Materials and methods

Sampling

Due to the ice-cover that usually persists until May, the investigations in 1978, 1979 and 1980 were performed only during the summer (July and August). In 1984 and 1985 we were supplied with water samples collected during spring (May and June 1984) from Kongsfjorden and from Hornsund (February to May 1985) (Table I). Some of the results from 1978 have been presented elsewhere (Schei *et al.*, 1979). Hydrographic measurements were taken with a Neil Brown CTD Sonde. The complete set of hydrographic observations from 1979 to 1983 is given in Normann and Pettersen (1984).

Seawater was collected with a non-toxic plastic water sampler (Niskin) and screened through a nylon net (mesh size 350 μm).

The sampling depths during the summer cruises were determined from continuous *in vivo* fluorescence (FL) profiles (50–0 m), and were usually 0, 2, 4, 8, 16, 32 and 50 m. During spring the sampling depths were 0, 5, 10 and 20 m.

Light

Sub-surface vertical attenuation was calculated on basis of measurements of scalar irradiance down to 50 m with a Lambda Instruments Model 185 quantum meter (400–700 nm). Scalar irradiance during the carbon assimilation experiments was measured with the same sensor coupled to a Lambda Model 500 integrator.

Chemical measurements

Nitrate, orthophosphate and silicate were analysed onboard according to Strickland and Parsons (1972). Chlorophyll *a* was analysed according to Edler (1979) using a Turner Model 111 fluorometer. Particulates were filtered onto GF/C filters and analysed immediately onboard the vessel.

Phytoplankton identification and enumeration

Water samples of 100 ml were preserved with 2 ml 40% formaldehyde neutralized with hexamine. Sub-samples of 2 ml were examined by the inverted microscope technique.

Table I. Variables measured in West Spitzbergen fjords

Date	Sampling area	Hydrography	Scalar irradiance	Chl*a*	Cell counts	C^{14}	Plant nutrients
1978	Van Mijen	x	x		x	x	x
1979	Van Mijen–Raudfjord	x	x	x	x	x	x
1980	Van Mijen–Woodfjord	x	x	x	x	x	x
1984	Kongsfjord				x		
1985	Hornsund	x			x	x	x

For a complete list of sampling stations and dates see Table VI.

Phytoplankton studies in the fjords of West Spitzbergen: physical environment and production in spring and summer

H.C.Eilertsen, J.P.Taasen and J.M.Węsławski[1]

Norwegian College of Fisheries Science, University of Tromsø, PO Box 3083, Guleng, 9001, Tromsø, Norway and [1]Institute of Oceanology, Polish Academy of Sciences, Powstańców, Warszawy 55, 81-967 Sopot, Poland

Abstract. The phytoplankton in the fjords of West Spitzbergen was investigated from 1978 to 1985. The spring bloom lasted longer than at the Norwegian coast: from mid March to early June. There is no delay in the onset of the spring bloom in Spitzerbergen fjords relative to fjords of northern Norway. This is probably related to the rapid daylength increase at high latitudes. The phytoplankton species composition during spring was comparable to that along the coast of northern Norway. Annual primary production in the investigated area was calculated to be 150 g C m^{-2} $year^{-1}$.

Introduction

Our knowledge of phytoplankton communities in the fjords of Spitzbergen is generally sparse, and most of the investigations in adjacent Arctic waters are descriptive studies of a taxonomic and biogeographic nature (Østrup, 1895; Cleve, 1899; Gran, 1902, 1904; Smayda, 1958; Zenkevich, 1963).

Data dealing with seasonal variations, primary production and growth physiology are few and primarily present results from oceanic localities (Braarud, 1935; Corlett, 1958; Ellertsen *et al.*, 1982; Heimdal, 1983; Rey and Loeng, 1985). There are also some reports from the sub-Arctic Russian region of the Barents Sea (Sokolova and Solov'yeva, 1971; Vedernikov and Solov'yeva, 1972; Bobrov, 1985).

The western side of Spitzbergen is strongly influenced by a branch of diluted Atlantic water that originates from the Norwegian Atlantic Current (Tantisiura, 1959). The investigated fjords (Hornsund, Van Mijenfjorden, Isfjorden, Kongsfjorden, Woodfjorden, Wijdefjorden, Smeerenburgfjorden, Magdalenefjorden and Raudfjorden) are heavily influenced by large amounts of freshwater runoff from glaciers during the summer.

