

Key Points:

- Picoplankton dominated the chlorophyll pool during peak spring bloom period
- Pigment data indicated haptophyte dominance of the phytoplankton community
- Chemotaxonomy and flow imaging microscopy indicated *Phaeocystis* sp. presence

Supporting Information:

Supporting Information may be found in the online version of this article.

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Phaeocystis Dominance of a Large-Scale Productivity Anomaly in the Northeast Atlantic Ocean During Spring 2024

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Abstract Changes to the North Atlantic spring bloom phytoplankton community structure are expected in response to regional warming trends. In 2024 an extensive body of low chlorophyll water, covering approximately 720,000 km² in area, dominated the Northeast Atlantic during the peak of the spring bloom period. Picoplankton (<2 μm) and small nanoplankton (2–10 μm) size fractions together accounted for ~90% of total chlorophyll-*a* implying a significant contribution by smaller phytoplankton cells to net primary production. Flow imaging microscopy of the phytoplankton community confirmed the dominance of smaller phytoplankton (<18 μm), whilst chemical taxonomy of phytoplankton pigments indicated the widespread presence of haptophyte species, most likely *Phaeocystis* sp. These results contrast markedly with recent descriptions of the North Atlantic spring bloom community structure which report larger nano- and micro-phytoplankton species dominance. However, these new results are consistent with model predictions showing a shift toward smaller sized phytoplankton species as water temperatures rise and with the appearance of increasingly favorable conditions for *Phaeocystis*. Our results further suggest that large scale regionally significant changes to the phytoplankton community can rapidly emerge in response to ocean warming which, in the case of a *Phaeocystis* dominated community, will likely have implications for carbon export fluxes due to changes in vertical flux attenuation efficiency.

Plain Language Summary The species of phytoplankton present at a point in space and time can have significant implications for productivity rates, carbon biomass, and whether newly produced biomass will reach the ocean interior thereby contributing to biological carbon export. It is therefore important to regularly reassess the community of species present during field campaigns. During the 2024 North Atlantic spring bloom we observed an unexpected shift in the phytoplankton community from larger toward smaller species. Results were consistent between different methodologies and indicated the widespread presence of the genus *Phaeocystis*, a member of the Haptophyte division of marine algae. Members of this genus are notable for their ability to form large colonies but also for the reduced likelihood of significant carbon fluxes to depth. The phytoplankton community sampled in 2024 was notably different to that reported in other recent studies from the same region, but consistent with model predictions that reveal the appearance of increasingly favorable conditions for *Phaeocystis* in the North Atlantic. Our results may therefore be indicative of future ocean conditions.

1. Introduction

The North Atlantic Ocean is estimated to produce a total annual carbon export flux of between 0.55 and 1.94 Gt C yr⁻¹, approximately 5%–18% of the total global carbon export flux (~11 Gt C yr⁻¹), with around half of North Atlantic flux derived from the spring bloom (Sanders et al., 2014). Interannual or interdecadal variability in the timing and magnitude of the spring bloom can therefore have significant impacts on local ecosystems, on trophic energy flows, and on the strength of carbon export fluxes to the ocean interior (Asch, 2019; Friedland et al., 2016, 2024; Kelly et al., 2025). In addition to the fundamental environmental controls of light, nutrients, and temperature on the magnitude and duration of the spring bloom, changes to the phytoplankton community structure may also directly impact carbon export potential. For the Northeast Atlantic Ocean both interannual and interdecadal variability in upper ocean pelagic community structure have now been shown to impact the spring-bloom driven export flux reaching 3,000 m depth (Lampitt et al., 2023), suggesting that the export potential of this

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globally significant region can change, and will change, as phytoplankton communities themselves are altered by rising ocean temperatures.

The Northeast Atlantic phytoplankton community structure is already known to be susceptible to warming trends in the upper ocean with evidence that both species composition and cell size are changing (Beaugrand et al., 2009). It is therefore prudent to regularly assess the internal dynamics of the spring bloom community to gauge how unusual environmental conditions, or changes in community structure, impact productivity cycles or temporal trends (Asch, 2019; Clevenger et al., 2024; Friedland et al., 2016, 2024; Johnson et al., 2024; Kelly et al., 2025; Meyer et al., 2024). During 2024 an anomalous and spatially extensive region of weak productivity formed in the Northeast Atlantic Ocean during the peak spring bloom timeframe and persisted throughout the summer months (Painter et al., 2026). Characterized by low surface chlorophyll concentrations ($<0.3 \text{ mg L}^{-1}$), weak productivity ($<0.6 \text{ g C m}^{-2} \text{ d}^{-1}$) and low particulate concentrations this feature covered $\sim 721,000 \text{ km}^2$ at its largest extent and was tentatively linked to silicate limitation ($\text{NO}_3:\text{Si} > 4$), warmer than average winter conditions ($\sim 1^\circ\text{C}$ warmer than the 1991–2023 average) and a shallow convective mixing period (Painter et al., 2026). These conditions followed extraordinary heating of the wider North Atlantic throughout 2023 and 2024 (England et al., 2025; Terhaar et al., 2025). Notably, this same sector of the Northeast Atlantic appears in most climate model projections as a region that will see rapid and significant declines in net primary production over coming decades due to weakening nutrient delivery (Tagliabue et al., 2021), appears prominently as a region experiencing reduced light attenuation/increased light penetration (Davies & Smyth, 2025), and was impacted by thermal anomalies throughout 2023 and 2024 (Berthou et al., 2024; England et al., 2025; Jacobs et al., 2024). Such observations imply the Northeast Atlantic is sensitive to environmental change. In addition, the presence of a large-scale productivity anomaly raises the possibility that predicted changes to the productivity regime of the Northeast Atlantic region may emerge sooner than estimated (Kelly et al., 2025). Yet, whilst changes to surface chlorophyll fields can be remotely assessed, coincident changes to the phytoplankton community remain harder to infer. Here we present a detailed investigation of the phytoplankton community associated with this productivity anomaly and compare it with both recent investigations and typical descriptions of the spring bloom community and with projected community changes in a warmer ocean.

2. Methods

2.1. Hydrography and Water Sampling

Samples were collected between 26th May and 9th June 2024 within a 1 km radius around a nominal position of $48.98^\circ\text{N } 16.368^\circ\text{W}$ (approx. 800 km southwest of Lands End, UK; Figure 1), in support of the PAP-SO program (Hartman et al., 2021). The observations are presented and interpreted as a time-series of upper ocean conditions. Hydrographic data and water samples were collected across the euphotic zone from depths corresponding to irradiance horizons of 97%, 55%, 33%, 14%, 4.5% and 1% of surface PAR (photosynthetically active radiation) on pre-dawn casts using a Seabird 9/11+ CTD and niskin bottle rosette. The euphotic layer, defined as the layer between the sea surface and the depth at which incident irradiance was 1% of surface irradiance, was calculated from a regression of natural log normalized irradiance intensity (PAR) against depth (Kirk, 2010). The mixed layer was calculated based on a density difference of 0.01 kg m^{-3} relative to 10 m (Thomson & Fine, 2003). Seawater was collected directly from the niskin bottles into clean 10 L carboys, which were covered with dark screens whilst being processed. A total of 13 daily profiles were sampled with days 1–6 located within the southern border of the low chlorophyll feature shown in Figure 1. In contrast days 7–13 were located outside of this feature.

2.2. Total and Size-Fractionated Chlorophyll-a

Chlorophyll concentrations measured via fluorometry were obtained for both natural and size-fractionated water samples. Total chlorophyll concentrations (Tchl_a) were obtained via filtration of 250 mL of water onto a 25 mm GF/F grade glass fiber filter. Pigment extraction was achieved via addition of 6 mL of 90% acetone with extraction taking place in the dark at 4°C for 18–20 hr. Extracted pigment fluorescence was measured on a Turner Triloby bench top fluorometer calibrated with a Chl-a standard (Sigma-Aldrich, UK).

Three chlorophyll size fractions were measured using polycarbonate filters with pore size of $2 \mu\text{m}$, $10 \mu\text{m}$ and $20 \mu\text{m}$. For each size fraction 250 mL of seawater was filtered and extracted as described above. The concentration in each fraction ($<2 \mu\text{m}$, $2\text{--}10 \mu\text{m}$, $10\text{--}20 \mu\text{m}$ and $>20 \mu\text{m}$) was subsequently estimated by difference.

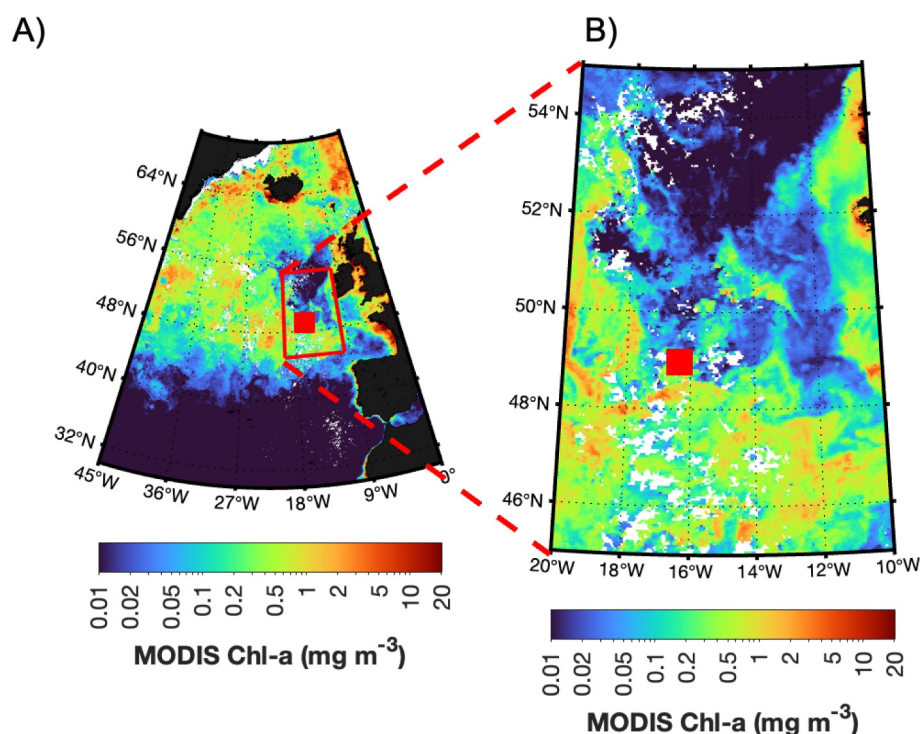


Figure 1. Modis Aqua monthly composite of surface chlorophyll distribution for June 2024 across (a) the wider North Atlantic Ocean with the location of sampling indicated by the small red square and (b) the subregion of the Northeast Atlantic indicated by the red polygon in panel (a). Image color scale has been adjusted to better highlight the spatial extent and anomalous nature of the region of low chlorophyll identified to the west of Ireland.

