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A B S T R A C T

The Jan Mayen Front is located in the Norwegian Sea to the east of the Jan Mayen Ridge and separates warm, salty Atlantic water and colder, less salty Arctic water. The effects of the light regime, hydrographical conditions and nutrients on the variations of chlorophyll a (chl a), quantum efficiencies of photochemistry in PSII (Fv/Fm) and effective absorption cross-section of PSII (φPSII) at the Front were studied in June 2007. Stratified waters were seen on both sides of the Front and lowered nutrient concentrations were seen shallower than 10–20 m. The lowest values of the spectral diffuse attenuation coefficient, k d (λ), were found at 500–550 nm (0.07–0.16 m −1). While k d (465 nm) ranged between 0.08 and 0.17 m −1 and k d (380 nm) between 0.13 and 0.20 m −1. Chl a concentrations seldom exceeded 1.0 mg m −3 outside pure Atlantic Water, while elevated concentrations (3–4 mg m −3) developed at depth (20–30 m) east of the Front in Atlantic Water. For the upper 100 m N/P, Si/P, N/Si and POC/PON ratios were 15.2, 8.0, 1.7 and 6.2, respectively. The quantum efficiency was strongly influenced by nutrients, suggesting nutrient limitation of phytoplankton biomass at the Front in June, but also light inhibition probably was a contributing factor in the upper part of the water column. High quantum efficiencies (0.5) and effective absorption cross sections (>700 Å2 quanta −1) were seen to the east of the Front and at depth (20–40 m) in stratified Atlantic waters. We therefore conclude that the Jan Mayen Front did not have a stimulatory effect on phytoplankton biomass enhancement and photosynthetic performance. This is in part due to the weak horizontal density front caused by density compensation of temperature and salinity characteristics of the adjacent water masses, and the associated weak vertical mixing.

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1. Introduction

Fronts are defined as a discontinuity in the horizontal distribution of water mass properties (Denman and Powell, 1984) and are formed at the transition between two well-defined water masses with different properties. This study examines the Jan Mayen Front situated south of the island of Jan Mayen and east of the Jan Mayen Ridge in the Norwegian Sea and was part of the IPY Project NESSAR (Norwegian component of the Ecosystem Study of Subarctic and Arctic Regions). The Jan Mayen Front is a permanent feature and part of the Arctic Front system which extends from the Iceland–Faroe Ridge in the south to Fram Strait in the north roughly following the mid-Atlantic Ridge. It separates colder and fresher Arctic waters from warmer and saltier Atlantic waters. In this paper we explore the nutrient distributions, spectral light penetration as well as the phytoplankton productivity potential and phytoplankton distribution, and their controlling factors at, and in the vicinity of, the Front.

Many of the earlier surveys of the Norwegian Sea are recognized as pioneer work and they represent milestones in the history of Norwegian marine research. They mostly focused on hydrographical conditions and quantitative aspects of phytoplankton vegetation (Braaud, 1935; Gran, 1902; Halldal, 1953; Paasche, 1960; Ramsfjell, 1960; Smydja, 1958). An other important work from the Norwegian Sea in the 1950s was conducted by Berge (1958), who used the C-14 technique for measuring primary production for the first time in Norwegian oceanic waters.

A number of studies have shown that changes in physical characteristics across a front result in special adaptation strategies, which give rise to different phytoplankton communities. On the stratified side of the transitional zone of the Ushant tidal front (west coast of France) Videau (1987) found that the physiological state of diatoms cells was improved, revealed by increased growth rates. Jones et al. (1984) and Carreto et al. (1986), on the other hand, emphasize the

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dominance of diatoms on the homogenous (mixed) side of the tidal front system at Jura (Scotland) and Valdés (Argentina), respectively. For the more permanent Kuroshio frontal system (Japan), Yamamoto et al. (1988) found that dominance of diatoms at the front was due to upwelling of nutrients.

Higher biomass of primary and secondary producers is often encountered in frontal areas compared with adjacent waters (Fernández et al., 1993; Hansen et al., 1990; Kahrul et al., 1984). This can be due to the accumulation of cells through physical forces or by enhanced in situ production in response to favorable growth conditions, such as access to increased nutrient supply. Fernández et al. (1993) concluded that primary production peaks within a slope current-induced front in the southern Bay of Biscay (Spain) were a result of active growth and not accumulation of cells. For the Catalan Front in the northwestern Mediterranean, the formation of a subsurface chlorophyll-μ maximum layer (SCML) seemed to be a prominent feature, both during winter and spring (Delgado et al., 1992). In Monterey Bay, California (USA), a tight physical–biological coupling at the frontal zone has been observed, and topographical conditions together with internal wave dynamics seemed to be important regulating mechanisms (Ryan et al., 2005).

Studies of phytoplankton growth dynamics in the Antarctic Polar Front region (170°W) revealed that stimulatory effects on primary production rates could first be seen in the main front and was thereafter displaced southwards (Landry et al., 2002). High diatom stocks were restricted to waters with silicate and iron concentrations above a critical minimum. Remotely sensed ocean color data suggest that the major front systems of the Southern Ocean are regions of elevated chlorophyll concentrations and high primary production rates with diatoms as the main contributor (Moore and Abbott, 2000). A similar pattern, with a marked surface bloom of diatoms in May responding to upwelling of silicate, was seen along the meanders of the Iceland–Faroe Front (Allen et al., 2005). In the Polar Front region of the southwestern Atlantic, active growth also occurs at depth in the SCML (Brandini et al., 2000). According to Laubscher et al. (1993), a coincidence of two or more factors, such as temperature gradients, upper mixed layer depth, silicate availability and grazing, is needed to generate and regulate phytoplankton blooms in these frontal systems.

A dominance of diatoms and the pynmesiophyte Phaeocystis pouchetti are a characteristic feature of the phytoplankton composition in the Norwegian Sea in June (Paasche, 1960; Ramsfjell, 1960). In the Norwegian Sea to the northeast of Jan Mayen during early summer, in a difference in the timing of the seasonal development of the plankton community was observed across the Arctic Front, with typical post-bloom conditions on the Atlantic side and bloom conditions on the Arctic side (Dale et al., 2001). The Arctic Front in the Norwegian Sea has also been associated with high numbers of the coccolithophorid Coccolithus pelagicus during summer, and it was concluded that other controlling factors than low temperature had to be taken into account for explaining their dominance (Baumann et al., 2000). A comprehensive data set from the central Greenland Sea revealed that the spring (May) phytoplankton was mainly composed of diatoms and the pynmesiophyte P. pouchetti, while the summer situation is generally characterized by depletion of nutrients and low phytoplankton biomass (Erga et al., 2005; Rey et al., 2000). Maximum primary productivity in June along a transect across the Greenland Sea from the Norwegian Sea to the Greenland Shelf was reported in the Arctic Frontal Zone (Legendre et al., 1993). They also found production was dominated by large cells (>5 μm) in the Arctic Water and small cells (<5 μm) in the Atlantic Water. This is also consistent with the results of Erga et al. (2005) who found a change from low biomass composed of small flagellates to a dominance of high biomass composed of large diatoms when crossing the Arctic Front from Atlantic to Arctic waters during late summer. In the ice edge region of the Fram Strait/Greenland Sea area, elevated chlorophyll a concentrations were encountered in the nutrient rich frontal boundaries (Spies et al., 1988). It was also suggested that the Arctic Front in the Western Norwegian Sea might be a region of high productivity based primarily on the presence of the large number of pelagic fish species that feed there in the late spring to early autumn period (Rey, 2004).

