Early spring microplankton development under fast ice covered fjords of Svalbard, Arctic^{*}

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Abstract

The chlorophyll *a* concentration, phytoplankton taxa succession, density, biomass and sedimentation was studied in three fjords of Svalbard in January, April and May 1995 and 1996. The fjords were covered with variable fast ice cover ranging in thickness from 0.4 to 1.5 m. Samples collected from the water column showed that only 10% of the algae could be classified as ice algae species. The fjord phytoplankton grew well under very poor light conditions (< 1% of incident radiation). The phytoplankton biomass ranged from $1.7 \,\mathrm{gC}\,\mathrm{m}^{-2}$ in winter to $15 \,\mathrm{gC}\,\mathrm{m}^{-2}$ in May. Heterotrophic flagellates made a significant contribution to the biomass (up to 98%), especially at stations with poor light conditions (inner fjord basins and thick ice cover).

1. Introduction

Among the growing literature on the biology of sea ice (recent reviews in the *Savonlinna conference papers* (1998) or from the 1996 Gordon Research Conference), very little attention has been paid to Arctic fast ice biota. The extensive studies of Svalbard fjords carried out hitherto have resulted in only a few papers dealing with phytoplankton and its links to the sea ice (Halldal & Halldal 1973, Schei *et al.* 1979, Heimdal 1983, Eilertsen *et al.* 1989, Węsławski *et al.* 1993, Keck *et al.* in press). There are even fewer studies

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from the winter and early spring: from Svalbard, only the papers by Eilertsen *et al.* (1989) and Węsławski *et al.* (1994). Although the stable fast ice cover in Svalbard is restricted to the inner fjord basins, this narrow zone seems to be of considerable ecological importance (Węsławski *et al.* 1993, 1994). For comparison I have selected data from three different sites – Adventfjorden – the westernmost inner fjord on Spitsbergen, supplied by a small river; Kongsfjorden – a glacier-fed fjord in west Spitsbergen, open to the sea, and Storfjorden and Burgerbukta – fjords in south and east Spitsbergen with thick and long-lasting ice cover, where the climatic conditions are the most severe. The aim of the present study was to discover the relationship between variable fast ice conditions and phytoplankton growth in Svalbard fjords. A further aim was to discover whether the fast ice cover seeds algae to the water column before the commencement of the spring bloom.

2. Material and methods

Phytoplankton was sampled in three fjords around the island of Spitsbergen in the Svalbard archipelago - Kongsfjorden, Adventfjorden and Storfjorden (Fig. 1) during three seasons (Table 1). Samples of phytoplankton were collected from water casts collected under the fast ice and the fast ice edge. In winter, samples were collected from open water, where fresh ice was starting to form. All samples were fixed in Lugol solution immediately after collection; 1 ml of formaldehyde was added 24 h later. 10 ml sub-samples were analysed under an inverted microscope (Utermöhl 1958) at 10x and 32x magnification. At the lower magnification the most numerous taxa were counted up to 50 individuals each, the less numerous ones were counted over the whole chamber surface. Small taxa were counted under 32x magnification, 50 cells usually being counted in 3–5 transects of the field of view. Flagellate forms (except Dinophyceans, and Prymnesio- and Prasinophyceans) were counted as flagellates not det. in three size classes -3-5, 5-10 and $10-15 \,\mu m$ without being classified as autoor heterotrophs. The phytoplankton data were evaluated by multivariate analyses (PRIMER and Systat software packages PML 1994). Temperature and salinity data were collected using a mini CTD (Bergen Sensor Data). The Photosynthetically Available Radiation (PAR) was measured with a LiCor. Chlorophyll a was measured with a Turner fluorimeter from an acetone extract of chlorophyll *a* obtained from water passed through GF/F filters. Sedimented phytoplankton was collected in cylindrical traps $70 \,\mathrm{cm}$ long and $10 \,\mathrm{cm}$ in diameter and exposed for 24-72 hours. These samples were processed in the same way as those taken from the pelagial.



Fig. 1. Study areas and sampling points (a-c). The arrow on the general map indicates the positions of the fjords studied

Area	Phyto- plankton samples	chl a	CTD profiles	$\begin{array}{c} {\rm PAR} \\ [\mu {\rm mol} \ {\rm m}^{-2} \ {\rm s}^{-1}] \end{array}$	Sediment traps	Period
Adventfjorden	80	80	10	9	16	January 1996, April, May 1995, 1996
Kongsfjorden	50	50	6	5	4	April, May 1996
Storfjorden, Burgerbukta	3	х	х	х	x	April 1996

Table 1. Samples considered in the present study

The carbon content was measured on a CHN analyser at the University of Gdańsk. The algal biomass was calculated according to the volume-to-biomass conversion factors given in the *Guidelines...* (1983). The cells of 30 specimens of each species were measured stereometrically.

