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# The coccolithophores *Emiliania huxleyi* and *Coccolithus pelagicus*: extant populations from the Norwegian-Iceland Sea and Fram Strait

C. V. Dylmer<sup>1</sup>, J. Giraudeau<sup>1</sup>, V. Hanquiez<sup>1</sup>, and K. Husum<sup>2</sup>

<sup>1</sup>Université de Bordeaux, CNRS, UMR5805 EPOC, Talence, France <sup>2</sup>Department of Geology, University of Tromsoe, Tromsoe, Norway

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Correspondence to: C. V. Dylmer (c.dylmer@epoc.u-bordeaux1.fr)

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	Title Page						
-	Abstract	Introduction					
2	Conclusions	References					
-	Tables	Figures					
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	•	•					
-	Back	Close					
	Full Screen / Esc						
1	Printer-frien	Printer-friendly Version					
	Interactive	Discussion					



## Abstract

Extant coccolithophores and their relation to the governing oceanographic features in the northern North Atlantic were investigated along two zonal transects of surface water sampling, both conducted during summer 2011 and fall 2007. The northern tran-

- <sup>5</sup> sects crossed Fram Strait and its two opposing boundary currents (West Spitsbergen Current and East Greenland Current), while the southern transects sampled the Norwegian and Iceland Seas (passing the island Jan Mayen) from the Lofoten Islands to the continental margin off Eastern Greenland. The distribution of the dominant coccolithophore species *Emiliania huxleyi* and *Coccolithus pelagicus* is discussed in view
- <sup>10</sup> of both the surface hydrology at the time of sampling and the structure of the surface mixed layer. Remote-sensing images as well as CTD and ARGO profiles are used to constrain the physico-chemical state of the surface water at the time of sampling. Both transects were characterized by strong seasonal differences in bulk coccolithophore standing stocks with maximum values of  $53 \times 10^3$  cells L<sup>-1</sup> for the northern transect and
- <sup>15</sup>  $72 \times 10^3$  cells L<sup>-1</sup> for the southern transect in fall and summer, respectively. The highest recorded bulk cell densities are essentially explained by *E. huxleyi*. This species shows a zonal shift in peak abundance in the Norwegian-Iceland Seas from a summer maximum in the Lofoten gyre to peak cell densities around the island Jan Mayen in fall. Vertical mixing of Atlantic waters west of Lofoten Island, a phenomenom related to per-
- vasive summer large scale atmospheric changes in the eastern Nordic Seas, on one hand, and strengthened influence of melt-water and related surface water stratification around the island Jan Mayen during fall, on the other hand, explains the observed seasonal migration of the *E. huxleyi* peak production area, as well as the seasonal change in dominating species within the Iceland Sea. In addition our datasets are indicative of a
- <sup>25</sup> well-defined maximum boundary temperature of 6 °C for the production of *C. pelagicus* in the northern North Atlantic.

The Fram Strait transects provides, to our knowledge, a first view of the zonal distribution of extant coccolithophores in this remote setting during summer and fall. Our





datasets are indicative of a seasonal change in the species community from an *E. hux-leyi*-dominated assemblage during summer to a *C. pelagicus*-rich population during fall. Here, higher irradiance and increased Atlantic water influence during summer favored the production of the opportunistic species *E. huxleyi* close to the Arctic Front, whereas the peak production area during fall, with high concentrations of *C. pelagicus*, lays in true Arctic/Polar waters.

# 1 Introduction

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The northern North Atlantic is experiencing unprecedented changes in physical and chemical conditions, which directly influence the ecosystem structure and processes (Hunt and Drinkwater, 2005). The impact of the last decades' increased temperatures linked to the recent "global warming" is particularly felt in those high latitude areas close to the boundary of maximum winter sea-ice extent, defined as the Arctic Front (AF) (IPCC, 2007). There, strong gradients in cryospheric, atmospheric and oceanic processes are prone to enhanced new production (Hunt et al., 2002).

- The water mass exchanges between the North Atlantic and Arctic Ocean taking place in the Nordic Seas and Fram Strait have been extensively studied throughout the last decades in order to investigate the manifestations and impacts of the recent global climate change in terms of poleward heat transfer and changes in ecosystem structure. Recent compilations of satellite observations (AVHRR, SeaWiFS and MODIS-Aqua)
- <sup>20</sup> suggest an increased occurrence of blooms of marine calcifying phytoplankton coccolithophores – in the Barents Sea and Nordic Seas since the late 80s (Smyth et al., 2004; Burenkov et al., 2011). These blooms are thought to be triggered by modifications in the stratification and temperature of the upper mixed layer linked with extensive sea-ice melting (Parkinson et al., 1999) and increased inflow of Atlantic Water (AW)
- into the Nordic Seas and adjacent areas (Hatun et al., 2005; Hegseth and Sundfjord, 2008; Dmitrenko et al., 2010). This group of unicellular marine phytoplankton, the most abundant calcifying species on Earth, plays an important role in many biogeochemical





cycles, and hence likely contributes to important internal feedbacks to climate changes (e.g. Westbroek et al., 1993).

Recent studies on the biogeography of extant epipelagic coccolithophores in the Northern North Atlantic, and on the distribution of their fossil remains – coccoliths – in

- <sup>5</sup> surface sediments of the Nordic Seas highlighted the close relationship between the distribution of this species group and major surface water masses of the northern North Atlantic (Samtleben and Schröder, 1990, 1992; Samtleben et al., 1995a, b; Andruleit, 1997; Baumann et al., 2000; Schröder-Ritzrau et al., 2001; Matthiessen et al., 2001; Balestra et al., 2004; Smyth et al., 2004; Dmitrenko et al., 2006; Hegseth and Sundfjord, 2008; Giraudeau et al., 2004, 2010; Burenkov et al., 2011; Charalampopoulou et al.,
- 2011).

