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The coccolithophores *Emiliana huxleyi* and *Coccolithus pelagicus*: Extant populations from the Norwegian–Iceland Seas and Fram Strait

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ABSTRACT

The distributions of the coccolithophore species *Emiliana huxleyi* and *Coccolithus pelagicus* (hetero-coccolith-bearing phase) in the northern North Atlantic were investigated along two zonal transects crossing Fram Strait and the Norwegian–Iceland Sea, respectively, each conducted during both July 2011 and September–October 2007. Remote-sensing images as well as CTD and ARGO profiles were used to constrain the physico-chemical state of the surface water and surface mixed layer at the time of sampling. Strong seasonal differences in bulk coccolithophore standing stocks characterized the northern and southern transects, where the maximum values of 53×10^3 cells/l (fall) and 70×10^3 cells/l (summer), respectively, were essentially explained by *E. huxleyi*. This pattern confirms previous findings of a summer to fall northwestward shift in peak coccolithophore cell densities within the Nordic Seas. While depicting an overall zonal shift in high cell densities between the summer (Norwegian Sea) and fall (northern Iceland Sea) conditions, the southern transects were additionally characterized by local peak coccolithophore concentrations associated with a geographically and temporally restricted convective process (Lofoten Gyre, summer), as well as an island mass effect (in the vicinity of Jan Mayen Island, fall).

Maximum coccolithophore abundances within Fram Strait were found during both seasons close to the western frontal zone (Polar and Arctic Fronts) an area of strong density gradients where physical and chemical properties of the surface mixed layer are prone to enhance phytoplankton biomass and productivity. Here, changes in species dominance from *E. huxleyi* in summer, to *C. pelagicus* in fall, were related to the strengthened influence during summer, of surface AW, as well as to high July solar irradiance, within an area usually characterized by *C. pelagicus*-dominated low density populations.

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1. Introduction

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 (i.e. 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).

Recent compilations of satellite observations (AVHRR, SeaWiFS and MODIS-Aqua) suggest an increased occurrence of summer blooms of a marine calcifying coccolithophore species,

Emiliana huxleyi, in the seasonally ice-covered eastern Barents Sea since the late 1980s (Smyth et al., 2004; Signorini and McClain, 2009; 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 delivery of Atlantic Water (AW) to the Barents Sea (Hatun et al., 2005; Hegseth and Sundfjord, 2008; Dmitrenko et al., 2010). Besides coastal Norway (e.g. Kristiansen et al., 1994), no coccolithophore blooms have been observed in the Nordic Seas so far, either from satellite or in-situ observations.

The coccolithophore populations in the Nordic Seas generally experience a north/north-westward decrease in species number, which is primarily explained by decreasing surface water temperatures (Baumann et al., 2000). Coccolithophore production is usually delayed by the diatom spring blooms until silica is depleted (Samtleben and Schröder, 1992; Baumann et al., 2000), and it is generally confined to surface waters above or close to the thermocline (Schröder-Ritzrau et al., 2001). In the southeastern

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Norwegian Sea, the coccolithophore production may be enhanced as early as May, with a progressive transition towards the Greenland Sea peaking in late summer/fall (Samtleben and Bickert, 1990; Samtleben et al., 1995a; Baumann et al., 2000; Schröder-Ritzrau et al., 2001). Hence the living coccolithophore community shows a broad summer/fall maximum in the Nordic Seas (Schröder-Ritzrau et al., 2001), with consistently higher cell numbers of living coccolithophores during this high production period than during the winter–spring low production period (Baumann et al., 2000).

According to 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 two species *E. huxleyi* and *Coccolithus pelagicus*. An ubiquitous species in the world ocean, *E. huxleyi* exhibits a high growth rate compared to other coccolithophore species (Brand, 1982, 1994), which makes it one of the most successful coccolithophores thriving in the North Atlantic Ocean (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 (Balestra et al., 2004; Hegseth and Sundfjord, 2008). Additional ecological studies have shown this species to be euryhaline and mainly influenced by variations in stratification, irradiance and to a lesser extent temperature of the photic layer (Samtleben and Schröder, 1990, 1992; Samtleben et al., 1995b; Baumann et al., 2000; Beaufort and Heussner, 2001).

C. pelagicus on the contrary represents the colder species of the fossilizable coccolithophore community, thriving preferentially within surface waters colder than 6 °C (Samtleben and Schröder, 1992; Samtleben et al., 1995a). Accordingly, *C. pelagicus* dominates the polar coccolithophore community of the EGC, albeit with low standing stocks (Samtleben and Schröder, 1992). *C. pelagicus* has previously been associated with mesostrophic to eutrophic waters in phytoplankton-rich frontal systems of the Nordic Seas (Andruleit, 1997; Samtleben et al., 1995a), suggesting an ecology controlled by factors other than temperatures e.g. nutrients and irradiance (Baumann et al., 2000; Schröder-Ritzrau et al., 2001; Balestra et al., 2004; Giraudeau et al., 2004). In addition, some studies have suggested turbulence as an important factor preventing the sinking of this heavily calcified species from the photic zone (Cachão and Moita, 2000) hence favoring its production in the highly mixed upper Arctic Water (ArW) mass. The calcareous skeletal remains – coccoliths – of *E. huxleyi* and *C. pelagicus* are distributed in surface sediments of the Nordic Seas according to their abundances in the extant populations, and dominate the fossil assemblages below AW and ArW masses, respectively (Samtleben and Bickert, 1990; Baumann et al., 2000).

