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Phytoplankton biomass, composition, and productivity along a temperature and stratification gradient in the Northeast Atlantic Ocean

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Abstract

The North Atlantic Ocean experiences considerable variability in sea surface temperature (SST, > 10 m) on seasonal and inter-annual time-scales. Relationships between SST and vertical density stratification, nutrient concentrations, and phytoplankton biomass, composition, and absorption were assessed in spring and summer from latitudes 30–62° N. Furthermore, a bio-optical model was used to estimate productivity for five phytoplankton groups. Nutrient concentration (integrated from 0–125 m) was inversely correlated with SST in spring and summer. SST was also inversely correlated with near surface (0–50 m) Chl *a* and productivity for stratified stations. However, near surface Chl *a* showed an exponential relationship with SST, whereas a linear relationship was found for productivity and SST. The response of phytoplankton to changes in SST is therefore most likely to be observed by changes in Chl *a* rather than productivity. The discrepancy between relationships of Chl *a* and productivity were probably related to changes in phytoplankton cell size. The contribution of cyanobacteria to water column productivity correlated positively with SST and inversely with nutrient concentration. This suggests that a rise in SST (over a 13–23 °C range) stimulates productivity by cyanobacteria at the expense of haptophytes, which showed an inverse relationship to SST. At higher latitudes, where rising SST may prolong the stratified season, haptophyte productivity may expand at the expense of diatom productivity. Depth integrated Chl *a* (0–410 m) was greatest in the spring at higher latitudes, where stratification in the upper 200 m was weakest. This suggests that stronger stratification does not necessarily result in higher phytoplankton biomass standing stock in this region.

1 Introduction

Phytoplankton growth in the oceans ultimately depends on seasonal and inter-annual climatological cycles that determine the availability of nutrients and light. In the open ocean, vertical density stratification is an important process in shaping the resource

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availability for phytoplankton growth. Stabilization of the water column allows phytoplankton to exploit higher irradiance intensities near the surface. However, stratification also inhibits exchange with nutrient rich deep water, potentially leading to nutrient limitation of phytoplankton near the surface. In the absence of stratification (winter, early spring) the depth range of vertical mixing due to wind and convection can expand by more than one order of magnitude, reducing phytoplankton light availability, and increasing nutrient concentrations. Furthermore, stratification may affect predator-prey and viral-algal host interactions by influencing encounter rates (Behrenfeld, 2010; Baudoux et al., 2008). Moreover, stratification is also an important factor in the seasonal development of phytoplankton composition in the open ocean. Changes in phytoplankton composition often coincide with changes in cell size, because an increased surface-to-volume ratio is advantageous under low nutrient concentrations typical of a stratified water column (Chisholm and Morel, 1991). High nutrient concentrations and turbulence due to winter mixing supports the growth of larger phytoplankton species such as diatoms, whereas the onset of stratification in spring leads to a succession towards smaller phytoplankton species (Litchman et al., 2007; Claustre et al., 2005). Low nutrient availability in the (sub)tropical oligotrophic ocean results in the dominance of cyanobacteria like *Synechococcus* and *Prochlorococcus* over pico-eukaryotic phytoplankton species (Li, 1994; Johnson et al., 2006). The changes in phytoplankton composition can affect productivity and carbon storage to the deep ocean (Claustre et al., 2005; Martin et al., 2011).

Apart from pronounced seasonal changes, the North Atlantic experiences fluctuations in sea surface temperature (SST, > 10 m) on inter-annual to multi-decadal scales due to the influence of the North Altantic Oscillation and the Atlantic Multi decadal Oscillation (changes in the range of 0.5 °C, Drinkwater et al., 2003; Enfield et al., 2001; Ting et al., 2009). In addition, the North Atlantic has experienced significant warming as a result of global climate change (Gleckler et al., 2012) and this process is expected to continue over the next decades. The response of ocean productivity to rising temperature is under debate. Models predict that increased SST will enhance stratification of

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the upper oceans (Steinacher et al., 2010; Hofmann et al., 2011), thereby reducing the depth of the mixed layer and decreasing nutrient exchange with the deep ocean. Remote sensing derived, globally averaged Chl *a* and productivity showed a significant negative relationship with density differences in the upper oligotrophic open ocean (Behrenfeld et al., 2006; Polovina et al., 2008). However, long term monitoring sites and historical records for estimated Chl *a* showed conflicting trends for the North Atlantic and other oceanic regions (Chavez et al., 2010; Boyce et al., 2010). Furthermore, no evidence for the inter-annual control of phytoplankton biomass and productivity by stratification was observed in the subtropical North Pacific and North Atlantic, although stratification correlated on a seasonal timescale with phytoplankton productivity (Dave and Lozier, 2010; Lozier et al., 2011). At mid and higher latitudes in the North Atlantic, stratification has been associated with bloom formation (Dutkiewicz et al., 2001). Here, termination of convection and the onset of stratification initiate the phytoplankton spring bloom (Siegel et al., 2002; Taylor and Ferrari, 2011; Mahadevan et al., 2012). Earlier onset of stratification in the subpolar North Atlantic may prolong the phytoplankton bloom season (Racault et al., 2012). As such, different responses to stratification can be expected between the sub-polar and subtropical North Atlantic (Richardson and Schoeman, 2004).

A pronounced gradient in SST and stratification can be observed from low (30° N) to higher (62° N) latitudes in the North Atlantic (Jurado et al., 2012a,b). We investigated seasonal changes in biomass, productivity, and composition of North Atlantic phytoplankton along this gradient in relation to stratification, sea surface temperature, nutrient concentration, and light availability. Furthermore, a model was used to estimate daily water column productivity in the euphotic zone, using in situ phytoplankton biomass (Chl *a*), phytoplankton composition (pigments), light, and temperature as variables, providing insight into the contribution of five phytoplankton taxonomic groups to community primary productivity.

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2 Methods

Two cruises were performed in the North Atlantic Ocean onboard the RV Pelagia covering the area between the Canary Islands and Iceland (summer: July/August 2009; spring: April/May 2011). The cruise track covered subtropical, temperate, and subpolar sections in the North Atlantic Ocean (Fig. 1). Samples were collected with a trace metal clean CTD frame equipped with 12 (summer) and 27 L (spring) sample bottles. Samples for macro nutrients, pigments, and chlorophyll specific absorption (see below) were obtained in a dedicated clean container.

2.1 Stratification index

The stratification index (Behrenfeld et al., 2006; Dave and Lozier, 2010; Lozier et al., 2011) was used as a measure of stratification. The stratification index was calculated as the difference in potential density (sigma-theta) between the upper 10 m (0–10 m average) and 200 m using the salinity and temperature profiles obtained by the CTD (Seabird 9+). When the difference in potential density was smaller than 0.125, the upper 200 m was considered as non-stratified (De Boyer Montegut et al., 2004).

