Irradiance and pH affect coccolithophore community composition on a transect between the North Sea and the Arctic Ocean

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ABSTRACT: Little is known about the distribution of coccolithophores in Arctic regions, or the reasons why they are absent from certain locations but thrive in others. Factors thought to affect coccolithophore distribution include nutrients, salinity, temperature and light, as well as carbonate chemistry parameters. Here we present data collected in summer 2008 along a transect between the North Sea and Svalbard (Arctic). Coccolithophore abundance and diversity were measured and compared with a set of environmental variables that included macronutrients, salinity, temperature, irradiance, pH and $\Omega_{calcite}$. Eighteen coccolithophore species were found in the southern North Sea where coccolithophores were previously thought to be absent. In the ice-covered region north of Svalbard, coccolithophores were scarce and dominated by the family Papposphaeraceae. A multivariate approach showed that changes in pH and mixed layer irradiance explained most of the variation in coccolithophore distribution and community composition (Spearman's $r_S = 0.62$). Differences between the Svalbard population and those from other regions were mostly explained by pH ($r_S = 0.45$), whereas mixed layer irradiance explained most of the variation between the North Sea, Norwegian Sea and Arctic water assemblages ($r_S = 0.40$). Estimates of cell specific calcification rates showed that species composition can considerably affect community calcification. Consequently, future ocean acidification (changes in pH) and stratification due to global warming (changes in mixed layer irradiance) may influence pelagic calcification by inducing changes in the species composition of coccolithophore communities.

KEY WORDS: Coccolithophore · *Emiliania huxleyi* · Arctic Ocean · pH · Irradiance · Ocean acidification

INTRODUCTION

Coccolithophores are a diverse group of calcifying marine phytoplankton that might be either positively or negatively affected by climate change and ocean acidification (Doney et al. 2009). Their response to such changes is of great importance as coccolithophores play a major role in the ocean carbon cycle by contributing to both the biological and carbonate pumps. They can contribute up to 20% of total primary production in selected oceanic regions (Poulton et al. 2007, 2010) and produce high numbers of coccoliths, thus dominating (50 to 80%) pelagic biogenic calcification (Milliman 1993, Broecker & Clark 2009). During

calcification, CO_2 is produced and as a result partial CO_2 pressure (pCO_2) is often elevated in bloom areas (Holligan et al. 1993a, Merico et al. 2006). Moreover, coccolithophores may facilitate the transfer of organic carbon from the surface to the deep ocean as a result of the 'ballast effect' imparted by their coccoliths (Klaas & Archer 2002). Hence, a change in coccolithophore calcite production, due to changes in either coccolithophore abundance or cellular calcification, could in turn affect the oceanic carbon cycle (Zondervan 2007) and ultimately feed back to climate change.

Predicted future changes in the ocean include sea surface warming (Barnett et al. 2005), shallowing of the mixed layer (Levitus et al. 2000), changing nutrient

concentrations and light conditions (Bopp et al. 2001, Sarmiento et al. 2004), as well as ocean acidification (Orr et al. 2005). Extensive experimental and field research on *Emiliania huxleyi*, the most common coccolithophore, indicates that calcification in this species depends strongly on irradiance and is stimulated by nutrient stress, even though cells grow well under high nutrient concentrations and low irradiance (see review by Zondervan 2007). However, elevated pCO_2 levels have varying effects on the calcifying ability of different *E. huxleyi* strains (Riebesell et al. 2000, Iglesias-Rodriguez et al. 2008, Langer et al. 2009) and different coccolithophore species (Langer et al. 2006). Moreover, effects of simultaneous changes in multiple environmental variables are diverse. For example, light saturation for *E. huxleyi* growth depends on temperature (Paasche 2001, Zondervan 2007) whereas the sensitivity of *E. huxleyi* calcification and organic C fixation to elevated pCO_2 depend on their replete or depleted nutrient status (Sciandra et al. 2003, Delille et al. 2005, Engel et al. 2005) as well as available light (Zondervan et al. 2002, Feng et al. 2008). Hence, more research on synergistic effects of environmental variables over a wider range of coccolithophore species is essential.

Coccolithophores are widespread in the oceans; they are found in oceanic and coastal waters and they extend from tropical to subarctic and subantarctic regions (Winter et al. 1994). They are most prominent in high latitude waters where *Emiliania huxleyi*, the most euryhaline and eurythermal species, forms blooms in regions such as the North Atlantic, the North Sea, the Barents Sea and the Bering Sea (Tyrrell & Merico 2004) when conditions are favourable, i.e. seasonally shallow mixed layer depths, high irradiances and high temperatures (Raitsos et al. 2006, Merico et al. 2004). Blooms also occur at the time of year when carbonate ion concentrations are seasonally high (Merico et al. 2006). Coccolithophore diversity, however, is highest in the warm oligotrophic subtropical gyres (Winter et al. 1994).

Although their biogeography is relatively well mapped, it remains unclear why coccolithophores are absent from some regions whilst thriving in others. They are thought to be scarce in the Arctic, perhaps because of the low temperatures (<0°C) relative to optimal (2 to 15°C) bloom temperatures (Holligan et al. 1993b, Raitsos et al. 2006, Merico et al. 2004), although the exact cause is unknown because very few studies have examined coccolithophores in polar waters. Early taxonomic work in Homer (South Alaska), Godhavn (West Greenland) and Resolute Bay (Northwest Passage) (Manton et al. 1976a, 1976b, 1977) indicated the presence of some coccolithophore species of *Papposhaera*, *Pappomonas*, *Turrisphaera* and *Wigwamma* in

low-temperature (<0°C) waters. The lack of quantitative data on Arctic coccolithophore assemblages and their calcification rates is a significant gap in current knowledge as the Arctic Ocean is particularly vulnerable to environmental changes: it has been warming 2 times faster than the rest of the world's oceans and models predict that it will be the first region to experience widespread calcite undersaturation of surface waters (Orr et al. 2005, Steinacher et al. 2009).

Coccolithophores are also absent from sediments in the southern North Sea (SNS) and the eastern English Channel, whereas they are found in high numbers in sediments of the northern North Sea (NNS) (Houghton 1991) and the western English Channel. The high coccolithophore numbers found in the NNS sediments can be explained by the *Emiliania huxleyi* blooms observed there regularly from both satellites and *in situ* sampling (Holligan et al. 1993b, Van der Wal et al. 1995, Buitenhuis et al. 1996, Marañón & González 1997, Burkill et al. 2002). However, such blooms are not observed in the SNS, and water column data for this region are scarce. Blooms in the NNS coincide with enhanced thermal stratification and low summer nutrient concentrations, whereas the possibly coccolithophore-barren SNS remains well mixed and, for this reason, has unusually high pCO_2 throughout the summer (Thomas et al. 2004), representing conditions potentially unfavourable for coccolithophores.

The main aim of the present study was to collect coccolithophore diversity, abundance and calcification data along a transect of strong environmental gradients. This provided the opportunity to investigate whole-community responses of natural coccolithophore populations to a wide range of environmental conditions. A sampling transect from the North Sea to Svalbard presented such strong environmental gradients and variability, as well as the opportunity to examine coccolithophore distribution in the SNS and in the high Arctic. A second goal was to use a multivariate approach to investigate which environmental variables, including temperature, salinity, irradiance, macronutrients and carbonate chemistry, most strongly influence coccolithophore distribution along this gradient. Finally, we added *in situ* calcification data to estimate cellular calcification rates and relate these to the assemblage composition.

MATERIALS AND METHODS

Study area. The study area included 4 main hydrographic regions (Fig. 1): (1) the North Sea, subdivided into the well-mixed southern part (SNS), the Atlantic-influenced central part (CNS) and the stratified northern part (NNS) influenced by the Baltic Sea outflow
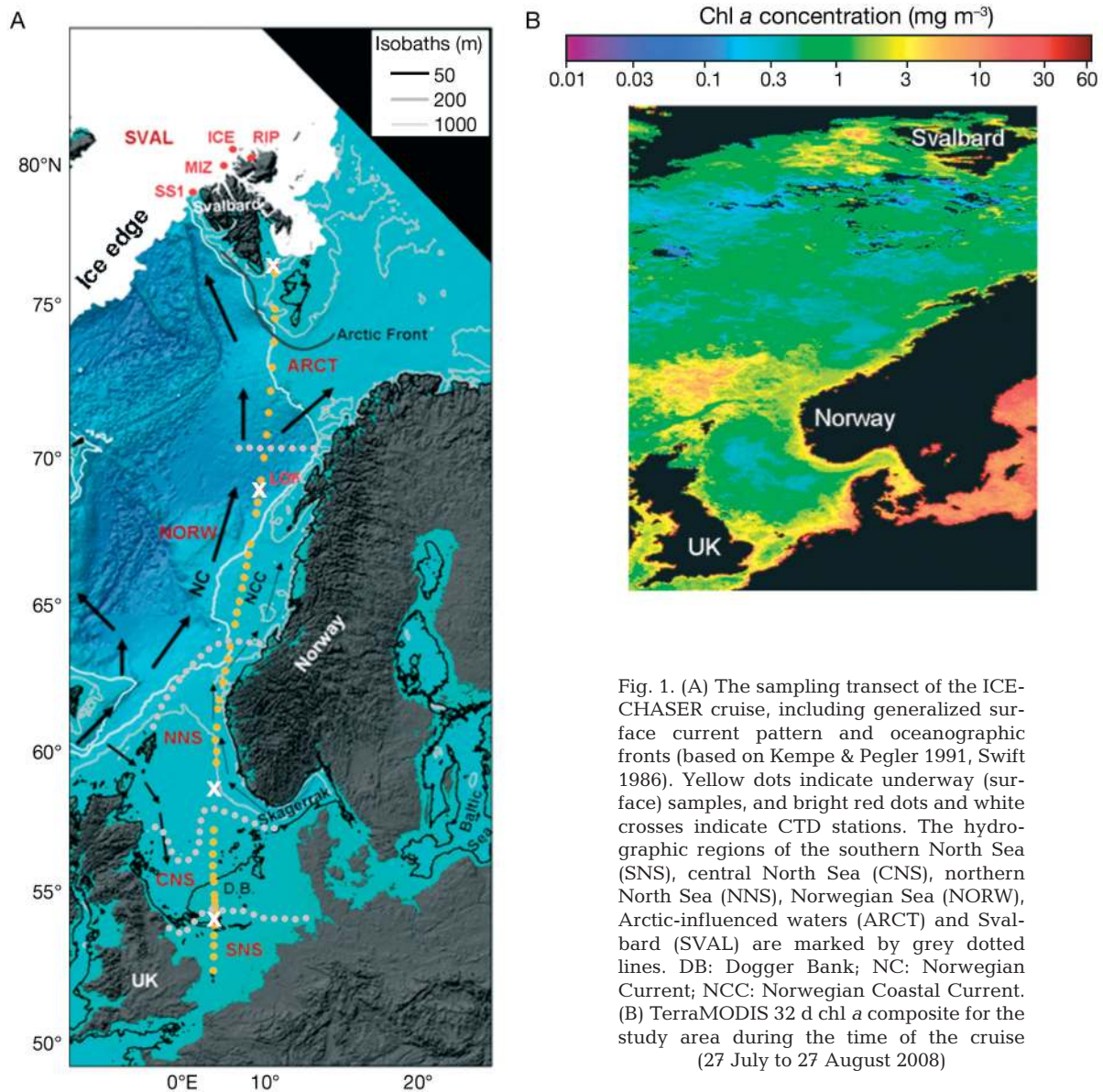
Fig. 1. (A) The sampling transect of the ICE-CHASER cruise, including generalized surface current pattern and oceanographic fronts (based on Kempe & Pegler 1991, Swift 1986). Yellow dots indicate underway (surface) samples, and bright red dots and white crosses indicate CTD stations. The hydrographic regions of the southern North Sea (SNS), central North Sea (CNS), northern North Sea (NNS), Norwegian Sea (NORW), Arctic-influenced waters (ARCT) and Svalbard (SVAL) are marked by grey dotted lines. DB: Dogger Bank; NC: Norwegian Current; NCC: Norwegian Coastal Current. (B) TerraMODIS 32 d chl a composite for the study area during the time of the cruise (27 July to 27 August 2008)

