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Quantum yield and photosynthetic parameters of marine microalgae from the southern Arctic Ocean, Svalbard

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The quantum yield and photosynthetic parameters of phytoplankton and sea ice microalgal communities were assessed from the Arctic Ocean and fjords of northern Svalbard. The phytoplankton community in Fram Strait was dominated by *Phaeocystis* while on Norskebanken it was dominated by diatoms. The quantum yield showed maximum values of 0.64 at 20–40 m below the surface and were consistent with nutrient replete waters elsewhere.

Sea ice infiltration communities were widespread and dominated by *Phaeocystis*. This is the first record of an Arctic infiltration ice community. Quantum yields were relatively low (0.247). Bottom ice communities, which were dominated by *Nitzschia frigida*, were extremely restricted and had moderate quantum yields (0.427). Communities growing on multiyear ice had quantum yields of only 0.126. All ice communities were well adapted to their light environment.

INTRODUCTION

Primary production in high latitudes is essentially partitioned between phytoplankton and ice algal production, with a small contribution from benthic algae in shallow areas. In the Barents Sea the areas north of the Polar Front (~75°N) are ice-covered for most of the year, but open for up to three to five months in summer. Primary production starts under the ice early in the season before the phytoplankton growth commences. Water column primary production continues into autumn for as long as there is light or open water, allowing for a growth season of up to seven months.

The ice algal growth season extends from March until melting starts in June. The most abundant species growing on the underside of the ice is the diatom *Nitzschia frigida* Grun, which is found under all annual pack ice, but other diatoms, mostly pennate forms, are also common (Hegseth, 1992). Even diatom species that are most commonly associated with the phytoplankton, such as *Chaetoceros* spp., *Corethron criophilum*, *Proboscia alata*, *Rhizosolenenia hebetata* and *Pseudo-nitzschia delicatissima*, may be found for a short period under the outermost, thinnest ice. The ice algae grow on the ice underside and not within the ice itself, unlike in Antarctic fast ice or in other Arctic areas such as the Canadian Arctic (Smith et al., 1990).

Phytoplankton growth is delayed by more than a month compared with ice production, and normally starts along the ice edge in mid April. It terminates as a result of refreezing and low light levels in September/October (Hegseth, 1997). Spring phytoplankton blooms are normally dominated by diatoms such as *Chaetoceros socialis* Lauder, *C. furcellatus* Bailey, *Thalassiosira nordenskioeldii* Cleve, *T. antarctica* var *borealis* Fryx., Douc. & Hubb, *T. hyalina* (Grun.) Gran, *Fragilariopsis oceanica* (Cleve) Hasle and others. *Phaeocystis pouchetii* (Hariot) Lagerheim is also very common in spring blooms and may sometimes completely dominate the blooms. Blooms later in the season are dominated by several other algal groups/species such as small flagellates, *Dinobryon* species, *Phaeocystis* and summer diatom species.

Primary production is dependant on the length of the growth season in ice and water, which is primarily a function of latitude. In the Barents Sea the highest annual production ($90\,g\,C\,m^{-2}$) is found south of the Polar Front in the open, Atlantic water masses; it then gradually decreases northward (Slagstad & Støle-Hansen, 1991). The shortest season is found in the area north of Kvitøya (White Island) with an annual production of only $15\,g\,C\,m^{-2}$. Annual production between Kvitøya and the Polar Front is twice as high at $30\,g\,C\,m^{-2}$. Annual ice algal production in the northern Barents Sea is $5\,g\,C\,m^{-2}$ and contributes 20% of the total production of that area (Hegseth, 1998). The Arctic Ocean primary production has recently been revised from the previous estimate of around $1\,g\,C\,m^{-2}$ (English, 1961) to $15–20\,g\,C\,m^{-2}$ (Pomeroy, 1997; Gosselin et al., 1997), which is similar to estimates for the northern limits of the Barents Sea. In the central Arctic Ocean a relatively larger proportion of the total production occurs in the ice, up to 57% (Gosselin et al., 1997). Unlike the Barents Sea, the ice-cover consists of multiyear ice but the ice flora is much the same with *N. frigida* being a dominant species, and other pennate diatoms occurring frequently. This ocean is also the home of some impressive colonies of the centric diatom *Melosira arctica* Dickie, which in zones of 'hydrodynamic shadows' may reach a length of 6 m (Melnikov & Bondarchuk, 1987). Phytoplankton communities are divided into different types, one close to the ice–water interface consisting of centric diatoms, and one in the deeper water masses dominated by flagellates (Gosselin et al., 1997).