For the Norwegian Sea it has been emphasized that the loss of phytoplankton biomass due to sedimentation during summer could be counteracted by phytoplankton production through nutrient regeneration in the upper part of the water column caused by zooplankton grazing. The effect of such a coupling will depend upon the timing between the bloom period and the appearance of zooplankton (Wassmann et al., 1991).

Intensive and high spatial resolution studies aiming at resolving fine scale structure in phytoplankton distributions, photosynthetic efficiencies and spectral light penetration in the Arctic frontal zone are scarce for the Norwegian Sea. In the present study these items are addressed using high resolution data collected during June field studies.

2. Material and methods

2.1. Study area

In 2007, the Institute of Marine Research (IMR) in Bergen, Norway, organized a cruise to the Norwegian Sea south of the island of Jan Mayen as part of the IPY NESSAR project. A study of the physical and biological processes at the Jan Mayen Front located east of the Jan Mayen Ridge was carried out onboard R.V. G.O. Sars from 1 to 22 June. Physical and biological sampling at a horizontal resolution of 1–10 km was principally conducted along an east–west transect located near 68 26’N. Additional sampling was undertaken between this transect and the island of Jan Mayen, mostly over and to the east of the Jan Mayen Ridge. Typical bottom depths in the study area are >2000 m.

2.2. Salinity, temperature and oxygen

At each station on the cruise (Fig. 1), depth profiles of temperature and salinity were measured by a Sea Bird CTD probe mounted on a General Oceanic Rosette water sampler. The CTD temperature sensor was calibrated before the cruise, and the salinities were calibrated by analyzing salinity samples collected routinely from the water bottle at the deepest sampling level on each cast. The salinity analyses were conducted by a Guildline 8400 AutoSal using IAPSO Standard Sea Water as a reference. Oxygen on the CTD was measured using a Sea-Bird (SBE43) instrument. Oxygen samples were also taken from water bottles on the rosette at 21 stations for a total of 251 samples and analyzed by titration using the Winkler method. The titrated oxygen levels were used to calibrate the CTD-measured oxygen concentrations.

2.3. Nutrients, particulate organic carbon and nitrogen

Dissolved inorganic nutrients (nitrite, nitrate, orthophosphate and silicate) at discrete depths collected from water bottles on the rosette were analysed onboard according to standard methods (Parsons et al., 1992) adapted to an auto-analyser (Rey et al., 2000). Triplicate samples for particulate organic carbon (POC) and nitrogen (PON) were taken at selected stations and depths. They were filtered onto precombusted Whatman GF/F filters and stored at −20 °C before analysis on a FlashEA 1112, Automatic Elemental Analyser for CHN determination. No corrections were made for detritus.

2.4. Chlorophyll-a and in situ fluorescence and turbidity measurements

Samples taken from water bottles for chl a measurements were filtered using GF/F filters and stored at −20 °C before analysis within 2 weeks of end of the collection. The analyses were done fluorometrically (Turner Designs-10) according to Holm-Hansen et al. (1965), using 90% acetone as solvent and acid corrections for phaeopigments.
Vertical profiles of in situ fluorescence (ISF) were obtained by a SeaTech active fluorometer attached to the CTD. Continuous profiles of chl-a emerge from ISF profiles calibrated with chl-a from discrete depths. Fluorescence and turbidity profiles were also obtained from a Web SLOCAN© autonomous glider, equipped with a Wet Labs FLNTU fluorometer-turbidity sensor. Turbidity was obtained by measurements of backward scattering from particles at 700 nm. The glider yo-yoed between the surface and 400 m, logging data every 4 s. It produced a profile approximately every kilometer.

2.5. Light measurements

Measurements of spectral cosine irradiance were performed with a RAMSES-ACC-VIS (TriOS GmbH, DE) spectral radiometer with 3.3 nm wavelength resolution at 9 stations along the transect (68.5°N) and 2 stations further to the north (69.8°N). It was lowered with a crane from the side of the vessel at a distance of ~5 m to avoid shipside reflection or shadow. The radiometer was mounted in a metal frame facing upwards to measure downwelling irradiance (\(E_d\)) and subsequently, on an immediate second run, re-mounted to face downwards in order to measure upwelling irradiance (\(E_u\)). At each measuring depth (read from the cable counter) three consecutive spectra were collected, with integration time set to ‘automatic’, while the instrument cable was held still. The correct average depth of the spectra used for the mean irradiance calculation was calculated from pressure data by a CTD model SD204 (SAIV A/S, NO) mounted on the same metal frame.

The spectral diffuse attenuation coefficient, \(K_d\), for each wavelength was found by fitting a linear function to the log-transformed irradiance depth profile between 0 and 20 m. \(K_d\) is given by:

\[
E = E_s \cdot \exp(-K_d \cdot z)
\]  

where \(E\) is irradiance at depth \(z\) and \(E_s\) is surface irradiance. Solving for \(z\) one gets

\[
z = -\ln(E/E_s)/K_d
\]

Thus the depth where the light intensity is reduced to a given percent, \(p\), of its surface value, can be expressed as:

\[
z = -\ln(p/100)/K_d
\]

Variation in the cloud cover during profiling of spectral irradiance potentially reduces the quality of the calculated attenuation coefficients as it can change the underwater irradiance during profiling. To ensure high data quality we therefore compared the spectrally-averaged \(K_d\) in the range 350 and 650 nm, from profiles with the sensor looking downward to \(K_d\) from profiles with the sensor looking upwards. Profiles with deviations larger than 15% were excluded. The remaining spectra have an overall average difference, between the downward and upward looking profiles of 8%. Note that one would expect some difference in downward and upward looking \(K_d\) caused by directional difference in

![Fig. 1. Map of the investigation area to the south of the island Jan Mayen in the Norwegian Sea. The sampling stations are marked by open circles.](image-url)
the ambient light field (Kirk, 1994). Variations in $F_D$ by depth could not be resolved within the measurement uncertainties.

