

Research



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Bio-optical evidence for increasing *Phaeocystis* dominance in the Barents Sea

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Increasing contributions of prymnesiophytes such as *Phaeocystis pouchetii* and *Emiliania huxleyi* to Barents Sea (BS) phytoplankton production have been suggested based on *in situ* observations of phytoplankton community composition, but the scattered and discontinuous nature of these records confounds simple inference of community change or its relationship to salient environmental variables. However, provided that meaningful assessments of phytoplankton community composition can be inferred based on their optical characteristics, ocean-colour records offer a potential means to develop a synthesis between sporadic *in situ* observations. Existing remote-sensing algorithms to retrieve phytoplankton functional types based on chlorophyll-a (*chl-a*) concentration or indices of pigment packaging may, however, fail to distinguish *Phaeocystis* from other blooms of phytoplankton with high pigment packaging, such as diatoms. We develop a novel algorithm to distinguish major phytoplankton functional types in the BS and apply it to the MODIS-Aqua ocean-colour record, to study changes in the composition of BS phytoplankton blooms in July, between 2002 and 2018,

creating time series of the spatial distribution and intensity of coccolithophore, diatom and *Phaeocystis* blooms. We confirm a north-eastward expansion in coccolithophore bloom distribution, identified in previous studies, and suggest an inferred increase in *chl-a* concentrations, reported by previous researchers, may be partly explained by increasing frequencies of *Phaeocystis* blooms.

This article is part of the theme issue 'The changing Arctic Ocean: consequences for biological communities, biogeochemical processes and ecosystem functioning'.

1. Introduction

The Barents Sea (BS) extends north of mainland Arctic Norway, spanning the continental shelf region between the Svalbard Archipelago, Franz Josef land and Novaya Zemlya, occupying some 1.4 million km², with a complex hydrography that results from the convergence of warmer, more saline Atlantic and fresher, cooler Arctic waters [1]. The BS is predominantly shallow, averaging only approximately 230 m depth. This shallow topography means that the movements of water-masses are guided by bathymetry such as the Barents Sea Opening (approx. 470 m deep), which serves as a gateway for the delivery of warmer, more saline and nutrient-rich Atlantic water onto the shelf [2]. These ocean dynamics are illustrated in figure 1.

Bathymetric features stabilize the position of the boundary between Atlantic and Arctic water-masses, known as the Polar Front (PF), which means that the front's position remains relatively constant year-on-year, insensitive to inter-annual variation in the flux of Atlantic water caused by climatological variability, such as the Arctic Oscillation [2]. Over the last 30 years, however, a sustained increase in the baseline rate of Atlantic water flux into the Arctic has doubled the volume occupied by Atlantic water in the BS, causing the northward displacement of the PF [2,4]. As the PF delimits the maximum extent of sea-ice cover [5], its retreat has resulted in the recession of average sea-ice extent in the BS, which has occurred at a disproportionately rapid rate compared with the rest of the Arctic [6].

The hydrography and climatology of the BS create an environment conducive to massive phytoplankton blooms, and the inter-annual variation in these environmental properties determine which phytoplankton groups will be most successful from year to year. The surface ocean is charged with nutrients in the winter when dense Atlantic waters are brought to the surface by vertical mixing [7] and this nutrient complement is further supplemented in spring by mineral-rich ice-rafted debris that is released by melting sea-ice imported through the Fram Strait region [8]. Thermal stratification of the water-column in spring, and salinity-based stratification associated with melting sea-ice, create a nutrient-replete sunlit surface layer that can support phytoplankton blooms in which chlorophyll-*a* (*chl-a*) concentrations exceed 10 mg m⁻³ [9]. Historically, these blooms have usually been dominated by large-celled diatom genera such as *Chaetoceros*, *Fragilariopsis* and *Thalassiosira* that can reproduce very rapidly when resources are abundant [10] and have been observed to form ice-edge blooms that follow the receding Marginal Ice Zone through summer [11]. Outside of the Seasonal Ice Zone, in waters where perennial freezing does not occur, summer mixing tends to be deeper and periodic recharging of the surface nutrient reservoir may occur, favouring smaller phytoplankton species with larger proportional surface areas, such as *Emiliania huxleyi* and *Phaeocystis pouchetii* [10].

We should, therefore, expect that environmental changes in the BS, caused by human-induced warming, will influence the community composition of phytoplankton blooms, with ramifications for overall new production, phenology and hence the supply of food to higher trophic levels in this great northern fishery, and influencing the ecosystem services that are rendered. Indeed, *in situ* investigations in the Eurasian basin during the summer 2012 sea-ice minimum revealed a rare mass-sedimentation of diatomaceous ice-algae filaments, consistent with the expectation of authors such as Krumpen *et al.* [8] that thinner sea-ice, carrying lower levels of exogenous sediment, should transmit more sunlight and hence permit greater under-ice

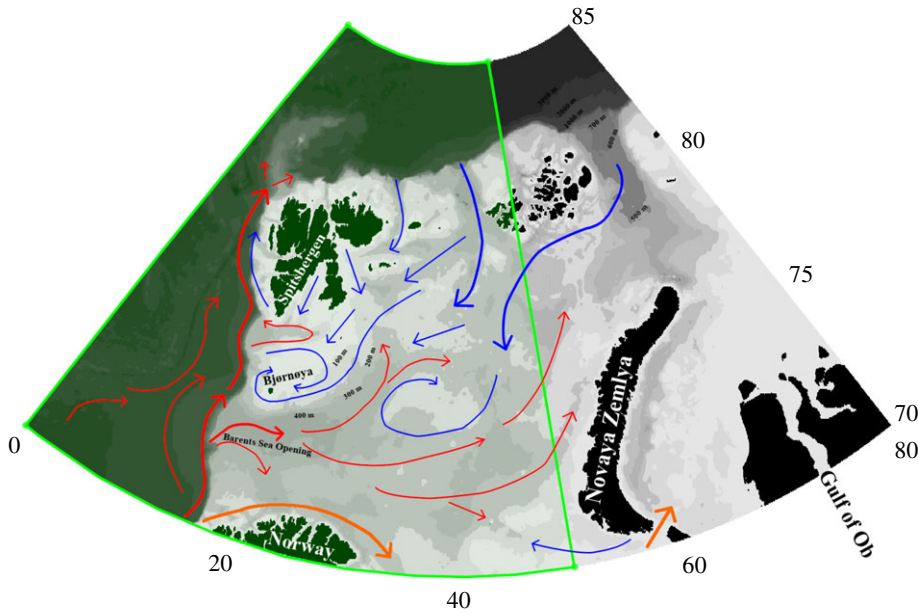


Figure 1. A bathymetric map of the Barents Sea, with inflowing Atlantic (red), Norwegian coastal current (orange) and Arctic (blue) water masses. A front forms between the warm and cold water masses. The area of interest in this study is outlined in green. Bathymetric data were sourced using the ETOPO1 NOAA global relief database (<https://www.ngdc.noaa.gov/mgg/global/>) with the **R** *marmap* package [3]. (Online version in colour.)

