Sea ice algae in the White and Barents seas: composition and origin

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To examine algae populations, three expeditions (in March 2001, April 2002 and February 2003) were conducted in the Guba Chupa (Chupa Estuary; north-western White Sea), and one cruise was carried out in the open part of the White Sea in April 2003 and in the northern part of the Barents Sea in July 2001. Sea ice algae and phytoplankton composition and abundance and the content of sediment traps under the land-fast ice in the White Sea and annual and multi-year pack ice in the Barents Sea were investigated. The community in land-fast sea ice was dominated by pennate diatoms and its composition was more closely related to that of the underlying sediments than was the community of the pack ice, which was dominated by flagellates, dinoflagellates and centric diatoms. Algae were far more abundant in land-fast ice: motile benthic and ice-benthic species found favourable conditions in the ice. The pack ice community was more closely related to that of the surrounding water. It originated from plankton incorporation during sea ice formation and during seawater flood events. An additional source for ice colonization may be multi-year ice. Algae may be released from the ice during brine drainage or sea ice melting. Many sea ice algae developed spores before the ice melt. These algae were observed in the above-bottom sediment traps all year around. Three possible fates of ice algae can be distinguished: 1) suspension in the water column, 2) sinking to the bottom and 3) ingestion by herbivores in the ice, at the ice–water interface or in the water column.

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High concentrations of organisms in polar sea ice have been well documented (e.g. Horner 1985; Lizotte 2003). Sea ice is inhabited by diverse communities, including bacteria, algae, protists and metazoans (e.g. Melnikov 1997). Often the flora and fauna are not evenly distributed in the ice, but occur in specific microhabitats in different parts of the ice floes (Horner 1985; Syvertsen 1991; Gradinger 1999). Such communities have been studied in detail, but the current knowledge of the biological processes involved during sea ice formation and melting are still inadequate (Gradinger & Ikävalko 1998; Weissenberger & Grossmann 1998). There are several hypotheses regarding the origin and fate of sea ice communities (Horner 1985). Sieving of water by densely packed ice crystals has been observed repeatedly and appears to constitute an important mechanism for accumulation of algae cells on the ice under-surface (Syvertsen 1991; Melnikov 1997). The composition of sea ice algae off the shelves suggests that this population derives from pelagic algae inhabiting underlying water masses or from sea ice algae at the ice edge or polynyas (Syvertsen 1991; Druzhkov et al. 2001). In shallow water areas benthic algae may be included in the succession cycle (Poulin 1990; Gogorev 1998).

Through various research programmes we studied and compared the ice flora of the White and Barents seas, two regions inadequately studied with regard to ice biota. We investigated in particular the peculiarities of the vertical distribution of the sea ice algae under different conditions and the succession of this distribution during the late winter/early spring in the land-fast ice in the White Sea. The differences in the algae species composition in different types of ice and the relationships between taxa within the ice and water column were also quantified.

Materials and methods

Three cruises were conducted to the Guba Chupa (Chupa Estuary; north-western White Sea) in February 2003, March 2001 and April 2002. One cruise was carried out in the open part of the White Sea (April 2003), where the stations were located in the Marginal Ice Zone (MIZ) in the southern part of Gorlo (north-eastern White Sea). One cruise was carried out in the MIZ of the northern part of the Barents Sea in July 2001 (Table 1). Ice cores from the White Sea were obtained with a ring corer (diameter 14.5 cm) and divided into three or four sections: upper 10 cm, lower 3 - 5 cm, and a middle part, which was cut into two parts if the total ice thickness exceeded 40 cm. The sections were melted at low temperatures (<2 °C) without addition of filtered water. The salinity of the White Sea ice is low (Krell et al. 2003), and we deem that the algae were not being exposed to osmotic stress during melting. In the Barents Sea, ice cores were collected with an ice auger (diameter 9 cm). The lowermost 20 - 30 cm of each ice core was melted in double its volume of filtered seawater at low temperatures. Samples from the water column below the ice were also obtained in both regions (Appendix). The volume of the sea ice and water samples ranged from 100 to 4500 ml, according to the abundance of the algae. To investigate the possible importance of sea ice algae for the vertical flux of biogenic matter, cylindrical sediment traps were deployed below the ice: in the White Sea (Guba Chupa) the traps were preserved with formaldehyde and exposed for a week at 20 m depth. Traps were also deployed above the bottom in the Kandalaksha Bay (depth 280 m) and nine samples (each representing one month) were taken from August 2002 to May 2003. In the Barents Sea, traps were deployed without preservation for one day at 30 m depth . The height/diameter ratio of the traps was 3.11 for the White Sea and 3 for the Barents Sea. Temperature and salinity were measured with standard CTD profilers.

All samples were preserved with a glutardialdehyde–lugol–ethanol solution and developed according to Ratkova & Wassmann (2002). Small flagellates were counted in a Fuchs-Rosenthal chamber at 600× magnification prior to any concentration of samples. After they had settled, larger algae were counted in chambers with rul-

Table 1. Biomass (mg C m^{-3}) of the sea-ice algae ("algae") in the lowermost layer of the ice in the Barents (5 - 34 cm of 100 - 135 cm cores) and in the White Sea (5 - 10 cm of 37 - 56 cm cores) and of phytoplankton ("phyto") below the ice.

	Barents Sea						White Sea (pack ice)		White Sea (land-fast ice)					
	77° 50'N, 29° 45'E		78° 20'N, 27° 20'E		82° 00'N, 26° 00'E		65° 40' - 66° 10'N, 40° 10' - 40° 50'E		66° 20'N, 33° 40'E					
	3 July 2001		6 July 2001		9 July 2001		19–20 April 2003		8 February 2003		18–26 March 2001		6–8 April 2002	
	algae	phyto	algae	phyto	algae	phyto	algae	phyto	algae	phyto	algae	phyto	algae	phyto
Diatoms	7.58	5-44	49.2	1-7	254.6	1-7	44-478	11-12	1.49	0. 07-0.31	94-598	1-64	1136-35188	1-94
Dino-flagellates	0.49	34-80	14.0	25-33	11.0	1-2	1.3 - 21.7	0.01-1.06	0.49	0.03-0.18	3.1-37.5	0.02-1	24.5-178.6	1-28
Other flagellates	17.0	82-299	86.8	82-173	76.5	32-74	36-49	27-94	4.4[a]	0.5-2.2[a]	8.6-35.7	11-359	3.8-61.7[b]	1-525[b]
Total	28.3	154-407	150	117-218	343.8	35-83	87-565	39-109	6.49	0.12-2.69	115.9-674.1	15-444	1164-35428	3-647

[a] According Sazhin et al. in press.
[b] According Sazhin et al. 2004.

ings, at 300× magnification in a 0.06 ml chamber and at 150× magnification in a 1.0 ml chamber. The carbon content of the algae was calculated according to Strathmann (1967) for diatoms with a cell volume >3000 μm^3, and according to Menden-Deuer & Lessard (2000) for all other protists.

Results

Physical environment

The temperature of the water in the White Sea seldom reached the freezing point, and the ice developed mainly from the surface (Krell et al. 2003; Pantyulin 2003). The ice was thin during all of the expeditions (thickness 34 - 57 cm) and often flooded with seawater. Granular snow ice dominated the entire ice column at all times in the White Sea. Only in March 2001 and in February 2003 was columnar ice observed in the middle part of the ice cores. The sea ice structure was determined by visual observation of the ice core, but was supported by investigation of the crystal structure of thin ice core sections (February and April 2002) (Krell et al. 2003).

The winter of 2001 was unusually mild and ice formation did not take place until February. The ice was rather porous, granular and white in the upper and in the lowermost parts and columnar and grey in the middle part of the ice cores. The ice was 44 - 57 cm thick and was covered with a layer of snow which increased in thickness from ca. 10 cm on the first day of the expedition to ca. 16 cm a day later, after a snowfall. Below the ice there was a < 1 m thick brackish layer (psu < 15 ‰) with a temperature of –1.2 °C—well above the freezing point.

In April 2002 a < 1 m thick brackish layer (psu < 6 ‰, temperature: –1.2 °C) was encountered below the ice; the sea ice below a thin snow cover was granular, white-grey and semi-transparent, and wide channels were observed in the lower 10 cm of ice cores (thickness 34 - 54 cm). A brownish discolouration was observed at the lowermost surface.

In February 2003 the white, dull granular ice was covered with a thick layer of slush (up to 15 cm) and snow (ca. 10 cm). In the middle part, columnar semi-transparent ice was observed. In the lowermost few centimetres, the ice was opaque, white and granular. The water salinity was high (psu 26.1 ‰) and the temperature was –1.2 °C directly beneath the ice (thickness 34 - 52 cm); both parameters increased with the depth.

