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Article

The Sub-Ice Algal Communities of the Barents Sea Pack Ice: Temporal and Spatial Distribution of Biomass and Species

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Abstract: This work summarizes ice algal studies, presented as biomass and species temporal and spatial distribution, during 11 cruises conducted between 1986 and 2012. The majority of the biomass was found as loosely attached sub-ice algal layers, and sampling required diving. A maximum of 40 mg chlorophyll m^{-2} and 15.4×10^9 cells m^{-2} was measured in May. The species diversity was separated in zones based on ice thickness, with the highest biodiversity in the medium-thick ice of 30–80 cm. *Nitzschia frigida* was the most common species. There was a significant positive relationship between the dominance of this species and ice thickness, and it dominated completely in thick ice. Other common species, such as *N. promare* and *Fossulaphycus arcticus* reacted oppositely, by becoming less dominant in thick ice, but the positive correlation between total cell numbers and number of these three species indicated that they would most likely dominate in most populations. *Melosira arctica* was found several times below medium-thick annual ice. Algae occurred from top to bottom in the ice floes and in infiltration layers, but in very low numbers inside the ice. The bipolar dinoflagellates *Polarella glacialis* inhabited the ice, both as vegetative cells and cysts. The algal layers detached from the ice and sank in late spring when melting started. The cells in the sediments form an important food source for benthic animals throughout the year. Fjord populations survive the winter on the bottom and probably form next year's ice algal inoculum. A few 'over-summer' populations found in sheltered locations might provide supplementary food for ice amphipods in late summer. The future faith of the ice flora is discussed in view of a warmer climate, with increased melting of the Arctic ice cover.

Keywords: Barents Sea; ice algae; algal species; algal biomass; spatial distribution; temporal distribution; over-vintering

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1. Introduction

Data on ice algal species from the Arctic, covering the last 140 years, have been found in a number of various sources. Recently they were compiled to a first assessment of pan-Arctic biodiversity of ice algae [1]. After an update, close to 1300 sympagic algae and other protists associated with sea ice have been recorded [2].

Quantitative ice algal investigations in the Arctic started in the 1960s, and the western part hosts the most extensively studied areas, from Chukchi Sea to Davis Strait. Chlorophyll measurements exist for a number of areas in the west [3]. Fewer investigations have been performed in the eastern Arctic: Greenland Sea [4], Fram Strait [5], Barents Sea [6], and the Laptev Sea [6]. A couple of studies exist from the Arctic Ocean [7,8]. Several of these investigations include few samples, so that the biomass distribution in the eastern Arctic is still fairly unknown. Even fewer data exist for cell numbers. A limited number of ice cores from the Barents Sea [9], the Kara Sea [10], and the Laptev Sea [11] have provided some information. The present set of data sum up our knowledge of the biomass, species distribution, and biodiversity of the Barents Sea sub-ice algal flora during 11 cruises from

1986 until 2004, covering the months April–September, and from the high north in the 2012 winter.

Qualitative studies of ice algae have been going on in the Barents Sea since the 1890s, but quantitative measurements only began in the last 30 years, starting with the Norwegian Marine Ecological Program (PRO MARE 1984–1988, [12,13]). The production of ice algae relative to phytoplankton increases with latitude, and for the northern Barents Sea about 20% of the total primary production may come from ice algae, amounting to 5 g C m^{-2} $year^{-1}$ [14,15]. For the central Arctic Ocean ice algal production has been calculated to represent up to 50% of the total production [7,16].

Most of the ice in the Barents Sea ice was found east of Spitsbergen [17]. In winter the ice used to cover the Arctic water north of the Polar Front (the mixing area between the Arctic and Atlantic water masses [18], during the years of our investigations. The Barents Sea is dominated by annual pack ice, fast ice is found only in the fjords in Svalbard and around Hopen Island. Earlier, as much as 75%, or more than 1 million km, could be covered by ice in winter. Now the Barents Sea region is the part of the Arctic where ice reduction has been the most dramatic in the last few years [19–22] particularly in winter. The same trend has also been observed in the Fram Strait [23–26]. The ice is formed locally, but during the years of investigation some inflow of multi-year ice from the Arctic Ocean was seen furthest north through the passages east of Svalbard and Hinlopen. This supply of sea ice from the Arctic Ocean, and from the Kara Sea, is still important for the Barents Sea ice cover. It produces fresh water during melting, keeping up the stable, upper layer and an Arctic Ocean climate in the northern Barents Sea [27].

All, or most, of the ice in the Barents Sea may melt in summer, as in our years of investigation. Maximum ice cover is found in April, and minimum ice cover is found in September. The trend, however, shows that the ice cover is withdrawing further north over time, both in summer and winter, although large interannual variations occur [28–30]. The northern ice border has now been found at 82–83° N in summer (National Snow and Ice data Center, Boulder, Colorado, USA, http://nsidc.org/arcticseaicenews/2021/09/arctic-sea-ice-at-highest-minimum-since-2014/, accessed on 16 September 2021), where the highest minimum of annual sea ice was measured in the Arctic.

There is always a high inter-annual variability in the extent of the ice cover in the Barents Sea, visualized by the position of the ice edge in spring and autumn [31]. The trend from 1979 in mean ice extent is slightly negative for the Barents Sea, with suggestions of a 3.5% reduction of ice cover per decade [31,32]. The thickness of the ice has been measured at selected sites in the Barents Sea, and the fast ice at Hopen Island has decreased in thickness by 10 cm per decade since 1966 [33], while few or no data are available for the Barents Sea pack ice after 1988 [18]. However, changes have been observed in the timing and geographical area of melting in spring, which may relate to a changing ice cover. The spring of 2006 was special in that the ice cover retreated early and uncovered a large open water area in the central Barents Sea, and the ice border was situated as far north as 80° N in May already [34]. Although the following years have had more ice, the year 2006 is an indication of changes in the Barents Sea ice cover that may come in the near future. Recently, the ice border in winter was found north of Svalbard, as in January 2012, which provided us with an opportunity to do winter studies far north.

Because it was a pack ice area with ice algae loosely attached to the ice underside, rather than inside the ice, sampling in the Barents Sea has required diving instead of coring. This has strongly restricted the amount of data collected each cruise, and consequently there has been necessary to merge several years of sampling to provide a realistic description of the ice flora in this area. The data will contribute to bridging the gap of knowledge, in particular about biomass, between the eastern and western part of the Arctic [3]. Additionally, these data may represent the 'normal' or 'pre-warming' conditions and may be used for comparison to future investigations, since no large changes in the ice conditions was observed during the years of investigation. Data include vertical and horizontal distribution of the ice flora, biomass, and biodiversity, as well as the seasonal development. They are discussed in relation to environmental factors, both for the whole communities and for a number of species, and in view of future changes to the ice environment. The last subject addressed is the overwintering of ice algae. Winter studies in the high Arctic are few, but the present data will add some information to this long-debated subject

The Arctic Sea ice cover has declined over the last 50 years (particularly in summer), but with a stronger trend for the last 25 years [30], followed by a thinning of the ice [35].

2. Material and Methods

2.1. Study Area

The ice edge zone is highly dynamic [36,37], and stretches from the Bear Island and the Central Bank in the south, to areas north of Spitsbergen, depending on the time of year. The southernmost spreading of the ice edge zone in the Barents Sea is mainly controlled by the position of the Polar Front, while summer melting is highly dependent on incoming radiation, air and water temperature, amount of snow on the ice, and wind. This produces seasonal variations, but short time variations, particularly caused by the wind, is common. Tides cause periodic movements of the ice [18]. As a result, the ice cover is constantly moving, causing ridging, floe break-up, and leads opening and closing, as we experienced during our cruises. In winter, up to 60% of the leads are less than 50 m wide and occur in the outer 10 to 50 km of the marginal ice zone (MIZ, [38]). Winds from the north, which were often dominating, pushed the ice cover southwards, causing a wide and loose MIZ. Opposing winds pushed the ice northwards, creating a sharp ice border. Gradients in ice quality and large fluctuations in size and form of ice floes thus signified the ice zone. The average thickness of the pack ice was (1966–1988) calculated earlier to be 95 cm at 75° N, and 170 cm at 80° N [18]. Our investigations covered annual ice from 40 cm to about 200 cm thickness during the spring season, and multi-year ice up to 3 m was found in late summer/autumn. Snow layer depth was 20–30 cm on first-year ice in winter and spring, decreasing to <10 cm in early summer during our investigations [13,14].

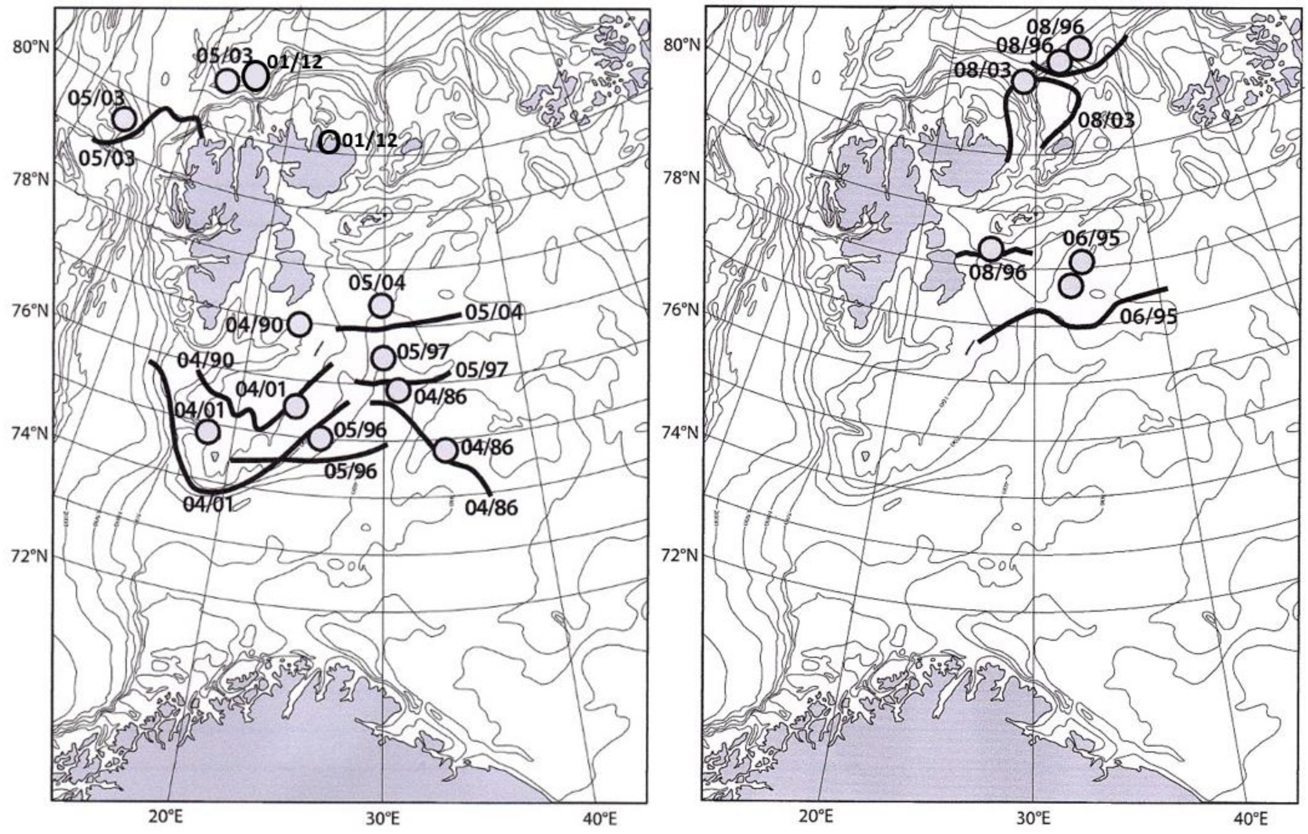
2.2. Analyses

Ice algal samples from 11 cruises from 1986 to 2012 at various times of the year are included in this work (Table 1). All but one cruise went to the northern part of the Barents Sea (north of the Polar Front and east of Spitsbergen, Figure 1a,b), but in May 2003 samples were collected north-west of Svalbard. The cruises were performed with three ships: the coast guard vessel 'Senja' (April 1986 and 1990), the 'Lance' from the Norwegian Polar Institute (June 1995, July/August 1996, August/September 2003), and the 'Helmer Hansen' (former 'Jan Mayen') from the University of Tromsö (May 1996, May 1997, April 2001, May 2003, May 2004 and the winter cruise in 2012).

