.46	0.17	148	77.00	28.13	2.5	10
	B51-09	20 May 1999	−1.38	34.42	0.16	111	76.93	28.09	2.5	10
B52	B52-01	21 May 1999	0.19	34.80	0.24	128	76.52	27.80	1	0
	B52-02	21 May 1999	−0.57	34.73	0.23	133	76.49	27.71	1	0
	B52-04	21 May 1999	−0.14	34.77	0.27	129	76.47	27.68	1	0
	B52-07	21 May 1999	0.14	34.84	0.27	129	76.49	27.76	1	0
	B52-08	21 May 1999	−0.21	34.77	0.25	135	76.35	27.67	1	0

Variability within dominant mesozooplankton taxa abundances among replicates and stations was examined by the Box Whiskers plots using the Statsoft software STATISTICA v. 6. Differences in the abundances of dominant zooplankton taxa among replicates and stations were identified using 1-way ANOVA (Table II). The normality of particular zooplankton taxa abundances at each station were tested with Shapiro−Wilk test and the homogeneity of variance with Brown−Forsyth test. To achieve homogeneity of variances, the abundances were log-transformed prior to analyses for *Calanus glacialis*, *C. finmarchicus* and *Pseudocalanus* spp. Fisher's least significant difference (LSD) test was used for *post hoc* comparisons.

To evaluate the effects of biotic and abiotic variables on multiple species assemblage, direct redundancy gradient analysis (RDA) was performed using CANOCO for Windows v4.5 (ter Braak and Smilauer, 2002). We chose RDA because it focuses on interspecies correlations and additionally has the advantage of treating the community as a multivariate entity (ter Braak and Smilauer, 2002). All zooplankton taxa abundances (ind. m^{-3}) were square-root transformed prior to analysis to reduce the patchiness effect (Krebs, 1989). The variability in abundance of mesozooplankton for each sampled layer was analysed in relation to biotic (fluorescence, bloom state) and abiotic parameters (depth stratum, temperature,

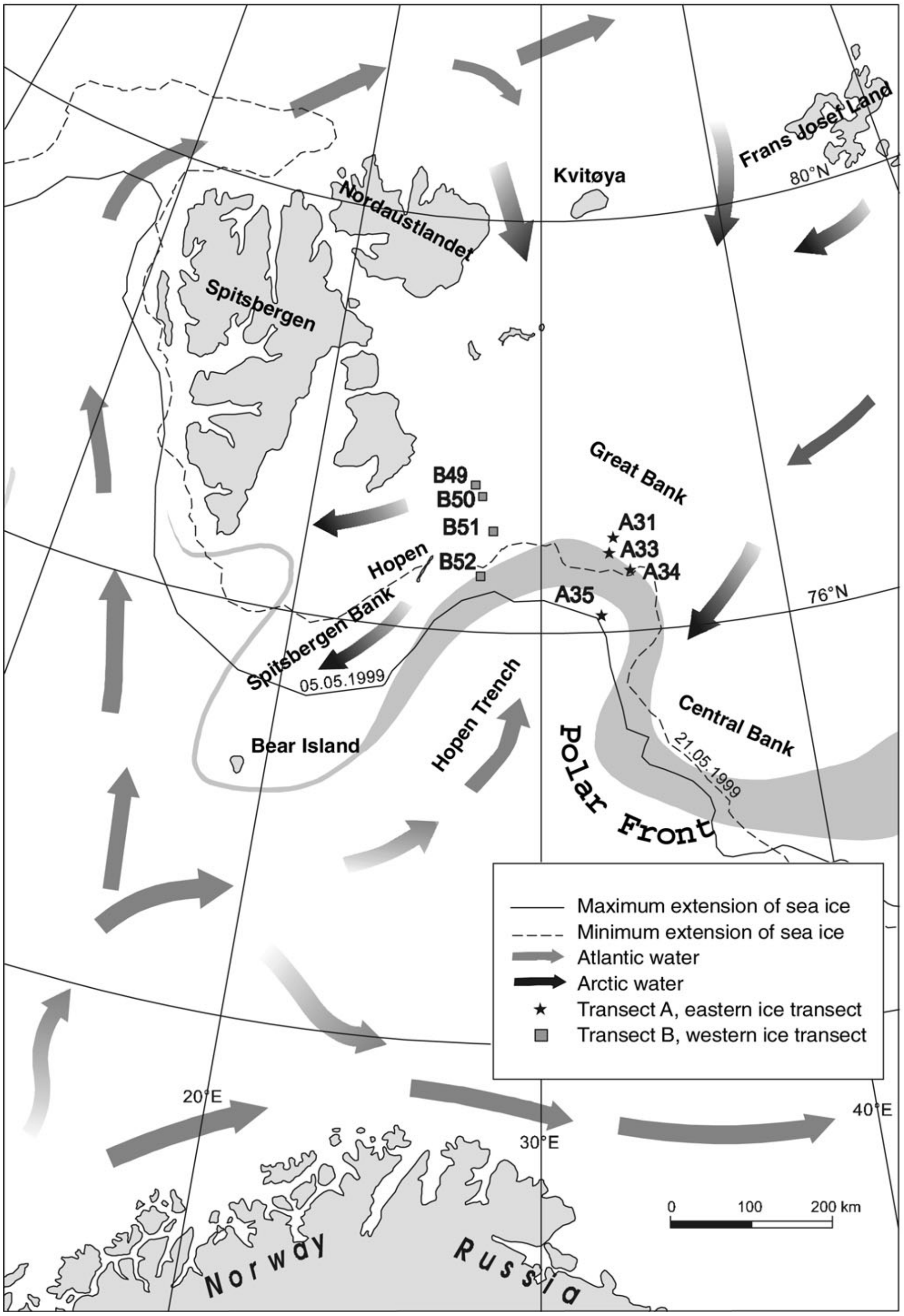


Fig. 1. Sampling area in the MIZ of the Barents Sea, May 1999.

