Polar Biol (2003) 26: 707–719
DOI 10.1007/s00300-003-0543-7

ORIGINAL PAPER

**Andreas Krell · Caroline Ummenhofer · Gerhard Kattner
Andrei Naumov · Dylan Evans · Gerhard S. Dieckmann
David N. Thomas**

The biology and chemistry of land fast ice in the White Sea, Russia—A comparison of winter and spring conditions

Received: 18 February 2003 / Accepted: 1 August 2003 / Published online: 26 September 2003

Abstract Various abiotic and biotic parameters, including phytoplankton distribution, were studied to investigate seasonal changes within the fast-ice cover in Chupa Inlet, a freshwater-influenced Arctic-like fjord in Kandalaksha Bay (White Sea). Sea ice and under-ice water were collected along transects in the inlet in February and April 2002. Ice-texture analysis, salinity and $\delta^{18}O$ values indicated that the complete ice sheet had transformed within 2 months. This resulted from an upward growth of snow ice and subsequent melting at the underside of the ice, which makes a comparison between the two sampling periods difficult in terms of defining temporal developments within the ice. Nutrients, DOC and DON concentrations in the under-ice water were typical for Russian Arctic rivers. Concentrations of nitrate, silicate and DOC in the ice were lower, which is attributed to a loss as the ice forms. The concentrations were also modified by biological activity. In February, there was a strong correspondence between the distribution of biological parameters, including particulate and dissolved organic carbon and nitrogen (POC and PON, DOC and DON) and inorganic nutrients (nitrate, nitrite, phosphate and silicate), which was not the case in April. The correlation between both DOC and DON with ammonium indicates heterotrophic activity within the winter ice collected in February. Sea-ice organisms were distributed throughout the ice, and several assemblages were found in surface layers of the ice. In April, a more ''typical'' distribution of biomass in the ice was measured, with low values in the upper part and high algal concentrations in the lower sections of the ice, characteristic of a spring ice-algal bloom. In contrast to the February sampling, there was evidence that the ice-algal assemblage in April was nitrogen-limited, with total inorganic nitrogen concentrations being <1 μM and a mean inorganic nitrogen to phosphorus ratio of 2.8. The ice assemblages were dominated by diatoms (in particular, *Nitzschia* spp.). There were temporal shifts in the assemblage composition: in February, diatoms accounted for 40% and in April for $>98\%$ of all organisms counted.

A. Krell (✉) · G. Kattner · G. S. Dieckmann
Alfred Wegener Institute for Marine and Polar Research,
Am Handelshafen 12, 27570 Bremerhaven, Germany
E-mail: akrell@awi-bremerhaven.de

A. Krell · C. Ummenhofer · D. Evans · D. N. Thomas
School of Ocean Science, University of Wales-Bangor,
Menai Bridge, Anglesey, LL59 5AB UK

A. Naumov
Zoological Institute, Academy of Sciences,
Universitetskaya nab.1, 199034 St. Petersburg, Russia

Introduction

The White Sea is a semi-enclosed Arctic sea comprising three larger bays (Dvina, Kandalaksha and Onega Bay), which are strongly affected by continental runoff. Chupa Inlet, where we performed our studies, forms part of Kandalaksha Bay, situated directly at the polar circle with a 4–5 months ice season lasting from mid-December to the end of April. Maximum ice extent is usually attained in March. Sea ice therefore probably plays a major role in structuring the White Sea ecosystem, since it strongly alters the exchange of energy and material between water and atmosphere.

During the formation of sea ice, 60–70% of the particulate and dissolved matter is not confined within the solid ice matrix but expelled into a system of interconnected channels and isolated pockets (Weissenberger et al. 1992), varying in size from <5 μm to >1 cm depending on the ice type (granular/columnar). Although freshwater-influenced White Sea waters are less saline (14–27) than open ocean waters, these principles hold even for brackish waters (Leppäranta et al. 1998). With decreasing temperature, salinity in the brine channels increases due to salt rejection during ice-crystal formation, and can attain values of 70–144 at −4 to −10°C, respectively (Cox and Weeks 1983). Incoming irradiance is strongly attenuated by the ice and overlying

snow cover. However, sea ice algae and, particularly, diatom species in the ice are able to grow at light intensities down to 2 μmol m^{-2} s^{-1} (Arrigo 2003). Despite these extreme conditions, the network of interconnected channels provides a habitat for a diverse grouping of heterotrophic and autotrophic organisms, at times resulting in a well-developed microbial food network within the ice (Lizotte 2003). At the onset of spring, algal blooms develop in and attached to the underside of the ice, triggered by the increased light availability after the dark polar winter.

So far, studies in the White Sea concerning hydrography, nutrient and biomass distribution (Howland et al. 1999; Mordasova 1999), as well as investigations on phytoplankton-species distribution and succession (Shanin and Mikhajlovskij 1996; Berger et al. 2001 and references therein), have focused mainly on ice-free seasons. Zhitina and Mikhajlovskij (1990) carried out studies during the winter season including sea ice, but concentrated only on species distribution. However, there are comparable studies on the chemistry and biota of fast-ice systems with a high degree of freshwater influence, which have been undertaken in other Arctic regions (Legendre et al. 1996; Weslawski et al. 1997; Wiktor 1999) and in the Baltic Sea (Haecky et al. 1998; Kaartokallio 2001; Meiners et al. 2002). Although the White Sea is situated in the same climate zone as the Baltic Sea, and is a similar type of semi-enclosed sea, it has a strong Arctic input and thus has a considerably higher salinity than the Baltic.

To our knowledge, no published research in the White Sea has so far focused on the coupling of biology with the physics and chemistry of sea ice. This is probably due to the relative inaccessibility of the region, harsh winter conditions and land stations mainly designed for summer activities. In this report, we discuss the findings of two expeditions to the White Sea, one at the beginning of February and the second in the middle of April. These were undertaken to investigate the seasonal changes in sea-ice texture, nutrient status and biology in a fast-ice-covered inlet, taking an intermediate position with respect to climate and salinity between the subpolar Baltic Sea and the high Arctic.

Materials and methods

Sampling site

The sampling site is located at 66°20′N and 33°40′E near the Kartesh field station of the Zoological Institute, St. Petersburg in Chupa Inlet. Chupa Inlet is a 37-km-long fjord-like estuary, the largest in Kandalaksha Bay, which itself forms the westernmost of three larger bays in the White Sea (Fig. 1). Although freshwater inputs are mainly situated mid- and down-estuary, salinity increases towards the mouth of the estuary. Tides are asymmetrical, having a 5 h flood and 7 h ebb period; maximum current velocities are between 10 and 25 cm s^{-1} and the tidal prism is approximately $4–10\times10^7$ m^3 depending on the tidal cycle. Chupa Inlet has comparatively small freshwater inputs, about 0.3–1% of tidal prism throughout all seasons. Effects of river plumes are detectable at a maximum distance of 1 km from the river mouth. A small creek, fed from a nearby lake situated at the northern end of the transect, provided freshwater input, having a measurable influence up to station WS 10 and WSII 10, respectively. Water depth in the middle of the transect reaches a maximum of 60 m. For a more detailed description of regional settings, refer to Howland et al. (1999). The two sampling periods were from 1 to 7 February 2002 and from 11 to 20 April 2002.

In order to understand the precipitation and air-temperature conditions during the investigation period, we used data provided by the Climate Diagnostics Center (CDC) at Boulder, Colorado (USA). The data, which are accessible at http://www.cdc.noaa.gov, are based on the NCEP Reanalysis Project (Kalnay et al. 1996).