Ice algae were sampled in the annual pack ice of the Barents Sea, except for some samples from multi-year ice and the 2012 winter cruise to the fast ice in Rijpfjorden. Samples were collected from the thin outer ice and inwards if conditions applied, otherwise from the ice the ship could enter. Sampling was in general conducted by diving under ice floes of variable size. The ship was anchored to a floe, and the diver, avoiding the anchor floe due to possible disturbance from the ship's propellers, started from a lead and sampled under several floes nearby. In rafted areas, ice algae from caves and various ice structures were also included.

Table 1. Positions and dates for the various cruises in the Barents Sea 1986–2004. Ice type describes ice in the sampling area, while ice thickness (cm) and snow depth (cm) are determined from sampling sites. Under-ice irradiance (µmol m^{-2} s^{-1}), chlorophyll (mg m^{-2}), and cell numbers ($\times 10^6$ m^{-2}) are given as average and range (in brackets), the same for the nutrient concentrations (nitrate, phosphate, and silicate, µmol L^{-1}) from surface waters at sampling sites.

Year	Date	Position	Ice Thickness, Sampling Site (cm)	Snow Depth (cm)	Ice Type and Thickness	Chlorophyll (mg m^{-2})	Cell Numbers ($\times 10^6$ m^{-2})	Nitrate (µmol L^{-1})	Phosphate (µmol L^{-1})	Silicate (µmol L^{-1})	Under-Ice Irradiance (µmol m^{-2} s^{-1})
1986	17–19 April	74°54′–75°54′ N 30°45′–32°59′ E	100–110	5–14	Annual, flat and rafted (80–150)	11.8 (1.31–17.7), $n = 4$	2065 (163–5695) $n = 4$	10.3 (9.5–11.0) $n = 2$	0.83 (0.75–0.91) $n = 2$	6.1 (5.7–6.5) $n = 2$	9 (5–14) $n = 3$
1990	20–28 April	76°46′–77°03′ N 23°44′–24°27′ E	100–140	20–30	Annual, flat and rafted and thicker multi-year floes	0.45 (0.31–0.65), $n = 4$	41 (35–46) $n = 2$	-	0.85 (0.6–1.1) $n = 2$	2.5 (1.5–3.5) $n = 2$	34 (23–45) $n = 2$
1995	15–21 June	77°30′–78°05′ N 34°17′–34°36′ E	100–200	5–10	Annual, flat and rafted (100–200)	0.11 (0.03–0.21), $n = 6$	300 (8–560) $n = 5$	2.0 (1.5–2.6) $n = 3$	0.26 (0.2–0.3) $n = 3$	1.63 (1.1–2.0) $n = 3$	-
1996	15–25 May	75°02′–75°14′ N 24°54′–26°27′ E	40–200	10–30	Annual, flat and rafted, with caves (40–200)	7.9 (0.80–39.0), $n = 17$	2520 (190–15,400) $n = 17$	6.3 (4.3–8.1) $n = 4$	0.47 (0.4–0.6) $n = 4$	2.75 (1.4–3.9) $n = 4$	28 (1–58) $n = 7$
1996	28 July–09 August	74°40′–81°34′ N 25°52′–34°50′ E	150–200	5–15	Old annual, rafted, with caves and large brine channels (150–340)	2.3 (0.03–9.60), $n = 10$	800 (81–2140) $n = 10$	Below detection	0.08 (0.04–0.2) $n = 4$	0.22 (0.05–0.4) $n = 4$	6 (2–19) $n = 5$
1997	20–25 May	76°10′–76°30′ N 29°56′–30°13′ E	30–80	2–20	Annual, flat, some rafted (30–300)	0.18 (0.04–0.48), $n = 20$	82 (18–270) $n = 18$	Below detection	0,07 (0.06–0.09) $n = 4$	0.82 (0.6–1.3) $n = 4$	72 (10–152) $n = 10$
2001	09–16 April	74°56′–75°20′ N 19°17′–23°59′ E	60–120	5–20	Annual, flat, thicker floes between thin new ice	0.26 (0.01–0.67), $n = 8$	-	9.9 (9.0 -11.0) $n = 4$	0.85 (0.83–0.87) $n = 4$	5.52 (5.5–5.9) $n = 4$	14 (3–31) $n = 4$
2003	12–26 May	79°31′ 80°49′ N 04°51′–11°37′ E	40	10–15	Thin, annual ice and thick, rafted multi-year ice (40–300)	0.21 (0.17–0.26), $n = 4$	47 (33–60) $n = 2$	2.2 (2.1–2.4) $n = 2$	0.22 (0.20–0.23) $n = 2$	3.36 (3.1–3.6) $n = 2$	13 (12–14) $n = 2$
2003	23–25 August	80°51′–81°03′ N 28°22′–28°39′ E	110–270	2–20	Multi-year ice (100–200)	5.58 (2.46–8.70), $n = 2$	850 (120–1260) $n = 2$	1.5 (0.5–2.5) $n = 2$	0.22 (0.20–0.23) $n = 2$	2.05 (1.8–2.3) $n = 2$	29 (13–45) $n = 2$
2004	23–31 May	77°03′–77°13′ N 29°17′–29°52′ E	100–150	10–30	Large, annual floe, flat (100–150)	16.3 (6.78–35.4), $n = 26$	1610 (670–2850) $n = 16$	1.3 (0.0–3.1) $n = 5$	0.19 (0.09–0.32) $n = 5$	2.86 (2.3–3.6) $n = 5$	16 (5–41) $n = 11$



(**a**) (**b**)

Figure 1. Map of the sampling area for ice algae in the Barents Sea 1986–2012. (**a**) Winter and spring cruises (January–May), (**b**) Summer/autumn cruises (June–September). Lines mark the average ice border for each cruise, numbers mark the month and year.

Diver sampling was performed by using an electric suction sampler [39], adapted to algal sampling, to collect the algal layer on the ice under the surface. Quantitative samples were collected by screwing a Plexiglas frame (diameter 19 cm) with a serrate end into the ice, and carefully sucking up the algae within the frame [14]. A net bag (10 or 20 µm mesh size) in the suction sampler collected the algae. The algal layer on the net walls was carefully washed out with pre-filtered seawater from the same locality, and the volume measured. All handling of samples was carried out in dim light in a tent on the ice. Subsamples were taken for measurements of chlorophyll, cell identification, and enumeration. In April 1986, a few samples were taken with a small corer (diameter = 10 cm, height = 15 cm) from the ice underside by the diver. A few ice cores from June 1995 and from January 2012 were sampled with a SIPRE corer (diameter = 9 cm) from the top of the ice floe. The cores were cut in 10 cm slices, and melted slowly at low temperature and in darkness. In 2012, the slices were melted in 400 mL pre-filtered seawater from the sampling site to avoid osmotic shock for the cells, except for cores used for nutrient analyses. Samples for chlorophyll, cell numbers, and species identification were taken from the melted cores, the latter preserved with 20% formalin (1986–1997) or Lugol (2003–2012). Nutrient samples were also taken from the surface water close to sampling sites. Phytoplankton in the water nearby was sampled with a Rosette sampler and Niskin water bottles.

Under-ice light irradiance (as PAR) was measured at sampling sites in two minutes intervals by means of a diver-operated integrating quantum scalar irradiance meter (QSL-140, Biosphaerical Instruments).

Nutrients were analysed by standard methods for nitrate, phosphate, and silicate [40,41] except for 2003 and 2004, when they were analysed by standard seawater methods in a Flow Solution IV analyser from O.I. Analytical, USA. The analyser was calibrated using reference seawater from Ocean Scientific International Ltd., Havant, Hampshire, UK. Chlorophyll was measured fluorometrically in triplicates, using GF/C (1986, 1990–1997) or GF/F filters and methanol as an extracting agent [42]. Samples for particulate organic carbon in ice cores were filtered onto pre-combusted GF/F filters, and later analysed in a Leeman Lab CHN analyser.

Cells were counted in a compound microscope using Palmer-Maloney counting chambers (0.1 mL volume, the samples were usually very dense) at 400× magnification and phase contrast. At least 100 cells of the dominating species were counted. The following microscopes were used: Leica DM 2500 (1986, 1990, 2001, 2003), Leica Aristoplan (1995–1997), and Olympus Axioscope [2004]. The 1995 ice core samples were counted in a 2 mL 4-well Nunclon chamber and a Leitz Labovert inverted microscope, while the winter samples in 2012 were counted as 50 or 100 mL in a Zeiss Primo Vert inverted microscope. Some of the samples were cleaned [43] and mounted in Naphrax to provide additional floristic composition. The cleaned samples were counted in a Leica Aristoplan compound microscope at 400× magnification. Identification is based on the following literature: [44–61].

Data from the spring stations (before melting) were selected for Pearson's correlation coefficient [62] and were used to investigate relationships amongst abiotic and biotic parameters. Those were ice thickness, snow depth, light under ice, nitrate and silicate in the surface layers, total number of species, total cell numbers, total chlorophyll, cell numbers, and percentage of total cell numbers of the most frequent species (*Nitzschia frigida*, *N. promare*, *Fossulaphycus arcticus*, *Porosira glacialis*, *Attheya septentrionalis*, and *Synedropsis hyperborea*). Correlations were calculated for the growth season, defined as the time between when the first algae were located (April), and until melting started in June. The species used in the correlations were picked out amongst those appearing in most of the spring samples, and both their actual cell numbers in the samples, as well as their percentage of total cell numbers were used, since a species could dominate in an area even with low cell numbers. The physical parameters were primarily related to the ice, but since these algae are in close contact with the seawater, nutrients in the surface water at the sampling sites were also included.

3. Results

In total, ice algal samples were collected from more than half the year under variable snow and ice thickness, both under flat and rafted ice with caves and structures. The variability was considerable, both on a temporal and spatial scale, for chlorophyll and cell numbers (Table 1). Maximum biomass was found in spring, with 39 mg chlorophyll m^{-2} and 15.4×10^9 cells m^{-2} (Figure 2) in May 1996 and May 2004, respectively. Observed species and their maximum cell numbers are given in Table S1, along with the month they occurred. Some species lack cell numbers, these were only found in the cleaned samples or in lumps of ice floating in leads. In total, 87 species were identified in the samples, 72 of these were diatoms (47 pennate, 25 centric), 11 dinoflagellates, and 4 others (in addition a group of unidentified small flagellates).