The overall surface circulation in the Nordic Seas is governed by two meridional boundary currents. The eastern boundary current is represented by the northward flowing warm and saline Norwegian Atlantic Current (NwAC) (< 500–600 m) (Furevik et al.,

- <sup>15</sup> 2007) (Fig. 1), a topographically steered two branch extension of the North Atlantic Current (NAC) (7–13 °C, ≥ 35), entering the Nordic Seas through the Iceland-Scotland ridge (ca. 7 Sv, Hansen and Østerhus, 2000; Orvik and Niller, 2002; Andersson et al., 2011). The eastern branch of the NwAC, is accompanied north by the baroclinic shallow Norwegian Coastal Current (NCC) (~ 34.4) along the continental slope of Norway,
- and splits into two branches North of Lofoten Island: a meridional branch, the West Spitsbergen Current (WSC), and a zonal component, the North Cape Current (NCaC) (Wassmann et al., 2006; Koszalka et al., 2011). The WSC flows along the continental margin of the western Barents Sea and western Spitsbergen and is further accompanied on its northern path by shallower Polar Waters (PW) on the shelf (e.g. the Bear
- Island Current (BIC) and the Sørkapp Current) (Saloranta and Svendsen, 2001; Wassmann et al., 2006) (Fig. 1). It enters the Arctic Ocean as a subsurface current insulated from the atmosphere by fresh PW in the upper mixed layer (3–5 Sv; Blindheim and Østerhus, 2005). The western branch of the NwAC (> 34.9) rounds the southern rim of the Lofoten Basin and flows north as a baroclinic jet along the Mohn Ridge contributing





with Atlantic Water (AW) to the development of the Nordic Sea Frontal Zone (Orvik and Niller, 2002; Jakobsen et al., 2003; Koszalka et al., 2011). The western boundary current is represented by the southward flowing East Greenland Current (EGC; < 0 °C, < 34.5), considered as the largest and most concentrated meridional ice flow in

- the World Oceans (Blindheim and Østerhus, 2005). Its two zonal components, the Jan Mayen Current (JMC) at the Jan Mayen Fracture Zone and the East Icelandic Current (EIC) in the Iceland Sea, supply fresh PW to the gyre systems and hence contribute to the Frontal Zone (Johannessen, 1986; Olsson et al., 2005) (Fig. 1). The mixing of PW and AW creates Arctic Water (ArW) (0–4°C, 34.6–34.9) (Johannessen, 1986).
- <sup>10</sup> The northeast-southwest trending boundary between PW and ArW is termed the Polar Front (PF) and characterizes the maximum summer sea-ice extent, whereas the boundary between ArW and AW is referred to as the Arctic Front (AF) and characterizes the maximum winter sea ice extent (Swift, 1986; Van Aken et al., 1995; Saloranta and Svendsen, 2001). Generally, the positions of the fronts in the Nordic Seas are well
- <sup>15</sup> correlated with bathymetry due to topographic steering of the currents (Johannessen, 1986). This is seen north of the island Jan Mayen along the mid-ocean ridge where the AF only exhibits small fluctuations in contrast to the zone between Iceland and Jan Mayen where large shifts within the position of the AF occur due to variations in the inflow of PW/ArW from the EIC (Blindheim et al., 2000). The Frontal Zone term is gen-20 erally used for the area where horizontal gradients in temperature, salinity and density
- are high in comparison with the mean parent water types (Van Aken et al., 1995).

A series of cyclonic gyres are present over the Greenland, Lofoten, and Norwegian Basins and the Icelandic Plateau, in-between the two main meridional boundary currents. These four gyres are strongly linked to the local bottom topography and are areas of strong mixing and transformation of water masses (Poulain et al., 1996; Jakobson et

al., 2003; Koszalka et al., 2011) (Fig. 1).

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Coccolithophores are generally confined to surface waters above or close to the thermocline and only a few species are known to thrive in subsurface waters below this boundary (Schröder-Ritzrau et al., 2001). In addition, coccolithophore production in the





Northern Atlantic is strongly related to the seasonal cycle of insolation, nutrient content, grazing pressure and weather conditions, and is usually delayed by diatom production until silica is depleted (Samtleben and Schröder, 1992; Baumann et al., 2000; Charalampopoulou et al., 2011). The Norwegian Sea is characterized by Atlantic surface waters with a seasonally established thermocline. The uppermost water mass stratification of the Greenland and Iceland Seas are essentially governed by highly variable sea-ice melting, although in years where sea-ice melt waters may be restricted to the margins, thermal warming might initiate the spring stratification. This regional difference obviously lead to important variations in the seasonal development and compo-

- sition of the fossilizable planktonic community (Wassmann et al., 1991; Samtleben et al., 1995a; Baumann et al., 2000; Schröder-Ritzrau et al., 2001). The coccolithophore production in the southeastern Norwegian Sea may be enhanced as early as May, with a progressive transition towards the Greenland Sea peaking in August (Samtleben and Bickert, 1990; Samtleben et al., 1995a; Baumann et al., 2000; Schröder-Ritzrau et al., 2000;
- <sup>15</sup> 2001). Hence the living coccolithophore community shows a broad seasonal maximum in the Nordic Seas as blooms occur throughout the summer season (Schröder-Ritzrau et al., 2001), with consistently higher cell numbers of living coccolithophores during the high-production periods (summer) than during the low-production periods (fall to early summer) (Samtleben et al., 1995a; Baumann et al., 2000).
- As evidenced earlier by Andruleit (1997) and Baumann et al. (2000), the coccolithophore communities in the surface waters across Fram Strait and the Norwegian-Iceland Seas are strongly dominated by the summer blooming species *Emiliania huxleyi* and *Coccolithus pelagicus*, which shows markedly different ecological preferences. An ubiquitous species in the world ocean, *E. huxleyi* exhibits a high growth rate com-
- pared to other coccolithophore species which makes it one of the most successful coccolithophores thriving in the world oceans (Baumann et al., 2000; Tyrrell and Merico, 2004). In the Nordic Seas it has been shown to have a strong affinity for the warm and saline Atlantic-derived surface waters and has only occasionally been reported in areas strongly influenced by sea-ice (Baumann et al., 2000; Balestra et al., 2004;