(Kempe & Pegler 1991); (2) the Norwegian Sea (NORW), characterised by the Norwegian Current flowing northward off the Scandinavian coast (Swift 1986); (3) the continental shelf and slope south of Svalbard (ARCT), influenced by the Arctic Front (Swift 1986); and (4), the partially ice-covered region north of Svalbard (SVAL).

Sampling. Sampling was conducted during the ICE-CHASER cruise (23 July to 23 August 2008) on board the RRS 'James Clark Ross' during a transect from Portland, UK, to Svalbard in the Arctic (Fig. 1). Both vertical CTD profiles and the ship's continuous non-toxic underway supply were used for water sampling. Water samples for coccolithophore community abundance and diversity, carbonate chemistry parameters

and ancillary measurements were collected from 47 underway locations (~5 m depth) and from 7 CTD deployments (see Fig. 1); one in each of SNS (SNScast), NNS (NNScast), NORW (off the Loffoten Islands, LOF), an open water shelf station west of Svalbard (SS1), the Marginal Ice Zone (MIZ), an Ice station (ICE) and an Arctic fjord station at Rijpfjorden (RIP). Samples for primary production and calcification rates were collected from all CTD deployments except from SNScast.

Coccolithophore community. Water samples (1 l) from either the underway supply or from each of 4 to 6 CTD depths were gently filtered onto Millipore Isopore membrane filters (25 mm diameter, 1.2 μm pore size), with a 25 mm diameter circle of 10 μm nylon mesh acting as a backing filter to achieve even distrib-

ution of cells. The membrane filters were oven dried overnight at 30°C and stored in the dark in sealed Petri dishes. A radially cut portion of each filter was mounted on an aluminium stub and gold-coated. For each filter, 225 fields of view (FOV; images), equivalent to ~1 mm², were taken at ×5000 magnification along a predefined meander-shaped transect, using a scanning electron microscope (Leo 1450VP, Carl Zeiss) combined with the software SmartSEM. For each sample, we enumerated both coccospheres and coccoliths until we reached 300 of each. The SmartSEM software allowed us to set the scanning for zero overlap between FOVs. We avoided counting specimens that were on the edge between FOVs twice by only counting the top and right edges of each FOV. The number of FOVs counted was used to calculate the area of the filter covered (the size of one FOV was 4.054×10^{-3} mm²). Both coccospheres and coccoliths were identified to species level following Young et al. (2003), and the abundance of these for each species (coccospheres or coccoliths ml⁻¹) was calculated as $C \times (F/A)/V$, where C is the total number of coccospheres or coccoliths counted, A is the area investigated (mm²), F is the total filter area (mm²) and V is the volume filtered (ml).

Diversity in each sample was determined by 3 indices: species richness (the total number of species, S), Shannon-Wiener diversity index (H') and Pielou's evenness (J'). H' accounts for both species richness and differing numbers of individuals whereas J' expresses solely how evenly individuals are distributed among the species:

$$H' = -\Sigma_i p_i \log(p_i) \tag{1}$$

$$J' = H'/H'_{max} \tag{2}$$

where p_i is the proportion of the total count arising from the ith species.

Macronutrients. Phosphate and nitrate concentrations were determined using a Lachat QuikChem 8500 flow injection autoanalyser following the manufacturer's recommended methods for orthophosphate and nitrate/nitrite (Lachat method nos. 31-115-01-1-G and 31-107-04-1-A). Samples were run in triplicate and salt-corrected by analyzing low nutrient seawater purchased from OSIL (Batch LNS 16) prior to and within each batch of samples. The precision of nutrient measurements was ±0.03 µM for both phosphate and nitrate.

Chlorophyll *a*. Water samples (200 to 500 ml) for chl *a* analysis were filtered onto Whatman GF/F (~0.7 µm pore size) filters and extracted in 7 ml 90% acetone for 24 h in the dark at 4°C. Chl *a* fluorescence was measured on a Turner Designs AU-10 fluorometer equipped with Welschmeyer (1994) filters and calibrated using a pure chl *a* standard (Sigma).

Mixed layer irradiance. In order to calculate mean daily irradiance over the mixed layer, we first deter-

mined mixed layer depth (MLD) as the shallowest depth corresponding to a density difference ($\Delta\sigma_t$) with the surface waters of more than $\Delta\sigma_t = 0.125$ g ml⁻¹ (Monterey & Levitus 1997). The vertical attenuation coefficient (k_d) for downward irradiance and the subsurface irradiance (E_0) at each of the 7 CTD deployments (and one additional deployment in ARCT, south of Svalbard; Fig. 1) were calculated from photosynthetically active radiation (PAR) data from a CTD-mounted sensor using the relationship describing the exponential diminution of downward irradiance (E_z) with depth (z):

$$E_z = E_0 \times \exp(-k_d z) \tag{3}$$

The fraction of daily PAR (mol PAR m⁻² d⁻¹) measured above the sea surface that reached below the sea surface was calculated using a ratio of instantaneous $E_0/E_{\text{above surface}}$ for each CTD station. Daily irradiance was then calculated at every 1 m down to the MLD:

$$E_{z,\text{daily}} = E_0/E_{\text{above surface}} \times \\ \text{daily PAR}_{\text{above surface}} \times \exp(-k_d z) \tag{4}$$

The mean irradiance over the mixed layer, E_{MLD} (mol PAR m⁻² d⁻¹), was calculated as the sum of $E_{z,\text{daily}}$ at every 1 m down to the MLD, divided by the MLD.

A highly significant relationship was found between k_d and surface chl *a* ($y = 0.1841x + 0.0685$, $R^2 = 0.9492$, p = 0.005, n = 5); this relationship was used to calculate k_d values for the 47 underway locations from chl *a* data only. These were used together with MLD and $E_0/E_{\text{above surface}}$ values extrapolated from the CTD stations and daily PAR to calculate E_{MLD} at each of the underway locations.

Comparison of daily PAR data from the ship's sensor with 32 d composite Aqua MODIS PAR data during the study period showed good agreement between the 2 and confirmed that daily PAR values were typical of the time of the year and were not biased by weather conditions at the time of measurement.

Carbonate chemistry. Samples for the determination of dissolved inorganic carbon (DIC) and total alkalinity (TA) were drawn in 250 ml Schott® SUPRAX borosilicate glass bottles following Dickson et al. (2007) to minimise gas exchange. A headspace of 1% was allowed for water expansion and samples were poisoned with 50 µl saturated mercuric chloride solution (7 g 100 ml⁻¹). Sample analysis was undertaken at 25°C using the VINDTA 3C (Marianda). DIC was determined coulometrically (coulometer 5011, UIC) and TA was determined using a semi-closed-cell titration (Dickson et al. 2007). Repeated measurements on the same batch of seawater (n ≥ 5) were undertaken every day prior to sample analysis to assess the precision of the method. Certified reference materials (from A. G. Dickson, Scripps Institute of Oceanography) were analysed as standards to calibrate the instrument at the

beginning and end of each day of analysis. Calcite saturation state ($\Omega_{calcite}$), carbonate ion concentration, pH and pCO_2 were calculated from DIC, TA, nutrients, temperature, salinity and pressure data using the CO2SYS.XLS program (Pierrot et al. 2006).

Multivariate data analysis. Multivariate statistics were used to assess spatial changes in coccolithophore community composition (biotic data) and environmental variables (abiotic data) following the methods described by Clarke (1993), using E-PRIMER (v. 6.0) (Clarke & Gorley 2006).

Analysis of biotic data was carried out on square-root-transformed species abundances, using Bray-Curtis similarity to determine changes in the abundance of dominant species as well as the less abundant species. Analysis of abiotic data was carried out on power-transformed (to reduce skewness and stabilize the variance) and standardised (to bring all variables to comparable scales) values of E_{MLD}, salinity, temperature, pH, $\Omega_{calcite}$, nitrate and phosphate, using Euclidean distance to determine spatial changes in these variables.