3.1. The Winter Season

The winter cruise (Polar Night Cruise) to the northern part of the Barents Sea in January 2012 went to Rijpfjorden on Nordaustlandet and to the ice edge during a period of open water in a limited area north of Svalbard (Figure 1a). The fjord at 80° N is facing north, and the inner part had a 50–60 cm-thick fast ice cover with a 5–10 cm snow layer. There was no light during the day. The cell numbers in the ice were extremely low, 2–300 cells L^{-1} throughout the ice, up to 800 at the bottom. The particulate organic carbon values followed the cell numbers, with a maximum of 1000 µg L^{-1} (Figure 3A). Most of the cells were pennate diatoms, amongst them a few cells of *Nitzschia frigida*, *Fragilariopsis cylindrus*, and *Pseudo-nitzschia* sp. Diatom spores were observed in low numbers all through the ice cores, with highest concentration in the bottom layers. Naked dinoflagellates and flagellates were also observed, and the dinoflagellate *Polarella glacialis* was the most common species

(Figure 4A). The ice edge over the Sophia Depth was not clearly defined, but started with a zone of freshly formed pancake ice, which changed into larger floes (up to 2 m thick) further into the ice. We sampled ice cores of different lengths (100–200 cm), and the longest cores exhibited a two-peak distribution of cells and carbon, each quite similar to the shortest cores (Figure 3B,C). This indicated that the thickest ice was two years old. Carbon concentrations were similar to the Rijpfjorden ice, but cells numbers were 103 times higher, with maximum concentrations of 2.4×10^6 cells L^{-1}. The species composition was also quite different. Diatom spores appeared in roughly the same numbers as in most of the Rijpfjorden ice, while diatoms cells were much more common (max 8×10^5 cells L^{-1}, Figure 4B,C). Pennate diatoms were common, mostly *Fragilariopsis oceanica*, *Cylindrotheca closterium*, and *Navicula* sp. and *N. frigida* was present, but in low numbers. However, the dominating species was *Polarella*, which occurred with a maximum of 2.2 mill cysts L^{-1}. Hardly any vegetative cells were present. Other dinoflagellates, mostly naked forms, were found in the upper part of the 2 m cores with a maximum of 3×10^5 cells L^{-1}.

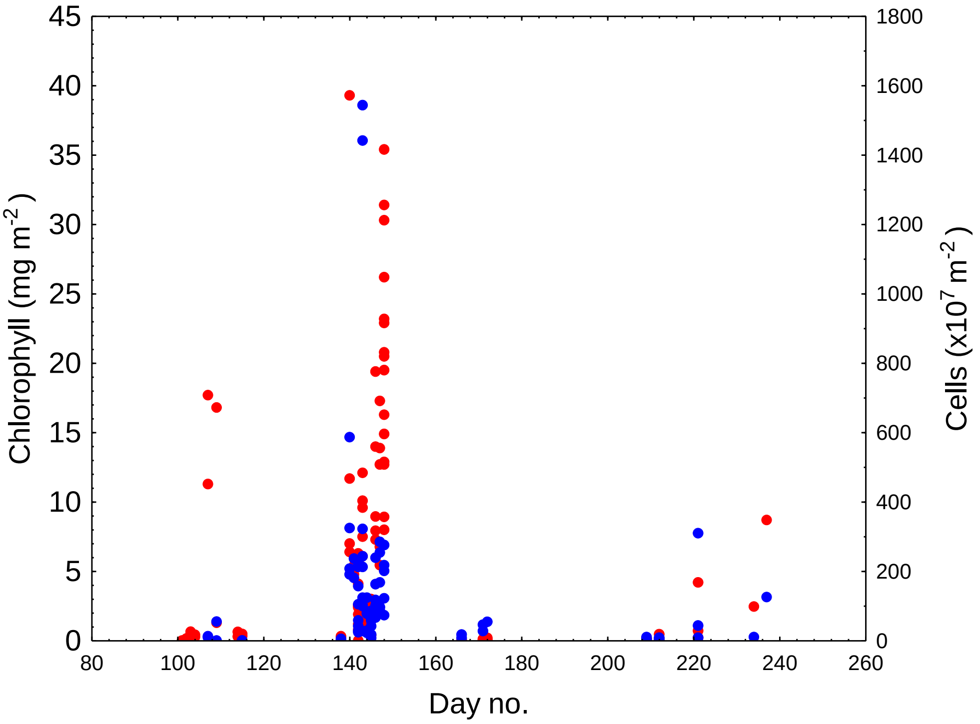


Figure 2. Temporal distribution of ice algal chlorophyll (mg m^{-2}) (red) and cell numbers (cells × 10^7 m^{-2}) (blue) in the Barents Sea pack ice 1986–2004.

3.2. The Spring Season

The spring season covers the cruises in April (1986, 1990, 2001) and May (1996, 1997, 2003, 2004), between 74° and 77° N (Figure 1a). With one exception, the surface water temperature at sampling sites was low, between −1.6 and −1.8 °C, which is not enough to induce melting of the ice cover. The ice conditions were different between the two months. The under-surface of the ice in April in the outer ice zone was soft and contained a visible layer of algae at the bottom; this ice was sampled by corer. Further into the ice, and for all samples in May, ice algae on the underside of more or less flat ice were growing as loosely attached thin layers, which were sampled by a diver with the suction sampler. In rafted ice, layers of algae were also found in caves and structures under the ice and were sampled in the same way.

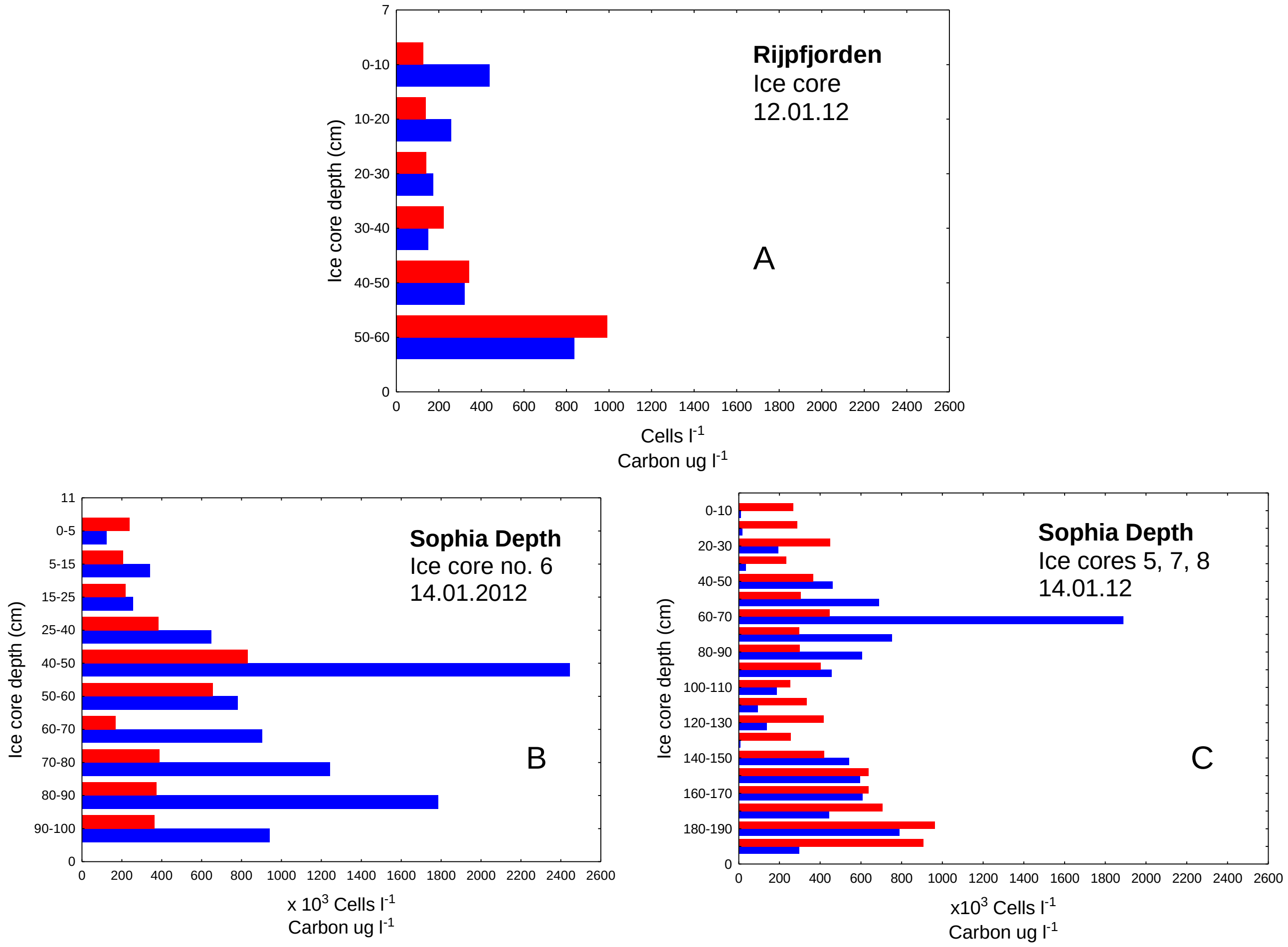


Figure 3. Vertical distribution of cells ($\times 10^3$ L^{-1}) and organic carbon (µg L^{-1}) in ice cores from Rijpfjorden (**A**) and the northern Barents Sea (Sophia Depth, **B** and **C**) pack ice in January.

The 1986 April cruise took place over the Hopen Depth and the western slope of the Central Bank. Northerly winds had pushed the ice south to 75° N. The ice cover was dense, and under-ice irradiance was low (Table 1). Chlorophyll in this ice was fairly high, max 17.7 mg m^2. The outer zone had thinner ice (20–40 cm), and several pelagic algal species were found (particularly *Thalassiosira* and *Chaetoceros* species). Further in, pelagic species still prevailed (*Chaetoceros gelidus*, *C. wighamii*, *Thalassiosira nordenskioeldii*, *Navicula vanhoeffenii*) together with several more algal species that thrive well in both ice and water (*Porosira glacialis*, *Shinodisus bioculatus*, *Fragilariopsis oceanica*, *N. kariana*, *N. pelagica*, *Entomoneis* sp.). The thicker ice was dominated by the typical ice algae *Nitzschia frigida* with epiphytes likes *Pseudogomphonema arcticum*, *Attheya septentrionalis*, and *Synedropsis hyperborea* (Table 2).

The cruises in April 1990 and 2001 both covered the Svalbard bank. No thinner outer zone was found, probably due to strong winds blowing the ice cover northward in the last days before the cruise. Sampling was carried out in thicker ice (approximately 1 m) with more snow and high nutrient concentrations in surface waters (Table 1). The biomass in the area was low, both in the algal layer and in the soft bottom layer of frazil ice crystals found in 2001. *N. frigida* and *F. oceanica* were the dominating species in the thin layers, while *N. frigida* with its epiphyte *P. arcticum*, *N. pelagica*, and several other species were found in the 2001 frazil ice. Lots of the *Nitzschia* cells were dividing, indicating active growth. No pelagic blooms were recorded (Table S2).