Knowledge of the distribution and ecology of modern fossilizable planktonic organisms is a prerequisite for paleoecologic and paleoceanographic studies of Quaternary sediments. The present investigation therefore aims at further improving our understanding of the distributional patterns of *E. huxleyi* and *C. pelagicus* in surface waters of the Northern North Atlantic. It is based on two zonal transects of surface water sampling across Fram Strait and the Norwegian–Iceland Seas (passing Jan Mayen Island), both carried out during fall 2007 and mid-summer 2011. Spatial and seasonal differences in coccolithophore abundances along both transects are discussed here in view of the large- to meso-scale surface circulation features as deduced from satellite-derived sea-surface temperature (SST) composite maps, as well as previous plankton survey studies of extant coccolithophore populations in the Nordic Seas.

2. Hydrological setting

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 North Atlantic Current (NAC) (5 °C, ≥ 35) (Skagseth et al., 2008) and its extension, the West Spitsbergen Current (WSC) (Koszalka et al., 2011) (Fig. 1). The WSC flows along the continental margin of the western Barents Sea and western Spitsbergen and enters the Arctic Ocean as a subsurface current insulated from the atmosphere by fresh Polar Water (PW) in the upper mixed layer (Blindheim and Østerhus, 2005). 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) (Fig. 1). Its two zonal components, the Jan Mayen Current (JMC) and the East Icelandic Current (EIC), supply fresh PW to the Greenland Sea and Iceland Sea gyre systems (Johannessen, 1986; Olsson et al., 2005). The mixing of PW and AW carried by the two boundary currents creates Arctic Water (ArW; 0–4 °C, 34.6–34.9) (Johannessen, 1986). The northeast–southwest trending boundary between PW and ArW is termed the Polar Front (PF), whereas the boundary between ArW and AW is referred to as the Arctic Front (AF) (Swift, 1986; Van Aken et al., 1995) (Fig. 1). Fronts in the Nordic Seas are generally defined as areas of high horizontal gradients in subsurface to surface temperature, salinity and density in comparison with the mean parent water types (Van Aken et al., 1995). The positions of the fronts in the Nordic Seas are well correlated with bathymetry due to topographic steering of the currents (Johannessen, 1986; Piechura and Walczowski, 1995).

The description of surface water conditions during the October 2007 and July 2011 sampling periods is based here on the interpretation of monthly-mean remote sensing-derived maps of sea-surface temperature (SST) (Fig. 1, see Section 3). The summer 2011 situation is characterized by a westward warming of the surface waters and a weaker expression of the polar EGC, JMC and EIC currents, compared to 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), explain to a high extent the observed shift from a dominance in the July 2011 situation of warmer AW carried by the NAC and WSC in the eastern part of the Nordic Seas to prevailing colder surface waters during the fall 2007 conditions (Fig. 1). These changes are particularly indicated, during fall 2007, by a narrower poleward tongue of AW west of Svalbard, as well as by a strengthened influence of the colder water masses carried by the EGC, JMC and EIC coupled to an increased temperature gradient across the AF and PF, compared to summer 2011.

3. Material and methods

The present study reports on extant populations of *E. huxleyi* and *C. pelagicus* collected along two zonal surface water transects across Fram Strait (ca. 73–78°N) and the Norwegian–Iceland Seas (ca. 70°N) during the fall 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. 1, Tables 1 and 2).

3.1. Coccolithophore analyses

Sampling was conducted en-route using the ship’s sea-water system (ship’s sea water inlet at ca. 5 m water depth), and involved onboard membrane filtration (pore size 0.8 μm) of sea water (2 to 3 l) as described by Andruleit (1996). In the laboratory, a ca. 20 mm² of the filter was cut out and mounted in 2–3 drops of immersion oil between slide and cover-slip for examination under a light microscope at $\times 1000$ magnification, as described by Giraudeau et al.