Biotic and abiotic data were used independently to cluster samples into groups that were mutually similar, by means of both hierarchical agglomerative clustering (CLUSTER) and non-metric multi-dimensional scaling (NMDS). Agreement between the 2 representations and an NMDS stress value of <0.1 was obtained for both biotic and abiotic data, which strengthened belief in the adequacy of both. Further confirmation of significant differences between clusters was assessed by performing an analysis of similarities (ANOSIM) on the *a priori* specified clusters.

The species typical of each group (characteristic species) and the species responsible for the differences between groups (discriminating species) were identified using the similarity percentages (SIMPER) routine. Characteristic species were defined as those cumulatively contributing approximately 90% to the Bray-Curtis similarity within each group and discriminating species were defined as those cumulatively contributing more than 50% to the Bray-Curtis dissimilarity between groups. The SIMPER routine was also used to identify the environmental factors responsible for differences between environmental clusters, i.e. those cumulatively contributing approximately 50% to the Euclidean distance between groups.

Spearman's rank correlation was used to search for relationships between the biotic and abiotic patterns and to identify which environmental variable(s) explained most of the variation in coccolithophore distribution (BEST routine).

Primary production and calcification. Water samples for rate measurements were collected before dawn or at the time of minimum light intensity at the Arctic stations, from 4 to 6 light depths (including 1, 4.5, 7, 14, 33 and 55% for SNScast, NNScast and LOF stations and 0.1 to 2, 6 to 9, 20, 50 or 80% of incident PAR for SS1, ICE, MIZ and RIP stations) from the upper 65 m of the water column. Daily rates of primary production (PP) and calcification (CF) were determined following the 'micro-diffusion' technique of Paasche & Brubak (1994), as modified by Balch et al. (2000). Water samples (150 ml, 3 replicates, 1 formalin-killed) were collected from each light depth, spiked with 100 µCi of ^{14}C-labelled sodium bicarbonate (Perkin Elmer) and incubated in on-deck incubators for 24 h. Light depths were replicated using a mixture of misty blue and neutral density filters, and samples were kept at ambient sea surface temperature by providing a continuous flow of water from the underway supply through the incubators.

Incubations were terminated by filtration through 25 mm 0.2 µm polycarbonate filters, which were then acidified with 1% phosphoric acid to separate the inorganic fraction (labile, CF) from the organic fraction (non-labile, PP). The inorganic fraction was captured as ^{14}C-CO_2 on a β-phenylethylamine soaked filter and placed in a separate vial. Liquid scintillation cocktail was added to both vials and activity was measured on a TriCarb liquid scintillation counter. Counts were converted to uptake rates using standard methods. The mean relative standard deviation (calculated as SD × 100/mean) of triplicate measurements was 18% (2 to 44%) for PP and 30% (2 to 99%) for CF. The formalin blanks represented a significant proportion of the CF signal (mean 61%) because of the low rates measured at all stations except LOF (see Results). Similarly high blank contributions have been reported in other studies, especially at the base of the euphotic zone where CF rates are low (Poulton et al. 2007, 2010). The blanks represented only 5% of the PP signal.

RESULTS

Physicochemical setting

The cruise transect covered a range of bathymetry (<50 to 3000 m) and water masses (Fig. 1) and hence strong environmental gradients. Temperature decreased with latitude, from >15°C in the SNS to <0°C in SVAL, but peaked at 17.8°C in the NNS (Fig. 2A). Salinity was generally >34 with the exception of the Skagerrak water mass in the NNS and NORW (min. 30.6), which was influenced by the low salinity Baltic Sea outflow, and SVAL (min. 30.7), which was influenced by ice melt (Fig. 2A). Both phosphate and nitrate concentrations were generally low (<0.5 and <0.2 µM, respectively), with the exception of 3 samples where
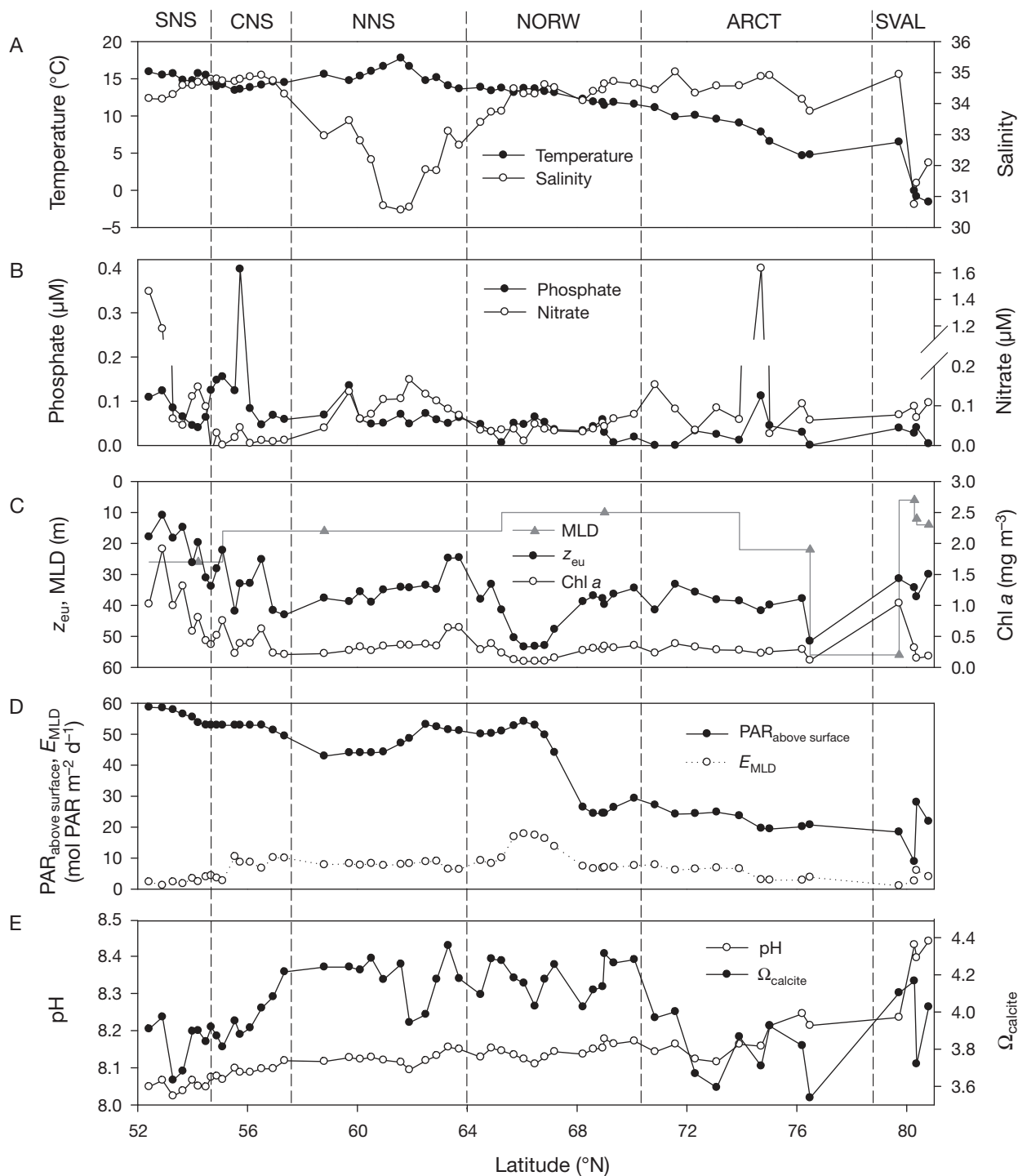
Fig. 2. Physicochemical variables along the UK–Svalbard transect. (A) Surface temperature and salinity. (B) Surface phosphate and nitrate. (C) Euphotic zone depth (z_{eu}), mixed layer depth (MLD, triangles indicate CTD stations from which MLD was extrapolated) and surface chl a. (D) Above surface photosynthetically active radiation (PAR$_{above\ surface}$) and mixed layer irradiance (E_{MLD}). (E) Surface pH and calcite saturation state ($\Omega_{calcite}$). SNS: southern North Sea; CNS: central North Sea; NNS: northern North Sea; NORW: Norwegian Sea; ARCT: Arctic-influenced waters; SVAL: Svalbard

high nitrate values (1.2 to 1.6 µM) were measured (Fig. 2B). pH increased with latitude from a minimum of 8.01 in the SNS to a maximum of 8.43 in SVAL, whereas $\Omega_{calcite}$ was higher in the NNS and NORW (up to 4.3) and lower in the SNS, CNS, ARCT and SVAL (typically ~3.5 to 4.0; Fig. 2, Table 1).