primary production. This carries potential implications for nutrient cycling mechanisms and carbon sequestration in a future Arctic Ocean that may be more conducive to perennial ice-algal sedimentation [12]. In the pelagic realm, some authors have reported that coccolithophore blooms are migrating eastward, further into historically more Arctic-influenced areas [13], and sampling in the Fram Strait has revealed an increasing predominance of *Phaeocystis pouchetii* and *Emiliana huxleyi* [14]. Average annual primary production, inferred from remotely sensed *chl-a*, has increased by 30% between 1998 and 2012 [15], but this picture of increasing primary production is difficult to reconcile with observations of declining end-winter silica inventories in the BS [16], critical for diatoms to build their frustules, and with studies of biochemical proxies in Greenlandic ice-cores that imply a centennial scale decline in the productivity of subarctic seas [17]. Remote-sensing inference of a decadal increase in Arctic dimethyl sulphide (DMS) production [18]—often associated with prymnesiophyte species that do not require silica, such as *Phaeocystis pouchetii* or *Emiliana huxleyi*—suggests that change in community composition may help to explain these seemingly conflicting findings, although the algorithm of Galí *et al.* [18] is based on comparisons of estimated productivity and inferred mixed-layer-depth, rather than the recognition of optical signatures of community composition. Time series of phytoplankton samples in the BS necessary to test the hypothesis of community compositional change are, however, sporadic and usually do not exceed the required decadal scales [19]. We, therefore, may ask whether a taxonomically informed study of changes in ocean-colour over the twenty-first century might help elucidate the matter.

There already exist several approaches towards this end. Remote sensing of ocean-colour has successfully detected coccolithophore blooms [13,20,21], owing to the strong scattering properties of calcite liths. However, the detection of other phytoplankton functional types has proved more challenging, although numerous attempts have been made; such as semi-analytical approaches based on forward-modelling from the optical properties of different phytoplankton groups to arrive at ocean-colour signatures that may distinguish them [22,23] or the inversion of systems of equations relating ocean-colour and phytoplankton size classes retrieved with high

performance liquid chromatography (HPLC) [24]. Some authors have explored linear unmixing models of phytoplankton light absorption [25] to infer community composition, but these have not yet been applied to remotely sensed ocean-colour. There have also been attempts to detect optical signatures of specific phytoplankton pigments [26], which have been demonstrated to be successful with *in situ* radiometry, but have not yet been extended to remotely sensed observations.

Some existing remote-sensing algorithms for the inference of phytoplankton functional types initially assume some *chl-a* dependences in their construction [24], which confounds the task of recognizing shifts in BS bloom composition, given that the inferred *chl-a* in this region has been increasing, and *chl-a* and community compositional change may therefore be convolved [13,15]. We also recognized that other algorithms to distinguish diatoms in high-latitude waters are predicated on differences in specific absorption coefficient between diatoms and mixed populations [22]. Pigment packaging is the phenomenon of the flattening of absorption spectra of suspensions of pigment as distributions change from dispersed to tightly packaged aggregates [27,28]. *Phaeocystis* forms aggregated colonies and therefore exhibits a normalized absorption spectrum that is indicative of levels of pigment packaging similar to diatoms [26], and we, therefore, may expect its optical properties to resemble those of diatoms—indeed this is indicated in fig. 2 of Alvain *et al.* [29], who recognized a *Phaeocystis*-like group in ocean-colour measurements in their development upon the PHYSAT algorithm for the inference of different phytoplankton functional types. Given diatoms and *Phaeocystis* blooms are typically associated with different styles of production (with *Phaeocystis* associated with greater regeneration [30]), remote-sensing approaches which treat these two groups as synonymous may produce results that provide misleading conclusions about ecosystem change—a salient observation that bears special consideration in the BS where gradients in remotely sensed production anti-correlate with the mass of benthic megafauna [31], suggesting that the direct interpretation of remotely sensed production as an indicator for export production is fraught. We reviewed the global PHYSAT algorithm and found that, while extensive *Phaeocystis*-like blooms are identified in the Southern Ocean, PHYSAT describes the Barents as nanophytoplankton-dominated [29], suggesting that the global PHYSAT algorithm struggles to detect different Barents phytoplankton communities. The '*Phaeocystis*-like' group identified in PHYSAT is based on ocean-colour observations from the Southern Ocean, where *Phaeocystis antarctica* predominates, as opposed to *Phaeocystis pouchetii* in the Arctic, so differences in ocean-colour between these two species may explain more pervasive identification of *Phaeocystis* in the Southern Ocean.

We hence opted to construct our own experimental bio-optical algorithm tuned to the bespoke phytoplankton functional types (coccolithophores, nanophytoplankton, diatoms and *Phaeocystis*) and conditions prevailing in the BS, to classify ocean-colour observations (see electronic supplementary material for a detailed description).