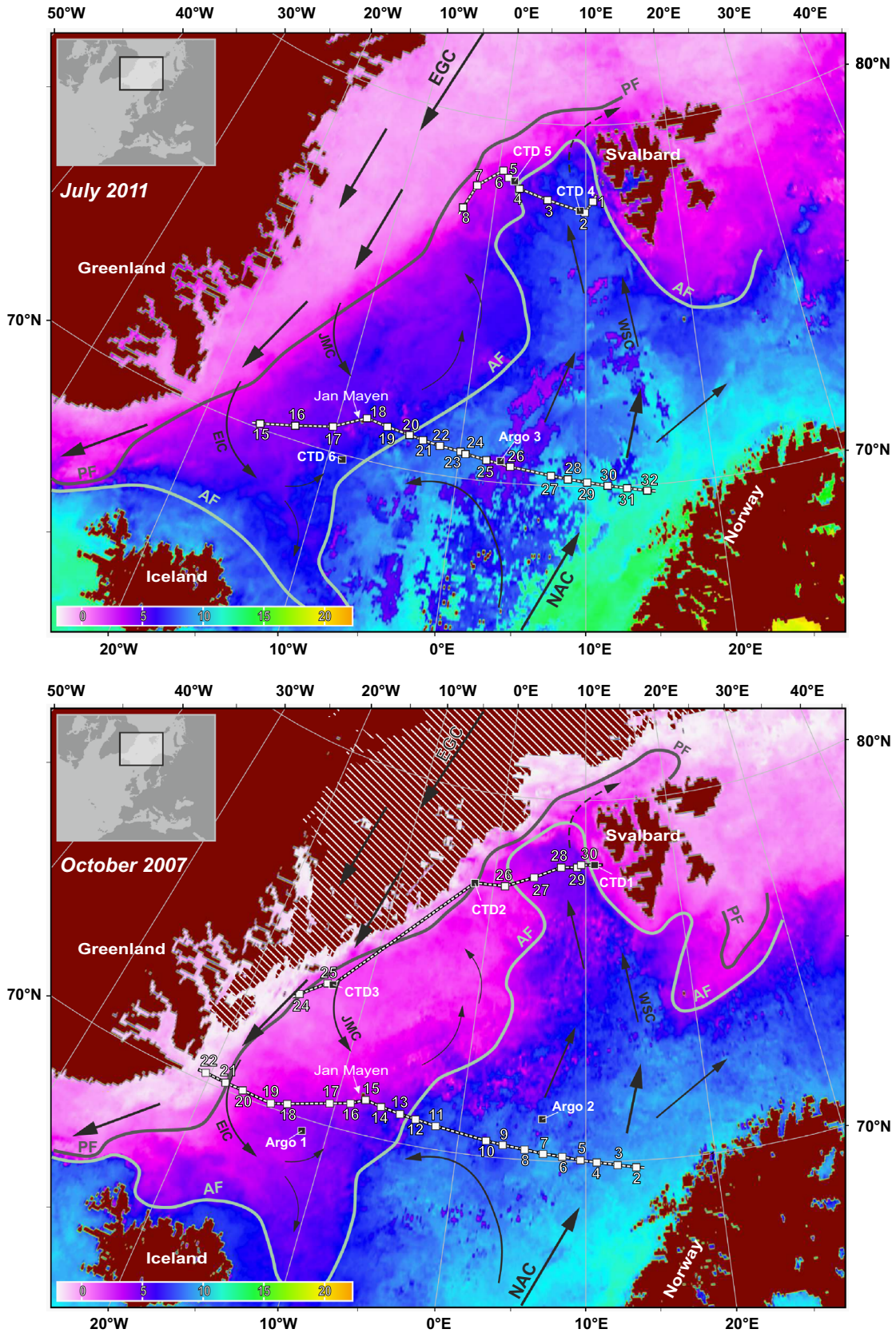


Fig. 1. Satellite derived, 32 days composite maps (see Section 3) of SSTs for July 2011 (top) and October 2007 (bottom), and schematic view of the surface circulation within the Nordic Seas. NAC: North Atlantic Current, WGC: West Spitsbergen Current, EGC: East Greenland Current, JMC: Jan Mayen Current, EIC: East Icelandic Current. The positions of the Arctic (AF) and Polar (PF) fronts are defined by the mean location of the maximal thermal gradients extracted from the SST satellite images. White squares: sample locations; black squares: locations of CTD casts and ARGO stations discussed in the text (see Appendix A). Shaded area (October 2007): no data.

Table 1
List of surface water samples for Sep.–Oct. 2007, with collection dates, locations, coccolithophore standing stocks and total number of counted coccolithophore cells.