3. Study areas and hydrographic conditions

The study sites are situated in the High Arctic, above latitude 78°N, where daylight is continuous from 22 April to 15 August. The sun remains below the horizon between 11 November and 12 February.

Adventfjorden is a small inner basin $(2 \times 3 \text{ km})$ of Isfjorden in west Spitsbergen, 120 km away from the open sea (Figs. 1a–b). Ice cover starts in early November and usually lasts until June. The ice thickness ranges from 0.5 to 1 m, with frequent break ups. Adventfjorden is supplied by two rivers, the discharge lasting from June to October. The freshwater discharge influences the hydrology and light conditions; in summer, the freshened surface layer (28 PSU) varies in thickness from 2 to 10 m. Winter and spring values show little thermohaline stratification (Fig. 2). Conditions in the water column in winter are almost isothermal and isohaline (Fig. 2a), while in April, the water under the fast ice surface is slightly less saline and rather warmer, the first signs of spring melting (Fig. 2b). Cold winds often cause the sea surface to freeze over again, which raises the salinity and lowers the temperature below the fast ice cover, owing to the elimination of brine pockets from freezing water (Fig. 2c). During the study period Adventfjorden was constantly covered with fast ice.

Kongsfjorden is a large fjord $(25 \times 5 \text{ km})$ on the west coast of Spitsbergen (Fig. 1c). Fast ice usually covers the inner basin from November to June, with frequent break- ups in the outer part. In sheltered bays the fast ice cover may be 1.5 m thick. The discharge of freshwater and suspensions is provided by glaciers and has been estimated at 0.5 km^3 annually (Beszczyńska-Möller



Fig. 2. Hydrological profiles in fast ice covered Svalbard fjords from station A1 on 17 April 1995 (a), 21 April 1995 (b) and station K6 on 7 May 1996 (c)

et al. 1997). The fjord was covered with stable fast ice in the inner basin and drifting pack ice in the outer part.

Storfjorden is a very large $(50 \times 250 \text{ km})$ longitudinally oriented basin on the east coast of Spitsbergen (Fig. 1a). From November till July most of it is covered by fast ice from 1 to 1.5 m thick. In summer, numerous glaciers discharge freshwater and sediments into Storfjorden. Burgerbukta, an inner

Taxon		15 January 1996					19 January 1996		
					Dept	h [m]			
		0	10	20	30	0	10	20	30
Flagellatae 3–5 $\mu \rm{m}$	A	5×10^{6}	10^{6}	10^{6}	2×10^{6}	9×10^{5}	3×10^{5}	2×10^{6}	3×10^{5}
Flagellata e $510\mu\mathrm{m}$	A B	$20 \\ 2 \times 10^{6} \\ 50$	4×10^{5} 10	$\frac{5}{8 \times 10^5}$	8×10^{5} 20	3×10^{6}	4×10^5		8×10^5
Flagellatae $1015\mu\mathrm{m}$	A B	7×10^5 80	3×10^4 3	$\begin{array}{c} 2 \times 10^5 \\ 20 \end{array}$	$\begin{array}{c} 10^5 \\ 10 \end{array}$	7×10^5 100	3×10^4 0	2×10^5 10	10^5 0
Navicula sp. 40 $\mu {\rm m}$	A B	$\begin{array}{c} 0 \\ 0 \end{array}$	$\begin{array}{c} 0 \\ 0 \end{array}$	$\begin{array}{c} 0 \\ 0 \end{array}$	$\begin{array}{c} 0 \\ 0 \end{array}$			$\begin{array}{c} 1000 \\ 0.1 \end{array}$	
<i>Emiliana huxlei</i> (Lohm.) Hay et Mohler	A B	$\begin{array}{c} 2\times 10^4 \\ 1 \end{array}$	$\begin{array}{c}9\times10^{3}\\0.5\end{array}$	$\begin{array}{c} 0 \\ 0 \end{array}$	0 0				
Thalassiosira sp.	A B	$\begin{array}{c} 0 \\ 0 \end{array}$	$\begin{array}{c} 0 \\ 0 \end{array}$	$\begin{array}{c} 0 \\ 0 \end{array}$	$\begin{array}{c} 100 \\ 0.04 \end{array}$				
total	A B	$\begin{array}{c} 7\times10^6\\ 151 \end{array}$	$ \begin{array}{c} 10^{6} \\ 18 \end{array} $	$\begin{array}{c} 2\times10^6\\ 45 \end{array}$	$\begin{array}{c} 3\times10^6\\ 37\end{array}$	$\begin{array}{c} 3\times10^6\\ 137\end{array}$	$\begin{array}{c} 4\times10^6\\ 3.5 \end{array}$	$\begin{array}{c} 2\times \ 10^6 \\ 31 \end{array}$	$\begin{array}{c} 3\times10^5\\ 2.5\end{array}$
total gC under 1 m^2 in 0–40 m water column			2	.5			1	.7	