In the near future NASA's PACE (Plankton, Aerosol, Cloud, Ecosystem) mission aims to measure ocean-colour at a 5 nm spectral resolution [32], which may offer researchers the capacity to detect subtle hyper-spectral features in ocean-colour attributable to key taxon-specific phytoplankton pigments, and may therefore facilitate increased confidence in the identification of distinct phytoplankton groups from ocean-colour. However, the legacy of ocean-colour measurements already collected will still represent a rich historic dataset and we should, therefore, retain an interest in exploring the detection of distinct phytoplankton groups in existing satellite records and assessing the extent to which bio-optical algorithms can be marshalled to describe ecosystem baselines or detect incipient signals of ecosystem change in our warming climate, especially as it is this historical record that will place future observations in context. Here we develop a bio-optical algorithm in the mould of Alvain *et al.* [29]. We constructed a training dataset of ocean-colour, in order to inform a linear discriminant analysis to identify blooms of phytoplankton with a high degree of pigment packaging (hereafter referred to as 'highly packaged phytoplankton'), such as diatom or *Phaeocystis* blooms. We employ an adaptation of the experimental chlorophyll-c3 algorithm of Astoreca *et al.* [26] to test whether it might also be possible to distinguish *Phaeocystis* from diatom blooms in the BS and assess whether it is possible

to confirm isolated reports of changing phytoplankton community composition and extend our understanding by using ocean-colour to construct a regional synthesis.

2. Methods

Level-3 daily binned ocean-colour observations during the month of July 2002–2018 were downloaded from the MODIS-Aqua website, for $\lambda = 412, 443, 469, 488, 531, 547, 555, 645, 667$ and 678 nm [33] between 0–50 degrees east and 70–85 degrees north. We chose to investigate only ocean-colour observations from July, because while annual net primary production has been increasing [15] lower ice extents are associated with decreased *chl-a* biomass in spring [13]. We hence chose to study summer blooms alone to avoid the convolution of these antithetical changes.

Our experimental algorithm is a stack of 3 individual algorithm modules, which is depicted as a flow-chart in electronic supplementary material, figure S1. The first module masks ocean-colour observations that are classified as being influenced by sediment, coloured dissolved organic matter (CDOM)-rich river plumes or coccolithophore blooms. These masks were based on MODIS-Aqua ocean-colour observations from July 2014 between 0–80 degrees east and 70–85 degrees north. Modes of ocean-colour variance associated with the Ob river plume—a feature of high CDOM output, the Svalbard coast—high sediment load, and coccolithophore blooms in the central BS were identified and used to inform criteria to establish masks (electronic supplementary material, figures S2 and S3). Only un-masked ocean-colour observations are passed on to the second module.

The second module uses a linear discriminant—trained on a slew of Level-3 daily binned MODIS-Aqua ocean-colour observations, measured on the same day and within 1 degree latitude or longitude as a series of natural phytoplankton samples collected in 2017–2018—to distinguish whether ocean-colour properties are compatible with blooms of highly packaged phytoplankton (either diatom or colonial *Phaeocystis* cells). The use of Level-3 daily data for the purpose of identifying distinct phytoplankton groups follows from the example set by the development of the PHYSAT algorithm, and our 1-degree criterion follows from that used in PHYSAT validation [29,34]. Hold-p-out cross-validation on our training dataset demonstrated that highly packaged phytoplankton could be distinguished from nanophytoplankton effectively (97 and 80% of diatom and *Phaeocystis*-affiliated ocean-colour observations were assessed to be highly packaged, and some 68% of nanophytoplankton were correctly identified).

After ocean-colour observations are classified as highly packaged phytoplankton or as unicellular nanophytoplankton populations, *chl-a* estimates are recalculated using the Lab-OC4L diatom algorithm for all highly packaged phytoplankton and the Lab-OC4L prymn relationship for all nanophytoplankton populations. We justified our choice to use the Lab-OC4L diatom algorithm to estimate *chl-a* for all highly packaged phytoplankton (whether they would subsequently go on to be classified as diatoms or as *Phaeocystis*) because Cota *et al.* had described remote-sensing algorithms developed by Arrigo *et al.* for the inference of diatom, *Phaeocystis* and (diatom + *Phaeocystis*) communities as ‘very similar, perhaps indistinguishable’ [35,36].

The final module takes all observations classified as blooms of highly packaged phytoplankton and uses the algorithm developed by Astoreca *et al.* [26] to distinguish between *Phaeocystis* and diatom blooms—on the basis that Stuart *et al.* [37] had used chlorophyll-c3 as a marker pigment to distinguish diatom and prymnesiophyte-dominated samples. Discrimination is informed by a suite of hydrolight simulated ocean-colour reflectances based on optical properties of *in situ* samples of diatom and *Phaeocystis* communities. It was found the ratio of retrieved *chl-a* to inferred chlorophyll-c3 absorption separated these simulations. We recognized that MODIS-Aqua ocean-colour reflectance may not be amenable to the detection of subtle hyperspectral features, so we performed a sensitivity analysis to evaluate the effects of noise and variable bandwidth on the resolution of this feature, and diatom and *Phaeocystis* hydrolight simulations remained distinct. We found that our discriminant for *Phaeocystis* from diatoms, when applied to our training dataset, corresponded to a bimodal feature in the optical properties of highly packaged phytoplankton (electronic supplementary material, figure S6).

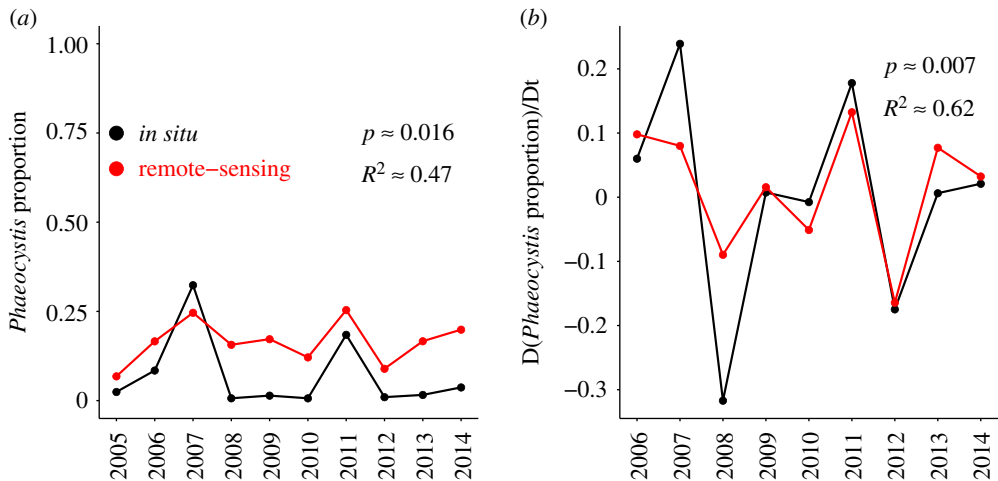


Figure 2. (a) Year-to-year variation in the dominance of *Phaeocystis* blooms in the *in situ* observations of Fragoso *et al.* [39] (black line) and from ocean-colour classifications across the Labrador Sea (red line). (b) Year-to-year variation in the derivative of *Phaeocystis* dominance. (Online version in colour.)