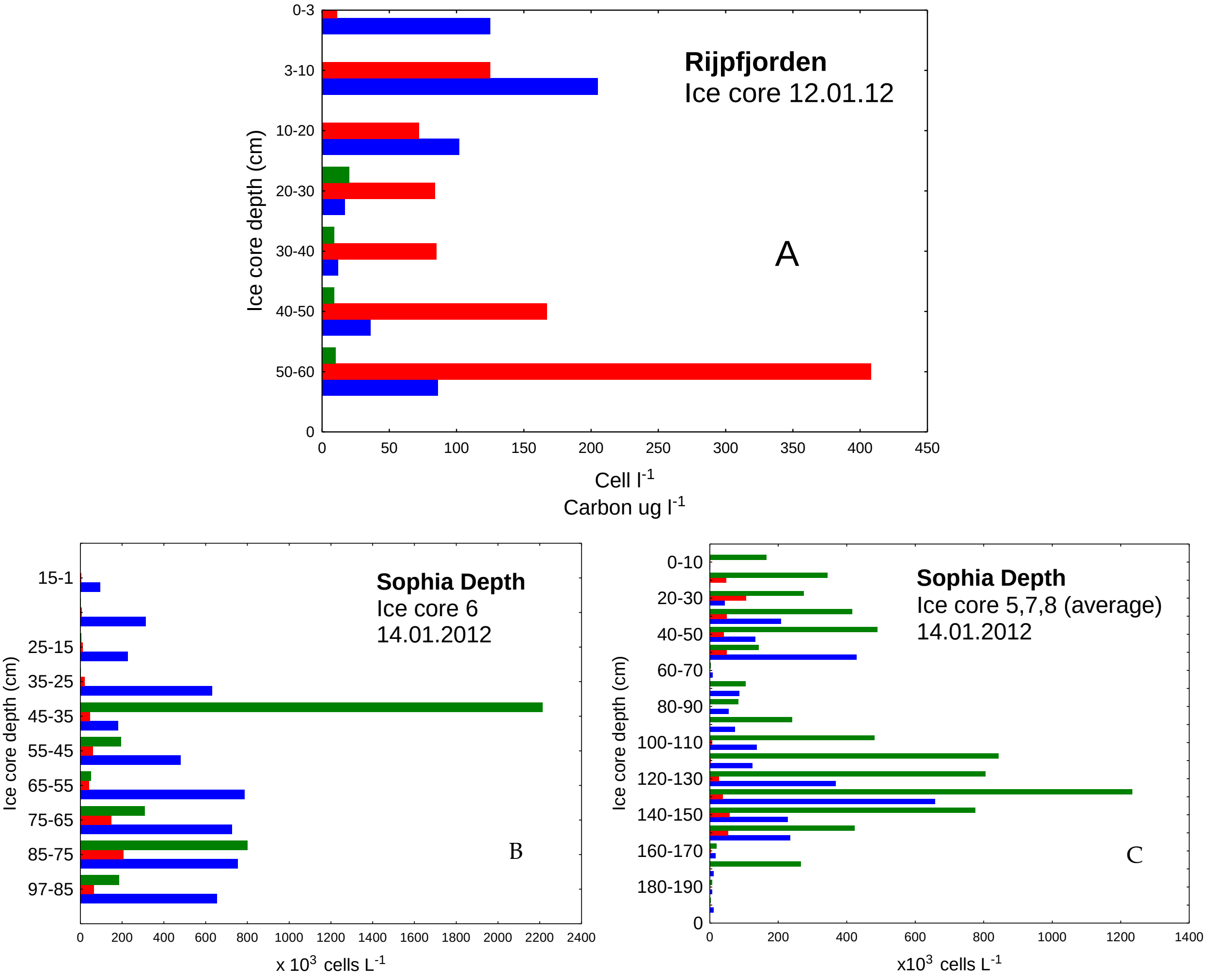


Figure 4. Vertical distribution of diatoms, spores and cysts of the dinoflagellate *Polarella glacialis* (cells L^{-1}) in ice cores from Rijpfjorden (**A**) and the northern Barents Sea pack (Sophia Depth, **B**,**C**) ice in January. Blue bars = diatoms, red bars = diatom spores, green bars = *Polarella* cysts.

Table 2. Dominating and common diatoms related to time of the year and ice thickness in the Barents Sea pack ice. Bold denotes dominating species.

Area	Time of Year	Dominating and Common Species
Outermost ice zone, 0–30 cm (Zone A)	March–April	Centric diatoms: *Thalassiosira* spp., *Porosira glacialis*, *Bacterosira bathyomphala*, *Chaetoceros* spp.
Average thick ice, 40–90 cm (Zone B)	April–June	Pennate diatoms: *Nitzschia frigida*, *N. promare*, *Fragilariopsis oceanica*, *Navicula kariana*, *Pseudogomphonema arcticum*, *Fossulaphycus arcticus*, *Synedropsis hyperborea*, *Navicula vanhoeffenii*, Centric diatoms: *Porosira glacialis*, *Schinodiscus bioculatus*
Thick annual ice, 100–120 cm (Zone C)	May–July	Pennate diatoms: *Nitzschia frigida*, *N. promare*, *Fossulaphycus arcticus*, Centric diatoms: *Melosira arctica*, *Attheya septentrionalis*
Multi-year ice, 150–200 cm (Zone D)	Probably all year	Centric diatoms: *Melosira arctica*, *Attheya septentrionalis* Pennate diatoms: *Ppseudogomphonema arcticum*, *Synedropsis hyperborea*

The May 1996 cruise, again over the Svalbard Bank, encountered ice cover reaching south to 74° N. A relative thin layer of ice (30–50 cm) was found in the ice edge zone. The ice algal populations, growing as thin layers, exhibited greater variability in this ice than otherwise observed, and a multitude of sub-populations were encountered within a limited area. Several species additional to *N. frigida* dominated (*N. promare*, *F. oceanica*, *Fossulaphycus arcticus*, *N. kariana*, *P. arcticum*) (Table 2), and even under the same flat floe, different populations were found virtually side by side. The thicker and more rafted ice (100–120 cm) exhibited caves and structures, and the caves in particular were as rich in species diversity as the thin ice. Different populations were found on the floor, on the walls, and in the ceiling of these caves. The average, as well as the maximum, biomass during this cruise (Table 1) was the highest encountered in the Barents Sea so far: max 39 mg chlorophyll m^{-2}, with an average of 7.9 mg m^{-2}. Maximum cell numbers (15,440 $\times$ 10^6 cells m^{-2}) were found below flat ice, dominated by *Fossulaphycus arcticus* (80%). No phytoplankton ice edge blooms were observed. The water masses were dominated by small flagellates (Table S2) in surface layers of high nutrient concentrations (Table 1).

The 1997 and 2004 cruises went to the Hopen Bank (Figure 1a). The ice edge was situated further north (76° and 77° N) than the previous May cruise. The thin outer ice observed in 1996 was not found. The ice thickness was in general 60–80 cm in 1997 and 120–150 cm in 2004, the latter consisted of large, old annual floes with 30–40 cm of snow. Light intensities were mainly low, but one high value (152 μmol m^{-2} s^{-1}) was measured below a floe of thin ice (30 cm) in 1997. This year's ice algal biomass was considerably lower than in 1996, maximum value was 9.6 mg m^{-2}. The 2004 biomass was variable, but in general high with max values of 35 mg chlorophyll m−2 (Table 1). The ice algal populations exhibited little variability in species composition, with dominance of *Nitzschia frigida* and some *N. promare* and *Fossulaphycus arcticus* in 1997, and *N. frigida* completely dominating (85–98% of cell numbers) in 2004 (Table S2). In the open water outside the ice, as well as in leads in the outer ice edge area, intensive *Phaeocystis pouchetii* blooms were going on (Table S2), and *Phaeocystis* cells were frequently found as brown spots on the snow cover on the ice floes and in the ice algal samples. When sampling started in 2004, a *Phaeocystis* late bloom with a biomass peak at 20–25 m depth surrounded the floe, and nutrients were almost exhausted in the upper layers (Table 1). During the four days of sampling, the ship and the anchor floe drifted further east out of the old bloom, into an area of another *Phaeocystis* bloom, apparently in a younger stage, with highest biomass in the surface layers and nutrient concentrations about half the winter water values. Nutrient concentrations in 1997 were extremely low and no measurable nitrate was ever found (Table 1).

The May 2003 cruise took place on the Norwegian Bank, north-west of Svalbard, in an area which was heavily influenced by the Atlantic Water (AW) flowing north along the western coast of Svalbard. This last branch of the AW turns eastward in this area, following the rim of the Arctic Ocean. The surface water temperature in these areas was only 0.5 °C. Multi-year ice dominated, and annual ice floes were either very thin and new, or in a state of melting. Hence, there was no algal layer on the underside of the majority of the annual ice. We encountered only a couple of floes with ice flora, both of about 40 cm ice thickness. Ice algal biomass was very low (Table 1). The populations were completely dominated by *Nitzscia frigida* (98%), but other species were also found, such as *Fragilariopsis oceanica* and dinoflagellate cysts (Table S2). However, in this area, infiltration layers were observed in a 10–15 cm-thick layer between the ice and the snow of some of the multi-year floes with about 30 cm of snow on top. The light intensity above the algal layer, but below the snow, was 450 μmol m^{-2} s^{-1} on a sunny day. Biomass in this layer was 4–5.5 mg chlorophyll m^{-2}. *Phaeocystis* dominated, but diatoms were also present, with *Chaetoceros furcellatus* and long chains of *F. oceanica* being the most common species. The species composition of the infiltration layers resembled that of the pelagic blooms in the area (Table S2), also dominated by *Phaeocystis* and a number of diatoms. Nutrient concentrations were reduced to about half of the winter values (Table 1).

3.3. The Summer and Autumn Season

Summer and autumn seasons cover the cruises in June [1995], July/August [1996], and August/September [2003]. Melting had started in June, and in late summer a lot of the ice cover was gone. Most of the sampling was then performed far north in the Barents Sea (north of 77° N), where old ice still remained (Figure 1b). The conditions were highly different from the spring, and most of the algal biomass was gone.

Ice cover in June 1995 over the Big Bank (Storbanken) was dominated by medium-to-thick, partially rafted annual ice, 50–150 cm, with some thicker, multi-year floes of 200 cm thickness or more in between. The ice underside was partly flat, partly cracked and structured. A large part of the sub-ice algal layers seemed to have disappeared due to melting; sea surface temperature was warmer than -1.5 °C and there was a pronounced melt water layer of 15–20 m depth in the area. The remaining biomass in flat parts of the floes was low (Table 1), consisting mainly of *Nitzschia frigida* (up to 60%) (Table S2). In a few sheltered habitats (structured parts) in annual ice *Melosira arctica* along with its most common epiphytes *Pseudogomphonema arcticum*, *Synedropsis hyperborea,* and *Attheya septentrionalis* was found in strands of up to 2 m length (Table S2). Some of the floes had softer ice on the underside, and ice cores from some of these floes exhibited low chlorophyll concentrations in most of the ice, except in the lower 15 cm in one of the cores. Species composition was variable inside the cores, but the most common species were *N. frigida*, together with vegetative cells and cysts of the dinoflagellate *Polarella glacialis*. In the high biomass bottom layer *N. frigida* (up to 60%) dominated along with *N. promare* (up to 30%). The phytoplankton populations at the ice edge were in a post-bloom phase with a deep chlorophyll maximum, dominated by old *Phaeocystis* colonies and summer species such as *Dinobryon balticum* and the dinoflagellate *Heterocapsa rotundata*, but diatoms like *Thalassiosira antarctica* var. *borealis* were also common (Table S2). Nutrient concentrations in the surface layer were low (Table 1).

The summer cruise in July–August 1996 covered a large part of the northern Barents Sea east of Svalbard (north of the Polar Front, Figure 1b). Melting was going on all over the area from 75° to 81.5° N. No real ice edge was observed; rather the ice melted and disappeared everywhere. Big holes from previous brine channels could be seen on edges of the floes and melt ponds were frequent. No ice algae were left in this heavily melting ice, but in a few locations in thick, annual ice (150–200 cm) furthest north remnants of the previous populations were found in sheltered parts, both in brine channels and below melt ponds; the latter acting as lenses collecting light. The populations exhibited lots of dead cells. 'Graveyard communities' or thanatocoenoses were found at some stations: all the cells were dead, only the diatom frustules remained, often with the epiphyte *Synedropsis hyperborea* as the dominant species. In the live communities, either various *Nitzschia* along with other pennate species dominated, or *Shinodiscus bioculatus* or *Melosira arctica* was the most common species (Table S2). The biomass was mostly less than 0.5 mg chlorophyll m^{-2} except for one station (Table 1), dominated (80%) by *Fragilariopsis oceanica*. Due to persisting fog, we could not go further north, hence we do not know how far north the melting processes proceeded, and if healthy populations still could be found at higher latitudes. No specific ice edge blooms were encountered in the area, but former blooms had absorbed virtually all the nutrients in the surface layers (Table 1).