Table 2. Abundance (A) [cell dm⁻³] and biomass (B) [mgC m⁻³] of phytoplankton in polar night samples, Adventfjorden, January 1996

branch of Hornsund, is similar in nature to Storfjorden, except that it is much smaller in size $(3 \times 3 \text{ km}, 25 \text{ km} \text{ from the fjord mouth})$. The last two sites were frozen solid during the study, with 10–15 cm of snow on top of the ice.

4. Results

Winter sampling

Polar night sampling was done at station A2 in Adventfjorden in January 1996. Analyses revealed 6 taxa only, ranging in density from 3×10^5 to 7×10^6 cells dm⁻³ and in biomass from 1.7 to $2.5 \,\mathrm{gC}\,\mathrm{m}^{-2}$ (Table 2). The chlorophyll *a* content was < 0.1 mg m⁻³. Phytoplankton sedimentation was $8 \,\mathrm{mgC}\,\mathrm{m}^{-2}$ day⁻¹. Samples were dominated by flagellates not det. (3 to $10 \,\mu\mathrm{m}$ in diameter); densities of autotrophic diatoms were very low (< 1000 cells dm⁻³; Table 2).

Spring sampling

Light transmission, expressed as the depth of 1% solar irradiance, was very variable between sites in Kongsfjorden and Adventfjorden. It ranged from 1 m below 1 m-thick ice topped by 15 cm snow to 27 m below 0.13 m-thick, snow-free ice, which was comparable to measurements at open-water stations (Table 3).

Table 3. The depth of 1% light penetration at different sampling sites in 1996

Ice thickness [cm]	Percentage of light (PAR)	Depth [m]	Date	Fjord, station
100	1.07	1	$5 { m May}$	Kongsfjorden, K6
100	0.76	3	9 May	Kongsfjorden, K6
100	0.76	3	11 May	Kongsfjorden, K6
65	0.89	4	24 April	Adventfjorden, A1
30	0.98	14	19 May	Kongsfjorden, K4
15	0.78	18	28 April	Adventfjorden, A1
15	0.83	15	1 May	Adventfjorden, A1
13	0.96	27	27 April	Kongsfjorden, K5
13	1.09	25	29 April	Kongsfjorden, K5
ice edge	0.89	19	11 May	Kongsfjorden, K6
ice edge	0.84	15	19 May	Kongsfjorden, K6
open water	0.85	25	6 May	Kongsfjorden, K7

104 phytoplankton taxa and 3 flagellate taxa were identified in 130 water samples; diatoms were dominant (Table 4). The numerically important flagellates were determined with respect to size classes only, so their