2.2 Nutrients

Nutrient samples (6 mL) were obtained from multiple bottles, sampling between 4 and 7 depths. The samples were filtered through 0.2 µm Acrodisc filters and measured onboard for inorganic PO_4, NH_4, NO_2, and NO_x using a Bran & Luebbe Quaatro auto analyzer. Depth profiles of PO_4 and NO_3 (calculated by subtracting NO_2 from NO_x) were fitted with a three or a five parameter sigmoidal function by non-linear regression (Sigma plot 11.0). Using the obtained function, nutrient concentrations were calculated over one meter depth intervals for the potential (0–125 m), upper (0–50 m), and lower (50–125 m) euphotic zone. Furthermore, N : P ratios were calculated for the upper and lower euphotic zone as $(NO_3 + NH_4)/PO_4$ for the respective depth intervals.

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In the present study, oligotrophic and mesotrophic stations were distinguished based on concentration of NO_3 in the upper euphotic zone (0–50 m). We defined oligotrophic stations as those stations where NO_3 in the upper euphotic zone was below the detection limit, whereas nutrients were detectable in the upper euphotic zone of mesotrophic stations (Fig. 2).

2.3 Chlorophyll specific absorption

Samples (5–10 L) for Chl *a* specific absorption were obtained from the chlorophyll maximum (oligotrophic stations: ~ 70 m, mesotrophic stations: ~ 40 m) and from the subsurface (oligotrophic stations: ~ 15–30 m, mesotrophic stations: ~ 10–15 m). The samples were filtered through 47 mm GF/F (Whatman), frozen in liquid nitrogen, and stored at −80 °C. Transmission and reflection from the filter was measured between 350–800 nm on a Varian CARY 3E UV/VIS double beam spectrophotometer with integrating sphere over 1 nm intervals, before and after bleaching with 1 % sodium hypochloride (Tassan and Ferrari, 1995). Chlorophyll specific absorption (a^*_{ph}) was calculated between 400–700 nm using the filter clearance area, sample volume, Chl *a* concentration (separate HPLC sample, see below), and the amplification factor β (set at 2 for all samples). The spectrally weighted mean specific absorption coefficient ($\overline{a}^*$) was calculated as the sum of a^*_{ph} between 400–700 nm and corrected by a normalized solar spectrum (maximum set to one).

2.4 Pigment composition

Four to seventeen samples (5–10 L) were obtained from multiple depths at each station and filtered through 47 mm GF/F (Whatman) under mild vacuum (0.3 mbar), frozen in liquid nitrogen, and stored at −80 °C. Prior to analysis, filters were freeze dried (48 h) and pigments were extracted in 90 % acetone (v/v) (48 h, 4 °C, darkness). Pigments were separated on a Waters 2695 HPLC using a Zorbax Eclipse XDB-C8 column (3.5 µm particle size) as described by Hooker et al. (2009). Diode array spectroscopy

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(Waters 996) and retention time were used for pigment identification and the system was calibrated against standards (DHI, Denmark) for chlorophyll a_1, divinyl (dv) chlorophyll a_2, chlorophyll b, chlorophyll c_2, chlorophyll c_3, 19-butanoyloxyfucoxanthin, 19-hexanoyloxyfucoxanthin, fucoxanthin, neoxanthin, prasinoxanthin, and zeaxanthin. Total Chl a (sum of Chl a_1 and dv Chl a) obtained from HPLC analysis served as phytoplankton biomass indicator and was used to calibrate the fluorescence sensor from the CTD (Chelsea Aquatracka Mk III). A single relationship between HPLC Chl a and Chl a fluorescence values was used for the summer cruise. However, during the spring cruise, the relationship between Chl a fluorescence and HPLC Chl a was more variable and three different relationships were used to calibrate the fluorescence profiles for data from latitude 28–40° N, 40–47° N, and 48–62° N. The calibrated fluorescence profiles were then used to calculate Chl a over 1 m depth intervals. Depth integrated Chl a was calculated for the euphotic zone and for defined depth intervals: Chl a integrated over 0–50 m (Chl $a_{0-50\,m}$) and total depth integrated Chl a (surface to 200–410 m, Chl a_t). The euphotic zone was defined as the depth with 0.1 % of surface irradiance. The 0.1 % light depth was calculated from the vertical attenuation coefficient (K_d), which was determined from linear regression of natural log transformed PAR vs. depth (PAR: photosynthetically active radiation, 400–700 nm, measured by a 2π Satlantic PAR sensor on the CTD).

2.5 Phytoplankton composition

Phytoplankton taxonomic composition was determined using CHEMTAX (Mackey et al., 1996) as described by Mojica et al. (submitted). In short, 13 pigments (Chl a, dv Chl a, Chl b, Chl c_2, Chl c_3, peridinin, fucoxanthin, 19-butanoyloxyfucoxanthin, 19-hexanoyloxyfucoxanthin, neoxanthin, prasinoxanthin, alloxanthin, and zeaxanthin) were used to distinguish 8 taxonomic groups (cyanobacteria, prochlorophytes, haptophytes, diatoms, dinoflagellates, cryptophytes, prasinophytes, and pelagophytes). Samples were grouped according to latitude. In oligotrophic waters, Chl a specific absorption showed differences between sub-surface samples and those from the

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chlorophyll maximum. In accordance, separate CHEMTAX analysis were performed for oligotrophic samples with depth < 50 m and > 50 m, using high light and low light acclimated initial pigment ratios, respectively. Mesotrophic stations showed no differences between sub-surface and chlorophyll maximum Chl *a* specific absorption, and for these stations, low light acclimated pigment ratios were used for all depths. Contributions of the taxonomic groups were expressed relative to Chl *a*. Initial pigment ratios for CHEMTAX were obtained from published pigment ratios (Zapata et al., 2004; Laviale and Neveux, 2011; Kulk et al., 2011, 2012) and from exponentially growing batch cultures (haptophytes: *E. huxleyi*, *P. globosa*, and diatoms: *D. brightwelii*, *T. pseudonana*, unpublished results). The current study focused on five phytoplankton groups used in the primary production model. Further details on phytoplankton species composition were published by Mojica et al. (2013).

2.6 Primary production

Depth integrated daily primary production in the euphotic zone (PP_{Zeu}) and in the upper 50 m ($PP_{0–50\,m}$) was calculated for each station using a diagnostic bio-optical model comparable to Claustre et al. (2005) and Uitz et al. (2008). The model uses in situ temperature, light, light attenuation, and Chl *a* profiles to estimate primary productivity of different oceanic phytoplankton groups. In contrast to the model presented by Claustre et al. (2005) and Uitz et al. (2008), the current model uses CHEMTAX based taxonomic groups and laboratory determined primary production rates. In situ Chl *a* specific absorption was used to reveal potential vertical structures in photoacclimation characteristics.

2.6.1 In situ data

In situ measurements obtained during the two cruises in the North Atlantic Ocean were used to set the irradiance climate, temperature, and biomass in the model. The daily light dose at each station was obtained using data (level 3, 9 d average) from the

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Moderate Resolution Imaging Spectroradiometer (MODIS) satellite. The time resolved surface PAR was then calculated using the formulations for the diurnal variation of solar irradiance from Kirk et al. (1994). PAR attenuation for 1 m depth intervals was calculated using the K_d determined from PAR profiles of the CTD (see above).

