



Dynamics of phytoplankton species composition, biomass and nutrients in the North Atlantic during spring and summer - A trans-Atlantic study

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ABSTRACT

During a return trip in May–June 2013 from Bergen, Norway, to Nuuk, Greenland, on the Institute of Marine Research's R/V "G. O. Sars", four ocean basins, the Norwegian, Iceland, Irminger and Labrador seas, were surveyed twice. Here we analyse the phytoplankton communities and their dynamics in the four basins, winter nutrient content, potential for new production, consumption of nutrients, phenology and algae biomass (Chlorophyll *a*). The primary production dynamics of the four basins are compared and related to physical forcing and top-down control and discussed in relation to vertical carbon flux. We focus on the primary production dynamics in the central, mostly Atlantic, water masses of the basin-wide gyres. The survey results are put into a larger scale context by comparison with MODIS surface chlorophyll estimates.

The timing of the phytoplankton bloom phase differed among the basins. In the Labrador Sea, there was a strong bloom already occurring during the first crossing in mid-May. This was confirmed by nitrate and silicate reduction, which was much larger in the Labrador Sea compared to the other seas in May. In the Irminger Sea the bloom lagged behind, whereas in the Norwegian and Iceland seas both a pre-bloom and a late bloom were observed during May–June.

There was a direct relationship between the mixed layer depth and the use of nitrate at the sampling stations, and a direct relationship between chlorophyll concentrations and the use of nitrate. The two relationships suggest that the use of nitrate can serve as a measure of the developmental state of the phytoplankton bloom, phenology, and that it is related to the shallowing of the mixed layer.

Flagellates were the most abundant algae in all regions, outnumbered by diatoms only at a couple of stations west of Greenland. Elevated ciliate numbers were observed in the Iceland and Norwegian seas on both sides of the Arctic front. The algae outnumbered the microzooplankton by at least an order of magnitude.

1. Introduction

The central Labrador, Irminger, Iceland and Norwegian seas are located at similar latitudes, thus having similar biological seasonal cycles (e.g. Harrison et al., 2013; Head et al., 2013). Hydrographically there are also similarities, the Labrador and Irminger seas being part of the sub-polar anti-clockwise gyre and the Iceland/Norwegian seas, all being filled with warm and saline Atlantic water from the south in the eastern and cold Arctic water from the north in the western side of the basins (Drinkwater et al., 2020). As is typical for Arctic and sub-Arctic regions, they all exhibit relatively pronounced seasonal production cycles with spring phytoplankton blooms and far less productive winters,

even though, there are differences in the phytoplankton community, their dynamics, and the prerequisites for primary production.

The study of the primary production of the Norwegian Sea has a long history (Braarud, 1935; Gran, 1902; Halldal, 1953; Paasche, 1960; Ramsfjell, 1960; Smayda, 1958; Berge, 1958) and reviewed by Rey (2004) and Erga et al. (2014). During winter, vertical mixing reaches to several hundred meters depth in Atlantic waters, bringing nutrients to the surface waters. The winter mixing is limited by permanent stratification at about 800 and 500 m in the eastern and western sections of the southern Norwegian Sea, respectively. The winter nutrient contents potentially available for new production have been measured at 12–13, 4–6 and 1 μM for nitrate (N), silicate (Si) and phosphate (P), respectively

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(Rey, 2004; Erga et al., 2014). By modelling and measurements in the Norwegian and Greenland seas, annual total and new production have been estimated at 62–70 g C m⁻² yr⁻¹ and 45–52 g C m⁻² yr⁻¹, respectively (Skogen et al., 2007; Slagstad et al., 1999; Rey et al., 2000). In June, new production in Atlantic water near the Arctic front of the Norwegian Sea was estimated at 30 g C m⁻² (Erga et al., 2014). The start of the bloom in the Norwegian Sea occurs when the mixed layer depth is less than the critical depth (Rey, 2004), thus complying with the critical depth hypothesis (Gran and Braarud, 1935; Sverdrup, 1953). Mixed layer depth for the Norwegian Sea in late spring normally is between 20 and 30 m (Dale et al., 1999). The phytoplankton spring bloom is not particularly prominent, and the chlorophyll concentrations seldom exceed 2 mg m⁻³. It has been suggested that large populations of zooplankton, particularly the copepod *Calanus finmarchicus*, are capable of grazing down the biomass of phytoplankton even during the bloom period (Rey, 2004). The bloom itself is dominated by diatoms and limited by Si, while primary production continues after the bloom, driven by flagellates until N-limited in June–July (Rey, 2004; Ibrahim et al., 2014). After that the primary production is based on regenerated nitrogen.

The Iceland Sea is more strongly influenced by cold water outflowing from the Arctic Ocean compared to the Norwegian Sea (Drinkwater et al., 2020 this issue). These Polar waters flow southwards off East Greenland as the East Greenland Coastal Current, eventually entering the Irminger Sea (see discussion of circulation patterns in Drinkwater et al., 2020 this issue). Prior to that, a branch of this cold coastal water heads eastward, entering the Iceland Sea north of Iceland to form the East Icelandic Current. As a result, the Iceland Sea is more stratified than the Norwegian Sea and the Irminger Sea, and this limits the winter overturning depth in the Iceland Sea to about 200 m (Ólafsson, 2003), which is shallow compared to the other seas. Ólafsson (2003) thus estimated nitrate and phosphate at about 11 and 0.7 μM, respectively, after the winter overturning. The Arctic Front, immediately to the east of the Jan Mayen Ridge separates the cold, lower salinity waters in the Iceland Sea from the warm, higher salinity waters in the Norwegian Sea, exhibits weak vertical mixing and little to no enhancement of primary production (Erga et al., 2014). During the spring bloom in May primary production in the Iceland Sea has been estimated at >1 g C m⁻² d⁻¹, decreasing to <0.6 g C m⁻² d⁻¹ during the post-bloom in June/July (Gudmundsson, 1998; Palsson et al., 2012).

The Irminger Sea is the least investigated of the four basins we studied, a fact probably due to its remote location with respect to populated lands and harsh weather conditions. The winter convection and mixing extend to a depth of 700–800 m, bringing high concentrations of nutrients to surface waters with little interannual variation (Ólafsson, 2003). The surface nitrate concentrations after the winter convection has been measured at 14–16 μM, higher concentrations than in the other seas mentioned (Ólafsson, 2003; Sanders et al., 2005). New production has been estimated at 65–30 g C m⁻² yr⁻¹ in the Irminger Sea (Henson et al., 2003, 2006; Sanders et al., 2005; Waniek and Holliday, 2006; Tilstone et al., 2014). Based on winter nitrate concentrations reported by Ólafsson (2003) and average seasonal mixed layer depth from Argos buoys (Henson et al., 2003), we estimate new production at around 58 g C m⁻² yr⁻¹. Thus, estimates of new production in the Irminger Sea are slightly higher than those of the Norwegian Sea, however, methods and data used to arrive at these numbers are different.

Based on hydrography and chlorophyll concentrations and distribution, the Irminger Sea was divided into four regions: The Central Irminger Sea, the Irminger Current, the East Greenland Current and the Reykjanes Ridge (Holliday et al., 2006). Like the Norwegian and Iceland seas the initiation of the bloom in the Irminger Current and the central Irminger Sea, follows solar warming causing spring stratification and favourable conditions for the bloom. However, in the East Greenland Current and the Reykjanes Ridge regions, horizontal advection of lighter surface water causes restratification and the earliest and strongest spring

blooms in the Irminger Sea (Holliday et al., 2006). In the central Irminger Sea, chlorophyll values were low through the whole growth season (<1.1 mg m⁻³), only silicate was depleted during summer and the mixed depth decreased from 50 to 20 m from spring until summer, and winter turnover did not reach beneath 200 m (Holliday et al., 2006). Using a coupled model including physics, nutrients, phytoplankton and zooplankton and initialised with field data, Waniek and Holliday (2006) explored the dynamics of the phytoplankton bloom in the same four regions of the Irminger Sea. Integrated chlorophyll content in the upper 100 m ranged from 86 to 97 mg m⁻², maximum daily production from 0.3 to 0.5 g C m⁻² d⁻¹, and annual production from 35 to 45 g C m⁻² yr⁻¹. Day of the year for the start of the bloom ranged from 120 to 133, peak of the bloom from day 166–200, and the bloom lasted between 70 and 90 days. The total annual primary production in the central Irminger Sea has also been estimated using satellite data at 190 g C m⁻² yr⁻¹ (Tilstone et al., 2014). The reason for the large discrepancies in the productivity estimates is unclear. The winter overturning depths, nutrient concentrations and annual primary production in the Irminger Sea based on observations, satellite data and models are highly variable, both spatially and temporally. This can be related to the fact that the Irminger Sea is a mosaic of many environmentally contrasting regions and hence a systematic comparison of the results arising from different methods is not easy. Never-the-less, the large discrepancies in results indicate that future studies need to compare and evaluate the different methods to resolve this issue.