salinity, ice cover conditions, bottom depth and geographical position).

The statistical significance of the relationship between species and the whole set of variables was examined by a Monte Carlo permutation test using "the global permutation test" in the CANOCO-package (ter Braak and Smilauer, 2002). Using ordination techniques and rules of interpretation of the redundancy diagrams, we followed the review and summary by ter Braak and Smilauer (ter Braak and Smilauer, 2002). The position of species can be determined using the "biplot rule". The closer a species clusters together with

Table II: Results of the one-way ANOVA F-tests for differences in variability of abundances of the main mesozooplankton taxa, based on five replicates per station

Zooplankton taxa/group	MS	df	*F* observed	*P*
Calanus finmarchicus	3.62	7	17.4	<0.0001
Calanus glacialis	2.99	7	15.7	<0.0001
Pseudocalanus spp.	2.19	7	21.67	<0.0001
Microcalanus spp.	2.63×10^7	7	2.66	0.027
Metridia longa	4.41×10^6	7	10.27	<0.0001
Oithona similis	1.77×10^9	7	9.40	<0.0001
Copepoda nauplii	2.80×10^8	7	6.01	0.0001
Total zooplankton	1.39×10^9	7	2.75	0.0237

Abundances of *Calanus glacialis*, *C. finmarchicus* and *Pseudocalanus* spp. were log-transformed prior to analyses to achieve homogeneity of variance. The other taxa were not transformed. d.f. = degrees of freedom; MS = mean square; F = test values; *P* = probability value.

environmental parameters, the stronger preference it has to this particular parameter. The angle between species and environmental parameter arrows indicates their correlation, i.e. they are uncorrelated if they are perpendicular to each other and highly correlated when the angle is small. Long arrows indicate higher correlation to the species pattern than shorter ones. To avoid multicollinearity problems, we examined the collinear factors by inspecting the Variance Inflation Factor (ter Braak and Smilauer, 2002).

Additionally, a generalized linear model (GLM) of response of *Oithona similis* to the ice cover conditions and depth stratum was constructed using CANOCO for Windows v. 4.5 (ter Braak and Smilauer, 2002). In a similar way, the response of all mesozooplankton was evaluated using Shannon–Wiener diversity index (H′) as a proxy of complex multispecies assemblage. GLMs represent a straightforward extension of the classical linear models based on modern regression methods. Important properties of the GLM are that individual predictors are mutually independent (additive) and that the effect of a particular predictor is expressed by a single parameter named linear transformation coefficient (the regression coefficient). The first GLM model was created on the real data (non-transformed abundances of *O. similis*, ind. m^{-3}). We specified GLM settings as the quadratic degree and Poisson distribution of response variables (depth stratum and ice situation) (ter Braak and Smilauer, 2002).

RESULTS

Hydrography and sea ice

The water masses of the MIZ were categorized into the following types: Atlantic water (AtW), Arctic water (ArW), Polar Front water (PFW), mixed Atlantic water (MAtW), melt water (MW), mixed melt water (MMW) and Barents Sea water (BSW) (Fig. 2). During the sampling period, the ice edge was located near the Polar Front at the inner part of the Hopen Trench. Cold ArW (<-1.2°C) with salinities close to 34.8 p.s.u. dominated over the slopes of the Great Bank, on the A transect (stations A31, A33, A34), whereas warm (>1°C), saline (>35.0 p.s.u.) AtW prevailed further south in the deeper Hopen Trench (station A35). Cold ArW, covered by the surface MW layer, dominated over the Spitsbergen Bank (stations B49, B50, B51). In the shallowest area, southeast of Hopen (station B52), cold MIX water (<0°C) prevailed (Figs 1 and 2).

The ice conditions at each station changed continuously, depending on wind and tides. The tidal effect was very pronounced over the banks and the divergence of the tidal wave opened or closed the ice pack regularly. The ice was <2 m thick and characterized as first-year ice.

Clustering of replicates

Two main clusters of stations were distinguished: one consisting of open water stations (A35 and B52) and the second linking together all "ice stations" from both transects (Fig. 3). The cluster generally revealed high similarities level (80–90%) among the five replicates belonging to each station. However, separation within ice stations from transect A (A31, A33 and A34) was less distinctive than those of transect B, except for one replicate (B49-05) that clustered with replications from station B50.