The in situ SST (CTD temperature at 10 m depth) during the spring and summer cruise in the North Atlantic Ocean ranged from 7.7–23.3 °C. Because the model is based on laboratory measurements at 20 °C, a temperature correction was applied. A linear relationship between carbon fixation and temperature was assumed. A mean slope ($-0.045\,\mathrm{mg\,C\,m^{-2}\,d^{-1}\,°C^{-1}}$) obtained from growth versus temperature experiments was used (Montagnes and Franklin, 2001).

Phytoplankton biomass (Chl *a*) was obtained from in situ fluorescence profiles (1 m depth intervals), which were calibrated to HPLC Chl *a* concentrations as described above.

2.6.2 Primary production calculations

Based on the taxonomic composition estimated by CHEMTAX, five different groups were distinguished to model primary production: group 1: *Prochlorococcus*, group 2: *Synechococcus*, group 3: Prasinophyceae, Pelagophyceae, and Cryptophyceae, group 4: Haptophyceae and Dinophyceae, and group 5: diatoms. Photosynthetic characteristics for these functional groups were obtained from ^{14}C based photosynthesis versus irradiances (PE) measurements of *Prochlorococcus marinus* (group 1), *Synechococcus* sp. (group 2), *Ostreococcus* sp. (group 3), *Emiliania huxleyi* (group 4), and *Thalassiosira oceanica* (group 5) (Kulk et al., 2011). Photosynthetic characteristic of low light ($50\,\mu\mathrm{mol\,photons\,m^{-2}\,s^{-1}}$) and high light ($125\,\mu\mathrm{mol\,photons\,m^{-2}\,s^{-1}}$) acclimated phytoplankton were used to calculate carbon fixation rates. To this end, a vertical structure in photosynthetic characteristics was assumed at oligotrophic stations, as was observed in Chl *a* specific absorption. The depth where the PAR dose exceeded the dose experienced by the high light acclimated cultures ($125\,\mu\mathrm{mol\,photons\,m^{-2}\,s^{-1}}$) was calculated from the K_d. Above this depth, phytoplankton were assumed to be high light acclimated,

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whereas low light acclimated phytoplankton (50 µmol photons m^{-2} s^{-1}) were assumed below this depth. In addition, phytoplankton were assumed to be low light acclimated when surface Chl *a* exceeded 0.5 mg m^{-3}. Depth integrated primary production was calculated according to Platt et al. (1980) for a 24 h period over 1 h time intervals in the euphotic zone (0.1 % PAR) for the five functional phytoplankton groups.

2.7 Statistics

Relationships between nutrient concentration (NO_3 and PO_4 integrated over 0–125 m: N, $P_{0–125\,m}$), SST, density differences (0–200 m), phytoplankton biomass, and phytoplankton productivity were assessed by calculating the Spearman rank order correlation coefficient (SigmaPlot 11.0, Systat Software). We used the following indicators for phytoplankton biomass: Chl *a* concentration in samples from 10–20 m (surface Chl *a*), Chl *a* integrated over 0–50 m (Chl $a_{0–50\,m}$), and total depth integrated Chl *a* (surface down to 200–410 m, Chl a_t). The daily integrated productivity in the euphotic zone (PP_{Zeu}) and the daily productivity integrated over 0–50 m ($PP_{0–50\,m}$) was used as a measure for productivity. In addition, relationships between contributions of five taxonomic groups to productivity were assessed.

Summer and spring cruises were tested separately ($n = 32$). Furthermore, relationships were assessed for stratified (spring and summer cruise pooled, $n = 52$) and non-stratified (spring, $n = 12$) stations. Chl *a* specific absorption data from oligotrophic and mesotrophic stations were pooled (sub-surface and Chl *a* maximum separately) and tested with a one way ANOVA using Statistica 8.0 (StatSoft). Differences were considered significant at $p < 0.05$.

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3 Results

3.1 Vertical density stratification

In summer, all stations were stratified, whereas weaker stratification was found in spring (Fig. 2). In spring, the upper 200 m of the 12 stations above 47° N were considered to be non-stratified (density difference < 0.125). In both seasons, the stratification index was highest at low latitudes and declined at higher latitudes, but the latitudinal gradient was less pronounced in spring compared to summer. The correlation between the stratification index (difference in potential density between the surface and 200 m) and SST (< 10 m) was stronger in summer than in spring (correlation coefficient 0.87 vs. 0.78, data not shown).

3.2 Nutrient standing stock

Oligotrophic conditions were encountered up to latitude 45° N in summer and 39° N in spring. N and P concentrations in the lower euphotic zone (50–125 m) increased linearly with latitude and did not show significant differences between spring and summer (Fig. 2). N and P in the upper euphotic zone (0–50 m) of mesotrophic stations increased with latitude and concentrations were higher in spring than in summer. N, $P_{0–125\,m}$ showed strong inverse correlations with SST in spring and summer and for stratified (summer and spring combined) and non-stratified stations (Table 1). The correlations between stratification index and N, $P_{0–125\,m}$ were stronger in summer than in spring and were not significant for stratified (summer and spring combined) and non-stratified stations. Integrated N and P concentrations in the euphotic zone were on average five times higher in non-stratified stations compared to stratified stations (data not shown).

Average N : P ratios for the upper euphotic zone of oligotrophic stations were 10.5 and 11.4 for spring and summer, respectively (data not shown). Four oligotrophic stations showed high N : P ratios due to extremely low P concentrations and were excluded

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from the N : P calculations. At mesotrophic stations, the average N : P ratio of the upper euphotic zone was 15.3 and 13.2 for spring and summer. Average N : P ratios for the lower euphotic zone were 14.0 and 18.7 for spring and summer in oligotrophic stations and 15.9 and 16.3 spring and summer in mesotrophic stations, respectively.

3.3 Phytoplankton Chl *a* specific absorption

At oligotrophic stations, the spectrally weighted mean specific absorption coefficient ($\overline{a}^*$) was significantly ($p < 0.01$) higher in samples from the sub-surface compared to the chlorophyll maximum in spring and summer (Fig. 3). In mesotrophic stations, $\overline{a}^*$ was not different between samples from the sub-surface and chlorophyll maximum in spring and summer. Chl *a* specific absorption was on average 37 % lower in spring compared to summer ($p < 0.001$).

3.4 Phytoplankton biomass

Oligotrophic stations showed low surface Chl *a*, whereas higher concentrations were found in a deep chlorophyll maximum (DCM). Mean surface Chl *a* was higher in spring (0.23 ± 0.07 mg Chl *a* m^{-3}) than in summer (0.08 ± 0.03 mg Chl *a* m^{-3}) for oligotrophic stations (Fig. 4). More variability in surface Chl *a* was observed in mesotrophic stations, with maximal surface concentrations (2.0 mg Chl *a* m^{-3}) at mid-latitudes during spring and at higher latitudes during the summer. Mean depth integrated Chl *a* (Chl a_t) for oligotrophic stations was 49 ± 11 and 23 ± 6 mg Chl *a* m^{-2} for spring and summer, respectively. Stronger seasonal differences were found in Chl a_t of mesotrophic stations with on average 112 ± 36 and 33 ± 11 mg Chl *a* m^{-2} in spring and summer, respectively. Non-stratified stations showed highest Chl a_t (up to 190 mg Chl *a* m^{-2}, integrated over 410 m). Depth integrated Chl *a* in the euphotic zone declined with increasing latitude from 80 to 30 % in spring, whereas 90 % of Chl *a* was found in the euphotic zone in summer (Fig. 4). In spring, Chl *a* in the euphotic zone correlated positively with SST (correlation coefficient 0.92) but not in summer.