2.6. Photosynthesis measurements

A Fast Repetition Rate Fluorometer (FRRF), type FASTtracka from Chelsea Technologies Group, UK, was used for obtaining vertical profiles of variable chl a fluorescence. At the optical head of the instrument there are dual light and dark chambers for measurement of fluorescence with and without actinic light, respectively. The instrument was fitted to an A-shaped stainless steel frame with both an external pressure sensor and PAR sensor connected, and placed in such a way to avoid self-shading. The instrument was lowered at a speed of 0.1 m s$^{-1}$. Shading of the FRRF profiles by the ship was avoided whenever possible by deploying the instrument on the side of the ship facing the sun, and by using a long crane to deploy it away from the ship’s shadow. The dark chamber was fitted with two L-shaped black tubes in order to increase the dark acclimation time for the measurement of fluorescence from dark-acclimated cells (Kolber et al., 1998). Blanks were obtained by using fresh Milli-Q water. Fluorescence measured under actinic light is distinguished from that in darkness by superscript ($*$). Throughout the data collection single turnover (ST) fluorescence measurements were obtained with an acquisition protocol of 100 saturation flashes, flash duration of 1.1 $\mu$s, spaced by 2.8 $\mu$s. A series of 8 sequences were averaged and recorded as one data acquisition. Minimum fluorescence ($F_O$), maximum fluorescence ($F_M$), steady state fluorescence ($F$) and functional absorption cross sections ($\delta F$) for each fluorescence acquisition were obtained by fitting the raw fluorescence data to the physiological model by Kolber et al. (1998) using the s software run in MATLAB (http://picasso.orce.orst.edu/ORSSO/FRRF/index.html). Variable fluorescence, ($F_v=F_m-F_o$), and the quantum efficiency of photochemistry, $\Phi = \delta F / F_m$, were calculated from the in situ FRRF fluorescence data. For the ST protocol a maximum $\Phi$ value of 0.65 has been obtained for algal cultures grown under optimal conditions (Falkowski and Kolber, 1995). Since the FRRF measurements are hampered by strong ambient light intensity, data have only been collected below 5 m (i.e. light intensities $<200 \mu$mol quanta m$^{-2} s^{-1}$).

The maximum light utilization parameter $a^2 P (mg C mg chl a^{-1} h^{-1} \mu$mol quanta$^{-1} m^2 s^2)$ was estimated from the FRRF parameters above using the equation adapted from Moore et al. (2003):

$$a^2 P = 7.29 \times 10^{-2} \times Q_P \times q_F \times n_{PSII} \times PQ^{-1}$$

where the factor $7.29 \times 10^{-2}$ accounts for the conversion from seconds to hours, $\mu$mol quanta to quanta, and $A^2$ quanta$^{-1}$ to $m^2 mol RCII^{-1}$, assuming a maximum quantum yield of 0.25 and a conversion of mol C and mol chl a to mg. $f = (F/F_m)/0.65$ is the proportion of potential functional reaction centers, $n_{PSII} = $ the ratio of PSII reaction centers to chl a (a value of $n_{PSII} = 0.002$ was used) and PQ is the photosynthetic quotient (assuming 1.2 mol O$_2$ mol C$^{-1}$).

$Q_F = (F_m-F)/(F_m-F_o)$ is the photochemical quenching coefficient (a measure of the fraction of open reaction centers that take part in photochemical work), where $F_m$ is the minimum fluorescence yield that would be measured after light adaptation/acclimation was estimated using equations involving $F_O$ (Oxborough and Baker, 1997).

3. Results

3.1. Hydrographic conditions

During the June cruise, the study of the Jan Mayen Front was principally focused along 68°26’N (SD $\pm 6’$) latitude, extending from 5°38’W to 7°36’W (Fig. 1). The Front was localized around 73°6’W ($\sim 7.6’$) where between 50 m and 200 m depth temperatures typically changed by 1–2°C and salinities by 0.1–0.2 over relatively short horizontal distances (a few kilometers; Fig. 2). Atlantic Water, defined as having salinities $>34.98$, lay to the east of the Front and Arctic Water (salinities $<34.91$) to the west. In spite of the relatively sharp temperature and salinity fronts, there was little density contrast across the Front (Fig. 2), owing to the density compensation associated with the hydrographic properties of the two water masses (see Rudnick and Ferrari, 1999). In the surface layers ($<50$ m), horizontal temperature gradients were much weaker with the highest temperatures ($\geq 6°C$) found east of the Front in Atlantic Water, while west of the Front in Arctic Water temperatures were $<4°C$. In contrast, a sharp surface salinity front was observed at 7°06’W, with the leading edge located east of the deeper Jan Mayen Front. West of this surface salinity front, the upper layers are characterized by thermally-heated Arctic Water. Vertically, the depth of the mixed layer, based on the location of the pycnocline, was around 30–50 m.

3.2. Nutrients

Data from the transect across the Jan Mayen Front show nutrient depleted Arctic Water to the west of the Front, especially for silicate (Fig. 2). In the upper layer (0–20 m), nitrate concentrations varied between 2 and 4 mmol m$^{-3}$ and phosphate between 0.2 and 0.4 mmol m$^{-3}$. Silicate, on the other hand, was almost exhausted (values $<0.5$ mmol m$^{-3}$) down to 50 m on the western (Arctic) side of the Front and down to 20–30 m on the eastern (Atlantic) side. At 630°W, there were elevated nutrient values as shallow as 10 m depth. At depth, the Arctic Water reached to 150 m on the western side of the Front and on the eastern side of the Front around 630°W (see temperature plot; Fig. 2). These water masses were characterized by elevated levels of both nitrate, phosphate and silicate. The bottom of the nutricline was restricted to the depth interval 40–60 m. At 200 m depth on both sides of the Front, the N:Si:P ratios were around 13.3:6:1:1 (atomic), a pattern that remained down to 500 m (deepest measurement), revealing that silicate is scarce also at depth when compared with the ratio of N:Si:P $= 16:16:1$, which is often the criteria for stoichiometric nutrient balance (Brzezinski, 1985). Farther to the north and close to the southern tip of Jan Mayen a similar N:Si:P ratio was observed at 500 m (data not shown). All together this pattern of relatively low levels of silicate compared to phosphate and nitrate for the upper 500 m indicates a slower regeneration of silicate compared with nitrate and phosphate.

3.3. Oxygen

The oxygen content varied between 310 and 345 mmol m$^{-3}$ (i.e. 4.96–5.52 mg L$^{-1}$ or 7.09–7.89 mL L$^{-1}$) with lower values below 50 m eastwards and below 100 m westwards from the Front (Fig. 2). Also for oxygen, the Front could only be recognized at depths below 50 m. Supersaturated water was encountered between 10 and 30 m depth within the Atlantic Water to the east of the Front, coinciding with the SCML. On the western side of the Front, the deeper extension of oxygen rich water between 50 and 150 m is associated with Arctic Water. It should be noted though, that the difference between maximum and minimum oxygen concentrations along the transect is $<10%$. Lower oxygen values were found below the SCML and could be due to aerobic mineralization of sinking organic matter.