In the Labrador Sea, primary production and phytoplankton growth are mainly limited by light levels, although once a phytoplankton bloom is established, the reduction in near surface nutrient concentrations during summer/autumn can constrain phytoplankton production (Harrison and Li, 2007). As in the Irminger Sea, winter convection and mixing can reach very deep, in some years extending to 1000 or even 2000 m (Drinkwater et al., 2020 this issue). However, according to Monterey and Levitus (1997), the climatological maximum monthly mean mixed layer depth in the central Basin is 300 m and occurs in March. In late spring and summer, the mixed layer depth shallows to 10–50 m depending on the year with an annual mean between 30 and 40 m (Harrison and Li, 2007). A deeper mixed layer depth reduces light levels in the near surface layer but tends to increase nutrients. In the spring/summer period, nitrate levels are 12–15 μM and silicates are 7–9 μM (Harrison and Li, 2007, based on Garcia et al., 2006). There are significant spatial differences in the phenology of the primary production. The earliest production occurs in the northeast Labrador Sea, north of 60°N and west of the West Greenland Shelf (Head et al., 2000; Frajka-Williams and Rhines, 2010). This is driven by offshore advection of low salinity waters from the West Greenland Shelf that increases the density stratification in the region allowing production to develop (Frajka-Williams and Rhines, 2010). Year-to-year variability in the bloom intensity was found to be related to offshore advection, eddy activity and runoff from Greenland. The timing of the bloom in the central Labrador Sea is later and weaker and was only correlated with irradiance levels (Frajka-Williams and Rhines, 2010). In this respect, the Labrador Sea differs from the other basins in that the primary production tends to occur earlier in the more northern regions. Annual primary production for the Labrador Sea and Baffin Bay has been estimated at around 60 g C m⁻² for the years 2003–2018 with an increase of 5.51 ± 1.87 g C m⁻² yr⁻¹ decade⁻¹ (Frey et al., 2019).

The present analysis focuses upon the phytoplankton communities and their diversity, seasonal dynamics, winter nutrient content, potential for new production, consumption of nutrients, phenology and algae biomass (as Chlorophyll *a*, hereafter denoted chlorophyll). The phytoplankton production dynamics of the four basins are compared and related to physical forcing, chemical conditions and also discussed in light of mesozooplankton biomass and stage composition. We focus our attention on the central and mostly Atlantic water masses of the basin-wide gyres. We provide an overview of observations from all regions in each basin, but in-depth analyses are not performed for regions with

permanently vertically stable water masses such as on shallow shelf regions or areas stratified by low salinity surface waters from coastal runoff or ice melt water, since phytoplankton bloom dynamics in such waters are different to the central ocean regions (e.g. Rey, 2004). Our aim is to compare the phytoplankton bloom dynamics of the central and largest regions of these seas.

2. Material and methods

The EURO-BASIN cruise with R/V G.O. Sars started in Bergen, Norway, May 1, 2013. The waters of the Norwegian, Iceland, Irminger and Labrador seas were surveyed twice as the ship crossed the four ocean basins on its voyage from Bergen to Nuuk, Greenland and return (Fig. 1). The ship reached Nuuk 22 May, left 24 May and reached Bergen 14 June.

2.1. Hydrography, chlorophyll, and nutrient sampling and post-cruise analyses

A total of 58 CTD stations were taken to 1000 m or less (although some deeper stations were taken to 2000 m or more). The CTD was a SBE 911plus CTD with sensors for temperature, conductivity, oxygen (SBE43), fluorescence (Aqua-III), and irradiance/PAR (Biospherical/Licor). The hydrographic and oxygen data are analysed in detail by Drinkwater et al., 2020 (this issue). A SBE 32 Carousel with 10-L sampling bottles was mounted on the CTD, and on all stations water samples were collected for chlorophyll, phaeopigments (not further analysed here) and nutrient analyses. The water-bottle depths sampled were standard ICES sampling depths that varies with total sampling depth of the CTD station. Additionally, a surface sample for chlorophyll analyses was obtained from a bucket at each station.

Chlorophyll samples (263 mL) were collected from the Niskin bottles in the upper 100 m and were immediately filtered (Munkell, Micro-Glassfibre filters, diameter 25 mm, pore retention 0.7 μm) and stored at -20°C until analysis on shore. The assay was performed by extraction with 90% acetone followed by centrifugation, and the measurements were conducted with a fluorometer (model 10 AU, Turner designs Inc., Sunnyvale, Ca., USA), according to Welshmeyer (1994) and Jeffrey and Humphrey (1975). Water samples for nutrients were collected from all water-bottle depths in 20 ml polyethylene vials, conserved with 0.2 ml chloroform and stored at 4°C for subsequent analyses in the laboratory on shore as described by Bagoien et al. (2012). In this paper, we only discuss nitrate and silicate concentrations.

The use of nitrate at any time were calculated as the nitrate concentration at 100 m, projected to the water column above 100 m and integrated for the 0–100 m, minus the integrated concentration of the nitrate measured for the 0–100 m water column.

$$N_u = \sum_{z=100}^0 c_{100} - c_z$$

where N_u is the nitrate used, z is depth, C_{100} is nitrate concentration at 100 m and c_z is the nitrate concentration at depth z . This difference represents the assumed winter concentration of nitrate in the upper 100 m after the winter convection having replenished the surface waters with new nutrients, minus the nitrate left at any time, which equals the amount of nitrate used for algal growth.

The winter nitrate concentrations were also used (with results from the literature) to calculate potential for new production in the four basins.

2.2. Sampling and analyses of protist diversity

During the cruise, quantitative and qualitative samples were taken for identification and enumeration of protists. Quantitative samples were taken at all standard CTD stations by obtaining 100 ml water samples at 10 m depth. The depth is assumed to be representative for the upper mixed layer. The samples were added to dark glass bottles and preserved with neutralized lugol solution. The samples were processed during the cruise using a compound light microscope (Leica DMR, 200 \times times magnification). The phytoplankton were enumerated using a Palmer-Malony chamber (0.1 ml) and semitransparent membrane filter (25 mL samples) according to Karlson et al. (2010). The method for enumeration is suitable for analysing onboard a moving ship, with a detection level of 10,000 cells L^{-1} (Palmer-Malony chamber) and 40 cells L^{-1} (filter method). The samples were analysed to the lowest taxonomic level possible, using a light microscope.

Qualitative samples were taken at approximately every second station, a total of 30 samples. A vertical phytoplankton net haul was made from 30 to 0 m. The phytoplankton net had a mesh size of 10 μm and was hauled at 0.1 m s^{-1} . The samples were preserved with neutralized formalin. The net samples were investigated using a light microscope (Leica DMR) during the cruise for identification of phytoplankton species.