The variability in abundances of dominant zooplankton taxa (ind. m^{-2}) was compared among replicates and stations for the most abundant and frequent species (*O. similis*, *C. finmarchicus*, *C. glacialis*, *Metridia longa*) and genera (*Pseudocalanus* spp. and *Microcalanus* spp.) as well as for Copepoda nauplii and total zooplankton (Fig. 4). For detailed list of all mesozooplankton species and taxa see Blachowiak-Samolyk *et al.* (Blachowiak-Samolyk *et al.*, 2006).

ANOVA and *post hoc* Fisher's LSD tests confirmed differences in abundances between stations (Table II). The notably high abundances of *C. finmarchicus* at stations B49 and B50 were confirmed by the statistical analysis (Fig. 4a). Abundances of *C. glacialis* from transect B, except at station B52, were different from those of transect A (Fig. 4b). The abundances of *O. similis* from both open water stations, A35 and B52, were similar but differed significantly from abundances at all other stations (Fig. 4c). A similar pattern was observed

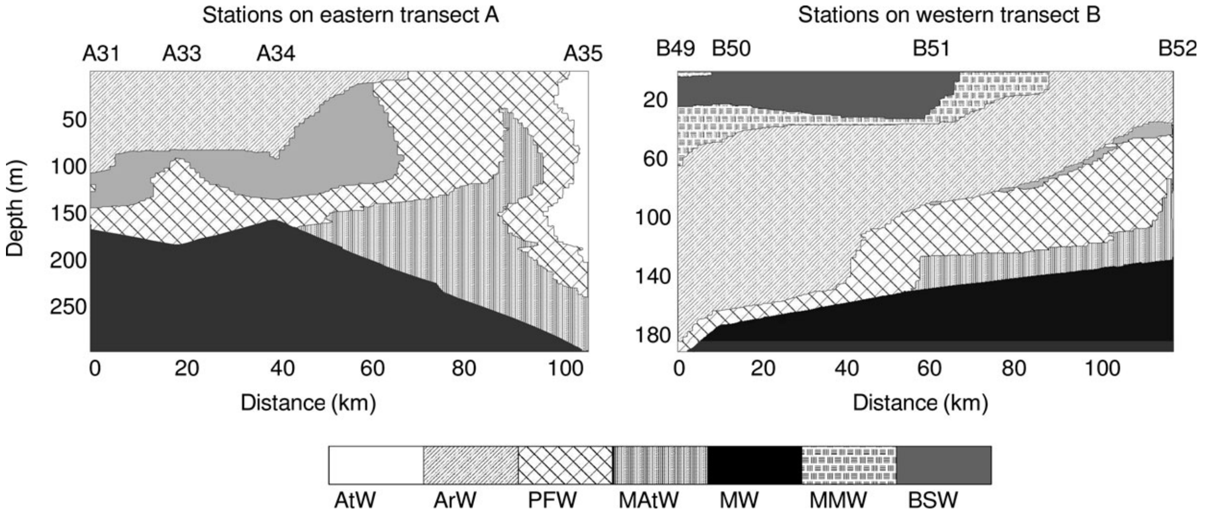


Fig. 2. Water masses determined from CTD casts along two transects (A and B) in the MIZ of the Barents Sea, May 1999. AtW: Atlantic Water ($>1°C$, >35.0 p.s.u.); ArW: Arctic Water ($<0°C$, 34.3–34.8 p.s.u.); PFW: Polar Front Water (-0.5 to $3°C$, 34.8–35.0 p.s.u.); BSW: Barents Sea Water ($<-0.5°C$, 34.8–35.95 p.s.u.); MAtW: Mixed Atlantic Water (-1 to $1°C$, >34.95 p.s.u.); MW: Melt Water (34.2 p.s.u.); MMW: Mixed Melt Water ($<0°C$, 34.2–34.3 p.s.u.). Note differences in scales.

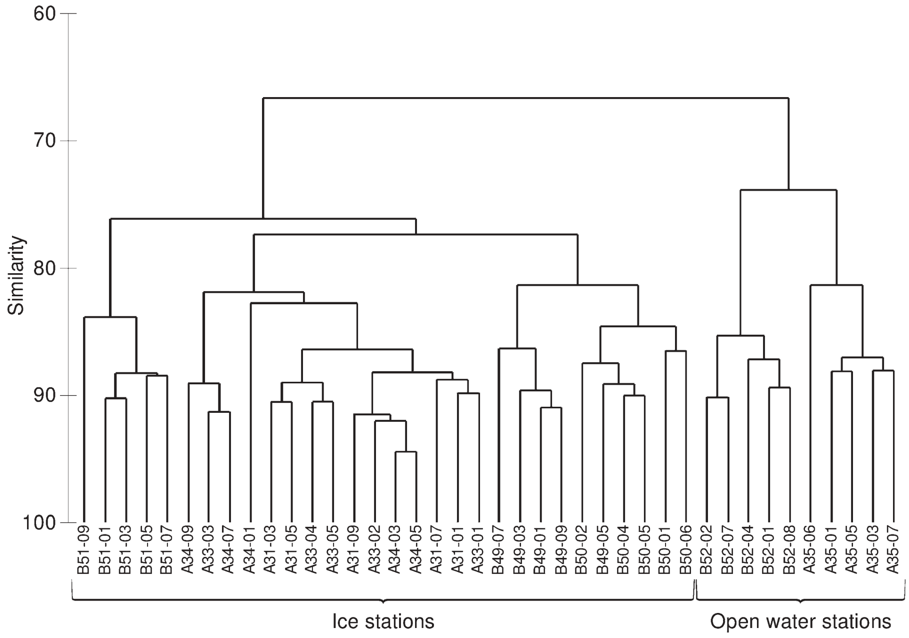


Fig. 3. Clustering dendrogram illustrating similarities among replicates as well as among different stations. The cluster analysis was performed on a data matrix of species abundances, integrated for the whole water column (ind. m^{-2}) for each of the five replicates per station.