Taxon	Month	Algae type [*]	Area**	References***
Achnanthes taeniata Grun.	May	Р	S, A, K	4, 5
Actinoptychus senarius Echr.	April	Р	A, K	5
Amphinidium sphaenoides Wuff		Р		2
Entomoneis paludosa Grun.	May, July	Р	S	5
Amylax triacantha (Jörg) Sournia	May, July	Р	S	5
Apenidella spinifera (Throndsen) Throndsen	July		K, Pack Ice	1, 2
Bacteriosira fragilis (Gran) Gran	May		S, K	3, 5
$Calcycomonas \ wulffi$	July		Κ	1
Cerataulina pelagica (Cleve) Hendey	May	Р	Κ	4
Ceratium arcticum (Ehr.) Cleve	May		S	4
Chaetoceros affinis Laud.	May		\mathbf{S}	5
Chaetoceros brevis Schütt	May		\mathbf{S}	5
$Chaetoceros\ ceratos por orus$	May		\mathbf{S}	5
$Chaetoceros\ constrictus\ {\it Gran}$	May	Р	S	5
Chaetoceros debilis Cleve	July		K, S	1, 5
$Chaetoceros\ decipiens\ Cleve$	May	Р	Κ	5
Chaetoceros diadema (Ehr.) Gran	May, July	Р	S	5
Chaetoceros furcellatus Bailey	April		Н	3
Chaetoceros holsaticus Schütt	May, July	Р	S, K	5
Chaetoceros lacinosus Shütt	July	Р	Κ	1
Chaetoceros septentrionalis Østrup	May	Р	S	5
Chaetoceros socialis Lauder	April, May	Р	A, S, H, K	3, 5
Chaetoceros sp.	May	Р	S	5
Chaetoceros subsecundus (Grun) Hudst.	May, July	Р	S	5
Coccolitophora tot.	July		A, K	1, 5

Table 4. Check list of phytoplankton found in the water column under the fast ice

 in Svalbard fjords and the adjacent area

Table 4. (continued)

Taxon	Month	Algae type*	Area ^{**}	References***
Cryptophyta	April, May, July	Р	S, A, K,	5
Detonula confervacea (Cleve) Gran	May	Р	Н, К	3, 5
Dictyocha speculum Ehrenberg	May	Р	А, К	5
Dinobryon balticum (Shütt) Lemm.	May, July	Р	S, K	3, 5
Dinobryon sp.	July	Р	Κ	1
Dinoflagellatae tot.	April, May, July	Р	A,K,S	1, 5
<i>Emiliana huxlei</i> (Lohm.) Hay et Mohler	April, May	Р	A, K	5
Eucampia groenlandica Cleve	April, May	Р	Pack Ice, A, K, S	2, 5
Flagellatae	January–May, July		А, Н, К	1, 3, 5
<i>Fragilariopsis</i> sp.	April, May	Р	H, S, A, K	3, 5
Fragilaria sp.	May, July	Р	A, S	5
Fragilariopsis oceanica (Cleve) Hasle	March–May, July	Р	S, K, A	4, 5
<i>Gymnodinium lohmanii</i> Pauls.			Pack Ice	2
Gymnodinium simplex (Lohm.) Kofoid et Swezy	March–May, July	Р	A,K,S	5
Gymnodinium sp.	March–May, July	Р	A,K,S	5
Gymnodinium wulffii Schiller	April, May	Р	A,K,S	5
<i>Gyrodinium grenlandicum</i> Braarud	July	Р	Pack Ice	2
Leptocylindricus danicus Cleve	May, July	Р	Pack Ice, K	2, 5
Leucocryptos marina (Braarud) Butch.	May	Р	Pack Ice, K	2, 5
<i>Licmophora</i> sp.	May		Κ	3, 5
Meringosphaera tenerrima Schiller	July		Κ	1

Table 4. (continued)

Taxon	Month	Algae type [*]	Area ^{**}	References***
Minuscula bipes Lebour	April, May	Р	S, K	5
Navicula pelagica Cleve	May	Р	Κ	5
Navicula sp.	March–May, July	P, S	S, K, A	4, 5
Navicula cf. transitans Cleve	May	P, S	S	4
Nitzschia delicatissima Cleve	May, July	P, S	Pack Ice, A, S	2, 5
Nitzschia frigida Grunow	April, May	Р	А, К	5
Nitzschia longissima (Bréb.) Ralfs	May	Р	S, A, K	4, 5
Nitzschia seriata Cleve	March–May, July	Р	S, K, Pack Ice	5, 2
Nitzschia sp.	May		S	4
Odontella aurita (Lyngb.) Agardh	April, July	Р	S, A, K	4
Pennatae n. det.	May		S	4
Phaeocystis pouchetii (Hariot) Lagerh.	May, July		S, H, K, A	3, 4, 5
Pleurosigma sp.	May		S	4
Protoperidinium curvipes (Ostenf.) Balech	May	Р	S	4
Protoperidinium depressum (Bailey) Balech	May	Р	Κ	3
Protoperidinium divergens (Ehr.) Balech	May, July	Р	S	4
Protoperidinium islandicum (Paulsen) Balech	May	Р	S	4
Protoperidinium minutum (Schiller) Wall and Dale	May	Р	S	4
Protoperidinium pellucidum Bergh	May	Р	S, A, K	4, 5
Protoperidinium spp.	May	Р	S	4
Protoperidinium subcurvipes (Lebour) Balech	May	Р	S	4
resting spores	May	Р	S	4
Rhizosolenia hebetata Bailey	July	Р	Pack Ice	2