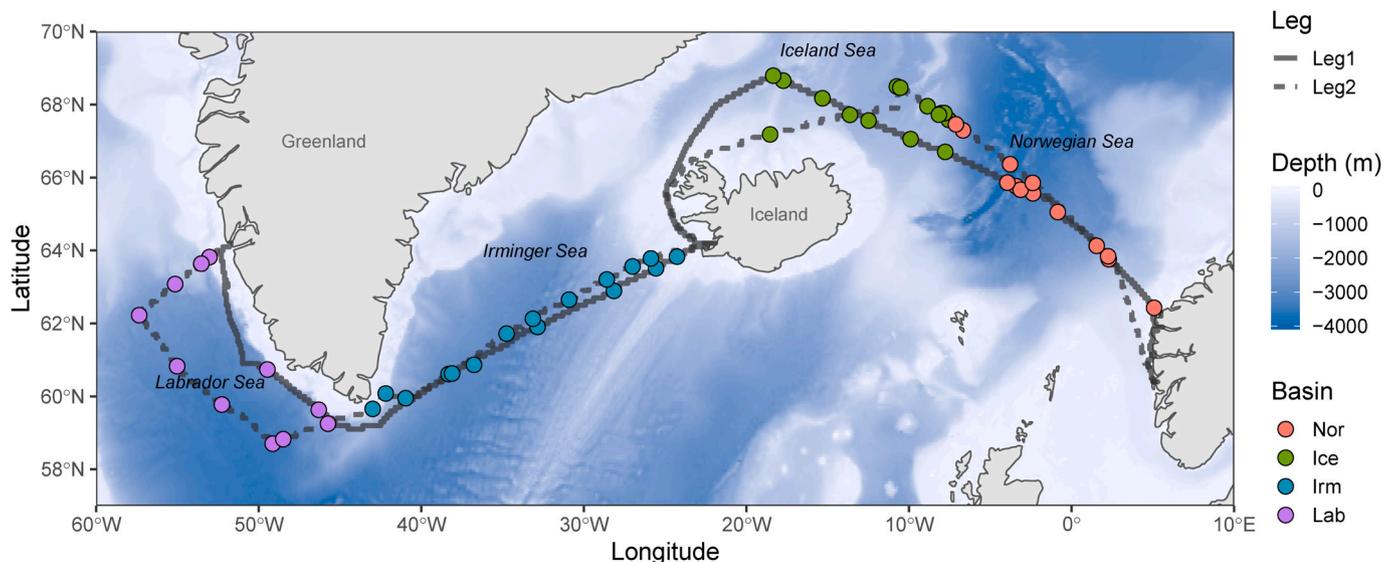


Fig. 1. Cruise map. CTD stations with water samples are shown as dots with colours based on basin. Lines are cruise track of Leg1 (westward) and Leg2 (eastward). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2.3. Underway sampling of hydrography and fluorescence

A thermosalinograph with a Wet Labs Wetstar WS3S-1253 fluorometer, measured temperature, conductivity and fluorescence continuously along the ship-track in water from an intake at 8.5 m depth. The data were written to file every 30 s with geographic position and time.

2.4. Satellite data

To put the survey results into a larger scale context, we downloaded 8-day averaged MODIS surface chlorophyll estimates (9-km resolution) for the period of the cruise.

2.4.1. Longer-term patterns

To assess differences in the patterns of annual primary production, we extracted MODIS A surface chlorophyll estimates for the years 2002–2019, for areas in the vicinity of the cruise track (see Fig. 1 and 10), inside the area covered by a box extending from 62°W to 8°E, and from 55°N to 75°N. Inside this area, grid cells were assigned to basins based on spatial positions.

Based on the 8-day satellite composite averages, geometric means, medians and maxima were computed for the different basins, for periods where the satellite data had at least 30 measurements (9-km resolution) per basin. To separate samples from open waters from more coastal water masses, data collected in areas with a bottom depth of <750 m were labelled as “coastal”.

2.4.2. Fluorescence and the calibration and intercalibration of the three fluorometers used

For calibration of the fluorometers, measured chlorophyll concentrations from 0, 5 and 10 m depths, were used. During the survey, three types of fluorometers, mounted on different platforms, were used. A Chelsea AquaTracka III on the Seabird 911plus CTD, a Seapoint Chlorophyll Fluorometer (SCF) on the MESSOR (data not used in the present analyses, but in Melle et al., 2020 and Strand et al., 2020 this issue), and a Wet Labs Wetstar WS3S-1253 fluorometer on the thermosalinograph, the latter giving continuous underway measurements at 8.5 m depth. All fluorometers were not calibrated prior to the survey. However, the Wet Labs Wetstar WS3S-1253 fluorometer was sent to the producer in the U. S. and checked by a factory pre-calibration undertaken after the cruise, on October 15, 2013. Thus, the calibrated WetStar data, along with chlorophyll data from the water bottles, were considered the best available from the cruise. These data were used to establish relationships between the different fluorometers and between fluorometers and chlorophyll measured from the water bottles. After calibration both *in situ* fluorescence and water bottle chlorophyll, were in the same unit ($\mu\text{g L}^{-1}$). See Supplement (A) for details.

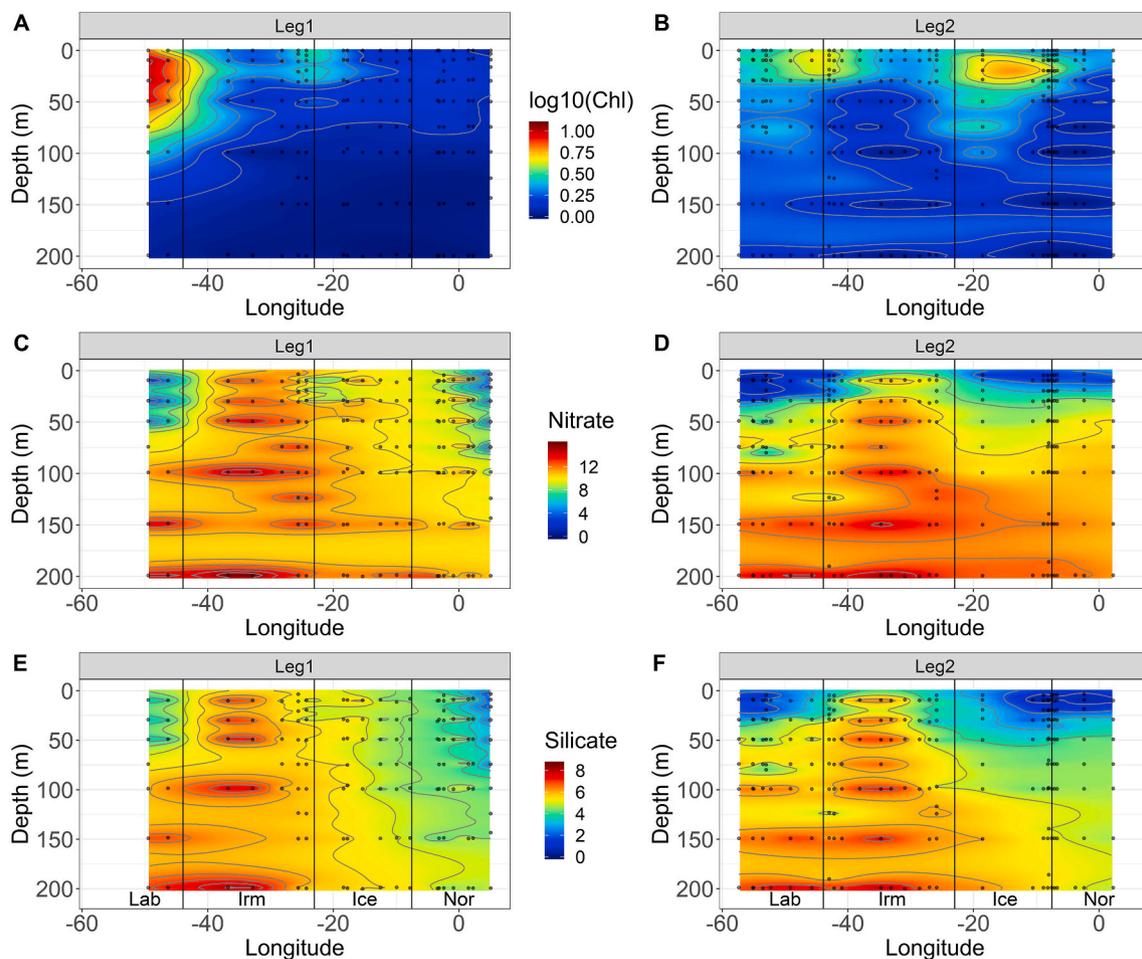


Fig. 2. Chlorophyll (Chl; $\mu\text{g L}^{-1}$, panels A&B), Nitrate (μM , panels C&D) and Silicate concentrations (μM , panels E&F) as a function of depth and longitude, during westward (Leg1, panels A,C,E) and eastward legs (Leg2, panels B,D,F). All data (black dots) measured from water bottle samples on the CTD Carousel. Vertical lines indicate what basin the samples belong to.

