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[1] Production and dispersion of coccolithophores are assessed within their ecologic and hydrographic context across enhanced spring chlorophyll production in the surface eastern North Atlantic. Within a 4 day period from 12 to 16 March 2004, a N–S transect from 47°N to 33°N was sampled along 20°W. Water samples from defined depths down to 200 m were analyzed for coccolithophores from 0.45 μm polycarbonate filters by scanning electron microscopy. At 47°N coccolithophores flourished when euphotic conditions allowed new production at deep mixing, low temperatures, and high nutrient concentrations. *Emiliania huxleyi* flourished at high turbulence during an early stage of the phytoplankton succession and contributed half of the total coccolithophore assemblage, with up to 150×10^3 cells L^{-1} and up to 12×10^9 cells m^{-2} when integrated over the upper 200 m of the water column. Maximum chlorophyll concentrations occurred just north of the Azores Front, at 37°N–39°N, at comparatively low numbers of coccolithophores. To the south, at 35°N–33°N, coccolithophores were abundant within calm and stratified Subtropical Mode Waters, and *E. huxleyi* was the dominant species again. Although the cell densities of coccolithophores observed here remained below those typical of plankton blooms visible from satellite images, the depth-integrated total mass makes them significant producers of calcite and contributors to the total carbon sedimentation at a much wider range of ecological conditions during late winter and early spring than hitherto assumed.

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1. Introduction

[2] Coccolithophores have been major producers of calcite in the open oceans since the late Jurassic [*Hay*, 2004]. Modern coccolithophores are assumed to produce about half of the open marine calcite flux and affect the turnover of oceanic and atmospheric CO_2 [e.g., *Wolf-Gladrow et al.*, 1999; *Schiebel*, 2002]. Phytoplankton production and composition are affecting the partitioning of CO_2 between the atmosphere and the ocean and may cause negative feedback on rising atmospheric CO_2 levels [e.g., *Ridgwell et al.*, 2009]. Blooms of phytoplankton are events of major biogeochemical turnover in the surface ocean, and cause mass sedimentation of organic remains, and seasonal phytoplankton blooms and mass sedimentation are the major source of calcareous open oceanic sediment formation on a regional scale [e.g., *Baumann et al.*, 2004]. Plankton that has accumulated at the seafloor during seasonal maxima hence constitutes the major part of the open oceanic sedimentary archive that is interpreted for reconstruction of oceanography and climate. Understanding the phytoplankton succession as the primary trophic level is therefore indispensable for reliable paleoceanographic analyses.

[3] Phytoplankton production is largely driven by seasonal changes in the availability of nutrients, light and other environmental parameters. Blooms and seasonal mass flux of coccolithophores are known to occur in the North Atlantic [e.g., *Broerse et al.*, 2000; *Sprengel et al.*, 2000], an ocean basin where most of the annual production takes place during spring. Coccolithophore production is assumed to occur over a wide range of turbulence and nutrient concentrations [e.g., *Brand*, 1994; *Balch*, 2004]. High production (blooms) of *Emiliania huxleyi* has been reported from different settings of the North Atlantic and Pacific [e.g., *Beaufort and Heussner*, 2001; *Beaufort et al.*, 2007, 2008]. All of these blooms of *E. huxleyi* occurred in the top 10–20 m of the water column [*Tyrrell and Merico*, 2004], and during the later stages of phytoplankton production in spring, i.e., during May through

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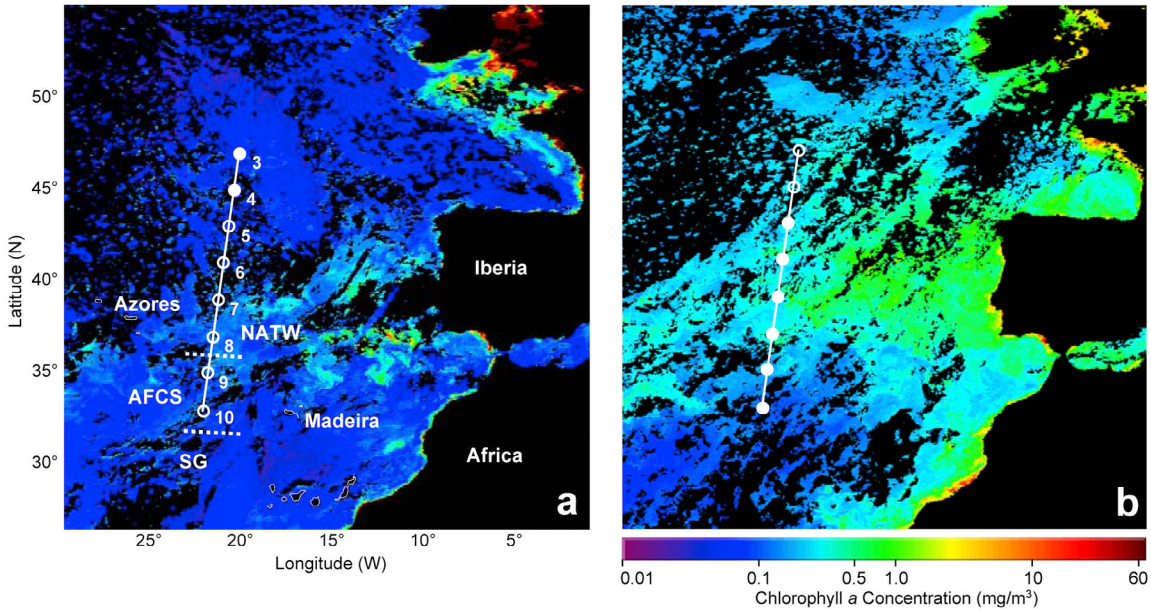

Figure 1. Stations 3–10 sampled during *Poseidon* cruise 308. Chlorophyll distribution during (a) 4–12 March 2004 and (b) 13–20 March 2004 (4 km resolution). Dashed lines between stations 8 and 9 and south of station 10 in Figure 1a delineate the northern and southern margins of the Azores Front–Current System (AFCS), respectively. NATW, North Atlantic Transitional Water; SG, Subtropical Gyre.

July in the North Atlantic at rather stratified conditions (low turbulence) and intermediate nutrient concentrations [e.g., *Holligan et al.*, 1983, 1993; *Balch et al.*, 1992; *Fernández et al.*, 1993; *Townsend et al.*, 1994; *Egge and Heimdal*, 1994; *Kristiansen et al.*, 1994; *Van der Wal et al.*, 1995; *Head et al.*, 1998; *Rees et al.*, 2002].

[4] To better understand distribution, ecology, and carbonate production of coccolithophores, we analyzed a north–to–south transect at the eastern North Atlantic during March 2004, anticipating sampling across a phytoplankton spring bloom. North Atlantic Transitional Waters (NATW) are ideally suited to study the phytoplankton succession during spring, representing a distinct biogeographical region with pronounced seasonality [e.g., *Longhurst*, 1998; *Beaufort and Heussner*, 2001]. We show that *E. huxleyi* flourishes under conditions of high turbulence during an early stage of the phytoplankton succession in spring, as well as during calm and stratified conditions following the spring bloom. We finally discuss the likely effect of total depth-integrated coccoliths production on carbonate sedimentation. Understanding the ecological context, production, and dispersion of coccolithophores in the modern ocean will facilitate better reconstruction of calcareous phytoplankton in paleoceanography and paleoclimate analyses, and modeling of future open marine carbonate budgets.