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Surface Chl *a* and Chl $a_{0–50\,m}$ correlated with N, $P_{0–125\,m}$, whereas inverse correlations were observed with SST (Table 2, Fig. 5). Correlations between these variables were weaker in spring compared to summer. In spring, Chl a_t correlated with N, $P_{0–125\,m}$, SST, and the stratification index. When tested for stratified stations (spring and summer combined), surface Chl *a* and Chl $a_{0–50\,m}$ showed significant inverse correlations with SST and a positive correlation with N, $P_{0–125\,m}$, whereas this was not found for the stratification index (Table 2). The relationships between Chl *a* (surface Chl *a* and Chl $a_{0–50\,m}$) and SST was best described by an exponentially declining function (Fig. 5). Chl *a* concentrations of non-stratified stations were not correlated with N, $P_{0–125\,m}$, SST, and stratification index (data not shown).

3.5 Primary production

Daily primary production in the euphotic zone (PP_{Zeu}) of oligotrophic stations showed about 2-fold lower carbon fixation in summer than in spring (on average 457 ± 242 and $979 \pm 236\,mg\,C\,m^{-2}\,d^{-1}$, respectively, Fig. 6). However, for mesotrophic stations, PP_{Zeu} showed no significant differences between spring and summer (on average 1210 ± 225 and $1330 \pm 232\,mg\,C\,m^{-2}\,d^{-1}$, respectively). In summer, PP_{Zeu} and $PP_{0–50\,m}$ correlated positively with N, $P_{0–125\,m}$, and inversely with SST and the stratification index ($n = 32$, Table 2). These correlations were weaker or not significant in spring ($n = 32$). PP_{Zeu} and $PP_{0–50\,m}$ showed an inverse correlation with SST in stratified stations (summer and spring combined) (Table 2, Fig. 5), and a positive correlation with N, $P_{0–125\,m}$ (Table 2). There was a weak inverse correlation between productivity and the stratification index for stratified stations (Table 2). Productivity of non-stratified stations showed no correlations with N, $P_{0–125\,m}$ and SST (data not shown).

Cyanobacteria contributed up to 30 % to productivity of oligotrophic stations (group 1 and 2 combined, Fig. 7). At stratified stations (summer and spring combined), the contribution of cyanobacteria was inversely correlated with N, $P_{0–125\,m}$ and positively with SST, whereas no significant relationship was found for the stratification index (Table 3). In mesotrophic stations, productivity of cyanobacteria was of minor importance

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(Fig. 7). On average 30 % of group 3 (prasinophytes, pelagophytes and cryptophytes) consisted of prasinophytes (data not shown). Group 3 showed a relatively stable contribution to productivity of stratified stations (on average 30 %). In non-stratified stations the contribution of group 3 increased up to 73 % and showed positive correlations with N, $P_{0–125\,m}$ and an inverse correlation with SST (Table 3). Haptophytes were the most important contributor of group 4 (haptophytes, dinophytes) in spring (91 %) and summer (75 %). On average, group 4 accounted for 50 % of the production in mesotrophic stations, whereas this was 37 % in oligotrophic stations (Fig. 7). At stratified stations (summer and spring), the contribution of group 4 correlated positively with N, $P_{0–125\,m}$ and inversely with SST (Table 3). At non-stratified stations, group 4 showed inverse correlations with N, $P_{0–125\,m}$ and a positive correlation with SST. The contribution of diatoms to productivity (groups 5) was maximal at higher latitudes (up to 60 %) during the spring compared to summer (on average 8 %, Fig. 7). The contribution of diatoms to the productivity in stratified stations did not show correlations with N, $P_{0–125\,m}$ and SST (Table 3). At non-stratified stations, this group was inversely correlated with N, $P_{0–125\,m}$ and positively correlated with SST (Table 3).

4 Discussion

4.1 Phytoplankton biomass and productivity in relationship to SST, stratification, and nutrients

The summer and spring comparison of open ocean stations in the North Atlantic (30–62° N) showed that phytoplankton biomass, productivity, and composition were correlated with N and P concentrations and SST. In the present study, the potential nutrient availability for phytoplankton was estimated by integration of nutrient concentrations over 0–125 m (N, $P_{0–125\,m}$). The positive correlation between N, $P_{0–125\,m}$ and Chl *a* suggested that open ocean phytoplankton biomass and productivity were controlled by the availability of these nutrients in the investigated region. SST was inversely correlated

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with phytoplankton biomass and productivity and with N, $P_{0-125\,m}$. This suggests that SST is important in determining nutrient availability for phytoplankton by influencing vertical exchange with deeper nutrient rich water. The relationships were stronger with SST than with the stratification index. A possible explanation for this may be that temperature influences phytoplankton growth rates (nutrient utilization) in addition to influencing nutrient availability in the water column. Correlations between SST and phytoplankton biomass and productivity were weaker under the weakly and non-stratified conditions in spring. Moreover, the fraction of the phytoplankton biomass in the euphotic zone correlated with SST. Combined, this indicates that convective and wind mixing exerted a stronger influence on the water column distribution of Chl *a* in spring.

The inverse relationships between SST and near surface phytoplankton biomass and $PP_{0-50\,m}$ for stratified stations suggests that within the SST range of 13–23 °C, North Atlantic open ocean phytoplankton productivity can co-vary with seasonal, inter annual, and multi-decadal SST changes. This also implies that anthropogenic warming of the ocean has a negative influence on phytoplankton biomass and productivity in the stratified open ocean within this temperature range. The relationship between productivity and SST in stratified stations indicated that a 0.5 °C increase in SST causes a 6.5 % decline in daily productivity in the upper 50 m. Gregg et al. (2003) reported a similar decline in productivity (6–7 %) in the central and northern section of the North Atlantic from a 0.3–0.7 °C SST increase. In addition, the non-linear response of Chl *a* to SST observed in the present study suggested that a SST rise of 0.5 °C would correspond to a 13–15 % decline in near surface Chl *a* (surface Chl *a*, Chl $a_{0-50\,m}$) for stratified conditions between 13–23 °C. Moreover, the non-linear nature of this relationship suggests that responses to changes in SST are more likely to be detected in Chl *a* compared to productivity.