Hegseth and Sundfjord, 2008). Additional ecological studies has shown this species to be euryhaline and mainly influenced by variations in stratification, irradiance and to a lesser extent temperature (0–22 °C) of the photic layer (Samtleben and Schröder, 1990, 1992; Samtleben et al., 1995b; Baumann et al., 2000; Beaufort and Heussner,

- <sup>5</sup> 2001; Schröder-Ritzrau et al., 2001). *C. pelagicus* represents the coldest species of the coccolithophore community, occurring at temperatures between –1 and 14 °C with an optimum at 8 °C (Samtleben et al., 1995a; Baumann et al., 2000). Such a temperature range might explain its very strong dominance, albeit with low standing stocks, in the polar community of the EGC (Samtleben and Schröder, 1992). It might also explain
- that this species constitutes the main component of the coccolith assemblages in surface sediments of the Greenland, Iceland, Irminger and Labrador Seas (Solignac et al., 2008). The species has no known salinity preferences, but it has previously been associated with the position of the AF, suggesting an ecology controlled by factors other than temperatures e.g. nutrients and irradiance (Baumann et al., 2000; Schröder-Ritzrau et al.)
- al., 2001; Balestra et al., 2004; Giraudeau et al. 2004). Furthermore, some studies have suggested turbulence as a possibly important factor preventing the sinking of this heavily calcified species from the photic zone (Cacha and Moita, 2000) hence favoring its production in the highly mixed upper ArW. In these upper water masses the low temperatures probably also further limit the occurrence of other species (Baumann et al.,
- 20 2000). In addition *C. pelagicus* has been suggested as a reliable proxy of mesostrophic to eutrophic waters in phytoplankton biomass-rich frontal systems of the Nordic Seas (Andruleit, 1997; Samtleben et al., 1995a).

The extant coccolithophore communities compare relatively well with the spatial distribution of their fossil remains in the surface sediments of the Nordic Seas (Samtleben et al., 1995a). Indeed, contrary to siliceous microfossils, dissolution in the water column and in the surface sediments does not alter the general composition of coccolith assemblages and their fluxes remarkably (Andruleit, 1997; Schröder-Ritzrau et al., 2001;

Matthiessen et al., 2001). This is consistent with sediment trap studies indicating a dominance of calcareous organisms in the export flux of plankton organisms within the





Norwegian Sea. Furthermore, the coccolithophores are the most dominant fossilizable plankton group in terms of mean annual daily flux rates in this region (Schröder-Ritzrau et al., 2001). Previous investigations have demonstrated that coccoliths of *E. huxleyi* and *C. pelagicus* are distributed in surface sediments of the Nordic Seas according to their distribution in extant populations, and accordingly dominate the fossil assem-

blages below AW and ArW (Baumann et al., 2000).

Remote sensing offers the opportunity to discuss the distribution patterns of phytoplankton communities collected in the upper photic layer, according to geographically and temporally well-constrained large- to meso-scale surface circulation features,

- and, as in the case of the Nordic Seas, sea-ice occurence. The present investigation, which relies on this analytical strategy to comprehend the seasonal surface hydrology, aims at improving our understanding of the modern distribution of the two dominant coccolithophore species in the Northern North Atlantic: *E. huxleyi* and *C. pelagicus*. It is based on two transects of surface water sampling across Fram Strait and the
- <sup>15</sup> Norwegian-Iceland Seas (passing Jan Mayen Island), perpendicular to the flow direction of the primary surface currents, and both carried out during the autumn of 2007 (September–October) and the mid-summer of 2011 (July). Annual and seasonal differences in coccolithophore abundances along both transects will be discussed in view of the surface hydrology at the time of sampling as deduced from Aqua MODIS and AVHRR Pathfinder images.
  - 2 Material and methods

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The present study reports on extant coccolithophore populations collected along two zonal surface water transects across Fram Strait (ca. 73–78° N) and the Norwegian – Iceland Seas (ca. 70° N) during the autumn of 2007 (29 September–14 October) and summer of 2011 (15–27 July), as part of the cruises SciencePub UiT/WARMPAST and GEO-8144/3144, respectively, of the R/V *Helmer Hanssen* (former "R/V *Jan Mayen*") (Fig. 2, Tables 1 and 2).





# 2.1 Coccolithophore analyses

Sampling was conducted en-route using the ship's deckwash pump (limiting the sampling to the near surface water masses < 5 m), and involved onboard membrane filtration of sea water (2–3 L). Air-dried filter were subsequently mounted between slide and coverslip, and examined under a light microscope at ×1000 magnification as described by Giraudeau et al. (1993). A total of 57 samples (31 samples, September/October 2007; 26 samples, July 2011) were investigated for living assemblages (Tables 1 and 2) and the results expressed as coccolithophore standing stocks per litre (number of cells L<sup>-1</sup>). In the present work, *C. pelagicus* includes both the motile holococcolithbearing phase (*C. pelagicus* f. *hyalinus*) and the non-motile heterococcolith-bearing phase (*C. pelagicus* f. *hyalinus*) (Cachão and Moita, 2000; Balestra et al., 2004)
While the use of a light microscope (compared with Scanning Electron Microscope

- SEM - examination) limits a precise taxonomical investigation of the extant coccolithophore population, this approach was found sufficient to identify and to conduct reliable census counts of the dominant fossilizable species in the recovered samples, i.e. *E. huxleyi* and *C. pelagicus*.