We found that a significant shift in mean retrieved chlorophyll-c3 signal (We use the term ‘signal’ rather than ‘absorption’ here because this metric sometimes takes negative values, for example Astoreca *et al.* [26] recorded a diatom bloom with an apparent negative chlorophyll-c3 absorption) occurred after 2009 in disparate parts of the global ocean (see electronic supplementary material, figures S7–S8) and adapted the method of Taylor *et al.* [38], who corrected for drift in the output of the IASI (infrared atmospheric sounding interferometer). Corrected chlorophyll-c3 absorption signal was then used in module 3 of our algorithm to infer the presence or absence of *Phaeocystis* blooms. The bio-optical algorithm was validated against a yearly time series of spring phytoplankton samples in the Labrador Sea, reported by Fragoso *et al.* [39] (dataset accessible at <https://doi.pangaea.de/10.1594/PANGAEA.871872>). A linear regression between the yearly *Phaeocystis* proportion of *in situ* samples, collected by Fragoso *et al.* [39] (defined as the portion of *chl-a* associated with *Phaeocystis* divided by the sum of *chl-a* associated with either *Phaeocystis* or diatoms) shows a highly significant correlation with the yearly *Phaeocystis* proportion in ocean-colour classifications (defined as the ratio of *Phaeocystis* to the sum of *Phaeocystis* and diatom classifications) (figure 2). The relationship between the inter-annual differences of these two curves is also highly significant. None of the curves show a significant linear trend over the time period 2005–2014.

We noted that the *Phaeocystis* dominance estimated across the Labrador Sea from remote-sensing was often biased high, compared to the *in situ* samples (figure 2a). This may be because the dataset of Fragoso *et al.* [39] does not contain observations along the East-Greenland coast, which we found was often pervaded by *Phaeocystis* classifications (see electronic supplementary material, figure S9, years 2007–2008, 2010–2012).

We believe we have demonstrated that our bio-optical algorithm facilitates the construction of time series of diatom and *Phaeocystis* blooms that show biogeographical patterns consistent with *in situ* observations in another Subarctic Atlantic system.

3. Results

We first tested for changes in the geographical distribution of phytoplankton blooms with time. We discuss the example of coccolithophores to clarify our approach. We controlled for

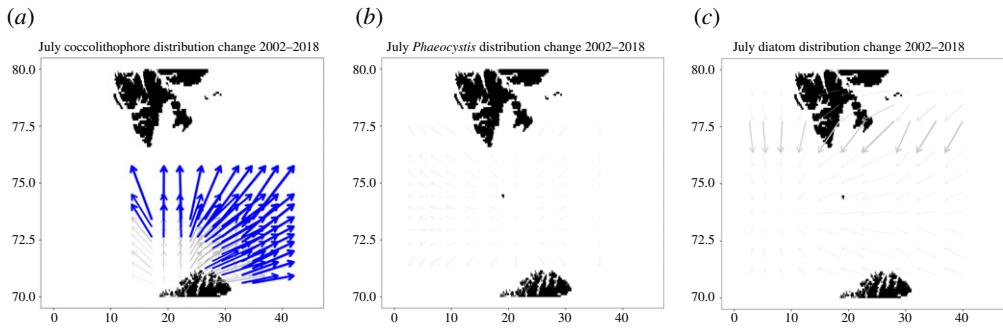


Figure 3. (a) Changing distributions of coccolithophore ocean-colour observations between 2002 and 2018. Significant (p -value < 0.05) vectors are coloured blue. (b) Vector field for *Phaeocystis* distribution change, no significant vectors. (c) Vector field for diatom distribution change, no significant vectors. (Online version in colour.)

changes in the geography of the sampled area, as a result of the inter-annual recession in sea-ice extents for example, by excluding pixels poleward of 80 degrees north—the approximate limit of ice at the start of our time series. We also excluded observations in the box between 10–30 degrees east and 76–80 degrees north, because the coastal regions of Svalbard are often identified as coccolithophore-dominated (electronic supplementary material, figure S10). It is not clear whether these classifications are spurious, but even if they are genuine their association with the coast means that they do not reflect any biogeographic changes in open-ocean coccolithophore blooms. We took all the unique pixels in our time series and computed the relative frequency of coccolithophores in each pixel for a given year—such that a pixel observed once as coccolithophore-dominated is 100% coccolithophore-dominated and a pixel observed four times, but classified as coccolithophore only twice, is 50% coccolithophore-dominated. The accuracy of the frequency estimate increases with greater observations. We then calculated the longitudes and latitudes of the quantiles of the pixel distribution, weighted by the coccolithophore frequencies in each pixel, for 10 equally-spaced values of τ between 0.1 and 0.9, corresponding to the 10th and 90th quantiles of the distribution. We performed this exercise for each year in the time series. We then took our time series of latitudes and longitudes for each quantile value and performed a linear regression with time, weighted by the number of coccolithophore observations in each year, so that a year with a strange geographical distribution but few observations would not exert undue influence. Finally, we inverted the linear models to predict changes over time in latitude and longitude for each value of τ . We built multiple linear regressions for all latitude-longitude combinations of varying τ against time, and assessed their significance by calculating p -values. The result is a field of vectors which visually describe the change in coccolithophore distribution with time (figure 3). The most north-eastern vector corresponds to the model for change in geography of the 90th quantiles for both latitude and longitude, while the most south-western vector corresponds to the model for change in the geography of the 10th quantiles for both latitude and longitude. Coccolithophores were the only phytoplankton community which demonstrated significant changes in biogeography between 2002 and 2018.