3. Results

3.1. Nutrients, chlorophyll and diversity from shipboard observations

3.1.1. Large-scale horizontal and vertical distribution of chlorophyll, diversity of protists, nitrate and silicate concentrations

During the westward survey across the North Atlantic basins, chlorophyll concentrations were low in all ocean regions (Fig. 2), except on the continental shelves west of Iceland and Greenland, in the Irminger and Labrador seas, respectively. Most of the phytoplankton was in the upper water layers, above 50 m depth as depicted by chlorophyll concentrations (Fig. 2). The overall low chlorophyll concentrations were reflected in the nitrate and silicate concentrations being close to winter values except for the shelf stations west of Iceland and Greenland where a bloom was ongoing (Fig. 2). On the Norwegian Shelf, both the nutrient and the chlorophyll concentrations in the surface waters were low, indicating that the spring bloom had already taken place (Fig. 2). From the Norwegian/Iceland and into the Irminger and Labrador seas, there was an increasing trend in concentrations of nutrients below 100 m, probably related to the winter nutrient concentrations in those seas (Fig. 2).

During the eastward survey, the same trend in deep nutrient concentration values was visible (Fig. 2), but a deeper utilisation of nutrients in the Iceland and Norwegian seas basin compared to the western basins cannot be excluded. Chlorophyll concentrations increased notably in the Irminger, Iceland and Norwegian seas from the first to the second survey (Fig. 2), and mostly were contained within the upper 25 m. The Irminger Sea chlorophyll concentrations were still lower than in the other basins. Except for in the Irminger Sea, nitrate and silicate levels were now approaching a state of depletion in the surface layers in all regions, and the surface reduction of nutrients seemed to reach deeper in the west (≤ 30 m; Fig. 2) than in the east (≤ 20 m). The Irminger Sea stands out with a considerable amount of nutrients left compared to the

other basins, which fits with the lower chlorophyll levels. Continuous measurements of chlorophyll from the underway fluorometer on the thermosalinograph (Data not shown), confirm the horizontal distribution of chlorophyll as depicted by the water bottle samples on the CTD.

The count-based abundances of algae and microzooplankton in all the four basins increased in the period between the westward and the eastward crossing (Fig. 3), though in the Labrador Sea, the difference in timing of the surveys was just a few days. Flagellates were the most abundant algae in all regions, outnumbered by diatoms only on a couple stations west of Greenland (Fig. 3). Diatoms were numerous at some stations in the Labrador and Iceland seas, whereas dinoflagellates were present in moderate numbers with higher concentrations in the Norwegian Sea during the eastward survey. Elevated ciliate numbers were observed in the regions of the East Greenland current, the shelf stations around Iceland and during the eastward crossing in the Iceland and Norwegian seas on both sides of the Arctic front. The algae outnumbered the microzooplankton by at least an order of magnitude (Fig. 3).

The protists were not only identified to the four higher taxonomic levels presented in Fig. 3, but also to lower taxonomic levels. Here a summary of the distributions of these taxa are presented. Within the Norwegian Sea, in early May, the phytoplankton were dominated by small flagellates and the dinoflagellate genus *Gymnodinium*. In the Iceland Sea, the phytoplankton community was dominated by smaller flagellates, where *Phaeocystis pouchetii* were numerous at several stations. At the shelf stations, diatoms from the genus *Chaetoceros* and *Fragilariopsis* were numerous. In general, the concentrations were low in the Irminger Sea in May. In the Irminger Sea, on the shelf station off West Iceland, diatoms from the genus *Chaetoceros*, *Thalassiosira* and *Asterionellopsis* were prominent. In the open sea areas, smaller flagellates such as *Phaeocystis*, dominated the algal community, while the dinoflagellate genera, *Gymnodinium* and *Gyrodinium*, were also present. The Labrador Sea was covered during mid-May by three stations along the west coast of Greenland. On the near-shelf stations, there was an

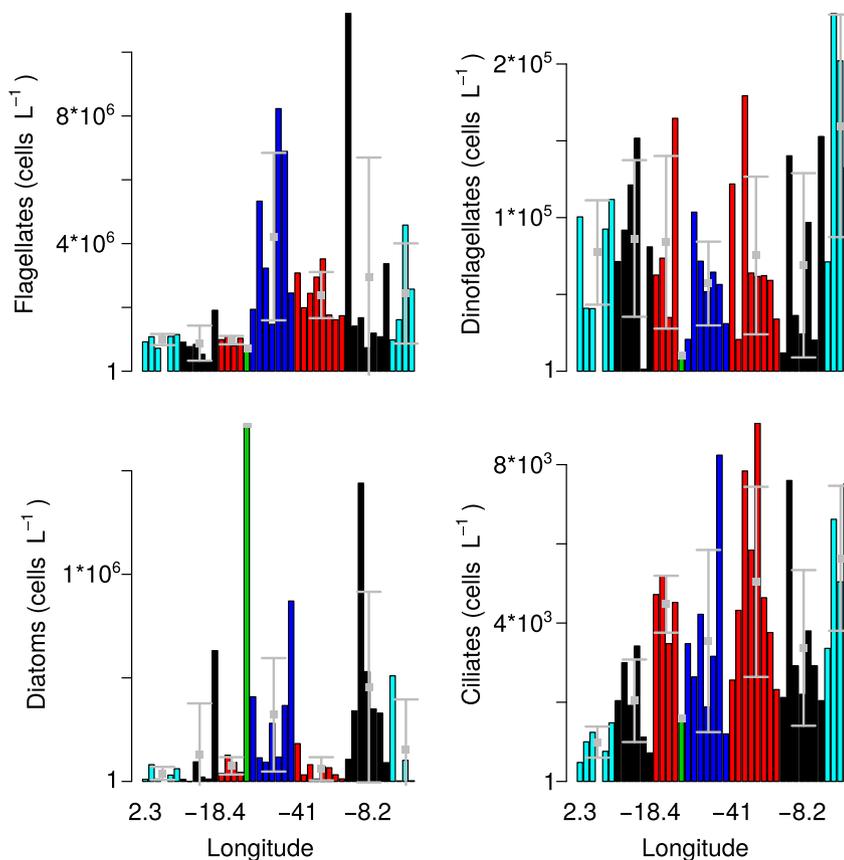


Fig. 3. Main groups of phytoplankton; flagellates, dinoflagellates, diatoms, and microzooplankton; ciliates, identified and counted from water bottle samples on the Carousel at CTD stations > 60 km from land, along the survey transects. Densities are plotted for stations, so the x-axis is categorical, and we have overlaid the longitude of select stations along the transect as labels. Colour of the bar indicates basin. Light blue: Norwegian Sea, Black: Iceland Sea, Red: Irminger, Green: Labrador, westward leg, Dark blue: Labrador, eastward leg. Grey points and error bars are basin crossing means ± 1 standard deviation. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

ongoing diatom bloom dominated by the genus *Chaetoceros* and *Thalassiosira*. In addition, there were high concentrations of the flagellate *Phaeocystis*.

The Labrador Sea was covered again during the eastward crossing at the end of May by some stations just off the Greenland coast and more stations farther west in the central Labrador Sea. In the off-shelf stations, the flagellate *Phaeocystis* was more numerous than diatoms. At the end of May, the concentrations of the diatoms *Chaetoceros* and *Thalassiosira*, and the flagellate *Phaeocystis* were high on the East Greenland Shelf of the Irminger Sea. In the central Irminger Sea, the phytoplankton community was dominated by smaller flagellates, as well as *Phaeocystis*. On the shelf northwest of Iceland at the beginning of June, the diatom *Fragilariopsis* was numerous, whereas at one station northeast of Iceland, the flagellate *Phaeocystis* dominated. Farther east in the Iceland Sea, the phytoplankton community was a mix of small flagellates (e.g. Coccolithophorids), dinoflagellate (*Gyrodinium*) and diatoms (*Fragilariopsis*). Compared to May, there was an increase in microzooplankton in the Iceland Sea. In the Norwegian Sea, diatoms were more prominent in the eastern part, whereas smaller flagellates were more numerous in the western areas. The silicate concentration was considerably lower compared to early May, and the diatoms may have been close to silicate limited.

Chlorophyll measurements from water samples, as well as diversity of protists confirmed that the shelf stations differ with respect to phytoplankton bloom dynamics and characteristics from the deep ocean basins. The use of nitrate and silicate was higher, and ciliates were more numerous on the shelf stations (data not shown), suggesting that these stations were further along in the bloom phenology. However, the main objective of this study was to compare the bloom dynamics of the four basins, thus in the remainder of this analysis we ignore the shelf stations (less than 60 km offshore) to enable a comparison of the oceanic realms.