3.4. Light conditions

Surface irradiances at the time of sampling (mostly cloudy conditions) varied between 30 and 600 $\mu$mol quanta m$^{-2} s^{-1}$ during 24 h of daylight in the Norwegian Sea with maximum around local noon and minimum at night (data not shown). Due to the fact that the FRRF data only were taken at depths deeper than 5 m and the maximum surface irradiance value along the transect was 600 $\mu$mol quanta m$^{-2} s^{-1}$, intensities at 5 m were $\leq 345$ $\mu$mol quanta m$^{-2} s^{-1}$. Detailed information of the spectral diffuse attenuation coefficient in the 350–650 nm wavelength band is given in Fig. 3. The nine
“light” stations on the transect along 68°26′N were all situated on the eastern side of the Front. Maximum light penetration was encountered within the spectral range 500–550 nm where $K_d$ values varied between 0.07 and 0.16 m$^{-1}$. From Eq. (3) it follows that the 1% light depth varies from 29 to 66 m. This corresponds to an optical depth (i.e. $K_d z$, where $z$ is depth in m) of 4.6 (see Kirk, 1994). From 570 nm and upwards into the red part of the spectrum the $K_d$ values increased sharply, mainly due to absorption by water itself (Kirk, 1994). At 600 nm, $K_d$ values were within the range 0.22–0.31 m$^{-1}$. At 380 nm (UV-A) and 465 nm, $K_d$ values varied between 0.13 and 0.20 m$^{-1}$, and 0.08 and 0.17 m$^{-1}$, respectively. For all of the stations with relatively high spectral attenuation, the chl $a$ absorption signature in the blue part of the spectrum (440 nm) was revealed by a higher $K_d$ value. This was especially obvious for two stations located close to the island of Jan Mayen. All stations with high $K_d$ values were restricted to Atlantic waters.

The Glider measurements revealed that the euphotic zone was characterized by relatively low turbidity at and around the Front, but the transparency decreased markedly moving eastwards from the Front and into more chl $a$ rich waters (Fig. 4). Below 30 m the turbidity was low, while maximum turbidity was encountered in the surface layer to the east of the Front.

3.5. Phytoplankton distribution

Along the frontal transect the highest chl $a$ concentrations were encountered within Atlantic waters to the east of the Jan Mayen Front (Fig. 2). For all stations, the highest concentrations were observed in the upper 40 m of the water column with a tendency within this layer of increasing values with depth. A more detailed picture of chl $a$–fluorescence

Fig. 2. Isopleth diagrams for temperature (°C), salinity, density ($\sigma_t$), chlorophyll $a$ (mg m$^{-3}$), phosphate, nitrate, silicate and oxygen (mmol m$^{-3}$) across the Jan Mayen Front in the Norwegian Sea, June 2007. Depth interval: 0–200 m.

Fig. 3. Spectral light attenuation coefficients $K_d$ (m$^{-1}$) for the 0–20 m depth interval at selected stations in the Norwegian Sea, June 2007.

variation near the Front on 12–13 June from the Glider data is shown in Fig. 4. Phytoplankton biomass was at its minimum within and close to the Jan Mayen Front (4–5 km). The deeper SCML to the west of the Front in Arctic Water contained less phytoplankton than the more pronounced and shallow SCML to the east of the Front in Atlantic Water. Elevated chl a values were observed in the depth interval 30 and 50 m along the section from 7.7W to 7.4W. A maximum chl a concentration of 3.5 mg m\(^{-3}\) was encountered in Atlantic Water between 25 and 30 m at 6.9W and ranged from 0.5 to 3.0 mg m\(^{-3}\) for the other stations (Fig. 2). For the Arctic waters to the west of the Jan Mayen Front (7.6W), maximum chl a values were at the base of the pycnocline between 40 and 50 m. Below 50 m, chl a concentrations were lower than 0.5 mg m\(^{-3}\) at all stations. Common for many of the stations was a dominance of flagellates and monads (<1 μm) in the upper part of the water column (L.J. Naustvoll pers. comm.).

It is interesting to note that north of this transect at a station situated on the shelf close to the southwestern tip of Jan Mayen, chl a concentrations exceeded 18 mg m\(^{-3}\) at 10 m (data not shown). Contrary to the frontal area, this bloom was dominated by diatoms (L.J. Naustvoll pers. comm.) which were restricted to the upper layer of the water column consisting of Atlantic Water. Here the Arctic Water was encountered below 60 m.

3.6. Photosynthetic performance

Since data from the dark and light chamber of the FRRF reveal the same variation patterns along the transect, only values obtained from the dark chamber are plotted (Fig. 5). However, data from both chambers are discussed.

The quantum efficiency of photochemistry in PSII in the dark-acclimated state \((F_{v}/F_{m})\) is shown for phytoplankton along the frontal transect (Fig. 5a). It seems to be influenced by the surface salinity front at 7.1°W (Fig. 2), with low values observed in the upper 15 m of the Atlantic waters expanding eastwards from this front, while maximum quantum efficiency was encountered closer to the position of the deeper Jan Mayen Front (situated at 7.6°W), but mostly to the east of it. Here values around 0.5 were seen between 10 and 40 m. These were associated with the stratified part of the water column and coincided with relatively low chl a concentrations (Fig. 2). In the stratified Atlantic Water \((F_{v}/F_{m})\) values slowly increased with depth, attaining 0.5 between 32 and 40 m, and were associated with the SCML. Close to the Front lower quantum efficiencies were seen between 16 and 28 m, more exaggerated in the light than in the dark chamber. In total, values ranged between 0.2 and 0.5. Our data reveal that phytoplankton cells with a high primary production potential were found within the upper 8–40 m of the water column in the vicinity of the Front, but mostly to the east, while farther eastwards into the Atlantic Water the high potential was restricted to cells being situated between 20 and 40 m.

The variations in functional/effective absorption cross-section of PS II (i.e. maximum efficiency of light utilization for photochemistry in PS II) for dark-acclimated (i.e. protected from ambient light) phytoplankton cells, \(\sigma_{PSII}\), across the Jan Mayen Front transect are shown in Fig. 5b. The profiles were obtained at different times during the day (0–24 h), but due to the midnight sun no profiles represent night darkness. Values for \(\sigma_{PSII}\) varied between 400 and 850 Å\(^2\) (quanta)\(^{-1}\), while \(\sigma'_{PSII}\) (cells in ambient light) varied between 400 and 900 Å\(^2\) (quanta)\(^{-1}\) (data not shown). Maximum values were seen in association with the Jan Mayen Front, but to the east of it.
and they were restricted to depths between 15 and 40 m. Another characteristic feature was the high $\text{PO}_{4}$ values seen between 10 and 40 m when passing the surface salinity front around 7.1°W. Farther to the east, into Atlantic Water, the effective absorption section increased gradually at depth. Minimum $\text{PO}_{4}$ values on the other hand, were encountered in the upper part of the water column in the transition zone between Atlantic and Arctic waters towards the Jan Mayen Front and during the whole water column to the west of it.

4. Discussion

External physical forces are often decisive for regulation of growth of individual phytoplankton species as well as their relative contributions to community structure (Reynolds and Reynolds, 1985). In this paper we examined the spatial distribution of phytoplankton biomass and its productivity at the Jan Mayen Front in the Norwegian Sea. In particular we were interested in whether there was increased primary production at the front and if the front represented a boundary separating different phytoplankton communities in the two adjacent water masses.

4.1. Environmental controls on phytoplankton distribution

Close to the Jan Mayen Front elevated chl $a$ concentrations were measured at depth on the Atlantic side and to a certain degree on the Arctic side (Fig. 4). This structure was further observed eastward on the transect where maximum values (3–4 mg m$^{-3}$) were encountered between 20 and 30 m, and farther from the Front where values $> 1$ mg m$^{-3}$ were observed close to 50 m depth (Fig. 2). Apparently this was caused by stable growth conditions in the lower thermocline. The fluorescence data obtained by the CTD fluorometer and the Glider showed similar patterns, but the absolute values from the Glider were higher. This is probably due to difference in time between the measurements and a higher spatial resolution in the case of the Glider.