Sample	Longitude (°E)	Latitude (°N)	Date	Total standing stocks ($\times 10^3$ cells/l)	<i>Coccolithus pelagicus</i> ($\times 10^3$ cells/l)	<i>Emiliania huxleyi</i> ($\times 10^3$ cells/l)	<i>Algirosphaera</i> sp. ($\times 10^3$ cells/l)	Total counted cells
1	13.85	69.82	29/09/2007	12.1	0.0	12.1	0.0	4
2	12.43	69.90	30/09/2007	4.8	0.0	2.4	2.4	4
3	10.83	69.98	30/09/2007	2.2	0.0	2.2	0.0	2
4	9.58	70.05	30/09/2007	5.2	0.0	3.9	1.3	8
5	9.58	70.05	30/09/2007	0.0	0.0	0.0	0.0	0
6	8.17	70.13	30/09/2007	1.5	0.0	1.5	0.0	2
7	6.67	70.20	30/09/2007	0.0	0.0	0.0	0.0	0
8	5.23	70.28	30/09/2007	0.0	0.0	0.0	0.0	0
9	3.50	70.37	30/09/2007	0.0	0.0	0.0	0.0	0
10	2.17	70.43	30/09/2007	0.0	0.0	0.0	0.0	0
11	–1.92	70.65	01/10/2007	0.0	0.0	0.0	0.0	0
12	–3.57	70.73	01/10/2007	1.3	1.3	0.0	0.0	4
13	–4.85	70.80	01/10/2007	2.2	0.0	2.2	0.0	6
14	–6.45	70.88	01/10/2007	11.8	0.0	11.8	0.0	36
15	–7.78	70.97	01/10/2007	23.5	0.0	23.5	0.0	72
16	–8.87	70.77	01/10/2007	23.5	2.6	20.9	0.0	72
17	–10.45	70.62	01/10/2007	66.4	0.0	66.4	0.0	254
18	–13.60	70.25	02/10/2007	20.7	0.0	20.7	0.0	68
19	–14.83	70.12	02/10/2007	13.1	0.0	13.1	0.0	40
20	–17.23	70.18	02/10/2007	2.5	2.5	0.0	0.0	6
21	–18.68	70.20	02/10/2007	1.9	0.5	1.4	0.0	8
22	–20.38	70.23	02/10/2007	6.1	3.1	3.1	0.0	16
24	–15.67	73.23	07/10/2007	6.5	3.3	3.3	0.0	20
25	–13.65	73.77	08/10/2007	16.3	10.5	5.9	0.0	50
26	1.25	77.50	11/10/2007	48.3	25.6	22.6	0.0	66
27	4.32	77.82	12/10/2007	11.5	1.6	9.9	0.0	14
28	7.23	78.13	12/10/2007	6.1	1.2	3.7	1.2	10
29	9.03	78.15	12/10/2007	12.7	2.3	9.2	1.2	22
30	9.48	78.22	12/10/2007	9.1	2.6	3.9	2.6	14
CTD 1	–13.15	73.78	08/10/2007	9.1	3.9	5.2	0.0	10
CTD 2	–2.03	77.47	11/10/2007	52.9	29.4	23.5	0.0	54
CTD 3	10.98	78.22	12/10/2007	7.0	0.0	5.6	1.4	28

(1993). A total of 57 samples (31 samples for September/October 2007; 26 samples for July 2011) were primarily investigated for *E. huxleyi* and *C. pelagicus* abundances (Tables 1 and 2) and the results expressed as coccolithophore cell densities (number of cells/l). At least 50 fields of view per sample (equivalent to 1.5 mm² at $\times 1000$ magnification) were investigated for coccolithophore census counts. An additional coccolithophore species, *Algirosphaera* sp., was only occasionally encountered within the investigated samples. Part of this apparent low species diversity might be induced by the “Funnel” method used as part of the sampling preparation (Herrle and Bollmann, 2004). We believe that the most important cause of the apparent low species diversity is related to the use of light microscopy in the present study. Previous studies comparing census counts derived from scanning electron microscope (SEM), on one hand, and light microscope observations, on the other hand, indicate a dramatic decrease in the species diversity between the two methods, up to 4/5th of the original assemblages (Silva et al., 2008; Poulton et al., 2010), this decrease affecting the rare, often poorly calcified, and morphologically complex species. The same studies (Poulton et al., 2010) however support the use of the standard light microscopy technique for reliable ship- or shore-based quantitative investigations of the dominant species, such as *E. huxleyi* and *C. pelagicus* in the present study. In the present work, *C. pelagicus* refers to the non-motile heterococcolith-bearing phase (*C. pelagicus*) only. While common in surface waters of the Nordic Seas based on SEM investigations of plankton samples (Balestra et al., 2004; Samtleben et al., 1995a), the holococcolith phase of *C. pelagicus* (e.g. *Crystalloolithus hyalinus*, Gaarder and Markalli) was hardly recognizable in the light microscope-based present study. In addition, this latter fragile form is barely preserved in marine sediments, contrary to coccoliths of the heterococcolith phase which, by far, often constitute the bulk of the carbonate fraction in the Nordic Seas sediments (Giraudeau et al., 2004). Our light microscope observations indicate

that *E. huxleyi* cells all belong to a single morphotype ca. 5–6 μ m wide, with characteristics (central area) close to morphotype B (sensu Paasche, 2001).

3.2. Satellite-derived method of hydrological setting

Sea surface temperature (SST) maps (Fig. 1) for the sampling periods were derived from Aqua MODIS 32 days composite, 0.08° (9 km) 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). The time and resolution windows selected for the satellite-based datasets was chosen in order to minimize the effect of common heavy cloudy conditions over the Nordic seas in summertime, as well as to fit with the overall objective of this study, i.e. comparing the distribution of the dominant *E. huxleyi* and *C. pelagicus* species with large scale hydrological features. The geographical distribution of the PF and AF was defined based on the Aqua MODIS dataset, according to the highest SST gradients surface expression, following Van Aken et al. (1995).

Nine conductivity–temperature–depth (CTD) profiles, 5 of them collected as part of the 2007 and 2011 cruises using a Seabird 911 Plus CTD, and 4 extracted from the Coriolis database (<http://www.coriolis.eu.org/>) among which 3 Argo floats, were included into the present study (Fig. 1; Appendix, Table A1 and Fig. A1). They were used as a mean to validate the satellite extracted monthly average SST profiles as well as to provide additional information on the vertical distribution of water masses and stratification within the top 500 m of the water column. An average temperature difference of $\pm \sim 0.6$ °C has been estimated between in situ measurements from CTD and Argo-floats and the MODIS-derived SST values. Two larger deviations (1.2 °C and 1.8 °C) were noticed for CTD 2 and 5 within Fram Strait, respectively, and are related to enhanced

Table 2

List of surface water samples for July 2011, with collection dates, locations, coccolithophore standing stocks and total number of counted coccolithophore cells.