Chlorophyll fluorescence has become a widely accepted method of measuring the photophysiology of terrestrial plants. The development of the fast repetition rate fluorometer (FRRF) and pulse amplitude modulation (PAM) fluorometer in the 1980s allowed the measurement of photosynthesis in marine plants (Falkowski & Kolber, 1993; Schreiber et al., 1994). Pulse amplitude modulation fluorometers are able to measure effective quantum yield ($\partial F/F'_m$), maximum quantum yield (Fv/Fm) and electron transfer rate (ETR) of photosystem II (PSII) in photosynthesis. Using rapid light curves (RLC), it is also possible to gain an insight of the photoadaptive state of the plant and to measure the photoadaptive index, E_k. The PAM method is based on weak, modulated light pulses (the measuring light) that allows chlorophyll fluorescence to be monitored without inducing photosynthesis. In the dark-adapted state, a minimum fluorescence (F_0) is determined when the measuring light is turned on. This mostly results from emissions from the antenna pigments. When the sample is exposed to actinic light, i.e. light that induces photosynthesis, a much higher fluorescence results. This fluorescence rapidly peaks and then declines until an equilibrium level, F, is attained. This characteristic behaviour is referred to as the Kautsky curve (Schreiber et al., 1995). Maximum fluorescence (F_m) is achieved by exposing the dark-adapted sample to a pulse of very intense light. The maximum quantum yield of PSII is defined as

$$\phi_{PSII}\ (F_m - F_0)/F_m = F_v/F_m \tag{1}$$

The relative electron transfer rate (rETR) can be calculated from

$$rETR = \phi_{PSII} \times E \tag{2}$$

where E is the irradiance.

The relationship between rETR and irradiance is comparable with a conventional photosynthesis versus irradiance (P vs E) relationship and allows the estimation of the photosynthetic parameters $rETR_{max}$, equivalent to P_{max}, photosynthetic efficiency, equivalent to α and the photoadaptive index, E_k, which is the same as that estimated by conventional methods.

The maximum quantum yield (Fv/Fm) of Southern Ocean phytoplankton was first investigated using fluorometric techniques by Strutton et al. (2000). They found that Fv/Fm was significantly depressed, with most values less than 0.5 and more than 40% of values less than 0.4. They suggested that nutrient depletion, most likely Fe, was the probable cause.

During on-board Fe incubations in the Ross Sea on the AESOPS experiments, most taxa responded to Fe enrichment but a difference was noted between the response of different phytoplankton groups (Olson et al., 2000). Fluorescence was subsequently used to follow the photosynthetic response of a Southern Ocean phytoplankton community during two iron release experiments; first SOIREE in February 1999 (Boyd et al., 2001) and then EisenEx in November 2000 (Gervais et al., 2002). During SOIREE, iron fertilization led to an increase in quantum yield from 0.2 to 0.6 over ten days. A similar increase from 0.3 to 0.55 was seen in EisenEx (Gervais et al., 2002). In the sub-Arctic Pacific Ocean Suzuki et al. (2002) found an east–west gradient in Fe limitation. They reported a gradient in Fv/Fm values from 0.27 to 0.49. There are no comparable studies of phytoplankton Fv/Fm from the Arctic Ocean.