Earlier experience from the Norwegian Sea (Rey, unpublished data) shows that little diffusive transport occurs through the pycnocline in summer. Rather the higher concentrations of chl $a$ could be partly due to low light acclimation and partly due to evisceration of the pycnocline as the biomass sinks down in the water column and later temporarily accumulates at the pycnocline.

Depending on ambient irradiance, nutrient availability and temperature, it has been found that POC/Chl $a$ for phytoplankton cultures could vary from less than 10 to over 200 g C g$^{-1}$ (Reynolds and Reynolds, 1985), but that the ratio at an ambient irradiance of 50 μmol quanta m$^{-2}$ s$^{-1}$ typically increases from 10 to 130 between 30 and 0 °C under nutrient sufficient conditions. Our data show that the POC/Chl $a$ ratios in most cases were relatively high between 20 and 40 m, on average $> 100$ (data not shown). Assuming a daily PAR surface irradiance of 300 μmol quanta m$^{-2}$ s$^{-1}$ for the investigation area in June (Rey, 2004) and a $K_{d}$ (550 nm) of 0.1 m$^{-1}$ as representative light conditions for our cruise (see Section 3.4), it follows from Eq. (3) that an ambient irradiance of 50 μmol quanta m$^{-2}$ s$^{-1}$ will be encountered at 18 m, coinciding with the position of the upper nutricline. Also taking into account that compensation light intensities for growth of phytoplankton in many studies have been found to be below 2 μmol quanta m$^{-2}$ s$^{-1}$ (see Erga, 1989a and references therein), we believe that the upper part of the SCML is maintained by actively growing phytoplankton cells, but that the lower part probably consists of low light acclimated phytoplankton cells, revealed by the fact that the 1% light depth in this case extends down to 46 m.

Vertical stratification was observed on both sides of the Jan Mayen Front (Fig. 2). At the Front, lowered nutrient concentrations were seen shallower than 10–20 m. Chl $a$ concentrations seldom exceeded 1.0 mg m$^{-3}$ outside pure Atlantic Water, peaking at temperatures around 4–5 °C and salinities around 35 (Fig. 6). For the upper 100 m along the frontal transect, silicate concentrations were about 50% of that of nitrate, and when silicate is depleted there is still 3.1 mmol m$^{-3}$ of nitrate of left (see Fig. 6). Phosphate, on the other hand, was more abundant, but for values higher than 0.7 mmol m$^{-3}$ there was a tendency of a relative steeper increase of nitrate than phosphate (Fig. 6). For the upper 100 m of the Norwegian Sea N/P, Si/P and N/Si ratios were 15.2, 8.0 and 1.7, respectively. It should be noted, however, that at 200 m silicate concentrations did not surpass 6 mmol m$^{-3}$ at any station along the transect (Fig. 2), while nitrate concentrations were around 12–13 mmol m$^{-3}$ (Fig. 2). In other parts of the Norwegian Sea it had earlier been seen that silicate concentrations increase from about 7 mmol m$^{-3}$ at 500 m to 13 mmol m$^{-3}$ at 2000 m (Blindheim and Rey, 2004). Compared with the balanced N: Si/P ratio of 16:16:1 (atomic), originally derived from deep water nutrient concentrations of the western Atlantic, this indicates that the lowered silicate levels relative to nitrate and phosphate are typical for the upper 2000 m. Atlantic derived waters of the eastern Arctic Ocean have typical nutrient concentrations of 12 mmol m$^{-3}$ and silicate of 6 mmol m$^{-3}$ between 200 and 300 m (Wheeler et al., 1997), while deeper water (300–500 m) of the central Greenland Sea during summer, comprising both Atlantic and Arctic waters, have nitrate concentrations of 12–13 mmol m$^{-3}$ and silicate of 5–7 mmol m$^{-3}$ (Rey et al., 2000). In general, the winter concentrations in the northeast Atlantic are 9–14 mmol m$^{-3}$ nitrate, 0.5–0.6 mmol m$^{-3}$ phosphate and 4–5 mmol m$^{-3}$ silicate (Koeve, 2001; Slagstad, 1992). According to Allen et al. (2005) typical silicate concentrations are around 6–8 mmol m$^{-3}$ when the diatom spring bloom commences in the Northeast Atlantic. It therefore seems that silicate regeneration is much slower than that of nitrate, both in the Northeast Atlantic and the Norwegian Sea. One would therefore expect that these waters could not support growth of diatoms to the same degree as for other types of phytoplankton that do not depend upon silicate. In accordance with this, Sieracki et al. (1993) found that the diatom spring bloom in the Northeast Atlantic is short lived because silicate is depleted to a minimum before nitrate is depleted. The same pattern of silica depletion prior to nitrate was found by Rey (2004) for the Norwegian Sea.

The POC/PON ratio for a restricted number of depths (most of them between 20 and 40 m) and stations along the transect were found to be 6:2 (atomic) (Fig. 6). This is higher than the ratio of 5.7 (atomic) found by Smith (1994) during a massive Phaeocystis bloom in the Greenland Sea. Our POC/PON ratio is lower than the Redfield ratio of 6.6 (atomic), and that of 7.7 and 7.4 found as seasonal averages for a western Norwegian fjord and the Greenland Sea (Erga, 1989a; Rey et al., 2000), which were obtained for substantially higher phytoplankton concentrations. Such low ratios reveal that phytoplankton at these depths are not N-limited (see Paasche and Erga, 1988).

The mean attenuation coefficient (0–30 m) for visible light (400–700 nm) in Atlantic Water was calculated to be 0.11 m$^{-1}$ (standard deviation 0.004 m$^{-1}$) in the Norwegian Sea, while waters of Arctic origin were more transparent with a mean value 0.08 m$^{-1}$ (standard deviation 0.008 m$^{-1}$) (data not shown). This is in accordance with the turbidity measurements that showed more transparent water at the Front and into Arctic waters to the west, while Atlantic waters to the east were markedly more turbid due to increased levels of phytoplankton biomass (Fig. 4). Due to the fact that inorganic particles contribute relatively stronger to backwards scattering than organic particles (Kirk, 1994), it can be seen from the chlorophyll and turbidity variation pattern that concentrations of inorganic particles were dominating in the upper 20 m on both sides of the Jan Mayen Front. From the surface circulation patterns of the northwestern Norwegian Sea (Blindheim and Rey, 2004; Holm et al., 2000), it follows that these particles probably originate from an earlier diatom bloom and/or snow/ice melt further north in Arctic waters (see Results), and have been advected southwards as

part of the East Greenland Current. Moving eastwards from the Front, the relative contribution of chlorophyll containing particles to the observed turbidity increased.

Our measurements represent the first detailed information on spectral light penetration for these waters covering 350–650 nm wavelength bands over the depth interval 0–20 m (Fig. 3). The contribution of chl a-absorption in the spectral attenuation can be distinguished in the blue part (430 nm) for the two north-most stations and the eastern-most on the main transect. From 7.0°W and westwards towards the Front, where chl a concentrations for depths shallower than 20 m were below 2.0 mg m$^{-3}$ (Fig. 2), the contribution from chl a-absorption could hardly be seen on the spectral attenuation. These stations also represent the most transparent water with $K_d$ (500 nm)$ < 0.1$ m$^{-1}$.