Sample	Longitude (°E)	Latitude (°N)	Date	Total standing stocks ($\times 10^3$ cells/l)	<i>Coccolithus pelagicus</i> ($\times 10^3$ cells/l)	<i>Emiliana huxleyi</i> ($\times 10^3$ cells/l)	<i>Algirosphaera</i> sp. ($\times 10^3$ cells/l)	Total counted cells
1	10.77	77.88	15/07/2011	1.3	0.0	1.3	0.0	2
2	9.88	77.58	15/07/2011	1.1	0.0	1.1	0.0	2
3	5.77	77.90	16/07/2011	27.3	0.0	27.3	0.0	116
4	2.55	78.15	16/07/2011	46.0	14.7	31.4	0.0	234
5	1.22	78.42	16/07/2011	29.3	2.0	27.3	0.0	146
6	0.50	78.60	19/07/2011	10.3	4.8	5.5	0.0	30
7	-2.17	78.08	19/07/2011	4.0	0.0	4.0	0.0	14
8	-3.27	77.42	19/07/2011	1.5	0.0	1.5	0.0	2
15	-15.72	70.13	25/07/2011	5.3	0.0	5.3	0.0	6
16	-13.10	70.40	25/07/2011	2.6	0.0	2.6	0.0	6
17	-10.25	70.68	25/07/2011	21.7	12.5	9.3	0.0	122
18	-7.78	71.15	25/07/2011	3.8	1.0	2.9	0.0	8
19	-6.03	71.05	25/07/2011	12.2	9.8	2.4	0.0	62
20	-4.17	70.95	26/07/2011	5.2	3.1	2.1	0.0	20
21	-3.03	70.88	26/07/2011	9.7	0.0	9.7	0.0	44
22	-1.65	70.80	26/07/2011	1.0	0.0	1.0	0.0	2
23	0.05	70.73	26/07/2011	3.6	0.0	3.6	0.0	10
24	0.47	70.68	26/07/2011	3.5	0.0	3.5	0.0	8
25	2.15	70.58	26/07/2011	17.9	0.0	17.9	0.0	88
26	4.05	70.47	26/07/2011	71.3	3.1	68.2	0.0	280
27	7.28	70.28	26/07/2011	12.6	0.8	11.8	0.0	62
28	8.60	70.20	27/07/2011	65.4	0.4	65.0	0.0	344
29	10.10	70.12	27/07/2011	35.8	0.4	35.4	0.0	170
30	11.67	70.02	27/07/2011	0.0	0.0	0.0	0.0	0
31	13.17	69.93	27/07/2011	8.9	0.0	8.9	0.0	26
32	14.70	69.83	27/07/2011	6.1	0.4	5.7	0.0	32

surface SST gradients over a limited geographic domain in vicinity of the PF and AF as well as biases induced by the nearby sea-ice edge (CTD 2) (Fig. 1; Appendix, Table A1 and Fig. A1).

4. Results and discussion

Considerable spatio-temporal variations in coccolithophore abundances can be observed across both transects. The bulk coccolithophore cell densities within the present study ranged from barren to “moderate” (i.e. max. 70×10^3 cells/l according to Samtleben and Schröder, 1992) (Tables 1 and 2). The average concentrations recorded in areas of highest abundances (ca. 40×10^3 cells/l) fall in the lower range of previous surveys for *E. huxleyi*, and correspond to the average concentrations recorded by Baumann et al. (2000) in the Nordic Seas during the winter and spring low coccolithophore production period (Table 3). A different figure concerns *C. pelagicus* whose average concentrations in areas of highest abundances (ca. 15×10^3 cells/l) were found within the range of previously estimated values for the summer high production period (Table 3). Although a comparison between previous coccolithophore surveys and our study suffers from heterogeneities in the investigated regions, surface waters around Jan Mayen Island are highlighted in both datasets as an area of enhanced concentrations for both species during the summer–early fall season (Table 3).

Applying a simple conversion of coccolithophore concentrations (cells/l) to coccolithophore biomasses ($\mu\text{gC/l}$) using previously published species-specific carbon biomass estimates (O'Brien et al., 2013), our abundance data translate into a biomass range of 0 to $1.7 \mu\text{gC/l}$, with a mean of $0.26 \mu\text{gC/l}$. These values fall well within the range of typical mean coccolithophore carbon biomass estimates (0.01 – $2 \mu\text{gC/l}$) in surface water masses (< 5 m) of the Nordic Seas (O'Brien et al., 2013). Although these typical biomass values are 3 times lower than the mean estimates of coccolithophore biomass for the global ocean (O'Brien et al., 2013), and lower by a factor of 3 of the mean diatom carbon biomass within the Nordic Seas (Leblanc et al., 2012).