Depth integrated total and size-fractionated chlorophyll concentrations were obtained via trapezoidal integration. The final size classes conform to the size distributions of Sieburth et al. (1978) namely picoplankton (<2 μm), small nanoplankton (2–10 μm), large nanoplankton (10–20 μm) and microplankton (>20 μm).

2.3. Phytoplankton Pigments

A total of 24 phytoplankton pigments were quantified via High Performance Liquid Chromatography (HPLC) analysis from preserved samples collected at sea. At each sampled depth up to 2 L of seawater was filtered onto a pre-combusted (450°C, >6 hr) glass fiber filter (Whatman GF/F). Filters were placed inside tinfoil envelopes, flash frozen in liquid nitrogen (−196°C), and stored in a −80°C freezer until analysis. Samples were analyzed by the French Naval Hydrographic and Oceanography Service (SHOM; Brest, France) using a reverse-phase C8 column and the method of Van Heukelem and Thomas (2001). Quantified pigments included chlorophyll c3 (chl c3), chlorophyll c2+c1 (chl c2c1), Mg-2,4-divinyl-pheoporphyryin-a5-monomethyl-ester (MgDVP), peridinin (per), 19-butanoyloxyfucoxanthin (19'-but), fucoxanthin (fuco), neoxanthin (neox), prasinoxanthin (pras), violaxanthin (viol), 19-hexanoyloxyfucoxanthin (19'-hex), astaxanthin (asta), diadinoxanthin (ddx), dinoxanthin (dino), alloxanthin (allo), diatoxanthin (dtx), zeaxanthin (zea), lutein (lut), chlorophyll b + divinyl chlorophyll b (chl-b), $\alpha + \beta$ carotene (caro), chlorophyllide a (childA), pheophorbide a (phbA), divinyl chlorophyll a (DVa), chlorophyll a (chl-a), and pheophytin a (phtA). HPLC calibration was by both an internal vitamin E tracer and external chlorophyll and carotenoid standards (DHI Laboratory; Hørsholm, Denmark). The mean limit of quantification for individual pigments was $1.05 \times 10^{-4} \pm 3.65 \times 10^{-4} \mu\text{g L}^{-1}$.

Pigment data were interpreted using the size-class based Diagnostic Pigment Analysis (DPA) method described by Uitz et al. (2006), which utilizes selected pigments to establish proportional representation by micro-, nano- and picoplankton size classes within the total diagnostic pigment pool (weighted sum of per, 19'-but, fuco, 19'-hex, allo, zea and chl-b). Due to a significant inconsistency between the size-fractionated chlorophyll observations and the DPA results obtained with this model we also explored a North Atlantic variant of the DPA methodology described by Brewin et al. (2017), which uses modified pigment weighting factors based on North

Atlantic observations and apportioned part of the 19'-hex pigment to the picoplankton pool under low chlorophyll concentrations. We also used the algal class model described by Barlow et al. (2014) to further explore the data.

2.3.1. Chemotaxonomic (CHEMTAX) Analysis

Algal class contributions to the total chlorophyll-*a* pool were estimated using CHEMTAX v1.95 (Mackey et al., 1996; Wright, 2017). 15 pigments (chl-*c*3, chl *c*2 + *c*1, per, 19'-but, fuco, 19'-hex, viol, allo, zeax, pras, chl-*b*, DVA, lut, neox and chl-*a*) were used to distinguish 9 taxonomic groups (chlorophytes, cryptophytes, diatoms, dinoflagellates, haptophytes, pelagophytes, prasinophytes, *Prochlorococcus* and *Synechococcus*). The initial input matrix of pigment ratios and weights was built using data from Higgins et al. (2011), with two groups of Haptophytes defined representing a *Phaeocystis*-like group (Hapto-8) and a *Gephyrocapsa huxleyi*-like group (Hapto-6) (Higgins et al., 2011; Jeffrey et al., 2011; Zapata et al., 2004). CHEMTAX analyses were performed for the whole euphotic zone using all samples, and again separately for the mixed layer, and the lower euphotic layer beneath the mixed layer, using the relevant subset of samples due to reported vertical distribution patterns amongst phytoplankton species (Mojica et al., 2015; Painter et al., 2016; van de Poll et al., 2013). In keeping with previous studies from these waters (e.g., van de Poll et al., 2013), no corrections were applied to the pigment ratios to account for photo-acclimation, a decision supported by the near constant proportions of photoprotective and photosynthetic carotenoids throughout the euphotic zone (which averaged $16 \pm 4\%$ and $84 \pm 4\%$ respectively).

2.4. Flowcam Analysis of Phytoplankton Community

Seawater samples (100 mL) were collected at the 6 sampled depths across the euphotic zone on all pre-dawn CTD casts and carefully poured into amber glass bottles inoculated with 2 mL of acidic Lugol's solution (2% final concentration) as preservative. Upon return to shore samples from a selected subset of CTD casts with ~1-4-day intervals (29/5/2024, 30/5/2024, 2/6/2024, 3/6/2024, 6/6/2024 and 9/6/2024; days 4, 5, 8, 9, 12, and 13) were analyzed via a FlowCam 8,000 imaging microscope (Yokogawa Fluid Imaging technologies) fitted with a 10X objective lens, a FOV100 flow cell and a 5 mL syringe with a quoted particle size resolution of 2–100 μm , though in practice a higher minimum of 10–20 μm is more typical (Alvarez et al., 2014; Camoying & Yniguez, 2016; Jakobsen & Carstensen, 2011; Owen et al., 2022). Samples were settled for >12 hr before the upper 50 mL of seawater was removed, thus ensuring a 2X concentration of samples. The remaining 50 mL sample was gently mixed before 4 mL of sample was transferred to the FlowCam and cells and particles imaged using Visual-Spreadsheet software (version 6.0) in auto-image mode at a rate of 0.15 mL min^{-1} , auto-image rate of 20 and estimated efficiency of 63%. The analysis was configured to stop after processing of the full volume. FlowCam was autofocused with a 15 μm microbead suspension (Duke Standards™) followed by a manual focus with a plankton sample. Particles with an equivalent spherical diameter <10 μm were ignored and not imaged.

2.4.1. Taxonomic Identification

The FlowCam raw images were exported and processed with the ZooProcess software before being imported into the EcoTaxa web platform (<https://ecotaxa.obs-vlfr.fr>) for machine-assisted classification. Images were cleaned to remove blanks, artifacts, duplicates, and detritus before being classified into 8 categories. Image recognition algorithms were used in EcoTaxa to predict categories and 86% of the total images were manually validated or corrected, and these data sets are presented here. Due to the resolution of the FlowCam the smallest organisms (~10–18 μm) were not classified due to poor precision so were grouped into a <18 μm category. The final categories included pennate diatoms, centric diatoms, dinoflagellates, flagellates, ciliates, *Phaeocystis*, Cryptophyta, *Dictyocha* and small (<18 μm) unidentified cells.

The percentage of relative abundance of images per group was integrated over the euphotic depth for each day.

2.5. Coccolithophore Community

Following completion of the primary sampling effort, and during transit away from the sampling site and back toward the NW European Shelf, small volume filtration was undertaken to collect surface water samples ($n = 10$) for identification of the coccolithophore community. Water samples (500 mL) were collected from the ship's underway seawater supply and filtered onto 0.4 μm 25 mm polycarbonate filters. Filtered volumes ranged from 285 to 500 mL due to rapid clogging of filters. After filtration filters were washed with borax buffered ultrapure