2. Materials and Methods

[5] During R/V *Poseidon* cruise 308 (Pos308, 2004), seawater was sampled for phytoplankton analyses from the upper 200 m of the water column from 12 to 16 March, on a N–S transect along 20°W in the North Atlantic (Figure 1 and Table 1). Samples were obtained with 10 L Niskin bottles attached to a 12-Rosette/CTD system (Sea-Bird SBE 9) from 10 m, 50 m, 100 m, 150 m (except station 10), and 200 m water depth. Additional samples were obtained from 30 m, 65 m, 75 m, 85 m, and 125 m depth at major changes in the vertical temperature profile (Figure 2 and Tables A1a–A1c). Samples for nutrient analyses were filtered through precombusted Whatman GFF filters immediately after rosette retrieval, and frozen (−20°C) until analysis. Phosphate, nitrite, nitrate, and silicate concentrations were determined using standard colorimetric methods [*Grasshoff et al.*, 1983] with a four channel autoanalyzer system (Evolution III, Alliance

Table 1. Stations Sampled on R/V *Poseidon* Cruise 308

Station Number	Date	Local Time	Year Day	Lunar Day[a]	Latitude (N)	Longitude (W)	Water Depth (m)	Chl Modis	PAR Modis (E m^{-2} d^{-1})
3	12.03.2004	4:35	72	6	46°59.607′	19°55.681′	4550	0.1	76.20
4	12.03.2004	18:20	72	6	44°59.817′	20°16.500′	4400	0.1–0.2	76.20
5	13.03.2004	08:44	73	7	42°59.870′	20°33.934′	3120	0.3–0.4	35.50
6	13.03.2004	22:20	73	7	41°00.191′	20°50.939′	3400	0.3–0.4	32.70
7	14.03.2004	12:06	74	8	39°00.148′	21°07.959′	4600	0.5–0.7	76.20
8	15.03.2004	01:40	75	9	37°00.549′	21°24.679′	3880	0.4	20.64
9	15.03.2004	14:12	75	9	34°59.785′	21°42.624′	5074	0.2	43.22
10	16.03.2004	18:36	76	10	33°00.039′	21°59.346′	5216	0.1	28.34

[a]Lunar day 0 = full moon.

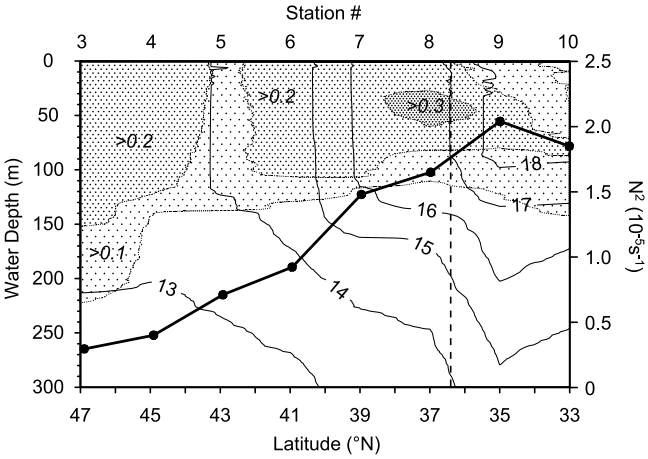

Figure 2. Temperature (°C) of the upper 300 m along transect. The northern limit of the AFCS is shown by the vertical dashed line. Stratification (bold line) of the upper water column is expressed as the Brunt-Väisälä frequency (N^2, arithmetic mean over 0–300 m; stronger stratification at higher values).

Instruments). Chlorophyll *a* concentrations, photosynthetically available radiation (PAR), and calcite concentration from MODIS level 3 satellite images (http://oceancolor.gsfc.nasa.gov/) are available as daily or weekly composites during the sampling period, 4–12 and 13–20 March 2004 (Figure 1 and Table 1).

[6] Plankton were filtered from two liters of seawater using 45 mm diameter polycarbonate membrane filters (0.4 μm Nucleopore) attached to inline gaskets [see *Bollmann et al.*, 2002]. Filters were air-dried for 12 h, stored in plastic petri dishes, and kept dry in closed boxes with silica gel. For the analyses in a scanning electron microscope (Philips XL30 SEM at 30 kV), radially cut pieces of the filter membrane were mounted onto aluminum stubs, coated with 15 nm of gold, and colloidal silver suspension was applied for optimal conductivity.

[7] 500 images were automatically acquired from each sample in five sequential tracks of 10 × 10 images, at a 2000X magnification, and stored on a PC computer. Image size is 1440 × 1152 pixels, with one pixel covering 0.04 μm^2, which amounts to an analyzed area of 5.76 mm^2 for each sample, corresponding to 10.7 mL of filtered seawater. An average of 325 coccolithophores specimens were taxonomically identified and counted, providing statistically significant assemblage data on a 95% confidence level [*Patterson and Fishbein*, 1989]. Collapsed coccospheres were counted as cells and the coccoliths aggregates were counted as cells if their number exceeded more than half of coccoliths known to occur on an average cell of the species. Coccolithophore taxonomy follows *Young et al.* [2003] (see Appendix A). The number of coccolithophores is given in cells per liter (Tables A1a–A1c). Multivariate analyses on coccolithophore assemblage data and ecological parameters were calculated with Systat (V.9), applying principal component analysis (PCA), and using Varimax rotation (Table A2).

[8] Stratification of the water column is expressed as Brunt-Väisälä frequency (N^2 [s^2]). Larger N^2 indicate larger change in water density per water depth interval, i.e., stronger stratification.

3. Results

[9] Different water bodies were sampled along transect (Figure 1), i.e., North Atlantic Transitional Water (NATW) between 47°N and 36.5°N, waters of the Azores Front–Current System (AFCS) between 36.5°N and 31.5°N including Subtropical Mode Waters (SMW), and waters of the subtropical gyre to the south of 31.5°N [cf. *Gould*, 1985]. Stratification of the water column increased from north to south. Mixing depth according to temperature distributions was greater than 200 m at the northern stations at 45°N–47°N, and shoaled to 100–150 m at 37°N–43°N

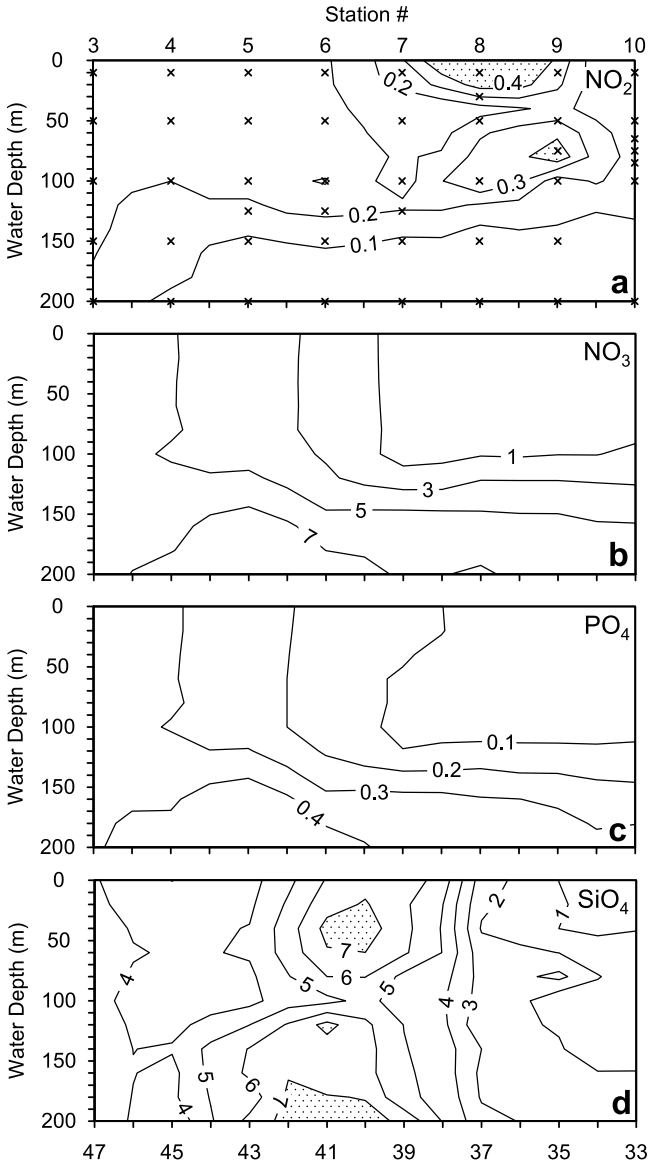

Figure 3. Concentration of (a) NO_2, (b) NO_3, (c) PO_4 and (d) SiO_4 (μmol L^{-1}). Maximum concentrations are indicated by dotted areas for NO_3 and SiO_4. The crosses mark the positions of samples.