4.1. Northern transects

The Fram Strait transects display prominent gradients in SST and coccolithophore standing stock 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 stocks) and fall 2007 (SST ~ -0.5 – 5°C , *C. pelagicus* dominated stocks) (Fig. 2). Coccolithophore cell densities of up to 53×10^3 cells/l were within the range of previous observations south of Svalbard (influenced by the WSC) for the summer and fall-winter seasons (10 to 100×10^3 cells/l; Samtleben et al., 1995a).

Table 3

Average concentrations of *E. huxleyi* and *C. pelagicus* in areas of highest abundances during High (summer–fall) and Low (winter–spring) coccolithophore production periods based on a mapping (not shown) of the published datasets of (1) Baumann et al. (2000), (2) Samtleben and Schröder (1992), and (3) Charalampopoulou et al. (2011). Data gathered in the present study are provided (right column) for comparison.

	High production period			Low production period			This study	
	Average concentration ($\times 10^3$ cells/l) in areas of highest abundances	Ref.		Average concentration ($\times 10^3$ cells/l) in areas of highest abundances	Ref.		Average concentration ($\times 10^3$ cells/l) in areas of highest abundances	
<i>E. huxleyi</i>	~ 140	Northern Norwegian Sea	(1,2)	~ 40	Northern Norwegian Sea	(1)	~ 30	Fram Strait
	~ 410	Southern Norwegian Sea	(3)	~ 30	Southern Norwegian Sea	(1)	~ 50	Central Norwegian Sea
	~ 150	ca. Jan Mayen Island	(1,2)				~ 40	ca. Jan Mayen Island
<i>C. pelagicus</i>	~ 20	Northern Norwegian Sea	(1)	~ 2	Northern Norwegian Sea	(1)	~ 25	Fram Strait
	~ 30	ca. Jan Mayen Island	(1)	~ 5	Central Norwegian Sea	(1)	~ 10	ca. Jan Mayen Island
	~ 25	Greenland Sea	(1)				~ 10	Greenland Sea

Peak coccolithophore abundances occurred on the western edge of the poleward flow of surface AW (Fig. 2), either associated with the AF (July 2011) or within ArW (October 2007). This open-ocean frontal area is characterized by some of the highest density gradients recorded in the upper water layer of the Nordic Seas (Korablev et al., 2014) triggered by the opposing boundary currents of AW and PW, within the narrow Fram Strait gateway. While vertical motions within such a dynamical feature set the supply of nutrients to the upper mixed layer, the strong density gradients acts as a barrier in the surface water (Bower et al., 1985), this combination of physical and chemical properties being prone to enhance phytoplankton biomass and productivity (Yoder et al., 1994).

Peak cell densities were characterized by an apparent seasonal change between the two years from a dominance of *E. huxleyi* during the summer period, to almost equally shared cell numbers with *C. pelagicus* during the fall situation (Fig. 2). Differences in the spatial development of the Frontal Zone between the summer and fall periods, as expressed by a reduced distribution of surface AW in October 2007 compared with July 2011 (Fig. 1), may partly explain this change in coccolithophore assemblage. Surface waters at the eastern edge of the Frontal Zone (AF) during July 2011 showed low concentrations of *C. pelagicus*, a species which has previously been found to be abundant, if not year-round dominant in ArW (Baumann et al., 2000). A strong stratification of the upper photic layer took place across the Frontal Zone in summer 2011 (Appendix, Fig. A1, CTD 4 and 5), under the combined influence of enhanced sea-ice melting, increased contribution of AW to the surface waters of Fram Strait, and higher irradiance. This scheme, linked with high SSTs and a weaker temperature gradient across the Frontal Zone (Fig. 2), resulted here in *E. huxleyi* dominated coccolithophore assemblages (Fig. 2). This situation agrees with previous observations which showed this species as occasionally highly successful in ArW close to the PF during the 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 SSTs within the Frontal Zone area during fall 2007 (Fig. 2; Appendix, Fig. A1, CTD 2), a situation associated here with a reduced westward influence of surface AW across Fram Strait (Fig. 1), favored an increased abundance of the well-mixed and cold water adapted *C. pelagicus*.

4.2. Southern transects

The SST profiles along the two Norwegian–Iceland Seas transects display a pattern of stepwise decreasing values from the NAC-bathed area off western Norway (Fig. 3; Appendix, Fig. A1, Argo 2 and 3) to the EGC-influenced margin off eastern Greenland. In both 2007 and 2011 the AF and the PF were identified by SST gradients of ca. 2.5°C at around 4°W and 18°W , respectively