for *Pseudocalanus* spp. (Fig. 4d). *Metridia longa* abundances at all A transect stations were different from all B transect stations, except at station B49. Also, the highest abundance of *M. longa* at station A35 was different from that of other stations (Fig. 4e). *Microcalanus* spp. showed maximum abundance at station A34, which differed from all these recorded at all B transect stations (Fig. 4f).

The maximum abundance of Copepoda nauplii was observed at station B51 but it was also high at stations A33 and A34, although high variability in abundances was observed within this group at all stations (Fig. 4g). *Post hoc* comparisons showed that the low total zooplankton abundance at station A35 differed significantly from the abundances at all other stations, except for A31 and B52 (Fig. 4h).

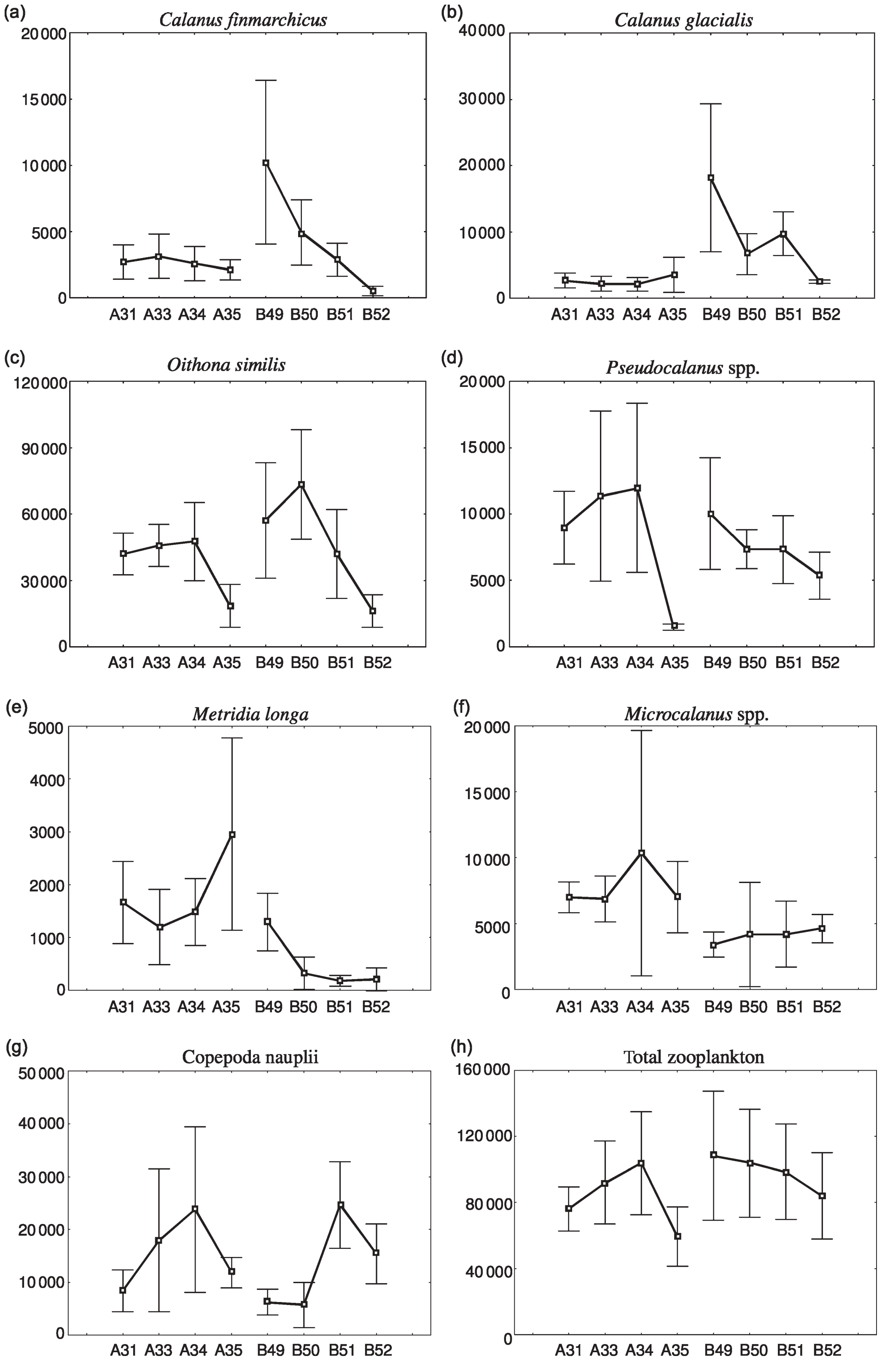


Fig. 4. Box Whiskers plots with the mean abundances (ind. m^{-2}) of main zooplankton taxa/groups: (**a**) *Calanus finmarchicus*; (**b**) *C. glacialis*; (**c**) *Oithona similis*; (**d**) *Pseudocalanus* spp.; (**e**) *M. longa*; (**f**) *Microcalanus* spp.; (**g**) Copepoda nauplii and (**h**) total zooplankton, based on five replications per station (mean and 95% confidence intervals). Note differences in scales.