At the north of Spitzbergen (79–80°N) the sun stays below the horizon from November 1 until February 25. At the southern part of Spitzbergen (77–78°N) the winter darkness lasts from November 10 until February 15. The midnight sun period lasts from May 1 until August 25 in the north of Spitzbergen and from May 10 until August 15 in the south (Brahde, 1970). The fjords are normally ice-covered for 6–10 months of the year. The Arctic region thus offers good opportunities to study the effects of extreme light variations and low temperature upon the marine ecosystem. As an expansion of our plankton investigations in the sub-Arctic north Norwegian fjords (Eilertsen *et al.*, 1981; Bech, 1982; Eilertsen and Taasen, 1984), our research program has since 1978 also included the fjords of West Spitzbergen.

Carbon assimilation experiments

The method for ^{14}C uptake followed the method described in Strickland and Parsons (1972). To *in situ* light and dark bottles (100 ml) was added 0.5 ml (1.85×10^5 Bq or 5 μCi) NaH_2CO_3 solution (Radiochemical Centre, Amersham). The duration of the experiments was 5–6 h around noon. Some of the samples were subsequently fractionated by screening the phytoplankton carefully through a nylon plankton net, mesh size 20 μm. We estimated annual production by first computing 24 h production values for the different stations in Van Mijenfjorden in 1978, 1979 and 1980 by assuming that carbon assimilation was linearly proportional to irradiance in 6 h increments, with the uptake rates around noon as base values (see Eilertsen and Taasen, 1984). We thereafter computed production for the summer by simple plane integration between the data points. Production during spring was calculated on the basis of carbon assimilation values for Hornsund in 1985, assuming that carbon net uptake occurred for 10 h on March 16 and for 16 h on April 30 (Table V). Finally, we assumed that the phytoplankton growth season ended in late October (Vowinckel and Orvig, 1970). The annual production was then calculated by integration.

Results

Hydrography

The investigated fjords have maximum depths of 100–200 m. Van Mijenfjorden and Raudfjorden (Figure 1) have sill depths of 35 m that affect the circulation pattern to a pronounced extent.

Surface temperatures during the summers of 1980 and 1981 varied between 2 and 4°C (Figure 2). The highest surface temperatures were observed in the innermost part of Van Mijenfjorden (5.1–6.7°C, station 2, see Figure 1).

The lowest temperatures (−1.75°C) were measured below 100 m depth in Raudfjorden in 1980. Also, Van Mijenfjorden had cold bottom water (−1.7°C) of high salinity (Figure 2). The northernmost fjords had lower maximum temperatures (Figure 2). In Van Mijenfjorden the temperatures were generally higher in the whole water column in 1980 than in 1979 (Figure 2). The hydrographic conditions in Van Mijenfjorden in 1978 were similar to the situation in 1979 (Schei *et al.*, 1979). Further north, temperatures were of similar range in all years.

Large amounts of freshwater runoff from the surrounding glaciers resulted in extremely low salinities at the head of some of the fjords. Near Sveagruva, at the head of Van Mijenfjorden, the mean salinity varied around 7‰ in all the investigated years. The brackish surface layer reached down to 15 m in Van Mijenfjorden. Further north, the halocline was found at shallower depths (Figure 2).

The water temperatures in Hornsund were constantly below −1.55°C in the entire water column from January until mid-April in 1985, and salinity varied around 33.5‰ until June (J.M.Węsławski, personal communication).

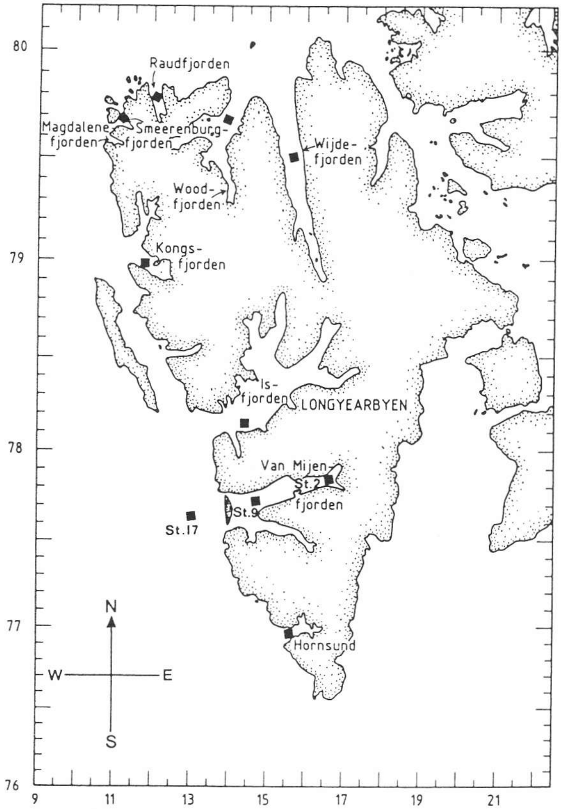

Fig. 1. Sampling stations in the fjords of West Spitzbergen.