The mean surface precipitation rate was calculated as the monthly average for the area studied, both as a long-term mean (1961–1990) and specifically for the 2001/2002 ice season (November 2001 to April 2002). Anomalies in surface precipitation rate were compared to the long-term mean (1961–1990) for a particular month and area, and associated probability determined with parametric 1-tailed *t*-test. At the 5% significance level, 80% of the precipitation data and 100% of surface-air temperature data were found to be normally distributed (Anderson Darling test). In addition, surface temperature recordings from the closest Russian

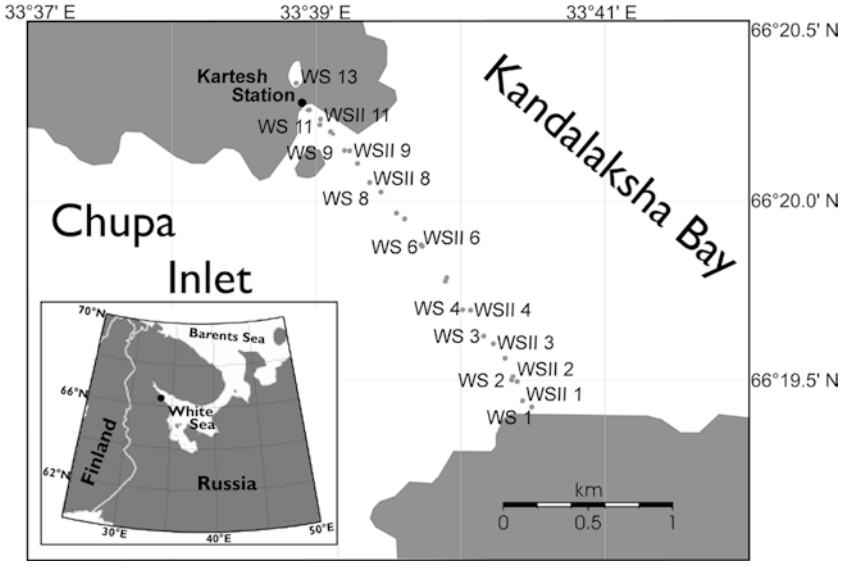

Fig. 1 Location of the study site with the two transects sampled in February and April 2002. For reasons of clarity not all station positions are labelled

weather station situated in Kandalaksha (67°10′N, 32°40′E; approx. 140 km northwest of the study site) were used.

Sampling and sample preparation

During both sampling periods, ice samples were obtained on a transect stretching across the inlet (approx. width of 2 km) at stations labelled 1–12, from south to north. On the February transect, three additional stations were sampled and labelled "b". A sample was also taken from the lake (WS 13). Although we attempted to sample at the same locations in February and April, there were slight differences in the locations from which the cores were taken. Ice cores were taken with a Kovacs ice auger at stations approx. 200 m apart. Parallel cores were taken at selected sampling locations, one for the chemical and biological parameters, and a second for the determination of the physical characteristics of the ice. Temperature profiles of the texture core were measured immediately the core was retrieved.

Temperature and salinity of the water column under the ice were measured once during each visit, using a CTD probe (SBE 19 Seacat Profiler, accuracy: conductivity ± 0.0001 S/m, temperature ± 0.01°C) close to station WS 6 and WSII 6, respectively.

The biology/chemistry cores were immediately cut into 10-cm sections and placed into clean plastic containers, returned to the laboratory and allowed to melt at $+2$°C in the dark. Prior to further treatment, the sample volume was measured and salinity recorded using a digital conductivity probe (WTW, Weilheim, Germany, precision of $\pm 0.2\%$). Aliquots of 100 ml were taken for species enumeration, and poisoned with hexamine-buffered formaldehyde to a final concentration of 2%.

The remaining sample was filtered through pre-combusted (500°C for 12 h) GF/F filters (Whatmann). Material retained on the filters was used for particulate organic carbon and nitrogen (POC, PON) analyses. On the second sampling in April, additional samples for the determination of chlorophyll *a* (Chl*a*) were filtered through GF/F filters.

The filtrates were subdivided: inorganic nutrients and dissolved organic nitrogen (DON) samples were poisoned with $HgCl_2$ and stored in acid-washed 50-ml PE bottles at $+5$°C (Kattner 1999). Dissolved organic carbon (DOC) sub-samples were poured into 20-ml precombusted (500°C, 12 h) glass ampoules, flame-sealed and frozen.

All filters and DOC samples were frozen at -15°C at the station and during transport to Bremerhaven (1–2 weeks) and then subsequently frozen at -80°C before analysis. The texture cores were treated similarly, but maintained at -25°C prior to analysis in Bremerhaven.

Sample analyses

Inorganic nutrients (nitrate, nitrite, ammonium, silicate and phosphate) and DON were analysed using a Technicon AII AutoAnalyser, following the protocols described in Kattner and Becker (1991). DOC was measured by high-temperature oxidation using an MQ1001 TOC Analyser (Qian and Mopper 1996).

Prior to the determination of POC and PON, filters were acidified with four drops of 0.1 N hydrochloric acid, and dried overnight at 60°C. They were then transferred to tin vials and analysed using a Carlo Erba Nitrogen Analyser 1500 CHN analyser calibrated with acetanilide standards. Filters for Chl*a* were homogenised in 10 ml 90% acetone. Extraction took place in the dark at $+4$°C for 24 h, and Chl*a* was measured using a Turner Designs TD-700 fluorometer after Evans et al. (1987).

Vertical thin sections on a selected number of texture cores were prepared in the ice laboratory at -25°C, and photographed under illumination between crossed polarisers, to identify crystal structure, following standard techniques (e.g. Lange 1988).

Stable oxygen isotope ratios ($^{18}O/^{16}O$) of melted core sections (2–3 cm thick, cut horizontally according to stratigraphic units) were measured on two texture cores, according to Mackensen (2001). All samples were run in duplicate and calibrated to Vienna Standard Mean Ocean Water (VSMOW) with an external reproducibility of $\pm 0.03‰$ at 1σ.

The Utermöhl method (Hasle 1978) was used for the analysis of micro-organisms in the ice cores. For each sample, micro-organisms in a 50-ml sub-sample were counted after being left to settle in sedimentation cylinders for >24 h. Enumeration of species followed the method described by Venrick (1978). Species identification of diatoms was verified using cleaned material under oil-immersion (R. Crawford, personal communication).

Cell counts were performed on samples from stations WS2, WS4, WS6, WS11 and the lake (WS13) of the first transect. The last was not sampled in April, so that micro-organisms were only analysed in samples from stations WSII 2, WSII 4, WSII 6 and WSII 11. However, not all ice depths were enumerated. Counts focused on diatom species, though other groups (ciliates, dinoflagellates and coccolithophorids) were counted, but not identified to genus or species level. Since counts from the February transect were performed on directly melted cores, fragile taxa (e.g. flagellates and ciliates) are likely to be underestimated in these cores, due to the damage caused by osmotic shock (Garrison and Buck 1986).

Inorganic nutrient and biological parameters (DOC, DON, POC, PON) for both transects were normalised to 1 dm^3 and analysed by correlation analysis (Pearson correlation coefficient). Cluster observation analysis (Euclidean distance, single linkage) using relative abundance was performed on micro-organism groups and then on diatom species for both transects, respectively. The lake station (WS 13) in the February transect was excluded from the statistical analyses.

Results

Sea-ice physics

Trends in the bulk salinity of cores were consistent within each transect, excluding the three northernmost stations. Cores from the February transect showed high values at the surface, decreasing downwards (Fig. 2a). This trend had reversed by April (Fig. 2b), and the overall bulk salinity range of 0–12 in February dropped to between 0 and 4 in April.

Photographs of vertical thin sections and corresponding $\delta^{18}O$ values are shown in Fig. 3. Samples from the February transect mostly contained ice of granular and columnar structure. The former was found in the upper portion varying in thickness between 5 cm (WS 6) and 13 cm (WS 2). The latter occupied the lower section, which had completely vanished in cores from the April transect, with the exception of the last 6 cm at WSII 8. Instead, a very porous texture of variable grain size was observed, with many distinct structural boundaries, probably related to different growth stages. Grain size in the lower 40 cm of the core most influenced by freshwater, WSII 11 was exceptionally large (>1 cm). The $\delta^{18}O$ value in the top 2.5 cm of core WS 6 was -4.72, corresponding to a granular structure, whereas values of -1.51 to -1.86 were found in the columnar part below 10 cm. The most negative (-8.72) $\delta^{18}O$ value was measured in the top 2.5 cm of core WSII 4. Below a depth of 4.5 cm, $\delta^{18}O$ values ranged between -3.71 and -4.15, falling in the same range as that on the surface of core WS 6.