In April 2003 the depth of the snow cover ranged from 10 to 20 cm on different ice floes. The ice floes, which remained intact after a storm event, showed no signs of surface melting. However, considerable ice melting occurred from the sides and from below, due to relatively warm water. The lower part of the ice cores (thickness 45 cm) was semi-transparent, granular and had large caverns. The middle part was greyish, opaque and dense. The upper part of the ice layer was not much different from the middle part, though it was softer. In the water column, salinity and temperature varied little from the surface to the bottom. From the north-west part of the Gorlo Strait (66° 10' N; 40° 10' E), where most of the water is from the Barents Sea, to the south-east part of the strait (65°40' N; 40°50' E), where White Sea water dominates, the temperature increased from –1.52 to –1.08 °C and the salinity decreased from 29.7 ‰ to 27.2 ‰ psu (Kosobokova et al. 2004).

A peculiar feature of the physical oceanography in the MIZ of the northern Barents Sea in July 2001 was a 20 m thick layer of meltwater (–1 to 0.4 °C; psu 31 ‰) above the Arctic Water (< –1 °C; psu 34 ‰). The ice conditions in the investigated floes varied from annual pack ice floes (thickness about 1 m) to multi-year pack ice (thickness > 1.35 m). Differentiation between the multi-year and annual ice was based mainly on ice thickness and the density of the *Melosira arctica* mats observed by the divers. The snow cover was rather thin (< 10 cm).

Phytoplankton and sea ice algae: composition

A total of 306 algae species (Appendix) were identified in the ice, in the water and in the sediment traps. In White Sea land-fast ice, 275 species were encountered. The White Sea pack ice was inhabited by fewer species (106), and only four of them were not also observed in the land-fast ice. In the Barents Sea, 201 species were found. In general, the algae composition in the two regions was rather similar: 156 species, including 73 diatoms, 39 dinoflagellates, all silicoflagellates and coccolithophorides and 31 other flagellates were observed in both regions. The main differences were encountered among the pennate diatoms. In the White Sea land-fast ice, 110 pennate species were found, while only 49 and 52 species were found in the White Sea and the Barents Sea pack ice, respectively.

Most of the species were found both in the water column and the ice, but 50 species were not observed in the ice. Most of these were benthic ones which only occasionally occurred in the water, but there were also some common planktonic species which were not found in the ice, for example, the diatoms *Chaetoceros borealis*, *C. brevis*, *C. decipiens*, *Corethron criophylum*, *Coscinodiscus centralis*, *C. radiatus*, *Proboscia eumorpha*, *Rhizosolenia hebetata* f. *semispina*; the dinoflagellates *Dinophysis contracta*, *D. arctica*, *Heterocapsa triquetra*, *Protoperidinium pallidum*, *P. pellucidum*, *P. pyriforme*, *Warnowia reticulata* and a few other flagellates.

Some species were observed only in the ice: 37 diatoms (e.g. *Navicula algida*, *N. glacialis*, *N. gelida*, *Nitzshia hybridae*, *N. polaris*, 22 other pennate and 10 centric species) and 7 dinoflagellates (e.g. *Gymnodinium wulfii*, *Karenia brevis*, *Protoperidinium granii*).

Diatoms and euglenophytes were represented by more species in the ice (178 and 5, respectively) than in the water (154 and 4, respectively). All other groups were represented by more species in the water; except for chlorophytes, which were represented by the same number of species in the ice and in the water.

The snow covering the ice demonstrated poor species diversity (44 species in the snow in comparison to 228 species in the ice). All the species observed in the snow were also found in the underlying ice.

The abundance of species also differed between sea ice and the water column: sea ice algae species were less abundant in the water, where plankton species had the higher abundance (Appendix).

On the basis of morphological and ecological distinctions, some assemblages of the sea ice species were selected for comparison: A) pennate ice plankton species that develop ribbon-shaped colonies (*Fossula arctica*, *Fragilaria striatula*, *Fragilariopsis* spp., *Pauliella taeniata* and some species of *Navicula* and *Nitzschia*—hereafter "ribbon diatoms"); B) single-celled ice-benthic pennate species that sometimes develop barrel-shaped colonies in ice (*Enthomoneis* spp., *Undatella* cf. *quadrata*, *Navicula lineola*—"barrel diatoms"); C) epiphytic species that are associated with *Melosira arctica* and *Nitzschia frigida* (*Synedropsis* spp., *Gomphonemopsis* cf. *exigua*, *Gomphonema septentrionalis*, *Pseudogomphonema kamchaticum* and *Atteya septentrionalis*—"associated diatoms").

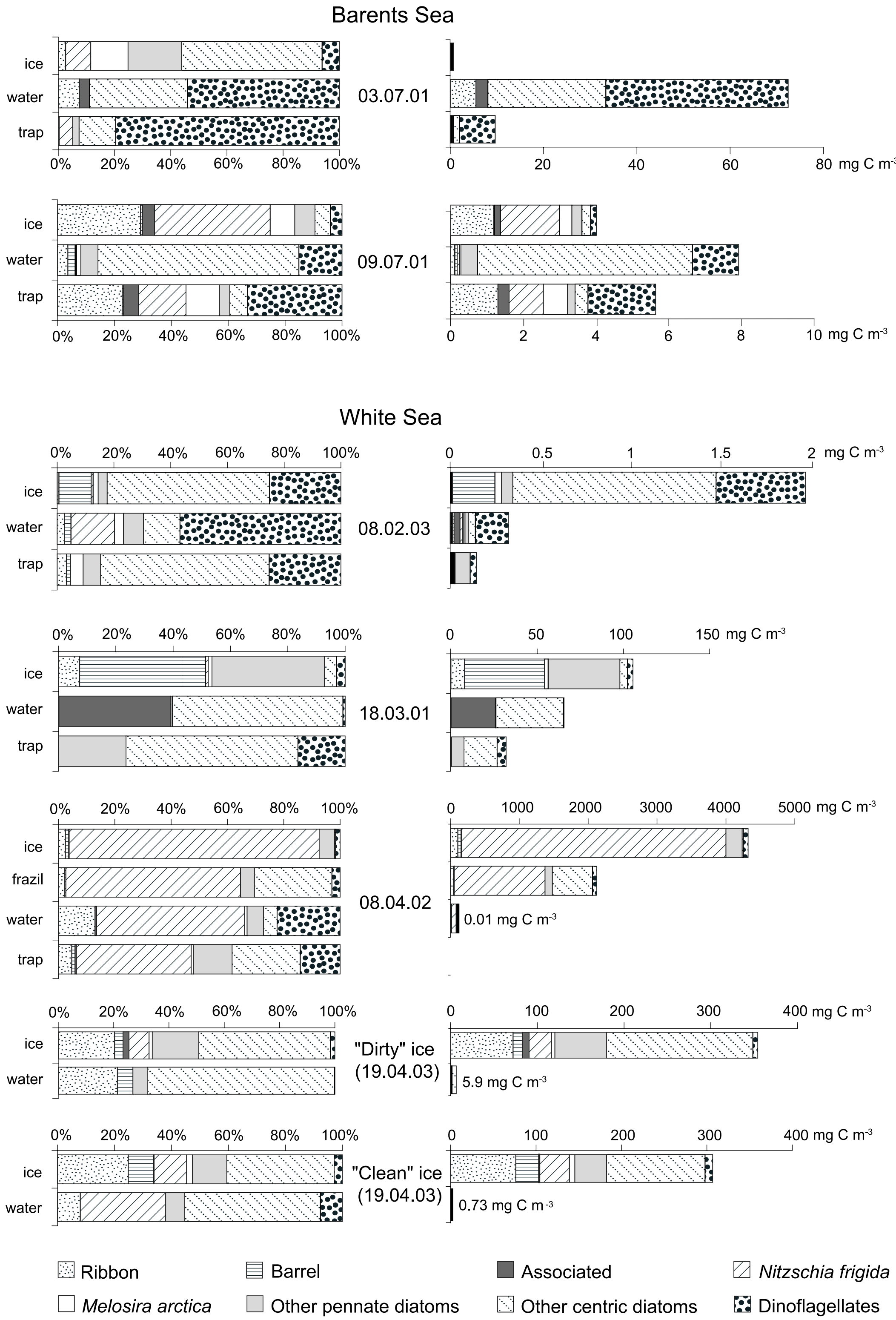
Phytoplankton and sea ice algae: abundance

In the White Sea land-fast ice, flagellates dominated the phytoplankton carbon in all samples, but diatoms dominated in the sea ice (Table 1). Flagellates comprised <25% in the ice and 73-80% in the water (3.8-62 and 0.5-525 mg C m^{-3}, respectively). In February 2003 the species composition and abundance of diatoms and dinoflagellates in the White Sea land-fast ice were rather similar to those in the annual ice of the Barents Sea in July 2001, i.e. centric diatoms dominated in a sparse sea ice algal assemblage (Fig. 1).