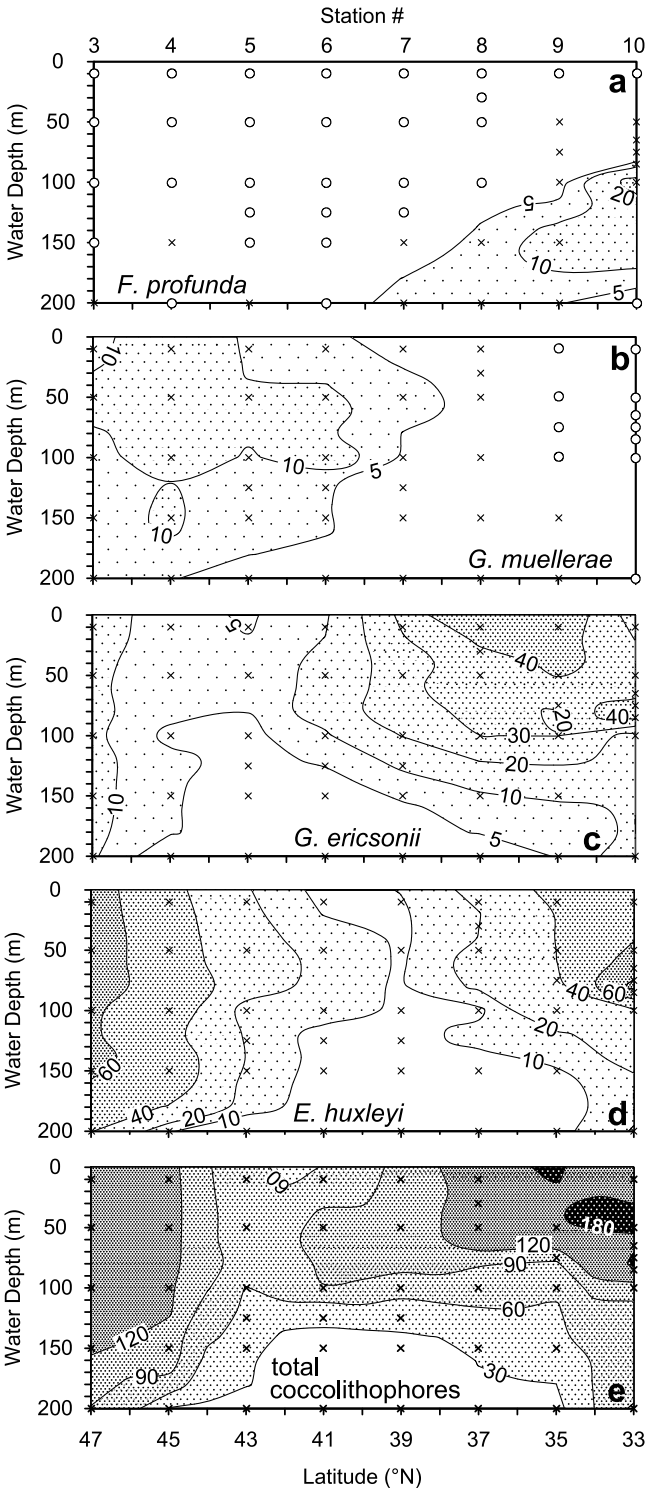

Figure 4. Standing stocks given as 10^3 cells L^{-1} of (a) *F. profunda*, (b) *G. muellerae*, (c) *G. ericsonii*, (d) *E. huxleyi*, and (e) total coccolithophores with data interpolation at 20 m depth intervals and 2° latitude. The crosses mark sampling positions, and the open circles mark samples without the respective species.

(Figure 2). A thermocline was developed at about 100 m between 33 and 37°N. During 1–12 March 2004, sea surface chlorophyll *a* concentrations along transect were low (0.1 mg m^{-3}) and significantly increased between 13–20 March 2004, ranging from >0.1 to 0.5 mg m^{-3} (Figure 1). Surface nitrate and phosphate concentrations decreased with increasing stratification (Figure 2) from north to south, and were generally low in surface waters (<100 m) south of 40°N (Figures 3b and 3c). Nitrite concentration was highest at surface waters (<100 m) at 34°N–38°N (Figure 3a). Maximum silicate concentration occurred at 39°N–43°N throughout the upper 200 m of the water column (Figure 3d).

[10] Coccolithophores were most abundant at the northernmost (45°N–47°N) and southernmost (33°N–37°N) sites, with maximum numbers of 151 × 10^3 and 240 × 10^3 cells L^{-1}, respectively (Figure 4e). North of 45°N, high cell numbers occurred down to 150 m water depth, and south of 37°N highest cell numbers were restricted to the upper 100 m. Coccolithophores were least frequent in the middle part of the transect at 39°N–43°N. Integrated over the upper 200 m of the water column, the total number of coccolithophore cells at 47°N amounted to 24.9 × 10^9 cells m^{-2}.

[11] *Emiliania huxleyi* was the dominant species at the northern and southern site down to the pycnocline, with more than 60 × 10^3 and 35 × 10^3 cells L^{-1}, in the upper 150 and 85 m, respectively (Figure 4d and Tables A1a–A1c). Integrated over the top 200 m, the total number of *E. huxleyi* cells at 47°N amounted to 12 × 10^9 cells m^{-2}. Maximum cell densities of *E. huxleyi* along transect occurred at a coincidence at (1) complete mixing and high nutrient concentration, or (2) at rather strong stratification and low nutrient concentration (Figure 5). At the northern station 3, *E. huxleyi* type A (with small "solid" liths) was the dominant morphotype with 81% of all morphotypes of *E. huxleyi*; the "closed morphotype" occurred at 13%, and *E. huxleyi* type B (large "fragile" liths) at 6% (Figure 6). At the southern station 10, only *E. huxleyi* type A was present.

[12] The second most abundant coccolithophore species was *Gephyrocapsa ericsonii*, which occurred throughout the transect (stations 3–10), and was most frequent in the upper 100 m south of 37°N (Figure 4c). *Gephyrocapsa muellerae* was present in high cell numbers at the north of transect (Figure 4b). *Florisphaera profunda* was frequent only at the southernmost end of transect between 33°N and 35°N, in waters around and below 100 m depth (Figure 4a and Tables A1a–A1c).

[13] The distribution of coccolithophore taxa, and their correlation among each other and to ecological parameters is confirmed by multivariate analyses (Table A2). Low factor loadings and low communalities (<0.9) of frequent and rare species indicate polymodal or heterogeneous distribution patterns.

4. Discussion

4.1. Production of Coccolithophores at Varying Ecological Conditions

[14] The most abundant coccolithophore species are discussed for their ecologic significance in the following. Ecologic conditions at the northern end of transect (stations 3–4) during 12 March 2004, were characterized by complete mixing of the upper water column, high nitrate and phosphate concentrations, and low chlorophyll *a* concentrations (Figures 1–4), which are typical of the aphotic winter conditions in the temperate North Atlantic (see http://ingrid.