Table 1. Physicochemical characteristics of hydrographic regions. Mean values are given with ranges in brackets. E_{MLD}: mixed layer irradiance, PAR: photosynthetically active radiation. Station SS1 has been included in the ARCT region, as it falls within the same range of temperature and salinity

Region	Latitude (°N)	Influences	Depth (m)	Temperature (°C)	Salinity	pH	Calcite saturation state ($\Omega_{calcite}$)	Phosphate (μM)	Nitrate (μM)	E_{MLD} (mol PAR m^{-2} d^{-1})
Southern North Sea (SNS)	52.4–54.5	British rivers	<50	15.4 (15.4–16.0)	34.4 (34.1–34.7)	8.04 (8.01–8.06)	3.82 (3.61–3.95)	0.08 (0.04–0.12)	0.45 (0.05–1.46)	2.5 (1.2–3.9)
Central North Sea (CNS)	54.7–57.4	Atlantic	<75	14.0 (13.6–14.6)	34.7 (34.3–34.9)	8.07 (8.06–8.11)	3.91 (3.80–4.20)	0.14 (0.05–0.40)	0.01 (0.00–0.04)	6.9 (2.7–10.1)
Northern North Sea (NNS)	58.8–64.1	Baltic Sea, Norwegian Coastal Current	100–400	15.3 (13.6–17.8)	32.1 (30.6–33.4)	8.11 (8.07–8.14)	4.10 (3.83–4.30)	0.07 (0.05–0.13)	0.10 (0.03–0.17)	7.9 (6.3–9.0)
Norwegian Sea (NORW)	64.5–70.1	Norwegian Current	400–3000	12.7 (11.4–13.8)	34.3 (33.4–34.7)	8.13 (8.10–8.17)	4.17 (4.01–4.30)	0.04 (0.01–0.06)	0.04 (0.01–0.08)	10.8 (6.6–17.8)
Arctic waters (ARCT) (incl. SS1: 79.7)	70.8–76.5	Arctic Front	<200–2000	8.0 (4.6–11.1)	34.6 (33.7–35.0)	8.17 (8.11–8.23)	3.81 (3.51–4.10)	0.03 (0.00–0.11)	0.23 (0.03–1.63)	4.7 (1.1–7.8)
North Svalbard (SVAL)	80.3–80.8	Ice edge	<200	−0.9 (−1.6 −−0.1)	31.4 (30.7–32.1)	8.40 (8.38–8.43)	3.88 (3.63–4.06)	0.02 (0.00–0.04)	0.09 (0.07–0.11)	4.2 (2.6–6.0)

The euphotic depth (z_{eu}, 11 to 52 m) was typically deeper than the MLD (6 to 56 m), apart from within the SNS region and at station SS1 (Fig. 2C). Daily PAR above the sea surface (PAR$_{above\ surface}$) decreased with latitude and was maximal at the SNS and NORW (Fig. 2D). E_{MLD} was lowest in the SNS (mean 2.5 mol PAR m^{-2} d^{-1}), which was characterised by a well-mixed water column, where MLD was deeper than z_{eu} (Fig. 2C,D). High values of E_{MLD} (mean: 6.9 to 7.9 mol PAR m^{-2} d^{-1}) were observed in the well-stratified CNS and NNS, but the maximum E_{MLD} (17.8 mol PAR m^{-2} d^{-1}) was observed in NORW, which was characterised by a very shallow MLD (~10 m) (Fig. 2C, D). Low E_{MLD} values were also found in ARCT and SVAL (mean: 4.2 to 4.7 mol PAR m^{-2} d^{-1}) which were characterised by a shallow MLD but low PAR$_{above\ surface}$ (Fig. 2C,D).

Satellite-derived sea-surface chl *a* concentrations in the study area during the sampling period were generally <1 mg m^{-3}, with slightly higher values in the SNS (up to 2 mg m^{-3}) and on the border between the NNS and NORW (Fig. 1B). *In situ* measurements of surface chl *a* confirmed this range of values (Fig. 2C). Integrated chl *a* over the euphotic zone ranged from 15.7 to 56.3 mg m^{-2} whereas integrated PP (data not shown) ranged from 1.8 to 28.6 mmol C m^{-2} d^{-1}. The lowest integrated PP values (1.8 to 5.6 mmol C m^{-2} d^{-1}) were measured at the ICE and SS1 stations, even though these had the highest integrated chl *a* values (45.1 to 56.3 mg m^{-2}). The highest PP values were measured at the LOF station, where chl *a* values were moderate (23.4 mg m^{-2}). Moderate values of PP were measured at the NNScast, MIZ and RIP stations (8.1 to 11.2 mmol C m^{-2} d^{-1}), where the lowest integrated chl *a* values were observed (15.7 to 18.7 mg m^{-2}).

Coccolithophore community composition

Coccolithophore abundance in surface waters was generally low (typically <200 cells ml^{-1}), but higher values were found in the CNS (max. ~950 cells ml^{-1}) and some areas of the SNS and NNS. Very low abundance values were observed in SVAL and throughout most of NORW (1 to 5 cells ml^{-1}; Fig. 3A). A total of 40 coccolithophore species were identified in the surface samples: 25 species were present in the NNS, 5 in SVAL and 16 to 21 in the other regions (Table 2). *Emiliania huxleyi* (Fig. 4A) was generally the most abundant coccolithophore in most regions, contributing 32 to 100% towards total abundance (Fig. 3A).

The highest values (1.5 to 2.1) of the Shannon-Wiener diversity index (*H'*) were observed in the CNS, NNS and NORW (Fig. 3B) where *Emiliania huxleyi* relative abundance was low (32–55%). Pielou's evenness (*J'*) was also high in these samples, suggesting a highly
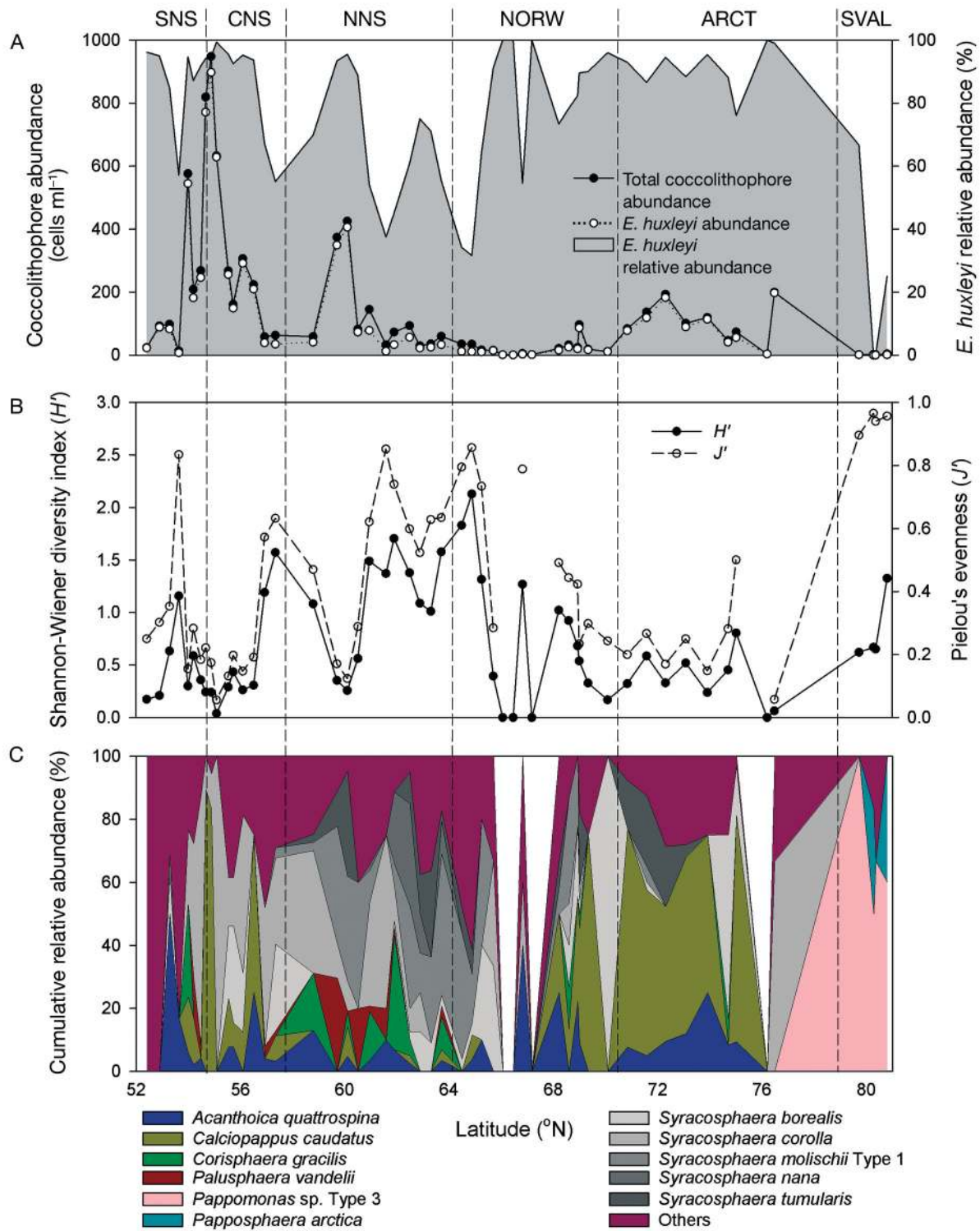
Fig. 3. Diversity of the coccolithophore population along the UK–Svalbard transect. (A) Total coccolithophore abundance, *Emiliania huxleyi* absolute abundance and *E. huxleyi* relative abundance. (B) Shannon-Wiener diversity index and Pielou's evenness. (C) Cumulative relative abundance of coccolithophores other than *E. huxleyi*. White blank areas correspond to points where the population consisted of 100% *E. huxleyi*. SNS: southern North Sea; CNS: central North Sea; NNS: northern North Sea; NORW: Norwegian Sea; ARCT: Arctic-influenced waters; SVAL: Svalbard

Table 2. Species list and occurrence (+) of coccolithophores in surface (<5 m) samples. SNS: southern North Sea; CNS: central North Sea; NNS: northern North Sea; NORW: Norwegian Sea; ARCT: Arctic-influenced waters; SVAL: Svalbard. HOL: holococcolithophore stage

Region Total number of species	SNS 18	CNS 16	NNS 25	NORW 21	ARCT 20	SVAL 5
Emiliania huxleyi	+	+	+	+	+	+
Acanthoica quattrospina	+	+	+	+	+	
Acanthoica quattrospina HOL				+		
Algirosphaera robusta	+		+	+	+	
Alisphaera extenta	+	+		+	+	
Alisphaera gaudii					+	
Braarudosphaera bigelowii	+	+	+			
Calcidiscus leptoporous			+	+		
Calciopappus caudatus	+	+	+	+	+	
Calciosolenia murrayi			+			
Calyptrosphaera sphaeroidea			+	+		
Coccolithus pelagicus	+				+	+
Coccolithus pelagicus HOL	+	+	+	+	+	
Corisphaera gracilis	+		+	+		
Florisphaera profunda					+	
Gephyrocapsa oceanica					+	
Helicosphaera carterii HOL *perforata*			+			
Helladosphaera cornifera	+	+	+			
Homozygosphaera vercelii		+	+			
Ophiaster formosus			+	+		
Ophiaster hydroideus			+			
Ophiaster sp.		+	+	+		
Palusphaera vandelii	+	+	+			
Pappomonas sp. Type 3[a]					+	+
Papposphaera arctica[b]						+
Rhabdosphaera xiphos	+		+	+	+	
Saturnulus helianthiformis				+		
Sphaerocalyptra sp. HOL					+	
Syracosphaera bannockii			+			
Syracosphaera bannockii HOL	+	+		+	+	
Syracosphaera borealis	+	+	+	+	+	
Syracosphaera corolla	+	+	+	+	+	
Syracosphaera exigua	+					
Syracosphaera marginaporata			+	+		
Syracosphaera molischii type 1	+	+	+	+	+	
Syracosphaera nana			+			
Syracosphaera ossa		+	+		+	
Syracosphaera tumularis			+	+	+	
Syracosphaera sp.	+	+			+	
Wigwamma sp.						+