The eastern limit of coccolithophore blooms has shifted some 7 degrees eastward over the study window, while the northern limit has expanded about 1.5 degrees poleward, in accord with the findings of previous studies [13,21]. Interestingly, figure 3 also shows that the western limit of coccolithophore blooms has expanded westward by 4 degrees. The vector field of coccolithophore distribution change in figure 3 implies that there are distinct eastern and western coccolithophore blooms. It appears that the eastern bloom dominates the distribution and is migrating to the northeast, while a minor branch of western blooms is migrating towards the Fram Strait region. These two pelagic blooms may be diverging as they migrate north, because the Svalbard archipelago separates the western and eastern portions of the BS, and consequently warm ocean currents bifurcate as they head north, steered by bathymetry (figure 1).

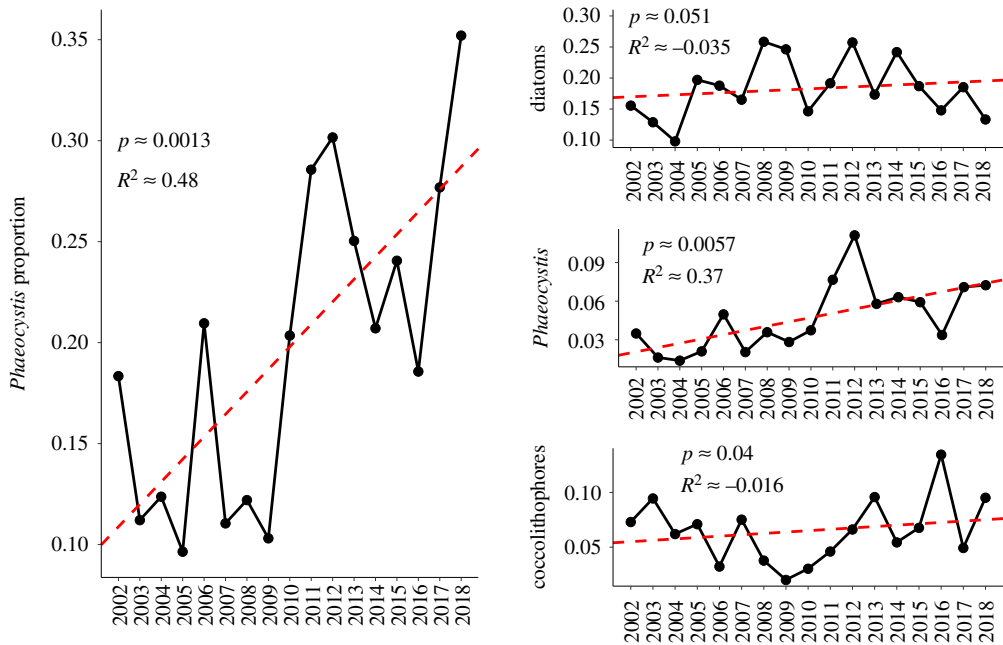


Figure 4. Evolution of the dominance of different phytoplankton groups in the Barents Sea in July. *Phaeocystis* proportion is defined as the number of *Phaeocystis* classifications divided by the sum of diatom and *Phaeocystis* classifications. All other subplots record the number of classifications of a specific phytoplankton group as a proportion of the total number of observations. Linear regressions with time are represented by red dashed lines. (Online version in colour.)

Coccolithophore blooms identified by Smyth *et al.* [20] between 1987 and 2002 were typically centred between 30 and 40 degrees east and rarely extended beyond 40 degrees east.

By contrast, this study shows that it has become routine in recent years for coccolithophore blooms to extend past 40 degrees.

We also constructed time series of the proportion of all pixels in the study area dominated by different phytoplankton communities (figure 4). Hovland *et al.* [21] commented that a large mass of Atlantic water penetrated far into the east of the BS during 2007, compared with 2010, which was a year with relatively less Atlantic influence. Figure 4 shows that 2007 has a greater proportion of coccolithophore detections than 2010, conforming to the results of these earlier studies. Although inter-annual variations in diatom frequency are large—varying between 10% and 25% of observations—no discernible pattern of biogeographic change prevails over the study window and there is no significant linear trend in their occurrence between 2002 and 2018 (figure 4). Sub-significant patterns in the vector field of figure 3 imply a slight gravitation of diatoms towards the Atlantic inflow region and this may reflect a local increase in diatom identifications here (figure 5). By contrast, *Phaeocystis* frequency is low at the start of the study window, but climbs rapidly in 2010 (figure 4). We find this particularly interesting, given that previous authors found a massive increase in the occurrence of *Phaeocystis* and associated marine gels in the Fram Strait in 2010 [40]. We also note a positive anomaly in *Phaeocystis* detections in 2006, coinciding with reports of an increase in *Phaeocystis* in the Fram Strait by Nöthig *et al.* [14]. We consider increasing *Phaeocystis* predominance compatible with the predictions that Atlantification of the Barents should be expected to increase *Phaeocystis* frequency and result in a northward expansion of more Atlantic-associated species such as *E. huxleyi* [41].

Given that a pronounced change in phytoplankton community structure was found over the study period, difference maps showing the change in the frequency of occurrence of different phytoplankton groups were created, so that we could identify the geographical regions driving