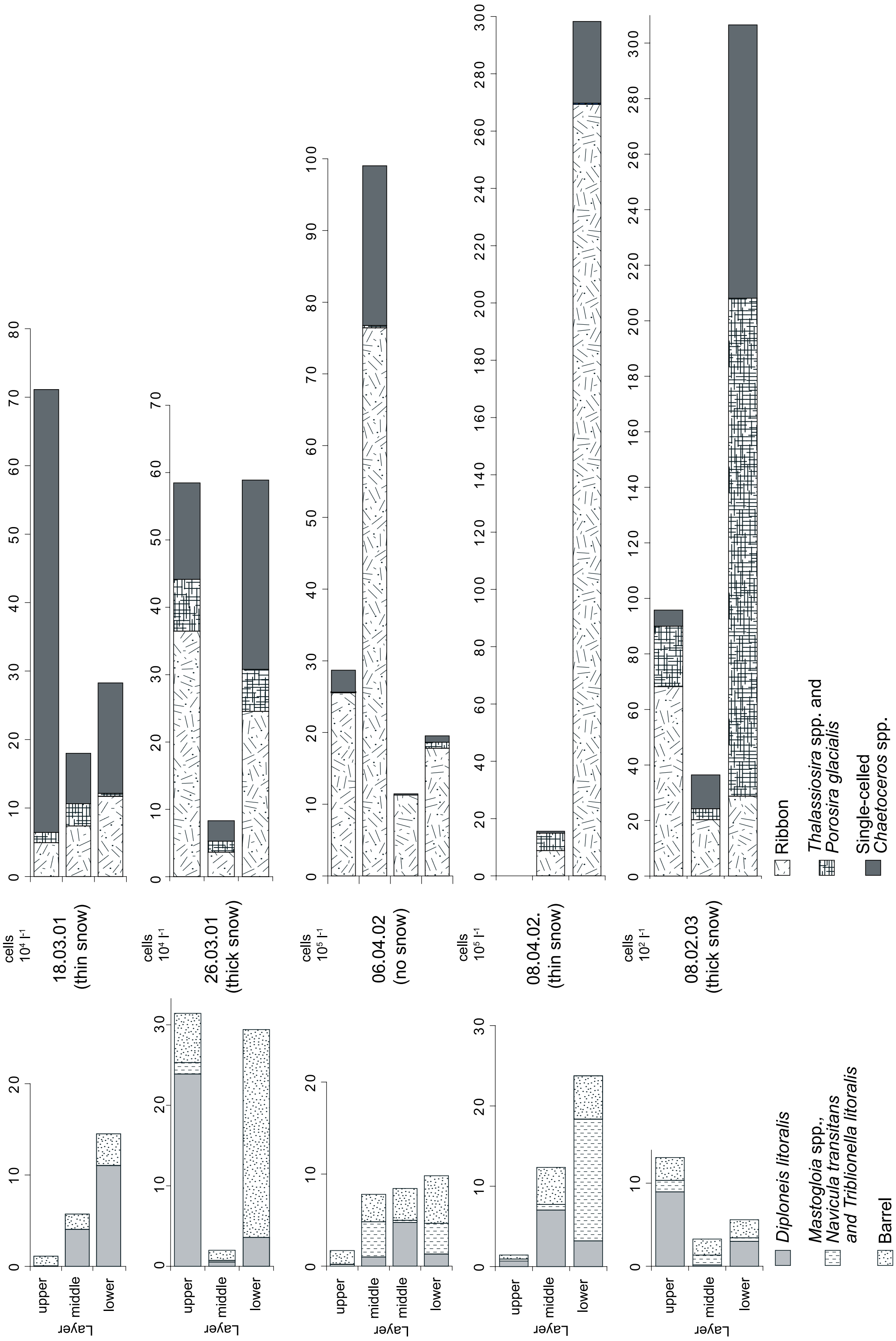
In March 2001 the species composition in the White Sea land-fast ice was quite different: barrel and other benthic and ice-benthic diatoms dominated the algae carbon in the ice. Benthic single-celled pennate diatoms were most abundant in the lowermost few centimetres of the ice core on 18 March before a snowfall ($>1 \times 10^5$ cells l^{-1}) and in the upper 10 cm of the ice (Fig. 2) after the snowfall on 26 March (2.5×10^5 cells l^{-1}). These species were rare in the water, where centric diatoms dominated (Fig. 1). In April 2002, *Nitzschia frigida* dominated the total carbon of diatoms and dinoflagellates in the sea ice and water column (Fig. 1).

Two types of White Sea pack ice were studied: pack ice floes in the southern part of the Gorlo Strait, probably formed far from the coast ("clean ice"), and fragmented ice in the northern part of the Gorlo Strait with characteristic brown mineral insertions ("dirty" ice). Algae biomass in the "dirty" ice (407 mg C m^{-3}) was close to the highest values in the "clean" ice (87-565 mg C m^{-3}). The composition of the algal populations differed

Fig 1 (opposite page). Composition of the diatoms and dinoflagellates abundance in the lowermost part of the ice, in the upper part of the water column and in sediment traps in the northern Barents Sea in July 2001 and in the White Sea in February 2003, March 2001, April 2002, and in the lowermost part of the ice and in the upper part of the water column in April 2003. "Ribbon" denotes plankton diatoms forming ribbon-shaped colonies; "barrel" is benthic single-celled diatoms forming barrel-shaped colonies in the ice; and "Associated" stands for species found in association with *Melosira arctica* and *Nitzschia frigida*. Each bar represents the value of the single sample in the Barents Sea and in March 2001 and April 2003 in the White Sea. The axes showing biomass are different. Each bar is the mean value from the 4-5 samples collected in April 2002 and in February 2003. Low biomasses of algae in the White Sea in the water in April 2003 and in the traps in February 2003 are indicated by numbers instead of bars.



Barents Sea
ice
water
trap
03.07.01
0% 20% 40% 60% 80% 100%
0 20 40 60 80 mg C m-3
09.07.01
0 2 4 6 8 10 mg C m-3
White Sea
08.02.03
0 0.5 1 1.5 2 mg C m-3
18.03.01
0 50 100 150 mg C m-3
frazil
08.04.02
0 1000 2000 3000 4000 5000 mg C m-3
0.01 mg C m-3
"Dirty" ice (19.04.03)
0 100 200 300 400 mg C m-3
5.9 mg C m-3
"Clean" ice (19.04.03)
0.73 mg C m-3
Ribbon
Barrel
Associated
Nitzschia frigida
Melosira arctica
Other pennate diatoms
Other centric diatoms
Dinoflagellates



cells 10⁴ l⁻¹
18.03.01 (thin snow)
cells 10⁴ l⁻¹
26.03.01 (thick snow)
cells 10⁵ l⁻¹
06.04.02 (no snow)
cells 10⁵ l⁻¹
08.04.02. (thin snow)
cells 10² l⁻¹
08.02.03 (thick snow)
Layer
upper
middle
lower
Ribbon
Thalassiosira spp. and Porosira glacialis
Single-celled Chaetoceros spp.
Diploneis litoralis
Mastogloia spp., Navicula transitans and Triblionella litoralis
Barrel

considerably: pennate ice-planktonic species were dominant in the "clean ice", while planktonic centric algae were dominant in "dirty" ice (Fig. 1). Compared to the White Sea land-fast ice, pack ice in the White Sea had higher concentrations of flagellates (Table 1).

Sedimentation of algae was low in Guba Chupa (0.28 - 2.2 mg C m^{-2} day^{-1}) and was dominated by plankton centric diatoms in February and March. In April, *Nitzschia frigida* was more abundant than centric diatoms. Planktonic centric diatoms dominated the vertical flux above the bottom in the deepest part of Kandalaksha Bay, but the permanent occurrence of sea ice algae, even during the summer months, was remarkable.

In contrast to the rather low abundance of phytoplankton below the ice in the White Sea, in the Barents Sea, the biomass of phytoplankton was two orders of magnitude higher than the biomass of sea ice algae (Fig. 1). Flagellates dominated the sea ice algae and phytoplankton carbon in all samples from the Barents Sea (Table 1). They comprised 60 - 90 % of the total (1.1 - 3.9 mg C m^{-3} in the ice and 30 - 300 mg C m^{-3} in the water). In the lowermost part of the annual ice, centric diatoms were abundant (> 50 % of total carbon of diatoms and dinoflagellates).