3.1.2. The dynamics of the phytoplankton blooms in the four basins

The average chlorophyll concentrations during the westward

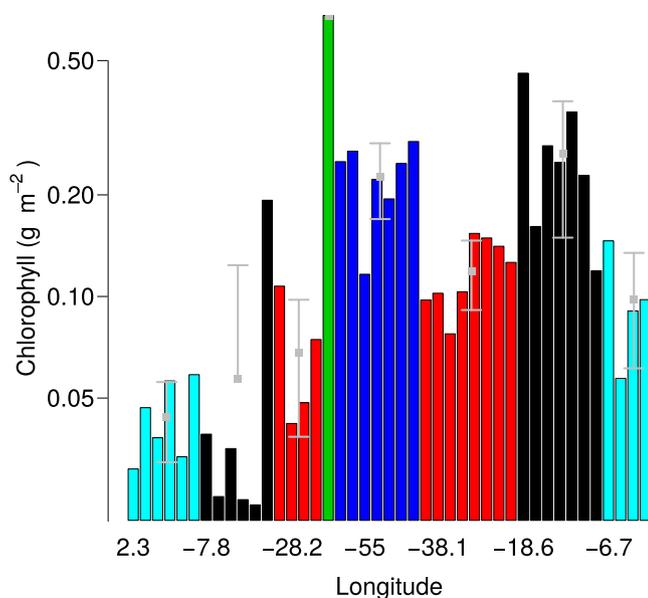


Fig. 4. Integrated chlorophyll concentrations (0–100 m, measured from water bottle samples on the Carousel) for all CTD stations > 60 km from land. Grey points and error bars are basin crossing means \pm 1 standard deviation, logarithmic scale. The x-axis is categorical, we have overlaid the longitude of select stations along the transect as labels. Light blue: Norwegian Sea, Black: Iceland Sea, Red: Irminger, Green: Labrador, westward leg, Dark blue: Labrador, eastward leg. Grey points and error bars are basin crossing means \pm 1 standard deviation. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

crossing were higher in the Labrador Sea than in the other basins (Fig. 4). The chlorophyll in the Iceland Sea and Norwegian Sea was on average the lowest compared to the other two regions. From the westward to the eastward crossing, chlorophyll concentrations remained high in the Labrador Sea, while there was an increase in the other basins. This relative increase was largest in the Iceland Sea. During the eastward crossing the chlorophyll concentrations were, on average, highest in the Iceland Sea and lowest in the Norwegian Sea. The basin-wide variations and changes in chlorophyll concentrations from the westward to the eastward crossings, were reflected in nutrient concentrations. During the westward crossing, the nitrate and silicate values of the Labrador Sea were lower than in the other basins (Fig. 5). At the time of the return, nitrate and silicate concentrations were much lower in the Norwegian and Iceland seas, while there was little difference between the two crossings in the Labrador Sea. The changes in nitrate and silicate concentrations from the westward to the eastward crossing were not pronounced in the Irminger Sea, except for some stations in the northeast (Fig. 6).

The amount of nitrate and silicate at any time will be the amount present after the deep winter convection minus the amount used by the algae during their growth (neglecting horizontal advection). During the westward crossing, the Labrador Sea was the only basin with a notable decline in nutrients, thus indicating phytoplankton production had taken place (Figs. 5 and 6). At the time of the eastward crossing the phytoplankton production had increased in the other three basins. There was no difference between the seas, although the Irminger Sea still had a lower use of nutrients. Within both the Labrador and the Irminger seas there was a trend in the use of silicate from west towards east (Figs. 5 and 6), indicating a larger diatom growth in the west.

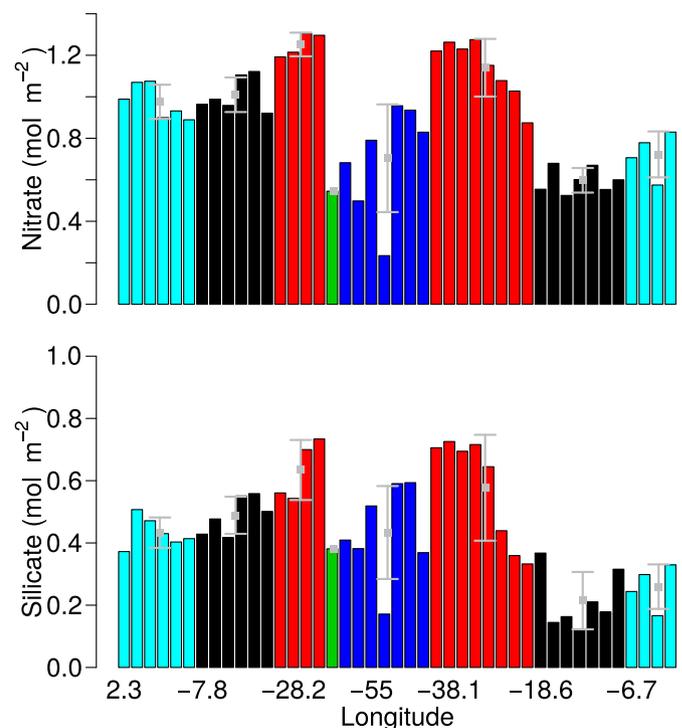


Fig. 5. Integrated nitrate (upper row) and silicate (lower row) (0,100 m) for CTD stations > 60 km from land along the survey transects. Colour of bar indicates basin, westward transect on the left, eastward on right, x-axis labels denote longitude. The x-axis is categorical, we have overlaid the longitude of select stations along the transect as labels. Light blue: Norwegian Sea, Black: Iceland Sea, Red: Irminger, Green: Labrador, westward leg, Dark blue: Labrador, eastward leg. Grey points and error bars are basin crossing means \pm 1 standard deviation. Nutrients measured from water bottle samples on the Carousel. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

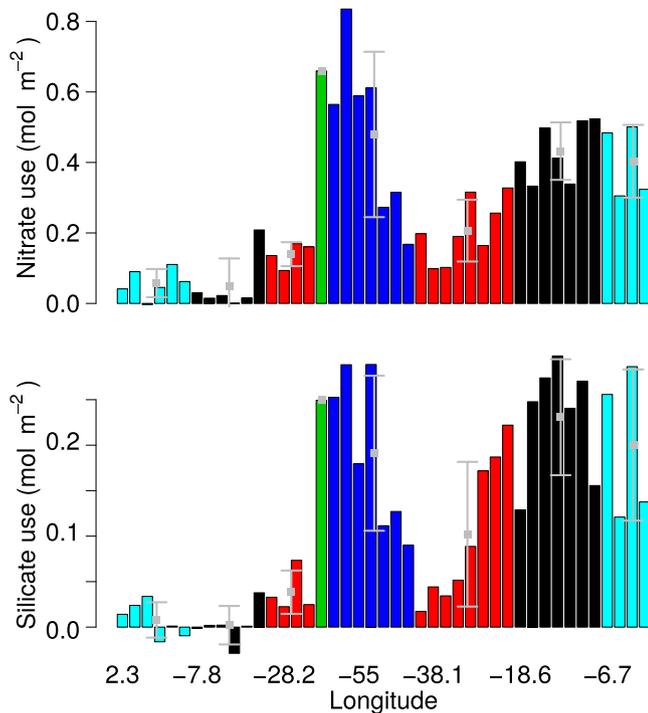


Fig. 6. Reduction of nitrate and silicate. Integrated nitrate and silicate (0–100 m) for all stations > 60 km from land, along the survey transects. The x-axis is categorical, we have overlaid the longitude of select stations along the transect as labels. Colour of bar indicates basin. Light blue: Norwegian Sea, Black: Iceland Sea, Red: Irminger, Green: Labrador, westward leg, Dark blue: Labrador, eastward leg. Grey points and error bars are basin crossing means ± 1 standard deviation. Nutrients measured from water bottle samples on the Carousel. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

During the time used traversing the North Atlantic basins, the mixed layer depth shallowed, particularly in the Iceland and Norwegian seas, where the timespan from the first to the last observations was greatest (Fig. 7). The shallowing of the mixed layer was also obvious in the Irminger Sea but showed spatial variation. Above, we showed how the use of nitrate increased over the same time span, though with