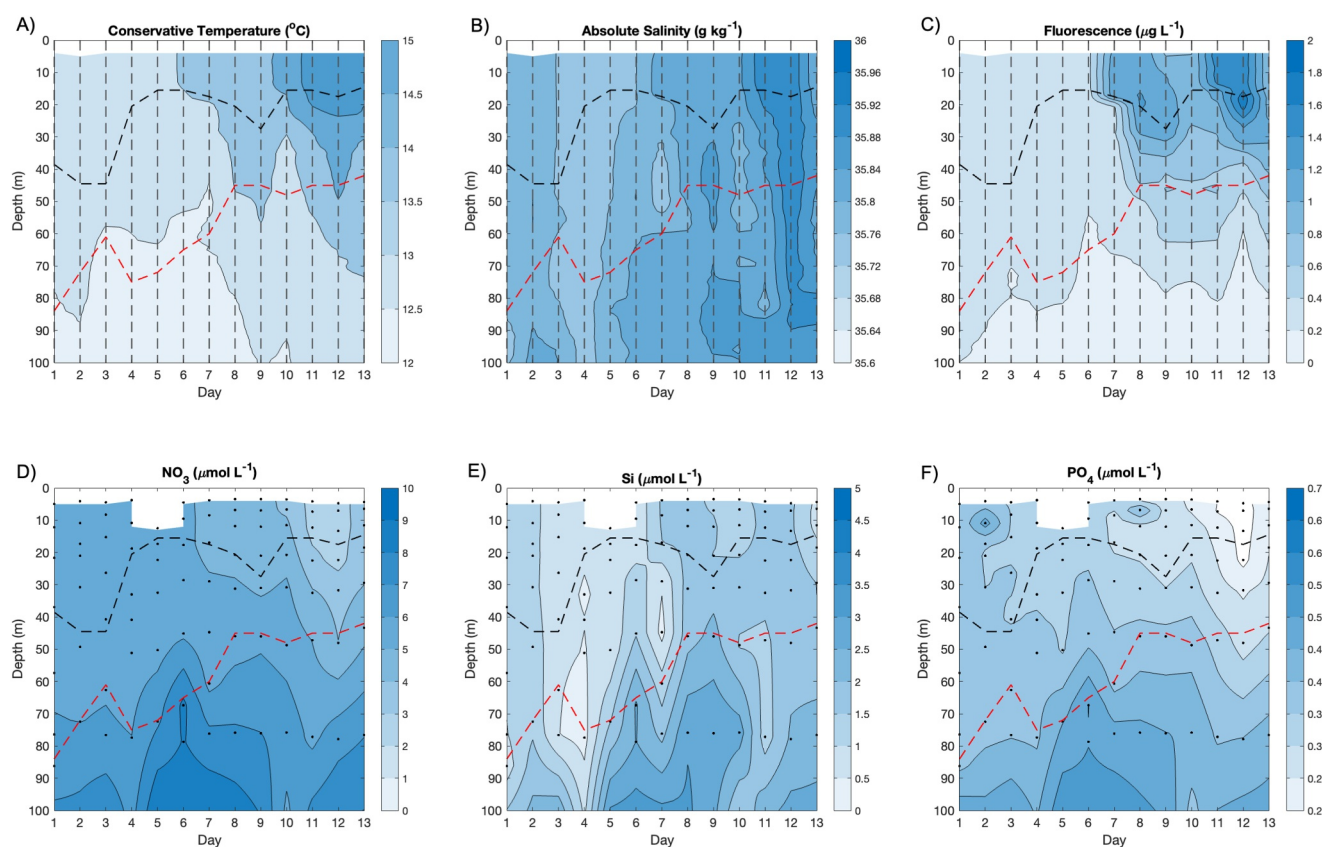


Figure 2. Upper ocean environmental conditions in the Northeast Atlantic during late May–early June 2024 including (a) temperature, (b) salinity, (c) chlorophyll fluorescence, (d) nitrate, (e) silicate and (f) phosphate concentrations. The surface mixed layer (Zmld) is indicated by the black dashed line and the euphotic zone (Zeu) by the red dashed line. The euphotic zone represents 1% of surface PAR irradiance.

water (Milli-Q purification system), placed into individual petrislide trays and oven dried over night at 40°C and then stored. In the laboratory, a subsection of each filter approximately 0.5 × 0.5 cm in size was subsequently mounted on to an aluminum stub and sputter coated with gold before being imaged using a Leo 1450VP scanning electron microscope (Carl-Zeiss, Germany), with x5000 magnification. An area of approximately 1 mm² was imaged producing 225 images in a 15 × 15 grid for each filter. Each individual image was manually inspected and loose coccoliths and complete coccospheres counted and identified using the taxonomic keys of Young et al. (2003) and Cros and Fortuno (2002). Counts were converted to per liter equivalents using the ratio between filter area imaged and total filter area used, an approximate ratio of 311:1.

3. Results

3.1. Environmental Conditions

Surface hydrographic conditions changed from relatively cooler and fresher waters (~12.7°C; ~35.76 g kg⁻¹), to warmer and more saline waters (~14.2°C; 35.91 g kg⁻¹), over the observation period. These changes were coincident with an increase in chlorophyll fluorescence from ~0.2 μg L⁻¹ to ~2 μg L⁻¹ (Figure 2). Both the euphotic zone and the mixed layer shoaled with time, with the euphotic zone reducing from 84 to 42 m, and the mixed layer reducing from a maximum of 45 m to a minimum of 15 m. Water column conditions may therefore be considered transitional lying somewhere between fully mixed winter and fully stratified summer conditions. Surface nutrient concentrations ranged from 2.64 to 6.06 μmol NO₃⁻ L⁻¹, 0.6–1.71 μmol Si L⁻¹, and 0.18–0.36 μmol PO₄³⁻ L⁻¹ (Figure 2). Surface NO₃⁻ and PO₄³⁻ concentrations decreased by ~50% over the observation period whilst surface Si concentrations were more variable and increased by ~30%. A notable transition in upper ocean conditions due to passage of a hydrographic front occurred between days 6 and 7, which

was accompanied with warmer temperatures (Figure 2a), increased chlorophyll fluorescence (Figure 2c), reductions in NO_3^- and PO_4^{3-} (Figures 2d and 2f) and an increase in Si (Figure 2e).

3.2. Fluorometric Chlorophyll

Total chlorophyll-a concentrations measured by fluorometry ranged from 0.09 to 1.35 $\mu\text{g L}^{-1}$. Averaged across the euphotic layer the cruise mean concentration was $0.6 \pm 0.38 \mu\text{g L}^{-1}$ (mean $\pm$ S.D.). Daily mean mixed layer total chlorophyll-a varied from 0.23 to 1.23 $\mu\text{g L}^{-1}$ with a cruise mean of $0.68 \pm 0.42 \mu\text{g L}^{-1}$. During days 1–6 the mean chlorophyll concentration in the mixed layer ranged from 0.23 to 0.34 $\mu\text{g L}^{-1}$ but this increased to 0.56–1.23 $\mu\text{g L}^{-1}$ between days 7–13. Chlorophyll concentrations for the $<2 \mu\text{m}$, 2–10 μm , 10–20 μm and $>20 \mu\text{m}$ size fractions ranged from 0.01 to 0.72 (mean $\pm$ S.D. of $0.36 \pm 0.21 \mu\text{g L}^{-1}$, 0.03 to 0.57 ($0.19 \pm 0.16 \mu\text{g L}^{-1}$); 0.01 to 0.12 ($0.02 \pm 0.03 \mu\text{g L}^{-1}$); and 0.01 to 0.14 ($0.02 \pm 0.02 \mu\text{g L}^{-1}$), respectively. Within the mixed layer sharp increases in the chlorophyll concentration of the $<2 \mu\text{m}$ and 2–10 μm size fractions were seen coincident with the increase in total chlorophyll from day 7 onwards (Figure S1 in Supporting Information S1). Mean chlorophyll concentrations in the $<2 \mu\text{m}$ fraction increased from ~ 0.1 to $\sim 0.7 \mu\text{g L}^{-1}$, whilst concentrations within the 2–10 μm fraction increased from ~ 0.07 to $\sim 0.5 \mu\text{g L}^{-1}$. No increase in chlorophyll concentration was observed in the larger 10–20 μm and $>20 \mu\text{m}$ size fractions over the same time period.

Size-fractionated chlorophyll measurements indicated that $61 \pm 11\%$ of Tchla was in the picoplankton size fraction ($<2 \mu\text{m}$), $30 \pm 10\%$ in the small nanoplankton (2–10 μm), $4 \pm 5\%$ in the larger nanoplankton (10–20 μm) and $5 \pm 5\%$ in the microplankton size class ($>20 \mu\text{m}$) (Figure 3). Only minor temporal changes in the average contribution by each size class were observed between days 1–6 and 7 to 13 with contributions changing from $63 \pm 6\%$ to $61 \pm 8\%$ in the picoplankton, from $26 \pm 6\%$ to $33 \pm 7\%$ in the smaller nanoplankton, from $5 \pm 6\%$ to $4 \pm 3\%$ in the larger nanoplankton and from $7 \pm 6\%$ to $2 \pm 2\%$ in the microplankton. Minor variations in the respective contribution by each size class to Tchla were evident with depth, particularly in the proportion of nanoplankton and microplankton size fractions, but this was less evident for the picoplankton size fraction which provided a more consistent contribution with depth. Microplankton, though variable in their contribution to Tchla across all sampled depths, tended to increase their contribution to Tchla with depth with contributions exceeding 5%, whilst smaller nanoplankton decreased their contribution from 20% to 40% of Tchla in surface waters to $<30\%$ at the base of the euphotic zone. The size fractionated results indicated a community dominated by picoplankton with the combined picoplankton plus small nanoplankton ($<10 \mu\text{m}$) size classes accounting for $\sim 90\%$ of Tchla.

Integrated chlorophyll concentrations for each size class are presented in Table 1 for both the euphotic zone and the mixed layer. For the euphotic layer, integrated Tchla concentrations ranged from 15.7 to 47.8 mg m^{-2} with the typical integrated concentration doubling abruptly from day 7 onwards. Integrated chlorophyll concentrations in the $<2 \mu\text{m}$ and 2–10 μm size fractions, which together accounted for $\sim 85\%$ – 95% of integrated Tchla, were between 8 to 59-fold and 3 to 40-fold greater than in the $>20 \mu\text{m}$ size fraction, respectively. Similar contributions were seen in the mixed layer where 85%–98% of integrated chlorophyll was contained in the $<10 \mu\text{m}$ size fraction and mixed layer integrated concentrations ranged from 2.3 to 23.9 mg m^{-2} .

3.3. Phytoplankton Pigments and Diagnostic Analyses

The total pigment concentration measured by HPLC ranged from 0.14 to 3.85 $\mu\text{g L}^{-1}$, a ~ 29 -fold variation. Concentration ranges for the major diagnostic pigments are shown in Table 2. Most pigments exhibited 20–40-fold variations in magnitude, comparable to that of the total pigment pool, except for prasinoxanthin (16-fold), violaxanthin (48-fold), and alloxanthin (144-fold). Divinyl chlorophyll-a concentrations were below detection during days 1–9, and only weakly present during days 10–13.