The different relationships of biomass (non-linear) and productivity (linear) with SST may be associated with the influence of phytoplankton composition on Chl *a* concentration. In the present study, Chl *a* specific absorption was significantly lower (37 %) in spring compared to summer, as was also observed by Claustre et al. (2005). This may

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be caused by increased pigment packaging due to the presence of larger phytoplankton species such as diatoms. Furthermore, the relationships between Chl *a* fluorescence (CTD) and HPLC determined Chl *a* concentrations showed a decreased Chl *a* specific fluorescence yield in spring as compared to summer (data not shown), providing additional evidence for seasonal differences in the Chl *a* package effect. Most variability in Chl *a* specific absorption has been associated with changes in phytoplankton size structure (Bricaud et al., 2004). In the present study, reduced nutrient concentrations coincided with a shift to smaller phytoplankton species, which was also found in other studies (Bouman et al., 2011; Agawin et al., 2000). Smaller species contain less Chl *a* per cell and therefore show less pigment packaging (Ciotti et al., 2002). Therefore, changes in phytoplankton cell size may contribute to the observed non-linear relationship between Chl *a* and SST. However, acclimation to different light and nutrient conditions can also influence cellular Chl *a* and Chl *a* specific absorption, but the magnitude of these changes can vary among phytoplankton species (Geider et al., 1993; Kulk et al., 2011). Stronger turbulence in spring (Jurado et al., 2012b) may have reduced the light dose experienced by the phytoplankton, thereby increasing cellular pigment concentrations compared to the more stable summer conditions. Therefore, contributions of phytoplankton composition and photoacclimation on pigment concentrations and packaging cannot be fully separated in the present study.

4.2 Stratification mediated shifts in phytoplankton biomass, productivity, and composition

In spring, stations above 47° N showed minimal stratification, with potential density differences in the upper 200 m of $0.029 \pm 0.02\,kg\,m^{-3}$. This is less than the reported $0.12\,kg\,m^{-3}$ difference for eddy driven stratification that preceded thermal stratification in the same region in 2008 (Mahadevan et al., 2012), but corresponds with values ($0.025\,kg\,m^{-3}$) where phytoplankton biomass accumulation in the upper 150 m was observed around New Zealand (Chiswell, 2011). At our non-stratified stations, we observed relatively low surface Chl *a* ($0.7 \pm 0.3\,mg\,Chl\,a\,m^{-3}$) and up to 70 % of the

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Chl *a* was below the euphotic zone. Comparable observations were reported during late winter-early spring by Backhaus et al. (2003) for the Icelandic Basin. Inevitably, the occurrence of phytoplankton below the euphotic zone will slow down growth rates of the phytoplankton standing stock. However, productivity estimates for non-stratified stations in the present study were not significantly different compared to the stratified mesotrophic stations in spring and summer.

Increased surface Chl *a* in response to stratification of the water column represents the classical view of the spring bloom at mid and higher latitudes (Sverdrup, 1953). However, the present study suggests that the pre-bloom conditions, with minimal stratification in the upper 200 m (beginning of May, latitude 49–62° N), were more productive in terms of depth integrated Chl *a* (129 ± 32 mg Chl *a* m^{-2}) compared with surface blooms at mid-latitudes in spring (44–45° N, up to 112 ± 13 mg Chl *a* m^{-2}) and surface blooms at higher latitudes in summer (59–62° N: 42 ± 13 mg Chl *a* m^{-2}). This also illustrates that surface Chl *a* concentration can be a poor indicator of phytoplankton standing stock, since surface Chl *a* was lower during pre-bloom conditions (0.7 ± 0.3 mg Chl *a* m^{-3}) compared with spring (1.8 ± 0.3 mg Chl *a* m^{-3}) and summer (1.3 ± 0.3 mg Chl *a* m^{-3}) blooms. It was earlier observed that phytoplankton growth increased with increasing light in winter and early spring in the absence of stratification (Behrenfeld, 2010). This increase in Chl *a* can be masked by the diluting effect of deep convective and wind induced vertical mixing as proposed by Boss and Behrenfeld (2010).

Relationships between the contribution of taxonomic groups to productivity and SST were different for stratified and non-stratified stations. In the latter stations, productivity of group 3 (prasinophytes, cryptophytes) was inversely correlated with SST (7–12 °C), whereas group 4 (haptophytes) and 5 (diatoms) were positively correlated with SST. This suggested that temperature constrains productivity of the latter groups within this temperature range. In the present study, the nutrient-rich conditions associated with non-stratified stations supported significant diatom productivity (up to 60 %) above SST of 8 °C. After stratification, the relatively large and heavy diatoms typically become

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nutrient (Si) limited and sink out of the euphotic zone (Alkire et al., 2012). Furthermore, contraction of the mixed layer and the euphotic zone due to stratification traps a large amount of the phytoplankton in the dark ocean (Backhaus et al., 2003). Estimated class-specific productivity from SeaWiFS observations showed that strongest productivity anomalies occurred in early spring in the temperate and sub-polar North Atlantic, coinciding with diatom productivity (Uitz et al., 2010). Therefore, it can be expected that differences in annual primary production are for a large part caused by variability in diatom productivity.

The nutrient concentrations in the euphotic zone of stratified stations were on average five times lower compared to those of the non-stratified stations. Furthermore, low N : P ratios indicated mostly N-limitation in the upper euphotic zone (0–50 m) of stratified stations. This is consistent with factorial nutrient addition experiments in the oligotrophic North Atlantic that have identified N as the primary limiting nutrient (Davey et al., 2008; Moore et al., 2008). Therefore, the ability to compete for nutrients can be expected to be an important driver of changes in phytoplankton composition in the stratified North Atlantic. In the present study, changes in phytoplankton groups that contributed to primary production were observed along the latitudinal gradient in N, $P_{0–125\,m}$. Overall, the haptophyte pigment signature was dominant in spring and summer. Moreover, an inverse correlation was observed for the contribution of group 4 (dominated by haptophytes) and SST, whereas there was a positive correlation between SST and group 1 and 2 (cyanobacteria) in stratified stations. This suggests that increased SST will increase the contribution of less productive species, such as *Prochlorococcus*, at the expense of more productive species, such as haptophytes, at low and mid-latitudes. Furthermore, the present study also suggests that haptophytes succeed diatoms after stratification in spring at higher latitudes. Therefore, earlier stratification in spring would prolong the growth season of haptophytes at higher latitudes in the North Atlantic Ocean.

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4.3 Productivity modeling and assumptions

Reported productivity in the North Atlantic subtropical gyre varied between 100–350 mg C m^{-2} d^{-1} (Morel et al., 1996; Maraňón et al., 2000, 2003). Claustre et al. (2005) estimated daily primary production rates of 939 ± 223 and 393 ± 80 mg C m^{-2} d^{-1} for spring and summer, respectively, in the North Atlantic between 39 to 45° N, which agrees well with our estimates for this region. In the present study, N and P were not depleted in summer in the upper euphotic zone (0–50 m) of mesotrophic stations. Therefore, wind events can temporarily raise nutrient concentration in the mixed layer in summer, making nutrient limitation less evident in these stations. At mesotrophic stations, reported productivity values do not show clear differences between summer and spring (500–2000 mg C m^{-2} d^{-1}, Bury et al., 2001; Weeks et al., 1993) and compared well to our estimates.

In the present study, several assumptions were made to model primary production from field measurements. Firstly, we applied a linear temperature correction to total modeled productivity. Typically, growth shows temperature dependence in specific oceanic phytoplankton species (Moore et al., 1995; Kulk et al., 2012). Eppley (1972) suggested that the temperature dependence of growth is exponential, with growth increasing with increasing temperature. However, compiled carbon fixation data and lab experiments suggest a linear response of productivity within the temperature range of 13–23 °C (Behrenfeld et al., 1997; Montagnes and Franklin, 2001). Secondly, the model assumes that nutrient availability is reflected by differences in phytoplankton biomass and composition. This is in line with the observation that nutrient availability does not influence Chl *a* specific net primary production in *Dunaliella Tertiolecta* (Halsey, 2011). Finally, the model assumes a sinusoidal irradiance distribution during the day and therefore does not include effects of cloud cover and/or vertical mixing. However, Kulk et al. (2011) showed that there were no significant effects of a dynamic irradiance regime on phytoplankton carbon fixation characteristics (under nutrient replete conditions). Validation of the productivity calculations with field productivity estimates was

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not possible in the present study. Therefore, the current productivity estimates should be viewed as potential productivity estimates, rather than actual measurements. Overall, this study showed that the model approach can expand the use of phytoplankton pigments and provided useful insight in group specific productivity.