In vivo chl a–specific light absorption seems to be more influenced by phytoplankton composition (dominant cell size and pigment composition) than optical acclimation (Staehr et al., 2002). For the stations with the strongest chl a–signature, there is also smaller attenuation peaks at 520 nm, probably caused by scattering from nonchlorophyllous particles (tripton) (Prieur and Sathyendranath, 1981), indicating decomposing processes being associated with the phytoplankton bloom. The absorption from pure seawater itself increases sharply above 600 nm (Kirk, 1994). Following the optical classification of coastal and oceanic waters based on the specific spectral absorption curves of phytoplankton pigments, dissolved organic matter and other particulate matter by Prieur and Sathyendranath (1981), the waters covered by our optical stations close to the Jan Mayen Front seem to be influenced by chlorophyllous particles to the north and east, but the importance of nonchlorophyllous particles increase westwards towards the Front. The importance of colored dissolved organic matter (CDOM) for spectral absorption is normally negligible in oceanic waters compared to coastal and fjord water, where spectral attenuation coefficients increase more rapidly down in the UV spectrum (Å400 nm) (Erga et al., 2005; 2012). This also appeared to be case for the present study (Fig. 3).

The few earlier publications from neighboring locations were mainly based upon light attenuation measurements restricted to certain wavelengths. Thus, Højerslev and Aas (1991) gave $K_d$ (465 nm) values within the range of 0.09–0.11 m$^{-1}$, 0.13–0.15 m$^{-1}$ and around 0.21 m$^{-1}$ to be representative for Faroe waters, Faroe-Shetland waters and east Icelandic waters during summer, respectively. This compares well with our $K_d$ values at this wavelength (0.08–0.17 m$^{-1}$). For the UV-A wavelength of 380 nm a $K_d$ of 0.16 m$^{-1}$ was found to be a typical average for the summer in the Greenland Sea (Erga et al., 2005) and compares favorably with the $K_d$ (380 nm) values found in the Atlantic waters on the eastern side of the Jan Mayen Front and in Arctic waters close to the island of Jan Mayen (0.13–0.20 m$^{-1}$) (Fig. 3). According to Morel (1988), attenuation coefficients (PAR) of <0.1 m$^{-1}$ are typical for “case I” Oceanic Water with average chl a concentrations for the entire euphotic zone of <1 mg m$^{-3}$ and >0.1 m$^{-1}$ for waters with chl a

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Fig. 6. Linear relationship between chlorophyll a (Chl; mg m$^{-3}$) and temperature (°C), chlorophyll a and salinity, nitrate and phosphate (mmol m$^{-3}$), nitrate and silicate (mmol m$^{-3}$), silicate and phosphate (mmol m$^{-3}$), and particulate organic carbon (POC) and nitrogen (PON) (mmol m$^{-3}$) at the Jan Mayen Front in the Norwegian Sea, June 2007. Depth interval: 0–100 m.
Nutrient consumption and production potential

The winter mixed layer in the Norwegian Sea in the Atlantic waters can vary from less than 200 to several hundred m depth (Rey, 2004). It is assumed that disappearance of nutrients from the water column is due to growth of phytoplankton and bacteria during the season prior to the cruise, and that nutrients shallower than 100 m are mixed into the euphotic zone (Reigstad et al., 2002) and consumed there, the biomass production potential can be calculated by depth integration of nutrient concentrations (Fig. 7). Doing this, the highest nitrate consumption (300 mmol m$^{-2}$) took place within the Arctic Water on the western side of the Front and within the Atlantic Water farthest to the east (370 mmol m$^{-2}$). This is in contrast to the findings of Dale et al. (2001), claiming that typical post-bloom conditions exist on the Atlantic side of the Front. Phosphate revealed a similar pattern, while silicate$^{1}$ was found (0.07 m$^{-3}$, 0.115 m$^{-3}$, 0.14 m$^{-3}$ and 0.22 m$^{-3}$) is defined as Oceanic types II (OII), III (OIII), Coastal 1 and Coastal 3, respectively.

4.2. Nutrient consumption and production potential

Norwegian Sea, mathematical modeling gives an annual primary production around 70 g C m$^{-2}$ (Skogen et al., 2007; Slagstad et al., 1999) of which 45 g C m$^{-2}$ is new production (Slagstad et al., 1999). Based on nitrate disappearance and 14C-incubations, a new production of 62 g C m$^{-2}$ and 52 g C m$^{-2}$ have been calculated, respectively, for the period May–August in the Greenland Sea (Rey et al., 2000). Given that our estimate is only until June, it seems our estimates compare favorable.

4.2.1. New production

If it is further assumed that the nutrient concentrations at 100 m depth are representative for the pre-bloom values (i.e. winter values) of the whole water column above, one obtains an estimate of 37% of the total nitrate reservoir was consumed at the eastern station on the transect during the growth season prior to the cruise. In the northern Barents Sea bacterial nitrate assimilation has been estimated to be substantial, representing more than 30% of the nitrate assimilation in the upper 80 m of the water column during summer (Allen et al., 2002). In late May–early June 2008 it was confirmed that bacterial growth within euphotic zone at the Jan Mayen Front was limited by mineral nutrients (L.A. Cuevas, pers. comm.). It is therefore likely that bacterial nutrient uptake is also considerable in the Norwegian Sea, and that the phytoplankton part of the new production potential should probably be reduced to at least 20 g C m$^{-2}$. This is roughly equal to 270 mg C m$^{-2} d^{-1}$ when assuming that the growth season in the Norwegian Sea commences in early April (Rey et al., 2000).

Luchetta et al. (2000) give 200–400 mg C m$^{-2} d^{-1}$ as typical for new production in the northern Barents Sea during summer.

The additional contribution of regenerated production to the total primary production has been calculated for the Arctic part of the Barents Sea (79°16′–81°05′ N) by Eliertsen et al. (1989). They concluded that at least one third of regenerated primary production could be supported by ammonia excreted by zooplankton, being positioned around the chl $a$ maximum in the summer. This also is in accordance with Kristiansen and Farbrot (1991) who found that a subsurface ammonia maximum is often associated with the chl $a$ maximum in the Barents Sea. Due to the fact that high abundances of the copepod Calanus finmarchicus have been recorded in the Atlantic domain of the Norwegian Sea in June (Dale et al., 2001), ammonia is probably an important supplementary nitrogen source also in these waters, and therefore may contribute significantly to the total primary production (i.e. the sum of new and regenerated production).