In February, the snow thickness along the transect was 5–24 cm and a negative freeboard (0 to -4 cm) was

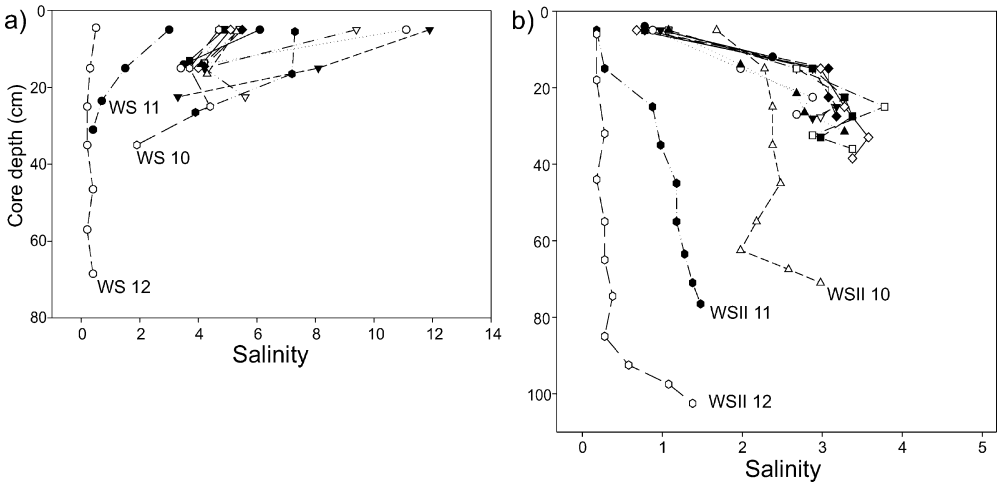

Fig. 2a, b Bulk salinity of **a** transect I (February), and **b** transect II (April). Data points correspond to middle of core section measured

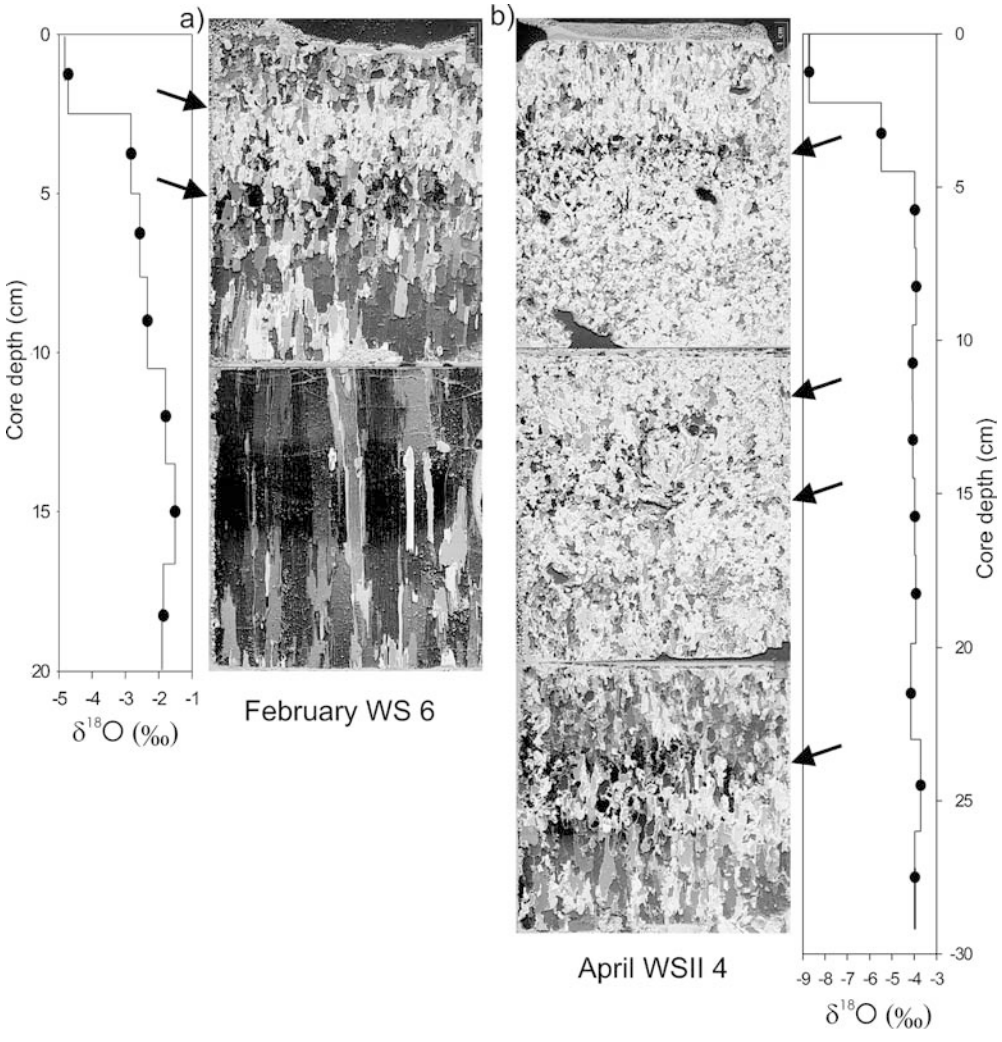

Fig. 3a, b Vertical thin sections, as well as corresponding $\delta^{18}O$ values of ice core **a** WS 6, and **b** WSII 4. *Arrows* denote structure boundaries

observed between stations WS 2b and WS 6. By the time of arrival in April (10.04.), all the snow on the ice surface had melted. Furthermore, the surface of the ice was marked by subsequent melting and freezing during day and night.

Weather and hydrography

Monthly data for precipitation rates (Table 1) and air temperature (Table 2) show the ice season 2001/2002 at Chupa Inlet to be anomalous in comparison to previous

Table 1 Summary of surface precipitation rate (mm day^{-1}) for 65.7–67.6°N, 31.9–33.8°E with long-term mean and standard error (SE) for 1961–1990, mean precipitation rate for November/December 2001 and January/April 2002, anomalous precipitation rate in comparison to long-term mean and its associated probability (according to 1-tailed *t*-test). Data provided by NOAA-CIRES/Climate Diagnostics Center

	Precipitation rate (mm day^{-1})			Probability
	Long-term mean (±SE)	Monthly mean	Anomaly	
November 2001	1.24 (±0.07)	0.81	−0.43	<0.001
December 2001	0.96 (±0.06)	0.25	−0.71	<0.001
January 2002	0.86 (±0.08)	1.30	+0.44	<0.001
February 2002	0.76 (±0.07)	1.12	+0.36	<0.001
March 2002	0.85 (±0.06)	0.69	−0.16	0.018
April 2002	1.09 (±0.07)	1.11	+0.02	0.791

Table 2 Summary of surface air temperature (°C) for 65–67.5°N, 32.5–35°E with long-term mean for 1961–1990, mean surface air temperature for September/December 2001 and January/April 2002, anomalous air temperature in comparison to long-term mean and its associated probability (according to 1-tailed *t*-test). Data provided by NOAA-CIRES/Climate Diagnostics Center

	Air temperature (°C)			Probability
	Long-term mean (±SE)	Monthly mean	Anomaly	
November 2001	−5.31 (±0.32)	−6.61	−1.30	<0.001
December 2001	−9.64 (±0.50)	−10.15	−0.51	0.318
January 2002	−13.15 (±0.62)	−10.54	+2.61	<0.001
February 2002	−12.16 (±0.68)	−8.92	+3.24	<0.001
March 2002	−7.45 (±0.51)	−6.68	+0.77	0.142
April 2002	−2.55 (±0.31)	−1.33	+1.22	<0.001

years. November and December were dry with a 35% to almost 75% reduction in precipitation, respectively. January and February, however, showed an abnormal 50% increase in precipitation. This trend was further confirmed by significantly colder (decrease by almost 25%) than normal air temperatures in November and a reversal to anomalously high temperatures in January and February. On average, very much warmer (up to 3.2°C) and wetter (up to 0.45 mm day^{-1}) conditions were observed early in 2002. Overall, the ice season 2001/2002, and especially the periods during which sampling was conducted, were extremely anomalous for Chupa Inlet.

Air-temperature recordings showed that, even in the middle of winter, the temperature occasionally rose to freezing point or even above, as experienced during the February stay (Fig. 4). The end of March was marked by a 14-day warm period.

CTD measurements in February directly beneath the ice yielded salinity and temperature values of 26.9 and −1.19°C, respectively. This is 0.27°C above the freezing point calculated for the given salinity. In April, an approximately 25-cm-thick, low salinity (17.16) and warm (−0.41°C) water layer was situated directly underneath the ice.