[a]*Pappomonas* sp. Type 2 was also found in samples deeper than 5 m.
[b]*Papposphaera borealis* was also found in samples deeper than 5 m

diverse community with little dominance by one or a few species. Along the rest of the transect, where relative abundances of *E. huxleyi* were high, both *H'* and *J'* were low, suggesting a less diverse community dominated by *E. huxleyi*. One exception was SVAL, where *H'* was low but *J'* was extremely high (Fig. 3B). The coccolithophore community in this case was species poor, with the individuals evenly distributed among *E. huxleyi* (Fig. 3A), 2 species of the family Papposphaeraceae (Fig. 3C) — *Pappomonas* sp. Type 3 (after Young et al. 2003; Fig. 4B) and *Papposphaera arctica* (Fig. 4C) — and *Coccolithus pelagicus* (included in 'other' in Fig. 3C). A highly significant relationship was found between diversity (*y*) and *E. huxleyi* relative abundance (*x*) ($y = 4 \times 10^{-6} x^3 - 0.001x^2 + 0.068x + 0.454$, $R^2 = 0.923$, $p < 0.0001$). The polynomial trend demonstrates that diversity was low both when *E. huxleyi* was dominant (100% relative abundance) and when *E. huxleyi* was virtually absent (<0.1% relative abundance, Papposphaeraceae dominance).

The cumulative relative abundance of the most numerous and commonly occurring species other than *Emiliania huxleyi* is shown in Fig. 3C. *Acanthoica quattrospina* (Fig. 4D) was present in all regions apart from SVAL; *Calciopappus caudatus* (Fig. 4E) made important contributions in the CNS, northern NORW and in ARCT; and *Syracosphaera corolla* was characteristic of the SNS and CNS. However, the NNS was very diverse, with significant contributions from *A. quattrospina*, *C. caudatus*, *Corisphaera gracilis*, *Palusphaera vandelii* and 5 different *Syracosphaera* spp. (Fig. 3C).

Multivariate analysis of environmental and coccolithophore community data

Environmental data

CLUSTER and NMDS analyses of all surface (0 to 5 m) samples based on temperature, salinity, pH, $\Omega_{calcite}$, nitrate, phosphate and E_{MLD} values revealed 6 significantly different clusters or groups ($p < 0.05$) at the 2.8 similarity level (Euclidean distance; similarity increases with decreasing distance) (Fig. 5A). An ANOSIM test further confirmed that the groups are significantly different from each other ($p < 0.002$). These 6 groups correspond to the hydrographic regions described in Fig. 2 and Table 1. At the 3.75 similarity level, 3 groups were formed: SNS samples clustered with ARCT ones; CNS, NNS and NORW clustered together; and SVAL remained a distinct group (Fig. 5A). The stress value of the 2-dimensional representation was 0.18, which indicates that the 2-dimensional plot (Fig. 5A) is a
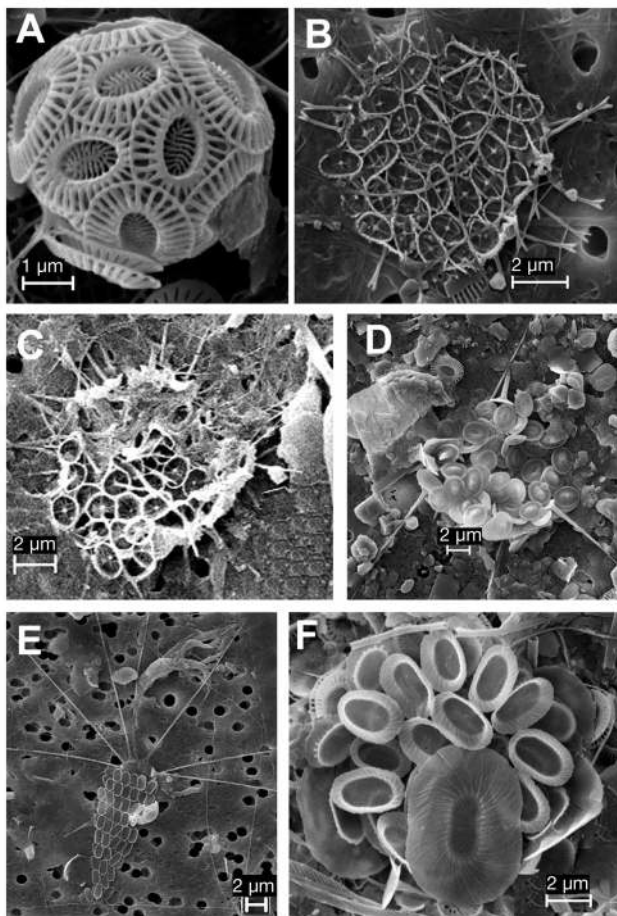
Fig. 4. SEM images of some characteristic coccolithophore species: (A) *Emiliania huxleyi*, (B) *Pappomonas* sp. Type 3, (C) *Papposphaera arctica*, (D) *Acanthoica quattrospina*, (E) *Calciopappus caudatus* and (F) *Syracosphaera corolla*

good representation of the high-dimensional pattern (Clarke 1993).

SIMPER analysis showed that differences between environmental clusters were driven mainly by pH, $\Omega_{calcite}$ and E_{MLD} at the 3.75 similarity level and by these and additional factors (temperature, salinity, nitrate and phosphate) at the 2.8 similarity level (Table 3). The high pH at SVAL explained at least 30% of the differences between SVAL and the rest of the groups, whereas high E_{MLD} at NORW consistently explained differences between NORW and the other groups (Table 3). Low salinity at the NNS accounted for >27% of differences between NNS and the other groups (Table 3).

Coccolithophore community data

CLUSTER and NMDS analysis of all surface (0 to 5 m) samples based on coccolithophore species composition
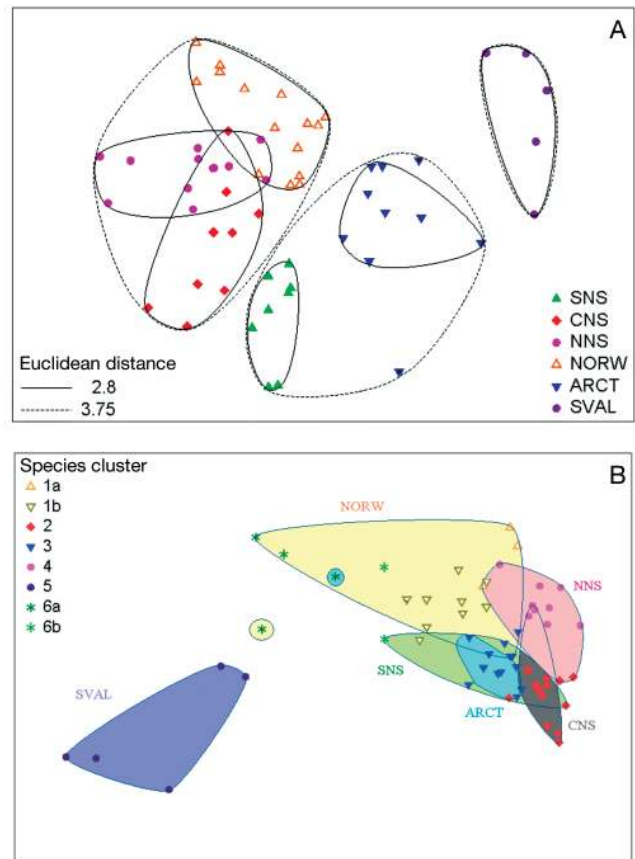

Fig. 5. Non-metric multidimensional scaling (NMDS) ordination of (A) environmental variables based on Euclidean distance and (B) coccolithophore abundance and species composition (symbols) based on Bray-Curtis similarity. (A) demonstrates spatial environmental changes; solid and dashed lines represent the superimposed sample clusters at the similarity levels of 2.8 and 3.75 Euclidean distance, respectively. (B) demonstrates spatial community changes; superimposed shaded areas represent the hydrographic regions associated with the species groups as identified by the independent NMDS analysis (A). SNS: southern North Sea; CNS: central North Sea; NNS: northern North Sea; NORW: Norwegian Sea; ARCT: Arctic-influenced waters; SVAL: Svalbard

and abundance rather than environmental data also revealed 6 significantly different clusters or groups (p < 0.05) (Fig. 5B). An ANOSIM test further confirmed the groups are significantly different from each other (p < 0.05). Overlaying the environmental clusters, as identified by the independent NMDS analysis (see Fig. 5A), onto the species clusters showed a clear match between the 2 patterns. Species cluster 1 was associated with the southern NORW, species cluster 2 with the CNS, species cluster 3 with ARCT, species cluster 4 with the NNS, species cluster 5 with SVAL, and species cluster 6 with northern NORW (Fig. 5B, Table 4). The biotic and abiotic characteristics of each of these groups are given in Table 4.