Incident and sub-surface radiation

The 1% irradiance depth varied between 15 and 35 m at most of the stations (Figure 3). In the inner parts of some of the fjords (Van Mijenfjorden) we registered no (measurable) light intensity at 0.1 m due to extreme amounts of silt in the uppermost water masses. Light penetration usually increased from the head to the mouth of the fjords (Figure 3).

Water chemistry

The measurements often showed higher nutrient concentrations below the pycnocline than above (Figure 4). Nitrate concentrations typically varied around 2–5 μmol l^{-1} and phosphate around 0.5 μmol l^{-1} during summer. Silicate concentrations were similar to those of nitrate. In Van Mijenfjorden in 1979 there were higher values of nitrate and phosphate under the pycnocline (Figure 4).

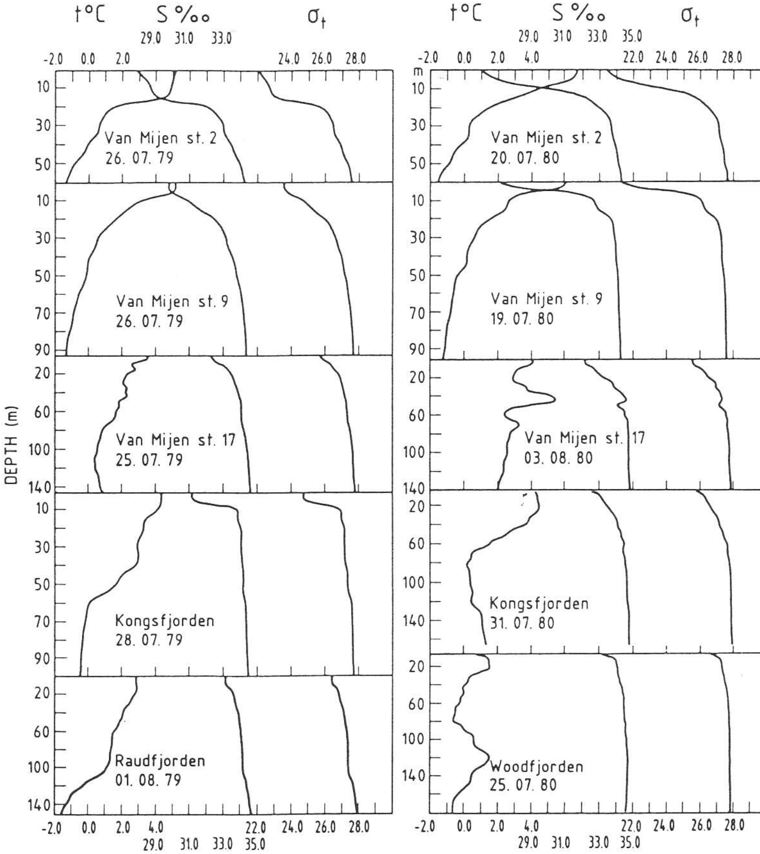

Fig. 2. Vertical distribution of temperature, salinity and σ_t at selected stations.

Phytoplankton abundance, species composition and carbon assimilation

The spring samples from Kongsfjorden and Hornsund showed high cell numbers, which indicate surface blooms (Table III). Predominant species in the spring were *Phaeocystis pouchetii* and *Chaetoceros socialis.* From April 9 large amounts of *Phaeocystis* colonies were found in Hornsund. At the same time *Chaetoceros socialis* was found for the first time. Other important spring species both in Hornsund and in Kongsfjorden were *Thalassiosira nordenskioeldii* and *Fragilariopsis* sp.

The carbon assimilation measurements from Hornsund yielded high values from March onwards (up to 10 mg C m^{-3} h^{-1}; Figure 5), decreasing in June.

During summer, cell counts and Chl*a* measurements indicated low phytoplankton biomass (Table IV, Fig. 6). The northernmost fjords had the greatest