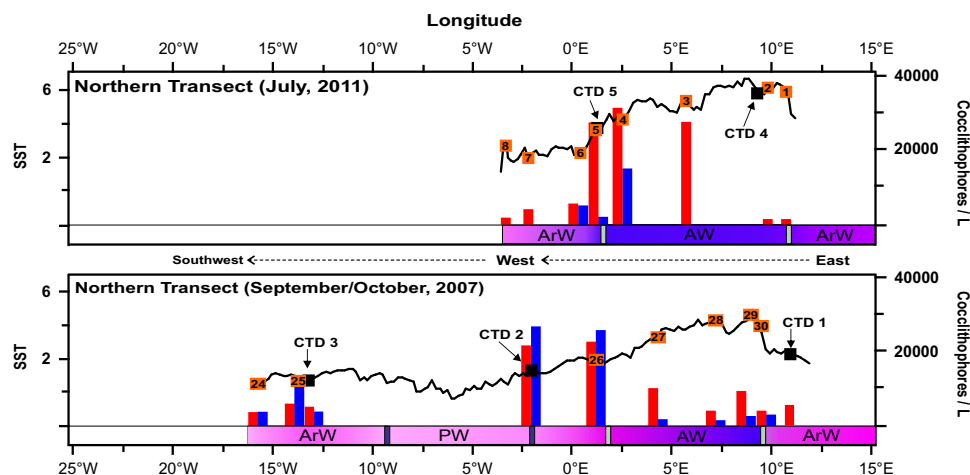


Fig. 2. Longitudinal plots of coccolithophore cell densities and SSTs across Fram Strait during July 2011 (top) and October/September 2007 (bottom). Red and blue bars refer to *Emiliana huxleyi* and *Coccolithus pelagicus*, respectively; orange boxes: sample locations; black boxes: locations of CTD casts 1–5; horizontal color bars: nature of surface water masses (the color code follows the one used in the satellite-derived SST maps); dashed arrows: overall transect direction. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Fig. 3). Despite a rather moderate (ca. 1 °C) summer to fall SST difference along this southern transect, the distribution of maximum coccolithophore cell densities, mostly explained by *E. huxleyi*, was governed by a zonal shift, from the eastern Norwegian Sea in July to the northern Iceland Sea, west of Jan Mayen Island in September–October (Fig. 3). This zonal shift refers to the common north–westward progression in coccolithophore standing stock across the Nordic Sea throughout the summer–fall season, as described by Samtleben et al. (1995a) and Schröder-Ritzrau et al. (2001) among others, and is usually delayed by the diatom spring bloom which initiate in May in the Norwegian Sea and progresses to the western Nordic Seas in summer (Samtleben et al., 1995a).

Beside zonal shift in bulk coccolithophore abundances, seasonality locally affected the composition of the assemblage in the ArW-bathed Iceland Sea, from a *C. pelagicus* in summer, to an *E. huxleyi* dominated assemblage in fall (Fig. 3). This change in species dominance occurred together with a modified hydrological setting of the surface waters in the northern Iceland Sea: there, ArW bore a strong signature of AW (salinity > 34.9) as well as a deep mixed layer (Appendix, Fig. A1, CTD 6) during July 2011, whereas a buoyant, lower salinity (< 34.8) and highly stratified upper photic layer of PW origin characterized this region during fall 2007 (Appendix, Fig. A1, Argo 1). The latter is likely a direct result of mild and sunny weather conditions during the period of sampling (Husum, 2007). The dominance of *C. pelagicus* in the summer of 2011 agrees well with previous indications that the primary distribution area of this cold-adapted species in the Nordic Seas is within ArW masses (Baumann et al., 2000). The transition to an *E. huxleyi*-dominated population in the northern Iceland Sea during fall 2007 suggests a control by other ecological factors than temperature alone, according to available data, stratification and irradiance.

Peak very localized coccolithophore concentrations, with values up to ca. 70×10^3 cells/l, were encountered at two occasions along the southern transects.

Abnormally high *E. huxleyi* cell concentrations in fall 2007 in close vicinity to Jan Mayen Island (Fig. 3) are likely to be induced by the so-called “island mass effect” (Doty and Oguri, 1956) and associated enhanced phytoplankton biomass, either via nutrient enrichments by run-off and re-suspended sediment from the shelf sea-bed (Sharples, 1998), and/or hydrodynamic processes (Hasegawa et al., 2008).

Another local area of excess *E. huxleyi* concentrations was found in July 2011 in the eastern Norwegian Sea (Fig. 3) and is strictly related to two successive sharp negative anomalies of SSTs up to 4 °C between ca. 2°E and 8°E (Figs. 1 and 3). This temperature

anomaly is related to the Lofoten Gyre, a semi-permanent feature of the Norwegian Sea forced by large-scale atmospheric rotational variations (Jakobsen et al., 2003). SST Aqua MODIS images (<http://oceancolor.gsfc.nasa.gov/>) indicates that this phenomenon occurs almost every year but is affecting the surface waters in July and August only. The Argo record for July 2011 (Appendix, Fig. A1, Argo 3) suggests deep mixing of AW-type waters within this gyre. Hence, our unique observation of *E. huxleyi* peak concentrations within the Lofoten Gyre might be explained by vertical mixing, and hence nutrient enrichment of the upper photic layer.

5. Conclusions

Coccolithophore samples investigated in the present study were collected on-route along two zonal surface water transects perpendicular to the major meridional boundary current systems and hydrological fronts of the Nordic Seas. The combined use of remote sensing images, CTD casts and Argo floats from existing databases, was found relevant for significantly improving our knowledge on the meso- to large scale biogeography of the dominant fossilizable coccolithophore species within the northern North Atlantic i.e. *E. huxleyi* and *C. pelagicus*.