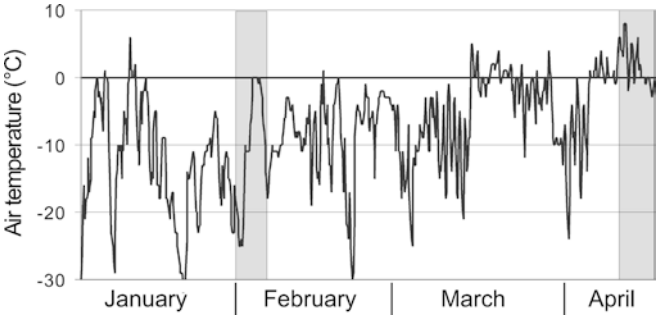

Fig. 4 Air temperature at Kandalaksha between 1 February and 16 April covering the time between the two expeditions and 1 month before. *Shaded* areas correspond to sampling periods

Nutrients, particulate and dissolved organic matter

Nutrient distributions are shown in Fig. 5 and mean values and range of nutrient concentrations with corresponding ratios in Table 3. Nitrate concentrations in sea ice of transect I, in February, were around 1 μM in the lower part and slightly higher in the upper 10 cm. There were two exceptions, one in the surface section of stations WS1b–WS2b, and the other in the upper part of station WS12, where increased nitrate concentrations up to 6.95 μM were measured. Nitrite concentrations were constantly below 0.8 μM. Ammonium reached maximum values of 5.31 μM in the upper part of the ice and the middle of the transect (WS 5–WS 7), whereas only slightly elevated values were recorded at station WS 2b and towards the northern end of the transect. Silicate concentration showed a similar distribution to nitrate (0.687; $P = 0.003$) with values of 2–4 μM in the surface and highest values at station WS 12. Phosphate varied between 0.44 and 0.74 μM and showed a slight relationship with ammonium.

The distribution of particulate and dissolved organic matter is presented in Fig. 6 and summarised in Table 3. DON and PON essentially showed the same distribution as ammonium, resulting in a significant correlation ($P \leq 0.024$) between these nitrogen compounds. A strong coupling between DOC/DON (0.74; $P = 0.001$) and DOC/ammonium (0.751; $P = 0.001$) was also measured in the February profiles. POC ranged between 14.4 and 130 μM, and the distribution pattern was similar to PON, which had concentrations about 10 times lower than POC. POC correlated significantly with DON and ammonium (0.917; $P = 0.001$ and 0.539; $P = 0.031$, respectively). Furthermore, silicate strongly correlated with DOC (0.847; $P < 0.001$).

In April, nitrate values in the lower part of the ice had decreased to <0.4 μM, whereas elevated values of up to 6.2 μM in the upper core sections were found along the entire transect. A similar pattern was also found in the ammonium distribution. However, apart from DON and nitrate (0.628; $P = 0.038$), no other significant correlation between nitrogen compounds was found in the April transect. Silicate values in the upper 20 cm of ice

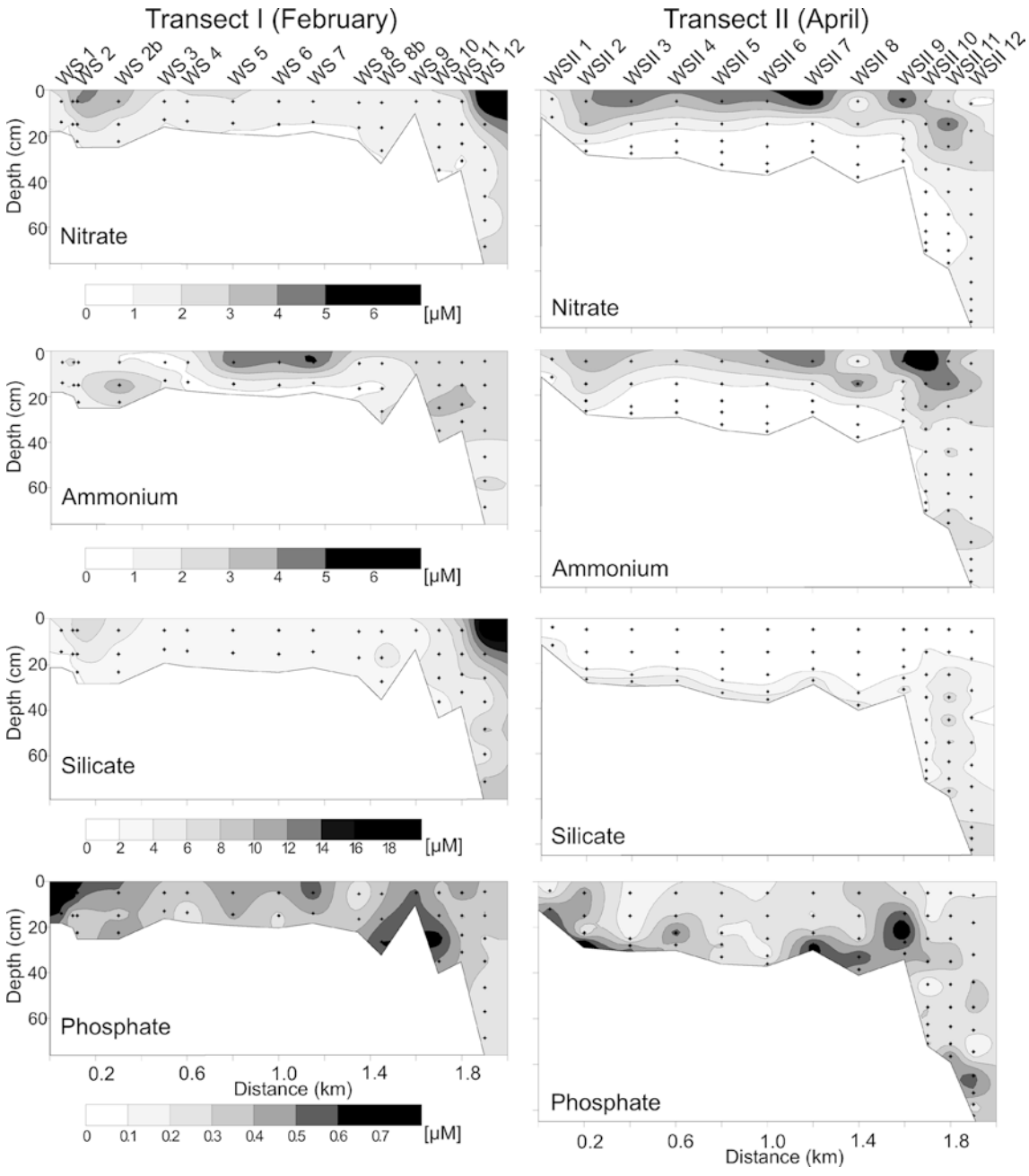

Fig. 5 Distribution of nitrate, ammonium, silicate and phosphate measured in the ice along transects in February and April. All concentrations are in µM

were depleted to less than 2 µM. However, a strong increase to more than 4 µM was measured in the bottom ice layer. Phosphate distribution was as variable as in February, and concentrations generally varied around 0.44 µM (Fig. 5). Values of phosphate in the underlying seawater decreased slightly between February and April (1.1–0.6 µM), which was higher than in the ice. This was similar to nitrate, which decreased from 7.6 to 4.7 µM. Silicate concentrations in the underlying water were considerable higher than in the ice during both periods, reaching values of up to 26 µM.

POC, PON and DOC essentially showed a similar distribution pattern as silicate; low concentrations in the upper part of the ice and high ones in the bottom section (Fig. 6). A most pronounced feature was a tenfold increase of POC and PON to a mean value of 620 µM C and 29.7 µM N, respectively, in bottom ice, between February and April (Table 3). The difference to the underlying water column, where PON values were < 1.7 µM, was even more prominent. Another most striking feature was the reduction of DON (mean of 16.57 to 7.42 µM) over the whole profile between February and April, and the corresponding increase in the DOC/DON ratio (Table 3), especially in the bottom section. Again, a significant correlation was found for DOC and DON (0.634; $P = 0.036$) and a new corre-

Table 3 Mean values and range of salinity, nutrient and biological parameters, measured in transect I (February) ($n = 27$–30) and transect II (April), excluding the two most freshwater-influenced stations. Due to the great differences in chemical and biological parameters between top and lower sections of the ice in the April transect, a distinction into upper part ($n = 34$–37) and bottom section ($n = 10$) was made