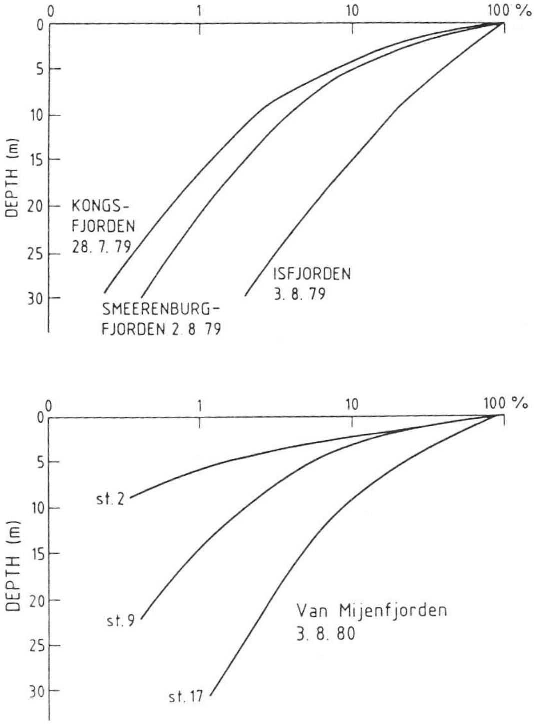

Fig. 3. Vertical attenuation of scalar irradiance, presented as a percentage of the quantum flux reaching the surface.

Table II. Average nutrient concentrations (0–20 m depth) in the fjords of West Spitzbergen, Northern Norway and the Barents Sea before and after the spring bloom

Nutrients (μmol l^{-1})	West Spitzbergen[a]		Barents Sea[b]		Tromsø/Finnmark[c]	
	Before	After	Before	Afer	Before	After
NO_3	–	1.5	11.0	0.0	7.0	1.0
PO_4	0.5	0.3	0.5	0.1	3.0	0.2
SiO_4	5.0	1.0	4.5	0.0	3.0	1.0

[a]Present investigation.
[b]Rey and Loeng (1985).
[c]Unpublished results.

relative abundance of diatoms. The other fjords were dominated by flagellates and 'monads'. The carbon assimilation values were generally low (Table V, Figure 5). In the inner part of Van Mijenfjorden during the summers of 1978–80, net carbon uptake at noon was only measurable down to 8 m depth (Figure 5).

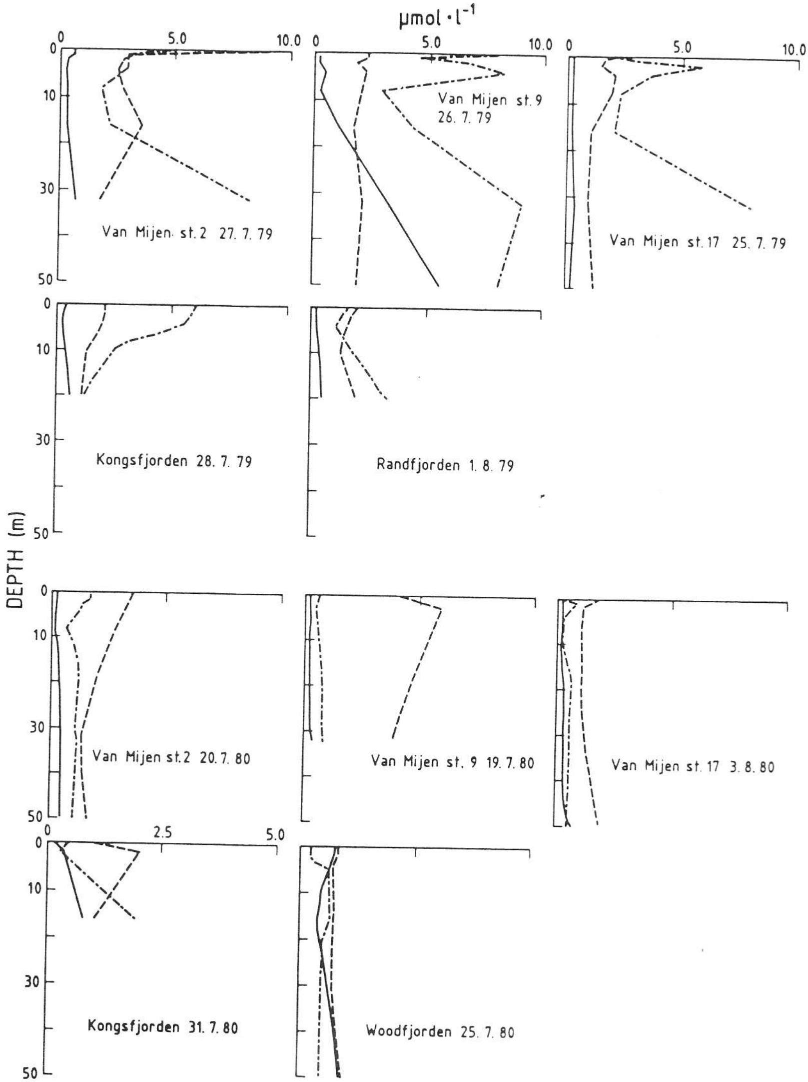

Fig. 4. Nutrient concentrations at selected stations: -·-·-·-· nitrate; ——— phosphate; -----silicate.