DPA results indicated an average size class distribution of $21 \pm 6\%$ microplankton, $69 \pm 9\%$ nanoplankton and $10 \pm 5\%$ picoplankton across individual samples (Figure 4a), or $21 \pm 4\%$, $69 \pm 6\%$ and $10 \pm 3\%$, respectively, for daily depth averaged estimates (Figure 4b). These size-class results contrast starkly with the pico-plankton dominance indicated by the size-fractionated chlorophyll measurements.

Examination of the percentage contribution by weighted diagnostic pigment to the summed total of all weighted diagnostic pigments showed that 19'-hex was dominant representing an average of $65 \pm 9\%$ of the diagnostic pigment pool within individual samples (Figure 4c). This major contribution by 19'-hex was consistent across all

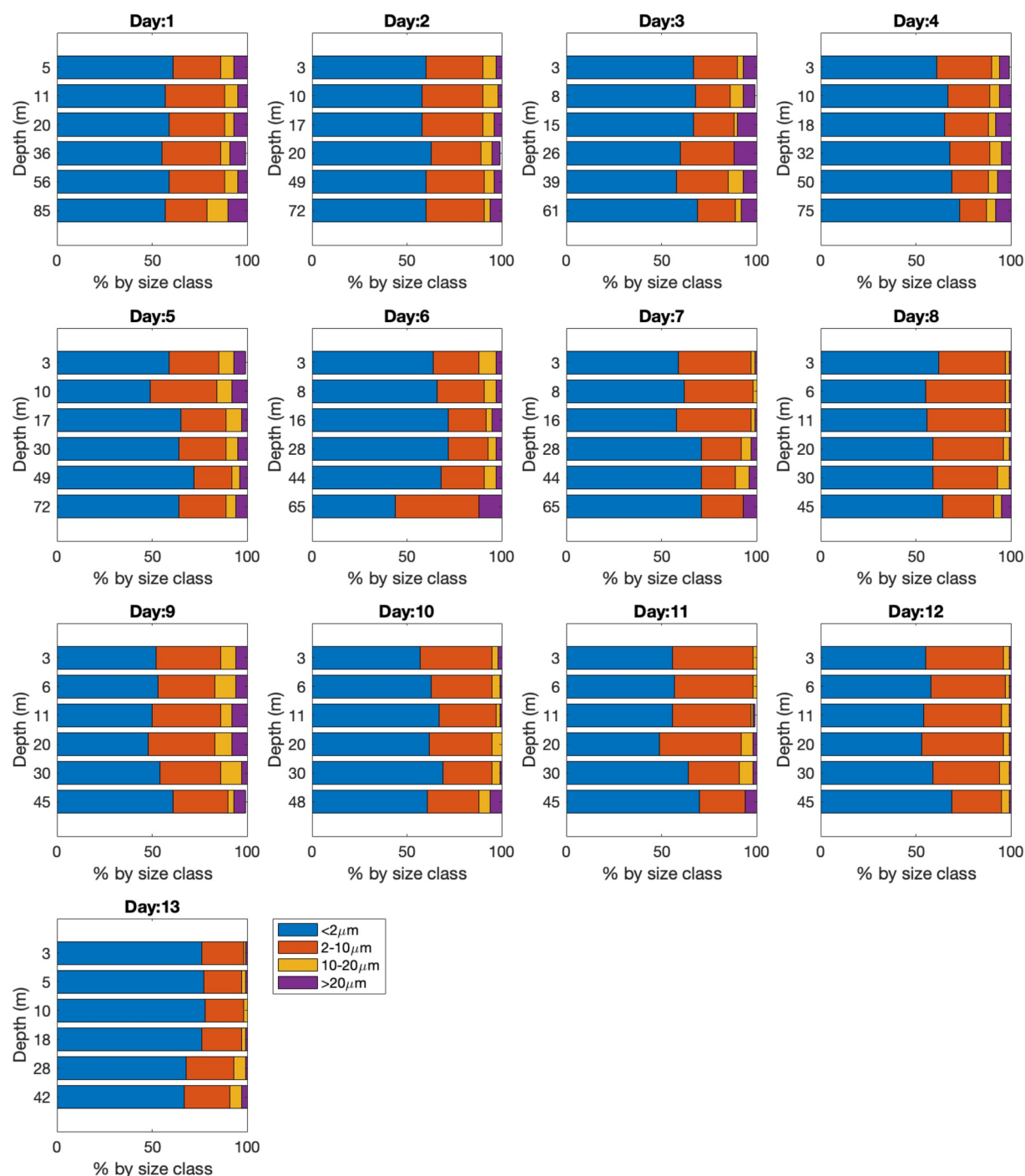


Figure 3. Daily profiles of size class contributions to total chlorophyll concentrations based on size-fractionated filtration and fluorometric measurement.

samples regardless of sampled depth (range 41%–82%) or sampling day (range 54%–74%; mean $65 \pm 6\%$; Figure 4d). In contrast the average per sample contribution by fucoxanthin, widely used as a diagnostic pigment for diatoms, was $18 \pm 6\%$ and implied a low diatom presence. All other diagnostic pigments represented $<7\%$ of the diagnostic pigment pool.

Application of the North Atlantic tuned version of the DPA methodology introduced by Brewin et al. (2015, 2017) to account for the presence of 19'-hex in both pico- and nanoplankton modified only slightly the daily depth averaged size-class contributions, with averages of $19 \pm 6\%$ microplankton, $67 \pm 9\%$ nanoplankton and $14 \pm 3\%$

Table 1
Euphotic Zone and Mixed Layer Integrated Total Chlorophyll and Size-Class Chlorophyll Concentrations

Day	Date (d/m/y)	Lat (°N)	Lon (°W)	Integration depth (m)	Total Chl-a (mg m ⁻²)	<2 μm fraction (mg m ⁻²)	2–10 μm fraction (mg m ⁻²)	10–20 μm fraction (mg m ⁻²)	>20 μm fraction (mg m ⁻²)
Euphotic zone									
1	26/5/24	48.9750	16.3583	85	19.7	11.4	5.5	1.3	1.4
2	27/5/24	48.9752	16.3580	72	21.6	13.0	6.5	1.2	0.9
3	28/5/24	48.9750	16.3581	61	18.8	11.9	4.5	1.0	1.5
4	29/5/24	48.9747	16.3583	75	21.0	14.2	4.3	1.0	1.4
5	30/5/24	48.9747	16.3582	72	20.8	13.6	5.0	1.2	1.0
6	31/5/24	48.9752	16.3571	65	15.7	10.6	3.7	0.7	0.7
7	01/6/24	48.9761	16.3562	60	33.6	21.2	10.9	0.8	0.7
8	02/6/24	48.9792	16.3615	45	43.0	25.3	15.6	1.5	0.6
9	03/6/24	48.9870	16.3607	45	46.8	24.2	15.6	4.0	2.9
10	04/6/24	48.9840	16.3589	48	36.9	23.7	11.0	1.5	0.7
11	05/6/24	48.9883	16.3649	45	38.3	22.0	14.2	1.3	0.7
12	06/6/24	48.9815	16.3651	45	47.8	27.2	18.4	1.9	0.5
13	09/6/24	48.9799	16.3805	42	29.1	20.9	6.6	1.1	0.4
Mixed layer									
1	–	–	–	39	8.4	4.9	2.4	0.5	0.6
2	–	–	–	45	5.7	3.4	1.8	0.4	0.2
3	–	–	–	45	12.5	7.9	3.0	0.6	1.0
4	–	–	–	21	5.4	3.5	1.3	0.2	0.3
5	–	–	–	16	2.3	1.3	0.7	0.2	0.2
6	–	–	–	16	2.7	1.7	0.7	0.2	0.1
7	–	–	–	18	16.9	10.2	6.3	0.3	0.2
8	–	–	–	21	22.2	12.8	8.7	0.5	0.2
9	–	–	–	28	23.9	12.0	8.3	1.9	1.8
10	–	–	–	16	8.5	5.2	2.9	0.3	0.1
11	–	–	–	16	13.5	7.6	5.6	0.2	0.1
12	–	–	–	18	13.2	7.4	5.3	0.4	0.1
13	–	–	–	15	5.6	4.3	1.1	0.1	0.1

picoplankton. Thus, the indication of nanoplankton size-class dominance within the community remained unchanged (Figure S2 in Supporting Information S1).

An additional modification of the DPA methodology, as introduced by Barlow et al. (2014), allowed the attribution of Tchl_a to different phytoplankton types. This approach indicated daily mean depth-averaged contributions of 18 ± 3% by diatoms, 3 ± 1% by dinoflagellates, 76 ± 5% by flagellates and 3 ± 2% by prokaryotes (*Synechococcus* and *Prochlorococcus*) respectively (Figure S3 in Supporting Information S1).

3.4. CHEMTAX Analysis

Input and final output matrices for the various CHEMTAX analyses are shown in Table 3. Within the mixed layer the algal group Hapto-8 contributed the most to the Tchl_a pool with per sample contributions of 54%–85% (mean 73 ± 9%). Other significant contributors were prasinophytes (range 2%–15%; mean 6 ± 4%), *Synechococcus* (range 2%–13%; mean 5 ± 4%) and Pelagophytes (range 0%–10%; mean 4 ± 3%). All other groups, including diatoms contributed on average <3% each to the Tchl_a pool of the mixed layer (Figure 5; Table 4).