There have been comparatively few attempts to investigate the Fv/Fm of sea ice microalgae using these fluorescent techniques. Schofield et al. (1995) used a pulse amplitude modulation fluorometer (PAM 101, Walz, Effleberg, Germany) to investigate the effects of ultraviolet-B radiation on incubated Antarctic frazil ice samples and Robinson et al. (1998) incubated samples of platelet ice algae from McMurdo Sound with a fast repetition rate fluorometer (FRRF). The first *in situ* measurements of the effective quantum yield (ϕ_{PSII}) of sea ice algae were made by Kühl et al. (2001) in summer fast ice in Greenland with a diving PAM (Waltz, Effleberg, Germany). They found that the ϕ_{PSII} of the under ice microalgae were between 0.20 and 0.65. Rapid light curves on these communities showed an E_k of 7.9 μmol photons $m^{-2} s^{-1}$. All communities were found to be well adapted to the low under-ice light climate and able to adapt to moderate changes in irradiance within minutes. Similarly, in Antarctic fast ice at Cape Evans, McMinn et al. (2003) documented rapid diurnal changes in effective quantum yield (i.e. quantum yield in the light) and a range of Fv/Fm between 0.2 and 0.70 with an average value of 0.45 ±0.15.

Quantum yield and photosynthetic parameters ($rETR_{max}$, α, E_k) of benthic microalgal mats from a shallow coastal site at Casey, eastern Antarctica were measured (McMinn et al., 2004). The only use of PAM techniques reported for Arctic benthic communities was by Kühl et al. (2001) working in north-east Greenland. They recorded maximum *in situ* effective quantum yields of up to 0.65 but noted the extreme shade adaptation of the Greenland benthic community, with an E_k of only 4.6 μmol photons $m^{-2} s^{-1}$, and evidence of photoinhibition at as little as 10–15 μmol photons $m^{-2} s^{-1}$.

The objective of this study is to assess the photosynthetic capacity and competency of Arctic microalgal communities. In particular we want to determine whether they are adapted to their light climates and whether other stresses, such as nutrient deficiency or senescence, are effecting photosynthetic performance.

MATERIALS AND METHODS

Quantum yield and photosynthetic parameters were measured between 12 and 26 May 2003 on Arctic sea ice algae, phytoplankton and benthic microalgae from the Norsebanken area, north of Svalbard and from the Smeerenburg Fjord, northern Svalbard (Figure 1). Water column samples were taken from 5-l Niskin bottles collected with a conductivity–temperature–depth probe (CTD). Additional water samples were taken from the ship's on-board seawater line with an intake 6 m below the surface. Surface ice samples were obtained by removing the snow from the surface of the floe and collecting the coloured ice at the snow-ice interface with a polycarbonate vial. Bottom ice samples were collected by diver using an electric suction pump, surface ice samples were collected by hand.

Measurement of quantum yield of PSII on dark adapted ice and water samples (minimum 15 min dark adaption)

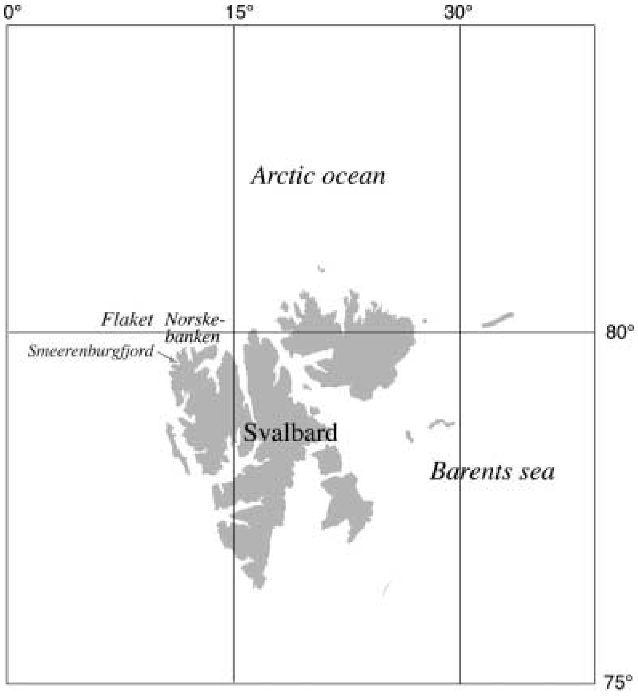

Figure 1. Location map of field stations off Svalbard.

was with a Water-PAM (Walz, Effeltrich, Germany) at ambient seawater temperature (0–2°C). This extended period of dark adaption was unavoidable given the time it took to bring CTD samples to the surface and the ice samples back on-board. Ice samples were not melted but the measurements taken on ice shavings. A minimum of five replicate measurements was made on all samples. Measurement of quantum yield on individual cells was with a Microscope-PAM (Walz, Effeltrich, Germany). Again, measurements were made on at least five different cells of each species.