	Transect I (February)		Transect II (April) upper		Transect II (April) bottom		Water	
	Mean	Range	Mean	Range	Mean	Range	February Mean (*n*)	April Mean (*n*)
Salinity	5.3	1.9–11.9	2.1	0.5–3.6	2.8	2.2–3.8	27.2 (3)	26.7 (2)
DOC (μM)	155	58.1–322	85	38.2–144	201	146–329	369 (3)	352 (2)
DON (μM)	16.6	4.2–50.6	7.4	2.9–17.2	8.1	5.2–14.9	7.7 (3)	7.1 (3)
DOC/DON	11	5.9–27.4	12.8	4.6–26.6	25.9	17.6–37	48.2 (3)	66.5 (2)
POC (μM)	45.9	14.4–130	69	21.5–251	620	245–1373	43.7 (3)	14.7 (3)
PON (μM)	3.3	1.4–10.3	3	1.1–9.8	29.7	9.8–71	1.2 (3)	1.7 (3)
POC/PON	13.8	10.5–19.5	21.9	11.3–58.7	21.3	14.6–28	34.0 (3)	8.3 (3)
Chl*a* (μg/l)			1.3	0.2–5.3	16.1	2.9–35.4	0.05 (2)	1.54 (3)
Nitrate (μM)	1.65	0.86–4.24	1.88	0.13–6.2	0.39	0.01–1.09	7.6 (3)	4.7 (3)
Ammonium (μM)	2.03	0.59–5.31	2	0.14–6.91	0.56	0.08–0.96	0.7 (3)	0.7 (3)
Silicate (μM)	3.41	1.79–7.03	1.16	0.07–2.94	4.68	2.82–5.83	15.0 (3)	19.0 (3)
Phosphate (μM)	0.44	0.22–0.74	0.29	0.09–0.73	0.44	0.15–0.77	1.1 (3)	0.6 (3)
N:P	8.7	4.8–15.3	16.5	0.7–49.9	2.8	0.5–9.6	7.5 (3)	10.4 (3)

spondence established between DOC and silicate (0.82; $P = 0.002$). Although there was good agreement in the open inlet cores, no significant correspondence could be found over the whole transect, between either DOC, or DON or POC as a biomass parameter. This was due to the high amount of DOC in the freshwater-influenced cores, reaching values of up to 262 μM. In the under-ice water, values even exceeded 1,000 μM.

Finally, it can be said that, during the course of the season, the close relationship between parameters disappeared, especially the correlation between the different nitrogen compounds. In April, the distribution of POC, PON and DOC resembled a spring-bloom pattern known from other investigations.

Chlorophyll

Chlorophyll *a* concentrations within the April cores showed a typically increasing trend from top to bottom (Fig. 6). In the upper part of the core, values ranged from 0 to 5 μg l^{-1}, whereas values of 10–35 μg l^{-1} Chl*a* were found in the lowest core section at stations WSII 1–8. This may be a reflection of the coarse sampling. Finer sectioning would have yielded even higher values confined to the lowest centimetre. A high biomass was already noticeable with the naked eye, as small green dots on the ice underside. Only at stations WSII 10–12 and near the freshwater input, did values not exceed 10 μg l^{-1} Chl*a*, even at the bottom of the ice. Water samples taken directly underneath the ice in the open inlet had values of 0.46 μg l^{-1}, an order of magnitude higher than in February when values did not exceed 0.1 μg l^{-1}. The distribution of Chl*a* along transect II in April corresponds significantly with POC and PON (0.857; $P = 0.001$, 0.905; $P < 0.001$).

Species distribution

Counts of micro-organisms revealed diatoms and coccolithophorids to be the most abundant groups in the February transect I (Table 4). Diatom abundance changed comparatively little over different ice cores and depths, while coccolithophorid numbers were more varied (Fig. 7). Multivariate cluster analysis of all four micro-organism groups shows all samples to be similar at almost 70%, with the exception of WS 6 (10–20 cm) (similar to all others at 53% only). This can be attributed to high relative abundance of coccolithophorids. For this reason, WS 2 (0–10 cm) can also be distinguished from the remaining samples. The proportion of ciliates increased towards the ends of the transect, i.e. stations WS 2 and WS11. With more than 60%, they were also the dominant group in the lake core, WS 13.

Particular emphasis was placed on diatoms and the following taxa were identified (roughly according to their relative abundance): *Nitzschia* spp., Cymatosiraceae, *Navicula* spp., *Navicula vanhoeffenii*, *Pinnularia* sp., *Chaetoceros* spp., *Entomoneis* sp., *Cylindrotheca closterium*, *Diploneis* sp., *Attheya* sp., *Mastogloia* sp., *Thalassiothrix* cf., *Coscinodiscus* sp. and *Aulacoseira* cf.

Within the diatoms, no particular differences in the species composition were visible along the transect in February (Fig. 7), except for station WS11, which was only similar at the 49% level. *N. vanhoeffenii* was the most abundant species (50–60%) at WS11, as well as in the bottom section of the lake core, WS13. This species was found at all stations, albeit in lower numbers. *Nitzschia* spp. dominated stations in the open inlet (30–40%), followed by *Navicula* spp. and Cymatosiraceae. With the exception of WS 2 (10–20 cm) (similar only at 66%), cluster analysis shows a grouping of the different samples of stations 2, 4 and 6 (all similar at over 80%) along a gradient. This can be attributed to the absence of most diatom species with the exception of *Nitzschia* spp., Cymatosiraceae, *Navicula* spp. and *Thalassiothrix* cf. (high relative abundance) in sample WS 2 (0–10 cm). Total cell numbers of single ice cores on the February transect were in the range of 0–1.6×10^4 cells l^{-1}, except for the bottom section of WS 6 where they reached 3.0×10^4 cells l^{-1}.

By April, cell numbers within the upper core sections of the open-inlet stations (WSII 2–WSII 8) had

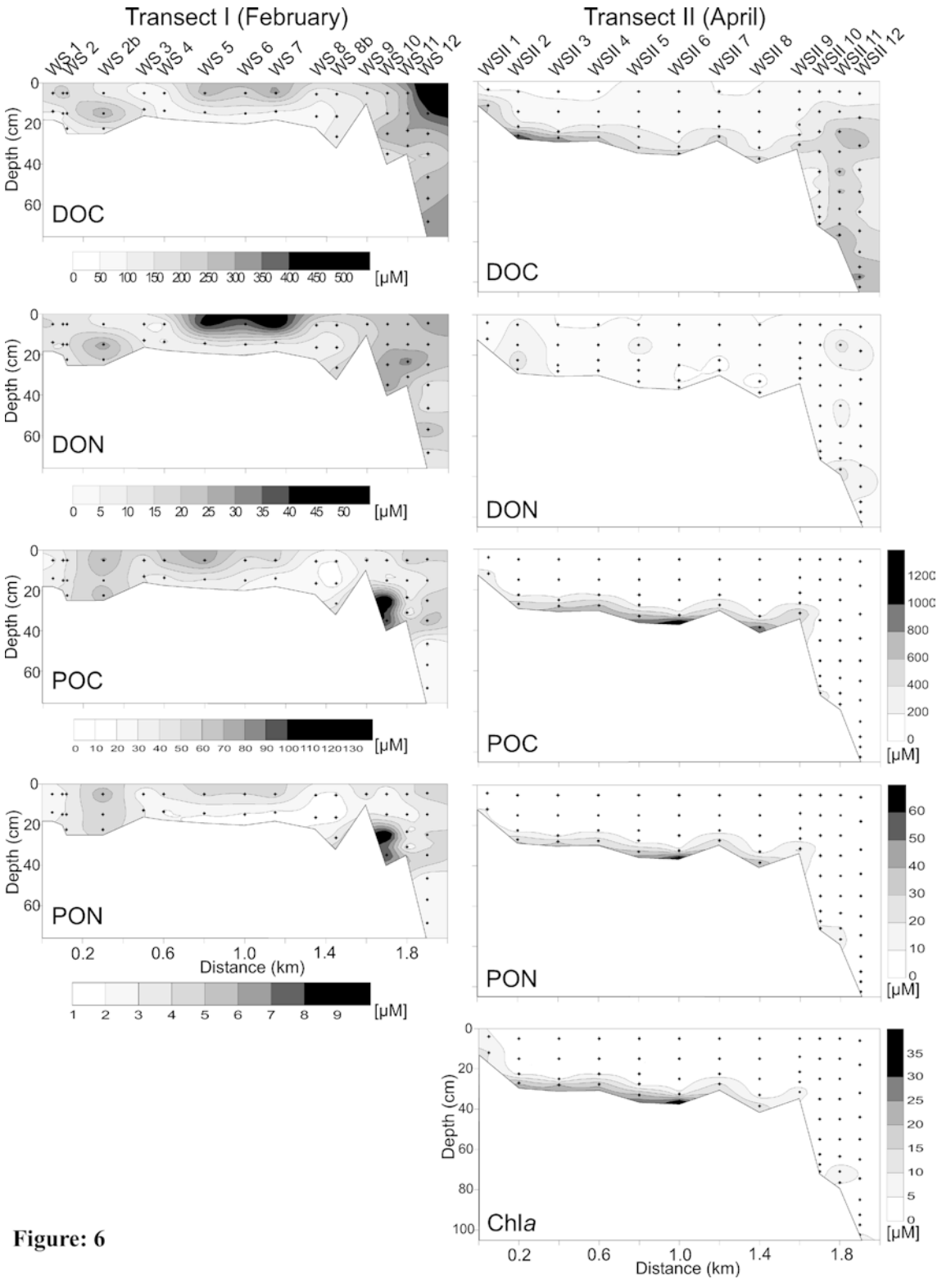

Figure: 6

Fig. 6 Distribution of DOC, DON, POC, PON and Chl*a* measured in the ice along transects in February and April. Concentrations given are in µM except for Chl*a*, which is in µg l^{-1}

increased a hundredfold, reaching 2×10^6 cells l^{-1}. A further tenfold rise was observed within the bottom ice section. WSII 11 differed completely from this observed trend. Only a maximum concentration of 3.9×10^5 cells l^{-1} was found in the 54- to 64-cm section, showing no increasing tendency towards the bottom. Values in the water directly underneath the ice were 0.4 to 1×10^6 cells l^{-1} from WSII 2 to WSII 6 and 0.03×10^6 cells l^{-1} at station WSII 11.