Environmental influence on species distribution pattern (RDA)

A model was constructed on the basis of abundances (ind. m^{-3}) of all 70 zooplankton taxa from all depth strata and replicates. The model illustrates the relationship between different variables and the 16 best fitted or most explained taxa (Fig. 5). Forward selection, applied to full set of environmental variables, discriminated eight variables with significant conditional effects: depth stratum, fluorescence, temperature, salinity, bottom depth, latitude, bloom situation and ice concentration (Table III), which together explained 55% of the total zooplankton variability during our survey. Longitude had no significant impact on the mesozooplankton patterns.

Depth stratum was the strongest contributor to the model, explaining 27% of the overall mesozooplankton variability. A close relationship between this parameter and increasing abundances of the two deeper water inhabitants, *Microcalanus* spp. and *M. longa*, was confirmed. Additionally, abundances of *Bradyidius similis*, *Eukrohnia hamata*, *Pareuchaeta norvegica*, *Thyssanoessa inermis* and *Triconia borealis* correlated well with increasing depth (Fig. 5).

Fluorescence explained 9% of the mesozooplankton variability pattern. *Fritillaria borealis*, *C. hyperboreus* and Copepoda nauplii showed the highest correlation with this parameter. Also, *Pseudocalanus* spp. and *C. glacialis* abundances were weakly correlated with this parameter.

Temperature, salinity and bottom depth explained 4–6% each of the total mesozooplankton heterogeneity. These parameters were correlated with abundances of *Microcalanus* spp., *M. longa*, *B. similis*, *E. hamata*, *P. norvegica*, *T. inermis* and *Triconia borealis*, whereas the relationship was inverse for abundances of *C. finmarchicus*, *C. glacialis*, *O. similis, Clione limacina* and *Pseudocalanus* spp.

Latitude together with bloom situation had rather small (2 and 1%, respectively) impact on the overall variability in the RDA model, although they were positively correlated with abundances of *C. finmarchicus*, *C. glacialis*, *O. similis* and *Pseudocalanus* spp.

Longitude explained 1% of the overall mesozooplankton variability although without a significant result.

Ice concentration did not contribute to the model explanation but significance of this parameter was confirmed by Monte Carlo permutation test (Fig. 5, Table III).

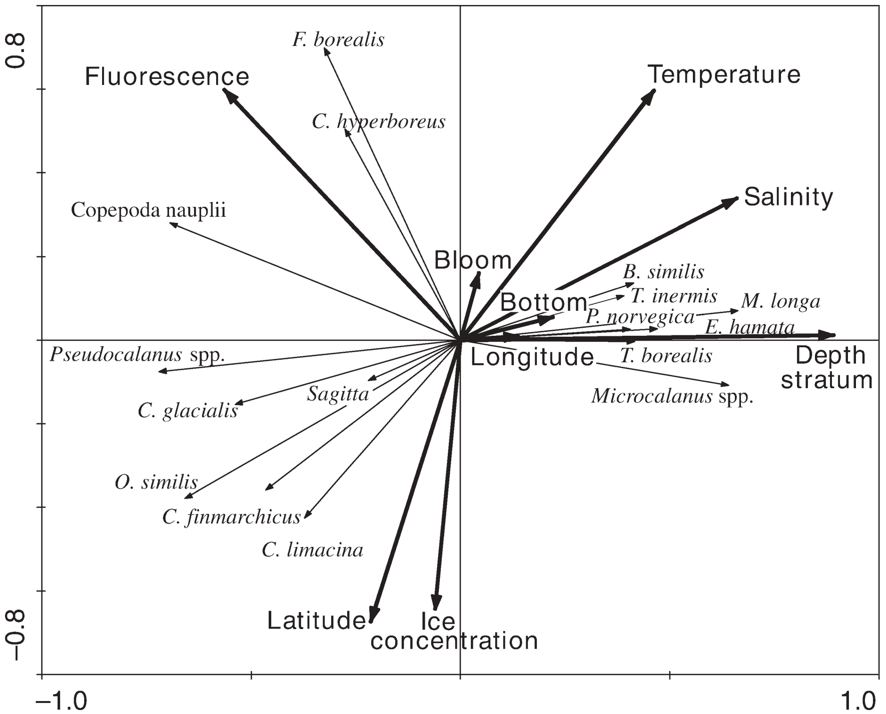


Fig. 5. Direct redundancy gradient analysis (RDA) of mesozooplankton square-root abundance (ind. m^{-3}) data (70 taxa) from the Barents Sea (May 1999), describing their relationship to selected environmental variables (arrows). The model explained 55% of all variability. The plot illustrates the relationship between different variables and 16 best fitted and most explained taxa. The first canonical axis (RDA-1) explains 57.6% of the species–environmental relationship, and the second axis (RDA-2) explains 28%. Variance of species data accounts for 34% and 16.5%, with regard to axes 1 and 2, respectively.