Table 4. (continued)

Taxon	Month	Algae type*	Area**	References***
Thalassiosira antarctica Comber	March–May, July	Р	Pack Ice, S, A, K	2, 4, 5
Thalassiosira baltica (Grun.) Ostenf.	May		S	4
Thalassiosira bioculata (Grun.) Ostenfeld	July		Pack Ice	2
Thal assios ira gravida Cleve	May		\mathbf{S}	4
$Thal assiosira\ nordenski oeldi i$ Cleve	May		Pack Ice, S, H, K	2, 3, 4

*Algae types: S – sympagic, P – pelagic;

**Area codes: K – Kongsfjorden, A – Adventfjorden, S – Sassenfjorden, H – Hornsund, Pack Ice – North of Spitsbergen;

***References: 1 – Halldal & Halldal 1973, 2 – Heimdal 1983, 3 – Eilertsen et al. 1989, 4 – Węsławski et al. 1993, 5 – present study.

contribution to the phytoplankton diversity is unknown. The microplankton biomass displays strong site-to-site variation in Kongsfjorden, where diatoms were found to make up from 20 to 90% of the algal biomass (Fig. 3a). The biomass ranged from 5 to 15 gC m^{-2} , with chlorophyll *a* concentrations between 3 and 7 mg dm^{-3} (Table 5). Sedimentation ranged from 100 to $260 \text{ mgC m}^{-2} \text{ day}^{-1}$, with a high proportion of diatoms (Table 6).

Temporal variations at station A1 in Adventfjorden revealed a slow decrease in the biomass of the dominant flagellates from 98 to 33% and an increase in that of diatoms (Fig. 3b). The same temporal changes in the water column show the algae almost evenly distributed from the undersurface layer to 30 m depth (Fig. 4). Like the algal groups, flagellates were the most abundant between 5 and 15 m depth (Fig. 4).

Bray-Curtis similarity clusters (based on taxonomic content and density) distinguish three groups of stations (Fig. 5). The first group (K5, K18/1, K18/2) are open-water stations in the outer part of the Kongsfjorden, dominated by *Navicula* sp. and *Thalassiosira nordenskioeldii*. The second cluster consists of mixed Kongsfjorden and Adventfjorden samples collected in the thick and medium ice, dominated by flagellates. The third cluster comprises mixed Adventfjorden and Kongsfjorden samples from thin ice and the ice edge, dominated by mixture of minor diatoms, flagellates and coccolithophorids (Fig. 5). These assemblages reflect the stages of succession from full ice conditions to broken-ice and open-water samples.

Cryptophyta

Flagellatae

Ø



Fig. 3. Biomass proportions among the major taxonomic groups in Kongsfjorden (a) and Adventfjorden (b); spring samples

Dinophyceae

Prymnesiophyceae

Bacillariophyceae

Prasinophyceae

Ice cover	Phytoplankton	Phytoplankton	Chlorophyll a	Biomass	Dominant	Date	Fjord, station
[cm]	$[mgC m^{-3}]$	$[10^6 \text{ cells m}^{-2}]$	$[mg(chl a) m^{-3}]$	$[\rm gCm^{-2}]$	taxa		
100	17.5	67	0.62	0.4	Flagellatae,	5 May 1996	Kongsfjorden, K6
					$Th.\ nordenski oeldii$		
100	124.8	151	_	1.24	$Th.\ nordenski oeldii$	9 May 1996	Kongsfjorden, K6
100	90.1	200	4.39	0.91	Flagellatae	11 May 1996	Kongsfjorden, K6
					$Th.\ nordenski oeldii$		
65	8.6	6.7	0.11	0.1	Flagellatae	11 April 1995	Adventfjorden, A1
65	2.4	4.1	0.51	0.05	Flagellatae	13 April 1995	Adventfjorden, A1
65	6.8	9.2	_	0.2	Flagellatae	16 April 1995	Adventfjorden, A1
65	8.5	12.7	0.2	_	Flagellatae	19 April 1995	Adventfjorden, A1
65	19.4	19.9	_	_	Flagellatae	22 April 1995	Adventfjorden, A1
30	66.5	285	0.6	0.5	Flagellatae	19 May 1996	Kongsfjorden, K4
					Th. nordenskioeldii	v	
15	11.8	10	0.6	0.1	Flagellatae	28 April 1995	Adventfjorden, A2
					Th. antarctica	-	v
15	33.3	10	1.7	0.4	Th. antarctica	1 May 1995	Adventfjorden, A2
					Flagellatae		•
15	72.2	51	0.17	2.0	Coccolitophora	2 April 1996	Adventfjorden, A1
					Th. nordenskioeldii	-	v
13	79	18	0.95	1.97	Flagellatae	27 April 1996	Kongsfjorden, K5
13	28.4	65	0.49	0.71	Flagellatae	29 April 1996	Kongsfjorden, K5
					Th. nordenskioeldii	-	- · · ·