Table 3. SIMPER results of variables responsible for 50% of differences between environmental groups at the 2.8 and 3.75 similarity levels. Contribution of each variable to Euclidean distance between groups is given in brackets. SNS: southern North Sea; CNS: central North Sea; NNS: northern North Sea; NORW: Norwegian Sea; ARCT: Arctic-influenced waters; SVAL: Svalbard; $\Omega_{calcite}$: Calcite saturation state; E_{MLD}: mixed layer irradiance

Similarity level 2.8	SNS	CNS	NNS	NORW	ARCT
CNS	Nitrate (54%)				
NNS	Salinity (34%) $\Omega_{calcite}$ (25%)	Salinity (39%) Nitrate (27%)			
NORW	E_{MLD} (35%) $\Omega_{calcite}$ (23%)	Phosphate (36%) E_{MLD} (25%)	Salinity (37%) E_{MLD} (18%)		
ARCT	Temperature (32%) Phosphate (22%)	Phosphate (36%) Nitrate (23%)	Temperature (27%) Salinity (24%)	$\Omega_{calcite}$ (31%) E_{MLD} (28%)	
SVAL	pH (45%) Temperature (26%)	pH (34%) Temperature (17%)	pH (38%) Temperature (34%)	pH (30%) E_{MLD} (16%)	pH (36%) Salinity (29%)
Similarity level 3.75	SNS–ARCT	CNS–NNS–NORW			
CNS–NNS–NORW	$\Omega_{calcite}$ (20%) E_{MLD} (19%)				
SVAL	pH (41%) Salinity (20%)	pH (34%) Temperature (21%)			

The characteristic species for each cluster, as identified by the SIMPER routine, agreed with those described in Fig. 3C. *Emiliania huxleyi* was present in all regions apart from SVAL; *Syracosphaera borealis* and *S. molischii* were typical of species cluster 1; *S. corolla* was typical of species cluster 2; *Calciopappus caudatus* and *Acanthoica quattrospina* were typical of species cluster 3; *S. corolla*, *A. quattrospina*, *S. molischii*, *Corisphaera gracilis*, *Paluasphaera vandelii* and *S. nana* were typical of species cluster 4; *Pappomonas* sp. Type 3 and *Papposphaera arctica* were typical of species cluster 5; and *E. huxleyi* was the only characteristic species of cluster 6 (Table 4). The same species were also good discriminators between groups, as demonstrated by the SIMPER routine.

Matching biotic to abiotic data

Multivariate analysis (Spearman's rank correlation, r_S) of the coccolithophore assemblage and environmental patterns showed that most of the variation in coccolithophore distribution could be explained by variation in pH and E_{MLD} (r_S = 0.62), and the single environmental variable explaining most of the variation in the biotic pattern was pH (r_S = 0.45) at the 0.1% significance level (Table 5). As SVAL was very different in terms of coccolithophore composition and environmental variables from all other regions, Spearman's rank correlation analysis was repeated on all samples except SVAL to identify which variables could explain coccolithophore variation within the more closely related SNS, CNS, NNS, NORW and ARCT regions. Again, variation in pH and E_{MLD} explained most of the variation in coccolithophore distribution (r_S = 0.45) at the 0.1% significance level (Table 5). The single environmental variable, however, explaining most of the variation in the biotic pattern in these regions was E_{MLD} (r_S = 0.40 at the 0.1% significance level) (Table 5). This is the first time, to our knowledge, that a recognised multivariate statistical approach has been used on observational data to relate coccolithophore distribution to all of the environmental variables influencing coccolithophore growth.

Calcification: total and cell-normalised

Discrete total calcification (CF) values ranged from <1 to ~300 µmol C m^{-3} d^{-1} (Fig. 6). At the NNScast and LOF stations, CF was high at the surface but also exhibited a deep maximum, well below the mixed layer. CF was uniform with depth at stations SS1 and MIZ, whereas a deep CF maximum below the mixed layer was observed at stations ICE and RIP (Fig. 6). The highest CF values were observed at the LOF station (100 to 300 µmol C m^{-3} d^{-1}), whereas low CF was measured at all other stations (<1 to 16 µmol C m^{-3} d^{-1}), except for a deep maximum (~50 µmol C m^{-3} d^{-1}) at 20 m at the ICE station.

Cell CF was generally <1 pmol C cell^{-1} d^{-1}. Exceptions included surface and deep maxima at the LOF station and SS1 and MIZ surface values, where higher cell CF was estimated (1.4 to 2.9 pmol C cell^{-1} d^{-1}),

Table 4. Summary of coccolithophore assemblage and physicochemical properties of each group identified by MDS analysis. Mean values are given with ranges in brackets. The regions associated with each cluster are given. SNS: southern North Sea; CNS: central North Sea; NNS: northern North Sea; NORW: Norwegian Sea; ARCT: Arctic-influenced waters; SVAL: Svalbard; E_{MLD}: mixed layer irradiance; PAR: photosynthetically active radiaton. Refer to Table 2 for full species names

Cluster	Total coccolithophore abundance (cells ml⁻¹)	*E. huxleyi* relative abundance (%)	Characteristic species	No. of species	Temperature (°C)	Salinity	pH	Calcite saturation state ($\Omega_{calcite}$)	Phosphate (µM)	Nitrate (µM)	E_{MLD} (mol PAR m⁻² d⁻¹)
1 NORW (south)	25 (12–35)	74 (32–96)	*E. huxleyi* *S. borealis* *S. molischii*	6 (2–12)	13.2 (11.6–15.9)	33.9 (31.8–34.7)	8.14 (8.05–8.17)	4.17 (3.91–4.36)	0.04 (0.01–0.06)	0.06 (0.03–0.11)	8.6 (6.4–16.9)
2 SNS, CNS	415 (161–948)	94 (87–99)	*E. huxleyi* *S. corolla*	6 (2–9)	13.8 (4.8–15.7)	34.4 (32.8–34.9)	8.09 (8.04–8.21)	3.91 (3.54–4.24)	0.11 (0–0.40)	0.07 (0–0.15)	5.4 (2.4–10.5)
3 ARCT	111 (46–224)	89 (76–95)	*E. huxleyi* *C. caudatus* *A. quattrospina*	6 (2–10)	11.4 (6.5–16.0)	34.4 (32.2–35.0)	8.13 (8.02–8.11)	3.94 (3.59–4.30)	0.03 (0–0.08)	0.06 (0.01–0.15)	6.2 (2.3–8.3)
4 NNS	71 (33–145)	57 (38–70)	*E. huxleyi* *S. corolla* *A. quattrospina* *S. molischii* *C. gracilis* *P. vandelii* *S. nana*	10 (5–13)	15.5 (13.6–17.8)	32.4 (30.6–34.7)	8.11 (8.09–8.15)	4.13 (3.94–4.26)	0.06 (0.05–0.07)	0.08 (0.01–0.17)	8.3 (6.3–10.1)
5 SVAL	2.5 (1.4–3.7)	9 (0–25)	*Pappomonas* sp. *P. arctica*	3 (1–4)	−1.0 (−1.6–−0.1)	31.8 (30.7–32.9)	8.40 (8.36–8.43)	3.89 (3.63–4.06)	0.03 (0–0.06)	0.16 (0.04–0.51)	3.8 (2.6–6.0)
6 NORW (north)	3.7 (0.5–13)	83 (55–100)	*E. huxleyi*	2 (1–5)	11.4 (4.6–14.8)	34.5 (34.1–34.9)	8.15 (8.04–8.25)	4.05 (3.68–4.25)	0.05 (0.03–0.06)	0.06 (0.01–0.11)	10.1 (1.1–17.8)

whereas the maximum cell CF was found at 20 m at the ICE station (5.9 pmol C cell⁻¹ d⁻¹) (Fig. 6). Cell CF was generally minimal at the base of the euphotic zone, except at the LOF station where a deep maximum was observed just below the base of the euphotic zone (Fig. 6).

DISCUSSION

Regional coccolithophore distribution

North Sea

In this study, we directly sampled surface waters to test the picture of diversity suggested by the sediments, i.e. that coccolithophores are more diverse in the NNS but are virtually absent south of ~54°N (Braarud et al. 1953, Houghton 1991). We found 30 coccolithophore species (as opposed to 13 recorded by Braarud et al. 1953) in the North Sea, and most were observed both in the SNS and the NNS, although decreasing diversity towards the south was also noted. *Emiliania huxleyi* was generally dominant, in agreement with studies by Braarud et al. (1953) and Houghton (1991). However, *E. huxleyi* numerically contributed as little as 30 to 60% of total counts in some of these samples.

A few of the characteristic species have not been recorded before in the North Sea. *Calciopappus caudatus* has only been previously reported in the low-salinity Skagerrak water mass (Schei 1975), whereas in the present study it was present in both the SNS and CNS. Most of the *Syracosphaera* species, as well as *Corisphaera gracilis* and *Palusphaera vandelii*, have not been reported in the North Sea before, either in water samples or in sediments. The disagreement with previous studies most likely results from more effective methods of preservation and species identification used in this study compared with those used in the past. Tidal activity might explain the absence of coccolithophores from sediments. Strong tidal currents characteristic of the North Sea may prevent accumulation and/or preservation of coccoliths on the seafloor through advective removal and mechanical breakdown.