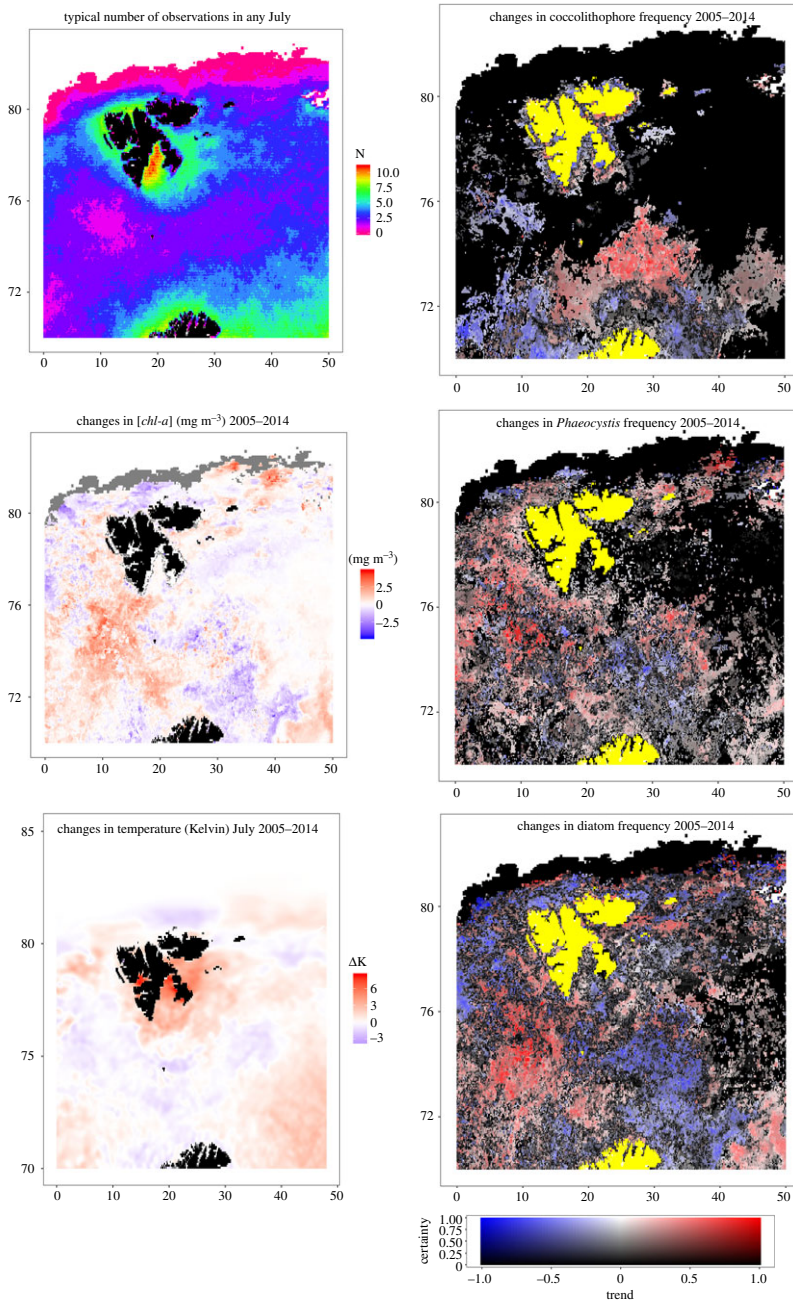


Figure 5. Maps of the changes of phytoplankton *chl-a*, temperature and community composition 2005–2014. The top-left subplot is a map of the average number of ocean-colour observations in a typical July. (Online version in colour.)

these patterns (figure 5). We limited the temporal extent to within 2005–2014 to match the period of our validation scheme in the Labrador Sea (figure 2), so that we could have confidence in the results. The difference maps were derived by computing linear models of the variable of interest—such as *chl-a* concentration or relative frequency of coccolithophores—in each unique pixel location as a function of time. We calculated the average change in each pixel that the linear models predicted and inferred significance of plankton community shifts from their *p*-values (expressed in figure 5 as ‘Certainty’, defined as $1 - p$ -value).

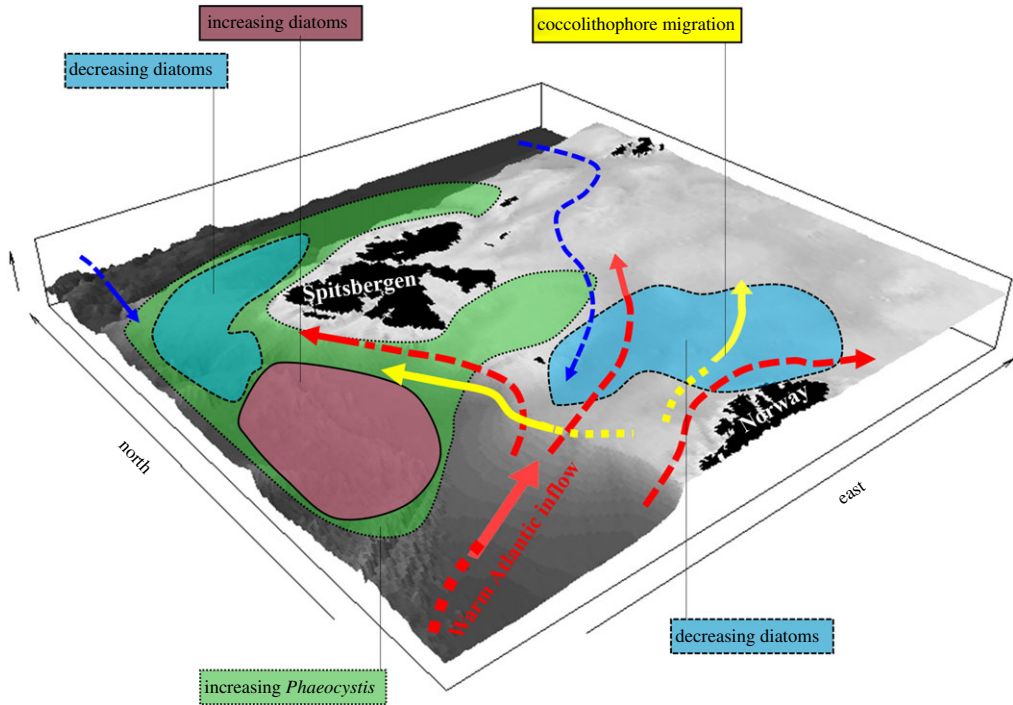


Figure 6. A synthesis of all the changes to phytoplankton community composition found in this study. Warm inflowing currents are represented in red, while cold waters flowing from the Nansen basin are represented in blue. (Online version in colour.)