Table 5. Dominant algae species, biomass (values integrated from 0, 5, 10 and 40 m depths) and phytoplankton abundance under different fast ice thicknesses, Adventfjorden and Kongsfjorden April, May 1996

Table 5.	(continued)
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Ice cover [cm]	$\begin{array}{c} Phytoplankton\\ biomass\\ [mgCm^{-3}] \end{array}$	Phytoplankton density $[10^6 \text{ cells m}^{-2}]$	Chlorophyll a concentration $[mg(chl a) m^{-3}]$	Biomass $[gCm^{-2}]$	Dominant taxa	Date	Fjord, station
ice edge	133	183	_	1.5	Th. nordenskioeldii	11 May 1996	Kongsfjorden, K6
ice edge	54	175	1.2	0.7	Flagellatae Th. nordenskioeldii	19 May 1996	Kongsfjorden, K4
open water	209	83	3.2	6.2	$Th.\ nordenski oeldii$	16 May 1996	Kongsfjorden, K7
open water	336	278	6.5	6.7	$Th.\ nordenski oeldii$	17 May 1996	Kongsfjorden, K7
open water	72	150	_	0.8	Th. antarctica Bacteriosira sp.	18 May 1996	Kongsfjorden, $K3/1$
open water	89.5	238	_	0.5	Navicula spp.	18 May 1996	Kongsfjorden, $K3/2$
open water	28	115	_	0.7	Flagellatae Th. nordenskioeldii	18 May 1996	Kongsfjorden, K3/3

 Table 6. Sedimentation rates of phytoplankton

Period	Area	Replicates	$\begin{array}{c} {\rm Rate} \\ [{\rm mgCm^{-2}day^{-1}}] \end{array}$	SD	$\begin{array}{c} \text{Rate} \\ [\text{mg}(\text{chl}a)\text{m}^{-2}\text{day}^{-1}] \end{array}$	SD	Dominant species
13-19.04.95	Adventfjorden	4	2.88	1.10	_		Th. antarctica Th. nordenskioeldii
25.04.95 23.04-28.05.96	Adventfjorden	5	26.40	19.66	_		Thalassiosira spp. Fragilariopsis oceanica
30.04 - 11.05.96	Kongsfjorden	3	1.39	0.50	0.16	0.04	Thalassiosira spp.

SD – standard deviation



Fig. 4. Temporal changes in the occurrence of major taxa in Adventfjorden, April 1995

Chlorophyll *a* and organic carbon values (Fig. 6) show that in samples dominated by flagellates (Adventfjorden under-ice samples), the observed carbon concentrations are unrelated to the chlorophyll values; hence these flagellates could be regarded as heterotrophic. The relationship was slightly better in the Kongsfjorden samples, where sampling was conducted under better light conditions and flagellates were not so dominant (Fig. 6). The proportion of flagellates in the microplankton was also high in Storfjorden and Burgerbukta, where flagellates made up 100% of the biomass in April, attaining values similar to those observed in winter (Table 7). The mean ratio of chlorophyll *a* to carbon was *ca* 0.05 (SD = 0.10) in the samples examined. The relationship between the ice type and the dominant algae in the water column underneath shows that flagellates prevail under poor light conditions (thick ice, early in the season), while the dominant diatom *Th. nordenskioeldii* appears later in the season at the ice edge and in the open water leads (Table 5).