Table 4 Summary of micro-organisms along transect I (February) and transect II (April), respectively, as cell numbers l^{-1} (± standard error) and their relative abundance (%)

	Transect I (February)		Transect II (April)	
	Cells l^{-1} (± SE)	Relative abundance (%)	Cells l^{-1} (± SE)	Relative abundance (%)
Diatoms	$8.7*10^3$ ($\pm 2.7*10^3$)	39.3	$2.9*10^6$ ($\pm 1.1*10^6$)	98.4
Coccolithophorids	$10.1*10^3$ ($\pm 8.6*10^3$)	45.9	$1.3*10^4$ ($\pm 0.8*10^4$)	0.5
Ciliates	$1.9*10^3$ ($\pm 0.3*10^3$)	8.5	$2.3*10^4$ ($\pm 0.7*10^4$)	0.8
Dinoflagellates	$1.4*10^3$ ($\pm 0.7*10^3$)	6.3	$0.9*10^4$ ($\pm 0.2*10^4$)	0.3

Compared to the transect in February, diatoms at single stations clearly dominated the microbial assemblages, reaching up to 98% of the cells counted (Table 4). *Nitzschia* spp. were the dominant group (55–80%, Fig. 8). The Cymatosiraceae were the second most abundant group, *Navicula* spp. barely attaining 10%. However, all samples at stations WSII 2, WSII 4, WSII 6 and WSII 11 appeared fairly similar (at over 75% similarity) at all ice depths, with regard to the relative abundance of diatom species. The only exception was station WSII 11 below ice (Fig. 8), caused by *Chaetoceros* spp. dominating this water-column sample by more than 80%. The species distribution in waters underlying the ice was almost identical at stations WSII 2 and WSII 4, similar to the overlying ice. At WSII 6, Cymatosiraceae dominated instead of *Nitzschia* spp. Although absent in core WSII 6, *N. vanhoeffenii* was found in all other cores, and at WSII 2 and WSII 4, mostly in the upper parts of the cores.

Generally, it seems that *Nitzschia* spp. increased in relative abundance from the February transect to that in April (on average from 20 to 40% in February to between 40 and 60% in April). No other general trends in species composition both in space (either over length of transect or with depth in ice core) or time were apparent.

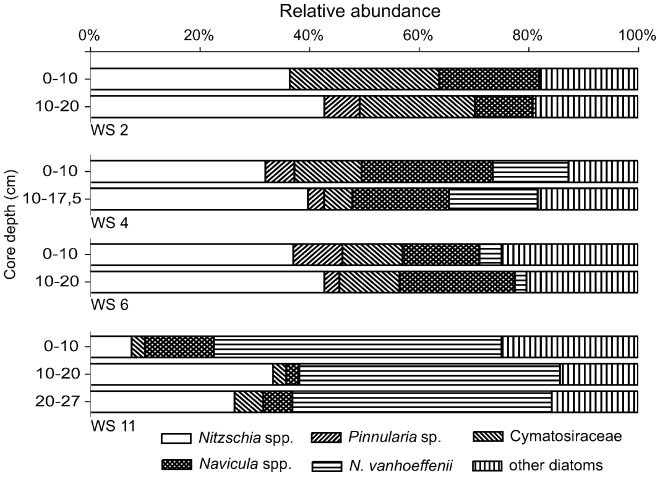

Fig. 7 Distribution of most common diatom species at different stations over ice-core depth as relative abundance (%) for transect I (February)

Discussion

The ice-structure components (Fig. 3) suggest that a downward growth of columnar ice occurred only at the beginning of the ice-growth season, brought about by low air temperatures, i.e. a strong temperature gradient in the ice, rather than low water temperatures. Later in the season, an upward growth took place caused by the formation of snow ice (a negative freeboard was measured in February). The strong decline in bulk salinity (Fig. 2) in the surface sections of the April cores suggests that, during the course of the season, snow-ice formation shifted to superimposed ice formation (Haas et al. 2001). This is further supported by more negative $\delta^{18}O$ values (−8.72 and −5.48) in the uppermost 4.5 cm compared to the rest of core WSII 4. These observations are substantiated by the weather data (Fig. 4), since melting and refreezing of snow are essential for the formation of superimposed ice. The results correspond to observations made in the northern Baltic Sea by Kawamura et al. (2001), although they found more negative $\delta^{18}O$ values in the columnar part than we did. This can be attributed to differences in the $\delta^{18}O$ signature of the originating water body. The $\delta^{18}O$ signature of the White Sea can be assumed to be less negative, due to a lowered freshwater input compared to the Baltic Sea. Furthermore, Kawamura et al. (2001) did not find such strong melting of the columnar portion, which can be attributed to a lower freezing point, since salinity in the White Sea is considerably higher than that of the Baltic Sea (2–4), or a higher heat flux from underlying water, as proposed by Lytle and Ackley (2001). These authors also found a complete melt-down of the columnar ice portion. A further time-series investigation on sea-ice texture would be important to validate the assumptions about ice development made here, especially since climate data (Tables 1, 2) indicate that unusual environmental conditions prevailed during this winter. The observed dramatic changes in the structural growth and development of sea ice between February and April preclude a direct comparison of temporal changes in other parameters related to the physical development of the sea ice.

The distribution of nitrate and ammonium along the April transect, with elevated values in the uppermost 20 cm and almost completely depleted in the bottom section, is comparable to results obtained by Kaartokallio (2001). According to Rahm et al. (1995),

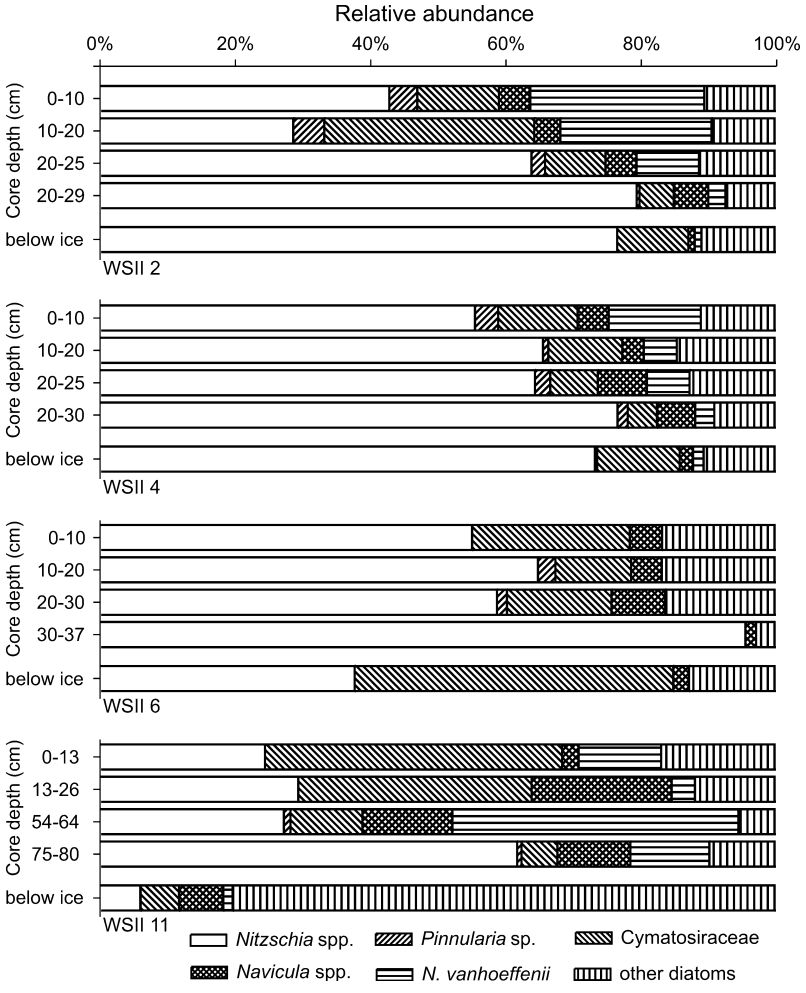

Fig. 8 Distribution of most common diatom species at different stations over ice-core depth and below the ice as relative abundance (%) for transect II (April)

nitrogenous compounds may accumulate due to atmospheric input in the upper ice layer. This input is probably also responsible for the elevated values in our study and is further supported by low salinity and $\delta^{18}O$ values, proving the atmospheric influence on the upper part of the ice.