Plankton algae dominated the sea ice assemblage and the vertical flux in the Barents Sea. In the water and sediment traps dinoflagellates were the second most abundant group. Only one sea ice species (*Nitzschia frigida*) was numerous in the traps. The composition of the sea ice algae population in the multi-year ice was rather similar to that of the sea ice algae in the White Sea in April 2002: *N. frigida* and ribbon diatoms comprised the bulk of the total diatom and dinoflagellate carbon.

However, in the water column of the Barents Sea, total carbon of diatoms was dominated by centric species, whereas in the White Sea it was dominated by pennates, *N. frigida* and ribbon species. Total algae concentration was higher in the water than in the ice in the Barents Sea, but the abundance of *Melosira arctica* and *N. frigida* was higher in the ice.

The sediment trap content under the multi-year ice in the Barents Sea was rather similar to the algae composition in the ice, in contrast to the traps under the annual ice, where the species *M. arctica* and *N. frigida* were sparse.

Fig 2 (opposite page). Vertical distribution of the sea ice diatoms in the White Sea in March 2001, April 2002 and February 2003. "Barrel" refers to benthic single-celled diatoms forming barrel-shaped colonies in the ice; "Ribbon" is plankton diatoms forming ribbon-shaped colonies. The axes are the same within each column, but the left and right columns have different axes. Each bar represents a single sample.

Discussion

Sea ice properties

The temperature of the water in the White Sea seldom reached the freezing point, and the ice developed mainly from the surface (Krell et al. 2003; Pantyulin 2003). The ice was thin during all expeditions (range: 34 - 57 cm) and was often flooded by seawater. In the White Sea, ice originated mainly from snow: $\delta^{18}O$ varied between –1.51 and –8.72 (Krell et al. 2003). The granular snow ice dominated the entire ice column at all times in the White Sea. Only during the coldest part of the year (March 2001, February 2002 and February 2003) was columnar ice observed in the lowermost layer of the ice. Congelation ice may only be found during the first stages of ice development in the White Sea (Melnikov et al. in press). The ice melted from below because the under-ice water temperature never dropped below –1.5 °C in the course of our investigations. The snow removed the bulk salinity from the brine channels and reduced the total sea ice salinity to psu 0 - 4 ‰. Thick snow cover insulated the ice from the cold air, and the temperature in the ice was rather high (>–2 °C). Low salinity and the high temperature of the ice led to wide brine channels and low salinity in the brine water (Melnikov et al. in press).

There are no data regarding the sea ice structure in the investigated region of the Barents Sea. However, it is well known that congelation ice dominates the total ice column in the Barents Sea, as in other Arctic areas. Only the uppermost 10 cm may be represented by snow ice. Salinity of the brine water may be as high as psu 70 - 144 ‰ (Gradinger et al. 1999). In summer, the total salinity and temperature of the lowermost part of the ice (psu 3 - 5 ‰ and –1.2 °C) appear to be comparable with the White Sea ice.

Composition and abundance

Most of the species that were observed in the sea ice were similar to those recorded from other parts in the Arctic. In the high latitude Arctic this similarity may be attributed to the long-range transport of ice (von Quillfeldt et al. 2003), but this explanation does not hold for the White Sea ice. The similarity between sea ice assemblages in the White Sea and in other ice-covered regions may be explained by a similar origin of the ice flora in all Arctic regions (Sazhin et al. 2004). Three types of sea ice organisms can be distinguished: ice specialists, ice-benthic and ice-plankton species. Additionally, plankton and benthic species may also be observed in sea ice. The sea ice specialists were neither observed in bottom sediments nor in plankton in summer, but they were found in the bottom water sediment trap, probably due to resuspension and stirring up of the sediment. As soon as the ice melted, sea ice specialists decayed or developed resting spores (e.g. *Undatella* cf. *quadrata*, *Melosira arctica*).

Closely related to these species were ice-benthic species (e.g. *Diploneis litoralis*, *Enthomoneis* spp., *Navicula lineola*), but these species were also observed in bottom sediments as active cells (Gogorev 1998). Benthic species may be included into the sea ice during its formation in shallow estuaries or bays. They may survive in the ice, but in contrast to the ice-benthic species, their abundance is not high (e.g. *Mastogloia* spp., *Pinnularia* spp., *Triblionella litoralis*). Most of these ice-benthic and benthic species were observed in the White Sea bottom sediments in March 2001 (F. Sapozhnikov, pers. comm.) and in the plankton in the Pechora Sea during the ice formation in November 2003 (T. Ratkova, unpubl. data). These species were observed in the bottom water trap in the White Sea deep throughout the year (T. Ratkova, unpubl. data).

Ice-benthic species were not abundant in pack ice, probably because they cannot recolonize ice from the bottom in deeper waters. The sea ice algae that inhabit the pack ice survive the summer in the water column (ice-plankton algae) or in the multi-year ice (sea ice specialists).

The ice-plankton species were frequent in land-fast and pack ice (e.g. ribbon diatoms and *Nitzschia frigida*, accompanied with *Atteya septentrionalis*, *Synedropsis hyperborea* and *Gomphonema*-like species). The plankton centric diatom species may be incorporated into the ice during ice formation and during flood events (Buck et al. 1998). However, they were not abundant in the interior of the ice, but only in the upper and lower layers, where the ice is in contact with the underlying water or floodwater. Centric diatoms are regarded as allochthonous for the ice realm. Thus, pennate diatoms dominate among the sea ice algae from the Chukchi, East Siberian and Laptev seas (Okolodkov 1992). The lower part of the annual sea ice in the northern Barents Sea was dominated by ice-plankton and plankton diatoms. The sub-ice assemblage was dominated by ice-plankton (ribbon diatoms and *Nitzschia frigida*). The ice specialist *Melosira arctica*, the ice-benthic species (*Enthomoneis* spp., *Diploneis litoralis*) and associated species were also observed. Planktonic algae dominated the water and sediment traps. Only one sea ice species (*N. frigida*) was numerous in the traps. The sea ice community of the annual ice in the northern Barents Sea included more planktonic algae than in the White Sea, but the same benthic species occurred in both areas.

The diatom population in the lower part of the multi-year ice was dominated by ribbon diatoms and by *N. frigida*. *M. arctica* developed into thick mats below the ice. The plankton diatom *Chaetoceros socialis* dominated the water below the ice, but in the upper few metres *M. arctica* was also abundant. *M. arctica* was abundant in the sediment traps below the multi-year ice, in contrast to those below annual ice, indicating that this species is primarily introduced to the Barents Sea from the Arctic Ocean. Many resting spores of M. arctica were observed in the water column and in sediment traps. Evidently, part of the *M. arctica* mats were detached from the lower surface of the ice.

Coastal sea ice of the White Sea forms in productive systems where a continuous nutrient supply from the water column (rivers, sediment, mixing by tidal currents) sustains high algal biomass, with diatoms as the dominating taxon (Krell et al. 2003). Oceanic ice habitats of the Barents Sea, however, are characterized by more regenerative food webs, with lower biomass and a higher contribution of flagellates (Gradinger 1999). This illustrates the main difference between the White Sea land-fast ice and White and Barents seas pack ice. These two different scenarios contribute to the observed differences in composition and abundance of the ice algae in these two types of sea ice.

The difference between the abundance of sea ice algae in the White Sea and in the Barents Sea may be attributed in part to the different timing of growth. In the northern Barents Sea the productivity of sea ice algae is highest in July (Kuznetsov & Schoschina 2003), but in the White Sea it is in April (Ilyash et al. 2003). Our observations in the Barents Sea were conducted at the end of sea ice algae vegetation and before and during the maximum of sea ice algae development in the White Sea.

The species composition in the ice changes little with the age of the ice, whereas the relative abundance of each species may change markedly: plankton species, which are more abundant and dominate total algae numbers and carbon in young ice, may be replaced by ice species, which are more abundant in older ice. The composition of the sea ice algae results primarily from the composition of algae in the underlying water masses in regions that are not ice-covered during a part of the year, or from the composition of the sea ice algae community in the ice-edge or in polynyas (Syvertsen 1991; Weissenberger 1998; Druzhkov et al. 2001). In shallow water areas benthic algae may also be included in the succession cycles (Poulin 1990; Gogorev 1998). The stickiness of pennate diatoms (Riebesell et al. 1991) may partially explain their high enrichment rates. Usually the planktonic and benthic algae entrapped by the ice crystals in autumn (Syvertsen 1991; Melnikov 1997; von Quillfeldt 1997) will be sparse during the entire winter. They start their development in spring (Zhitina & Mikhailovsky 1990). However, if sea ice forms earlier (in October in the northern Barents Sea), the entrapped algae may develop immediately (Horner 1990; Druzhkov et al. 2001), overwintering as a well-organized community. The timing of the development of the sea ice algae community can be explained mainly by the light conditions and the taxonomic composition of the algae: benthic algae may be better adapted to lower irradiance and lower temperature than planktonic ones (Gogorev 1998).