The photosynthetic parameters $\mathrm{rETR_{max}}$ (maximum electron transfer rate), α (photosynthetic efficiency) and E_k (light adaption parameter) were obtained by running rapid light curves (RLCs) from either the Water-PAM (Walz, Effeltrich, Germany) or Microscope-PAM (Walz, Effeltrich, Germany).

A weak measuring light (0.15 μmol photons $\mathrm{m^{-2}\,s^{-1}}$) was used to measure the fluorescence yield (F, open PSII reaction centres), while a saturating pulse ($>3000\,\mu$mol photons $\mathrm{m^{-2}\,s^{-1}}$ for 0.8 s) was used to determine the maximum steady-state fluorescence (Fm, closed PSII reaction centres). Chlorophyll fluorescence was detected at wavelengths above 710 nm. Red light emitting diodes (LEDs) provided actinic light used in the rapid light curves at levels of 0, 85, 125, 194, 289, 413, 577, 960, and 1441 μmol photons $\mathrm{m^{-2}\,s^{-1}}$ for phytoplankton and 0, 26, 37, 56, 85, 125, 194, 289 and 413 μmol photons $\mathrm{m^{-2}\,s^{-1}}$ for ice algae. Relative electron transport rate was derived according to $\mathrm{rETR = Fv/Fm * PAR}$ (Schreiber et al., 2004). The $\mathrm{rETR_{max}}$ of fluorometric analyses is directly proportional to P_{max} of conventional P vs E curves and can be thought of in a similar way, although the exact relationship cannot be quantified.

Rapid light curves, are described using several characteristic parameters such as E_k, α and $\mathrm{rETR_{max}}$ (McMinn et al., 2003). To determine these parameters, the RLCs were fitted to an exponential curve following Harrison & Platt (1986). This process described the photosynthetic response as a single continuous function of light, covering both the initial linear response, as well as the photoinhibited region at elevated light. Data were exported from WinControl (Walz, Effeltrich, Germany) into Systat (v 5.2 for Macintosh Systat Inc.). Empirical data were mathematically fitted to a double exponential decay function (Platt et al., 1980), using a Marquardt–Levenberg regression algorithm.

$$P = P_s(1 - e^{-\alpha E_d/P_s})e^{-(\beta E_d/P_s)} \qquad (3)$$

In the absence of photoinhibition (β=0), the function becomes a standard rectangular hyperbola, with an asymptotic maximum rETR value (Harrison & Platt, 1986), and eqn 5 can be simplified to:

$$P = P_m(1 - e^{-(\alpha E_d/P_m)}) \qquad (4)$$

where P_s is a scaling factor defined as the maximum potential rETR in the absence of photoinhibitory processes, P_m is the photosynthetic capacity at saturating light, α is the initial slope of the RLC before the onset of saturation, E_d is the downwelling irradiance (400–700 nm), and β characterizes the slope of the RLC beyond the onset of photoinhibition. E_k is the photoadaptive index or minimum saturating irradiance and is calculated as:

$$E_k = \mathrm{ETR_{max}}/\alpha \qquad (5)$$

All reported error measurements are standard deviations.