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Taxon		Storfjor	rden (11 Apr	ril 1996)	Burgerb	Burgerbukta 1 (1 May 1996)			Burgerbukta 2 (1 May 1996)		
						Depth [m]					
		0	0.5	1	0	0.5	1	0	0.5	1	
Gymnodinium sp.	А						3131				
$1015\mu\mathrm{m}$	В						0.4				
Flagellatae	А	1.4×10^6	2.6×10^5	8.6×10^5	8.7×10^5	5.3×10^5	6.4×10^5	6.2×10^5	4.2×10^5	6.3×10^5	
$35\mu\mathrm{m}$	В	5.2	0.96	3.2	3.2	2.0	2.4	2.3	1.5	2.3	
Flagellatae	Α	$7.3 imes 10^5$	6.2×10^4	2.6×10^5	3.6×10^5	2.6×10^5	2.9×10^5	1.7×10^5	8.9×10^4	1.4×10^5	
$5-10 \mu \mathrm{m}$	В	21.6	1.8	7.7	10.8	7.7	8.6	5.2	2.6	4	
Flagellatae	Α	$7.8 imes 10^4$	0	2.6×10^4	1.9×10^5	1×10^5	1.3×10^5	6.2×10^4	7.5×10^3	1.6×10^5	
$1015\mu\mathrm{m}$	В	8.8	0	2.9	21.5	11.7	14.1	7.1	0.8	17.6	
Flagellatae	Α									10^{5}	
$1525\mu\mathrm{m}$	В										
Navicula sp.	Α			1044							
$5070\mu\mathrm{m}$	В			0.15							
Fragilariops is	Α			2088	10^{6}	6×10^4	$4.7 imes 10^5$	8.1×10^4	0	1.4×10^5	
oceanica	В	0	0	0.1	49.7	3	23	4	0	7	
Peridinium sp.	Α			1044							
$2550\mu\mathrm{m}$	В										
Pleurosigma sp.	Α						1044				
	В										
total	Α	2.2×10^6	3.2×10^5	1.2×10^6	2.4×10^6	$9.7 imes 10^5$	1.5×10^6	9.4×10^5	5.1×10^5	1.1×10^6	
	В	36	2.8	14	85	24	49	19	5	31	

Table 7. Abundance (A) [cell dm⁻³] and biomass (B) [mgC m⁻³] of phytoplankton from Storfjorden and Burgerbukta, April, May 1996



Bray-Curtis similarity

K - samples taken in Kongsfjorden A - samples taken in Adventfjorden

Fig. 5. Bray-Curtis similarity clusters for spring samples







Fig. 6. Relation between chl *a* values and organic carbon in the samples from Adventfjorden (a) and Kongsfjorden (b)

5. Discussion

Water column algae and ice algae

Are the algae found in the water column under the ice the same as ice-associated species? There are different answers to this question in the literature, since both cases have been observed (Apollonio 1961, Horner & Alexander 1972, Gradinger *et al.* 1991, Horner 1985). Data from net phytoplankton collected under fast ice in Sassenfjorden shows 23% of typically ice-associated species, 37% found only in the water, and the remaining 39% found in both habitats (Węsławski *et al.* 1993). Colonial ice diatoms like *Melosira* sp. tend to sink fast once detached from the ice undersurface (Gutt 1995). Among the phytoplankton taxa identified in this study, only 8 (10%) were noted in the literature as ice-associated (sympagic); the others are typical pelagic marine and neritic species.

Temporal changes - succession

The phytoplankton succession under fast ice observed in the present study could be summarised as a change from mostly heterotrophic flagellates to diatoms, followed later in the season by dinophyceans. A secondary flagellate peak, as in the observations by Halldal & Halldal (1973), Eilertsen et al. (1989) and Keck et al. (in press), is caused on the one hand by nutrient depletion, on the other by poor light conditions due to the increase in mineral particles during the melting season. This pattern is similar to that reported from the pack ice in the Arctic Sea (Melnikov 1989). The algae dominant at the onset of the diatom bloom were not the same as those found in ice samples, hence the seeding hypothesis seems unlikely. Eilertsen et al. (1989) observed a well-developed bloom under stable ice cover, long before ice melting and water column stratification, *i.e.* before any possible seeding of the ice algae. In the ice-covered Canadian Arctic, sedimentation of ice algae was found to be out of phase with that of phytoplankton (Tremblay et al. 1989, Michell et al. 1993).