The vertical distribution of sea ice algae

The benthic algae entrapped by the ice crystals during ice formation in February 2001 may have developed immediately in the lower part of the thin granular ice because the light conditions in newly formed ice are favourable for algae growth. When the irradiance decreased after a heavy snowfall, they may have actively moved through the brine channels to the upper part of the ice. Consequently, on 26 March 2001 the highest biomass of these species was observed in the upper 10 cm of the ice. The same vertical distribution was also observed in February 2003, when the snow cover was exceptionally thick. The ice-planktonic and ice-benthic species may demonstrate new morphological peculiarities when they live in ice. Some of the species became longer (*Fragilariopsis cylindrus*, *F. oceanica*, *Nitzschia longissima*); others (*Enthomoneis* spp, *Undatella* cf. *quadrata* and *Navicula lineola*) developed large barrel-like colonies. These morphological changes may indicate an adaptation to new conditions.

In March 2001 we also observed an upward movement of the ice-benthic diatom *Diploneis litoralis*. It had its highest abundance in the lower 5 cm of the ice core on 18 March and was displaced to the upper 10 cm by 22–26 March. We speculate that the vertical species succession, which usually occurs over a time span of months (Syvertsen 1991), took place in a week in 2001 because of the late development of the sea ice.

Conclusion

A total of 306 algae species were identified in ice, water and sediment traps in the Barents and White seas. In the White Sea land-fast ice, 275 species were recorded. In the White Sea pack ice, species were less numerous (106 species), and only four of these species were not observed in the land-fast ice. In the Barents Sea, 201 species were found.

In general, the algae composition in the two regions was rather similar. The main differences were encountered among the pennate diatoms: in the White Sea land-fast ice, 110 pennate species were found, while only 49 and 52 species were found in the White Sea and Barents Sea pack ice, respectively. Most of the species were found both in the water column and in the ice, but a few species were not observed in the ice. The algae communities of the ice and ice-covered waters in the White and Barents seas are highly variable in space and time (Sazhin et al. 2004; von Quillfeldt et al. 2003). To understand the dynamics of these algae assemblages, one must take into account the formation history of the ice.

The algae communities of the land-fast ice, dominated by pennate diatoms, are more closely related to the bottom sediments than the community of the pack ice, which is dominated by centric diatoms. The algae in the land-fast ice community are more numerous and variable than those of the pack ice. Motile benthic and ice-benthic species find favourable conditions in the ice because of the close proximity and similarity between the bottom sediments and the sea ice interior (Gogorev 1998). The plankton and ice-plankton species find stable illumination and refuge from grazers in the ice. However, conditions here are less favourable for plankton algae, which are well-adapted to life in the water column, where algae circulate passively with the turbulent flow and where conditions for nutrient uptake are better. Algae living in ice, in contrast, must contend with the laminar flow in the narrow channels of the ice, where the nutrient supply in the upper layer may be very low (Gradinger & Ikävalko 1998). Benthic and ice-benthic ice algae are better adapted to such conditions, attaching themselves to the substrates or actively moving along the walls of the channels.

The pack ice community is related to that in the surrounding water. It originates from it and is released into it after the ice melt. An additional source for ice algae colonization may be the multi-year ice. Algae may be released from the ice during warming events, because of the brine drainage, or during the sea ice melting.

Some of the sea ice algae develop spores before the ice melt. These spores may be transported to other ice floes, or sink down to the bottom of shelf regions until the next season. Grazers may quickly ingest the released algae: in the White Sea almost none of the released diatoms reach the bottom. The sedimentation rate of the algae is therefore extremely low and a high rate of faecal pellet export was observed (Kosobokova et al. 2003).

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Appendix

The following table indicates the relative abundance, geographic ranges and ecology of the species recorded from ice cores and sub-ice water in the White Sea in February, March and April 2001–03 and in the Barents Sea in July 2001. (Identifications are based on Krishtofovich & Proshkina-Lavrenko [1949, 1950], Hendey [1964], Semina [1974], Semina & Sergeeva [1983], Medlin & Priddle [1991], Thomsen [1992], Snoeijs [1993], Snoeijs & Vilbaste [1994], Snoeijs & Potapova [1995], Snoeijs & Kasperovičienė [1996], von Quillfeldt [1996, 2000], Konovalova [1997], Tomas [1997], Okolodkov [1998], Snoeijs & Balashova [1998], Tuschling [2000], Ulanova [2003], Throndsen et al. [2003] and von Quillfeldt et al. [2003].) Geographic ranges (in the column headed "Range") are: cosmopolitan (c), Arctic–boreal (Ab), bipolar (b), tropical–Arctic–boreal (tAb), tropical–boreal (tb) and tropical (t). Ecological categories ("Ecology") are: freshwater (F), brackish water (B), marine (M), eurihaline (E), neritic (N), ice–neritic (In), marine–neritic (Mn), epiphytic (Ep) and benthic (Be). Relative abundance (mean number of cells for all available samples) categories are: 1 (<1 10^4), 2 (1 10^4 - 1 10^5), 3 (1 10^5 - 1 10^6) and 4 (>1 10^6 cells l^{-1}.

	Cell vol. (mμ^3)	Range	Ecology	Abundance: White Sea Ice	White Sea Snow	White Sea Water	Bar. Sea Ice	Bar. Sea Water
Division Chromophyta								
Class Bacillariophyceae								
Achnanthes brevipes Agardh	4000	c	B, Be	1	-	1	-	-
A. flexella (Kütz.) Brun	9000	-	F, Be	-	-	1	-	-
Achnantidium minutissima (Kütz.) Czarm.	250	-	F, Be	1	-	1	-	-
Actinocyclus curvatulus Ehrenberg	67 500	c	M	1	-	1	-	-
A. octonarius Ehrenberg	48 000	c	M	1	-	-	-	-
Amphora spp.				1	-	1	-	1
Asterionella formosa Hassal	800	c	F	-	-	1	-	-
Attheya septentrionalis (Øestrup) Crawford	150	Ab	M, Ep, In	3	2	1	3	1
Bacterosira bathyomphala (Gran) Syvertsen & Hasle	2200	Ab	M, N	1	-	1	-	1

Table continued from previous column.

	Cell vol. (mμ^3)	Range	Ecology	Abundance: White Sea Ice	White Sea Snow	White Sea Water	Bar. Sea Ice	Bar. Sea Water
Caloneis sp.				1	-	-	-	-
Campylodiscus fastuosus Ehrenberg	42 000	Ab?	M, Be	-	-	1	-	-
Chaetoceros affinis Lauder	4600	Ab?	M, N	1	-	1	-	-
C. borealis Bailey	11 250	tAb	M	-	-	1	-	-
C. brevis Schütt	1500	Ab	M, N	-	-	-	-	1
C. ceratosporus Ostenfeld	50	Ab	M, N	2	-	1	-	2
C. compressus Lauder	600	tAb	M	1	-	1	-	1
C. concavicornis Mangin	2200	Ab	M	1	-	1	-	-
C. danicus Cleve	7500	tAb	B, N	1	-	1	-	-
C. debilis Cleve	600	tAb	M, N	1	-	1	-	1
C. decipiens Cleve	13 500	c	M	-	-	1	-	1
C. diadema (Ehrenberg) Gran	3100	Ab	M, N	1	-	-	1	1
C. diversum Cleve	720	tb	M, N	-	-	1	-	-
C. fallax Proshkina-Lavrenko	1100	-	-	1	-	-	-	-
C. furcellatus Bailey	200	Ab	M, N	1	-	1	-	1
C. gracilis Schütt	110	Ab	M, N	1	-	1	1	1
C. holsaticus Schütt	720	Ab	B, N	1	-	-	-	-
C. invisibilis Gogorev	30	-	M, In	2	-	1	3	-
C. laciniosus Schütt	400	tAb	M, N	1	1	-	-	1
C. perpusillus Cleve	300	tAb	M, N	-	-	-	-	1
C. similis Cleve	300	Ab	M, N	1	-	-	-	-
C. simplex Ostenfeld	350	tAb	E, N	1	3	1	-	1
C. socialis Lauder	100	c	E, N	2	3	3	3	3
C. wighamii Brightwell	600	Ab	E, N	1	-	-	-	-
Cocconeis costata Gregory	4600	Ab?	M, N	1	-	1	-	-
C. pediculus Ehrenberg	1440	-	B, Ep	-	-	1	-	-
C. scutellum Ehrenberg	9000	c?	M, N	1	-	1	-	-
C. stauroneiformis (Van Heurck) Okuno	4050	-	B, Ep	-	-	1	-	1
Corethron criophyllum Castracane	25 200	c	M	-	-	1	-	-
Coscinodiscus asteromphalus Ehrenberg	1012 500	c	M	-	-	1	1	-
C. centralis Ehrenberg	844000	c	M	-	-	1	-	-
C. concinnus W.Smith	1350 000	c	M	1	-	1	-	-
C. radiatus Ehrenberg	42 300	c	M	-	-	1	-	-
Ctenophora pulchella (Ralfs & Kützing) Williams & Round	6370	Ab	E, Be	1	-	1	1	-
Cyclotella choctawhatcheana (Proshkina-Lavrenko) Prasad	1700	Ab	E, N	1	-	1	1	-
C. litoralis Lange & Syvertsen	16 000	b	E, N	1	-	1	-	-
C. striata (Kützing) Grunow	3000	Ab?	E, N	1	-	1	-	-
Cylindropyxis tremulans Hendey	140	-	-	1	-	1	-	-
Cylindrotheca closterium (Ehrenberg) Lewin & Reimann	450	c	E, N	1	1	1	1	1