Table 5. Spearman's rank correlation (r_S) of coccolithophore assemblage distribution and environmental variables using data from all regions and excluding Svalbard (SVAL). Correlations of $r_S > 0.3$ are significant (p < 0.001)

——— All regions ———		— Excluding SVAL —	
Environmental variable	r_S	Environmental variable	r_S
pH, E_{MLD}	0.622	pH, E_{MLD}	0.447
pH	0.454	E_{MLD}	0.399
Temperature	0.311	pH	0.149
E_{MLD}	0.292	Salinity	0.085
Salinity	0.258	$\Omega_{calcite}$	0.082
$\Omega_{calcite}$	0.058	Temperature	0.041
Phosphate	0.008	Nitrate	−0.009
Nitrate	−0.072	Phosphate	−0.075

Norwegian Sea

Coccolithophores have been relatively well studied in the Norwegian Sea (Samtleben & Schröder 1992, Samtleben et al. 1995). Up to 20 species have been previously recorded (Samtleben & Schröder 1992, Samtleben et al. 1995), with *Acanthoica quattrospina*, *Syracosphaera borealis*, *S. corolla*, *S. molischii*, *S. nana* and *Corisphaera gracilis* all being characteristic of the region and occurring at temperatures of >9 to 10°C. A similar species composition was found in the present study, with 21 species recorded in total. In addition, *Calciopappus caudatus*, which is known to tolerate cooler temperatures and to have a distribution similar to that of polar species such as *Coccolithus pelagicus*
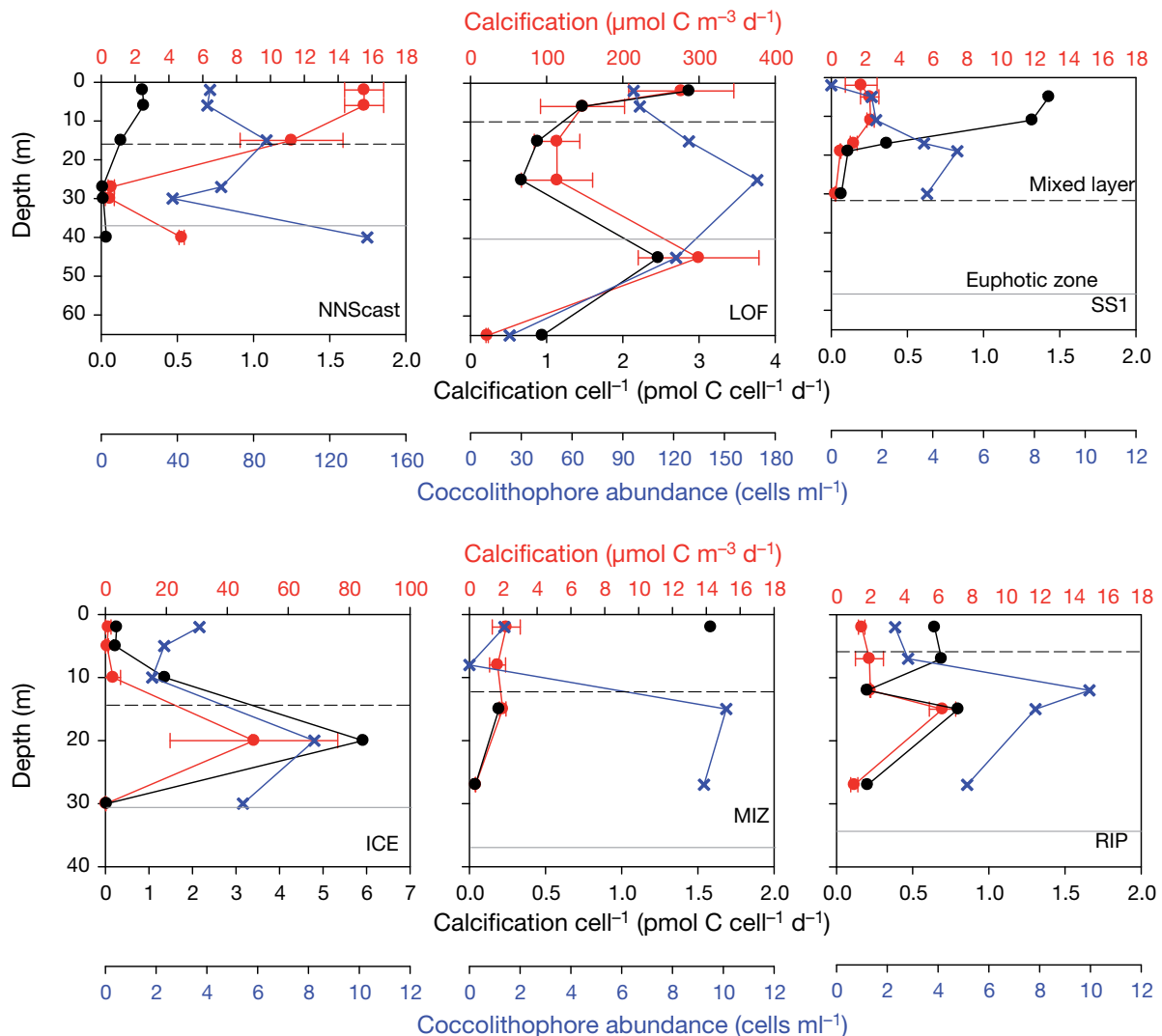

Fig. 6. Total calcification rates (red), calcification rates per cell (black) and coccolithophore abundance (blue) at NNScast, LOF, SS1, ICE, MIZ and RIP stations. For station locations see Fig. 1A

(Samtleben & Schröder 1992), was observed in the northern part of the Norwegian Sea. The low abundances (<100 cells ml^{-1}) found in early August agree with other studies of the same area at similar times of the year (e.g. max. 70 cells ml^{-1} in the Norwegian Current east of Jan Mayen; Samtleben & Schröder 1992).

Arctic Ocean

Two different Arctic assemblages (Fig. 5B) were observed in this study. One assemblage, south of Svalbard (ARCT) in an area of mixed Arctic surface waters of Atlantic origin (4 to 10°C), was dominated by *Emiliania huxleyi*, with contributions from *Acanthoica quattrospina*, *Calciopappus caudatus*, *Syracosphaera borealis* and *S. tumularis*. The other assemblage, north of Svalbard (SVAL) and influenced by retreating ice (<0°C), was characterised by *Pappomonas* spp. and *Papposphaera* spp.

Emiliania huxleyi and *Calciopappus caudatus* are thought to be characteristic of Atlantic–Arctic mixed waters (Samtleben & Schröder 1992, Samtleben et al. 1995), and cell densities observed in the present study (mean: 111 cells ml^{-1}) agree with those reported in previous studies south of Svalbard (Baumann et al. 1997, 2000, Samtleben et al. 1995). However, the only other studies, to our knowledge, that have recorded coccolithophores in high Arctic regions such as the area north of Svalbard (SVAL) are early taxonomic studies in which most of these species were first described (Manton et al. 1977, Thomsen 1981 and references therein). The genera *Pappomonas*, *Wigwamma*, *Turrisphaera*, *Papposphaera*, *Balaniger*, *Calciarcus*, *Trigonaspis* and *Quaternariella* were reported in Godhavn (West Greenland) in 1972 and 1977. *Wigwamma* and *Turrisphaera* were also found in Resolute Bay (Northwest Passage) in 1973, and the genera *Pappomonas*, *Papposphaera*, *Calciarcus*, *Wigwamma* and *Turrisphaera* were all present in Homer (South Alaska) in 1975. Our findings of *Pappomonas* spp. and *Papposphaera* spp. north of Svalbard are consistent with these previous studies. We also found individuals of *Wigwamma* spp. in surface and subsurface (>15 m) samples of the ICE, MIZ and RIP stations. We did not find any individuals of *Calciarcus*, *Turrisphaera* or *Trigonaspis*; however, these genera are thought to be holococcolith-bearing phases of the genera *Wigwamma*, *Papposphaera* and *Pappomonas*, respectively (Thomsen et al. 1991).

Coccolithus pelagicus was occasionally found at low cell densities (up to 4 cells ml^{-1}) in SVAL samples, in contrast to the relatively high densities of this species (up to 100 cells ml^{-1}) usually encountered in the Greenland Sea (Baumann et al. 2000). Hence, it ap-

pears that the Svalbard assemblage was more similar to other polar assemblages from continental shelf locations (Godhavn, Resolute Bay and Homer) rather than the oceanic assemblage usually found in the Greenland Sea. *Emiliania huxleyi* cells were also occasionally found at very low densities (<2 cells ml^{-1}) at the SS1 and ICE stations, whereas Manton et al. (1977) and Thomsen (1981) found this species to be completely absent from Godhavn, Resolute Bay and Homer during the 1972–1977 period. *E. huxleyi*, however, was found in moderate densities (8 to 69 cells ml^{-1}) north of Svalbard from September to October 1979 (Heimdal 1983) and more recently in August 2003 (19 to 95 cells ml^{-1}; Hegseth & Sundfjord 2008). Most likely, *E. huxleyi* cells from the northern North Atlantic are occasionally transported along the west coast of Svalbard by the West Spitsbergen Current and into high Arctic areas, as has been found for other Atlantic phytoplankton species (Hegseth & Sundfjord 2008). Similarly, *E. huxleyi* blooms in the Barents Sea also follow the Atlantic water distribution (Smyth et al. 2004). However, the absence of *E. huxleyi* from the Northwest Passage and the West Greenland shelf could be attributed to the fact that these areas are influenced by Arctic water masses (i.e. the West Greenland Current) rather than currents of Atlantic origin; or it could simply mean that previous sampling was inadequate and further sampling in these regions is required.

Environmental variables influencing coccolithophore community composition and distribution

This is the first multivariate approach in which carbonate chemistry parameters (pH and $\Omega_{calcite}$) have been used together with other environmental variables (light, nutrients, temperature and salinity) to determine which factors influence coccolithophore species distribution. Previous studies have included in their approach nutrient and light availability in addition to temperature and salinity (seasonal variability: Cortés et al. 2001, Haidar & Thierstein 2001; spatial variability: Boeckel & Baumann 2008), or have related carbonate chemistry parameters with coccolith mass (Beaufort et al. 2008), but all of these variables have not been considered simultaneously before.

Spearman's rank correlation showed that pH and mixed layer irradiance (E_{MLD}) are the combination best able to explain variatio in coccolithophore distribution in the North Sea, the Norwegian Sea and the Arctic ($r_S = 0.62$). The high pH values and low temperatures at SVAL are most likely responsible for this cluster separating from the rest in terms of hydrography, species composition (Papposphaeraceae do-

minance) and abundance (very low, 3 cells ml^{-1}). Boeckel & Baumann (2008) found that temperature explained much of the variation in coccolithophore distribution across the subtropical frontal zone in the South Atlantic. However, our results show that pH explained more of the coccolithophore variation between the SNS and SVAL (r_S = 0.45) than did temperature (r_S = 0.31). In both studies, the colder frontal zone and Arctic waters could be considered as more productive and hence associated with higher pH values due to uptake of DIC, creating a pH gradient that matches the temperature gradient. Indeed, in our study, pH and temperature were strongly negatively correlated (R^2 = 0.83). However, apart from primary production and respiration, pH is also affected by physical mixing and air–sea CO_2 exchange (Chierici & Fransson 2009) and our results suggest that pH controls coccolithophore distribution to a greater degree than temperature. As mentioned earlier, in laboratory studies, different coccolithophore species and even strains exhibit different responses to changes in pCO_2 and/or pH (e.g. Langer et al. 2006, 2009), and recent studies have begun to consider metabolic pH balance as an important component of cellular physiology in terms of the calcification process and its interaction with the environment (Mackinder et al. 2010, Rickaby et al. 2010). Rickaby et al. (2010) recently hypothesized that cell size within the coccolithophores influences cellular pH balance and carbon acquisition. However, a considerable amount of further research is required in testing this hypothesis and the role of other environmental parameters on coccolithophore physiology and growth.