Table 2
Concentration Ranges of Major Diagnostic Pigments

Pigment (abbreviation)	Concentration range ($\mu\text{g L}^{-1}$)	Mean $\pm$ s.d. ($\mu\text{g L}^{-1}$)
Total chlorophyll- <i>a</i> (Tchl _a) ^a	0.06–1.85	0.43 $\pm$ 0.31
Total chlorophyll- <i>b</i> (Tchl _b) ^b	<0.01–0.16	0.03 $\pm$ 0.03
Total chlorophyll- <i>c</i> (Tchl _c) ^c	<0.01–0.27	0.08 $\pm$ 0.07
Fucoxanthin (fuco)	0.01–0.49	0.06 $\pm$ 0.06
Peridinin (per)	<0.01–0.03	0.01 $\pm$ 0.01
19'-hexanoyloxyfucoxanthin (19'-hex)	0.03–0.54	0.23 $\pm$ 0.16
19'-butanoyloxyfucoxanthin (19'-but)	<0.01–0.16	0.06 $\pm$ 0.04
Alloxanthin (allo)	<0.01–0.07	0.01 $\pm$ 0.01
Zeaxanthin (zea)	<0.01–0.03	0.01 $\pm$ 0.01
Violaxanthin (viol)	<0.01–0.08	0.01 $\pm$ 0.01
Diadinoxanthin (ddx)	<0.01–0.16	0.04 $\pm$ 0.03
Lutein (lut)	<0.01	0.001
α + β carotene (caro)	<0.01–0.05	0.01 $\pm$ 0.01
Prasinolanthin (pras)	<0.01	0.003 $\pm$ 0.002
Total pigments	0.14–3.85	1.0 $\pm$ 0.71
Total photosynthetic ^d	0.04–2.18	0.54 $\pm$ 0.41
Total carotenoids ^e	0.03–1.45	0.44 $\pm$ 0.32
Photosynthetic carotenoids (PSC) ^f	0.02–1.07	0.36 $\pm$ 0.26
Photoprotective carotenoids (PPC) ^g	<0.01–0.38	0.08 $\pm$ 0.07

^aSum of chlorophyll-*a*, divinyl chlorophyll-*a* and chlorophyllide-*a*. ^bSum of chlorophyll-*b* and divinyl chlorophyll-*b*. ^cSum of chlorophyll-*c*2 + *c*1 and chlorophyll-*c*3. ^dSum of Tchl_a + Tchl_b + Tchl_c. ^eSum of per, 19'-but, fuco, viola, 19'-hex, ddx, allo, zea, lut, and α + β carotene. ^fSum of per, 19'-but, fuco, 19'-hex. ^gSum of viola, ddx, allo, zea, lut, α + β carotene.

In the lower euphotic zone beneath the mixed layer, the relative contribution by algal groups to Tchl_a changed slightly with the average Hapto-8 contribution decreasing to 60 $\pm$ 10%, whilst the average prasinophyte and pelagophyte contributions increased to 11 $\pm$ 1% and 7 $\pm$ 4%, respectively. The contribution by Hapto-6 (8 $\pm$ 6%), and *Synechococcus* (4 $\pm$ 3%) remained comparable to their respective contributions within the mixed layer. Other algal groups exhibited minor variations in their respective contributions (Table 4).

Some algal groups exhibited temporal changes in their contribution to euphotic zone Tchl_a. For example, the chlorophyte contribution rose steadily between day 1 and day 12 but still represented only a minor component (maximum 1.4%) of Tchl_a. The pelagophyte contribution also increased over time reaching 10% by the end of sampling. The cryptophyte contribution, which was <0.5% between days 1 and 6, increased abruptly from day 7 onwards reaching 2.5%. Changes in this group most closely tracked changes in Tchl_a even though the overall cryptophyte contribution was small compared to the Hapto-8 group, which made a high and sustained contribution averaging 68 $\pm$ 7% to euphotic zone Tchl_a across all days. Diatom contributions decreased from ~16% (day 1) to ~0% (day 13), whilst prasinophyte contributions reduced from 10% to 12% at the start of sampling to ~4%–5% by the end. The dinoflagellate contribution to euphotic zone Tchl_a was generally low and less variable compared to other algal groups averaging 3 $\pm$ 1% and exhibiting no clear temporal trend.

3.5. Flowcam Assessment of Phytoplankton Community

Assessment of the phytoplankton community by Flowcam imaging was restricted to 6 profiles with two profiles sampled before the passage of the front (days 4 and 5), and 4 profiles sampled in the period of higher productivity afterward (days 8, 9, 12 and 13) (Figure 6). Collectively, *Phaeocystis* sp., and the <18 μm unidentified cell groups numerically dominated the community both pre- and post-front and the sum of their integrated relative abundance was >81% over the observation period. Although cells in the <18 μm group could not be fully identified, approximately 20%–25% of the images in this group corresponded to single or two-cell images of *Phaeocystis*,

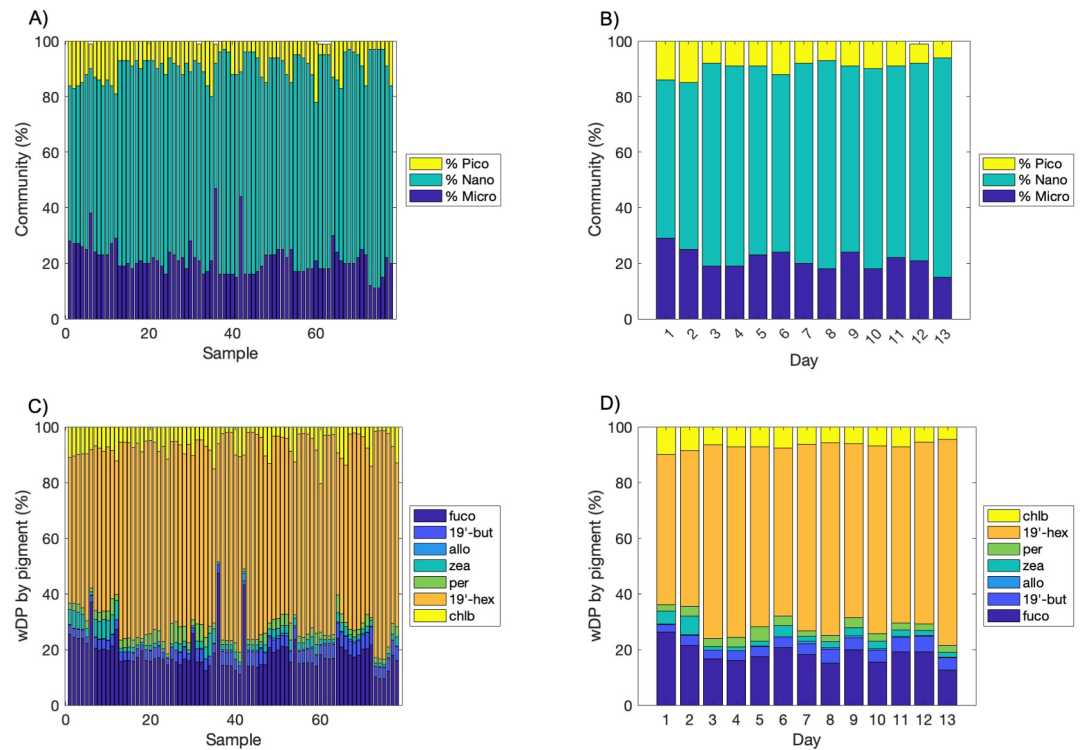


Figure 4. Pigment based breakdown of the phytoplankton community showing (a) size-class proportions by sample, (b) depth-averaged size-class proportions per day, (c) individual pigment contributions to the weighted diagnostic pigment pool by sample, and (d) depth-averaged pigment contributions to the weighted diagnostic pigment pool per day. Results are based on the methodology and weights described by Uitz et al. (2006).

Table 3

Initial and Final CHEMTAX Matrices for Chemotaxonomic Analyses of the Whole Euphotic Zone (1% Surface Irradiance), the Surface Mixed Layer and the Lower Euphotic Zone Lying Between the Base of the Mixed Layer and the Euphotic Zone Depth

	CHL _{c3}	Chl _{c2+c1}	PER	BUT	FUCO	HEX	VIO	ALLO	ZEA	PRAS	CHLb	DVa	Lut	NEO	CHLa
<i>Input matrix</i>															
Chlorophytes	0	0	0	0	0	0	0.03	0	0.02	0	0.317	0	0.177	0.2	1
Cryptophytes	0	0.17	0	0	0	0	0	0.36	0	0	0	0	0	0	1
Diatoms	0	0.09	0	0	0.71	0	0	0	0	0	0	0	0	0	1
Dinoflagellates	0	0.23	0.54	0	0	0	0	0	0	0	0	0	0	0	1
Haptophytes-6	0.16	0.19	0	0.002	0.06	0.23	0	0	0	0	0	0	0	0	1
Haptophytes-8	0.07	0.14	0	0.05	0.09	0.12	0	0	0	0	0	0	0	0	1
Pelagophytes	0.22	0.46	0	0.55	0.66	0	0	0	0	0	0	0	0	0	1
Prasinophytes	0	0	0	0	0	0	0.07	0	0.04	0.2	0.7	0	0.06	0.04	1
<i>Prochlorococcus</i>	0	0	0	0	0	0	0	0	0.22	0	0	0	0	0	0
<i>Synechococcus</i>	0	0	0	0	0	0	0	0	0.52	0	0	1	0	0	1
<i>Output matrix (euphotic zone)</i>															
Chlorophytes	0	0	0	0	0	0	0.029	0	0.020	0	0.287	0	0.195	0.237	1
Cryptophytes	0	0.157	0	0	0	0	0	0.408	0	0	0	0	0	0	1
Diatoms	0	0.087	0	0	0.615	0	0	0	0	0	0	0	0	0	1
Dinoflagellates	0	0.210	0.581	0	0	0	0	0	0	0	0	0	0	0	1
Haptophytes-6	0.136	0.199	0	0.002	0.056	0.299	0	0	0	0	0	0	0	0	1