Table continued from previous column.	Cell vol. ($m\mu^3$)	Range	Ecology	Abundance White Sea Ice	Snow	Water	Bar. Sea Ice	Water
Dactyliosolen fragilissimus (Bergon) Hasle	5100	c?	-	1	-	-	-	-
Detonula confervacea (Cleve) Gran	270	Ab	M, N	-	-	1	-	1
Diatoma tenuis Agardh	800	-	F	1	-	1	-	-
Didymosphaenia geminata (Lyngb.) M.Schmidt	56 900	-	F, Be	-	-	1	-	-
Diploneis didyma (Ehrenberg) Ehrenberg	10 000	Ab?	B, N	1	-	1	-	-
D. litoralis var. *litoralis* (Østrup) Cleve	2300	Ab	M, N	2	-	1	1	1
D. litoralis var. *arctica* (Østrup) Cleve	2700	Ab	M, In	1	-	-	-	-
D. litoralis var. *clathrata* (Østrup) Cleve	5300	Ab	M, In	1	-	1	-	-
Ditylum brightwellii (West) Grunow	11 800	tb	M	1	-	1	1	-
Entomoneis alata (Ehrenberg) Poulin & Cardinal	3000	-	-	1	-	1	1	1
E. kjelmanii (Cleve in Cleve & Grunow) Poulin & Cardinal	78 000	Ab	M, In	1	1	1	-	-
E. kjelmanii var. *subtilis* (Grunow) Poulin & Cardinal	16 000	Ab	M, In	1	-	1	-	-
E. paludosa (W. Smith) Poulin & Cardinal	28 800	Ab	B, In	1	-	1	1	-
E. paludosa var. *hyperborea* (Grunow in Cleve & Grunow) Poulin & Cardinal	29 400	Ab	M, In	1	-	1	-	-
E. pseudopulex Osada & Kobayasi	23 600	-	-	1	-	-	-	-
E. punctulata (Grunow) Osada & Kobayasi	18 700	Ab	B, In	1	-	1	1	-
Entomoneis sp.	25 200			1	-	1	-	-
Eucampia groenlandica Cleve	1500	Ab	M, N	1	-	1	-	1
Fallacia forcipata (Greville) Stickle & Mann	23 520	c	M	1	-	1	-	-
Fossula arctica Hasle, Syvertsen & von Quillfeldt	1400	Ab	M, In	2	1	1	3	1
Fragilaria striatula Lyngbye	2560	Ab	M, In	2	1	1	1	-
F. ulna (Nitzsch) Lange-Bertalot	7300	-	F	1	-	1	-	-
Fragilariopsis cylindrus (Grunow) Krieger	100	b	M, In	2	1	1	2	1
F. oceanica (Cleve) Hasle	400	Ab	M, In	2	1	1	1	1
Gomphonemopsis cf. *exigua* (Simonsen) Medlin	1920	Ab?	M, Ep, In	2	1	1	1	1
Grammatophora arctica Cleve	12000	Ab?	M, N	1	-	1	-	-
G. oceanica (Ehrenberg) Grunow	9000	Ab?	M, N	-	-	1	-	-
Guinardia delicatula (Cleve) Hasle	7000	c	M, N	1	-	1	-	-

Table continued from previous column.	Cell vol. ($m\mu^3$)	Range	Ecology	Abundance White Sea Ice	Snow	Water	Bar. Sea Ice	Water
Gyrosigma compactum Greville	4300	-	-	1	-	1	1	-
G. fasciola var. *tenuirostris* (Grunow) Cleve	7000	Ab?	M, N	1	-	-	-	-
G . hudsonii Poulin & Cardinal	18 000	Ab	M, In	1	1	-	-	-
G. tenuissimum var. *hyperborea* (Grunow) Cleve	3400	-	M, N	1	-	1	1	-
Hannaea arcus (Ehrenberg) Patrick	3200	-	F	-	-	1	-	-
Hantzschia sp.				-	-	1	1	-
Haslea sp.				1	-	-	-	1
Lauderia annulata Cleve	22 800	tb	M	1	-	-	1	1
Leptocylindrus danicus Cleve	1200	tAb?	M, N	1	-	1	-	1
L. minimus Gran	600	tAb	M	1	-	1	-	-
Licmophora communis (Heiberg) Grunow	4100	Ab?	M, N	1	-	1	-	-
L. gracilis (Ehrenberg) Grunow	18 200	-	M, N	1	-	1	-	-
Mastogloia sp.				1	-	1	1	-
Melosira arctica Dickie	1500	Ab	M, In	1	-	1	2	1
M. moniliformis (O.F.Müller) Agardh	25 200		B, N	1	-	-	-	-
M. nummuloides Agardh	43 500	c	M, N	1	-	1	-	-
Melosira sp.				-	-	1	-	-
Meridion circularis (Grev.) Agardh	400	-	F	-	-	1	-	-
Meuniera membranacea (Cleve) P.C. Silva	15 000	Ab	-	1	-	-	-	-
Navicula algida Grunow	120 000	Ab	M, In	1		-	-	-
N. directa (W.Smith) Ralfs	9000	Ab	-	1	-	1	-	-
N. distans (W.Smith) Ralfs	56 300	Ab?	Be	1	-	1	-	-
N. gelida Grunow	15 000	Ab	M, In	1	-	-	-	-
N. glacialis Cleve	7300	Ab	M, In	1	-	-	-	-
N. granii (Jørgensen) Gran	2700	Ab	M, In	2	-	1	1	-
N. cf. *lineola* Grunow	9050	Ab	M, In	1	-	1	1	-
N. menisculus var. *meniscus* (Schum.) Hust.	2200	-	F	1	-	-	-	-
N. microcephala Grunow	540	-	F	1	-	-	-	-
N. monilifera Cleve	10 000	Ab?	M	1	-	-	-	-
N. pelagica Cleve	1100	Ab	E, N	2	-	1	2	1
N. pellucidula Hustedt	7200	Ab	M, In	1	-	-	-	-
N. septentrionalis (Grunow) Gran	800	Ab	M, N	1	-	1	-	-
N. superba Cleve	9600	Ab	M, In	1	-	-	-	-
N. transitans var. *derasa* (Grunow) Cleve	34 900	Ab	-	1	-	1	-	-
N. vanhoeffenii Gran	2200	Ab	E, N	1	-	1	-	-
Nitzschia angularis W.Smith	3200	-	-	-	-	1	-	-
N. dissipata (Kützing) Grunow	2250	-	F	1	-	-	-	-