5 Conclusions

Our results show an inverse relationship between phytoplankton productivity and biomass with SST for the stratified North Atlantic Ocean with SST between 13 and 23 °C. Furthermore, increasing SST was associated with a change in phytoplankton species composition from haptophytes to cyanobacteria at mid and low latitudes. Since increases in North Atlantic SST are expected for the coming decades, we expect the phytoplankton to respond accordingly. Due to the exponential decline of Chl *a* and the linear decline in productivity with increasing SST, responses to a future temperature rise are more likely to be observed in Chl *a* than in productivity.

Increasing SST has been suggested to mediate different effects on phytoplankton biomass in subtropical (less productivity) and sub-polar regions (increased productivity due to a longer growth season) in the North Atlantic. However, our data showed highest depth integrated Chl *a* at higher latitude non-stratified stations in spring, suggesting that phytoplankton blooms can start under minimal stratification. This indicated that possible earlier onset of stratification (and surface blooming) would not necessarily result in a longer and more productive season. In contrast, delayed stratification may prolong the growth season of diatoms, the most productive phytoplankton group that contributes significantly to carbon export into the deep ocean, whereas earlier stratification may expand the contribution of haptophytes at the expense of diatoms.

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Table 1. Spearman rank order correlation coefficients of sea surface temperature (SST) and density differences in the upper 200 m (density), between nitrate (N) and inorganic phosphate (P) concentration in the potential euphotic zone (0–125 m). Data are shown for spring and summer cruises ($n = 32$) and for stratified ($n = 52$) and non-stratified ($n = 12$) stations from both cruises combined. Significant correlations are bold.

	Spring		Summer		Stratified		Non-stratified	
	SST	density	SST	density	SST	density	SST	density
$N_{0–125\,m}$	**−0.99**	**−0.75**	**−0.99**	**−0.87**	**−0.84**	−0.10	**−0.91**	−0.24
$P_{0–125\,m}$	**−0.98**	**−0.74**	**−0.99**	**−0.86**	**−0.84**	−0.10	**−0.97**	−0.35

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Table 2. Spearman rank order correlation coefficients of nitrate (N) and inorganic phosphate (P) concentration in the potential euphotic zone (0–125 m), sea surface temperature (SST), and density differences in the upper 200 m (density) versus phytoplankton biomass and productivity. Surface chlorophyll *a* (Chl *a*), Chl *a* in the upper euphotic zone (0–50 m), and Chl *a* integrated from the surface to 200–410 m (Chl a_t) were used as biomass indicators. Productivity in the upper euphotic zone ($PP_{0–50\,m}$) and productivity in the euphotic zone (PP_{Zeu}) were used as indicators for productivity. Data are shown for spring and summer cruises (n = 32), and for the stratified stations from both cruises (n = 52). Significant correlations are expressed in bold.

		$N_{(0–125\,m)}$	$P_{(0–125\,m)}$	SST	density
Spring	surface Chl *a*	**0.59**	**0.59**	**−0.61**	−0.34
n = 32	Chl $a_{0–50\,m}$	0.41	0.40	−0.41	−0.05
	Chl a_t	**0.89**	**0.89**	**−0.91**	**−0.72**
	$PP_{0–50\,m}$	0.16	0.17	−0.20	0.06
	PP_{Zeu}	0.22	0.23	−0.24	0.09
Summer	surface Chl *a*	**0.95**	**0.95**	**−0.96**	**−0.86**
n = 32	Chl $a_{0–50\,m}$	**0.92**	**0.92**	**−0.92**	**−0.83**
	Chl a_t	**0.66**	**0.66**	**−0.66**	**−0.51**
	$PP_{0–50\,m}$	**0.87**	**0.87**	**−0.85**	**−0.79**
	PP_{Zeu}	**0.87**	**0.84**	**−0.83**	**−0.77**
Stratified	surface Chl *a*	**0.69**	**0.69**	**−0.91**	**−0.62**
n = 52	Chl $a_{0–50\,m}$	**0.72**	**0.72**	**−0.88**	**−0.60**
	Chl a_t	0.17	0.17	**−0.56**	**−0.79**
	$PP_{0–50\,m}$	**0.70**	**0.71**	**−0.84**	**−0.52**
	PP_{Zeu}	**0.64**	**0.65**	**−0.79**	**−0.52**

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Table 3. Spearman rank order correlation coefficients of estimated contribution to primary production of group 1 (*Prochlorococcus*), group 2 (*Synechococcus*), group 1 and 2 combined (cyanobacteria), group 3 (prasinophytes, cryptophytes and pelagophytes), group 4 (haptophytes and dinophytes), and group 5 (diatoms) between nitrate ($N_{0–125\,m}$) and inorganic phosphate ($P_{0–125\,m}$) concentration in the potential euphotic zone, sea surface temperature (SST), and density differences in the upper 200 m (density). Data are shown for stratified (n = 52) and non-stratified (n = 12) stations from spring and summer cruises.

	$N_{0–125\,m}$	$P_{0–125\,m}$	SST	density
Stratified stations (n = 52)				
Group 1 (*Prochlorococcus*)	**−0.81**	**−0.80**	**0.86**	0.46
Group 2 (*Synechococcus*)	**−0.62**	**−0.63**	**0.69**	0.43
Group1, 2 (Cyanobacteria)	**−0.78**	**−0.78**	**0.80**	0.40
Group 3 (Prasinophytes)	0.16	−0.18	0.01	0.19
Group 4 (Haptophytes)	**0.74**	**0.74**	**−0.72**	−0.29
Group 5 (Diatoms)	−0.25	−0.25	0.01	−0.30
Non-stratified stations (n = 12)				
Group 3 (Prasinophytes)	**0.90**	**0.87**	**−0.79**	−0.22
Group 4 (Haptophytes)	**−0.76**	**−0.75**	**0.78**	0.35
Group 5 (Diatoms)	**−0.73**	**−0.73**	**0.59**	0.01