# 2.2 Synoptic views of sea-surface temperatures and sea-ice extents

The presented Sea Surface Temperature (SST) maps (Fig. 2) are based on Aqua MODIS 32 days composite, 0.08° resolution satellite grid images, extracted from http: //oceancolor.gsfc.nasa.gov/ for fall 2007 (22 September–23 October 2007) and summer 2011 (4 July–4 August, 2011). In order to convert grid raw values to STTs and to extract SST values along the studied transects, spatial analysis and geoprocessing were performed using ArcGIS (Esri Company). SSTs were calculated from the follow-ing equation, derived from information stored in Aqua MODIS grids:

 $_{25}$  SST = (V × 0.0007178) – 2, (where V represents grid raw values)





(1)

Information on sea-ice fraction in the form of 50 % sea-ice concentration were taken from daily AVHRR Pathfinder 5.2 satellite images extracted from http://data.nodc.noaa. gov for 5 October, 2007 (night), and 20 July 2011 (day). They are reported as isolines on the SST maps.

Six Conductivity-Temperature-Depth (CTD) profiles, 5 of them collected as part of the 2007 and 2011 cruises using a Seabird 911 Plus CTD and one extracted together with 3 Argo-floats from the Coriolis database (http://www.coriolis.eu.org/), were all included into the present study (Fig. 2; Appendix Table A1 and Fig. A1), as a mean to validate the satellite extracted monthly average SST profiles as well as to provide additional information on the vertical distribution of watermasses and stratification within the top 500 m of the water column.

#### 3 Results and discussion

The remote sensing-derived maps of surface water conditions during the sampling periods highlight strong differences in temperatures between October 2007 and July 2011 across the northern North Atlantic in terms of both mean average values and horizontal gradients (Fig. 2). The observed differences between the two investigated seasons clearly appear in the temporal and spatial distribution of AW masses between July 2011 and October 2007, showing a generally stronger longitudinal dominance of warmer waters towards the west during summer conditions, which can also be identi-

- fied by a weaker surface expression of the northern North Atlantic cold currents (EGC, JMC, BIC and EIC), compared to the autumn distribution, where surface ArW masses (0–4 °C) contribute to an inverse situation (Figs. 1 and 2). Previous findings of a topographical steering of the AF north of the island Jan Mayen (Blindheim et al, 2000), is hence not obvious based on these observations, in fact the zonal maximum distribution
- of the AF, with the exception of Fram Strait, show a strong seasonal migration towards the east from summer until autumn, a result which might however be an artifact of the stronger influence of solar irradiance during summer conditions on the upper surface





layer, directly influencing the satellite imagery. Sea-ice extent, represented here as the 50 % sea-ice concentration limit, do not show any obvious geographical shift between the two periods, with the exception of the area around Svalbard where sea-ice occupied most of the western and southern shelf in July 2011 but is virtually absent in fall 2007.

Sea-ice melting, initiated in summer and completed by fall, might, in addition to seasonal changes in solar irradiance (Cokelet et al., 2008), dominating windpatterns and AW flow (Blindheim et al., 2000), to a high extent explain the observed shift from a dominance in July 2011 of warmer AW carried by the NwAC and WSC in the eastern part of the Nordic Seas to prevailing colder surface waters during the fall of 2007. These changes are particularly indicated by a narrowing of the poleward AW tongue west of Svalbard, as well as by a strengthened influence of the colder water masses carried by the EGC, JMC, BIC and EIC coupled to an increased temperature gradient across the AF and PF between summer and autumn conditions.

#### 15 3.1 Northern transects

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The Fram Strait transects display prominent SST and coccolithophore standing stock gradients over a rather narrow area, as well as noticeable differences in SST ranges and coccolithophore assemblages between summer 2011 (SST ~ 1.5-7°C, *E. huxleyi* dominated peak coccolithophore standing stocks) and autumn 2007 (SST ~ -0.5-5°C, *C. pelagicus* dominated peak coccolithophore standing stocks) (Fig. 3).

# 3.1.1 Hydrological setting during the sampling periods

Both SST (sea surface temperature) profiles across Fram Strait show an abrupt temperature increase of ca. 2 °C around ~  $10^{\circ}$  E, which relates to the location of the AF off western Svalbard (Fig. 3). Saloranta and Svendsen (2001) investigated the AF positive increase of ca. 2 °C around ~  $10^{\circ}$  E, which relates to the location of the AF off western Svalbard (Fig. 3).

tion immediately west of Svalbard and identified it as a clear topographically steered temperature-salinity front at the shelf break, separating ArW carried by the Sørkapp





Current over the shelf from AW (WSC) over the slope. Our fall 2007 CTD profile recovered east of this frontal boundary (Fig. A1, CTD 1), also shows AW-type waters with temperatures and salinities in the range of  $\sim 4-5$  °C and  $\sim 35$ , respectively, submerged under a 50 m thick surface mixed layer of ArW (~2-3°C; <34.8). Both transects reach their highest surface temperatures west of  $\sim 10^{\circ}$  E, as they cross the main path of 5 the WSC-carried AW. The geographic distribution of WSC varies from  $\sim 1.5^{\circ}$  E in the summer 2011 to  $\sim 5^{\circ}$  E in the fall 2007 showing the widest extension during summer. The western boundary of surface AW is marked by a ca. 2°C SST decrease, however the boundary is less pronounced than its eastern counterpart over the Svalbard shelf break, representing the AF and the entrance into the EGC-influenced domain 10 (ArW/PW) (Fig. 3). Temperature differences between the two sampling periods in terms of mean values and width of the surface AW, are most probably related to the seasonal changes in solar irradiance (higher in July) and in distribution of meltwater (higher in October), as well as potential changes in the strength of the meridional currents. ArW located west of the AF is characterized by very homogeneous upper surface tempera-15

tures of ca. 1–2°C, as well as a deep mixed layer down to 100 m water depth (Fig. 3; Fig. A1, CTD 2). PW characterized by a highly stratified upper mixed layer (Fig. A1, CTD 3) is found during the fall 2007 close to the sea-ice edge within surface waters with SST around 0°C (Fig. 2).