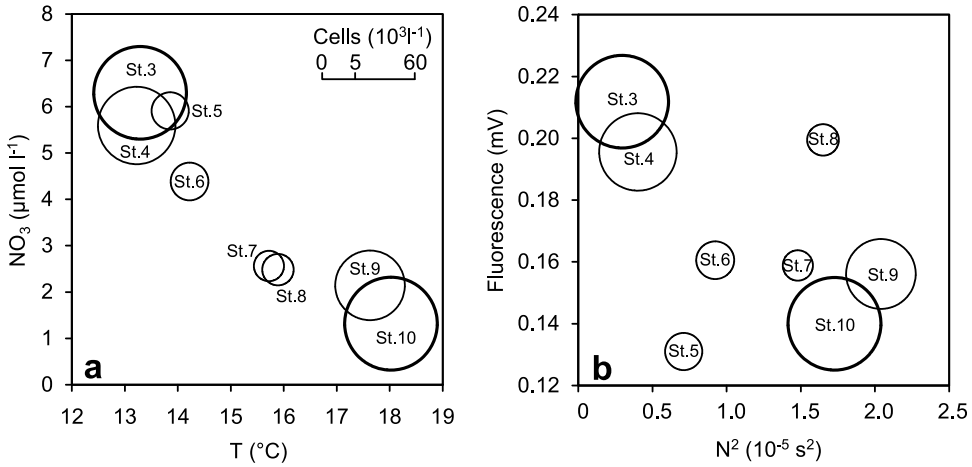

Figure 5. Weighted mean cell densities (area of circle) of *E. huxleyi* per station with respect to [NO_3] and stratification (N^2). The northernmost and southernmost stations are given in bold.

ldeo.columbia.edu/SOURCES/.LEVITUS94/.SEASONAL/.temp/) [*Glover and Brewer*, 1988]. During mid-March, aphotic conditions change to euphotic and new spring production is initiated in the eastern North Atlantic between 30°N and 45°N [*Obata et al.*, 1996]. During our cruise, between 13 and 20 March, phytoplankton production increased as evidenced by chlorophyll *a* concentration at the sea surface (Figure 1), corresponding to the timing predicted by *Obata et al.* [1996], and local radiation (PAR) between 20 and 76 E m^{-2} d^{-1} along transect (Table 1). During the early stage of phytoplankton spring production, *E. huxleyi* was the dominant coccolithophore species throughout the upper 200 m of the water column at 45–47°N (Table 1). *E. huxleyi* may be the first species that benefits from photic conditions and high nutrient concentration in early spring. Along with maximum *E. huxleyi* at the north end of our transect *G. muellerae* was most frequent, a coccolithophore species, which is supposed to flourish in rather cool waters and under well mixed conditions [cf. *Jordan*, 1988; *Ziveri et al.*, 1995; *Boeckel et al.*, 2006; *Boeckel and Baumann*, 2008]. With increasing stratification and lower NO_3 and PO_4 concentrations toward the south of transect coccolithophores decreased in numbers (Figures 3 and 4e).

[15] Cell densities of *E. huxleyi* increased again at the southern part of our transect within surface waters of the AFCS, with standing stocks similar to those recorded at the northern end of transect, but under different ecologic conditions (Figure 5). The abundance of the coccolithophore species *G. ericsonii* and *F. profunda* (Figures 4c and 4a) south of 36°N is indicative of Subtropical Mode Waters (e.g., of the AFCS and Canary Current (CC)) and of the oligotrophic and well stratified conditions of the subtropical gyre [*Sprengel et al.*, 2000; *Schiebel et al.*, 2002]. *F. profunda* has been discussed to occur at the intersection of decreasing light availability and increasing NO_3 concentration [*Cortés et al.*, 2001; *Haidar and Thierstein*, 2001; *Thierstein et al.*, 2004], conditions which are realized at thermocline depth at the northern limit of the subtropical gyre south of the Azores (Figure 1). *Gephyrocapsa ericsonii* has been assumed to be similar to *E. huxleyi* in ecologic demands [*Haidar and Thierstein*, 2001], abundant at a wide range of ecologic conditions, and a preference for subsurface waters with an enhanced nutrient concentration [*Baumann et al.*, 2008, and references therein]. Along transect, *G. ericsonii* was most frequent across the AFCS (Figures 1 and 4), and associated with Subtropical Mode Waters rather than of North Atlantic Transitional Waters. Analogously, *Bollmann* [1997] found *G. ericsonii* (reported as morphotype GM) to be dominant in subtropical surface sediment assemblages.

4.2. Mass Production of *E. huxleyi*

[16] High cell concentrations of plankton are referred to as bloom, usually, but not limited to, certain seasons, colora-

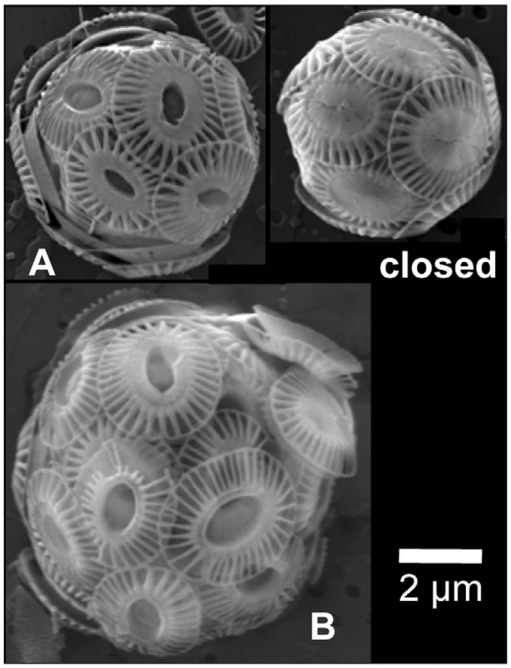

Figure 6. *E. huxleyi* type A (maximum diameter 3.5 ± 0.3 µm, n = 284), type B (maximum diameter 4.0 ± 0.3 µm, n = 17), and "closed morphotype" (maximum diameter 3.7 ± 0.3 µm, n = 40), from station 3.

Table 2. Cell Concentrations of Total Coccolithophores and *E. huxleyi* Analyzed From Natural Seawaters[a]

Location	MLD (m)	$[NO_3]$	$[PO_4]$	T°C	cells L^{-1}	cells m^{-2}	Remarks	Reference
Clear Waters								
Hawaii (HOT)	50–125	<0.2–4.2 μM kg^{-1}	–	~20–25°C	up to 60×10^3	–	total coccolithoph.	*Cortés et al.* [2001]
Hawaii (HOT)	50–125	<0.2–4.2 μM kg^{-1}	–	~20–25°C	up to 9×10^3	–	*E. huxleyi*	*Cortés et al.* [2001]
Bermuda (BATS)	70–>200	0.05–4.6 μM kg^{-1}	–	~20–25°C	up to 106×10^3	–	total coccolithoph.	*Haidar and Thierstein* [2001]
Bermuda (BATS)	70–>200	0.05–4.6 μM kg^{-1}	–	~20–25°C	up to 93×10^3	–	*E. huxleyi*	*Haidar and Thierstein* [2001]
N.Atlantic, 47°N, 20°W	>200	6.17–6.45 μM L^{-1}	~0.38 μM L^{-1}	13.3°C	up to 151×10^3	25×10^9	total coccolithoph.	this study
N.Atlantic, 47°N, 20°W	>200	6.17–6.45 μM L^{-1}	~0.38 μM L^{-1}	13.3°C	up to 68×10^3	12×10^9	*E. huxleyi*	this study
N.Atlantic, 33°N, 20°W	100	0.01–1.46 μM L^{-1}	<0.06 μM L^{-1}	17.7–18.6°C	up to 240×10^3	17×10^9	total coccolithoph.	this study
N.Atlantic, 33°N, 20°W	100	0.01–1.46 μM L^{-1}	<0.06 μM L^{-1}	17.7–18.6°C	up to 105×10^3	7×10^9	*E. huxleyi*	this study
Turbid Waters and/or Referred to as Bloom								
South of Iceland	-	–	–	10.5–12.7°C	up to 20×10^3	–	*E. huxleyi*, 3 m	*Holligan et al.* [1993]
Gulf of Maine	15	–	~0.3–0.5 μM	~25–26°C	$>10^6$	15×10^9	*E. huxleyi*	*Townsend et al.* [1994]
North Sea	20–30	~0.008–0.03 μM	<0.05 μM	8.5–11.7°C	up to 2.3×10^6	$<33 \times 10^9$	*E. huxleyi*	*Rees et al.* [2002]
North Sea	30	0.00–4.95 μM	0.26–0.70 μM	9.3–11.9°C	up to 4.5×10^6	–	*E. huxleyi*	*Head et al.* [1998]
Off southern Norway	~30	<4.3 μM L^{-1}	0.08–0.35 μM	10.4–12.2°C	up to 1.2×10^6	$\sim 27 \times 10^9$	*E. huxleyi*	*Van der Wal et al.* [1995]
Samnanger Fjord	<20	0.1–0.9 μM L^{-1}	<0.17 μM	–	$0.01–7.04 \times 10^6$	$0.08–55 \times 10^9$	*E. huxleyi*	*Kristiansen et al.* [1994]
48°N, 8°W	-	0.3–6.2 μM	–	12.5–13.5°C	$0.02–8.5 \times 10^6$	max.~3×10^{11}	*E. huxleyi*, 0–60 m	*Holligan et al.* [1983]