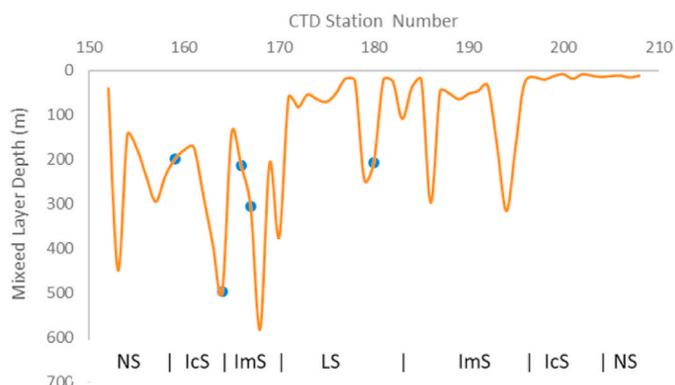


Fig. 7. Mixed layer depth by CTD station based on the depth where the difference in sigma-theta with the surface is > 0.125 . The blue dots indicate stations where the difference in sigma- θ at the surface and the maximum depth of the CTD profile is < 0.125 . In these cases, the MLD is plotted as the maximum depth of the CTD profile whereas the actual MLD is deeper than indicated. After Drinkwater et al. (this issue). NS=Norwegian Sea, IcS=Iceland Sea, ImS=Irminger Sea, LS=Labrador Sea. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

pronounced basin-wise differences (Fig. 6). There was a direct relationship between the seasonal shallowing of the mixed layer and the decline of nitrate in the upper 100 m (Fig. 8), and at the same time a direct relationship between the use of nitrate and integrated chlorophyll concentrations (Fig. 9). Note that Figs. 8–9 are based on all stations, including the shelf stations. This indicates a functional relationship between the shallowing of the upper mixed layer and the start and development of the phytoplankton production. In Strand et al., 2020 (this issue) and Melle et al., 2020 (this issue), they show how this energy progresses further up the food web.

3.2. Comparing annual cycles across the 4 basins based on satellite data

The 8-day satellite data (Fig. 10) show patterns that were consistent with the *in situ* observations of chlorophyll and changes in nutrients: during the early phase of the cruise there was an active bloom in the Labrador Sea, with relatively low chlorophyll levels (< 1 mg m^{-3}) found in the other basins. During the last part of the cruise the bloom was clearly over its peak in the Labrador Sea, and chlorophyll levels were patchy, but clearly higher (e.g. high proportion > 1 mg m^{-3}) than in the early phase in the 3 other basins. In June (last part of covering), there were areas north and northeast of Iceland showing high phytoplankton growth activity (Fig. 10), a pattern that fits with the *in-situ* observations (Fig. 4). The overall annual cycles of satellite-detected chlorophyll levels were somewhat similar between the areas (Fig. 11), with low average values during the first part of the year, increase in spring, and levels well above the winter minimum maintained during summer and fall. Overall average values (medians and geometric means) were low, and only the Labrador Sea showed average values exceeding 1 mg m^{-3} during any time of year (Fig. 11). Maximum values registered by the satellites, e.g. “bloom levels”, were however much higher, with local (e.g. 9 km) bins registering values above 50 mg m^{-3} most years in the Labrador Sea (Fig. 11), and above 30 mg m^{-3} most years in the Iceland Sea. In comparison, local bin levels above 25 mg m^{-3} were absent from the Irminger and Norwegian seas.

4. Discussion

4.1. Phytoplankton blooms and the use of nutrients; *in situ* measurements

Previous studies have addressed factors affecting primary productivity across the basins covered by this study (Tilstone et al., 2014, 2015), but, to our knowledge, no field-based studies have compared these factors across all areas. We believe that the results obtained by this comparative approach are important additions to the pelagic ecology knowledge-base of the four basins, and that they highlight some important differences among them. However, the design of this survey

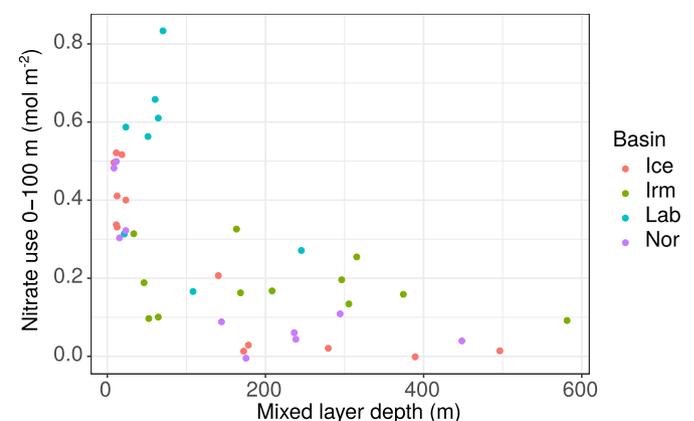


Fig. 8. Nitrate depletion (Fig. 9) versus mixed layer depth (Fig. 10). Including shelf stations.

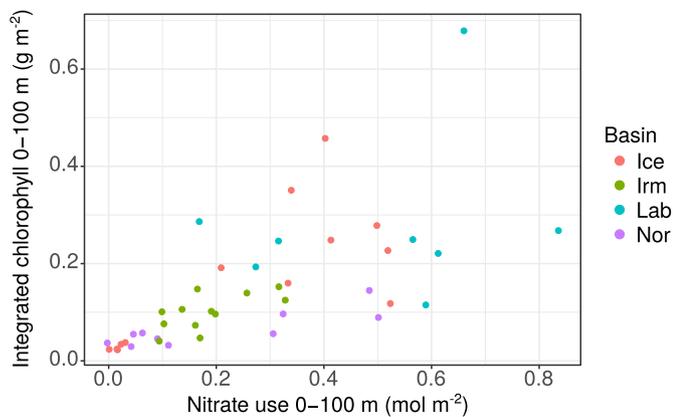


Fig. 9. Concentration of chlorophyll integrated over the upper 100 m (Fig. 7) versus nitrate depletion (Fig. 9). Including shelf stations.

of the four North Atlantic basins introduced some uncertainty to the analysis and interpretation of the data. All basins were visited twice, but obviously not at the same time. Additionally, particularly in the Labrador Sea the eastward crossing surveyed different areas than those surveyed during the westward crossing, and the time span between crossings were less than for the other seas.

The timing of the phytoplankton bloom phase differed among the basins. In the Labrador Sea, there was a strong bloom already occurring during the first crossing in mid-May, even if we do not consider the shelf stations with physical conditions facilitating an early bloom (e.g. Rey, 2004). This was confirmed by nitrate and silicate reduction, which was much larger in the Labrador Sea compared to the other seas in May. This is in accordance with Frajka-Williams and Rhines (2010) that described the timing of the bloom in the Labrador Sea to be related to the spring increase in irradiance, and mixed layer depth to be governed by an earlier offshore advection of low salinity waters from the West Greenland Shelf that increases the density stratification in the region allowing phytoplankton biomass increase in the surface layer. Therefore, the timing of the bloom is earlier than in the other basins, and the mechanism that allows the bloom to start is different as well. During the return survey, the bloom had also accelerated in the other seas, particularly in the Iceland Sea where the highest chlorophyll concentrations occurred. The coverage in 2013 fit with a previous study showing reduced nutrient concentrations and high phytoplankton production north of Iceland in the period May–June (Gudmundsson, 1998). Also, in the Norwegian Sea, there was a reduction in nutrient concentrations (Figs. 5 and 6) between the two transects that indicated increased phytoplankton production between the start of May and mid-June. The timing of the spring production will vary within the Norwegian Sea area, but the observation from 2013 fit with the observations by Dale et al. (1999) where the spring production peaked in May–June. Chlorophyll concentrations during the eastward crossing were lowest in the Norwegian Sea, while the use of nutrients was slightly lower in the Irminger Sea compared to the other seas. However, in the Irminger Sea, the winter nitrate values were also the highest. Possible top down effects that can explain the difference in the development of the blooms are discussed below.

In accordance with the critical depth theory (Gran and Braarud, 1935; Sverdrup, 1953), net growth in the phytoplankton population occurs when growth exceeds the losses, which is facilitated when the mixed layer depth during its shallowing following the deep overturning during winter, becomes equal to or less than the critical depth. The spring bloom has also been described as a decoupling between the growth and losses, with a positive net growth phase starting in winter and peaking at the time of the spring bloom, not being related to the stabilisation of the water column and allowing blooms to occur in so-called unestablished water columns (Behrenfeld and Boss, 2018).