Table III: Ranking of environmental variables in the Barents Sea (May 1999) that influenced the distribution of mesozooplankton significantly (Monte Carlo permutation test in RDA, P< 0.05), with significant values in bold

Variable	λ	*F*	*P*
Depth stratum	0.27	67.32	**0.002**
Fluorescence	0.09	26.73	**0.002**
Temperature	0.06	18.99	**0.002**
Bottom depth	0.04	13.32	**0.002**
Salinity	0.05	15.77	**0.002**
Latitude	0.02	7.74	**0.002**
Bloom situation	0.01	4.39	**0.004**
Longitude	0.01	2.20	0.056
Ice concentration	0.00	2.26	**0.046**
Total	0.55		

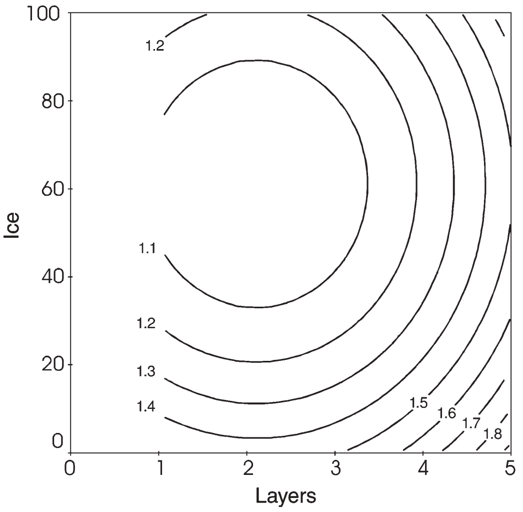
The eigenvalue (λ) for each variable indicates the portion of the total variance explained by the model.

Additionally, the two GLM models framed possible and clear relationship between overall mesozooplankton diversity (Shannon–Wiener diversity index H′), the concentration of *O. similis* and ice cover conditions and depth stratum (Fig. 6).

DISCUSSION

To estimate correctly the abundance of zooplankton is a difficult task, and there is surprisingly little knowledge about how representative are zooplankton net samples. A crucial question associated with plankton ecology is how representative a single sample is, when compared with several replicates in space and time. The accuracy of sampling may be hampered by a number of factors, including the patchiness (Wiebe and Holland, 1968; Wiebe and Benfield, 2003 and citations therein), filtering efficiency, net clogging and net avoidance (e.g. Clarke *et al.*, 2001). Additionally, mesozooplankton variability might be strongly modified by different biological factors, such as growth, life cycle, diel vertical migration (DVM) and ontogenetic seasonal migration of zooplankters (Mackas and Tsuda, 1999, Blachowiak-Samolyk *et al.*, 2006; Cottier *et al.*, 2006; Willis *et al.*, 2006). One of the most important problem, which could be the case in the current examination is DVM issue. The last results of Blachowiak-Samolyk *et al.* (Blachowiak-Samolyk *et al.*, 2006) based on the same material, as the current study, together with a comprehensive literature survey on Arctic zooplankton DVM revealed that dominant zooplankton taxa in the MIZ of the Barents Sea do not perform DVM under the midnight sun conditions.

(a) H' versus Layer and Ice



(b) *Oithona similis* abundance versus Layer and Ice

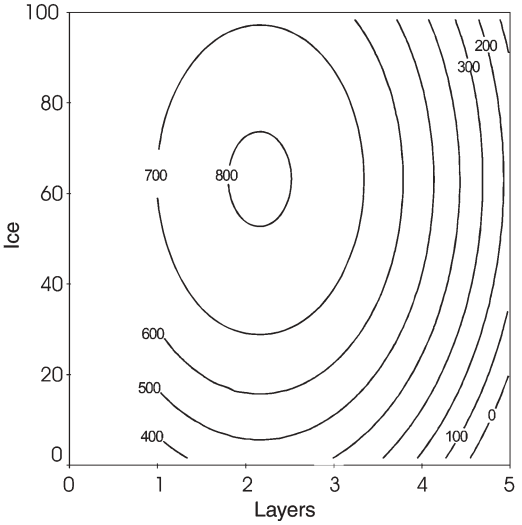


Fig. 6. Model of response to ice conditions (%) and particular depth stratum: 1 (0–10 m), 2 (10–30 m), 3 (30–50 m), 4 (50–100 m) and 5 (100 m-bottom) of: (**a**) Shannon–Wiener diversity index (H′); (**b**) *Oithona similis* abundances (ind. m^{-3}).

Taking advantage of having five replicates per station, from hard to access polar region, we tested how mesozooplankton vary locally in the MIZ of the Barents Sea. Generally, the five replicates from each station clustered together, showing high similarity level (80–90%). The results of clustering stations into groups can be interpreted in the light of the variability of the oceanographic conditions in the area. The two open water stations (A35 and B52), separated from the remaining stations, were located in parts of the study area where water masses of Atlantic origin predominated (AtW and

MIX, respectively). The stations were also different from the remaining stations with respect to bottom depth. Stations A31, A33 and A34 from transect A, which formed a well defined cluster, were all in this part of the Hopen Trench where Arctic water prevailed. Samples from stations preoccupied by ArW and MW (stations B49, B50, B51) were clustered separately too, with station B51 occupying a transient position between Arctic and Atlantic influenced stations. Station, B52, with MIX water masses had significantly lower zooplankton diversity than the other stations also with respect to macrozooplankton community (Søreide *et al*., 2003).