The assimilation numbers for waters near the surface varied between 2.0 and 3.5 mg C mg Chl*a* h^{-1} and decreased with depth to ~1.0 at 32–50 m. Carbon assimilation in the size fraction <20 µm in Smeerenburgfjorden and in Isfjorden was 50–85% of total production (Table V).

Table III. Maximum cell concentrations (l^{-1}) in Hornsund and in Kongsfjorden

	1985			
	Feb 21	Mar 30	Apr 9	May 28
Hornsund				
Chaetoceros furcellatus			26 000	
C.socialis			245 000	983 000
Chaetoceros sp.				6600
Detonula confervacea			26 400	
Fragilariopsis sp.			491 000	
Thalassiosira nordenskioeldii			61 440	
Thalassiosira sp.			2000	
Flagellates	81 000	37 109 000		
Phaeocystis pouchetti			3 031 000	7 168 000
	1986			
	May 24			June 12
Konsfjorden				
Bacterosira fragilis	117 100			
Chaetoceros socialis	4 687 000			600
Thalassiosira nordenskioeldii	50 000			
Licmophora sp.				50 000
Protoperidinium depressum	25 000			8000
Dinoflagellates indet.	100 000			
Flagellates	146 000			
Phaeocystis pouchetti	11 952 000			2 577 000

Table IV. Maximum cell concentrations (l^{-1}) at selected stations in summer, 1978–1980

Van Mijenfjorden (station 9, 22 July 1978)	
Dinoflagellates indet.	13 500
Flagellates	11 000
Monads	299 000
Kongsfjorden (28 July 1979)	
Chaetoceros debilis	3500
C.laciniosus	1500
C.socialis	8500
Nitzschia delicatissima	6000
Thalassiosira anguste-lineata	600
Emiliania huxleyi	2500
Flagellates	340 000
Dinoflagellates indet.	12 000
Wijdefjorden (29 July 1980)	
Chaetoceros affinis	60
C.breve	1500
C.compressus	3000
C.decipiens	16 000
C.furcellatus	1500
C.socialis	28 600
Flagellates	225 000

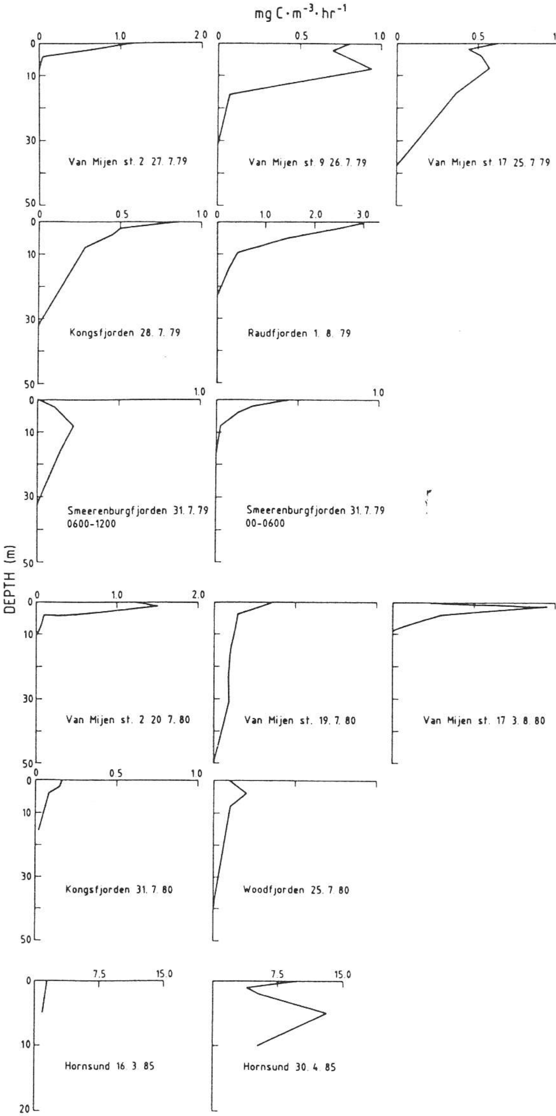

Fig. 5. Vertical distribution of carbon assimilation at selected stations.

Measurements at night (00.00–06.00 h) in Smeerenbergfjorden indicated a carbon assimilation of 50% of the uptake during the preceding day (06.00–12.00 h) (Table V).