There is a debate about the role of physical and biological factors in the formation and triggering of the spring bloom (Behrenfeld and Boss, 2018; Mignot et al., 2018). Data indicate that the spring bloom could start up during the winter with a deep mixed layer, but only at a low production rate (Mignot et al., 2018). Growth under suboptimal conditions, low light and deep mixing layer, may be possible due to low grazing pressure in winter. Mignot et al. (2018) argued that the rapid increase in phytoplankton growth and biomass, accumulation of biomass in the surface layer, takes place when the convection in the upper layer stops and with the shallowing of the mixed layer depth. During our cruise, there was a direct relationship between the mixed layer depth and the use of nitrate at the sampling stations (Fig. 8). There was also a direct relationship between chlorophyll concentrations and the use of nitrate (Fig. 9), but with much variation. The two relationships suggest that the use of nitrate can serve as a measure of the developmental state of the phytoplankton bloom, phenology, and that it is related to the shallowing of the mixed layer. However, we do not say whether there is a causal relationship between the bloom development and the mixed layer depth as suggested by the critical depth theory. Nevertheless, nitrate consumption and mixed layer depth can serve as indices of phytoplankton phenology. Nitrate consumption integrates past new production, until the nitrate is depleted. Even though some stations were not sampled until early June, we did not see a reduction in the chlorophyll concentrations at levels of high nitrate use, indicating that we did not observe post-bloom conditions. There are differences in how the mixed layer develops among the basins, particularly in the Labrador Sea and on the shelves, where low salinity water tends to overlay denser and more saline water. The timing and mechanisms behind the relationship between mixed layer depth and bloom dynamics (Figs. 7–9) are unique for each basin. In the Iceland and Norwegian seas, the mixed layer depths were more than 150 m during the westward crossing, while on the return towards east the mixed layer depths were consistently less than 30 m. In the Labrador Sea, the mixed layer depths during the westward crossing were greater than 50 m, even though we observed a strong bloom. During the return trip across the Labrador Sea mixed layer depths were variable, but in general deeper than in the Iceland and Norwegian seas. Similarly, the mixed layer depths in the Irminger Sea were greater than 50 m, even during the return trip, when nutrient use and chlorophyll levels suggested that the bloom had started. These differences in mixed layer depths during the blooms may have an important influence on the total annual phytoplankton production, since more nutrients will be available for new production (and thus total annual primary production) when mixed layer depths are deeper. In addition, winter nitrate values are greater for the Labrador Sea, and particularly the Irminger Sea compared to the other two seas. If we assume winter nitrate concentrations in the Irminger Sea to be 14 and in the Norwegian sea 12 μM , while mixed layer depths are 50 and 30 m, respectively, new production in the Irminger Sea will be twice that of the Norwegian Sea. Even if recycled production may to some extent mask this difference in terms of annual total production, it indicates that the potential for vertical carbon export and support of higher trophic levels is higher in the Irminger Sea. This is further discussed in 4.2.

In the survey of the Norwegian Sea in May, the nutrient data indicated a pre-bloom situation at most stations with relatively high surface concentrations of nitrate and silicate. The phytoplankton were dominated by smaller flagellates during this period, a phytoplankton composition that has been observed in other studies (Dale et al., 1999). When the area was revisited in mid-June, the reduced silicate concentrations indicated a bloom or post-bloom situation. In the microscope samples, diatoms (*Fragilariopsis* spp.) were only present in moderate concentrations in the western part of the Norwegian Sea, whereas flagellate, dinoflagellates and microzooplankton were more prominent in the eastern part, typical of a post-bloom situation. In the Iceland Sea, there were no large differences based on the species composition between the two survey times, except for the total number of cells. During both transects, there were stations dominated by the flagellate

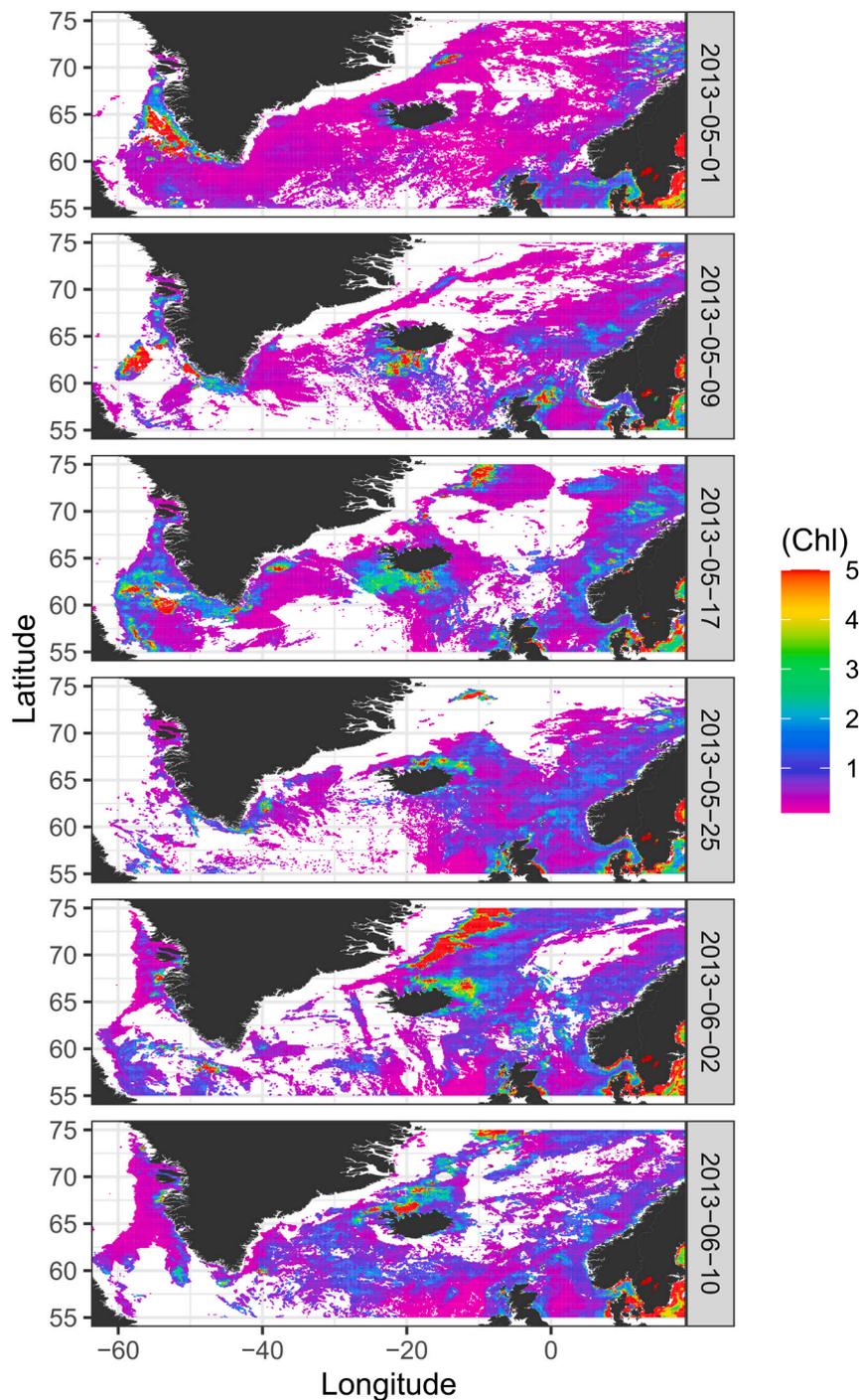


Fig. 10. MODIS A May - June 2013: 8d satellite derived chlorophyll values (mg m^{-3}) for the period May 01 to June 18. We use a linear scale to highlight areas with high chlorophyll concentrations (e.g. “blooms”), but had to truncate at 5 mg m^{-3} prior to plotting, lest only the areas in the Labrador Sea be visible.

Phaeocystis and the diatoms *Fragilariopsis*. However, during the June transect, diatoms were more common in the eastern part and as well there were reduced nutrient concentrations and increased concentrations of microzooplankton. In mid-May, the phytoplankton most likely were in a pre-bloom situation, whereas in early June, a late bloom or post-bloom was observed. High concentrations of the flagellate *Phaeocystis* in the western Iceland Sea explained the highest consumption of nitrate and low silicate reduction. This western station probably was influenced by low salinity water advected from the nearby East Greenland Current, and as such was not typical for the rest of the Iceland Sea. In the Irminger Sea and the open sea areas covered in the Labrador Sea, flagellates (*Phaeocystis*) were most numerous. The presence of

Phaeocystis results in a reduction of nitrate in the Labrador Sea and to some degree in the Irminger Sea. Along the Labrador Sea coast there was an ongoing bloom of diatoms (*Chaetoceros* and *Thalassiosira*) resulting in strong reduction in silicate and nitrate.