Interestingly, pH was more important when there were larger differences between locations (~0.4 unit difference between the SNS and SVAL). E_{MLD} became more important when the pH range was smaller (~0.2 unit difference between the SNS and ARCT), as the Spearman's rank correlation showed when SVAL was excluded from the analysis. In this case, high mean E_{MLD} (~8.7 mol PAR m^{-2} d^{-1}) was associated with high diversity in the NNS and southern NORW (low *Emiliania huxleyi* relative abundance and significant contributions of *Syracosphaera* spp., *Palusphaera vandelii* and *Corisphaera gracilis*) and explained much of the variation in coccolithophore distribution (r_S = 0.40). However, maximum E_{MLD} in NORW (~17.8 mol PAR m^{-2} d^{-1}) was associated with *E. huxleyi* contributing 100%, albeit to a low abundance (<3 cells ml^{-1}). This might be a result of *E. huxleyi* showing no photoinhibition in contrast to other phytoplankton species (Zondervan 2007 and references therein). Boeckel & Baumann (2008) found that, other than temperature, sampling depth (upper or lower photic zone) and nutricline depth best explained variation in species

composition in the subtropical frontal zone in the South Atlantic. In our study, nutrients did not seem to be important as both phosphate and nitrate concentrations were generally low across the transect and the photic zone was relatively shallow (<50 m) compared with subtropical waters (100 to 150 m). Sampling depth relates to how much light is available to coccolithophores and this controls the vertical distribution of coccolithophore species at the Hawaii Ocean Time-Series station ALOHA (Cortés et al. 2001). However, Boeckel & Baumann (2008, p 268) did not include light availability in their multivariate approach and their results implied that 'other unidentified and more important variables accounted for species variation, light availability being a potential control'. In our approach, both light availability and mixed layer depth are accounted for in our E_{MLD} calculation, which explains the relatively high Spearman's r_S value (0.399) for this variable. A possible explanation as to why irradiance levels would have a different effect on different coccolithophore species is the fact that there is extraordinary diversity in the pigment composition of different species, and even different strains of the same species (Van Lenning et al. 2004). These variations include different pigment contents with an efficient light energy transfer function or with photoprotective function, and have an evolutionary origin that may result from adaptations to low or high irradiance.

Multivariate data analysis also showed salinity to be less important than pH and E_{MLD} in explaining species variation. However, examination of individual samples shows that high diversity in the NNS was also associated with low salinity in this region. Similarly, $\Omega_{calcite}$ did not appear to influence coccolithophore distribution, as Spearman's r_S deviated little from 0. However, NMDS analysis showed that the SNS, CNS and ARCT coccolithophore assemblages were very similar to each other (high mean coccolithophore abundance, high *Emiliania huxleyi* relative abundance, low diversity and contribution of *Calciopappus caudatus*, *Acanthoica quattrospina* and *Syracosphaera corolla*) and that the 2 regions had very similar $\Omega_{calcite}$ values (mean ≈ 3.8), which were the lowest of the transect. The lack of correlation between coccolithophore distribution and $\Omega_{calcite}$ might be due to the relatively small range encountered (3.5 to 4.5) compared with the much larger pH range (8.0 to 8.4).

Finally, it is important to mention that growth and mortality, with the latter including grazing, competition and viral infection, also control coccolithophore abundance and distribution. These biotic controls may or may not be related to environmental variation, and could potentially explain the remaining variation in coccolithophore distribution.

Species composition and calcification rates

Coccolithophore species composition in the surface ocean ultimately affects calcite fluxes to the sediments, as the coccoliths of each species contain different amounts of calcium carbonate (Beaufort & Heussner 1999, Young & Ziveri 2000). This is also mirrored in the total CF rates measured, as 'heavier' species tend to calcify at higher rates than 'lighter' species. *Emiliania huxleyi* cellular CF rates are <1 pmol C cell^{-1} d^{-1} (Poulton et al. 2010) whereas *Calcidiscus leptoporus* and *Coccolithus pelagicus* can calcify at rates as high as 8 and 18 pmol C cell^{-1} d^{-1}, respectively (Langer et al. 2006). Hence, cell CF, growth rate and each species' contribution to total abundance determine how high the community CF is.

Species of the weakly calcified Arctic genera (Fig. 4) *Pappomonas*, *Papposphaera* and *Wigwamma* dominated the Arctic stations ICE, MIZ and RIP. Cell CF rates were generally <1 pmol C cell^{-1} d^{-1} (0.03 to 0.8 pmol C cell^{-1} d^{-1}) at these stations. Assemblage composition for these rates varied from 100% Arctic species (RIP station) to 50% Arctic species and 6 to 25% *Emiliania huxleyi*, 30 to 50% *Coccolithus pelagicus* HOL (holococcolith-bearing) and 15% *Algirosphaera robusta* (MIZ and ICE stations). Coccolith calcite content information does not exist for these species (except for *E. huxleyi*), so for the weakly calcified Arctic genera (coccolith length ~1 µm) we used a value equivalent to that estimated for a small *Syracosphaera* coccolith (coccolith length ~1.5 µm, calcite content ~0.001 pmol C; Young & Ziveri 2000) and calculated that in the 100% Arctic species assemblages, cell CF rates were equivalent to a coccolith production rate of 200 to 800 coccoliths cell^{-1} d^{-1}. These rates appear physiologically unrealistic: *E. huxleyi* can produce up to 30 coccoliths cell^{-1} d^{-1} (Poulton et al. 2010), indicating that either the calcite content of these weakly calcified coccoliths is higher, or that we have overestimated total CF rates or underestimated coccolithophore abundance.

These coccolith production rates can, however, be reduced to more realistic values of 9 to 35 coccoliths cell^{-1} d^{-1} if we use a calcite content equivalent to that of *Emiliania huxleyi* (coccolith length ~3.5 µm, calcite content ~0.023 pmol C; Young & Ziveri 2000). At the MIZ and ICE stations, the few exceptionally high cell CF rates calculated (1.4 to 5.9 pmol C cell^{-1} d^{-1}) can potentially be justified by the 13 to 33% contribution of the 'heavier' *Coccolithus pelagicus* and *Algirosphaera robusta* to total abundance (*C. pelagicus* coccolith calcite content = 1.4 pmol C; Young & Ziveri 2000).

At the NNScast, LOF and SS1 stations, *Emiliania huxleyi* usually dominated (70 to 90%) the total species abundance in the upper euphotic zone, but co-

occurred in the lower part of the euphotic zone with *Calciopappus caudatus*, *Algirosphaera robusta*, *Coccolithus pelagicus*, *Acanthoica quattrospina* and *Syracosphaera* spp. Cell CF rates were generally <1 pmol C cell^{-1} d^{-1}, thus within the *E. huxleyi* calcification range, but with a few exceptions. High rates (1.3 to 2.9 pmol C cell^{-1} d^{-1}) were measured at 5 to 10 m at the SS1 and LOF stations, and also at 45 m at the LOF station. Because the relative abundance of *E. huxleyi* ranged between 33 and 90% at these depths and species diversity was high, it was difficult to attribute these high rates to a certain species. However, again using the *E. huxleyi* coccolith calcite content (0.023 pmol C), we estimated a coccolith production rate of 56 to 126 coccoliths cell^{-1} d^{-1} for these depths. These are somewhat higher than previous measurements (7 to 29 coccoliths cell^{-1} d^{-1}; Poulton et al. 2010), but the high ratio of detached coccoliths to cells observed at these stations (40 at LOF, ≤250 at SS1) might justify the high rates.

These rough estimates of cell CF rates highlight the need for more calcite content and CF data across a wider range of coccolithophore species. It is obvious that highly diverse coccolithophore communities have very different community CF rates depending on their species composition. The contribution of *Coccolithus pelagicus* to the ICE assemblage increased integrated community CF by an order of magnitude in comparison to the SS1, MIZ and RIP assemblages (0.51 compared with 0.04 to 0.08 mmol C m^{-2} d^{-1}). If pH and E_{MLD} affect species composition and distribution, as our data suggest, then they must also indirectly influence community CF rates.

Wider implications

In this study, multivariate analysis of coccolithophore community composition and environmental data indicates that pH and mixed layer irradiance are best able to account for species composition and distribution between the North Sea and Svalbard. These results also show that low temperature and high pH are associated with a very distinct assemblage north of Svalbard whereas high irradiance and low salinity are associated with highly diverse assemblages in the northern North Sea.

Overall, the results imply that in a changing ocean there may well be significant community shifts within coccolithophore assemblages. Sea surface warming, retreating sea ice and changes in oceanic currents are already influencing polar ecosystems. Increased temperatures and reduced seasonal ice cover are likely to result in increased primary productivity (Arrigo et al. 2008), raising pH values in the Arctic surface waters

throughout summer (although the main trend will be towards lower pH values; Orr et al. 2005). These changes might already be assisting Atlantic species such as *Emiliania huxleyi*, which has been blooming with increasing frequency in the Barents Sea for the last few years (Smyth et al. 2004), to advance into colder Arctic waters. Whether these Atlantic species will outcompete weakly calcified Arctic species in the future remains to be determined. Moreover, changing light conditions due to shallower mixed layers (stratification) could also lead to changes in coccolithophore community structure and calcification rates in some regions, hence affecting the overall efficiency of the carbonate pump. It is also important to consider the effects of climate change and ocean acidification, not only on single coccolithophore species, but on whole communities. Changes in future pelagic calcite production may result from physiological changes acting on single species and/or from shifts in the species composition of coccolithophore assemblages induced by ocean acidification and stratification.

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