Table 3
Continued

	CHL _{c3}	Chl _{c2+c1}	PER	BUT	FUCO	HEX	VIO	ALLO	ZEa	PRAS	CHLb	DVa	Lut	NEO	CHLa
Haptophytes-8	0.036	0.086	0	0.101	0.081	0.314	0	0	0	0	0	0	0	0	1
Pelagophytes	0.238	0.400	0	0.604	0.620	0	0	0	0	0	0	0	0	0	1
Prasinophytes	0	0	0	0	0	0	0.125	0	0.042	0.112	0.777	0	0.038	0.038	1
<i>Prochlorococcus</i>	0	0	0	0	0	0	0	0	0.285	0	0	1.304	0	0	0
<i>Synechococcus</i>	0	0	0	0	0	0	0	0	0.589	0	0	0	0	0	1
<i>Output matrix (mixed layer)</i>															
Chlorophytes	0	0	0	0	0	0	0.027	0	0.0189	0	0.278	0	0.185	0.225	1
Cryptophytes	0	0.185	0	0	0	0	0	0.379	0	0	0	0	0	0	1
Diatoms	0	0.099	0	0	0.716	0	0	0	0	0	0	0	0	0	1
Dinoflagellates	0	0.218	0.607	0	0	0	0	0	0	0	0	0	0	0	1
Haptophytes-6	0.160	0.168	0	0.002	0.053	0.263	0	0	0	0	0	0	0	0	1
Haptophytes-8	0.037	0.086	0	0.088	0.073	0.314	0	0	0	0	0	0	0	0	1
Pelagophytes	0.222	0.471	0	0.734	0.671	0	0	0	0	0	0	0	0	0	1
Prasinophytes	0	0	0	0	0	0	0.168	0	0.041	0.141	0.656	0	0.044	0.032	1
<i>Prochlorococcus</i>	0	0	0	0	0	0	0	0	0.257	0	0	1.243	0	0	0
<i>Synechococcus</i>	0	0	0	0	0	0	0	0	0.499	0	0	0	0	0	1
<i>Output matrix (lower euphotic)</i>															
Chlorophytes	0	0	0	0	0	0	0.031	0	0.017	0	0.322	0	0.169	0.175	1
Cryptophytes	0	0.175	0	0	0	0	0	0.336	0	0	0	0	0	0	1
Diatoms	0	0.087	0	0	0.728	0	0	0	0	0	0	0	0	0	1
Dinoflagellates	0	0.246	0.544	0	0	0	0	0	0	0	0	0	0	0	1
Haptophytes-6	0.176	0.173	0	0.002	0.056	0.244	0	0	0	0	0	0	0	0	1
Haptophytes-8	0.027	0.053	0	0.064	0.086	0.370	0	0	0	0	0	0	0	0	1
Pelagophytes	0.205	0.500	0	0.786	0.575	0	0	0	0	0	0	0	0	0	1
Prasinophytes	0	0	0	0	0	0	0.100	0	0.037	0.097	0.768	0	0.026	0.049	1
<i>Prochlorococcus</i>	0	0	0	0	0	0	0	0	0.388	0	0	1.164	0	0	0
<i>Synechococcus</i>	0	0	0	0	0	0	0	0	0.552	0	0	0	0	0	1

implying an underestimation of the true *Phaeocystis* abundance (Figure S4 in Supporting Information S1). In contrast, diatoms were comparatively rare (<5% integrated relative abundance) and were predominately pennate diatom cells. There were day-to-day changes in the integrated relative abundance of dinoflagellates with relative abundances ranging from 3% to 14%, but no clear overall temporal trend.

3.6. Scanning Electron Microscopy Assessment of Coccolithophores

Surface water samples indicated low coccolithophore diversity and low coccosphere and coccolith abundances. For the two most abundant species, *Gephyrocapsa huxleyi* (formally *Emiliana huxleyi*; (Bendif et al., 2023; Filatov et al., 2021; Wheeler et al., 2023); and *Syracosphaera molishii* abundances were 15.3 cells mL⁻¹ and 1,359 liths mL⁻¹, and 15 cells mL⁻¹ and 13 liths mL⁻¹, respectively. Such concentrations are comparable to observations made in this region in autumn months for example, 13.2 cells mL⁻¹ *Gephyrocapsa huxleyi* and 10.8 cells mL⁻¹ for *Syracosphaera* spp. (Painter, 2021) but are not otherwise indicative of high cellular abundances. Whilst the low coccolithophore abundances appear at odds with the dominance of the haptophyte diagnostic pigment 19'-hex in the diagnostic pigment pool, deeper coccolithophore distributions were not sampled, thus the surface results may be indicative only.

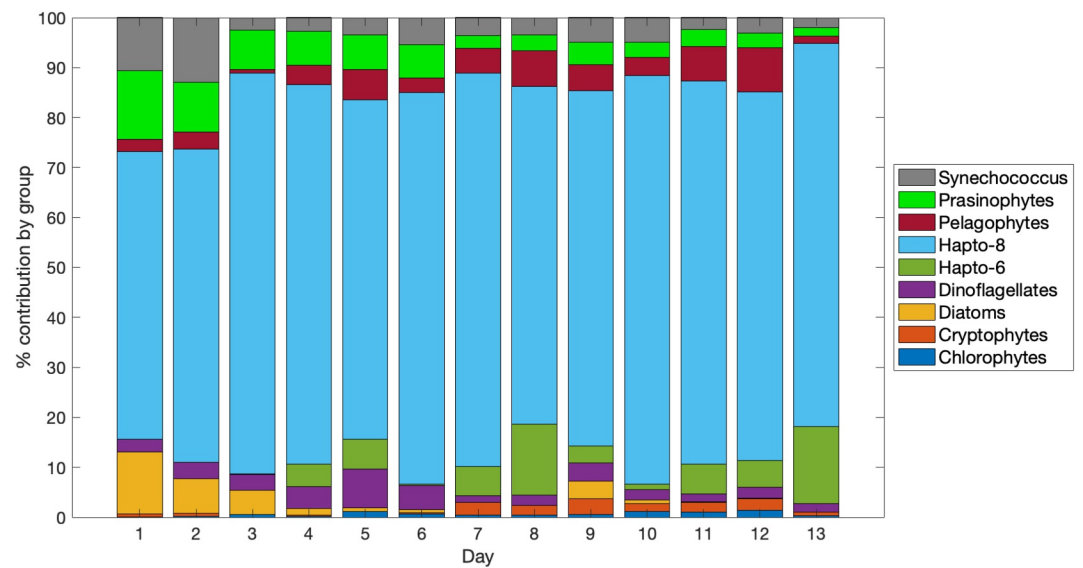


Figure 5. Percentage contribution by algal group to total chlorophyll-*a* (Tchl-*a*) within the mixed layer as determined by CHEMTAX. Hapto-8 represents a *Phaeocystis*-like algal group and Hapto-6 represents a *Gephyrocapsa huxleyi*-like group.

Table 4

Mean Percentage Contribution by Phytoplankton Type to Layer Averaged Chlorophyll-*a* Concentration

Day	Chl ^a ($\mu\text{g/L}^{-1}$)	Chlorophyte Chl (%)	Cryptophyte Chl (%)	Diatom Chl (%)	Dinoflagellate Chl (%)	Hapto-6 Chl (%)	Hapto-8 Chl (%)	Pelagophyte Chl (%)	Prasinophytes Chl (%)	Synechococcus Chl (%)
Euphotic zone										
1	0.16	0	0.5	16.6	2.4	4.0	56.1	1.4	11.9	7.0
2	0.18	0	0.5	9.2	3.6	0.5	62.8	2.7	9.8	10.9
3	0.18	0.5	0.1	5.6	2.9	1.4	79.7	0.1	7.7	2.0
4	0.18	0.1	0.2	3.1	3.6	5.9	75.5	1.6	8.3	1.7
5	0.18	0.7	0.2	4.5	5.5	6.8	68.8	3.0	8.1	2.4
6	0.16	0.4	0.2	8.0	3.3	4.4	65.6	3.5	8.5	6.1
7	0.67	0.6	2.6	5.4	2.0	11.8	65.5	3.1	6.7	2.4
8	0.64	0.6	1.8	0.6	2.4	16.6	62.1	7.1	5.8	3.1
9	0.65	0.6	2.5	3.4	3.8	8.6	64.5	5.9	6.3	4.4
10	0.46	0.8	1.4	1.9	2.8	1.1	77.5	2.9	7.2	4.4
11	0.63	1.4	1.3	1.8	2.8	3.7	69.9	8.0	7.6	3.5
12	0.65	1.3	1.5	0.7	2.5	3.3	72.6	9.6	5.8	2.7
13	0.41	0.9	0.6	0.0	2.7	17.4	66.3	4.9	4.7	2.6
Mixed layer										
1	0.15	0.1	0.6	12.4	2.5	0	57.5	2.4	13.7	10.7
2	0.18	0.1	0.6	7.0	3.2	0	62.7	3.4	9.9	13.0
3	0.19	0.5	0.1	4.9	3.1	0.1	80.2	0.7	7.9	2.5
4	0.20	0.2	0.2	1.4	4.4	4.5	75.9	3.9	6.8	2.7
5	0.16	1.1	0.0	0.8	7.7	6.0	67.9	6.1	6.8	3.5
6	0.19	0.6	0.3	0.6	4.8	0.2	78.4	3.0	6.6	5.4
7	0.64	0.4	2.5	0	1.4	5.8	78.7	4.9	2.7	3.5