Particulate organic carbon and nitrogen were low compared to values from

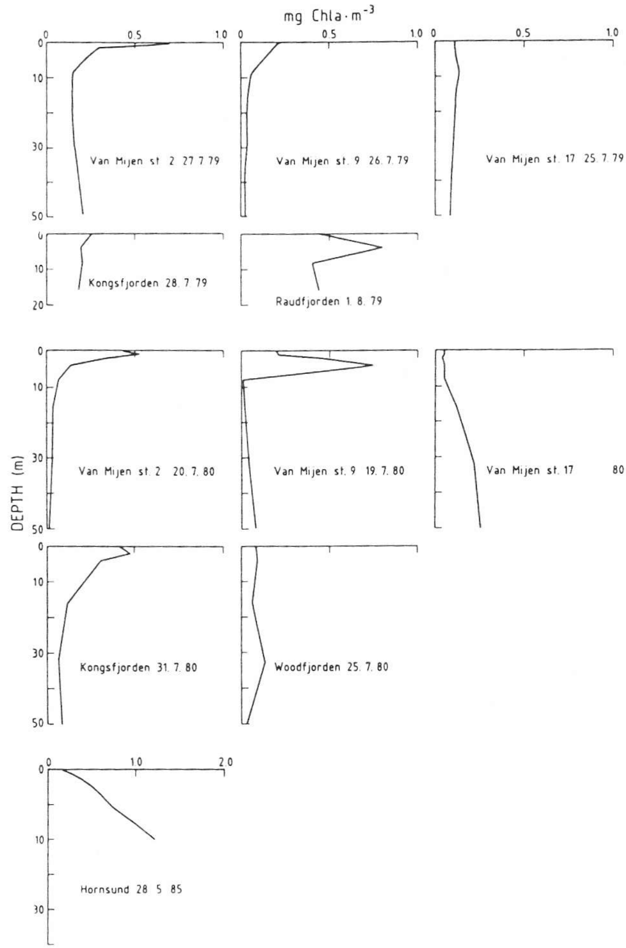

Fig. 6. Depth distribution of Chl*a* at selected stations.

summer in Norwegian coastal areas. Nitrogen varied from 9 to 28 $\mu g\ l^{-1}$ and carbon from 26 to 480 $\mu g\ l^{-1}$ (unpublished data).

Mean annual primary production was estimated to 150 g C m^{-2} $year^{-1}$, when including the values from Hornsund in 1985 as representative for spring values, and using the integrated values from Van Mijenfjorden (mean value from the two years) as estimates for the summer.

Table V. Carbon assimilation and scalar irradiance reaching the surface during the 6 h of incubation experiments

			$E\ m^{-2}\ 6\ h^{-1}$	$mg\ C\ m^{-2}\ 6\ h^{-1}$
1978	Jul 23	Van Mijen station 2	3.2	27.5
	Jul 29	Van Mijen station 2	1.2	5.7
	Jul 22	Van Mijen station 9	3.0	143.0
	Jul 30	Van Mijen station 9	0.8	49.0
1979	Jul 27	Van Mijen station 2	1.2	13.0
	Aug 6	Van Mijen station 2	1.9	19.0
	Jul 26	Van Mijen station 9	0.9	50.6
	Aug 6	Van Mijen station 9	1.5	63.6
	Jul 25	Van Mijen station 17	3.1	229.0
	Aug 7	Van Mijen station 17	1.2	114.3
	Aug 7[a]	Van Mijen station 17	1.2	54.2
	Jul 28	Kongsfjorden	1.1	42.2
	Jul 30	Magdalenefjorden	1.2	11.3
	Jul 31	Smeerenburgfjorden	1.5	21.6
	Aug 1[b]	Smeerenburgfjorden	0.3	9.2
	Aug 1	Raudfjorden	0.9	114.3
	Aug 2	Smeerenburgfjorden	2.3	55.6
	Aug 2[b]	Smeerenburgfjorden	2.3	24.3
	Aug 3[b]	Isfjorden	1.0	53.5
	Aug 3[b]	Isfjorden	1.0	46.1
1980	Jul 20	Van Mijen station 2	1.0	16.0
	Aug 2	Van Mijen station 2	1.2	2.2
	Jul 19	Van Mijen station 9	1.2	17.3
	Aug 2	Van Mijen station 9	1.0	39.5
	Jul 18	Van Mijen station 17	1.0	19.3
	Aug 3	Van Mijen station 17	0.7	8.3
	Jul 24	Smeerenburgfjorden	0.9	84.4
	Jul 25	Woodfjorden	1.0	18.3
	Jul 27	Raudfjorden	0.7	0.7
	Jul 31	Kongsfjorden	1.0	7.8
1985	Mar 16	Hornsund	–	81.0
	Apr 30	Hornsund	–	693.0

[a]Experiments performed on the nanoplankton fraction, i.e. cells that passed through a nylon net mesh size 20 μm.
[b]Carbon uptake between 00.00 and 06.00 h.