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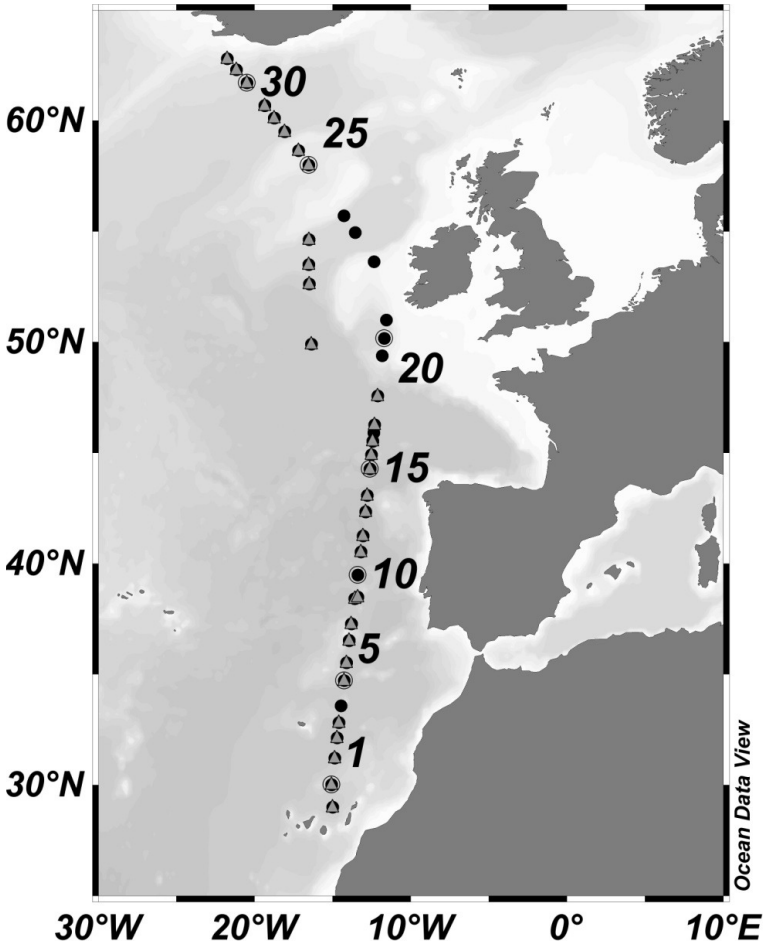

Fig. 1. Sample locations of the spring (2011, triangles) summer and (2009, circles) Stratiphyt cruises. The numbers represent the station numbers.

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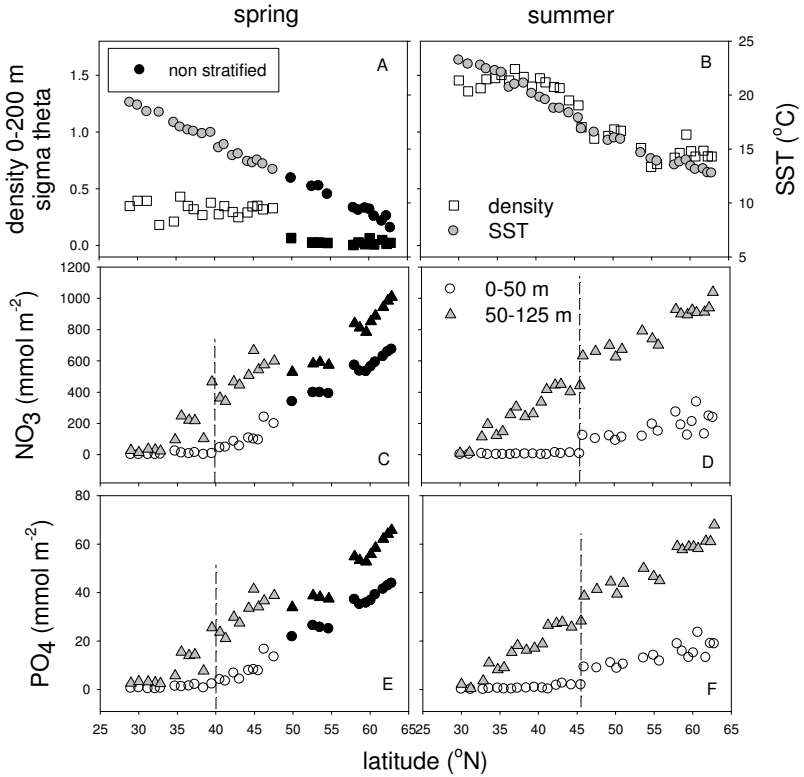

Fig. 2. Latitudinal changes in abiotic data from the spring **(A, C, E)** and summer **(B, D, F)** cruises. **(A)** density differences in the upper 200 m and sea surface temperature (SST, secondary y-axis). **(B)** Depth integrated nitrate (NO_3) concentration in the upper (0–50 m) and lower (50–125 m) euphotic zone. **(C)** Depth integrated inorganic phosphate (PO_4) concentration in the upper (0–50 m) and lower (50–125 m) euphotic zone. Black symbols represent data from non-stratified stations. The vertical lines indicate the transition from oligotrophic (left) to mesotrophic (right) conditions.

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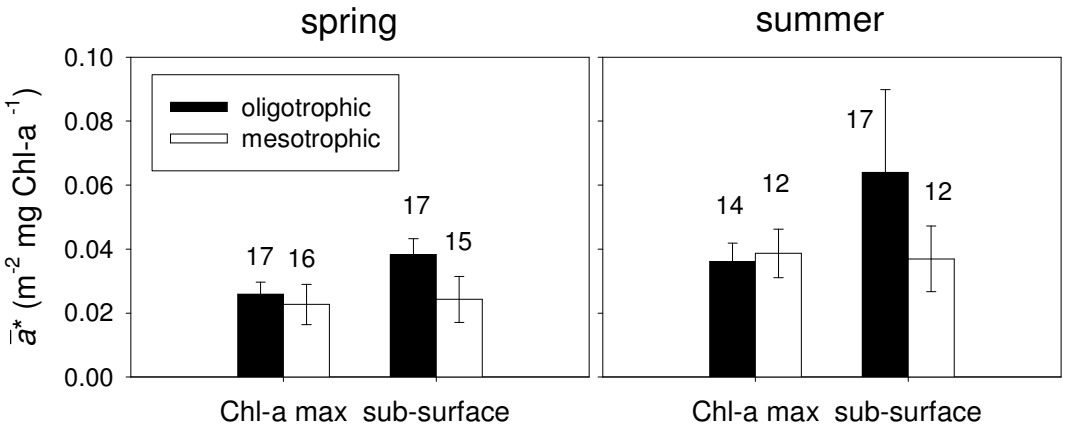

Fig. 3. The spectrally weighted mean specific absorption coefficient ($\overline{a}^*$) for the chlorophyll maximum (Chl a_{max}) and sub-surface samples for oligotrophic and mesotrophic stations, obtained during the spring and summer cruises. The graphs show the average and standard deviation and the number of replicates is shown above the bars.