[a]Concentrations of coccolithophores, NO_3, and PO_4 are given for the surface mixed layer of the ocean. MLD, mixed layer depth. Data given by *Holligan et al.* [1983, 1993] refer to 0–60 m and 3 m water depth, respectively.

tion of water caused by excessive growth, and outnumbering of other species. The term "bloom" has a connotation of rapid proliferation and high abundance [cf. *Smayda*, 1997]. Blooms of coccolithophores have been used in connotation with "whitings" of surface waters [*Brown and Yoder*, 1994; *Iglesias-Rodríguez et al.*, 2002]. *Head et al.* [1998] and *Tyrrell and Merico* [2004] have defined blooms of *E. huxleyi* by $>10^6$ cells L^{-1}, a concentration that is not reached in any of our samples (Table 2). However, if cell densities are integrated over the entire depth of the mixed surface layer the total standing stock of *E. huxleyi* per area (m^2) is similar to those typical of blooms observed previously in the upper photic zone. Depth integrated standing stocks of 14–44 × 10^9 cells m^{-2} of *E. huxleyi* in the photic zone of North Sea waters west of southern Norway during June [*Rees et al.*, 2002], are in the same order of magnitude as cell densities observed in the mixed layer at the northern and southern end of the Pos308 transect of 12×10^9 cells m^{-2} (Table 2).

4.3. Timing of *E. huxleyi* Production

[17] Blooms of *E. huxleyi* have so far been reported for the late stage of phytoplankton spring blooms during May through July, at rather stratified conditions, and intermediate nutrient concentrations [e.g., *Holligan et al.*, 1983, 1993; *Balch et al.*, 1992; *Fernández et al.*, 1993; *Townsend et al.*, 1994; *Egge and Heimdal*, 1994; *Kristiansen et al.*, 1994; *Van der Wal et al.*, 1995; *Head et al.*, 1998; *Rees et al.*, 2002]. In contrast, maximum abundance of *E. huxleyi* at the northern end of transect during mid-March 2004 occurred at complete mixing and high nutrient concentration, possibly during an early stage of the spring phytoplankton production (Figure 5). Similarly high cell numbers (up to 44×10^3 cells L^{-1}) were observed at the northern edge of the Azores Front–Current System (35°N), at complete mixing down to 125 m during mid-February [*Rickli*, 2003]. All of these assemblages of *E. huxleyi* would not have been detected by satellite observation because coccolithophore cells and coccoliths were dispersed over expanded surface water layers and no significant surface ocean signal occurred [cf. *Gordon et al.*, 2001; *Mouw and Yoder*, 2005]. In addition, satellite derived total calcite concentration (daily data, 4 km resolution) was the same at all sampling locations (0.056 mol m^{-3}) along Pos308 transect. Thus coccolithophore cell density profiles indicate that satellite-based estimates may not be representative of the changes of calcite concentration and biomass over the entire photic zone [*Fuentes-Yaco et al.*, 2005]. These findings indicate that high cell numbers and calcite production of coccolithophores may be a so far undetected feature during early stages of phytoplankton blooms in spring.

4.4. Early Production and Dispersion of Coccolithophore Cells

[18] Surprisingly, relatively high cell concentrations of *E. huxleyi* occurred down to 150 m water depth at the northern end of transect on 12 March 2004. We emphasize that this increase of *E. huxleyi* occurred in early spring at high nutrient concentrations (Figure 3). *Obata et al.* [1996] predicted earliest seasonal new phytoplankton production in the area analyzed here to occur in mid-March. Coccospheres of *E. huxleyi*, which were sampled at 150 m depth at the northern site of transect were likely mixed down to depths. Intense vertical mixing is referred to as phytoconvection, which can reach as deep as 300 m at 47°N and still 200 m at 42°N, affecting nutrient and CO_2 profiles and triggering new production [*Backhaus et al.*, 1999; *Perez et al.*, 2005]. Sinking of coccospheres seems unlikely to have caused vertical dispersion. Because of the low average sinking velocity of 1.3 m d^{-1} [*Sikes and Wilbur*, 1982; *Lecourt*

Table A1a. Hydrographic and Trophic Data and Plankton Count Data ($\times 10^3$ cells L^{-1}) Recorded During *Poseidon* Cruise 308 for Sites 3–5[a]