N:P ratios found both in February and April, in water and ice were mostly far below the Redfield ratio, which is indicative of phosphate-replete conditions in the ice and water. Phosphate values in the water are 2–5 times higher compared to the Baltic Sea (Kaartokallio 2001; Meiners et al. 2002), whereas ammonium and nitrate were in the same range. Silicate and DOC values in the ice increased towards the bottom, but were still lower compared to water values. This points to passive release during ice formation. Later in the season, during April, incorporation/exchange of silicate and DOC with the underlying water column seems to be the functional mechanism, rather than the release from a fast-growing ice community as proposed by Lara and Thomas (1995). Enrichment of nitrate and phosphate in the bottom ice layer due to exchange with the underlying water is limited, owing to the generally low concentrations in Russian rivers entering the Arctic Ocean (Lobbes et al. 2000).

Dissolved organic matter (DOM) found in the water column in February and April was essentially of terrestrial origin and not attributed to in-situ release by algae and bacteria, as generally reported for Russian Arctic rivers (Dittmar and Kattner 2003). A high input of DOC via the nearby creek is apparent, since surface-water values of the lake and the two most freshwater-influenced stations were elevated (765–1,002 μM) compared to water values further out and at greater depth (321–395 μM). The high DOC values found here were similar to those from closely neighbouring rivers (Mezen, Vizhas) and were at the upper end of the range measured for the large Russian rivers (Lobbes et al. 2000). In contrast to DOC, DON values in water and ice were similar or even higher in the ice.

The lower DOC/DON ratios of the ice compared to the underlying water column contrast with findings from other sea-ice studies (Thomas et al. 1995, 2001), although ratios are highly variable (Thomas and Dieckmann 2002). However, this is the first study of DOC and DON in a land fast-ice ecosystem, which limits the comparison to pure sea-ice systems. The DOC/DON ratios of the underlying water are very similar to the small adjacent rivers (Lobbes et al. 2000). The lower ratios of the ice may be caused by the variable release of

DOC and DON during ice formation and development, different degree of recalcitrant character or different biotic release and utilisation. Thomas et al. (1995) attributed high DOC/DON ratios in sea ice to an uncoupling of carbon and nitrogen metabolism such that the nitrogen pool is hydrolysed much faster than the carbon pool. Since the DOM pool found in this study is initially of terrestrial origin and therefore highly recalcitrant (Dittmar and Kattner 2003), release during ice formation is more likely, which is reflected by the low DOC values in the upper part of the ice from April. The bottom layer of this ice is characterised by high concentrations of POC due to accumulation of algae, which has a considerable influence on the biogeochemistry of the ice layer. A further characterisation of the DOC pool in the water and ice would be helpful to distinguish between origins and allow statements on the degradability. However, in February, the high correlation of POC with ammonium, as well as between DON and ammonium, indicates heterotrophic activity based on DOC and DON pools as observed by Kaartokallio (2001). Although these processes are probably temperature-limited at this time of the year (Pomeroy and Wiebe 2001), heterotrophic activity clearly dominates over autotrophic activity.

The high biomass (POC, Chl*a*, cell counts) (Fig. 6, Table 4) in the bottom section measured in April, indicates the formation of a spring bloom in the ice. Values assessed in the open inlet were within the range of results obtained in the Arctic (Gradinger et al. 1999; Mock and Gradinger 1999) and two- to sevenfold higher than those from the Baltic Sea (Haecky et al. 1998; Meiners et al. 2002). However, values at the freshwater-influenced stations were comparable to those in the Baltic Sea, clearly showing the imprint of salinity on biomass development, which agrees with the positive correlation between salinity and biomass found by Legendre et al. (1996). Although ice-diatom species from the Arctic are euryhaline and can grow over a wide range of salinities (Grant and Horner 1976), they obviously prefer higher salinities. Whereas a clear imprint of salinity on biomass abundance can be detected, the influence of salinity on species composition of the algal community was less pronounced. Tidal mixing might, to a large extent, be responsible for the relatively uniform community structure in the uppermost water layer, as can be seen from underwater samples of stations WSII 2 and WSII 4. Only in direct proximity to the freshwater input were differences in species composition detectable. No marked differences between ice and water are indicative of a passive incorporation into the ice.

The autotrophic community in April can be assumed to be very productive under given light conditions. Maximum incident irradiances of 1,200 μmol photons m^{-2} s^{-1} and sub-ice irradiances of 85 μmol photons m^{-2} s^{-1} were measured on clear days (M. Steffens, personal communication). However, depleted nitrogen resources in the bottom section (Fig. 4) might limit further algal development, as found in the coastal sea ice of the Canadian Arctic (Cota et al. 1987). Although the existence of strong tidal currents favours a constant supply of nutrients in the bottom section, the nitrogen demand of the fast-growing community may exceed supply. This is supported by an exceptionally low N:P ratio of 2.8, since all available pools (NH_4, NO_3, DON, Figs. 5, 6) were depleted in the bottom ice layer. This contrasts with findings from the Baltic Sea, where autotrophic production during spring-bloom events was generally phosphate-limited (Haecky and Andersson 1999; Meiners et al. 2002). However, similar limiting nitrogen resources were found in coastal sea ice of the Canadian Arctic (Cota et al. 1987). As melting proceeds, nitrate and ammonium from the upper part of the ice sheet will be released and, hence, might foster phytoplankton growth in the water column.

The diatom community composition in the White Sea ice differed from the community found in the adjacent Barents Sea. *Fragilariopsis* spp., a dominant group in the southeastern Barents Sea (Pautova and Vinogradov 2001), and also *Thalassiosira* spp. were absent in samples from the White Sea, both in the water column and the ice. However, those authors found *Nitzschia* spp. to be less dominant in the Barents Sea. The assemblage found here resembles the one described by Syvertsen (1991) from 60 cm first-year ice in the Barents Sea ice-edge, with *Nitzschia* species (especially *Nitzschia frigida*) dominant and *Navicula vanhoeffenii* sub-dominant. Therefore, different diatom communities exist in the White and Barents Seas, probably mainly caused by differences in salinity. Although coccolithophorids have been reported in sea ice, such high numbers as found in February have not been recorded either Arctic or Antarctic regions (Lizotte 2003).

Conclusions

Our observations on sea-ice development have, as yet, not been made for other fast-ice systems. However, due to the abnormal weather conditions, which prevailed during this winter, further investigations are needed to clarify if this was an anomaly or the natural course of events in the White Sea.

The Arctic coastal areas are special ecosystems because of low inorganic nitrogenous nutrients but high concentrations of silicate. The high amount of recalcitrant terrestrial DOM in the rivers may have a considerable impact on biological processes within the ice. The behaviour of DOC and DON during sea-ice formation and their changes due to biotic and abiotic processes are widely unknown and need further investigations. The observed atmospheric nitrogen input via snow agrees with observations reported from the Baltic Sea. Chl*a* concentrations found in the freshwater-influenced cores of land fast ice in the White Sea were in the range of those reported for sea ice from the Baltic Sea, whereas open-inlet cores had concentrations that resembled those from other Arctic regions, showing the

positive correlation of salinity and biomass. Furthermore, species composition in the White Sea was found to be different from the adjacent Barents Sea, and of particular interest is the first report of the occurrence of coccolithophorids in sea ice.

Finally, it can concluded that the sea-ice ecosystem plays a substantial role in organic-matter transfer and carbon flux in the White Sea, predominantly in regions with low freshwater impact.