Analyses of all replicates revealed consistent patterns in the abundances variability of the main mesozooplankton taxa (Fig. 4). The two *Calanus* species showed low abundances and rather narrow range of their variability on transect A, contrary to transect B. *Calanus finmarchicus* is an oceanic species with its main over-wintering site in the Norwegian Sea, in the Atlantic marine zoogeographic domain, but with the prevailing current system parts of the main population are transported northwards into the Arctic, often in high concentrations (Conover and Huntley, 1991; Head *et al*., 2003; Arnkværn *et al*., 2005; Falk-Petersen *et al*., 2006). *Calanus glacialis*, on the other hand, is a true Arctic shelf species, but the two species can co-occur in high numbers where Arctic and Atlantic water masses meet. We think that majority of our sampling stations were within a broad frontal zone, therefore co-occurring of the two *Calanus* species resulted from mixing of Atlantic and Arctic water masses. The highest abundance of the species at B49 could be an effect of concentrating the wintering populations in the depression of the sea bed nearby the station. The Barents Sea is generally shallow therefore even small depressions may offer favourable habitat for wintering populations of these species. Station B49 was the deepest station on Transect B. On the other hand, the high variability could be in part due to changing sampling location, because of unplanned drifting of the anchored ship together with ice. The station depth varied between 196 and 172 m during the 24 h sampling.

A characteristic feature of *O. similis* and *Pseudocalanus* spp. distribution was the low abundance at both open water stations, A35 and B52, and high abundance, but also high variability, at the ice stations B49 and B50, and at stations A33 and A34, respectively. Global distribution and high numerical abundance suggest that *O. similis* should be very tolerant to different environmental conditions (Gallienne and Robins, 2001). Head *et al*. (Head *et al*., 2003) found no relationship between *O. similis* distribution and water mass variability in the Labrador Sea, in contrast to Richter (Richter, 1994) and Gislason and Astthorsson (Gislason and Astthorsson, 2004), who described it as a cold adapted species with the highest occurrence in the Greenland Sea as well as in cold waters around Iceland. The present study confirms that *O. similis* showed the highest abundances in ice covered areas with Arctic water masses. *Pseudocalanus* was found in very low numbers at the deepest, open water station (A35) in the five replicates. This result concurs with other studies, which characterize representatives of *Pseudocalanus* as a neritic species both in the Barents Sea and in the Canadian Arctic (Conover and Huntley, 1991). *Metridia longa* is known to inhabit deep waters in Norwegian fjords (Balino and Aksnes, 1993), which is similar to what we observed in the Barents Sea, where the species attained the highest abundance at the deepest station A35. The maximum abundances, but also the largest variation, of *Microcalanus* spp. were found at station A34 at the ice edge, where oceanographic and ice conditions were extremely unstable. Interestingly, a substantial contribution of *Microcalanus* spp. to the total zooplankton abundance (10–20%) was reported in a similar region of the Barents in May 1998 (Arashkevich *et al*., 2002). High variability in the abundances of Copepoda nauplii was observed at all stations, although the peak of this group occurred at the ice edge, which is in agreement with earlier studies in the MIZ (Falk-Petersen *et al*., 1999). The highest total zooplankton abundances, as well as the largest variability, were observed at the stations with the heaviest ice conditions on both transects (B49, B50 and A34). These results were in agreement with those of Falk-Petersen *et al*. (Falk-Petersen *et al*., 1999), who found the highest numbers of mesozooplankton in consolidated pack ice.

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). To obtain synthetic information on the quality and scale of the interactions between the various environmental factors and zooplankton abundance, a correspondence analysis was performed using RDA ordination model (CANOCO). Gradients in mesozooplankton community and population structure from close pack-ice to open water in the Barents Sea have been recorded previously (Falk-Petersen *et al*., 1999). The authors indicated great impact of both oceanographic conditions and bottom topography on the mesozooplankton community structure. However, scale and magnitude of the observed changes have generally not been assessed, except for the study of Søreide *et al*. (Søreide *et al*., 2003), which assessed the horizontal distribution of macrozooplankton with respect to changes in environmental conditions in the same area over two seasons, May 1999 and March 2000.