# 20 3.1.2 Geographic distribution of coccolithophores

The coccolithophore standing stocks recorded in the present study across Fram Strait ranges from 1 to  $53 \times 10^3$  cells L<sup>-1</sup> (Fig. 3). The maximum values fall within the range of cell densities from previous observations south of Svalbard, within the influence of the WSC, for the summer and fall-winter seasons (10 to  $100 \times 10^3$  cells L<sup>-1</sup>; Samtleben et al., 1995a).

Peak coccolithophore cell densities occurred on the western edge of the poleward flow of surface AW (Fig. 3), either associated with the AF (July 2011) or within ArW (October 2007). These peak productions are also characterized by a change in dom-





inating species from *E. huxleyi* during the summer period, to *C. pelagicus* during the fall situation. Reduced irradiance from summer until autumn may have had a negative effect on the production of the blooming *E. huxleyi* species (Baumann et al., 2000). Additionally, the differences in the spatial development of the turbulent Frontal Zone between the summer and fall periods, as seen by a reduced distribution of AW in October 2007 compared with July 2011 (Figs. 2 and 3), may also explain this change in coccolithophore assemblage.

*C. pelagicus* has previously been found to be abundant, if not dominant in ArW (Baumann et al., 2000), hence the onset of the Frontal Zone seems to be surprisingly underrepresented by this species during July 2011. This discrepancy is better explained by the combined influences, during summer, of enhanced sea-ice melting close to the sea-ice edge, increased importance of AW and higher irradiance, causing strong stratification of the upper photic layer (Fig. A1, CTD 4 and 5). This scheme, linked with higher SSTs and a weaker temperature gradient across the Frontal Zone, resulted in

- *E. huxleyi* dominated coccolithophore assemblages in July 2011 (Fig. 3), in agreement with previous observations (though in more southern latitudes west of the island Jan Mayen) which showed this species as highly successful in ArW close to the PF during summer high production periods (Samtleben and Schröder, 1992; Baumann et al., 2000). The opposite situation, i.e. enhanced mixing of the photic layer and cooler SST
- <sup>20</sup> within the Frontal Zone area during fall 2007 (Fig. A1, CTD 2), a situation associated with a reduced westward influence of surface AW across Fram Strait (Fig. 3), favored the production of the well-mixed and cold water -adapted *C. pelagicus*.

### 3.2 Southern transects

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The Norwegian-Iceland Seas transects display, as expected, markedly higher SSTs (up to 11 °C, summer 2011) and coccolithophore standing stocks (up to 72 × 10<sup>3</sup> cells L<sup>-1</sup>, summer 2011) than the Fram Strait transects. Seasonal differences between July 2011 and October 2007 are limited to an overall SST difference of ca. 1 °C, and, more prominently, by a zonal shift in peak *E. huxleyi*-dominated coccolithophore densities (Fig. 4).



### 3.2.1 Hydrological setting during the sampling periods

Both SST profiles display a pattern of stepwise decrease of SSTs from the NwACbathed area off western Norway (~7–11 °C, ~35.1; Fig. 4; Table A1, Argo 2 and 3) to the EGC-influenced margin off eastern Greenland. The temperature is reduced ca.

- <sup>5</sup> 2.5 °C twice around 3° W and 17° W, respectively. This show the average locations of the AF and PF. The PF has only been sampled during fall 2007, when favourable seaice conditions allowed the transect to be extended to the eastern Greenland shelf off Scoresby Sund (Figs. 2 and 4). According to Van Aken et al. (1995), the AF and PF bounded Frontal Zone (ArW) is here defined as an area of mixed PW and AW fed
- by the JMC and EIC branches of the EGC and the poleward NwAC (western branch, > 34.9) (Fig. A1, Argo 1 and CTD 6). Surface waters of the Frontal Zone show an AW signature as well as a deep mixed layer during July 2011 (Fig. A1, CTD 6), whereas a buoyant, low salinity (< 34.8) and highly stratified upper photic layer of PW origin has been found during fall 2007 as a result of mild weather conditions during the period of</p>
- sampling (Husum, 2007), as well as eastward spreading of melt waters from the nearby eastern Greenland shelf (Fig. A1, Argo 1).

While both transects are characterized by an overall ~ 2  $^{\circ}$ C SST decrease from east to west across the AW-influenced Norwegian Sea, the July 2011 SST profile displays a low temperature anomaly between ca. 2 $^{\circ}$ E and 8 $^{\circ}$ E with values occasion-

- ally as low as 4°C. This is up to ~4°C lower than the surrounding water masses (Fig. 4). The Aqua MODIS image extracted for this period (Fig. 2) suggests that this anomaly is part of the Lofoten Gyre, a semi-permanent feature which is forced by large-scale atmospheric rotational variations effecting the governing wind patterns and the strength of the surface circulations (Jakobsen et al., 2003). The 32 days composite
- SST Aqua MODIS images representative of spring and fall situations (see database in http://oceancolor.gsfc.nasa.gov/) indicate that the surface water expression of the Lofoton Gyre was observable during 2007 and 2011, but was limited in both cases to





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July and August. The Argo record for July 2011 (Fig. A1, Argo 3) suggests deep mixing of AW-type waters within this gyre.

#### 3.2.2 Geographic distribution of coccolithophores

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Our profiles of coccolithophore standing stock values across the Norwegian-Iceland Seas are within the lower range of previously published extant coccolithophore datasets within the Nordic Seas during the summer production period (~3 to  $300 \times 10^3$  cells L<sup>-1</sup>) (Samtleben and Schröder, 1992; Baumann et al., 2000). In addition, the current dataset show and highlight a migration of the peak production (dominated by *E. huxleyi*) toward the west from summer until autumn (Fig. 4).