In 2003, the late summer cruise followed the northern coast of Svalbard, through Hinlopen, northwards past Kvitøya, and back again. The ice edge was situated far north (81° N), and the ice cover consisted of thick, annual ice or multi-year floes (110 to 270 cm thickness). Sampling was performed in the area north of Kvitøya (Figure 1b). The ice was beginning to melt, and most of the ice algal layers were gone, comparable to the summer cruise of 1996. In a few sheltered locations, low biomass of algae was found under fairly flat ice. More than 80% of the species were similar to the pelagic blooms in the area (Table S2), dominated by a mixture of *Dictyoca speculum*, *Thalassiosira* spp. and *Fragilariopsis* spp. Some samples contained high numbers of a small, naked, unidentified dinoflagellate, which also dominated in the water masses in the area. Nutrients were low or exhausted, depending on the development of the pelagic blooms (Table 1).

3.4. Statistics

There were a limited number of significant correlations between physical and biological parameters (Table S3). However, the total number of species showed a significant negative relationship with ice thickness (Figure 5) and snow depth, and positive relationship with under-ice light. Total cell numbers were significant, positively correlated to nitrate in the water, and to the three most common species: *Nitzschia frigida*, *N. promare*, and *Fossulaphycus arcticus*.

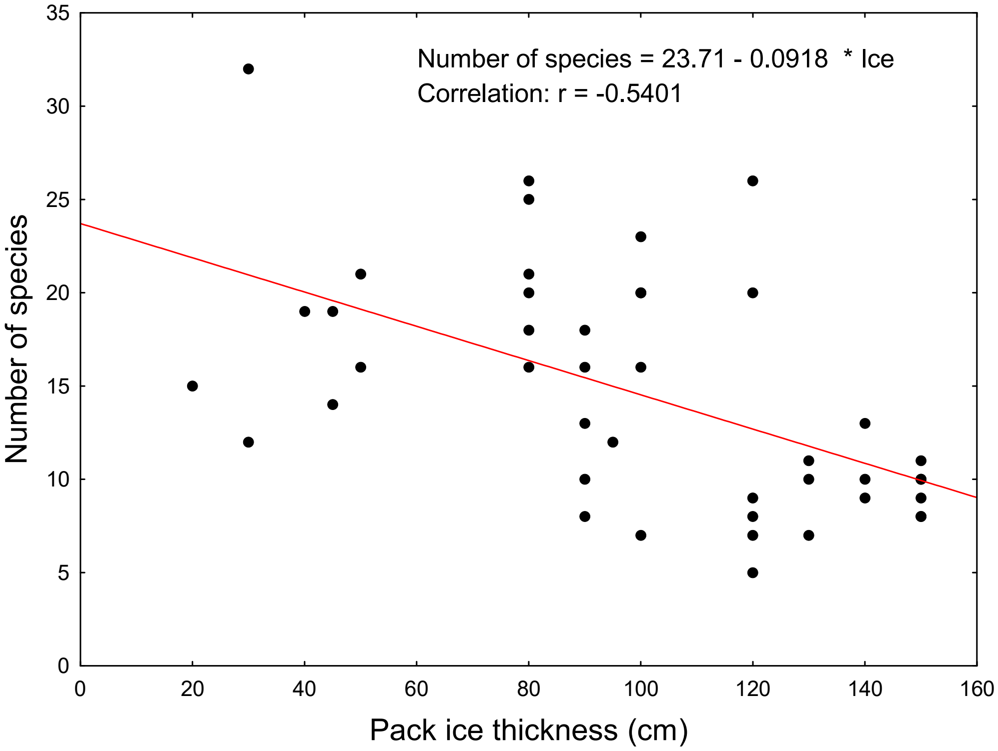


Figure 5. Regressions of the pack ice thickness and the total number of ice algal species in the Barents Sea.

Ice thickness and under-ice light showed a significantly negative relationship. Under-ice chlorophyll was significantly negatively correlated to under-ice light, but positively correlated to total cell numbers. The latter was also significantly positively correlated to ice thickness. No relationship between the thickness of the snow cover and total chlorophyll was found. This could indicate less accurate snow depth measurements since no relationship was found between under-ice light and snow depth either.

N. frigida exhibited a strong, significant positive relationship between the percentage of total cell numbers and ice thickness (Figure 6) and with snow cover, and a negative relationship with under-ice light. Cell numbers were positively correlated to ice thickness, and additionally to silicate in the water. *Attheya septentrionalis* reacted in much the same way as *N. frigida*. Its cell numbers showed a significantly positive relationship with ice thickness, while the percentage of total cells was significantly negatively correlated to cell numbers of *N. promare* and *F. arcticus*. It showed a positive relationship with the other epiphyte, *Synedropsis hyperborean*.

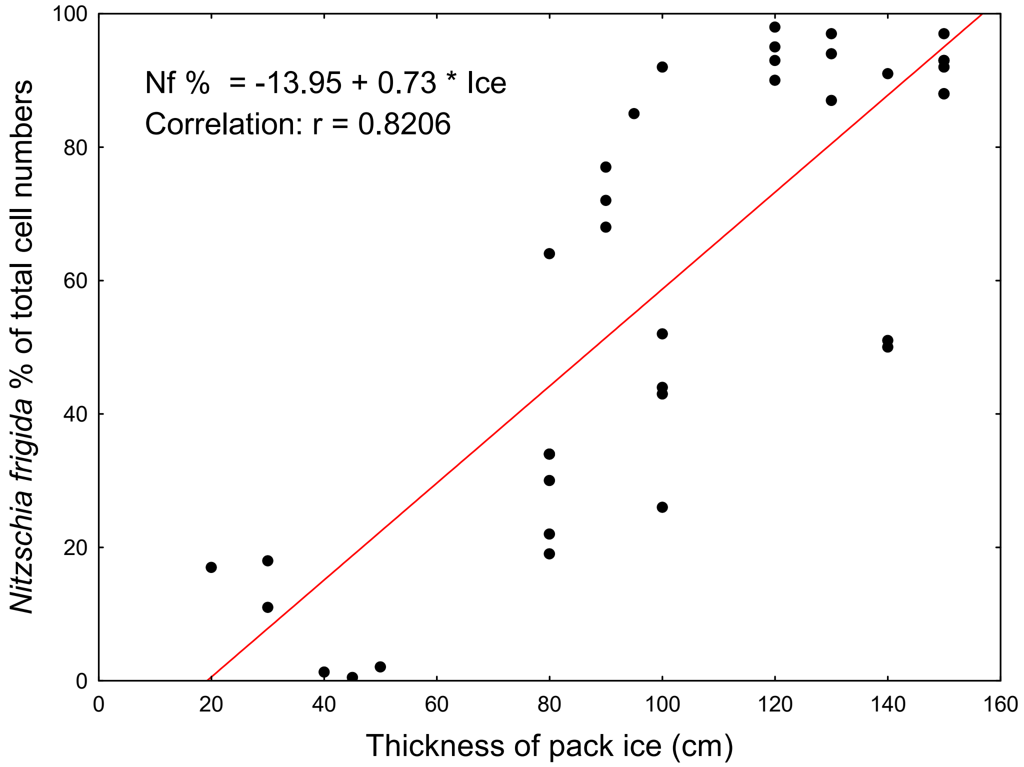


Figure 6. Regressions of the pack ice thickness and the percentage dominance of the ice diatom *Nitzschia frigida* in the Barents Sea.

The two common species, *N. promare* and *F. arcticus*, both showed a significant negative relationship for dominance and for cell numbers with *N. frigida* % cell dominance. Both *N. promare* and *F. arcticus* had a significant positive relationship with surface water nitrate, *N. promare* also with silicate. There was a significantly negative relationship between snow depth and dominance of *F. arcticus*. The co-occurrence of these two species was significantly positively related.

Thick ice had a strong negative influence on the occurrence of cells of *Porosira glacialis*, Cell numbers of this species was correlated to cell numbers of *N. promare*, and positively correlated to cell numbers of *F. arcticus*.

4. Discussion

4.1. Biomass Distribution and Biodiversity in Relation to Environmental Factors

The active growth period for the Barents Sea ice algae is 3–4 months in spring/early summer, comparable to both timing and duration of ice algal blooms in the Chukchi and other Siberian seas [11]. The observed maximum annual biomass of 40 mg chlorophyll m^{-2} may at first seem low, compared to the Canadian Arctic with its maximum of 360 mg m^{-2} [63], but average values are comparable to other Arctic seas and the Central Arctic Ocean [7,8,64–67]. The Barents Sea is a pack ice area, and similar areas like the Bering Sea and Davis Strait have comparable or even lower biomass [67–69]. The Canadian Arctic is primarily covered with fast ice, and the algae grow in the bottom layers of the ice. The highest biomass values are all found in ice located in the main flow-through areas of the water from the Arctic basin to the Baffin Bay, forming part of the Labrador Current [70]. These water masses include Bering Sea water from the Pacific, which has higher nutrient content [71]. Hence, the water masses flowing through parts of the Northwest Passage (Barrow Strait and Lancaster Sound) are especially rich in nutrients, compared to the Barents Sea waters, and may thus produce higher ice algal biomass. Additionally, the well-developed sub-ice communities observed in the Chukchi Sea experience a mixture of different, but nutrient-rich water masses [72].

The growth form of the Barents Sea ice algae is special. Cells commonly grow as sub-ice communities in a thin layer attached to the ice under-surface. Other areas reported to have similar types of communities are Hudson Bay [73], with a comparable maximum biomass, and the Chukchi Sea [72]. The ice algal layers below non-melting ice in the Barents Sea are not embedded in ice, but surrounded by water. Hence, the ice algae and the phytoplankton in the ice edge zone are competing for nutrients in the surface waters, and a substantial pelagic bloom may render little nutrients left for the ice algal production. However, ice edge blooms are patchy, both in time and place, and in May 1996 there was no such blooms observed in our sampling area. The nutrient concentrations in the water were high, and maximum ice algal biomass was recorded. Lower biomass the next May could be an effect of pelagic ice edge blooms having consumed most of the nutrients, as seen in May 2004, but that year the ice algal biomass was almost as high as in 1996. The sampled ice floe drifted through the pelagic bloom, but originated from an area with no such blooms. In a pack ice area, low nutrient concentrations in the surface waters may not necessarily imply low ice algal biomass, since this will very much depend on the pre-history of the ice cover drift, in addition to the ice and snow conditions. Phytoplankton and ice algal blooms may occur side by side below the ice cover, but with different species composition. *Phaeocystis pouchetii* is extremely common in the Barents Sea in spring, but at the same time a diatom bloom is found under the ice. These blooms may have only a few similar species, and even when diatoms bloom in the water they are different from the ones in the ice. How far into the ice these pelagic blooms in spring could occur is not known, but massive phytoplankton blooms have been observed in summer north of Svalbard [74], and in the Chukchi Sea [75] as far as 100 km into the ice-covered areas with lots of leads. Earlier ice melting, later freeze-up and more transparent ice cover (more melt ponds and leads) will have the potential to increase the frequency and intensity of phytoplankton blooms under the ice and reduce the relative contribution of ice algae to total primary production [76].

Good correspondence between ice algal biomass and ice/snow has been described from Canadian Arctic where the occurrence of fast ice allows for repetitive sampling stations, and the possibility to follow the bloom development during spring [63,77]. However, in the Chukchi Sea, no relationship was found between the percent cover of sub-ice algae and physical factors at the kilometer scale, only at the scale of individual ice floes where the cover of sub-ice algae was positively correlated with distance from the floe edge and negatively correlated with snow depth [72].