By considering the relative importance of silicate (Si(OH)$_4$) as input to the total primary production and comparing it with the nitrate input, the relative contribution of diatoms to the whole phytoplankton community primary production can be estimated. In this case we have used a particulate carbon to silicon ratio of 12:1 (atomic). This is based upon an investigation on biogenic silica production during a yearly cycle of diatom growth in the Oslofjord, Norway (60°N), and applying the winter values (at 2.5 °C) for Skeletonema costatum (Paasche and Østergren, 1980). By similar calculations as conducted for nitrate, silicate consumption of the upper 100 m of the water column at the eastern most station on the transect indicates new primary production of 21 g C m$^{-2}$, which is close to the value obtained based upon nitrate consumption. From Fig. 7 it can be seen that silicate consumption was higher on the Arctic side of the Front. We found that 45% of the total silicate reservoir of the upper 100 m, being formed during the winter convection, had been consumed by June. Therefore diatoms probably dominated in Arctic waters during the growth season prior to the cruise. Such a pattern had earlier been reported for the Barents Sea, where the pynmesiohyphete P. pouchetii was found to dominate in weakly stratified Atlantic Water, while diatoms dominated in the strongly stratified Arctic waters (Degerlund and Eliertsen, 2010; Reigstad et al., 2002). With respect to primary production $P$. pouchetii was also the most important contributor in Atlantic waters of the Norwegian Sea in June 1954 (Paasche, 1960).

It was earlier found that the temperature response of assimilation numbers (maximum photosynthetic rate of the water column) is typically 0.5 mg C mg chl $a^{-1} h^{-1} °C^{-1}$ in coastal waters of eastern

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$^{1}$A disclaimer is necessary to clarify that the silicate values used in this study are not directly comparable to the silicate values used in previous studies due to the differences in sampling, processing and analysis methods. The calculated nutrient concentrations are within the range 0.025–0.060 m$^{-1}$, while in our case an average $K_0$ (500 nm) value of 0.094 m$^{-1}$ was found (0.07–0.16 m$^{-1}$). According to the classification of optical water types by Jerlov (1976), a $K_0$ (500 nm) value for the 1–10 m depth interval of 0.07 m$^{-1}$, 0.115 m$^{-1}$, 0.14 m$^{-1}$ and 0.22 m$^{-1}$ is defined as Oceanic types II (OII), III (OIII), Coastal 1 and Coastal 3, respectively.
Canada and western Norway (Erga, 1989b; Harrison and Platt, 1980). For the lower temperature range (1–3 °C) a maximal photosynthetic response to temperature of 1.1 mg C chl a⁻¹ h⁻¹°C⁻¹ has been found (Erga, 1989b). Typical assimilation numbers for cold waters are 1–3 mg C chl a⁻¹ h⁻¹ (Eilertsen et al., 1989; Erga, 1989b; Hansen et al., 1990; Li et al., 1984; Rey, 1991). Assuming a photosynthetic rate of 0.2 mg C chl a⁻¹ h⁻¹ as an average for the euphotic zone (Erga, 1989b; Erga et al., 2005) and chl a concentrations of 2 mg m⁻³ as typical for the productive areas of the Norwegian Sea (Fig. 2c) during days with maximum surface irradiance of 300 μmol quanta m⁻² s⁻¹, one obtains an average primary production rate of 0.4 mg C m⁻³ h⁻¹ or 10 mg C m⁻³ during 24 h (midnight sun conditions). This is in accordance with values given by Eilertsen et al. (1989) for the chl a maximum being positioned around 20–30 m depth in the Barents Sea in July–August. For a euphotic zone extending down to 40 m (1% light depth in our case varied between 29 and 66 m, see Section 3.4 above), which has been verified for the adjacent Greenland Sea (Erga et al., 2005; Rey et al., 2000), and a mean chl a concentration for the euphotic zone of 1 mg m⁻³ for waters close to the Arctic Front, this gives a daily integrated water column primary productivity of 200 mg C m⁻² d⁻¹ for these waters. Based on ¹⁴C-incubations, Legendre et al. (1993) and Rey et al. (2000) give values around 500–700 mg C m⁻² d⁻¹ as typical under spring bloom conditions in the Greenland Sea, while Berge (1958) found 1 g C m⁻² d⁻¹ to be representative for Atlantic waters to the south east of Jan Mayen in June. Comparing these data with the calculated primary productivity values presented above for the transect, it seems that not only does the Jan Mayen Front not have elevated primary production, but it is rather low.

4.3. Photosynthetic performance

Among the environmental factors controlling quantum efficiency, light and nutrients are the most important (Geider et al., 1993; Vaillancourt et al., 2003). At the Jan Mayen Front nutrient depletion typically extended deeper in the water column on the Arctic side of the front compared with the situation further to the east (Fig. 2). Plots of quantum efficiencies versus nutrients (Fig. 8) suggest that phytoplankton within Atlantic waters respond to increasing nutrient levels. This is in accordance with enhanced quantum efficiencies from the upper nutricline and downwards (Figs. 2, 5a). By comparing Stn 216 (6.98°W) and Stn 230 (5.58°W) it seems that phytoplankton photosynthetic activity is more acclimated to low nitrate and phosphate concentrations farthest to the east in Atlantic waters. Close to the Front, on the other hand, high quantum efficiencies were encountered within the upper 8–40 m of the water column in spite of low chl a and nutrient concentrations in the upper 20 m (Fig. 2). Such conditions are advantageous for small cells with high surface to volume ratios. In accordance with this pico-phytoplankton quantum efficiencies were only found to be adversely affected at very low N and P concentrations (Timmermans et al., 2005). The lack of direct relationship between the concentrations of chl a and the quantum efficiencies are to be expected as the latter is a relative measure, and is biomass independent. From Fig. 8 it can be seen that high quantum efficiencies (>0.5) were obtained for chl a concentrations varying from <0.5 mg m⁻³ to >3.5 mg m⁻³, revealing that phytoplankton cells with a good physiological status were present at all stations. In most cases chl a concentrations >1 mg m⁻³ were associated with SCML within Atlantic waters and <1 mg m⁻³ with Arctic waters. It has earlier been emphasized by Paasche and Erga (1988) that low nutrient concentrations do not imply that the single algal cell is physiologically limited, even if there is a systemic limitation that prevents formation of a higher biomass. According to Parkhill et al. (2001) Φp is not a good indicator of nutrient limitation under balanced growth conditions.

It should be noted that the response to silicate differed from the other nutrients by the high quantum efficiencies obtained when silicate was exhausted. This could be due to dominance of non-silicate requiring phytoplankton in the upper part of the water column (i.e. most likely flagellates and monads <5 μm, see Section 3.5 above), at the time of the cruise. From our data it may also be inferred that high Φp values

![Fig. 8. Relationship between quantum efficiencies of photochemistry in PSII (Fv:Fm) and chlorophyll a (Chl; mg m⁻³), Fv:Fm and silicate (mmol m⁻³), Fv:Fm and nitrate (mmol m⁻³), and Fv:Fm and phosphate (mmol m⁻³) at the Jan Mayen Front in the Norwegian Sea, June 2007. Depth interval: 8–40 m. Stations 216 and 230 are within Atlantic waters, while Station 226, 228 and 233 are within Arctic waters. Note the different scales on the y-axis.](image-url)
were indeed obtained when silicate surpassed 1 mmol m⁻³. According to Egg and Aksnes (1992), diatoms will dominate when silicate concentrations are higher than 2 mmol m⁻³. In the Northeast Atlantic, silicate concentrations will control diatom blooms when depleted to < 1 mmol m⁻³ (Allen et al., 2005).