RESULTS

Quantum yield of PSII

Sea ice algae

Dense surface-ice algal communities were found growing beneath the snow at the freeboard level of multi-year floes at several locations on Norskebanken (Table 1). Samples were collected from both surface and surface brine communities. The surface communities were overwhelmingly dominated (99% by cell numbers) by *Phaeocystis pouchetii,* presumably derived from the intense *Phaeocystis* phytoplankton blooms occurring in the same area. Quantum yield of the snow/ice communities were 0.247 ±0.099. Quantum yield of the surface brine community, most probably the same infiltration community but further from the ice floe edge, differed very little and was 0.212 ±0.096. These results were not significantly different ($P<0.05$). Examination of individual cells showed that *Phaeocystis* had a quantum yield of 0.360 ±0.065, consistent with the bulk sample. Other cells measured ($N>5$) included *Nitzschia frigida* (quantum yield=0.469 ±0.004) and *Thalassiosira nordenskoeldiii* (quantum yield=0.311 ±0.134).

An actively growing bottom ice community was located at only one site. Here, on a 0.5 m thick annual ice floe with a 10 cm thick snow cover, a diffuse community (0.30 mg Chl*a* $\mathrm{m^{-2}}$) dominated by *Nitzschia frigida* (77%) and *Fragilaria oceanica* (12%) had a quantum yield of 0.427 ±0.029. This was the highest value of any ice algae found in this region.

Table 1. *Sampling stations for phytoplankton (P), ice algae (I) and sediment samples (S) during the May 2003 cruise.*

Date	Station no.	Position	Depth	Ice concentration	Area	Samples
15.05	383	80°03′N 11°03′E	241	8/10	Norskebanken	P
16.05	402	79°56′N 10°52′E	157	6/10	Norskebanken	P, I
	405	79°48′N 10°21′E	266	8/10	Shelf	P
18.05	414	79°54′N 05°07′E	2700	7/10	Fram Strait	I
19.05	420	79°31′N 04°51′E	2700	5/10	Fram Strait	P, I
20.05	436	80°06′N 08°48′E	515	9/10	Flaket	P, I, S
21.05	442	80°07′N 08°47′E	509	7/10	Flaket	P
	450	80°07′N 08°54′E	507	5/10	Flaket	P, I, S
	458	80°03′N 08°53′E	502	7/10	Flaket	I
22.05	463	80°02′N 09°06′E	500	8/10	Flaket	P, S

Additional bottom samples were obtained from protected pockets in multiyear ice. These communities were extremely spatially limited, usually covering less than 5 cm^2, were dense but had quantum yields of only 0.126 ±0.081 and 0.030 ±0.0198. They probably represented the remains of a community from a previous season. Examination of individual cells showed that *N. frigida* had a quantum yield of 0.215 ±0.047, *F. oceanica* 0.208 ±0.053 and *Phaeocystis* 0.452 ±0.062.

Phytoplankton

The phytoplankton communities at most locations on the bank were strongly dominated by a large *Phaeocystis pouchetii* bloom (up to 4.33 μg chlorophyll-*a* [Chl*a*] l^{-1} at 5 m on 18 May). In the fjord samples Fv/Fm was 0.422 ±0.061, which compares with similar values of surface water from across the bank of 0.488 ±0.067. The fjord samples were dominated by diatoms.

There was a strong relationship between the Fv/Fm of the phytoplankton communities and both the depth in the water column and the biomass (i.e. μg Chl*a* l^{-1}). Maximum quantum yield (0.646 ±0.051) was typically 20–40 m below the surface and mostly coincided with the maximum phytoplankton biomass (Figure 2). Quantum yield was typically depressed by 20–30% at the surface relative to the maximum level.

Benthic sediments

Benthic sediments were obtained from water depths of between 300 m and 500 m, however, only one benthic sediment sample contained photosynthesizing cells (Tables 1 & 2). Sediment from the sediment–water interface contained abundant settled algae, mostly diatoms. Long chains of *Fragilariopsis oceanica*, with spores, were frequent. Spores of *Chaetoceros furcellatus*, *Chaetoceros socialis*, *Chaetoceros debilis* Cleve *and Thalassiosira antarctica* var *borealis* were also present. While most quantum yield values were close to zero, at this one location the quantum yield was 0.131 ±0.052, indicating photosynthetic competency of the microalgae.