In a pack ice area such as the Barents Sea, some environmental factors are more difficult to measure, and logistically it is impossible to follow the growth of one particular population over a long time. The growth form and sampling method of the ice algae complicate precise measurements of ice thickness and snow depth. The given data are arbitrarily measured by the diver at the sampling site, and prone to be less accurate than core measurements. However, when all data from the pre-melting season were pulled together and analysed, some interesting patterns emerged. Thicker ice had lower under-ice light intensities, which was to be expected. The fact that under-ice chlorophyll increased with decreasing under-ice light, indicated that the algal cells were shade adapted by increasing their cellular chlorophyll in low light conditions [78]. The positive, but weak correlation between total cell numbers and total chlorophyll indicated that the chlorophyll values were dependent of other factors than just cell numbers, and both photoadaptation and species composition would likely interfere with this correlation. Overall, sea-ice communities show a high capacity for photoacclimation, but low maximum productivity compared to pelagic phytoplankton [79].

By breaking down the data to single species, it became obvious that *Nitzschia frigida* in particular reacted differently to the environment than the other species by increasing its dominance with ice thickness, snow cover, and reduced under-ice light. Since this species is by far the most important and numerous in the Arctic [1,11,69,80–82], and also in the Barents Sea, its reactions to environmental factors will strongly influence that of the total populations. This species will dominate totally in thick one-year-old ice, as confirmed by the in situ observations. Autecological data from *N. frigida* are scarce, but laboratory experiments have shown that the growth rate is strongly reduced by low light [13]. This is an indication that cells may not necessarily grow well under thick ice with heavily reduced light conditions, although cell numbers were also correlated to ice thickness. Ice algae have been observed to start growth in extremely low light conditions in NE Greenland, but unfortunately no information on species were given [83]. However, *N. frigida* survived well under the harshest conditions when other species had disappeared, but it was losing in competition to others in good light conditions.

N. frigida was often accompanied by epiphytes, and one of the most common species, *Attheya septentrionalis*, reacted in much the same way as *N. frigida*, but it never became a dominating species. Its importance decreased with increasing cell numbers of *N. promare* and *Fossulaphycus arcticus*, probably indicating that these two species are less suited as substrates for *A. septentrionalis*. Its positive relationship with the other epiphyte, *Synedropsis hyperborea*, indicated that they, to some degree, co-existed in the populations. Another possibility is that they both became outcompeted by high numbers of *N. promare* and *F. arcticus*, and with low numbers of host cells they are able to use the ice itself as a substrate.

The opposite reaction of the two common species, *N. promare* and *F. arcticus*, to *N. frigida* meant that high dominance of N. frigida would be followed by lower occurrence of the other two species, and that there would be a tendency in the populations for dominance either by N. frigida, or by the two other species. They also showed a stronger tendency to prefer high-nutrient waters, particularly rich in nitrate, *N. promare* also with silicate, whereas nitrate apparently was not that important for the *N. frigida* cell numbers. *F. arcticus* reacted negatively to snow depth, which is an indication that also the under-ice light conditions were important for the inter-specific competition. *F. arcticus* is the only one of the three that may also be found amongst the dominant species early in a spring phytoplankton bloom [84].

Porosira glacialis reacted to the environment in much the same way as *N. promare* and *F. arcticus*, and quite opposite to *N. frigida* with its epiphytes. *N. frigida* was obviously the different species here, since the total number of species reacted in the same way as *N. promare* and *F. arcticus* to increased ice thickness and snow depth and reduced under-ice light. The close coupling between total cell numbers and the three most common species: *N. frigida*, *N. promare*, and *F. arcticus* means that these species would be the most likely species to dominate in populations, *N. frigida* for itself and the other two either together or individually. The various ways individual species react to environmental factors emphasized the importance of knowing the species distribution when dealing with ice algal ecology.

4.2. Vertical Distribution

Algae have been located from top to bottom in the pack ice. The finding of infiltration layer communities makes the Barents Sea ice algal growth more comparable to the pack ice in Antarctica, where such communities are common [85]. The species distribution points to a pelagic inoculum, and these layers of algae probably developed from cells supported by the seawater, living in an environment of high light and sufficient nutrients to reach a fairly high biomass. Infiltration layers have only been found far north, and the importance for the total ice algal production is not known [86] but is likely to become increasingly important in some regions as a result of an increase in Arctic precipitation in combination with the thinning sea ice [87].

Algae are also growing inside the ice. Soft bottom layers are less common in the Barents Sea pack ice, but when present, either early or late in the season, algae were found to grow in these layers. In April, *Nitzschia frigida* dominated the bottom populations, and again in June when melting had started and the ice under-surface was softer. Algae were found throughout the June ice cores, and Syvertsen [12] reported these interstitial communities to be common. However, their appearance may be related to ice structure, and maximum biomass was always found in the bottom 10–15 cm, as is common in the

Arctic fast ice [10,63,81,88,89]. *N. frigida* was either dominating or common also in the interior of the ice.

Another common species was the dinoflagellate *Polarella glacialis*, found either as cysts or as vegetative cells. Cysts were found as the dominating growth form throughout the ice in winter (Figure 4A–C), similar to the Southern Ocean sea ice [90,91], and lasted at least till June. Then they were mainly found in the upper half of the cores, whereas vegetative cells were concentrated either at the top or at the bottom. *Polarella* is a bipolar species [60] which forms large number of cysts and blooms in brine channels. Encystment is a way to survive the, often tough, environment in the brine. *Polarella* was originally described from Ross Sea in Antarctica [92] and has now been found all around the continent [60,93]. Arctic reports most likely include cysts from the Barents Sea (called *Echinus,* [94]), and from the Polar Ocean (called *Xanthiopyxis polaris,* [47]). Later it was found from Greenland [95] and probably from Franz Josef Land, where the cysts were found to dominate in the ice [80], but not from the Kara Sea [10]. Ice cores have scarcely been studied in the Barents Sea, but there are indications of an equally diverse flora and fauna during the growth season. There are many flagellates [9], comparable to other arctic areas e.g., the Greenland Sea ice [81,95], in the Arctic Ocean [8], and in the Chukchi Sea [82] even if the biomass observed until now has been low.

However, the main ice algal biomass of the Barents Sea is, found as sub-ice populations [12,13], occurring as thin layers on the ice underside. The species diversity of these algal layers may be high and will depend on the thickness of the ice and the time of the year (see below).

4.3. Horisontal Distribution

A common feature when dealing with ice algae is the patchy distribution of cells. This has been observed in the entire Arctic, both on a small [96] and large scale [72,97]. Video recordings have illustrated this to non-divers in a convincing way ([98], own obs.), and sampling over many years in the Barents Sea have yielded highly scattered biomass data. This is an effect of a multitude of environmental physical factors such as snow and ice thickness (i.e., light conditions, [99,100]), ice structure [72], as well as biological factors such as growth rate, photoadaptation, and grazing. There is no guarantee that the maximum biomass measured so far in the Barents Sea is the actual maximum for the whole area, but the observed horizontal distribution of species seemed to be more consistent than biomass, although large-scale variability of species distribution occurred both on a temporal and spatial scale.

The season when live ice algae could be found under the ice has turned out to be surprisingly long, from the beginning of March until the end of October [13], although cells may exist in resting stages both very early and very late in the season [12]. Nevertheless, ice algae prolong the productive period of the Barents Sea for as much as two months, since the cells will start to grow well ahead of the phytoplankton spring blooms.

Early in the season some of the phytoplankton species, mainly centric diatoms of the *Thalassiosira* and *Chaetoceros* genera, temporarily use the outermost, thinnest ice (zone A: Table 2, Figure 7) as a convenient habitat with sufficient light and without deep mixing. However, they are not true ice algae, and are often seen less in the ice after this early phase (April). These populations probably seed the water masses in early spring and thereby serve as an inoculum for the ice edge spring blooms [12], but they probably do not originate from the ice, as will be discussed in more detail later. Ice slush sometimes found between floes in spring and summer may also contain a higher representation of phytoplankton species, particularly centric diatoms. The pennate *Navicula pelagica* (also common in the ice), however, has occasionally been found to dominate, with *Thalassiosira antarctica* var. *borealis*, *T. nordenskioeldii*, *Chaetoceros gelidus,* and *C. wighamii* as subdominant species. The ice obviously again acts as a temporary habitat for pelagic algae and some of these species have been reported earlier as common on ice or between ice floes in other Arctic areas [101].

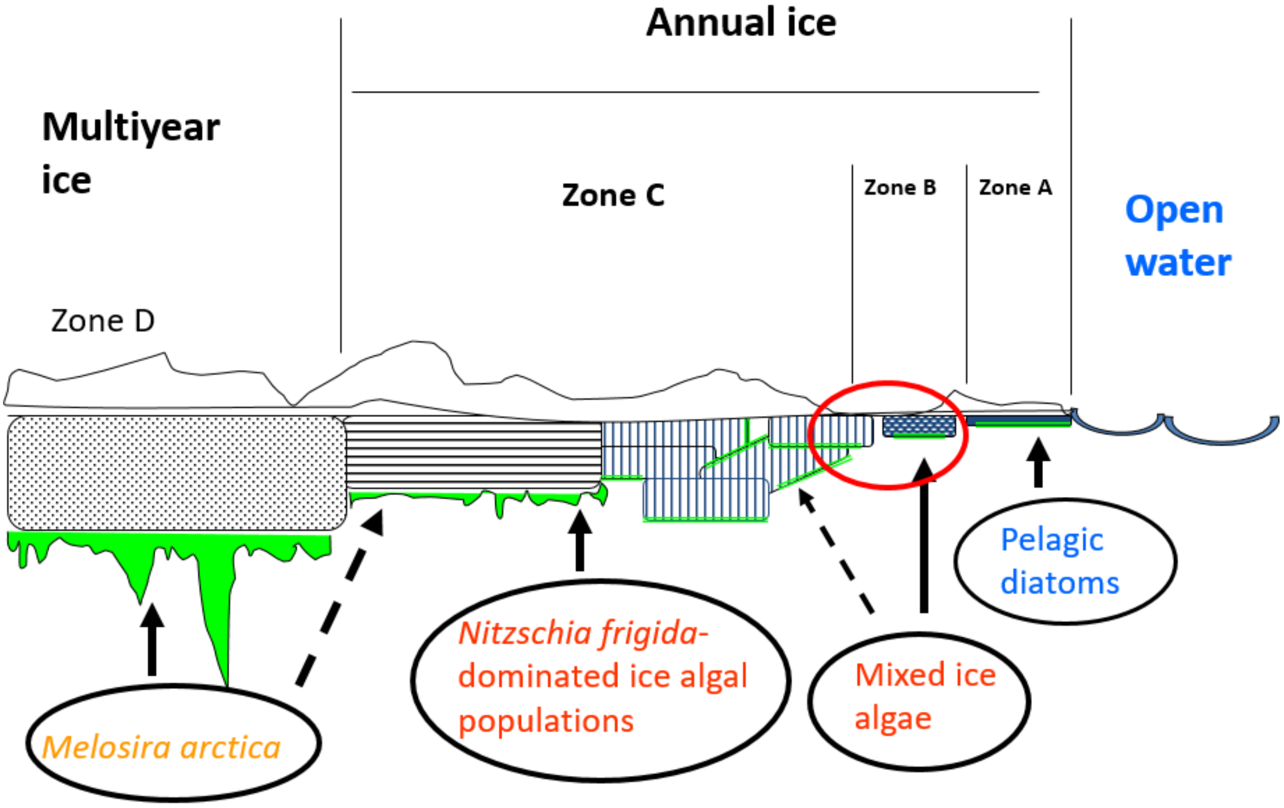


Figure 7. Spatial distribution of ice algal species in the Barents Sea pack ice in relation to increasing ice thickness from open water to multi-year ice.