The coccolithophore peak production area during July 2011 occurs within the Lofoton 10 Gyre system and might be explained by vertical mixing, and hence nutrient enrichment of the upper photic layer. Despite the low abundance the presence of C. pelagicus (Fig. 4, sample 26) seems to confirm the particular trophic conditions indicated in the Lofoten Basin during the summer season of 2011, as C. pelagicus has previously been related to other similar gyre systems south of the Iceland-Scotland Ridge (Tarran et al., 15 2001).

The Frontal Zone production area is marked by an overall change in species dominance from C. pelagicus during summer 2011, when surface waters were affected by deep mixing, to *E. huxleyi* during fall 2007, a period characterized by a highly stratified photic layer.

Both southern transects suggest a maximum boundary temperature of 6°C for the occurence of C. pelagicus (Fig. 4), a value which strictly corresponds with earlier suggestions based on the analysis of extant coccolithophore populations across the Norwegian-Greenland Sea (Samtleben and Schröder, 1990). However, our observa-

tions in the Fram Strait area also indicate that this upper SST limit becomes somewhat 25 lower (ca. 4 °C) in the northermost latitudes (Fig. 3).





### 4 Summary and perspectives

Although an increased amount of investigations during the recent decades on the distribution of extant coccolithophore populations (e.g. Matthiessen et al., 2001, and references herein) has strongly added to our knowledge of the ecology of this major

- calcifying species group within the Nordic Seas, our understanding is still hampered by the lack of surface water samples. Phytoplankton samples investigated in the present study were collected en-route using a simple, cost- and time effective method, along two zonal transects perpendicular to the major meridional boundary current systems and hydrological fronts. The combined use of easily accessible remote sensing im ages, CTD casts and Argo floats from existing databases, although not sufficient to investigate small-scale physical and biological processes, was found highly relevant for significantly improving our knowledge on the biogeography of the dominant fossilizable coccolithophore species within the northern North Atlantic i.e. *E. huxleyi* and *C. pelagicus*.
- <sup>15</sup> Seasonal changes in the distribution and stratification of the main water masses related to sea-ice melts and changes in the drift of Atlantic surface water masses results in an overall westward shift of the peak cocolithophore production areas dominated by the opportunistic *E. huxleyi*. Our datasets across the Norwegian-Iceland Seas confirm previous studies indicating high cell densities in the Vøring Plateau area in July
- and west of the island Jan Mayen in September-October (Samtleben et al., 1995a). Peak coccolithophore production within the Lofoten gyre in July 2011 was related to increased vertical mixing and nutrient enrichment of the photic layer due to large scale atmospheric changes. In contrast, the change in the dominating species around the island Jan Mayen from *C. pelagicus* in summer to *E. huxleyi* in fall, resulted from a
- <sup>25</sup> change in stratification from well mixed (summer) to stratified (fall) surface waters. In addition our data are indicative of a strong temperature limitation of *C. pelagicus* production, the maximum boundary value being estimated at 6 °C, with a somewhat lower (ca. 4 °C) limit in the northern most latitudes (Fram Strait).





Our dataset obtained in Fram Strait represent to our knowledge a first view of the zonal distribution of extant coccolithophores within this climatically sensitive area during summer and fall. There, seasonal changes in dominance from *E. huxleyi* (summer) to *C. pelagicus* (fall), are related to the combined influence, during summer, of enhanced sea-ice melting close to the sea-ice edge, as well as increased influence of AW and higher irradiance leading to the high production of the opportunitic species *E. huxleyi* within an area usually characterized by *C. pelagicus*-dominated low density populations.

The ongoing intensification of sea-ice melting and sea-ice thinning within the Arctic Ocean, and the associated naturally increased export of ice and melt water to the Nordic Seas (Kwok, 2009), directly results in an overall increased surface water stratification in the western northern North Atlantic (Furevik et al., 2002), a condition which is likely to favor the production of *E. huxleyi*. Remote-sensing investigations already point to the occurence of pervasive blooms of *E. huxleyi* in Arctic to Polar environ-

- <sup>15</sup> ments such as the Barents Sea (Smyth et al., 2004) under the influence of increased sea-ice melts and increased inflow of AW, conditions which are equally supposed to characterize the Greenland-Iceland Seas. While the impact of the anthropogenicallyforced ocean acidification upon calcifying plankton in polar environments is still debated (Charalampopoulou et al., 2011), ongoing changes in the physico-chemical structure
- of the surface mixed layer of the northern North Atlantic (stratification, temperature, salinity) might induce regional changes in the structure of the phytoplankton communities with major effects on the carbon cycle as well as the entire food web of the Nordic Seas. Continuing surveys on the distribution of extant coccolithophores, a presumably highly successful group in the presently changing high latitude oceans, are therefore of tremendous importance.

Acknowledgements. This work is a contribution to "The Changing Arctic and Subarctic Environment" (CASE) Initial Training Network funded by the European Community's 7th Framework Programme FP7 2007/2013, Marie-Curie Actions, under Grant Agreement No. 238111. Thanks are due to the captain and crew of the R/V *Helmer Hanssen* and S. Iversen





for CTD collections. Some of the material used in this study was collected as part of the IPY project no. 786 "Arctic Ocean Warming in the past" (WARMPAST).



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Discussion Pa	<b>BGD</b> 10, 15077–15106, 201						
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Discussion

Paper

Discussion Paper

Discussion

Pape



Conclusions References **Figures** Tables 14 Close Back Full Screen / Esc **Printer-friendly Version** Interactive Discussion

**BGD** 

10, 15077-15106, 2013

The

coccolithophores

E. huxleyi and

C. pelagicus

C. V. Dylmer et al.

**Title Page** 

Introduction

Abstract

Discussion Paper

**Discussion** Paper

**Discussion** Paper

**Discussion** Paper

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**Table 1.** List of surface water samples for September–October 2007, with collection dates, locations and coccolithophore cell densities.