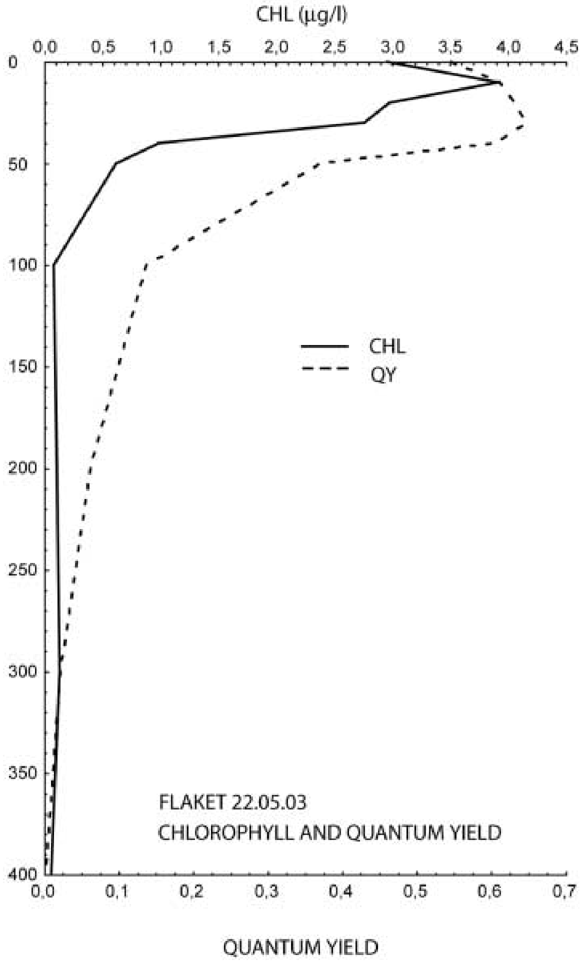

Figure 2. Vertical profiles of chlorophyll and quantum yield of phytoplankton north of Svalbard in May, 2003.

Photosynthetic parameters

Sea ice

The surface community had a $rETR_{max}$ (equivalent to P_{max} of P vs E curves) of 10.35 ±1.77, an α of 0.119 ±0.026 and an E_k of 90.3 ±20.0 μmol photons $m^{-2} s^{-1}$. The maximum under ice irradiance here was 13 μmol photons $m^{-2} s^{-1}$ below 40 cm ice with 14 cm of snow. The irradiance at the base of the snow layer would have been higher but was unable to be reliably measured. The surface brine community had a $rETR_{max}$ of 6.52 ±0.763, an α of 0.109 ±0.038 and an E_k of 68.1 ±36.1 μmol photons $m^{-2} s^{-1}$. The healthy bottom community from an annual ice floe had a $rETR_{max}$ of 7.12 ±2.89, an α of 0.121 ±0.013 and an E_k of 61.1 ±29.9 μmol photons

Table 2. *Quantum yield and photosynthetic parameters from microalgae measured in ice and water north of Svalbard in May, 2003.*

Algal type	Φ_{PSII}	α	E_k	rETR$_{max}$
Sea ice				
Annual bottom ice	0.427 ±0.029	0.121 ±0.013	61.1 ±29.9	7.12 ±2.89,
Multiyear bottom	0.125 ±0.060	0.022 ±0.003	385.1 ±87.6	8.59 ±1.425
Surface ice	0.247 ±0.099	0.119 ±0.026	90.3 ±20.0	10.35 ±1.77
Surface brine	0.212 ±0.096	0.109 ±0.038	68.1 ±36.1	6.52 ±0.763
Sediments	0.131 ±0.052	0.051 ±0.008	288.9 ±70.4	14.73 ±4.12
Phytoplankton				
Fjord surface	0.422 ±0.061	0.150 ±0.021	172.3 ±45.1	25.63 ±6.76
Surface water	0.488 ±067	0.278 ±0.119	191.4 ±76.7	46.53 ±16.12
CTDs				
0 m	0.562 ±0.091	0.255	170.9	43.589
10 m	0.594 ±0.039			
20 m	0.646 ±0.021	0.274	216.3	59.27
30 m	0.637 ±0.024			
40 m	0.646 ±0.051			
50 m	0.581 ±0.114	0.338	127.5	43.08
100 m	0.469 ±0.193	0.136	390.4	53.01
200 m	0.311 ±0.172			
300 m	0.128 ±0.062			
400 m	0.064 ±0.044			