Discussion

Spring

The spring bloom started in mid-March and lasted for nearly 2 months in Hornsund (Table III). In Kongsfjorden the spring bloom probably culminated at the end of May/early June (Tables III and IV). At both localities the first part of the spring bloom took place under ice cover. This ice broke up and disappeared during May. It thus appears that the spring bloom in the fjords of West Spitzbergen starts at approximately the same time as the spring bloom in the coastal areas of northern Norway (Eilertsen and Taasen, 1984). This may be surprising considering Spitzbergen is 8–10° of latitude further north.

At the coast of Norway there is a delay of ~3 weeks in the phytoplankton spring maximum at Vesterålen (69°N) relative to that of Møre (63°N) due to the time lag in the seasonal increase in total radiation (Braarud *et al.*, 1958; Braarud and Nygaard, 1978). Data for fjords in Finnmark (70°N), north of Tromsø (69°30′N, Table VI), indicate, however, that the peak of the spring bloom does not occur later at these localities than in the Tromsø area. Nevertheless, a delay in the timing of the spring bloom has been observed between Skjomen (68°30′N) and Balsfjorden (69°30′N) (Table IV).

At all the localities north of Skjomen the spring bloom did take place in unstratified water masses (Table VI), in fjords with depths of ~200 m (Eilertsen and Taasen, 1984). The seasonal warming of the upper water layers and freshwater runoff does not start in these areas until after the spring bloom has occurred (Eilertsen *et al.*, 1981).

It is widely accepted that the timing of the spring phytoplankton bloom is dependent upon a stable upper mixed layer (Braarud and Klem, 1931; Sverdrup, 1953). In other words, a null hypothesis that phytoplankton cannot stratify in the absence of a density gradient can be formulated.

Until March 21 (vernal equinox), the length of the day increases from north to south in the northern hemisphere. After the vernal equinox, daylength increases further north (Table VII). The reason why there is no delay in the phytoplankton maximum north of Tromsø is probably that daylength increases faster at high latitudes, and that this rapid daylength increase enhances primary production compared to areas further south. The 'critical depth' theory states

Table VI. Timing of the spring bloom maximum at various locatilities in Norway, surface irradiance at the onset of the bloom, and vertical stability (0–20 m)

Fjord/area	March	April	May	June	Irradiance (Ly day^{-1})	Vertical stability[h]
Korsfjord (Bergen)[a]	x				150	+
Lofoten[g]		x			100	+
Skjomen[c]		x			60–90	0
Tromsø[d]		x			60	0
Øksfjorden[b]		x			50	0
Altafjorden[b]		x			50	0
Porsangerfjorden[b]		x			40	0
Barents Sea south[e]				x	250	+
Hornsund[f]		x			45	0
Kongsfjorden[f]		x			45	0

[a]Matthews and Heimdal (1980); [b]unpublished results; [c]Eilertsen (1983); [d]Eilertsen and Taasen (1981); [e]Rey and Loeng (1985); [f]present investigation; [g]Schei (1974).
[h]Vertical stability: '0' denotes not significantly different σ_t in upper 20 m relative to underlying 20 m and '+' means measureable σ_t difference.

Table VII. Global radiation and daylength in north Norway and at Spitzbergen

	Global radiation (Ly day^{-1})			Daylength (h)		
	March	April	May	March	April	May
North Norway (70°N)	130	240	350	9.3	13.8	18.3
Spitzbergen (78°N)	80	240	340	7.0	14.5	23.0

that at some instances the combination of the depth of the mixed layer and the degree of mixing is of such an order that the phytoplankton receives insufficient light for net photosynthesis to occur. All the blooms in the Tromsø area and northwards took place in unstratified water masses. This demonstrates that phytoplankton can stratify in the absence of a density gradient, but it must here be noted that our physical criteria for identifying mixed layers was observation of a density gradient, and not actual measurements of the degree of mixing. Thus the absence of a density gradient does not give absolute criteria about the ability of phytoplankton to stratify.

Culture experiments with 11 arctic phytoplankton species has shown that all species had significantly increased growth rates at increased daylengths (Gilstad, 1987). Sakshaug and Andresen (1986) have also shown for *Skeletonema costatum*, that increased light period results in higher growth rates. Sakshaug *et al.* (1987) have designed a general model that simulates growth and light absorption in *Skeletonema costatum*, and they also conclude that it is of utmost importance to include daylength when estimating the onset of blooms and the magnitude of primary production in polar areas.