Figure 5 shows that there have been increases in the mean July *chl-a* concentration in the western BS, southern Fram Strait and far south-eastern BS. The largest increases exceed 1 mg m^{-3} , west of Bjørnøya. There is an equivocal pattern of change in the frequency of diatom occurrence; while there are strong increases in the Atlantic inflow region west of Bjørnøya there are decreases further down-stream in the northern Fram Strait or over the Sentralbanken. *Phaeocystis* increases are also achieved throughout much of the western and southern BS, but are absent beyond the typical position of the PF in the Arctic-derived waters of the northeast. Changes in patterns of coccolithophore occurrence are consonant with figure 3; the frequency of coccolithophores has declined in the southwest of their geographic range and increased in the northeast. The migration of coccolithophores into the Sentralbanken region may offer an explanation for declines in the frequency of diatom detections here. Curiously, patterns of change in sea surface temperature data from the ESA SST CCI reprocessed sea surface temperature analyses (temperature maps for the 15th of July in each year downloaded from CMEMS; Copernicus Marine Environment Monitoring Service: <http://marine.copernicus.eu/>) did not correspond clearly to changes in phytoplankton community composition. The pattern of change reproduces the regional change described for 2005–2016 in Barton *et al.* figure 2C [5]. We might tentatively suggest that a broad region of declining sea surface temperature in the Atlantic inflow region aligns with increasing *chl-a* concentrations, while warming regions of the northern Fram Strait align with declines in diatoms and increases in *Phaeocystis*. Interestingly patterns of temperature change in the Fugløya Atlantic inflow section (corresponding to the BS Opening: <https://ocean.ices.dk/iroc/>) show that there has been a broad increase in sea temperatures between 50 and 200 m between 2002 and 2018, whereas surface temperature data from CMEMS implies a decline over this same period. This emphasizes that consideration of sea surface temperature in isolation may provide misleading explanations for variation in the state of ecosystems.

The sum of all the changes to phytoplankton community composition that have been found in this study are presented in a synthesis as a single cartoon in figure 6.

4. Discussion

(a) Phytoplankton community shift in the context of ‘Atlantification’

The most significant trend we have uncovered is an inferred increasing predominance of *Phaeocystis* in midsummer in the BS. The distribution of change illustrated in figure 6 suggests that the findings of ship-board sampling by Nöthig *et al.* [14] apply generally to the more Atlantic-influenced portions of the BS, consistent with expectations expressed in Reigstad *et al.* [1]. This may well be consistent with predictions by Randelhoff *et al.* [42] that enhanced Atlantic water input onto the western shelves of the BS would alleviate late summer nutrient limitation and hence support increased pelagic primary production. It is also compatible with the report of Oziel *et al.* [13] of increasing *chl-a* concentrations in the BS in late summer, and the observation of Arrigo & Van Dijken [15] of increasing annual pelagic primary production in the region. The Fram Strait region has also experienced a significant increase in *Phaeocystis* occurrence, consonant with the existing literature [14]. Given the association of *Phaeocystis* blooms with the influx of warmer Atlantic derived waters into the Fram Strait [14], it is perhaps no surprise that the least Atlantified waters of the BS prove the most resistant to increases in *Phaeocystis* predominance. These findings are complementary to our investigations of coccolithophore biogeography, that expand upon the work of authors such as Oziel *et al.* [13], Smyth *et al.* [20] and Hovland *et al.* [21], showing that coccolithophore blooms have dispersed downstream in Atlantic inflow currents. The co-association of these changes is strongly suggestive of a signal of ‘Atlantification’ in midsummer Barents phytoplankton communities—especially as patterns in change appear to be delimited by the position of major fronts—implying a bottom-up control of inter-annual variation in phytoplankton community structure. We think it is curious that no significant change in biogeography for *Phaeocystis* was recovered, but this may be a result of this genus already having a cosmopolitan distribution in the BS [19]. We note that increases in *Phaeocystis* incidence illustrated in figure 6 generally occur downstream of the sites of intense coccolithophore blooms and beyond the ‘Southern Front’ identified in Oziel *et al.* [2] but not beyond the PF, perhaps implying that phytoplankton communities of different Barents water-masses exhibit subtly different responses to environmental change. Diatom detections exhibited a complex change between 2005 and 2014, increasing their incidence in inflow regions but declining further downstream. This might result from the dual changes of increasing Atlantic inflow and decreasing Atlantic inflow silica inventories [16]. Proximity to the inflow silica may not be limiting, so an increased flux may justify higher diatom growth, but further downstream, the declining silica content of Atlantic water may mean that phytoplankton groups less reliant on this nutrient are favoured. We stress that simple studies of *chl-a* concentration or the use of bio-optical algorithms that do not subdivide highly packaged phytoplankton into diatom and *Phaeocystis* dominated assemblages would provide a much coarser impression of ecosystem change (for example, see figure 5 *chl-a* change). Coarser products such as these might be interpreted as being concomitant with suggestions of increasing new production [15]. However, our finding of increasing *Phaeocystis* predominance suggests that the style of production is likely becoming increasingly regenerated in character. This was explicitly considered by Arrigo & Van Dijken [15] as a possibility, and might be inferred from isolated *in situ* records [14,40], but we have here provided the first bio-optical evidence of this. Other authors have also pointed out that deepening mixed layers in midsummer could explain greater regenerated production [13], a hypothesis compatible with increasing *Phaeocystis*, which is a shade-tolerant genus that prospers under conditions of deep mixing [39]. These interpretations are consistent with observations that remotely sensed *chl-a* increases are concentrated in mid and late summer—when episodic mixing prevails—and that *chl-a* concentrations detected in spring—when production depends on the nutrient inventory stocked over winter—have declined in years with lower sea-ice [10,13]. This shows that the retrieval of dominant phytoplankton groups from ocean-colour can inform a more nuanced understanding of incipient ecosystem change in the

Arctic in the face of human-induced climate change. We anticipate that the launch of hyperspectral sensors (PACE) into space will further invigorate taxonomically informed approaches in the study of ocean-colour.

(b) Implications

The ecological significance of increasing *Phaeocystis* predominance is difficult to ascertain. Previous authors have argued that zooplankton may modify their diets, buffering any substantial effects on higher trophic levels [43]. By contrast, other authors have suggested that the efficiency of the biological pump should decline under *Phaeocystis* predominance [44], because descending *Phaeocystis* aggregates are remineralized faster than diatoms [30]—an observation consistent with the faster sinking rates reported for more massive diatom cells [45,46]. Suggestions of declining biological pump efficiency can be contrasted in turn with rare reports of mass-sedimentation of *Phaeocystis* [47], when colonies are ballasted by gypsum crystals rejected from sea-ice [48], or the frustules of senescent diatom blooms [49,50]. *Phaeocystis* blooms frequently succeed diatoms in the BS and the co-occurrence of diatoms ballasting *Phaeocystis* colonies has been frequently recorded [51,52]. Hence, there are credible reasons in the literature to believe that increasing *Phaeocystis* should decrease carbon export, perhaps increase it or have little effect at all.