$m^{-2} s^{-1}$. The maximum irradiance below 40 cm ice with ice slush on top was 109 μmol photons $m^{-2} s^{-1}$; this decreased to a minimum of 5 μmol photons $m^{-2} s^{-1}$ shortly after midnight. The older multiyear floe community had a rETR$_{max}$ of 8.59 ±1.425, an α of 0.022 ±0.003 and an E_k of 385.1 ±87.6 mol photons $m^{-2} s^{-1}$. Irradiance beneath the small but thick multiyear ice floes was highly variable due to the presence of abundant cracks and leads.

Phytoplankton

Surface water samples typically had a high rETR$_{max}$ (46.53 ±16.12), a high α (0.278 ±0.119) and a high onset of saturation irradiance (191.4 ±76.7 mol photons $m^{-2} s^{-1}$). The fjord samples were similar with a rETR$_{max}$ of 25.63 ±6.76, α of 0.150 ±0.061 and onset of saturation irradiance of 172.3 ±45.1 μmol photons $m^{-2} s^{-1}$.

The data from the CTD samples were noisy with the greatest values for each of the three photosynthetic parameters occurring at a different depth.

The euphotic depth was consistently between 15 and 22 m.

Benthic sediments

The benthic sediments had a rETR$_{max}$ of 14.73 ±4.12, an α of 0.051 ±0.008 and an E_k of 288.9 ±70.4 μmol photons $m^{-2} s^{-1}$.

DISCUSSION

The Norskebanken area is heavily influenced by Atlantic water masses. This water is the last branch of the North Atlantic Current flowing northward along the western coast of Spitzbergen before turning east on the northern side of Svalbard. Hence the water temperature during the cruise was relatively high, between -0.5 and 0°C and in the surface layers, and almost no annual ice was found in the area. More than 90% of the sea ice comprised multiyear floes (from the Arctic Ocean) that contained virtually no ice algae, and the occasional bottom algal communities were extremely spatially limited. Very small, isolated pockets (less than 10 cm^3) of old algae were found on a few floes. A healthy bottom algal community on an annual floe was only found in one small area in the Fram Strait and this had dropped off within 24 hours due to rapid surface and bottom ice melting.

Infiltration communities, growing in the snow–ice interface, were recorded for the first time from the Arctic. They have previously been considered as a unique Antarctic community type (Horner et al., 1992), and have never been recorded from the Barents Sea. They have now been found both in the Fram Strait and on the shelf north of Svalbard ('Flaket') in multiyear or old annual ice floes, and appeared as visible brown layers of about 10–15 cm thickness. In both areas the communities were dominated by *Phaeocystis pouchetii*, but the shelf samples were mixed with diatoms. The most numerous species were *Chaetoceros furcellatus* and *Fragilariopsis oceanica*. Some ice algae were also present: *Nitzschia frigida*, *Attheya septentrionalis* (Oestrup) Crawford and *Synedropsis hyperborean* (Grunow) Hasle, Medlin and Syvertsen. The *Phaeocystis* colonies in the last area were large, misshaped and apparently old. Biomass was 15–20 mg m^{-2} (150–200 mg m^{-3}) in the algal layer, and light intensity in the middle of the day during weak sun was about 450 μmol photons $m^{-2} s^{-1}$ under the snow, but above the algal layer. The phytoplankton communities in the water masses in both areas were also dominated by *Phaeocystis*, and on the shelf mixed with diatoms. These were mostly the same species as in the infiltration layers, indicating the origin of these layers. The algae were growing within the ice floe and not just along the edge.