	Site 3					Site 4					Site 5					
	10 m Depth	50 m Depth	100 m Depth	150 m Depth	200 m Depth	10 m Depth	50 m Depth	100 m Depth	150 m Depth	200 m Depth	10 m Depth	50 m Depth	100 m Depth	125 m Depth	150 m Depth	200 m Depth
Temperature (°C)	13.28	13.29	13.29	13.30	13.29	13.27	13.28	13.28	13.25	13.03	14.13	14.12	14.13	13.91	13.59	13.27
Salinity	35.79	35.79	35.79	35.79	35.79	35.78	35.79	35.78	35.80	35.77	35.62	35.89	35.89	35.87	35.83	35.79
Fluorescence (mV)	0.228	0.227	0.235	0.223	0.147	0.305	0.273	0.225	0.096	0.079	0.187	0.177	0.175	0.114	0.067	0.067
NO_2 (μmol L^{-1})	0.22	0.21	0.21	0.21	0.18	0.23	0.20	0.20	0.15	0.06	0.26	0.24	0.26	0.16	0.05	0.04
NO_3 (μmol L^{-1})	6.32	6.17	6.26	6.29	6.45	4.70	4.59	4.68	5.85	8.16	4.14	3.90	4.23	5.70	8.26	9.24
PO_4 (μmol L^{-1})	0.39	0.37	0.37	0.38	0.39	0.29	0.28	0.29	0.36	0.49	0.24	0.24	0.24	0.32	0.47	0.54
SiO_4 (μmol L^{-1})	4.1	4.6	4.2	5.0	4.5	2.6	3.8	3.2	3.2	3.2	4.0	4.5	3.7	5.8	7.8	6.3
Counted specimens	599	617	556	573	411	766	762	709	655	225	218	259	299	140	118	74
E. huxleyi	67.7	67.1	61.1	64.1	40.7	38.3	46.1	54.5	61.1	10.2	15.0	15.0	13.8	9.0	4.8	0.6
G. ericsonii	13.2	11.4	11.4	12.0	10.8	4.8	3.0	3.6	3.6	0.6	4.2	10.2	3.6	2.4	1.2	1.2
G. muellerae	7.2	13.2	6.6	8.4	6.0	20.4	15.0	15.6	13.8	5.4	4.8	7.8	9.0	6.0	3.6	1.8
O. hydroideus	-	12.6	-	-	-	22.8	-	7.2	-	-	5.4	-	-	4.2	-	-
O. formosus	6.0	-	6.6	12.6	5.4	8.4	7.2	-	3.0	-	-	11.4	9.6	-	-	-
R. parvula	8.4	25.2	9.6	-	-	3.0	3.6	-	-	3.0	1.2	-	1.2	-	-	-
C. rigidus	-	2.4	-	-	2.4	-	27.6	16.8	20.4	3.0	1.8	-	1.8	-	1.8	1.2
P. vandelii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.6	-
S. molischii	3.6	4.8	3.0	9.6	1.8	4.2	1.2	-	1.8	0.6	3.0	1.2	0.6	0.6	1.2	-
F. profunda	-	-	-	-	0.6	-	-	-	0.6	-	-	-	-	-	-	0.6
A. quattrospina	0.6	1.2	3.0	0.6	3.6	11.4	9.0	9.0	-	-	-	0.6	0.6	1.2	-	-
U. tenuis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
M. elegans	4.8	2.4	18.0	4.2	-	-	0.6	3.0	1.8	-	1.2	-	1.8	-	-	-
C. murrayi	-	-	-	0.6	-	-	-	-	-	-	-	-	-	-	-	-
G. ornate	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
S. anthos	1.8	0.6	3.0	-	1.8	1.2	3.0	-	1.2	-	-	-	-	0.6	-	-
C. leptoporus	-	-	-	-	-	0.6	3.6	7.2	1.2	-	0.6	0.6	-	-	0.6	0.6
S. pulchra	-	-	-	-	-	-	-	-	-	-	0.6	-	-	-	-	0.6
D. tubifera	0.6	1.8	1.2	-	0.6	2.4	4.8	2.4	1.8	-	-	-	-	-	-	-
R. clavigera	-	-	-	-	-	-	-	-	-	-	-	-	-	1.8	-	-
A. robusta	-	-	-	-	-	-	-	0.6	-	-	-	-	-	-	-	-
U. sibogae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
A. unicornis	1.2	1.8	-	2.4	-	1.2	-	-	-	-	0.6	-	1.2	0.6	-	-
G. flabellatus	-	-	-	0.6	-	1.2	-	-	-	-	-	-	-	-	-	-
G. oceanica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
A. ordinate	-	0.6	0.6	-	-	-	-	-	-	-	-	-	-	-	-	-
C. mediterranea	3.0	-	0.6	-	-	-	-	-	-	-	-	0.6	-	-	-	-
C. oblonga	-	-	-	0.6	-	-	-	-	-	-	-	-	-	-	-	-
H. carteri	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Syracosphaera spp.	5.4	5.4	12.0	25.2	19.2	16.2	10.2	6.0	16.2	7.8	25.2	20.4	23.4	10.8	4.8	4.2
Holococcolithophore spp.	1.2	1.8	-	-	-	-	-	-	-	-	-	-	-	1.2	-	-
Undetermined species	9.0	4.2	0.6	2.4	6.6	6.6	1.8	2.4	-	1.2	3.0	2.4	3.6	3.6	0.6	-
Total	128.2	151.0	128.2	125.8	88.1	131.8	129.4	125.2	116.8	27.6	52.1	59.3	58.1	36.0	16.2	5.1

[a]Coccolithophore taxa are arranged according to absolute frequency. ND, not determined.

et al., 1996; *Poulton et al.*, 2006] *E. huxleyi* would have taken about 30–100 days to sink from 20 m to 150 m depth.

[19] High numbers of coccolithophore cells in the water column below coccolithophore blooms have earlier been reported from the North Atlantic [e.g., *Samtleben et al.*, 1995], and are possibly a frequent but largely neglected feature of blooms and postbloom episodes. Enhanced production of coccolithophore calcite in the North Atlantic from January to early April at 34°N, and between March and early June at 48°N, seems to be seasonally and interannually recurring, and to result in calcite fluxes of similar magnitude at both latitudes analyzed 34°N and 48°N [*Honjo and Manganini*, 1993; *Broerse et al.*, 2000; *Ziveri et al.*, 2000].

[20] Assuming that early production and dispersion of *E. huxleyi* occurs across the entire domain of North Atlantic Transitional Water (NATW), the global budget of coccolith calcite production may be much higher than estimated so far. The area of NATW (~1.5×10^6 km^2) is similar to the area of spring coccolithophore blooms south of Island [cf. *Holligan et al.*, 1993], and may hence contribute the same amount of coccolithophores. A large part of the coccolith calcite produced in the NATW in early spring is mixed to depth, and contributes to the carbonate pump of particulate inorganic carbon (PIC) to the twilight zone.

5. Conclusions

[21] Bimodal distribution of coccolithophores occurs along a north–to–south transect at 20°W in the North Atlantic during spring. Representing about half of the coccolithophore assemblage, *E. huxleyi* occurs at depth integrated cell densities of 12×10^9 cells m^{-2} at either end of transect, albeit under different ecologic conditions. Morphological differentiation of bimodal populations of *E. huxleyi* is indicated by the occurrence of different morphotypes at the northern and southern end of transect. Maximum total coccolithophore cell densities of 150–240 $\times 10^3$ cells L^{-1} occur under (1) well-

Table A1b. Hydrographic and Trophic Data and Plankton Count Data ($\times 10^3$ cells L^{-1}) Recorded During *Poseidon* Cruise 308 for Sites 6–8[a]