Table continued from previous column.	Cell vol. (mµ³)	Range	Ecology	Abundance: White Sea Ice	White Sea Snow	White Sea Water	Bar. Sea Ice	Bar. Sea Water
N. frigida Grunow	4500	Ab	M, In	4	1	1	3	1
N. hybrida Grunow	2400	Ab	B, In	1	-	-	-	-
N. longissima (Brebisson) Ralfs	830	b	M, N	1	1	1	1	-
N. neofrigida Medlin	19 000	Ab	M, In	1	1	1	-	-
N. pellucida Grunow	1100	Ab?	B	1	-	-	-	-
N. polaris Grunow	6500	Ab	M, In	1	-	-	-	-
N. promare Medlin	560	Ab	M, In	2	1	1	1	-
N. recta Hantzsch.	1400	-	F	1	-	-	-	-
N. scrabra Cleve	12 000	Ab	M	1	1	1	-	-
N. sigmoidea (Ehrenberg) Wm. Smith	9000	-	B	1	-	1	1	-
Odontella aurita Agardh	10 500	c?	B, N	1	-	1	-	1
Paralia sulcata (Ehrenberg) Cleve	3300	c?	M, Be	1	-	1	1	-
Pauliella taeniata (Grunow) Round et Basson	1000	Ab	E, Mn	2	1	1	3	1
Pinnularia guadrataera var. *baltica* Grun	15 000	tAb	M, N	1	-	1	-	-
P. semiinflata (Øestrup) Gran	5400	Ab	M, In	1		-	-	-
Plagiotropis lepidoptera (Gregory) Poulin & Cardinal	60 000	tAb	M, N	1	-	1	-	-
P. scaligera Grunow in Cleve & Grunow	10 000	-	-	1	-	1	1	-
Planotidium delicatulum (Kützing) Round & Bukht.	200	Ab?	E, N	1	-	-	-	-
Pleurosigma angulatum (Quekett) Wm.Smith	6000	tAb?	B, N	1	1	1	1	-
P. clevei Grunow in Cleve & Grunow	35 000	Ab	M, In	1	-	1	1	-
P. finmarchicum Cleve & Grunow	67 500	Ab?	Mn	1	-	1	1	-
P. formosum Wm.Smith	18 700	-	-	1	-	1	-	-
P. normanii Ralfs	4500	c?	-	1	1	1	1	-
Porosira glacialis (Grunow) Jørgensen	38 800	b	N	1	-	1	1	1
Proboscia eumorpha (Castracane) Takahashi, Jordan & Priddle	3200	c	M, Mn	-	-	-	-	1
Pseudogomphonema kamtchaticum (Grunow) Medlin	7200	-	Ep	1	-	1	2	-
P. septentrionale (Øestrup) Medlin	3200	Ab?	M, Ep, In	1	-	-	-	-
Pseudo-nitzschia australis (Cleve) Heiden	3100	tb	M, Mn	1	-	1	-	1
P. calliantha (Hasle) Lundholm, Moestrup & Hasle	100	Ab	M, Mn	1	-	1	1	-
P. delicatissima (Cleve) Heiden	200	Ab	M, Mn	1	-	1	-	-
P. granii (Hasle) Hasle	30	Ab?	-	1	-	1	-	1
P. pungens (Grunow & Cleve) Hasle	1400	c	M, Mn	1	-	-	-	-
P. seriata (Hasle) Hasle	3200	Ab	M, Mn	-	-	1	-	-
P. seriata f. obtusa (Hasle) Hasle	2200	Ab	-	1	-	1	-	-
Rhabdonema arcuatum (Lyngbye) Kützing	49 500	Ab	Ep	1	-	1	-	-
Rhizosolenia hebetata f. *semispina* (Hensen) Gran	37 500	Ab	M, Mn			-	-	1
Rhizosolenia setigera Brightwell	18 000	c	M, Mn	1	-	-	-	-
Rhoicosphenia curvata (Kützing) Grunow	4000	-	B, N	1	-	1	-	-
Skeletonema costatum (Greville) Cleve	200	c	M, Mn	2	1	1	2	1
Stauroneis amphioxys Gregory	24 000	Ab?	N	1	-	-	-	-
Stenoneis sp.				1	-	-	-	-
Synedropsis hyperborea (Grunow) Hasle, Medlin & Syvertsen	270	Ab	M, In	2	-	1	2	1
Synedropsis hypeboreoides Hasle, Medlin & Syvertsen	250	Ab	M, In	1	-	1	1	-
Tabellaria binalis (Ehrenberg) Grunow	4800	-	F	1	-	1	-	-
T. fenestrata (Lyngbye) Kützing	30 000	-	F	1	-	1	1	-
T. flocculosa (Roth.) Kützing	18 700	-	F	-	-	1	1	-
Thalassionema nitzschioides (Grunow) Grunow & Hustedt	400	tAb	M, Mn	1	1	1	-	-
Thalassiosira angulata (Gregory) Hasle	4300	Ab	M, Mn	1	1	1	1	1
T. anguste-lineata (A.Schmidt) Fryxell & Hasle	12 000	tAb	M, N	1	-	1	-	1
T. antarctica var. borealis Fryxell, Douc. & Hubb.	14 580	Ab	M, Mn	1	1	1	1	1
T. bioculata (Grunow) Ostenfeld	18 000	Ab?	-	1	-	-	-	-
T. bulbosa Syvertsen	400	Ab	-	1	-	1	-	1
T. conferta Hasle	2000	tb	-	2	1	1	-	-
T. eccentrica (Ehrenberg) Cleve	23 400	tAb	E, Mn	-	-	1	-	-
T. gravida Cleve	9000	b	M, Mn	1	-	1	-	-
T. hyalina (Grunow) Gran	6500	Ab	M, Mn	2	1	1	1	-
T. hyperborea (Grunow) Hasle & Lange	25 000	Ab	B, In	1	1	1	1	-
T. nordenskioeldii Cleve	2900	Ab	E, N	1	1	1	1	1
Trachyneis aspera (Ehrenberg) Cleve	160000	Ab	M, N	1	-	1	-	-
Tryblionella litoralis (Grunow) D.G.Mann	18 000	-	M, Be	1	-	1	1	-
Undatella cf. *quadrata* (Bréb. in Kütz.) Padd. et Sims	24 300	tAb?	M, Be	1	-	1	1	-

Table continued from previous column.