The Fv/Fm of the Arctic phytoplankton communities showed a strong depth dependence. Maximum values of approximately 0.65 were recorded from between 20 and 40 m below the surface. These values are close to the theoretical optimum and are consistent with other values from nutrient replete polar and temperate phytoplankton communities (Gervais et al., 2002; Suzuki et al., 2002). They imply absolutely no nutrient or micronutrient (e.g. iron) limitation. Surface values were typically 20–30% below maximum values and imply shallow mixing depths and photoinhibition. The euphotic depth was consistently between 15 and 22 m. E_k values were between 170 and 216 μmol photons $m^{-2} s^{-1}$ indicating that the phytoplankton were well adapted to the light climate. Fv/Fm values below 40 m gradually declined to less than 0.1 at 400 m.

The phytoplankton bloom on Norskebanken was apparently sinking, the biomass being almost the same from the surface to the sea-floor at nearly 150 m. Diatoms dominated the bloom, and typical spring species such as *Fragilariopsis oceanica*, *Chaetoceros socialis*, *Thalassiosira nordenskioeldii*, *T. antarctica* var *borealis* were frequently observed along with resting spores, another sign of a bloom in its late stage.

In the Fram Strait the conditions were more like a late spring or summer with a phytoplankton biomass maximum at 15–20 m depth, and communities dominated by *Phaeocystis pouchetii*. Some diatom spring species were still around, but mainly as resting spores.

Phaeocystis also dominated the bloom on 'Flaket', but the number of diatoms was considerably higher than in the Fram Strait. The cells occurred in long colonies, and only a few spores were seen. The biomass distribution exhibited near-surface peaks and little sinking material, all pointing to a bloom close to its peak and in a better condition than in the other two areas.

Unlike the phytoplankton communities, the sea ice communities mostly showed reduced Fv/Fm and elevated E_k values. The quantum yield of sea ice bottom communities has previously been measured from the Antarctic (McMinn et al., 2003) and from Greenland (Kühl et al., 2003). McMinn et al. (2003) reported values between 0.20 and 0.75 (mean=0.45 ±0.15, N=101) while Kühl et al. (2002) reported values of between 0.20 and 0.65. The values reported here from the Arctic Ocean are generally lower. The bottom community was clearly the healthiest of all the ice algal communities measured. It had a Fv/Fm of 0.427 and an E_k of 61 μmol photons $m^{-2} s^{-1}$. This was the highest ice algal quantum yield measured and the lowest E_k. The ambient irradiance was between 5 and 109 μmol photons $m^{-2} s^{-1}$, which suggests that the algae were well acclimated to the light field. The ice at this time was clearly melting and the salinity was lowered to 29.0 psu. This reduced salinity probably explains the depressed quantum yield. Several other studies have shown that reduced salinity depresses photosynthesis and growth of sea ice algae (Bates & Cota, 1986).

The ice algae from the multiyear ice were clearly unhealthy; their low Fv/Fm (0.125) suggests little photosynthetic activity and a senescent state. They also had a very low photosynthetic efficiency ($\alpha = 0.022$) but a very high E_k (385.1 μmol photons $m^{-2} s^{-1}$)). This implies a low level of acclimation to the ambient irradiance.

The surface infiltration ice algal community, which experienced the highest light levels, had a quantum yield of 0.247 ±0.096, which was lower than both the bottom sea ice algae community and the phytoplankton. E_k was 90.3 ±20.0 1 μmol photons $m^{-2} s^{-1}$. This is considerably lower than the E_k of the phytoplankton community (191.4 ±76.7 μmol photons $m^{-2} s^{-1}$), which had the same *Phaeocystis*-dominated species composition, and suggests the community had at least partly adapted to the high light conditions at the surface. The surface brine community mostly demonstrated a similar response to the surface community.

While most bottom sediments proved to be physiologically inactive, one sample had a quantum yield of 0.131. This sample was taken from a depth of approximately 500 m, which was clearly well below the euphotic zone. The activity of this sample indicates relatively rapid transport from the surface to the bottom and also indicates the resilience of the photosynthetic apparatus. How long phytoplankton cells can remain alive in complete darkness is unknown. However, on-board experiments with phytoplankton samples showed no decline in quantum yield after seven days. Further experiments are needed to quantify this further.

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