	Site 6						Site 7						Site 8					
	10 m Depth	50 m Depth	100 m Depth	125 m Depth	150 m Depth	200 m Depth	10 m Depth	50 m Depth	100 m Depth	125 m Depth	150 m Depth	200 m Depth	10 m Depth	30 m Depth	50 m Depth	100 m Depth	150 m Depth	200 m Depth
Temperature (°C)	14.40	14.41	14.32	14.33	14.19	13.69	16.23	16.20	16.15	15.92	15.51	14.32	16.49	16.40	16.40	16.28	15.29	14.49
Salinity	35.86	35.88	35.86	35.89	35.89	35.84	36.15	36.16	36.15	36.13	36.09	35.94	36.16	36.17	36.17	36.17	36.07	35.98
Fluorescence (mV)	0.230	0.224	0.232	0.127	0.082	0.069	0.250	0.257	0.224	0.088	0.070	0.065	0.281	0.321	0.332	0.121	0.072	0.069
NO_2 (μmol L^{-1})	0.25	0.29	0.31	0.24	0.12	0.04	0.08	0.10	0.15	0.23	0.04	0.05	0.90	0.11	0.15	0.40	0.04	0.02
NO_3 (μmol L^{-1})	2.77	2.81	2.81	4.15	5.03	8.74	0.13	0.14	0.25	1.79	6.24	6.83	0.26	0.30	0.36	0.83	5.73	7.42
PO_4 (μmol L^{-1})	0.18	0.16	0.16	0.23	0.28	0.50	BD	BD	BD	0.08	0.32	0.37	BD	BD	0.01	0.04	0.30	0.40
SiO_4 (μmol L^{-1})	5.5	7.4	4.7	8.7	5.5	8.9	7.8	8.5	4.5	5.7	5.9	6.8	3.3	2.2	2.6	2.6	2.9	3.4
Counted specimens	174	368	318	106	120	60	463	389	245	90	71	32	375	296	454	238	103	29
E. huxleyi	5.4	24.0	15.6	3.6	7.8	3.6	9.6	7.2	7.8	5.4	6.6	1.8	12.5	4.2	15.0	7.8	1.8	0.6
G. ericsonii	3.6	7.2	9.0	3.0	0.6	-	24.0	21.6	20.4	7.2	3.6	1.2	57.2	23.4	42.5	30.0	9.0	0.6
G. muellerae	6.0	13.8	14.4	4.2	8.4	3.6	3.6	8.4	4.2	2.4	1.2	0.6	6.0	1.8	6.6	0.6	1.8	1.2
O. hydroideus	6.0	-	-	-	-	-	22.8	26.4	13.8	-	-	-	8.7	31.8	22.2	-	2.4	0.6
O. formosus	6.0	18.6	10.8	1.2	-	-	-	-	-	-	-	-	-	-	-	4.8	-	-
R. parvula	-	-	-	-	-	-	3.0	4.2	4.2	-	-	-	12.0	7.8	10.2	7.2	3.0	-
C. rigidus	6.0	13.2	9.6	1.8	1.8	1.2	-	-	-	-	-	-	-	4.8	4.8	0.6	-	-
P. vandelii	-	-	0.6	0.6	-	-	-	-	0.6	0.6	-	-	1.1	0.6	-	0.6	-	-
S. molischii	-	-	4.8	1.2	0.6	-	0.6	1.8	0.6	-	-	-	3.8	2.4	6.6	1.8	1.2	-
F. profunda	-	-	-	-	-	-	-	-	-	-	0.6	8.4	-	-	-	-	3.0	6.6
A. quattrospina	-	3.0	0.6	-	-	0.6	1.2	6.0	2.4	-	-	-	-	4.2	-	-	-	-
U. tenuis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
M. elegans	-	-	1.2	-	-	-	-	-	0.6	-	-	-	-	-	-	-	0.6	-
C. murrayi	-	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-	-	-	-
G. ornate	-	-	-	-	-	-	1.2	1.8	-	-	-	-	2.2	3.0	3.6	1.8	1.2	-
S. anthos	1.8	6.0	0.6	0.6	1.8	0.6	1.8	2.4	1.8	0.6	-	-	-	-	-	-	-	-
C. leptoporus	-	0.6	-	-	-	-	-	1.2	-	0.6	0.6	0.6	-	-	1.2	2.4	-	1.2
S. pulchra	-	1.2	-	-	-	-	-	-	-	-	-	-	8.7	1.2	4.2	1.2	-	-
D. tubifera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.6	-	-	-
R. clavigera	-	-	-	-	-	-	0.6	-	0.6	0.6	0.6	-	0.5	0.6	4.2	-	-	1.2
A. robusta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
U. sibogae	-	-	-	-	-	-	-	-	-	-	0.6	-	-	-	1.2	0.6	-	-
A. unicornis	-	-	-	-	-	-	0.6	3.0	1.2	-	-	-	-	1.8	-	0.6	-	0.6
G. flabellatus	-	-	-	-	-	-	-	-	0.6	-	1.2	-	-	-	-	-	-	-
G. oceanica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
A. ordinate	0.6	1.2	-	-	-	-	-	-	-	-	-	-	0.5	-	2.4	-	-	-
C. mediterranea	-	1.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C. oblonga	1.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
H. carteri	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Syracosphaera spp.	12.6	21.6	31.8	4.2	4.8	1.8	38.3	41.3	33.6	19.8	8.4	-	37.6	21.6	62.3	10.2	4.8	1.2
Holococcolithophore spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	4.8	1.8	0.6	-	-
Undetermined species	9.0	13.2	9.0	7.8	2.4	1.2	1.8	3.0	2.4	-	0.6	0.6	10.4	4.2	7.8	8.4	2.4	1.8
Total	51.5	110.3	89.3	25.2	24.6	11.4	88.7	105.5	76.7	27.0	19.8	13.2	150.4	105.5	160.0	72.5	28.2	15.0

[a]Coccolithophore taxa are arranged according to absolute frequency. ND, not determined; BD, below detection limit.

mixed high-nutrient conditions, and (2) stratified low-nutrient conditions at the northern and southern end of transect, respectively. Due to the dispersion of coccolithophore cells, early spring mass production at complete mixing of the upper water column might have been overlooked by satellite imagery and earlier studies, and would need to be taken into consideration when quantifying carbonate budgets.

Appendix A

[22] This appendix includes information on coccolithophore species and species groups, including hydrographic and trophic data and plankton count data (Tables A1a–A1c) and Varimax rotated factor loadings (Table A2). Coccolithophore species and species groups recorded during Poseidon Cruise 308 are (in alphabetical order): *Acanthoica quattrospina* Lohmann 1903; *Algirosphaera robusta* (Lohmann 1902) Norris 1984; *Alisphaera ordinata* (Kamptner 1941) Heimdal 1973; *Alisphaera unicornis* Okada and McIntyre 1977; *Calcidiscus leptoporus* (Murray and Blackman 1898) Loeblich and Tappan 1978; *Calciopappus rigidus* Gaarder and Ramsfjell 1954; *Calciosolenia murrayi* Gran 1912; *Calyptrosphaera oblonga* Lohmann 1902; *Coronosphaera mediterranea* (Lohmann 1902) Gaarder; *Discosphaera tubifera* (Murray and Blackman 1989) Ostenfeld 1900; *Emiliania huxleyi* (Lohmann 1902) Hay and Mohler, in Hay et al. 1967; *Florisphaera profunda* Okada and Honjo 1973; *Gephyrocapsa ericsonii* McIntyre and Bé 1967; *Gephyrocapsa muellerae* Bréjéret 1978; *Gephyrocapsa oceanica* Kamptner 1943; *Gephyrocapsa ornata* Heimdal 1973; *Gladiolithus flabellatus* (Halldal and Markali 1955) Jordan and Chamberlain 1993; *Helicosphaera carteri* (Wallich 1877) Kamptner 1954; Holococcolithophore spp.; *Michelsarsia elegans* Gran 1912 emend. Manton et al. 1984; *Ophiaster formosus* Gran 1912 emend Manton and Oates 1983; *Ophiaster hydroideus* (Lohmann 1903) Lohmann 1913 emend. Manton and Oates 1983; *Palusphaera vandelii* Lecal 1965 emend. Norris 1984; *Reticulafenestra parvula* (Okada and McIntyre 1977) Biekart 1987; *Rhabdosphaera clavigera* Murray and Blackman 1989; *Syracosphaera anthos* (Lohmann 1912) Janin 1987; *Syracosphaera molischii* Schiller 1925; *Syracosphaera pulchra* Lohmann 1902; *Syracosphaera* spp.; *Umbilicosphaera sibo-*

Table A1c. Hydrographic and Trophic Data and Plankton Count Data ($\times 10^3$ cells L^{-1}) Recorded During *Poseidon* Cruise 308 for Sites 9 and 10[a]