The thin-to-medium thick ice in the outermost zone (zone B: Table 2, Figure 7) is an area of considerably higher biodiversity. More diatom species have been found to dominate in the communities here than in thicker ice, particularly under relatively flat ice. Different populations are found almost side by side, even under the same floe. Contradictory to the thinnest ice, this zone is dominated by pennate diatoms such as *Nitzschia promare*, *N. frigida*, *Fossulaphycus arcticus*, *Fragilariopsis oceanica*, *Navicula kariana,* and *Pseudogomphonema arcticum*, in addition to a lot of other species, i.e., a combination of true ice algal species and species thriving equally well in ice or as part of the plankton community. Centric diatoms, dinoflagellates, and other flagellates have also been found, the latter group, however, mainly in the interstitial communities. Sampling methods (suction sampler) as well as type of fixative could discriminate small flagellates if present, and also some small, naked dinoflagellates, because of the mesh size of the net in the pump. Motile, naked, and flagellated algal types seem (at present) to be less common in the sub-ice communities. It is, however, questionable if flagellates (including single cells of *Phaeocystis*) should be defined as true members of these ice algal communities due to the open contact between the sea water and the algal mats.

There was a smooth transition into the thickest and oldest annual ice (zone C: Table 2, Figure 7), which is almost exclusively dominated by the typical ice specialist *N. frigida*. The cells were often overgrown with the epiphytes *P. arcticum* and *Synedropsis hyperborea*, occasionally also *Attheya septentrionalis*, which are the same species commonly reported as epiphytes on *Melosira arctica* and sometimes also on *Fragilariopsis cylindrus*, *F. oceanica* and *Fossulaphycus arcticus* [81]. Additionally, *A. septentrionalis*, *P. arcticum* and *S. hyperborea* may be regular members of ice communities, despite low numbers of their most common supporting algae [102], i.e., the sea ice is being used as a substitute for their more common “habitat”. However, in our samples, they mainly occurred together with a ‘host’ species. *N. frigida*, which is also a dominating species in the Davis Strait pack ice, but apparently occurs here without the epiphytes [69]. Epiphytes in ice algal populations are an interesting, but not yet quite understood factor.

Whilst *N. frigida* particularly dominated under relatively flat ice, caves and structures in rafted ice were often habitats for a diverse flora, comparable to the one found in zone B. Cave floors, walls and, ceilings may exhibit different populations, indicating variable microclimatic conditions. The light climate in caves may be highly different from that found under flat ice, even though integrated PAR-values are comparable. Divers have reported the colours of light to be different, more yellow-orange, corresponding to the spectral distribution of light, which has passed through an algal layer [103]. Light beneath pure ice otherwise has a blue-green colour. Hence, the light climate inside caves may vary considerably from ceiling to floor, acting as a possible species-regulating factor.

Melosira arctica was occasionally found in the medium-thick annual ice (Zone C) of the Barents Sea in May and June, always with a patchy distribution. Gran [47] and Usachev [104] found this species on ice floes turned upside-down and thought it to be the dominant species of Arctic Sea ice communities. Today it has been reported from both multi-year and older annual ice in the Northern Hemisphere and demonstrates no obvious preference to a certain ice type [12,13,72,101,105–107].

The *Melosira* communities in the Arctic Ocean (zone D: Table 2, Figure 7) have previously been found to show preference to habitats with low hydrodynamic energy (‘hydrodynamic shadow’), such as under-ice hummocks, cracks, and low-current areas at least in multi-year ice [105]. However, this species have recently been found over large areas along the Chukchi Sea shelf [72] under relatively flat, annual ice where cells could form substantial nets, curtains, and strands, additional to its occurrence under flat multi-year ice in the Arctic Ocean [7]. The most recent reports talk about massive *Melosira* growth under the thinning ice in the Arctic Ocean, which is now, at least in some areas, mainly first-year instead of multi-year ice [108]. Very little about its preferences to light and nutrients are known, but it can obviously grow well below thick ice, either annual or multi-year [7,72,105]. If its first habitat priority is old ice, lack of suitable ice may prevent its mass occurrence in the Barents Sea, more than available light and nutrients, although this can obviously not be the full answer to the question of preferences, as have been proven for the Chukchi Sea and the Arctic Ocean. Strong under-ice currents and/or lack of suitable seeding populations may be other controlling factors for its distribution [109]. However, we have observed both resting spores and auxospores floating in lumps between ice floes and under the ice in the Barents Sea. They potentially represent an inoculum for recolonizing new floes, hence the question of its scanty occurrence in the Barents Sea is still open.

4.4. Seasonal Occurrence

As long as the ice cover is fairly intact ice algae will remain under the ice during the growth season. This season, starting in mid-March, is more or less over when melting becomes significant from mid/late June. However, thinning sea ice is a factor affecting sympagic algae, and bottom communities develop earlier in the season because light penetration increases with decreasing ice thickness [79]. The thin algal layers, loosely attached to the ice under-surface by a slimy mucilage of carbohydrates, the EPS (ExoPolymeric Substances, [110–112]), begin to detach from the ice. Currents may pack the layers into lumps, often concentrated in brine channels and other structures on the ice under-surface [12]. In sheltered areas, particularly in rafted ice, the layers may grow into short strands, which we observed in May for species such as *Fragilariopsis oceanica* and *Nitzschia frigida*. Finally, most of this algal material will loosen from the ice underside.

Melting proceeds from south and northwards in the Barents Sea, but melting may occur over a large area more or less simultaneously in summer [113]. During the two summer/late summer cruises to the northern Barents Sea, only remnants of the former ice flora were left even if the ice cover was about to open up and a ‘spring’ phytoplankton bloom were developing in the water masses [114]. Accordingly, in the high north there may be a larger time gap between the ice algal and the phytoplankton spring bloom (ice algae bloom in April/May, phytoplankton bloom in August/September).

Some ice algae may still be found in summer in the high north. There seem to be (at least) three kinds of 'over-summer' populations in the Barents Sea. The first is a true remnant of the spring populations, most often dominated by *N. frigida*, and always with a lot of dead cells and detritus. The populations survive in sheltered areas only, such as caves and other structures in rafted ice and in brine channels. During the melting period, fresh water drained through the brine channels of ice floes may provide unfavourable conditions for the algae. Additionally, the fresh water is virtually devoid of nutrients (it was drained out during freezing the previous winter), hence the algae may also suffer from serious nutrient deficiency which add to deteriorate life conditions. These populations often occur in lumps, which may loosen from the ice underside and appear in leads or holes in the ice [115] and may also be of the same type of populations observed collecting in open melt ponds in other arctic areas [116].

The other type of population is represented by the true 'cave-dwellers', the species that almost exclusively are found in caves in rafted ice, such as *Actinocyclus curvatulus* and to some degree also *Shinodiscus bioculatus*, earlier *Thalassiosira bioculata* [12,13,87]. Caves obviously offer a more protected and longer-lasting habitat. Other species may inhabit caves as well (as previously described), but they also grow under flat ice and are not confined to one type of habitat. Cave populations may survive as long as the rafted ice does not melt.

The third population type is found far north and is dominated by pelagic species, such as in early spring under thin ice and in ice slush. These populations were seen in 2003, and the species composition resembled the surrounding pelagic blooms of diatoms and dinoflagellates; however, not for species such as *Emiliania huxleyi* [114] which were not found in the ice samples. Ice algal species were present in low numbers, and there was lots of detrital material present. The populations were found in connection with the east-going branch of the Atlantic water north of Svalbard, which inhabited a bloom of several oceanic species, and it is possible that the sub-ice populations here are special for these physical environments.

It is not known to what extent any of these ice algal populations survive in the ice over winter. The growth season, however, is obviously terminated by October, when *Actinocyclus* cells, as the last observed, had entered a resting stage [13].

4.5. The Fate of the Ice Algal Blooms

Ice algae are important food for ice amphipods for as long as the cells remain under the ice [117,118]. Even though the amphipods share the same habitat, they occupy different trophic niches and have different diets [119–121]. Dead cells may also serve as food items in late summer, given that they still hang on to the ice (see below). Lots of different sea-ice meiofauna and copepods have been observed at the ice bottom where it was soft and contained ice algae and sediments, both in Baffin Bay [122] and in the Laptev Sea [123]. The hard under-ice structure of the Barents Sea pack ice prevents in general algal growth inside the ice. The ice algal mats will be available for zooplankton, but only in spring. Both *Calanus glacialis* and *C. finmarchicus* are found to graze ice algae in spring [124]. Eggs of *C. glacialis* have been found in high numbers below the ice in the Barents Sea, indicating that the ice algae function as an important food source for the females in early spring [125–127].

The significance of the 'over-summer' populations to the ice ecosystem is not well understood, but they may serve as a food supply for the ice fauna, which in general increases in numbers during summer [105,128–130]. The ice fauna biomass in the Barents Sea also increases geographically towards the Arctic Ocean [131]. Ice amphipods feed primarily on detritus in late summer, but live ice algae, given that they exist, act as additional food items [132]. Detritus lumps seem to attract these animals [133], and they usually contain amorphous plant material (probably former ice algae, [134]), so that both dead and alive algae are grazed by the ice fauna.

Before melting has started in spring, water temperature is still −1.8 °C, but an increase of less than 0.5 °C is enough to detach the algal layers from the ice (personal obs.). The algae may then be ingested in the water column, stay in suspension, or sink to the bottom. The fate of the ice algae in the Barents Sea is most probably sinking, since mass sinking of algal mats have been observed by the divers, similar to the Canadian Beaufort Shelf [135]. These are episodic events and take place in late spring. Few measurements of sedimentation from the ice of the Barents Sea exist, but maximum sedimentation has been measured at the time of melting [136], comparable to the Mackenzie Shelf [137]. Often the ice algal biomass entering the water would likely be too high for any zooplankton populations to cope with, as seen in the Canadian Arctic [138] and in the Bering Sea [139]. This will, however, also depend on the timing of the ice spring bloom, and earlier bloom will favour less zooplankton grazing and more sinking [140]. Historical data from the Canadian Arctic have shown great variability in the fate of the ice algae due to the variability of biological and ocean climate factors. However, without more data, it is not possible to know how much of the populations sinks in the Barents Sea. Many of the cells finally reaching the bottom may enter the benthic food chain [72,141–145]. Experiments have demonstrated that these ice algae are readily consumed and assimilated by Arctic benthic animals, and may even be preferred by some benthic species, due to their better fatty acid composition [142], which may be preferentially utilized [143]. Sedimenting ice algae may cause increased benthic activity, since consumption of these algae may lead to enhanced respiration rates in the benthic animals [146]. Areas with a high abundance of benthic animals in the northern part of the Barents Sea could be an indication of high ice algal sinking [147,148]. Recent investigations from Rijpfjorden, Svalbard suggest that the ice algae in sediments may act as a food source for benthic feeding animals even in winter, both for invertebrates and fish [149]. The ice algal biomarker IP25 may be a useful tool in the future to help identify the fate of these algae in the arctic ecosystems [150].

4.6. Initiation of Ice Algal Blooms

The sinking cells probably also serve as an inoculum for next year's season by forming resting cysts or resting cells, known to be alternatives of resting spores [151]. Pelagic blooms in the ice edge zone of the Barents Sea hardly ever consist of specific ice algal species except for the aforementioned phytoplankton species temporarily resting under the thin ice of the outermost zone. Genuine ice algae do not serve as inoculum for phytoplankton blooms, which has frequently been discussed for other areas [152]. In most cases, blooms in open water and in ice are dominated by different species, although quite a few species are common both in ice and in the water column, the most frequent in the Barents Sea being *Fragilariopsis oceanica*, *F. cylindrus*, *Fossulaphycus arcticus*, *Navicula vanhoeffenii*, *N. septentrionalis*, *N. pelagica*, *Pauliella taeniata*, *Shinodiscus bioculatus*, and *Porosira glacialis*. These common species may contribute to the maintenance of ice edge blooms, but except for *F. oceanica* and *F. arcticus*, probably do not initiate them. Timing is not coherent either, ice edge blooms have been going on for a prolonged period, usually more than a month, when the ice cover starts melting in late spring. Only if the ice edge is situated south of the Polar Front over the warmer Atlantic water melting will start early, and the phytoplankton species inhabiting the thinnest ice for a short period may initiate an ice edge bloom.