Sample	Longitude	Latitude	Date	Total	Coccolithus	Emiliania	Algirospheara
				Coccolithophores	pelagicus	huxleyi	robusta
				$(\times 1000  \text{L}^{-1})$	$(\times 1000  L^{-1})$	$(\times 1000  L^{-1})$	$(\times 1000  \text{L}^{-1})$
1	13.85	69.82	29/09/2007	12.1	0.0	12.1	0.0
2	12.43	69.90	30/09/2007	4.8	0.0	2.4	2.4
3	10.83	69.98	30/09/2007	2.2	0.0	2.2	0.0
4	9.58	70.05	30/09/2007	5.2	0.0	3.9	1.3
5	9.58	70.05	30/09/2007	0.0	0.0	0.0	0.0
6	8.17	70.13	30/09/2007	1.5	0.0	1.5	0.0
7	6.67	70.20	30/09/2007	0.0	0.0	0.0	0.0
8	5.23	70.28	30/09/2007	0.0	0.0	0.0	0.0
9	3.50	70.37	30/09/2007	0.0	0.0	0.0	0.0
10	2.17	70.43	30/09/2007	0.0	0.0	0.0	0.0
11	-1.92	70.65	01/10/2007	0.0	0.0	0.0	0.0
12	-3.57	70.73	01/10/2007	1.3	1.3	0.0	0.0
13	-4.85	70.80	01/10/2007	2.2	0.0	2.2	0.0
14	-6.45	70.88	01/10/2007	11.8	0.0	11.8	0.0
15	-7.78	70.97	01/10/2007	23.5	0.0	23.5	0.0
16	-8.87	70.77	01/10/2007	23.5	2.6	20.9	0.0
17	-10.45	70.62	01/10/2007	66.4	0.0	66.4	0.0
18	-13.60	70.25	02/10/2007	20.7	0.0	20.7	0.0
19	-14.83	70.12	02/10/2007	13.1	0.0	13.1	0.0
20	-17.23	70.18	02/10/2007	2.5	2.5	0.0	0.0
21	-18.68	70.20	02/10/2007	1.9	0.5	1.4	0.0
22	-20.38	70.23	02/10/2007	6.1	3.1	3.1	0.0
24	-15.67	73.23	07/10/2007	6.5	3.3	3.3	0.0
25	-13.65	73.77	08/10/2007	16.3	10.5	5.9	0.0
26	1.25	77.50	11/10/2007	48.3	25.6	22.6	0.0
27	4.32	77.82	12/10/2007	11.5	1.6	9.9	0.0
28	7.23	78.13	12/10/2007	6.1	1.2	3.7	1.2
29	9.03	78.15	12/10/2007	12.7	2.3	9.2	1.2
30	9.48	78.22	12/10/2007	9.1	2.6	3.9	2.6
CTD 1	-13.15	73.78	08/10/2007	9.1	3.9	5.2	0.0
CTD 2	-2.03	77.47	11/10/2007	52.9	29.4	23.5	0.0
CTD 3	10.98	78.22	12/10/2007	7.0	0.0	5.6	1.4

**BGD** 10, 15077-15106, 2013 The coccolithophores E. huxleyi and C. pelagicus C. V. Dylmer et al. **Title Page** Introduction Abstract Conclusions References Tables Figures 14 Þ١ . Back Close Full Screen / Esc Printer-friendly Version Interactive Discussion

**Discussion** Paper

**Discussion** Paper

**Discussion Paper** 

**Discussion Paper** 



**BGD** 10, 15077-15106, 2013 The coccolithophores E. huxleyi and C. pelagicus C. V. Dylmer et al. **Title Page** Abstract Introduction Conclusions References Figures **Tables** Þ١ 14 ► Close Back Full Screen / Esc **Printer-friendly Version** 

**Discussion** Paper

**Discussion** Paper

**Discussion Paper** 

**Discussion Paper** 

Interactive Discussion



Table 2. List of surface water samples for July 2011, with collection dates, locations, and coccolithophore cell densities.

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Total

Coccolithus

Emiliania

Algirospheara

Sample

Longitude

Latitude

Date

	-			Coccolithophores	pelagicus	huxleyi	robusta
				$(\times 1000 L^{-1})$	$(\times 1000 L^{-1})$	$(\times 1000  L^{-1})$	$(\times 1000  L^{-1})$
1	10.77	77.88	15/07/2011	1.3	0.0	1.3	0.0
2	9.88	77.58	15/07/2011	1.1	0.0	1.1	0.0
3	5.77	77.90	16/07/2011	27.3	0.0	27.3	0.0
4	2.55	78.15	16/07/2011	46.0	14.7	31.4	0.0
5	1.22	78.42	16/07/2011	29.3	2.0	27.3	0.0
6	0.50	78.60	19/07/2011	10.3	4.8	5.5	0.0
7	-2.17	78.08	19/07/2011	4.0	0.0	4.0	0.0
8	-3.27	77.42	19/07/2011	1.5	0.0	1.5	0.0
15	-15.72	70.13	25/07/2011	5.3	0.0	5.3	0.0
16	-13.10	70.40	25/07/2011	2.6	0.0	2.6	0.0
17	-10.25	70.68	25/07/2011	21.7	12.5	9.3	0.0
18	-7.78	71.15	25/07/2011	3.8	1.0	2.9	0.0
19	-6.03	71.05	25/07/2011	12.2	9.8	2.4	0.0
20	-4.17	70.95	26/07/2011	5.2	3.1	2.1	0.0
21	-3.03	70.88	26/07/2011	9.7	0.0	9.7	0.0
22	-1.65	70.80	26/07/2011	1.0	0.0	1.0	0.0
23	0.05	70.73	26/07/2011	3.6	0.0	3.6	0.0
24	0.47	70.68	26/07/2011	3.5	0.0	3.5	0.0
25	2.15	70.58	26/07/2011	17.9	0.0	17.9	0.0
26	4.05	70.47	26/07/2011	71.3	3.1	68.2	0.0
27	7.28	70.28	26/07/2011	12.6	0.8	11.8	0.0
28	8.60	70.20	27/07/2011	65.4	0.4	65.0	0.0
29	10.10	70.12	27/07/2011	35.8	0.4	35.4	0.0
30	11.67	70.02	27/07/2011	0.0	0.0	0.0	0.0
31	13.17	69.93	27/07/2011	8.9	0.0	8.9	0.0
32	14.70	69.83	27/07/2011	6.1	0.4	5.7	0.0