	Site 9						Site 10						
	10 m Depth	50 m Depth	75 m Depth	100 m Depth	150 m Depth	200 m Depth	10 m Depth	50 m Depth	65 m Depth	75 m Depth	85 m Depth	100 m Depth	200 m Depth
Temperature (°C)	18.15	18.50	18.50	17.92	16.67	16.05	18.58	18.73	18.64	18.58	18.37	17.74	15.55
Salinity	ND	36.55	36.55	36.48	36.29	36.21	ND	36.73	36.73	36.72	36.67	36.53	36.14
Fluorescence (mV)	0.130	0.280	0.224	0.142	0.086	0.074	0.090	0.102	0.159	0.233	0.211	0.120	0.066
NO_2 (μmol L^{-1})	0.20	0.30	0.60	0.14	0.03	0.03	0.07	0.06	0.08	0.09	0.16	0.14	0.09
NO_3 (μmol L^{-1})	0.10	0.25	0.24	0.94	5.38	5.95	0.06	0.01	0.10	0.16	0.60	1.46	6.84
PO_4 (μmol L^{-1})	BD	0.01	BD	0.03	0.25	0.33	BD	BD	BD	BD	0.02	0.06	0.36
SiO_4 (μmol L^{-1})	0.2	0.3	4.0	1.1	1.9	2.8	1.2	1.3	1.1	1.1	1.6	1.0	2.3
Counted specimens	444	409	279	264	170	51	204	448	277	436	313	226	201
E. huxleyi	58.1	55.7	38.3	35.4	10.2	6.6	34.8	68.3	74.3	105.5	80.3	37.8	21.0
G. ericsonii	47.3	46.1	27.6	30.0	10.2	5.4	17.4	36.6	25.2	65.9	44.9	16.2	13.8
G. muellerae	-	-	-	-	0.6	1.2	-	0.6	-	-	-	-	-
O. hydroideus	7.8	-	4.8	-	0.6	-	-	2.4	-	7.8	6.0	0.6	1.8
O. formosus	25.2	35.4	18.0	7.8	-	-	1.2	-	6.6	-	-	-	-
R. parvula	3.0	-	6.0	3.6	1.8	0.6	1.2	8.4	2.4	7.2	0.6	1.2	1.2
C. rigidus	-	-	-	-	-	-	-	-	1.8	3.6	1.8	2.4	-
P. vandelii	3.0	-	-	-	-	-	18.0	36.6	12.0	6.0	1.2	1.2	9.6
S. molischii	6.0	4.8	1.8	-	-	-	3.0	4.2	1.2	-	1.2	-	3.6
F. profunda	-	0.6	1.2	2.4	19.8	5.4	-	2.4	1.8	1.2	2.4	24.6	-
A. quattrospina	4.8	1.2	0.6	-	1.2	-	4.2	2.4	-	-	0.6	-	1.2
U. tenuis	-	-	-	-	-	-	12.0	21.6	6.6	6.0	1.8	-	12.6
M. elegans	1.2	4.8	3.6	-	-	-	-	0.6	1.2	1.8	-	-	-
C. murrayi	2.4	5.4	1.8	1.2	-	0.6	-	3.6	4.8	5.4	11.4	0.6	-
G. ornate	4.2	3.0	1.2	1.8	-	-	1.2	4.2	1.2	5.4	-	-	1.2
S. anthos	0.6	0.6	-	-	-	-	-	-	1.8	0.6	-	-	-
C. leptoporus	-	0.6	1.2	-	0.6	-	-	-	-	-	1.2	0.6	-
S. pulchra	0.6	2.4	-	-	-	-	0.6	-	2.4	0.6	0.6	-	1.8
D. tubifera	0.6	0.6	0.6	-	-	-	1.2	3.6	-	0.6	0.6	-	0.6
R. clavigera	-	-	-	-	-	-	-	7.8	-	-	-	0.6	4.2
A. robusta	1.2	4.2	3.6	3.6	1.2	-	0.6	-	-	3.6	-	3.0	-
U. sibogae	0.6	1.2	0.6	0.6	-	-	0.6	-	1.2	5.4	3.0	1.8	0.6
A. unicornis	-	-	-	-	-	-	-	-	-	-	-	-	-
G. flabellatus	-	-	-	-	8.4	-	-	0.6	-	-	-	6.0	-
G. oceanica	-	3.6	-	1.2	-	-	-	-	-	0.6	1.2	-	-
A. ordinate	-	-	-	-	-	-	-	-	-	-	-	-	-
C. mediterranea	-	-	-	-	-	-	-	-	-	-	-	-	-
C. oblonga	-	-	-	-	-	-	-	-	-	-	-	-	-
H. carteri	-	0.6	-	-	-	-	-	-	-	-	-	-	-
Syracosphaera spp.	53.9	37.8	6.6	9.6	1.2	2.4	14.4	36.6	6.6	3.6	11.4	-	5.4
Holococcolithophore spp.	2.4	3.0	2.4	-	-	-	3.0	3.0	1.8	0.6	0.6	-	1.8
Undetermined species	8.4	8.4	19.8	12.6	1.2	0.6	5.4	10.2	6.6	11.4	5.4	4.2	21.0
Total	200.7	197.1	81.9	63.4	56.3	21.6	109.7	233.1	153.4	240.3	169.6	100.7	95.9

[a]Coccolithophore taxa are arranged according to absolute frequency. ND, not determined; BD, below detection limit.

Table A2. Varimax Rotated Factor Loadings[a]

	Factor Number					
	1	2	3	4	5	Communality
Water Depth (m)	−0.24	−0.73	0.03	0.31	−0.12	0.70
Temperature (°C)	0.80	0.25	0.25	0.26	−0.33	0.93
Salinity	0.82	0.12	0.33	0.20	−0.31	0.93
Fluorescence (mV)	0.22	0.79	−0.17	−0.39	0.25	0.92
NO_2 (μmol L^{-1})	0.16	0.49	−0.27	−0.01	0.26	0.40
NO_3 (μmol L^{-1})	−0.60	−0.66	−0.06	0.03	0.23	0.86
PO_4 (μmol L^{-1})	−0.61	−0.64	−0.06	−0.02	0.28	0.87
SiO_4 (μmol L^{-1})	−0.65	0.00	−0.32	0.12	0.02	0.54
E. huxleyi	0.53	−0.02	0.34	−0.42	0.35	0.70
G. ericsonii	0.71	0.53	0.24	0.14	−0.01	0.87
G. muellerae	−0.44	0.21	−0.19	−0.69	0.29	0.83
O. hydroideus	−0.08	0.77	0.03	−0.15	−0.27	0.70
O. formosus	0.45	0.07	−0.30	−0.08	0.65	0.72
R. parvula	0.01	0.52	0.31	−0.06	0.13	0.39
C. rigidus	−0.07	−0.05	−0.07	−0.77	0.05	0.61
P. vandelii	0.18	0.01	0.90	0.02	−0.03	0.85
S. molischii	−0.03	0.46	0.27	0.03	0.55	0.58
F. profunda	0.29	−0.34	−0.07	0.04	−0.55	0.50
A. quattrospina	−0.11	0.19	0.02	−0.81	0.01	0.71
U. tenuis	0.19	−0.04	0.92	0.04	−0.01	0.88
M. elegans	0.10	−0.03	−0.01	−0.15	0.59	0.39
C. murrayi	0.75	−0.02	0.23	0.02	0.06	0.62
G. ornate	0.53	0.48	0.47	0.14	−0.04	0.75
S. anthos	−0.13	0.16	−0.20	−0.41	0.25	0.31
C. leptoporus	0.06	−0.07	−0.09	−0.69	−0.13	0.52
S. pulchra	0.19	0.56	0.05	0.24	0.07	0.41
D. tubifera	0.04	−0.01	0.47	−0.78	0.18	0.86
R. clavigera	−0.02	0.19	0.85	0.12	−0.06	0.78
A. robusta	0.82	−0.08	−0.17	0.03	0.01	0.71
U. sibogae	0.72	0.01	0.12	0.01	−0.16	0.55
A. unicornis	−0.27	0.45	−0.07	−0.06	0.06	0.28
G. flabellatus	0.20	−0.22	−0.09	−0.05	−0.49	0.34
G. oceanica	0.75	−0.02	−0.16	0.11	0.40	0.76
A. ordinata	−0.12	0.53	0.03	0.01	0.12	0.31
C. mediterranea	−0.11	0.02	−0.06	−0.08	0.42	0.19
C. oblonga	−0.10	0.09	−0.15	0.04	0.08	0.05
H. carteri	0.57	0.01	−0.17	0.12	0.50	0.62
Syracosphaera spp.	0.02	0.78	0.09	0.05	0.16	0.65
Holococcolithophore spp.	0.35	0.35	0.47	0.11	0.19	0.51
Total variance explained	7.22	5.77	4.16	3.76	3.21	24.11
Percent of total variance explained	18.51	14.80	10.65	9.64	8.22	61.82

[a]The number of factors was selected from scree plot.

gae (Weber-van Bosse 1901) Gaarder 1970; *Umbellosphaera tenuis* (Kamptner 1937) Paasche in Markali and Paasche 1955.

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