	Cell vol. (mμ³)	Range	Ecology	Abundance: White Sea Ice	White Sea Snow	White Sea Water	Bar. Sea Ice	Bar. Sea Water
Class Dinophyceae								
Alexandrium insuetum Balech	1500	tAb?	N	1	-	1	1	2
A. ostenfeldii (Paulsen) Balech & Tangen	147000	tAb?	N	1	-	1	-	-
A. tamarense (Lebour) Balech	19000	tAb?	N	1	-	1	1	-
Amylax triacantha (Jørgensen) Sournia	5000	Ab	N	-	-	1	-	-
Amphidinium crassum Lohmann	2300	Ab?	N	1	-	1	1	1
A. fusiformis Martin	1050	Ab?	N	1	-	1	1	1
A. larvale Lindemann	190	-	E, N	1	-	1	-	1
A. latum Lohmann	1350	Ab?	N	-	-	-	-	1
A. longum Lohmann	1300	c	N	1	-	1	1	1
A. sphenoides Wulff	1100	Ab	M	1	-	1	-	1
Ceratium fusus (Ehrenberg) Dujardin	91800	c	M	1	-	1	-	-
C. lineatum (Ehrenberg) Cleve	46900	tb	M	-	-	1	-	-
Cochlodinium archimedes (Pouchet) Lemmermann	1400	Ab	M	1	-	1	1	1
Cochlodinium brandtii Wulff	8000	Ab	Mn	-	-	1	1	-
Cochlodinium schuetti (Kofoid & Swezy) Shiller	6000	-	-	1	-	1	1	1
Dinophysis acuminata Claparède & Lachmann	19000	c	N	-	-	1	-	-
D. acuta Ehrenberg	18000	b	M	1	-	-	-	-
D. arctica Mereschkowsky	9000	b	N	-	-	1	-	-
D. contracta (Kofoid & Skogsberg) Balech	6000	tAb	M	-	-	1	-	-
D. islandica Paulsen	36000	Ab	N	-	-	1	-	-
D. norvegica Claparède & Lachmann	35000	Ab	N	1	-	1	-	-
Diplopelta parva (Abé) Matsuoka	5900	Ab	N	1	-	1	1	-
Enthomosigma peridinioides Shiller	1200	tAb?	N	1	-	1	1	-
Glenodinium gymnodinium Penard	50000	-	B, N	1	-	-	-	-
Gonyaulax digitalis (Pouchet) Kofoid	40000	b	Mn	-	-	1	-	-
G. grindleyi Reinecke	18000	Ab	N	1	-	1	1	-
G. spinifera (Claparède & Lachmann) Diesing	9900	c	Mn	1	-	1	-	-
Gymnodinium albulum Lindermann	150	-	B, N	1	1	1	1	2
G. arcticum Wulff	4000	Ab	Mn	1	-	1	-	1
G. blax Harris	260	-	F	1	-	1	-	-
G. frigidum Balech	13500	b	N	1	-	-	-	1
G. japonica Hada	400	-	N	1	-	1	1	1
G. heterostriatum Kofoid & Swezy	4700	tAb?	N	-	-	1	-	-
G. lebourii Pavillard	108000	-	-	1	-	1	-	-
G. simplex (Lohmann) Kofoid & Swezy	190	tAb	N	1	-	1	-	1
G. wulfii Schiller	4000	tAb	N	1	-	-	-	-
Gyrodinium cf. *aureolum* Hulburt	24000	Ab	-	1	-	-	1	1
G. cohnii (Seligo) Schiller	4500	Ab?	-	1	-	-	-	-
G. esturiale Hulburt	1700	c	N	-	-	1	-	-
G. fusiforme Kofoid & Swezy	1620	tAb	Mn	1	-	1	1	1
G. lachryma (Meunier) Kofoid & Swezy	36700	Ab	Mn	1	-	1	-	1
G. prunus (Wulff) Lebour	47000	c	-	1	-	-	-	1
G. spirale (Berg) Kofoid & Swezy	17000	c	-	1	-	1	1	1
Heterocapsa rotundatum (Lohmann) Loeblich	400	c	N	1	-	1	-	2
H. triquedrum (Lohmann) Hansen	6900	c	B, N	-	-	1	-	-
Karenia brevis (Davis) G.Hansen & Moestrup	4000	Ab	N	1	-	-	-	-
Karlodinium micrum (Leadbeater & Dodge) J.Larsen	1700	-	-	1	1	1	-	-
K. veneficum (Ballantine) J.Larsen	900	-	-	1	1	1	1	1
K. vitiligo (Ballantine) J.Larsen	1700	-	-	1	1	1	1	1
Katodinium glaucum (Lebour) Loeblich	2100	tAb	N	1	-	1	1	-
Micracanthodinium claytonii (Holmes) Dodge	3800	-	-	-	-	-	-	1
Oblea baculifera Balech	1700	b	-	1	-	1	-	-
Oxyrrhis marina Dujardin	6500	tAb?	E, N	1	-	-	-	-
Oxytoxum belgicum Meunier	5250	-	-	-	-	1	-	-
Peridinella catenata (Lev.) Balech	4700	Ab	N	1	-	1	1	-
Preperidinium meunieri (Pavillard) Elbrächter	10000	t	M	1	-	1	-	1
Pronoctiluca acuta (Lohmann) Schiller	1600	tAb	Mn	-	-	1	-	-
P. pelagica Fabre-Domergue	9400	c	M	-	-	-	1	1
Prorocentrum balticum (Lohmann) Loeblich	400	c	M	1	-	1	1	1
P. cordatum (Ostefeld) Dodge	1600	tAb	N	1	-	1	-	1
P. micans Ehrenberg	6000	tAb	N	1	-	1	-	-
P. minimum (Pavillard) Schiller	720	c	N	1	-	1	-	-
Protoperidinium bipes (Paulsen) Balech	2000	c	N	1	-	1	-	1
P. brevipes (Paulsen) Balech	10100	Ab	N	1	-	1	-	1
P. depressum (Bailey) Balech	130000	c	M	-	-	1	-	-
P. granii (Ostefeld) Balech	66000	c	N	1	-	-	1	-
P. islandicum (Paulsen) Balech	36000	Ab	N	-	-	-	-	1

Table continued from previous column.	Cell vol. ($m\mu^3$)	Range	Ecology	Abundance White Sea Ice	Abundance White Sea Snow	Abundance White Sea Water	Abundance Bar. Sea Ice	Abundance Bar. Sea Water
P. nudum (Meunier) Balech	9400	Ab	Mn	1	-	1	-	-
P. pallidum (Ostenfeld) Balech	13 500	b	M, N	-	-	1	-	-
P. pellucidum Bergh	51 800	c	N	-	-	1	-	1
P. pyriforme subsp. *pyriforme* (Paulsen) Balech	24 000	c	-	-	-	1	-	-
P. pyriforme subsp. *breve* (Paulsen) Balech	23 300	Ab?	-	-	-	-	-	1
P. subinerme (Paulsen) Loeblich III	62 500	c	-	1	-	-	-	1
Scrippsiella trochoidea (Stein) Loeblich III	5900	c	N	1	1	1	1	1
Torodinium robustum Kofoid & Swezy	4500	-	-	1	-	1	-	1
Warnowia maculata (Kofoid & Swezy) Lindemann	15 750	-	-	-	-	-	-	1
Woloszynkia reticulata Thompson	1700	-	B, N	-	-	-	1	1
Class Prymnesiophyceae								
Corimbellus aureus Green	260	-	Mn	1	-	1	-	-
Emiliania huxleyi (Lohmann) Hay & Mohler	400	c	-	1	2	1	2	1
Zigosphaera massilii (Borsetti & Cati) Heimdal	700	-	-	1	-	1	-	1
Phaeocystis pouchetii (Hariot) Lagerheim	35	b	M	3	4	3	3	4
Primnesium sp.				1	-	-	-	2
Class Cryptophyceae								
Chroomonas marina (Büttner) Butcher	1100	-	N	1	-	1	-	1
Hilea fusiformis (Schiller) Schiller	64	tAb?	N	1	-	2	1	2
H. marina Butcher	18	tAb?	N	2	2	3	1	1
Leucocryptos marina (Braarud) Butcher	480	Ab	Mn	-	-	1	-	1
Plagioselmis prolonga Butcher	750	-	-	1	1	1	-	1
Teleaulax acuta (Butcher) Hill	340	-	Mn	1	1	1	-	2
Class Chrysophyceae								
Calicomonas gracilis	20	-	-	2	2	2	-	-
Calicomonas sp.				-	-	-	-	3
Dinobryon balticum (Schütt) Lemmermann	800	Ab	M	1	-	2	2	3
D. belgica Meunier	600	Ab	M	1	-	1	-	1
D. faculiferum (Willén) Willén	260	Ab	Mn	1	-	1	-	1
Ochromonas crenata Klebs	300	-	B, N	1	1	1	3	3
O. marina Lackey	480	Ab	N	-	-	1	-	1
Class Dictyochophyceae								
Dictyocha fibula Ehrenberg	5500	tAb?	M	1	-	1	-	-
D. speculum Ehrenberg	6900	c	E, N	-	-	1	1	1
Division Chlorophyta								
Class Chlorophyceae								
Carteria sp.				1	-	1	-	2
Chlamidomonas sp.				1	2	1	-	-
Tetraselmis sp.				1	-	-	-	-
Class Euglenophyceae								1
Eutreptiella braarudii Throndsen	7500	Ab	N	1	-	1	1	1
E. eupharyngea Moestrup & Norris	600	Ab	N	1	1	1	1	1
E. gymnastica Throndsen	2000	-	N	1	-	1	2	1
E. hirudoidea Butcher	560	-	N	1	-	-	-	-
Eutreptia sp.				-	-	1	1	-
Euglena acus	12000	-	-	1	-	1	1	-
Class Prasinophyceae								
Halosphaera viridis Schmitz	171 500	c	-	1	-	1	-	1
Micromonas pusilla (Butcher) Manton & Parke	4	tAb?	Mn	-	-	-	-	2
Pachysphaera marshalia Parke	100	tAb?	M	1	-	-	-	1
Pterosperma vanhoffenii (Jørgensen) Ostenfeld	32 000	-	Mn	1	-	1	-	-
Pyramimonas grossii Parke	50	c?	-	2	1	1	2	2
P. orientalis McFadden, Hill & Wetherbee	30	tAb?	N	1	-	2	-	1
Resultor micron (Throndsen) Moestrup	4	-	N	-	-	-	1	-
Cyanobacteria								
Anabaenopsis sp.				-	-	1	-	-
Synechococcus sp.				-	-	1	-	2
Phylum Zoomastigophora								
Class Kinetoplastida								
Telonema subtilis Griessmann	300	-	N	1	-	1	1	1
Class Choanoflagellidea								
Calliacantha natans (Grøntved) Leadbeater	32	Ab	Mn	2	2	2	-	-
Parvicorbicula socialis ? (Meunier) Deflandre	20	Ab	N	3	4	3	2	3
Monosiga marina Grøntved	100	tAb?	M	3	3	2	-	2
Pleurasiga reinoldsii Throndsen	6900	tAb?	N	-	-	1	-	-
Class Raphidophyceae								
Heterosigma akashiwo (Hada) Hada	768	tAb?	b, N	1	-	1	3	1