Empirical studies of benthic carbon flux and trawls of benthic organisms also yield conflicting results. Lalande *et al.* [53] reports greater biogenic and faecal pellet export under high sea-ice conditions—suggesting a warmer less diatom-dominated BS should have a weaker biological pump—while Cochrane *et al.* [54] report lower macrobenthic animal biomass and sediment carbon content north of the oceanic PF, implying that Atlantification and the northward recession of the PF ought to increase nourishment to the benthos. These conflicting reviews can perhaps be resolved by Jørgensen *et al.* [55], who notes that the benthic expression of the PF extends much further south than the ocean surface outcrop. Jørgensen *et al.* found that megafaunal (greater than 1 cm body length) biomass distribution differed from macrofaunal (greater than 1 mm body length, but less than 1 cm), with greater mass north of the benthic PF. They hypothesized that a longer equilibration time-scale for larger benthic animals may mean changes in the benthos lag environmental change and subsequent research showed that gradients in benthic megafaunal biomass are decoupled from surface production and therefore that carbon flux must be controlled to a first order by biological pump efficiency—perhaps mediated by bloom composition, dynamics or ice-edge physics [31].

We may, therefore, synthesize these findings to suggest that a history of frequent fast-sinking diatom blooms justifies greater megafaunal biomass in northern sites, and that the Atlantification of these waters, and a switch to *Phaeocystis* predominance, will result in a poorer nourishment of the benthos and a shift in the long term to lower megafaunal biomass. We must also consider that, during mid and late summer, phytoplankton blooms in the BS descend toward the nutricline to form subsurface chlorophyll maxima (SCMs) [56], meaning some production is missed by remote-sensing approaches. In this study, this may have the effect of giving us the false impression that phytoplankton communities north of the PF are resistant to environmental change (figure 5), when communities residing at depth here may, in fact, be changing. As there is currently much debate in the literature as to the effects of neglecting the SCM on production estimates (e.g. [57–59]), Arctic shelf SCMs clearly warrant further investigation.

(c) Limitations to our experimental bio-optical algorithm

Overall, much greater confidence can be invested in the detection of coccolithophore blooms, which are clearly defined by the characteristic light-scattering properties of their shed coccoliths. Our approach is also necessarily limited by the available spectral resolution of the MODIS-Aqua sensor and by the underlying assumption in our bio-optical algorithm's construction that CDOM is invariant. This assumption is fair in the BS, where CDOM absorption remains constant even across major hydrographic features [60], but is not true outside of the BS, limiting the wider

application of our algorithm to other Arctic regions. We must also acknowledge that Astoreca *et al.* [26] caution that their reflectance algorithm for the retrieval of chlorophyll-c3 may require modification in turbid waters and that accurate quantification of chlorophyll-c3 concentrations may not be possible even under ideal conditions—only the recognition of high concentrations indicative of *Phaeocystis* blooms. We believe that we have taken care to use Astoreca's algorithm within these limitations. We might also regard the requirement to use the MODIS landbands (such as 469 nm) as a limitation, but we note that previous authors such as Hu *et al.* have made successful use of these bands for the inference of phytoplankton functional types [61]. We caution that our approach to correct for temporal drift in the inferred signal of chlorophyll-c3 absorption is specific to the MODIS-Aqua r2018.1 ocean-colour reprocessing, and that this approach may need to be modified for future reprocessings, which may subtly vary the values of different ocean-colour bands. The results from our bio-optical algorithm suggest that it is possible to construct regional algorithms for the retrieval of major phytoplankton functional types in the Arctic, and that the output from such algorithms can form a useful supplement to incomplete *in situ* records of phytoplankton community composition.

5. Conclusion

We have developed a bio-optical algorithm to retrieve dominant phytoplankton groups in the BS and probed its applicability to investigate incipient changes in community composition. We have presented evidence that an expansion of coccolithophore range further down-stream in Atlantic inflow currents is ongoing, consistent with the expectations of previous authors. We have suggested that *Phaeocystis* predominance in the BS in midsummer is likely increasing in more Atlantic-influenced regions, which is consistent with a signal of Atlantification in the Barents phytoplankton community and the expectations of several previous authors. The combination of these changes may mean that reported increases in remotely sensed production in the BS are driven in part by higher standing stocks of phytoplankton associated with regenerated styles of production increasingly mediated by the microbial loop—a change with potential significance for higher trophic levels. The retrieval of these signals of Atlantification by our bio-optical algorithm emphasizes that existing records of ocean-colour will remain useful for interpretation alongside newer ocean-colour products from up-coming missions such as PACE.

Data accessibility. The datasets of optical properties used in the construction of the phytoplankton community composition algorithm used in this study are available at [doi:10.5285/97daa7ea-8792-6cff-e053-6c86abc0dd46] [doi:10.5285/982b6da2-7e11-060a-e053-6c86abc09389] [doi:10.5285/982b6da2-7e12-060a-e053-6c86abc09389], accompanying datasets for chlorophyll-a concentration are available at [doi:10.5285/97daa7ea-8793-6cff-e053-6c86abc0dd46] [doi:10.5285/982b6da2-7e13-060a-e053-6c86abc09389] [doi:10.5285/982b6da2-7e14-060a-e053-6c86abc09389] MODIS-A data is available from NASA's website for ocean-colour. [https://oceancolor.gsfc.nasa.gov/data/10.5067/AQUA/MODIS/L3M/RRS/2018/]

Authors' contributions. A.O. carried out analyses and drafted the manuscript. H.A.B. supervised analysis and the drafting of the manuscript. T.P. edited the manuscript. B.N. assisted in the interpretation of the significance of our results for the structure of benthic communities. I.K. set up Hydrolight simulations. All authors read and approved the manuscript.

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