Seasonal differences in the distribution and stratification of the main water masses resulted in an overall westward shift of the location of peak coccolithophore standing stocks dominated by the opportunistic *E. huxleyi* from the summer to the fall situations. Our datasets across the Norwegian–Iceland Seas confirm previous studies indicating a zonal shift in coccolithophore cell densities from the eastern Norwegian Sea in July to the northern Iceland Sea, west of Jan Mayen Island in September–October (Samtleben et al., 1995a). The change in dominating species west of Jan Mayen Island from *C. pelagicus* in summer to *E. huxleyi* in fall was related to a change in stratification from well mixed (summer) to stratified (fall) surface waters. An island mass effect might additionally explain the highest *E. huxleyi* concentrations recorded in close vicinity of Jan Mayen Island in fall 2007. Local peak coccolithophore abundances recorded within the eastern Norwegian Sea in July 2011 were related to a geographically- and temporally-restricted, pervasive hydrological process, the Lofoten gyre.

Our dataset obtained in Fram Strait represent to our knowledge a first view of the zonal distribution of extant coccolithophores

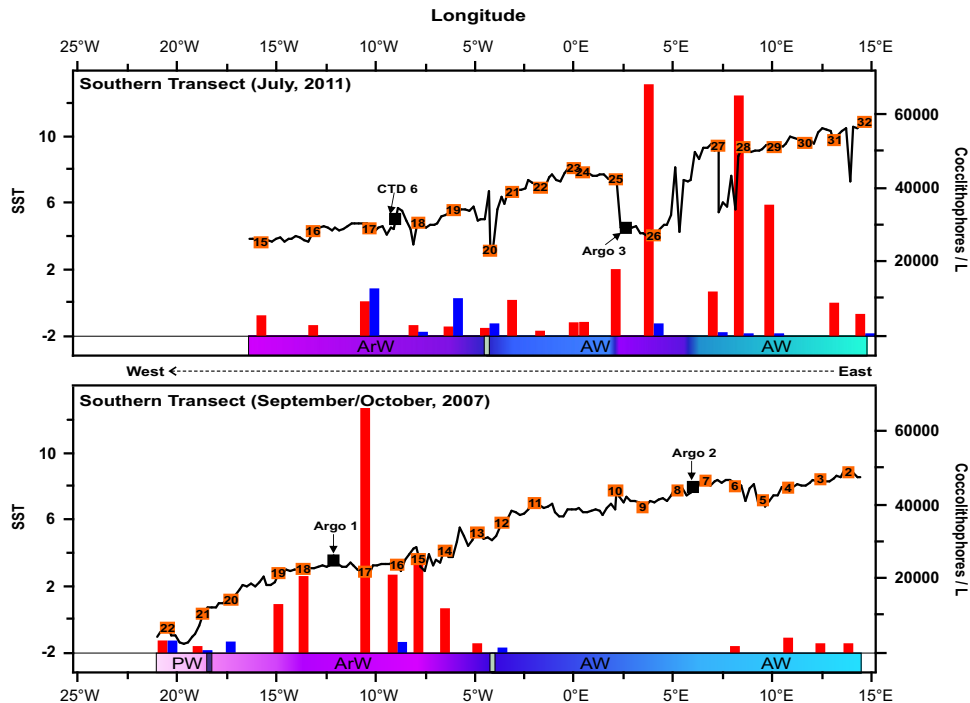


Fig. 3. Longitudinal plots of coccolithophore cell densities and SSTs across the Norwegian–Iceland Seas during July 2011 (top) and October/September 2007 (bottom). Red and blue bars refer to *E. huxleyi* and *C. pelagicus*, respectively; orange boxes: sample locations; black boxes: locations of CTD 6 and Argo casts 1–3; horizontal color bars: nature of surface water masses (the color code follows the one used in the satellite-derived SST maps); dashed arrows: overall transect direction. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

within this climatically sensitive area during summer and fall. The physical and chemical conditions at play within the narrow frontal zone of the PF and AF, and related to strong density gradients, explain the location of maximum cell densities at the western edge of the AW mass, if not west of the AF, during both the summer and fall sampling periods. Seasonal changes in dominance from *E. huxleyi* (summer) to *C. pelagicus* (fall), are possibly 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 seasonally higher irradiance leading to the high abundance of the opportunistic species *E. huxleyi* within an area usually characterized by *C. pelagicus*-dominated low density populations.

The ongoing intensification of sea-ice melting and thinning within the Arctic Ocean, and the associated increased export of ice and melt water to the Nordic Seas (Kwok, 2009), directly result in an overall increased surface water stratification in the north-western North Atlantic (Furevik et al., 2002). These changes combined, in recent decades, with enhanced flux of AW through the Arctic gateways (Skagseth et al., 2008) might trigger a more frequent seeding of opportunistic coccolithophore species into the high Arctic, as already identified off Northern Svalbard (Hegseth and Sundfjord, 2008). Continuing surveys on the distribution of extant coccolithophores are therefore of crucial importance to fully comprehend and further elaborate on the influence of the presently changing high latitude Ocean on this group of calcifying marine phytoplankton.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr.2014.11.012>.

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