4.2. Satellite data

The longer time-series of satellite data documents the annual cycle, with a pronounced spring/summer increase in chlorophyll levels, for all areas. In the Iceland Sea, and especially the Labrador Sea, there was a clear indication of an annual peak in average chlorophyll levels during the spring bloom, as expected. However, in the Irminger Sea, the

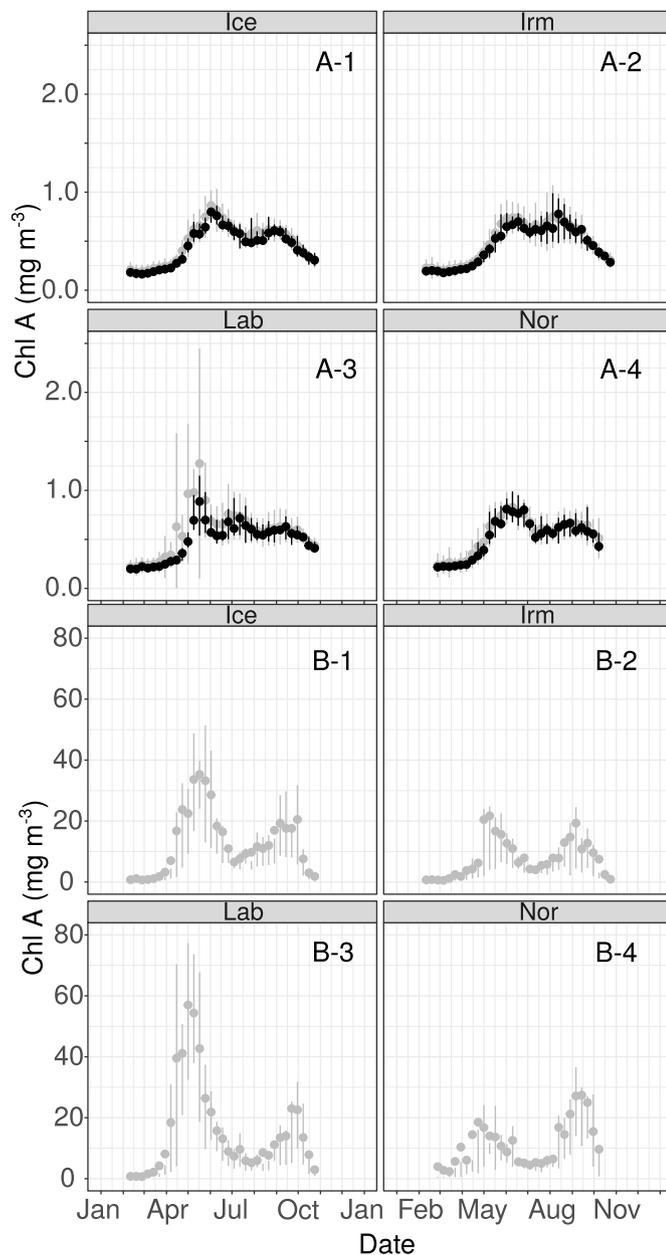


Fig. 11. A1-4: Annual progression of average MODIS-A satellite derived chlorophyll levels, for areas adjacent to the cruise track (Fig. 1), and the period 2002 to 2019. Black dots and bars: geometric means and ± 1 SE. Grey dots and error bars: medians and interquartile range. B1-4: Grey dots show the annual progression of median value of maximum satellite derived chlorophyll levels for the period 2002 to 2019, error bars show the interquartile range.

average springtime “bloom” levels were barely above average chlorophyll levels found during both summer and fall (e.g. until at least mid-September; Fig. 11). Based on satellite chlorophyll data alone, it may therefore be more correct to talk of the “spring increase” of chlorophyll in these areas; the average chlorophyll levels attained during the spring increase are basically maintained until winter sets in again. Due to the high skewness in the satellite data, the averages are reported as geometric means, which will give very conservative estimates if the overall biomass levels are driven primarily by extremely high values. During the spring bloom chlorophyll reaches considerably higher maximum (per bin) levels in the Iceland Sea and especially the Labrador Sea, documenting that the distribution of chlorophyll values, and hence “bloom dynamics” is different for these areas when compared to the Irminger and Norwegian seas.

A phytoplankton bloom will occur when the phytoplankton community grows quick enough to overcome its losses in the surface layer, which occur as a result of community respiration, grazing and dilution (Boss and Behrenfeld, 2010). The differences in both average and maximum chlorophyll during the spring bloom in the Labrador vs. Norwegian and Irminger seas, suggests that either the growth or the loss terms are very different in the Labrador Sea compared to the other basins. For the Norwegian Sea, it was previously suggested that the zooplankton can exert enough grazing pressure to keep chlorophyll levels relatively low, even during the bloom (Bodungen et al., 1995; Rey, 2004). During our cruise, the stage composition of *Calanus finmarchicus* in the Norwegian Sea was dominated by older stages, whereas the stage composition in the Labrador Sea was dominated by younger stages (Strand et al., 2020 this issue). In addition, the Norwegian Sea had higher densities of smaller species of copepods, such as *Oithona* spp. and *Pseudo-* and *Paracalanus* spp., and the abundance of microzooplankton for one specific station in the Norwegian Sea was close to an order of magnitude higher compared to the other seas. Thus, differences in grazing pressure from the meso- and possibly the microzooplankton can be expected, either directly or through trophic interactions with other (i. e. microzooplankton) grazers (Vadstein et al., 2004).

One likely consequence of the different spatial patterns and magnitude of chlorophyll accumulation between the areas, are differences in the dynamic of the gravitational export flux. If grazing is indeed keeping the chlorophyll more in check in the Norwegian and Irminger seas, we would expect a relatively higher importance of gravitational flux through fecal material in these areas. Conversely, we would expect that sinking out of senescent algal material to be relatively more important to the total gravitational flux in the Labrador Sea. In concordance with this, we did observe increased background levels as well as distinct spikes in fluorescence at depth in the Labrador Sea (Strand et al., this issue), suggesting that we were observing relatively fresh algal material in transition through the water column there.

5. Conclusions

Phytoplankton bloom development, or phenology of the phytoplankton communities, differed among the four seas. In the Labrador Sea, a strong bloom was already present at the time of our first survey of the seas, while in the other seas, and particularly the Irminger Sea, bloom development lagged behind. In the Norwegian and Iceland seas, the state of the blooms changed from a pre-bloom to a late bloom situation from the first to the second crossing, while the bloom did not appear to have started in the Irminger Sea. In the Labrador, Iceland and Norwegian seas the use of nitrate was evident, with reduced amounts in the upper 100 m. While the bloom in the Irminger Sea was particularly late and its development slow, the high winter nutrient values and somewhat deeper spring and summer mixed layer suggests that new production in the Irminger Sea likely exceeded that of the Norwegian Sea by 100%. A direct relationship between the depth of the shallowing mixed layer and the use of nitrate suggest that bloom development and phenology of the phytoplankton are related to water column stabilisation. There was also a direct relationship between the use of nitrate and chlorophyll concentrations. Satellite data confirmed that the Norwegian and Irminger seas are characterised by low chlorophyll levels during spring and summer, without pronounced chlorophyll accumulation. The Iceland Sea, and particularly the Labrador Sea, showed more intense blooms, with higher chlorophyll levels. The satellite data also confirmed that the bloom in the Labrador Sea commenced earlier than in the other seas. The early and strong bloom in the Labrador Sea has been related to early water column stabilisation by advection of low salinity surface waters from the West Greenland Shelf. At the time of the survey, there were no clear signs of nutrient limitation of the blooms in any of the four basins. Flagellates were the most abundant algae in all regions, outnumbered by diatoms only in a couple of stations west of Greenland. Elevated ciliate numbers were observed in the regions of the East

Greenland Current, the shelf stations around Iceland and during the eastward crossing in the Iceland and Norwegian seas on both sides of the Arctic front. The algae outnumbered the microzooplankton by at least an order of magnitude.

In the Labrador Sea, the presence of chlorophyll at depth was a direct indication of vertical loss of biomass and carbon from the mixed layer during the vigorous bloom taking place. The potential for carbon vertical transport in the Irminger Sea is probably high due to the high winter nutrient concentrations, but the late and slow bloom may prevent this from happening if grazing within the mixed layer can match the primary production. The same may be the case for the Norwegian Sea.

Author statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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