Table 4
Continued

Day	Chla ^a (μg/L ⁻¹)	Chlorophyte Chl (%)	Cryptophyte Chl (%)	Diatom Chl (%)	Dinoflagellate Chl (%)	Hapto-6 Chl (%)	Hapto-8 Chl (%)	Pelagophyte Chl (%)	Prasinophytes Chl (%)	Synechococcus Chl (%)
8	0.69	0.4	2.0	0	2.0	14.3	67.5	7.2	3.1	3.5
9	0.72	0.6	3.1	3.6	3.6	3.4	71.1	5.3	4.4	5.0
10	0.47	1.1	1.6	0.7	2.1	1.1	81.8	3.7	3.0	4.9
11	0.80	1.1	1.9	0.2	1.5	5.9	76.6	7.0	3.4	2.4
12	0.71	1.4	2.3	0.2	2.1	5.4	73.8	8.8	2.9	3.1
13	0.36	0.3	0.7	0	1.7	15.5	76.7	1.4	1.8	2.0
Lower euphotic zone										
1	0.17	0	0.2	17.0	2.1	10.3	53.5	1.8	12.0	3.2
2	0.20	0	0.3	8.3	4.4	2.4	54.1	5.9	12.5	12.1
3	0.16	0.3	0	5.8	1.6	3.5	75.4	1.4	11.0	1.0
4	0.17	0	0.3	0.9	2.8	3.9	76.8	3.0	11.0	1.3
5	0.20	0.3	0.4	3.2	4.5	6.0	68.2	4.9	9.9	2.4
6	0.13	0.0	0.2	12.4	1.7	8.2	51.4	6.5	11.3	8.3
7	0.70	0.6	3.4	9.0	2.8	14.2	51.6	4.3	12.3	1.9
8	0.52	1.0	2.0	1.1	3.4	16.1	53.2	7.9	11.6	3.6
9	0.51	0.7	2.0	2.0	4.1	16.0	50.0	9.0	10.9	5.2
10	0.45	0.3	1.6	1.4	3.8	0.3	68.8	6.6	12.1	5.2
11	0.45	1.8	1.0	1.4	4.3	0.3	61.3	11.9	12.6	5.4
12	0.60	1.1	1.0	0	2.9	1.7	67.7	13.3	9.3	3.0
13	0.46	1.7	0.6	0	4.0	15.5	55.8	11.0	7.7	3.8

^aMean HPLC chlorophyll concentration by layer for each daily profile.

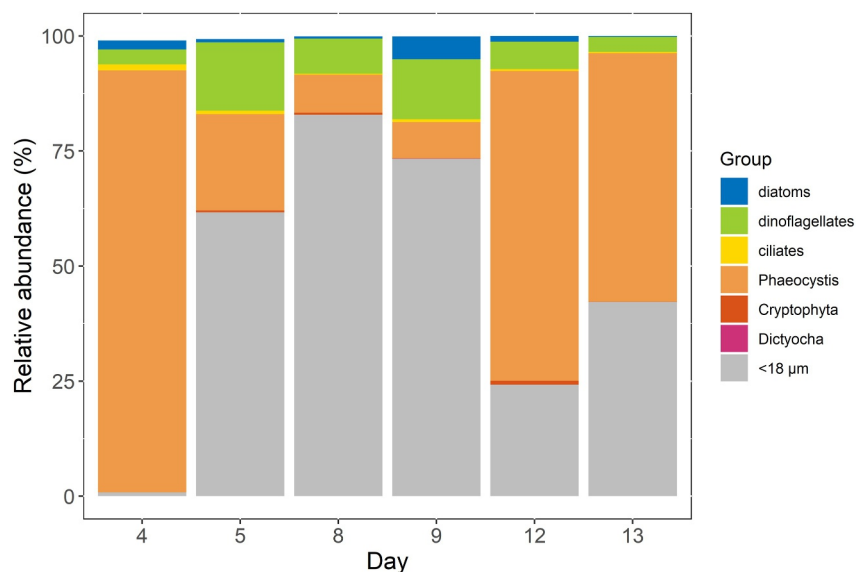


Figure 6. FlowCam derived phytoplankton relative abundances for selected daily profiles.

4. Discussion

Sampling during the 2024 Northeast Atlantic spring bloom encountered an extensive region of weak productivity (Painter et al., 2026). Results presented here corroborate satellite data showing low surface chlorophyll concentrations ($<0.3 \text{ mg L}^{-1}$) but also reveal an unusually high picoplankton contribution to the total chlorophyll pool (60%), whilst pigment-based analyses indicate a phytoplankton community dominated by haptophytes with a limited contribution by diatoms. Coincident observations of primary and new production, and of the particulate carbon, nitrogen and phosphorus pools, found rates and concentrations $>50\%$ lower in these low chlorophyll waters than in surrounding waters (Painter et al., 2026). Results from HPLC pigment and FlowCam microscopy analyses broadly agree with the conclusion derived from size-fractionated chlorophyll measurements that the community was dominated by smaller cells, though methodological differences mean that these techniques do not directly compare the same size intervals. The HPLC based DPA suggested that nanoplankton (traditionally $2\text{--}20 \text{ }\mu\text{m}$; Sieburth et al., 1978) were dominant and the FlowCam microscopy analyses supported this finding with cells $<18 \text{ }\mu\text{m}$ in size (i.e., nanoplankton) having the highest relative abundance. Size fractionated chlorophyll data indicated that 95% of the total chlorophyll was in the $<20 \text{ }\mu\text{m}$ fraction, and 90% in the $<10 \text{ }\mu\text{m}$ fraction. We note that whilst picoplankton cannot be assessed via FlowCam analyses due to the size limitation imposed by a $\times 10$ magnification (Camoying & Yniguez, 2016), both Flowcam and HPLC analyses ultimately indicated a phytoplankton community dominated by smaller cells.

One critical assumption of the size-class based diagnostic pigment methodology is that the diagnostic pigment 19'-hex is assigned exclusively to the nanoplankton size-fraction (Uitz et al., 2006) and specifically to haptophytes and some dinoflagellates (e.g. Jeffrey et al., 2011; Kramer & Siegel, 2019; Wright & Jeffrey, 2006). Consequently, because 19'-hex was dominant in this HPLC data set this led to the large nanoplankton contribution to Tchla indicated by the DPA method and the apparent difference between the dominant size class identified by the size-fractionated chlorophyll measurements (picoplankton) and the DPA analyses (nanoplankton). Notably, 19'-hex may also be found in picoeukaryotes, particularly picoflagellates, which can make correctly resolving the picoplankton contribution to Tchla difficult via DPA (Aiken et al., 2009; Brewin et al., 2017; Brotas et al., 2022; Liu et al., 2009).

The high contribution made by picoplankton ($\sim 60\%$) to total Chl-a was nevertheless unexpected given prevailing assumptions that larger size classes such as microplankton, but increasingly nanoplankton, are dominant in this part of the Northeast Atlantic Ocean during the spring bloom period (McQuatters-Gollop et al., 2007; Taylor et al., 1993). The dominance of the chlorophyll biomass by picoplankton coupled with only minor contribution ($\sim 5\%$) from larger microplankton was also at odds with traditional expectations and previous observations that larger cells should dominate the spring bloom (e.g., Joint et al., 1993; Lochte et al., 1993; Mojica et al., 2015; Savidge et al., 1995; Ward & Van Oostende, 2016). This suggests either that the phytoplankton community remained broadly reflective of typical winter community composition (e.g., cyanobacteria and pico-eukaryotes (Bolanos et al., 2020)), or that the community was different to a normal year. Of these two possibilities the former can be discounted as surface nutrient pools appeared to have been partially depleted compared to mean winter conditions by the time of sampling (<6 vs. $8\text{--}11 \text{ }\mu\text{mol NO}_3^- \text{ L}^{-1}$), whilst the latter seems more likely as sampling was ideally placed to coincide with the mean long-term peak timing of the spring bloom (Longhurst, 1995, 1998; Painter et al., 2016).

The pigment and size-fractionated chlorophyll results contrast markedly with the results from Meyer et al. (2024) who sampled a diatom dominated community in this region during May 2021 as part of the NASA Exports study (Siegel et al., 2016). In that study, fucoxanthin represented $\sim 30\text{--}80\%$ of the diagnostic pigment pool, whereas in this study a comparatively low contribution of $21 \pm 9\%$ was found. Furthermore, the size-fractionated chlorophyll data reported by Meyer et al. (2024) indicated a clear dominance by the $>5 \text{ }\mu\text{m}$, or co-equivalence between the $<5 \text{ }\mu\text{m}$ and $>5 \text{ }\mu\text{m}$ size fractions. Though the size classes are not directly comparable between studies this does contrast with the high contribution reported here for the $<2 \text{ }\mu\text{m}$ size fraction. These differences imply a significant taxonomic shift in the springtime phytoplankton community composition can be identified between studies.

Low surface silicate and moderate nitrate and phosphate concentrations observed at the start of sampling (Figure 2) were coincident with low rates of primary production ranging from 0.5 to $0.6 \text{ g C m}^{-2} \text{ d}^{-1}$ during days 1–6 (Painter et al., 2026). The community structure data reported here show that the composition of the phytoplankton community is relevant to wider investigation of the observed weak productivity regime. In particular, the shift toward smaller cell sizes tends to indicate reduced productivity, lower overall biomass and

shallow recycling of phytoplankton biomass. Previous observations that the spring bloom phytoplankton community can be shifted from larger cells to smaller cells were reported by Sieracki et al. (1993), who noted a shift from diatoms toward small flagellates during the 1989 spring bloom when comparable conditions of low surface silicate and residual nitrate concentrations were encountered. At that time however, surface chlorophyll concentrations remained high ($2\text{--}4\text{ }\mu\text{g L}^{-1}$), and a more heterotrophic community developed. Thus, whilst some similarities can be drawn between studies regarding the role of silicate limitation in shaping the community size class, the net impact on surface chlorophyll concentrations appears to have been very different.