# **Discussion** Paper **BGD** 10, 15077-15106, 2013 The coccolithophores E. huxleyi and **Discussion** Paper C. pelagicus C. V. Dylmer et al. **Title Page** Abstract Introduction **Discussion** Paper Conclusions References Tables Figures 14 Back Close **Discussion** Paper Full Screen / Esc Printer-friendly Version Interactive Discussion

**Table A1.** List of CTD casts and Argo Stations used in the present study, with collection dates, locations and water depths.

Station Nr.	Location	Station	Date	Latitude	Longitude	Water Depth (m)
CTD 1	Fram Strait	# 424	12/10/2007	78°13.84 N	11°00.57 E	340
CTD 2	Fram Strait	# 421	11/10/2007	77°28.61 N	02°02.54 W	3029
CTD 3	Fram Strait	# 417	08/10/2007	73°46.14 N	13°00.60 W	2570
CTD 4	Fram Strait	# 306	16/07/2011	77°36.05 N	09°53.30 E	1381
CTD 5	Fram Strait	# 309	18/07/2011	78°13.98 N	01°36.07 E	1707
CTD 6	Norwegian-Iceland Sea	# 249 (ship 10)	15/07/2011	69°92.98 N	08°70.63 W	717.4
Argo 1	Norwegian-Iceland Sea	# 134	26/09/2007	69°34.90 N	11°51.00 W	1273.9
Argo 2	Norwegian-Iceland Sea	# 6	02/10/2007	71°16.40 N	05°88.00 E	> 1963.4
Argo 3	Norwegian-Iceland Sea	# 39	26/07/2011	70°58.30 N	02°72.60 E	> 1976.3



**Fig. 1.** Bathymetric map of the Nordic Seas showing major surface currents after Jakobsen et al. (2003), Olsson et al. (2005) and Andersson et al. (2011). Red arrows show the flow direction of warm saline Atlantic Water. NwAC: Norwegian Atlantic Current, WB: Western Branch (NwAC), EB: Eastern Branch (NwAC), NCaC: North Cape Current, WSC: West Spitsbergen Current. Blue arrows show the flow direction of cold low saline Arctic/Polar waters. EGC: East Greenland Current, JMC: Jan Mayen Current, EIC: East Icelandic Current, BIC: Bear Island Current. Green arrow show the flow direction of coastal waters. NCC: Norwegian Coastal Current. Other abbrevations; NB: Norwegian Basin, LB: Lofoten Basin, GB: Greenland Basin, IP: Icelandic Plateau.







iscussion Paper **BGD** 10, 15077-15106, 2013 The coccolithophores E. huxleyi and **Discussion** Paper C. pelagicus C. V. Dylmer et al. **Title Page** Abstract Introduction **Discussion** Paper Conclusions References Tables **Figures** Close Back **Discussion** Paper Full Screen / Esc **Printer-friendly Version** Interactive Discussion

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**Fig. 2.** Monthly Sea Surface Temperature (SST) composite maps of the studied area based on satellite grid images (Aqua MODIS 32), extracted from http://oceancolor.gsfc.nasa.gov/ for 29 September–14 October in 2007 and 15–27 in July 2011. White squares: sample locations; black squares: CTD and ARGO locations; dashed light blue line: sea-ice margin as the 50 % sea-ice concentration isoline extracted from AVHRR Pathfinder 5.2 images (http://data.nodc.noaa. gov) from 5 October 2007, and 20 July 2011. Shaded area (October 2007): no data.



**Fig. 3.** Longitudinal plots of coccolithophore cell densities (Coccolithophores/L, coccolithophore standing stock) and SSTs across the Fram Strait transects during July 2011 and September/October 2007. Red bars: *Emiliania huxleyi* coccolithophore standing stocks; blue bars: *Coccolithus pelagicus* coccolithophore standing stocks; black dashed line: maximum temperature of *Coccolithus pelagicus* occurrence observed along the transect; orange boxes: sample locations; black boxes: locations of CTD 1–5; shaded white bars: sea-ice margin (50 % sea-ice concentration); light red bars: surface AW masses; light blue bars: surface ArW masses; purple bars: surface PW masses; dashed arrows: overall transect direction.







**Fig. 4.** Longitudinal plots of coccolithophore cell densities (Coccolithophores/L, coccolithophore standing stock) and SSTs across the Norwegian-Iceland Seas transects during July 2011 (top) and September/October 2007 (bottom). Red bars: *Emiliania huxleyi* coccolithophore standing stocks; blue bars: *Coccolithus pelagicus* coccolithophore standing stocks; black dashed line: maximum temperature of *Coccolithus pelagicus* occurence observed along the transect; or ange boxes: sample locations; shaded white bars: sea-ice margin (50 % sea-ice concentration); light red bars: surface AW masses; light blue bars: surface ArW masses; purple bars: surface PW masses; dashed arrows: overall transect direction.







**Fig. A1.** CTD and ARGO profiles (see Fig. 2 and Table A1 for locations) showing temperatures (°C) and salinities within the top 500 m of the water column. NT, Northern transect; ST, Southern Transect.