The RDA model explained 55% of the total zooplankton variability in the MIZ of the Barents Sea in May 1999. Depth stratum was the most important contributor to the model, describing 27% of the species variation. Many authors have indicated consistent patterns of vertical distribution of the main zooplankton taxa, specific for each region (e.g. Søreide *et al.*, 2003) and depths (e.g. Pedersen *et al.*, 1995). Our study confirmed the tendency to attain higher densities with increasing depth stratum for species such as *Microcalanus* spp., *M. longa*, *B. similis*, *Triconia borealis*, *P. norvegica*, *E. hamata* and *Thyssanoessa inermis* (e.g. Conover and Huntley, 1991; Hansen *et al.*, 1996; Head *et al.*, 2003). On the other hand, *C. finmarchicus*, *C. glacialis*, *O. similis*, Copepoda nauplii and *Pseudocalanus* spp. were found in the upper layers during May 1999 in accordance with their epipelagic preferences (Melle *et al.*, 1987; Arashkevich *et al.*, 2002; Kwasniewski *et al.*, 2003). Interesting was also the close relationship between distribution of the Arctic associated copepods *C. glacialis* and *Pseudocalanus* spp. (Jaschnov, 1970; Frost, 1989) as well as the Atlantic *C. finmarchicus* and *O. similis* (Brodskii, 1967; Jaschnov, 1970), which were observed in areas where Arctic and Atlantic water masses meet (Fig. 5). This observation concurs with results of earlier studies (e.g. Falk-Petersen *et al.*, 1999; Arashkevich *et al.*, 2002; Søreide *et al.*, 2003) characterizing our study area as a broad frontal zone of mixing Atlantic and Arctic water masses that is inhabited by mixed Atlantic and Arctic zooplankton.

Fluorescence explained 9% of the whole mesozooplankton distribution model. This factor has not been used very commonly in evaluation of different sources of zooplankton variability. Close association between herbivorous species, such as *Calanus*, *Pseudocalanus* and Copepoda nauplii, and fluorescence is consistent with their trophic preferences (Mauchline, 1998). It also suggests that in lack of proper chlorophyll-*a* measurements fluorescence might be a good proxy of this environmental factor. In this study, high fluorescence was also correlated with appendicularian abundance, which is in agreement with observed correlation between distribution patterns of *F. borealis* and chlorophyll-*a* in Toyama Bay, southern Japan Sea (Tomita *et al.*, 2003).

Temperature, salinity and bottom depth had very similar influence on the total mesozooplankton pattern. These variables were located very close to each other on the RDA diagram, suggesting close relation among them as well as to the overall zooplankton community structure. Earlier study on species–environment relationship in the Barents Sea from March to May 1989 (Pedersen *et al.*, 1995) showed that zooplankton community could not be grouped according to temperature and/or salinity. Recently, Søreide *et al.* (Søreide *et al.*, 2003) presented rather high impact of salinity and temperature on macrozooplankton distribution in the same area as in our study. It is well-known from the experimental studies that small changes in temperature may limit zooplankton distribution through altered growth, reproduction and/or mortality rates (Kinne, 1970). On the other hand, experimental evidence suggests that a small salinity difference of 2.5 p.s.u., which exceeds the difference between ArW and AtW, has no measurable effect on zooplankters physiology (Kinne, 1971). The Barents Sea is highly advective ecosystem, and many species, especially those with centres of distribution in temperate regions, may not successfully reproduce there. These expatriate populations will eventually become depleted, unless they are not supplied by advected individuals (Pedersen *et al.*, 1995). Unfortunately, in our study temperatures and salinities used are means for zooplankton sampling layers, so advective processes most probably might not been addressed here properly.

Latitude and bloom situation contributed only 1–2% each to the overall variability of the studied zooplankton, although their input was found still significant by the statistical analysis. Pedersen *et al.* (Pedersen *et al.*, 1995) found that the Barents zooplankton could not be grouped according to latitude due to a fairly stable physical conditions prevailing over larger areas in March–May 1989. The authors claimed that factors of biological nature (i.e. differences in growth rates or in vertical migration capability) were the major contributors responsible for maintaining variability within the region. On the contrary, Søreide *et al.* (Søreide *et al.*, 2003) reported significant influence of location on macrozooplankton distribution in the MIZ of the Barents Sea. Their conclusion was coherent with results of parallel studies (Falk-Petersen *et al.*, 2000; Engelsen *et al.*, 2002), which postulated that at high latitudes, the solar angle and thus the onset of spring, changes markedly over short latitudinal distances. According to our model, *C. finmarchicus*, *O. similis* and *C. limacina* were closely associated with latitude and ice concentration. Similar relationship was described recently for *C. limacina* and latitude by Søreide *et al.* (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 most likely the effect of ice diminishes pelagic biota quite rapidly with increasing depth and increasing distance from surface. One should expect stronger relationship between ice cover and zooplankton component that shows preference to inhabiting surface layers (e.g. Copepoda nauplii) and weaker or no relationship between ice cover and deep dweller (e.g. *M. longa*), which was displayed on our RDA model. Ice concentration did not contribute to the total mesozooplankton variability explained by the RDA model in our survey, which was also indicated by earlier investigations in the same area (Falk-Petersen *et al.*, 1999; Søreide *et al.*, 2003). Ice cover as well as Arctic waters, however, did influence the distribution of all the major species, being *C. finmarchicus*, *C. glacialis*, *O. similis* and *Pseudocalanus*.

The results of the GLM models confirmed anticipated negative relationship between overall zooplankton diversity and abundance of the dominant *O. similis* (Fig. 6a and b). In fact, this finding is in accordance with Shannon–Wiener index definition, which includes both species richness and species dominance (Magurran, 2004). The highest H′ is achieved for an even distribution of many species, and a dominant species, such as *O. similis*, will therefore tend to lower the diversity index.

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