Acknowledgements The authors are grateful to the staff of Kartesh Biological Station for their co-operation and assistance throughout the two field trips. Andreas Mackensen is thanked for his assistance in the oxygen isotope analyses. We thank Erika Allhusen and Marthi Wolff for excellent technical support and Zuzana Krell-Laluhová, Matthias Steffens and Oleg Fajans for their help during the fieldwork. This work was supported by EU funding through the Copernicus Programme, research project WOMP (ICA2-CT-2000-1003). D.N.T. is also grateful for the support of the Hanse Institute of Advanced Study and the Royal Society (Joint Project).

References

Arrigo KR (2003) Primary production in sea ice. In: Thomas DN, Dieckmann GS (eds) Sea ice—an introduction to its physics, chemistry, biology and geology. Blackwell, Oxford, pp 143–183

Berger V, Dahle S, Galaktionov K, Kosobokova X, Naumov A, Rat'kova T, Savinov VM, Savinova TN (eds) (2001) White Sea ecology and environment. Derzavets, St. Petersburg

Cota GF, Prinsenberg SJ, Bennett EB, Loder JW, Lewis MR, Anning JL, Watson NHF, Harris LR (1987) Nutrient fluxes during extended blooms of Arctic ice algae. J Geophys Res C 92:1951–1962

Cox GFN, Weeks WF (1983) Equations for determining the gas and brine volumes in sea-ice samples. J Glaciol 29:306–316

Dittmar T, Kattner G (2003) The biogeochemistry of the river and shelf ecosystem of the Arctic Ocean: a review. Mar Chem (in press)

Evans CA, O'Reilly JE, Thomas JP (1987) A handbook for the measurement of chlorophyll a and primary production. Biological investigations of marine Antarctic systems and stocks (BIOMASS). Texas A&M University, College Station, Texas

Garrison DL, Buck KR (1986) Organism losses during ice melting: a serious bias in sea ice community studies. Polar Biol 6: 237–239

Gradinger R, Friedrich C, Spindler M (1999) Abundance, biomass and composition of the sea ice biota of the Greenland Sea pack ice. Deep Sea Res II 46:1457–1472

Grant WS, Horner RA (1976) Growth responses to salinity variation in four Arctic ice diatoms. J Phycol 12:180–185

Haas C, Thomas DN, Bareiss J (2001) Surface properties and processes of perennial Antarctic sea ice in summer. J Glaciol 47:613–625

Haecky P, Andersson A (1999) Primary and bacterial production in sea ice in the northern Baltic Sea. Aquat Microb Ecol 20: 107–118

Haecky P, Jonsson S, Andersson A (1998) Influence of sea ice on the composition of the spring phytoplankton bloom in the northern Baltic Sea. Polar Biol 20:1–8

Hasle GR (1978) The inverted-microscope method. In: Sournia A (ed) Phytoplankton manual. UNESCO Monogr Oceanogr Methodol 6:88–96

Howland RJM, Pantiulin AN, Millward GE, Prego R (1999) The hydrography of the Chupa Estuary, White Sea, Russia. Estuarine Coast Shelf Sci 48:1–12

Kaartokallio H (2001) Evidence for active microbial nitrogen transformations in sea ice (Gulf of Bothnia, Baltic Sea) in midwinter. Polar Biol 24:21–28

Kalnay E, Kanamitsu M, Kistler R, Collins W, Deaven D, Gandin L, Iredell M, Saha S, White G, Woollen J, Zhu Y, Chelliah M, Ebisuzaki W, Higgins W, Janowiak J, Mo KC, Ropelewski C, Wang J, Leetmaa A, Reynolds R, Jenne R, Joseph D (1996) The NCEP/NCAR 40-year reanalysis project. Bull Am Meteorol Soc 77:437–471

Kattner G (1999) Storage of dissolved inorganic nutrients in seawater: poisoning with mercuric chloride. Mar Chem 67:61–66

Kattner G, Becker H (1991) Nutrients and organic nitrogenous compounds in the marginal ice zone of the Fram Strait. J Mar Syst 2:385–394

Kawamura T, Shirasawa K, Ishikawa N, Lindfors A, Rasmus K, Granskog MA, Ehn J, Leppäranta M, Martma T, Vaikmäe R (2001) Time-series observations of the structure and properties of brackish ice in the Gulf of Finland. Ann Glaciol 33:1–4

Lange MA (1988) Basic properties of Antarctic sea ice as revealed by textural analysis of ice cores. Ann Glaciol 10:95–101

Lara R, Thomas D (1995) Formation of recalcitrant organic matter: humification dynamics of algal derived dissolved organic carbon and its hydrophobic fractions. Mar Chem 51:193–199

Legendre L, Robineau B, Gosselin M, Michel C, Ingram RG, Fortier L, Therriault JC, Demers S, Monti D (1996) Impact of freshwater on a subarctic coastal ecosystem under seasonal sea ice (southeastern Hudson Bay, Canada). II. Production and export of microalgae. J Mar Syst 7:233–250

Leppäranta M, Tikkanen M, Shemeikka P (1998) Observations of ice and its sediments on the Baltic Sea coast. Nord Hydrol 29:199–220

Lizotte MP (2003) The microbiology of sea ice. In: Thomas DN, Dieckmann GS (eds) Sea ice—an introduction to its physics, chemistry, biology and geology. Blackwell, Oxford, pp 184–210

Lobbes JM, Fitznar HP, Kattner G (2000) Biogeochemical characteristics of dissolved and particulate organic matter in Russian rivers entering the Arctic Ocean. Geochim Cosmochim Acta 64:2973–2983

Lytle VI, Ackley SF (2001) Snow-ice growth: a fresh-water flux inhibiting deep convection in the Weddell Sea, Antarctica. Ann Glaciol 33:45–50

Mackensen A (2001) Oxygen and carbon stable isotope tracers of Weddell Sea water masses: new data and some paleoceanographic implications. Deep Sea Res I 48:1401–1422

Meiners K, Fehling J, Granskog MA, Spindler M (2002) Abundance, biomass and composition of biota in Baltic sea ice and underlying water (March 2000). Polar Biol 25:761–770

Mock T, Gradinger R (1999) Determination of Arctic ice algal production with a new in situ incubation technique. Mar Ecol Prog Ser 177:15–26

Mordasova NV (1999) Chlorophyll in the White Sea. ICES J Mar Sci 56:215–218

Pautova L, Vinogradov G (2001) Southeastern Barents Sea plankton in April 2000. Russian Academy of Sciences. Oceanology 41:211–217

Pomeroy LR, Wiebe WJ (2001) Temperature and substrates as interactive limiting factors for marine heterotrophic bacteria. Aquat Microb Ecol 23:187–204

Qian J, Mopper K (1996) Automated high-performance, high-temperature combustion total carbon analyzer. Anal Chem 68:3090–3097

Rahm L, Hakansson B, Larsson P, Fogelqvist E, Bremle G, Valderama J (1995) Nutrient and persistent pollutant deposition on the Bothnia Bay ice and snow fields. Water Air Soil Pollut 84:187–201

Shanin SS, Mikhajlovskij GE (1996) Species diversity and seasonal succession of phytoplankton in the White Sea. Oceanology 36:407–412

Syvertsen EE (1991) Ice algae in the Barents Sea: types of assemblages, origin, fate and role in the ice-edge phytoplankton bloom. Polar Res 10:277–288

Thomas DN, Dieckmann GS (2002) Biogeochemistry of antarctic sea ice. Oceanogr Mar Biol Annu Rev 40:143–169

Thomas DN, Lara R, Eicken H, Kattner G, Skoog A (1995) Dissolved organic matter in Arctic multi-year ice during winter: major components and relationships to ice characteristics. Polar Biol 15:477–483

Thomas DN, Kattner G, Engbrodt R, Giannelli V, Kennedy H, Haas C, Dieckmann GS (2001) Dissolved organic matter in Antarctic sea ice. Ann Glaciol 33:297–303

Venrick EL (1978) How many cells to count? In: Sournia A (ed) Phytoplankton manual. UNESCO Monogr Oceanogr Methodol 6:167–196

Weissenberger J, Dieckmann G, Gradinger R, Spindler M (1992) Sea ice: a cast technique to examine and analyze brine pockets and channel structure. Limnol Oceanogr 37:179–183

Weslawski JM, Wiktor J, Koszteyn J, Zajaczkowski M, Wieczorek P, Kotwicki L (1997) The coastal edge of the Northeast Water polynya in spring 1993. J Mar Syst 10:429–444

Wiktor J (1999) Early spring microplankton development under fast ice covered fjords of Svalbard, Arctic. Oceanologia 41:51–72

Zhitina LS, Mikhajlovskij GE (1990) Ice and plankton flora of the White Sea as the subject of monitoring. Biological monitoring of the White Sea coastal waters. IOAN, Moscow (in Russian)