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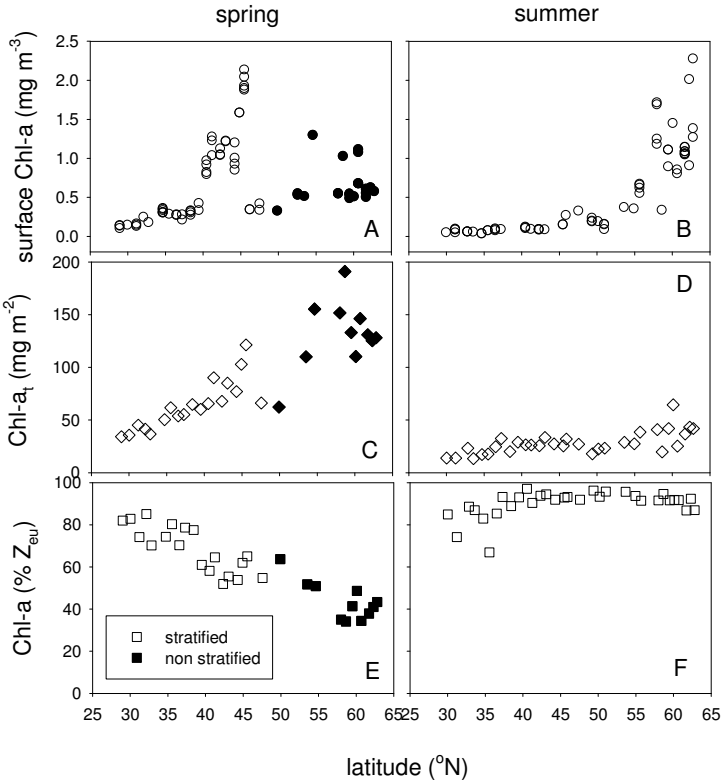

Fig. 4. Latitudinal changes in biomass (chlorophyll *a*) for the spring **(A, C, E)** and summer **(B, D, F)** cruise. **(A, B)** Surface Chl *a* (samples from 10–20 m) determined by HPLC. **(C, D)** Depth integrated Chl *a* (Chl a_t) as determined from HPLC calibrated CTD fluorescence profiles from the surface to 200–410 m. **(E, F)** Percentage of Chl *a* in the euphotic zone (0.1 % light depth). Black symbols represent data from non-stratified stations.

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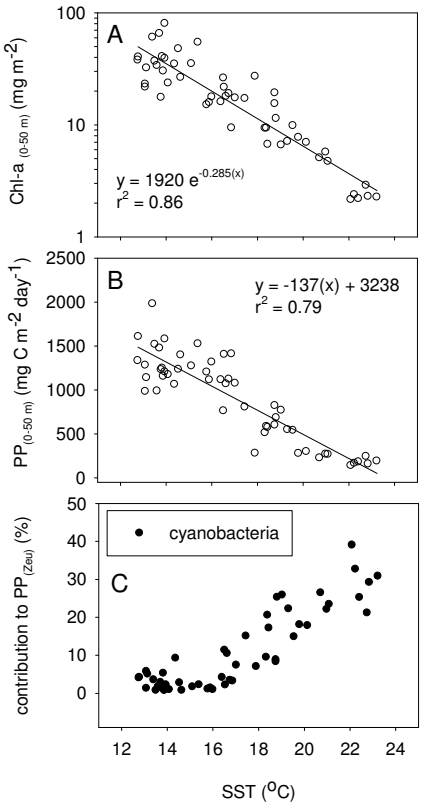

Fig. 5. (A) Relationship between depth integrated (0–50 m) Chl *a* (Chl $a_{0-50\,m}$) and sea surface temperature (SST) for stratified stations from the summer and spring cruise ($n = 52$). Note the exponential scale on the y-axis. **(B)** Relationship between depth integrated (0–50 m) daily productivity ($PP_{0-50\,m}$) and SST for stratified stations from the spring and summer cruises ($n = 52$). **(C)** Estimated productivity by cyanobacteria (group 1 and 2 combined) versus SST for stratified stations from the spring and summer cruises ($n = 52$).

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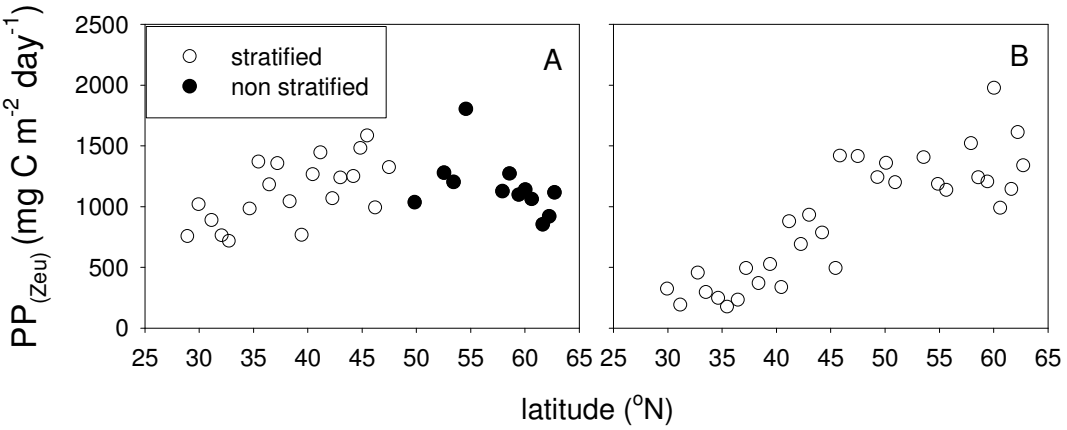

Fig. 6. Latitudinal changes in daily primary production in the euphotic zone (PP_{Zeu}) during the spring **(A)** and summer **(B)** cruise. Productivity was estimated from in situ phytoplankton biomass and composition, light, light attenuation, and temperature using a bio-optical model (see method for details). Black symbols represent data from non-stratified stations.

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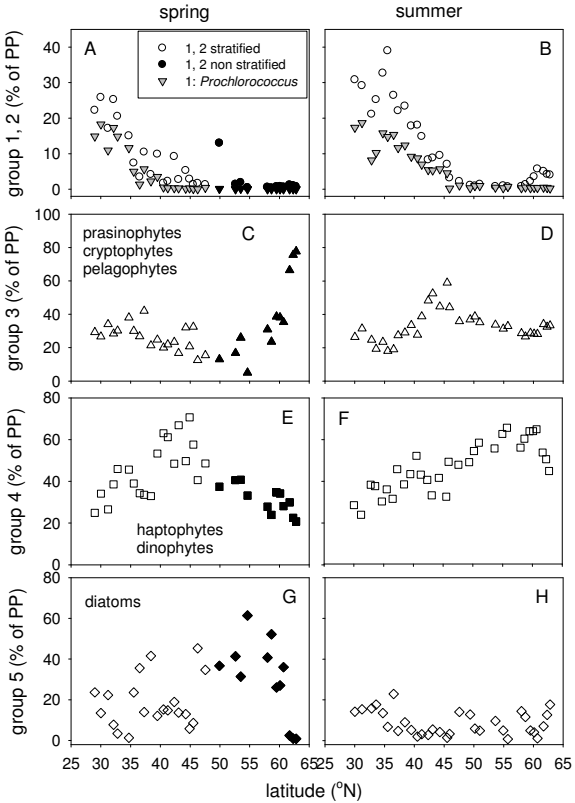

Fig. 7. Contributions to daily primary production in the euphotic zone of **(A, B)** group 1 (*Prochlorococcus*) and cyanobacteria (group 1 + 2); **(C, D)** group 3 (prasinophytes, cryptophytes, pelagophytes); **(E, F)** group 4 (haptophytes, dinophytes); **(G, H)** group 5 (diatoms) for the spring **(A, C, E, G)** and summer **(B, D, F, H)** and cruises. Black symbols represent data from non-stratified stations.

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