Spatial changes

The phytoplankton was patchily distributed. Even though the ice edge and the open water were only a few hundred metres apart, the phytoplankton assemblages in the two habitats differed with respect to density and taxonomic structure. Differences in phytoplankton assemblage distribution were observed in summer, where the inner fjord basin was dominated by small flagellates, the central part by chrysophyceans and the outer part of Kongsfjorden by diatoms (Keck *et al.* in press). Summer data from the Svalbard shelf collected in three different years shows three relatively stable algal assemblages (West Spitsbergen Current, Barents Sea and fjord assemblages) (Markowski & Wiktor 1998). However, the dominant species are different from those noted in the present study, and the fjord phytoplankton could be regarded as a separate assemblage.

Ice type and phytoplankton

The type of ice and its snow cover are the key factors determining light conditions in the water column beneath (Perovich 1998). A 50 cm-thick layer of snow transmits 1 to 0.3% of the radiation, while snow-free ice 1 m thick transmits 20% of the light (Maykut & Grenfell 1975, Gradinger *et al.* 1991). The observed differences in algal assemblages could well be attributed to the light conditions. Thick fast ice in fjords is similar to some extent to drifting pack ice. According to Heimdal (1983), samples collected from the North Spitsbergen pack ice in September were dominated by a post-bloom community of minute diatoms, different from those noted in the present study. Personal observations made in Eastern Svalbard in July show phytoplankton assemblages differing with respect to biomass and taxonomy from those reported from the fjords in the present paper. The summer pack-ice phytoplankton was dominated by *Phaeocystis pouchetii, Chaetoceros socialis, Fragilaria islandica* and

Fragilariopsis oceanica, attaining high densities $(5 \times 10^6 \text{ cells } \text{dm}^{-3})$ and biomasses of $63 \,\mathrm{mgC}\,\mathrm{m}^{-3}$ at ice margins (Andreassen & Wassman 1998, Owrid et al. in preparation). The summer post-bloom phytoplankton in fjords is adversely affected by a glacial, sediment-laden water discharge resulting in a reduction in transparency below 1 m (Halldal & Halldal 1973, Keck et al. in press). Shelf and open-sea pack ice is not affected by this phenomenon. In spring, when fjord water is still transparent, the thin ice (< 0.5 m thick) provides good light conditions and is similar in its optical properties to open-sea water. Even without snow cover, 1 m-thick ice transmits 20% of the solar radiation to the surface water layer (Maykut & Grenfell (1975). Hegseth (1992) demonstrated the change in the chlorophyll a-to-carbon ratio in ice algae in relation to decreasing light conditions. In poor light, under thick ice cover the chl a/C was ca 0.1 in value, while in good light it was 0.02. Since the average chl a/C ratio in our samples was ca 0.02, this may suggest good light conditions; on the other hand the high proportion of flagellates alters the chl a/C factor. The open water between ice floes and local polynyas was characterised by a higher proportion of large diatoms, and a reduced number of flagellates, the typical picture of coastal phytoplankton in north-east Greenland (Węsławski et al. 1997). Gradinger et al. (1991) observed a fall in flagellate density and a rise in diatom density following the removal of snow from the ice cover. The fast ice observed during the present survey was unstable, its average thickness of 0.5 m suggesting an age of more than 2 months (Gorlich & Stepko 1992). Frequent break-ups are characteristic of Spitsbergen fjords, when the winter ice cover is $ca 0.5 \,\mathrm{m}$ thick (Gorlich & Stepko 1992). The instability and frequent re-freezing of the ice cover prevents ice algae from forming larger and dense colonies, such as are observed under stable fast ice in the Canadian Arctic (Cross 1982).

The phytoplankton observed under the fast ice in Spitsbergen fjords is less diverse than that from shelf-water and pack ice assemblages. In winter and early spring the phytoplankton is heavily dominated by heterotrophic flagellates; these taxa again become dominant, after the spring diatom bloom. Because of the differences in the taxa observed in ice cores and the lack of correlation between the ice melt and the start of the spring bloom, it seems unlikely that fast ice seeds the algae that start the spring bloom in Svalbard fjords. Even if it does not support the phytoplankton bloom, the fast ice neither inhibits no delays it there; in most cases it allows for sufficient solar energy transmission. This is probably in contrast to the very thick, stable and snow-covered fast ice usually observed in the Canadian Arctic (Cross 1982). Alexander *et al.* (1974), Matheke & Horner (1974) and Apollonio (1961) have shown that the ice algae bloom and the water column bloom are processes separate in time and space. In the fjord area studied, the advection of algae from the open sea is more likely to contribute to the early spring algal growth than algae from the fast ice cover.

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