The Barents Sea water masses during winter are virtually devoid of autotroph microalgae, comparable to the fjords and coastal areas of Northern Norway and Svalbard, due to lack of light for several months and ice cover [149,153,154]. If cells should survive a winter in the ice, they would either have to rest in multi-year ice, or freeze into new, annual ice the previous autumn. Winter studies in January from Rijpfjorden, Svalbard exhibited extremely low cell numbers in the fjord (fast) ice, and only few of these cells were diatoms (pennate species), with some *N. frigida* cells. Spores were also found (Figure 4A), and since their main abundance was in the bottom layers, they may add to the spring biomass. However, growth of sediment samples from the fjord bottom revealed a lot of ice algal species, amongst them colonies of *N. frigida* (Figure 8). Other species observed were

Attheya septentrionalis, *Navicula transitans*, *Porosira glacialis*, *Pleurosigma* sp., *Entomoneis* sp., *Fragilariopsis oceanica* [149]. Previous sediment samples from Smeerenburgfjorden and the shelf north of Svalbard have produced several ice algal species in culture (*Navicula kariana*, *Entomoneis* sp., *P. glacialis*, *Pseudogomphonema arcticum* (own obs.). Spores sampled from the Barents Sea sediments germinate (in lab cultures) into the same spring bloom species as in the north Norwegian fjords, where spores are numerous [153,155]. Even if the majority of ice algae are pennate species, and only a few are known to form resting spores, they may well be capable of forming resting cells, and thereby survive on the bottom.

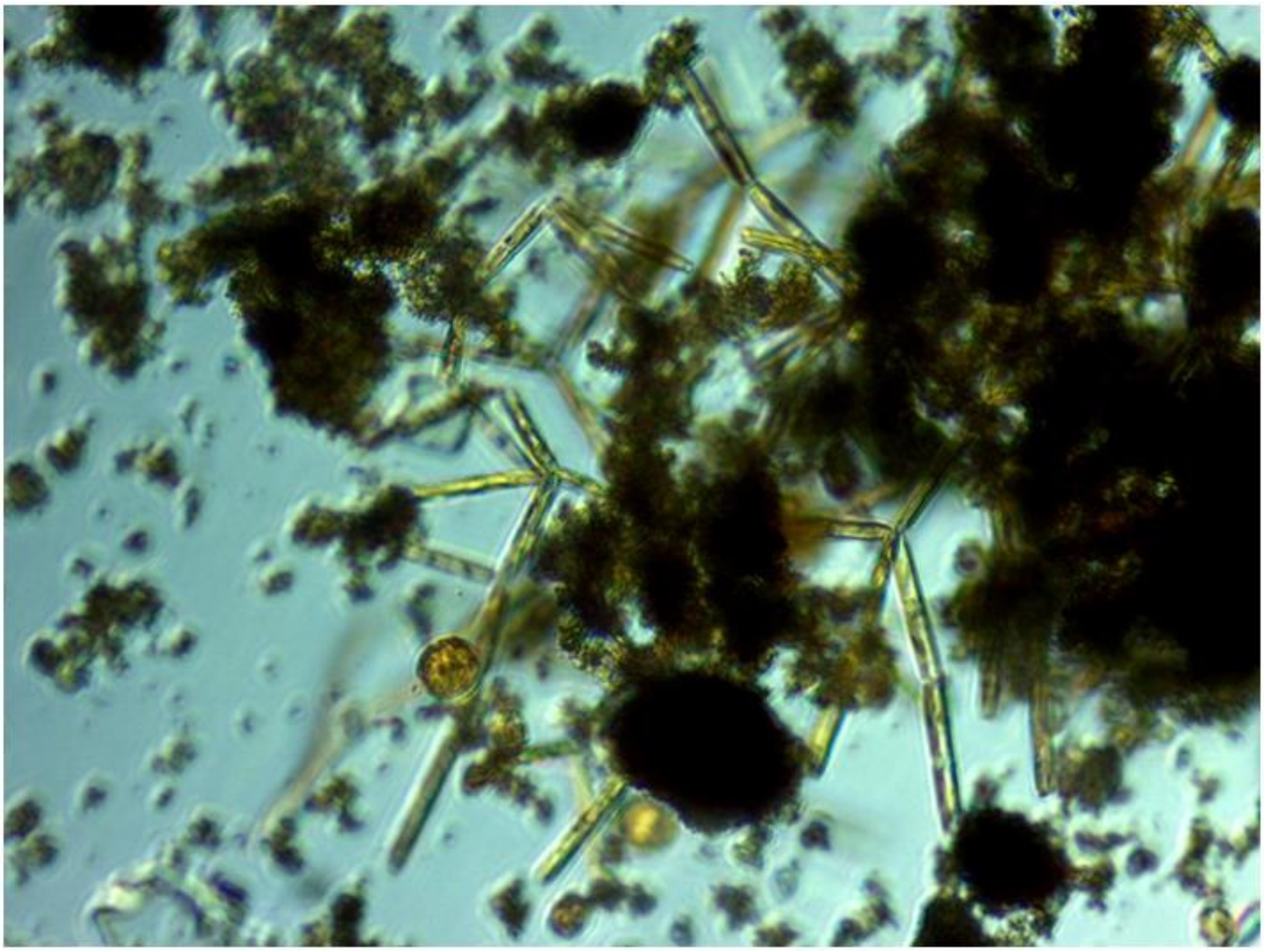


Figure 8. Colonies of the ice diatom *Nitzschia frigida* growing in lab cultures from sediment samples collected in Rijpfjorden in January.

In the Chukchi Sea, cells or spores of obligate ice algal taxa have been collected from sediments from 44 m to 1000 m depth [72]. Furthermore, many common benthic species also occur as regular components in ice from other arctic areas [49,50,69,72,84]. Modelling has shown that winter convection may reach down to the bottom of the fjords in Northern Norway, bringing diatom resting spores from the sediment surface to the upper water layers [156]. When the environmental conditions are appropriate, the spores will germinate and create the necessary inoculum for a pelagic bloom. To inoculate the ice, cells and spores must primarily be brought up from the bottom in ice-covered areas. This is possible in a pack ice area such as the Barents Sea. Leads open and close, and in a lead that stays open for some time, not only wind mixing, but also convection will take place [157]. Over the shallow banks convective mixing may reach the bottom very quickly and bring up material from the sediments, as observed in the ice samples from late February/early

March which were taken over the Svalbard and Hopen Banks and typically contained silt and clay particles along with algal cells [13]. Over deeper waters, however, cells will probably survive in the ice. Over the deep parts of the shelf slope north of Svalbard, winter ice was found to contain high numbers of ice algal cells and spores, up to 1000 times as many as in the fast ice from Rijpfjorden (Figure 4B,C). Although they did not dominate, both diatom cells and spores occurred in high numbers. *Polarella* was the main dominating species with up to 2.2 mill cysts L^{-1}, so obviously this species uses the sea ice as a survival habitat just as it does in the Antarctica [60]. The particulate organic carbon content was almost the same in all of the ice (Figure 3A–C), and given the large difference in cells numbers, meaning that the fast ice in Rijpfjorden must contain high amounts of organic material, or that the *Polarella* cysts have low carbon content (or both). The differences in cell concentrations in the two ice areas -fast ice in a shallow fjord and pack ice over deep waters of 2400 m-indicate that there exist several strategies of winter survival for the ice algae, varying between areas of different bathymetry and possibly also hydrography. Winter ice in the main part of the Barents Sea over the shelf areas which should be looked into before finally concluding about the ice algal winter survival.

4.7. The Future of Barents Sea Ice Algae

The declining (and disappearing?) ice cover in the Arctic is a relevant threat to the ice flora in its present form. Thinner ice may still be advantageous up to a certain point (when photoinhibition sets in), allowing more light to reach the under-surface of the ice cover. Changes to the timing of ice formation (and incorporation of organisms) are likely to lead to a greater presence of Atlantic species in the ice [109]. Together with species-specific mechanisms in coping with high light and high pCO2 (which may reflect ecological niches) this could potentially alter the balance between sympagic and pelagic primary production in a future Arctic [158]. The ice algal primary production is always low, but variable, and the available set of data give no clear indication of the relationship between measured under-ice irradiances and production rates in the pack ice [14,15,159]. Enhanced light availability may, however, allow bottom sea-ice communities to reach higher biomass, though over a shorter period, as nutrients will be consumed more rapidly [3]. Infiltration layers are likely to become increasingly important in some regions as a result of an increase in Arctic precipitation in combination with the thinning sea ice [87].

Biodiversity in the Barents Sea seems to benefit from thinner ice, judged by the present investigations (fewer species in thicker ice). However, the decline in multi-year ice in recent decades has already resulted in a decrease in sea-ice protist diversity in the Arctic Ocean [109]. It has been suggested that in general, the proportion of first-year ice and young ice will continue to increase compared with multi-year ice and result in less complex ice-associated communities [160]. The growth season and areal coverage may be drastically shortened if the ice cover changes. Long before the summer ice is gone, the ice algal layers beneath the Barents Sea pack ice may actually have disappeared. The reason for this is the loose attachment to the ice underside, with its high sensitivity to increasing temperature. High water temperature may come from two sources: either warmer Arctic water (a general increase in the Barents Sea water temperature, as predicted by models), or from more Atlantic water inflow. We have already seen the effect of warm, Atlantic water on the ice cover and the algae. The spring cruise in 2003 north-west of Spitsbergen took place over the east-going branch of the Atlantic water flowing north along the West Spitsbergen coast. Water temperature in the surface layers was too high for new ice to be formed (−0.5 °C), and the thin, annual ice drifting into this area from the north rapidly started to melt, losing the algal layer on the underside.

The cruise appeared to provide an unpleasant look into a warmer future, with an ice cover devoid of ice flora. The Arctic ecosystems depend on the high-quality food that ice algae provide, both for ice amphipods, zooplankton, and benthic animals [118,124,142,143,149]. Thus, changes in the sea ice cover and ice algae production are likely to have major consequences for the function of the food web and carbon dynamics in the pelagic system [120,161,162]. We do not know what will happen to the Arctic ecosystems if the ice flora is gone.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/jmse10020164/s1, Table S1. Algae found in and under pack ice in the Barents Sea. Species marked with an * are observed in cleaned samples or in qualitative samples (ice lumps). *Polarella* is found in the ice, the others as sub-ice species. Species inside the ice are given as cell L^{-1}, the rest as cells m^{-2}, Table S2. Comparison of dominating and/or most common algal species in sea ice and in concurrent ice edge blooms of the Barents Sea, Table S3. Correlation matrix for physical parameters from the Barents Sea ice: ice thickness (cm), snow depth (cm), under-ice light (µmol m^{-2} s^{-1}), nutrients in surface water (nitrate, phosphate, silicate, µmol L^{-1}). Biological parameters are: cell numbers and % of total cell numbers of the most common species [*Nitzschia frigida* (Nf), *N. promare* (Np), *Fossulaphycus arcticus* (Fa), *Porosira glacialis* (Pg), *Attheya septentrionalis* (As), *Synedropsis hyperborea* (Sh)], total number of species and total cell numbers. Values used are from the spring season, numbers show Pearson correlation coefficient between two and two variables. Symbols giving statistical significance level: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. Non-significant values ($p \leq 0.05$) are not presented.

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