Due to the fact that quantum efficiencies decrease with increasing irradiance (Suggett et al., 2003) and that our FRRF measurements in Arctic and Atlantic waters were conducted at different times during the 24 h light cycle (midnight sun), variations in light intensities cannot be neglected as a contributing factor to the observed variation pattern in quantum efficiencies. Also the fact that light acclimation in the case of fluorescence yield occurs on a time scale of minutes and changes in the antenna size of the light harvesting complex II (LHCLII) on a time scale of hours to days (Huner et al., 1998), support such a view. Besides this it can be seen from Fig. 3 that the water transparency in the Atlantic Water increases westwards towards the Front and continues into the Arctic Water, but despite this high transparency in the Atlantic Water increases westwards towards the Front. This can be due to the fact that the FRRF stations in Arctic waters were visited during midnight sun hours when light intensities were only 10% of those around local noon.

Most of the results being published from frontal studies are about stimulation of phytoplankton productivity by active front systems. From these studies it emerges that there are no consensus with respect to quantum efficiency responses at the front. Values within the range of 0.3–0.55 are typical for both sides of the frontal systems (Kolber et al., 1990; Moore et al., 2003; Smyth et al., 2004). These values are also consistent with our data for the waters at and around the Jan Mayen Front (Fig. 5a), but as opposed to the above studies we could not find a specific Front effect. Kolber et al. (1998) concluded that F/Fm values around 0.65 are achievable for physiologically healthy algae when using a ST flash. For the high productive upwelling areas, as off the coast of north western Africa, Falkowski and Kolber (1995) found values around 0.65, while values <0.3 are typical for surface layers of oligotrophic oceanic waters.

From the FRRF dataset, the initial slope of the P-E curve, $\alpha^8$ (mg C mg chl $^{-1}$ h $^{-1}$ mυm quanta $^{-1}$ m²s) can be calculated (see Material and methods). Average value of maximum $\alpha^8$ along the transect in the Norwegian Sea was 0.05 mg C mg chl $^{-1}$ h $^{-1}$ mυm quanta $^{-1}$ m²s. Based upon $^{14C}$ uptake measurements, $\alpha^8$ values in the Barents Sea ranged between 0.01 and 0.16 mg C mg chl $^{-1}$ h $^{-1}$ mυm quanta $^{-1}$ m²s with most of the values <0.05 mg C mg chl $^{-1}$ h $^{-1}$ mυm quanta $^{-1}$ m²s (Rey, 1991). Within the euphotic zone of open fjord waters of western Norway they ranged between 0.0056 and 0.0537 mg C mg chl $^{-1}$ h $^{-1}$ mυm quanta $^{-1}$ m²s during the year (Erga, 1989b).

As stated by Falkowski and Kolber (1995) the effective absorption cross section of PSII, $\sigma_{psii}$, can be used to obtain information about the rate of photon absorption by PSII, the maximum quantum efficiency for oxygen production, and photosynthetic electron transport rates at ambient irradiance. We found a tendency for the highest values to be within the warmer and more saline Atlantic waters (Fig. 5b) where values increased both with depth and distance eastwards from the Front. Here, values >700 Å² quanta $^{-1}$ were encountered between 15 and 30 m. Elevated values (about 600 Å² quanta $^{-1}$) were also encountered at depth westwards close to the Jan Mayen Front. This could be interpreted to be due to light acclimation of the phytoplankton cells. However, for the waters on the eastern side of the Front and close to the surface salinity front at 71°W, low $\sigma_{psii}$ values (450 Å² quanta $^{-1}$) revealed low degrees of light acclimation in the upper 32 m. For active tidal fronts $\sigma_{psii}$-values around 500–750 Å² quanta $^{-1}$ are representative for the stratified region and values around 320–500 Å² quanta $^{-1}$ for the mixed side (Moore et al., 2003; Smyth et al., 2004).

For a great variety of eukaryotic algal cultures $\sigma_{psii}$-values (measured with FRRF) have been found to vary between 270 and 1451 Å² quanta $^{-1}$ under low light and high light (18–300 μmol quanta m⁻² s⁻¹) growth conditions (Suggett et al., 2004). Kolber et al. (1988) found that both nutrient limitation, especially nitrogen, and light acclimation over a longer period could influence the effective absorption cross section. The low values often found within other frontal systems are probably due to nonphotochemical quenching (Falkowski and Kolber, 1995) caused by the mixing which prevents acclimation to the changing ambient light. Among the nonphotochemical quenching factors, antenna quenching released by thermal deactivation in the pigment bed, is one that can effectively reduce $\sigma_{psii}$ (Vassiliev et al., 1994).

From our study we find no evidence of increased primary productivity at the Jan Mayen Front compared with the adjacent waters. This is based on the low phytoplankton biomass, high transmittivity, low turbidity, low nutrient consumption and low quantum efficiencies. On the contrary, growth conditions were better to the east into Atlantic Water. This is in contrast with the findings of Legendre et al. (1993), investigating the Arctic Front (active) further to the north in the Greenland Sea (75°N). They found that the total primary production was especially high in the Arctic Front in June. This may be due to timing as the spring bloom occurs later farther to the north. On the other hand, farther south in the Northeast Atlantic, Popova and Srokosz (2009) showed that surface phytoplankton biomass distribution in June had a distinctive minimum along the Iceland—Faroe Arctic Front (active), while water column primary production peaked south of the Front in Atlantic Water where the upper mixed layer extended deeper. From this it may be inferred that phytoplankton biomass of the northwestern Norwegian Sea is higher within Atlantic Water than Arctic Water in June, after the spring bloom, due to a deeper depletion of nutrients in Arctic Water (see Fig. 2). The effect of this was most severe for silicate. Lack of significant vertical mixing and upwelling at the Jan Mayen Front prevents nutrients from being replenished in the upper layer.

5. Conclusions

Our data show that variations in quantum efficiency and effective absorption cross section along the transect across the Jan Mayen Front in the Norwegian Sea were related to water type. Measurements of the spectral diffuse attenuation coefficient $K_d$ (500 nm) suggest that the waters on the eastern side of the Front should be characterized as OII—OIII (Jerlov system). High quantum efficiencies were seen to the east of the Jan Mayen Front and at depth in stratified Atlantic waters. High chl $a$ concentrations were restricted to pure Atlantic waters. Maximum values of the effective absorption cross section were found within the stratified Atlantic Water. We could not observe any relationship between quantum efficiency and chl $a$ concentration. Our data also indicate that the quantum efficiency was partly controlled by nutrients and partly by light. Low phytoplankton biomass at the Front in June is probably due to nutrient limitation. The low silicate concentrations at depth are most likely related to the origin of water masses, putting constraints on the duration of the diatom spring bloom in the northwest Norwegian Sea. We conclude that the Jan Mayen Front did not have a stimulatory effect on phytoplankton growth and photosynthetic capacity, and that no changes in phytoplankton distribution could be observed across the Front. This is in part due to the weak horizontal density front because of the density compensation of the temperature, salinity characteristics of the adjacent water masses. This leads to weak vertical mixing and little or no associated vertical upwelling, as opposed to that observed in many temperate fronts.

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