Carbon assimilation measurements from Smeerenburgfjorden showed that carbon uptake during the night (00.00–06.00 h) amounted to 50% of uptake during the day (06.00–12.00 h). Measurements from the Atlantic Barents Sea south to Spitzbergen has shown that uptake during the night increases the critical depth compared to areas further south (Eilertsen *et al.*, 1989).

Our conclusion from this is that the critical depth (Sverdrup, 1953) increases (is deeper) in northerly areas compared to areas further south in May and April, since days are longer further north, and global radiation values are comparable (Table VII). Measurements of specific carbon assimilation (P/I measurements) from the Barents Sea have also shown that the phytoplankton has high photosynthetic efficiences at low light intensities (Eilertsen *et al.*, 1989). The quantitatively most important species are the same at Spitzbergen as in the Tromsø area (Table III, see also Eilertsen *et al.*, 1981) and in the Barents Sea. The physiological response to light and temperature is assumed by us to be comparable, though we do not have experimental results that confirm this. In total, this indicates that the onset of the spring bloom at high latitudes is closely governed by the yearly increasing daylength, and further work should aim at quantifying this effect relative to stabilization and mixing. This effect is clearly demonstrated by results from three succeeding years of investigations in Skjomen (north of Tromsø) before and after regulation (caused by a power plant) of the freshwater runoff. This regulation induced a much earlier stabilization of the surface layers, but the timing of the spring bloom did not alter significantly (Eilertsen, 1983).

The spring blooms in Kongsfjorden and Hornsund seem to last considerably longer than blooms at the Norwegian coast, where they usually last for about 1 month (Matthews and Heimdal, 1980; Eilertsen, 1983). The initial nutrient concentrations in the Spitzbergen fjords are comparable to initial concentrations from Balsfjorden outside Tromsø (Eilertsen *et al.*, 1984). It was therefore not probable that larger total amounts of new nutrients (accumulated during winter) prolonged the bloom at Spitzbergen. A more plausible explanation may be that the progress of the spring bloom at Spitzbergen is slowed down by heavy grazing, and that further progress continued on the basis of recycled ammonia. In Kongsfjorden we also sampled zooplankton, and the wet wt volumes were ~1.5 ml m^{-3}, with a pronounced predominance of barnacle larvae (unpublished data). This is high compared to oceanic values and clearly indicates that grazing plays an important part in regulating the progress of the spring bloom. Two of the most important phytoplankton species in Hornsund and Kongsfjorden, *Phaeocystis pouchetii* and *Chaetoceros socialis*, are also typical spring species along the coast of Norway (Eilertsen *et al.*, 1981).

Summer

The carbon assimilation rates in summer were generally low (Table V), and amounted to 10–50% of summer values for other Norwegian inshore areas (Matthews and Heimdal, 1980). The results were, however, comparable to results for coastal areas near Murmansk and waters off Spitzbergen (Heimdal, 1983; Sokolova and Solov'yeva, 1971). These low carbon assimilation values measured by us are in accordance with cell numbers (Table IV) and Chl*a* measurements (Figure 6). In the inner part of Van Mijenfjorden, net carbon uptake was measurable only down to ~8 m depth on a clear day (Figure 5). This is due to large amounts of 'silt' contained in the inner parts of the fjords. The nutrient concentrations during summer were surprisingly high (Figure 4). It is therefore a paradox that phytoplankton biomass values were not higher. This has also been observed from coastal areas in northern Norway (Eilertsen and Taasen, 1984). Zooplankton was abundant in Van Mijenfjorden in 1978 (Schei *et al.*, 1979), so grazing may have been important in regulating the phytoplankton crop in summer.

A considerable autotrophic carbon assimilation takes place at night in northerly areas (Eilertsen and Taasen, 1984; Table V). For some species (*Skeletonema costatum* and *Thalassiosira nordenskioeldii*) it has been documented that continuous light increases the growth rate (Baars, 1982; Sakshaug and Andresen, 1986). From Figures 3 and 6 (Van Mijenfjorden station 9) it is evident that the compensation depth during the day is below 1% light depth, and hence also allows the phytoplankton to take advantage of the enhanced nutrient concentrations under the pycnocline. Assimilation numbers were also relatively high at 32–50 m (1.0), again indicating net uptake during the day below 1% light depth (Figure 3).

Fractionation experiments performed in several of the fjords revealed that 50–85% of total production took place in the size fraction <20 μm. This may also have resulted from selective grazing on larger phytoplankton species.

Annual production

Estimated annual primary production in the southern Spitzbergen fjords is calculated as ~150 g C m^{-2} $year^{-1}$. This is in accordance with the revised figures for polar areas given by Subba Rao and Platt (1984). The primary production in inshore high latitude areas is thus comparable to primary production in Norwegian fjords (Matthews and Heimdal, 1980).

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