4.1. Picoplankton Haptophyte Identification

FlowCam analysis indicated most cells were in the $<18\text{ }\mu\text{m}$ size fraction (i.e., nanoplankton), but this technique does not adequately resolve smaller picoplankton cells, which can only be resolved via appropriate techniques such as flow cytometry, or accurately determine coccolithophore abundances, due to degradation of cells within the Lugol's fixative. HPLC data and the various DPA methodologies indicated high 19'-hex contributions to the diagnostic pigment pool and a dominance by flagellated haptophytes. SEM data indicated low coccolithophore abundances in surface waters. Collectively these data imply a community of small haptophytes were dominant during the observation period with a bias toward picoplankton sized cells. Whilst picoplankton sized haptophytes are widespread in open ocean waters and can be easily overlooked (Liu et al., 2009), contenders most likely belong to the genera *Phaeocystis* (cell size $<10\text{ }\mu\text{m}$), *Chrysochromulina* (size $3\text{--}13\text{ }\mu\text{m}$), or as a remote possibility *Prymnesium* (size $<12\text{ }\mu\text{m}$).

Reported distributions of *Phaeocystis* spp. include waters to the southwest of the UK and Ireland (Claustre et al., 1990; Gieskes et al., 2007; Owens et al., 1989; Schoemann et al., 2005) and the open waters of the North Atlantic (Smith & Trimborn, 2024). *Chrysochromulina* spp. are considered cosmopolitan but poorly studied (Chretiennot-Dinet et al., 2014; Estep & MacIntyre, 1989; Hansen et al., 1995; Kaas et al., 1991; Parke et al., 2009), yet most species are also known to display spines around the central cell increasing the effective cell size considerably (Hansen et al., 1995). The presence of spines would have increased the likelihood of *Chrysochromulina* spp. being retained by the $10\text{ }\mu\text{m}$ filter used for the size-fractionated chlorophyll measurements. Blooms of *Prymnesium* spp., meanwhile are typically reported from coastal and brackish waters (Edvardsen & Paasche, 1998; Eikrem et al., 2016), thus it is unlikely that *Prymnesium* spp. were present.

Whilst *Phaeocystis* spp. contains significant quantities of the pigment 19'-hex (Zapata et al., 2004) this pigment is also found within other haptophyte species (Jeffrey et al., 2011; Wright & Jeffrey, 2006) and for this reason is not generally sufficient on its own to infer the presence of *Phaeocystis* (Antajan et al., 2004; Mejanelle et al., 1995; Schoemann et al., 2005). However, in keeping with the haptophyte pigment types identified by Zapata et al. (2004), and in particular haptophyte Type-8 which was attributed to *Phaeocystis* sp., the contributions by the pigments 19'-hex and 19'-but represented $22\%\text{--}78\%$ (mean $65 \pm 9\%$) and $6\%\text{--}25\%$ (mean $14 \pm 4\%$) of the total fucoxanthin pigment pool, values comparable to the ranges reported by Zapata et al. (2004), and which therefore strongly imply *Phaeocystis* presence. Additionally, none of the other haptophyte pigment types described by Zapata et al. (2004) replicate the high contribution of both 19'-hex and 19'-but to the total fucoxanthin pool. Elsewhere, the presence of 19'-hex, 19'-but and chlorophyll-*c3* in pigment samples (Table 2) is generally accepted as a reliable indicator of *Phaeocystis* presence (Wang et al., 2022; Zhang et al., 2022).

4.2. Implications

Several lines of evidence indicate sampling occurred within a *Phaeocystis* bloom. The CHEMTAX analysis and size fractionated chlorophyll observations both suggest a general lack of other larger phytoplankton groups such as diatoms present during sampling. Whilst the occurrence of *Phaeocystis* sp. in the open waters of the Northeast Atlantic is not unusual (Smith & Trimborn, 2024), nor is the spring timing of this encounter unexpected (Gieskes et al., 2007; Leblanc et al., 2009), the overall dominance by this species as indicated by the analysis of the pigment pool was surprising. Whilst CHEMTAX analyses are more usually applicable to identification of algal groups rather than specific genera, the presence of *Phaeocystis* is supported by the independent FlowCam analyses. Such blooms, nevertheless, remain infrequently reported with most Northeast Atlantic regional studies emphasizing locations within the North Sea (Claustre et al., 1990; Eikrem et al., 2016; Gieskes et al., 2007; He et al., 2025; Lancelot et al., 1987; Marra et al., 1995; Owens et al., 1989; Vogt et al., 2012) or across the Northwest European continental shelf more generally (Smith & Trimborn, 2024).

At the time of sampling surface nutrient concentrations were $<2 \mu\text{mol Si L}^{-1}$, $2.6\text{--}6.1 \mu\text{mol NO}_3^- \text{L}^{-1}$ and $0.2\text{--}0.4 \mu\text{mol PO}_4^{3-} \text{L}^{-1}$ (Figure 2). Conditions of low silicate and moderate nitrate availability are known to be beneficial to *Phaeocystis* sp. (Wang et al., 2011). *Phaeocystis* blooms have also been positively correlated with temperature (Wang et al., 2025), and the weak productivity rates measured alongside the community structure observations reported here followed a prolonged period of unusual warming across the North Atlantic region (England et al., 2025; Terhaar et al., 2025). Thus, the recent thermal history of the North Atlantic was likely a relevant factor contributing to the dominance by *Phaeocystis* in spring 2024. Previous studies have highlighted how higher temperatures can alter North Atlantic coccolithophore blooms (Guinaldo & Neukermans, 2026), and are likely to lead to increased significance of *Phaeocystis* within a warmer North Atlantic Ocean (Bopp et al., 2005), whilst the emergence of unusually large *Phaeocystis* blooms in the Labrador Sea in 2015 and 2022 were considered significant for altering productivity and carbon export fluxes (Devred et al., 2025; Roca-Martí et al., 2025).

The dominant presence of *Phaeocystis* sp. in spring 2024 is ecologically noteworthy as the presence of *Phaeocystis* sp. has been shown to induce changes to both phytoplankton and zooplankton community structure, including reduced diversity and altered grazing patterns (Gasparini et al., 2000; Hansen & Boekel, 1991; Wang et al., 2025), with the latter change linked to the poor nutritional value provided by *Phaeocystis* (Claustre et al., 1990). *Phaeocystis* has also been implicated in changes to fisheries with some fish species reported to actively avoid *Phaeocystis* (see discussions in Schoemann et al., 2005; Weisse et al., 1994). Year-to-year changes in the phytoplankton community structure during the spring bloom period is also a key driver of interannual variability in carbon fluxes to depth (Lampitt et al., 2023). Consequently, the dominance of *Phaeocystis* sp., its higher flux attenuation efficiency relative to diatoms, and a general shift towards smaller cells likely reduced export fluxes in spring 2024 compared to previous years (Reigstad & Wassmann, 2007; Roca-Martí et al., 2025; Wolf et al., 2016). Indirect support for weak export potential can be inferred from the ratio of biogenic silica to particulate organic carbon. Using data reported in Painter et al. (2026) we calculate that the euphotic zone BSi:POC ranged from <0.01 to 0.45 and averaged 0.06 ± 0.06 . Most samples in the euphotic zone were <0.1 . Low BSi:POC ratios indicate weak ballasting of POC with opal suggesting low likelihood of *Phaeocystis* biomass export (Roca-Martí et al., 2025). Low BSi:POC ratios also indicate weak contributions by silicifying phytoplankton to POC biomass and to export potential, a result consistent with the pigment-based observations reported here.

Links between North Atlantic long-term climate variability and the occurrence of *Phaeocystis* sp., in open waters of the Northeast Atlantic indicate complex interannual and interdecadal patterns (Gieskes et al., 2007; Owens et al., 1989). Model predictions suggest that changing environmental conditions, particularly higher temperatures, will increasingly favour *Phaeocystis* sp., in the North Atlantic (He et al., 2025), with consequences for the marine carbon cycle and energy transfer. Our observations, during a period of unusual warming across the North Atlantic throughout 2023–2024 (England et al., 2025; Terhaar et al., 2025), appear to support these, and other model projections (Bopp et al., 2005). Significantly, the presence of a large low productivity anomaly in the NE Atlantic during what should have been the peak of the spring bloom, and the absence of diatoms makes conditions in spring 2024 unusual. The many parallels between the observed in situ conditions and those predicted by climate models to emerge in the coming decades (e.g., warmer temperatures, reduced nutrients, decreased primary production, a reduction in diatom and coccolithophore abundance, a shift towards smaller species, increased optical clarity), is particularly concerning as it implies early onset or shifts to a lower productivity regime may occur abruptly or earlier than predicted by models. Observations comparable to those presented here may therefore become more regularly reported for the Northeast Atlantic Ocean as upper ocean temperatures continue to rise.

5. Conclusions

In-situ sampling timed to coincide with the peak of the 2024 spring bloom found an extensive and persistent body of low chlorophyll waters in the Northeast Atlantic corroborating satellite data. These waters contained pigment markers indicative of haptophyte dominance and limited diatom presence. Surface chl-*a* concentrations of $\sim 0.2\text{--}0.3 \text{ mg m}^{-3}$ were less than half of concentrations observed across the wider North Atlantic region ($\sim 0.5 \text{ mg m}^{-3}$), and around one-quarter of concentrations considered typical for the spring bloom period. Analysis of phytoplankton pigments, and flow imaging microscopy of the phytoplankton community indicated a pico- and nanoplankton dominance within the phytoplankton community, and the widespread presence of

Phaeocystis sp. The change in the phytoplankton community toward smaller phytoplankton species and the likely dominance of *Phaeocystis* within the pigment pool supports model projections of how phytoplankton community structure may change in the near-future as the North Atlantic continues to warm. These observations also suggest that early or abrupt onset of those changes is possible.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Availability Statement

All cruise data are available via the British Oceanographic Data Centre (www.bodc.ac.uk). The pigment data set is available as a published data set via Hartman et al. (2025). Particulate and productivity data sets are available via Painter et al. (2025). Flowcam data are available via the EcoTaxa website (<https://ecotaxa.obs-vlfr.fr>; EcoTaxa ID 17483). Modis Aqua data products were obtained from the NASA Ocean Biology Distributed Active Archive Centre (OB.DAAC) via oceancolor.gsfc.nasa.gov.

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