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## Vertical and horizontal distribution of coccolithophores in the Caribbean Sea

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**Abstract** Coccolithophores are one of the major, living phytoplankton groups and play important roles in geochemical cycles and climate. They are a particularly dominant group in oligotrophic waters, yet a lot more needs to be learned about their horizontal and vertical distributions. Coccolithophores were collected at different photic depths from 15 stations across the Caribbean Sea during cruise 35/1 of the RV *Meteor* from April to May 1996. A total of 67 species was identified, with an average of 19 species per station. Coccolithophores were encountered at nearly all stations but abundances were fairly low ( $10^2$ – $10^3$  cells  $l^{-1}$ ). Coccolithophore assemblages in the four oceanographical provinces identified (Granada Basin waters, Atlantic surface waters, northern Caribbean waters, and Pedro Bank waters) differed in their species composition and abundances. Abundance peaks occurred near the surface and in the deeper photic zone (140–150 m) just below the deep chlorophyll-a maximum at the top of the nitrate nutricline.

### Introduction

Coccolithophores are one of the major phytoplankton groups in the oceans. There are about 200 species which have been classified so far (Jordan and Green 1994; Cros et al. 2000; Jordan et al. 2000), although newly discovered hetero/holococcolith combinations are continually reducing their number (Cros et al. 2000). The biogeographical zonations and depth habitats of a few of these species have been well documented and show that they prefer to live within certain depth ranges and latitudinal zones (Winter et al. 1994). *Emiliana huxleyi* and *Gephyrocapsa oceanica*, two species which are probably closely related (Medlin et al. 1996), are bloom-forming organisms which are thought to modify biogeochemical cycles of, amongst others,  $CO_2$  (Tyrrell and Taylor 1995; Winter 1996), climate (DMS-cloud cover; Charlson et al. 1987; Ayers et al. 1991) and light scattering-albedo (Balch et al. 1991; Tyrrell et al. 1999). Most of our understanding of coccolithophores stems from work undertaken in intense coastal upwelling regions and high latitudes where they often occur in great numbers (exceeding  $10^6$  cells  $l^{-1}$ , Balch et al. 1991). Much less is known about the role of coccolithophores in oligotrophic nutrient-depleted regions where they are often the dominant taxa, perhaps because of their special adaptation to these environments (extreme k-selection; Young 1994). Successful strategies of coccolithophores may include using coccoliths as buoyancy-control to reach prevailing nutrients (Wilbur and Watabe 1963; Klaveness and Paasche 1979), and reducing diffusion limitation of nutrient uptake by possessing higher sinking rates than other phytoplankton in the same size group (Smayda and Bienfang 1983). In the laboratory *E. huxleyi* showed the fastest nutrient uptake (=lowest half-saturation constant) for nitrate and ammonium uptake out of 16 species (Eppley et al. 1969). In general, oceanic coccolithophores are able to grow at much lower iron, zinc and manganese concentrations than other coastal phytoplankton (Brand et al. 1983). Most other

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tropical oceanic species remain at low abundances during natural and artificial nutrient enrichment (Hulburt 1983).

Coccolithophore diversity is lowest for strongly eutrophic communities but it is also low in extreme oligotrophic conditions. The highest diversity of coccolithophores is found in oligotrophic waters like subtropical oceanic gyres (Hulburt 1963, 1964). The miscellaneous group (> 80% of the species assemblage but < 20% of the total abundance) shows substantial abundance in intermediate conditions (e.g., Honjo 1976). The oligotrophic regions of the world's oceans are often overlooked but these regions have a deeper mixed layer and a deeper photic zone than eutrophic regions. Consequently, the total phytoplankton biomass production in oligotrophic regions may often be underestimated. The ratio of oligotrophic (low nutrient supply, coccolithophore-carbonate dominated) vs. eutrophic (high nutrient supply, diatom-organic matter dominated) volume of the world's ocean has been implicated as an important mechanism for changes in the partition of CO<sub>2</sub> between the ocean and atmosphere (Dymond and Lyle 1985). Therefore, it is important to understand the role of coccolithophores in oligotrophic regions. This paper addresses some of these questions, including the vertical and horizontal distributions of coccolithophores in the Caribbean Sea.

### The Caribbean Sea

The Caribbean Sea (Fig. 1) is well situated for studying the response of coccolithophores to different oceanographic features under tropical oligotrophic

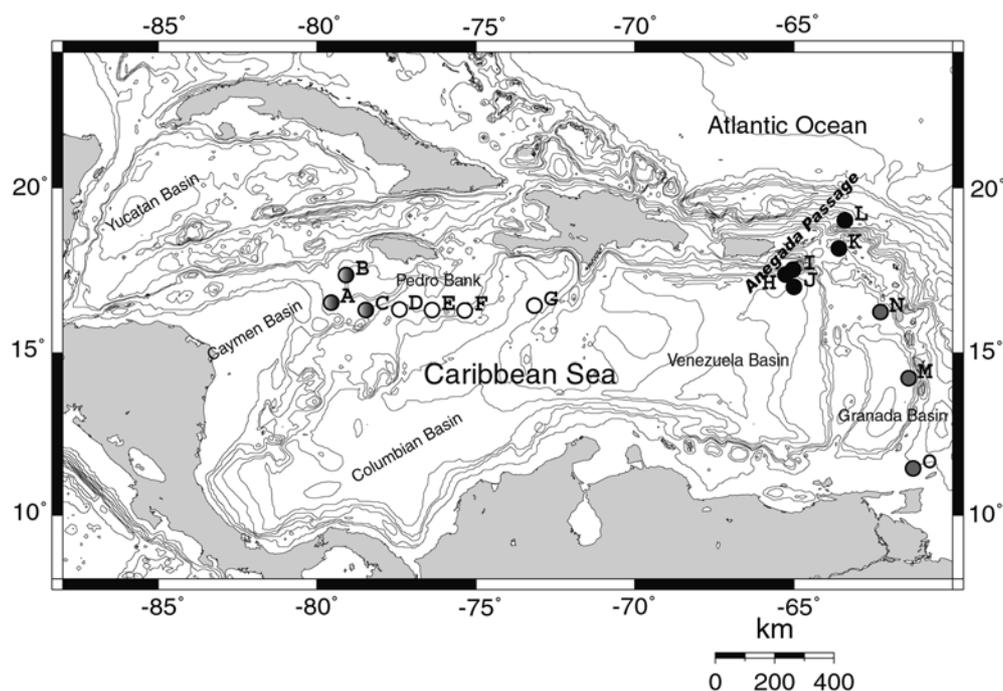
conditions. During *Meteor* cruise M35/1 we encountered four oceanographical settings which we designate northern Caribbean waters (stations A to C – which combine stations C1 and C2; gradient circles), Pedro Bank waters (stations D to G; open circles), Atlantic surface waters (stations H to L; closed circles), and Granada Basin waters (filter stations M to O; shaded circles).

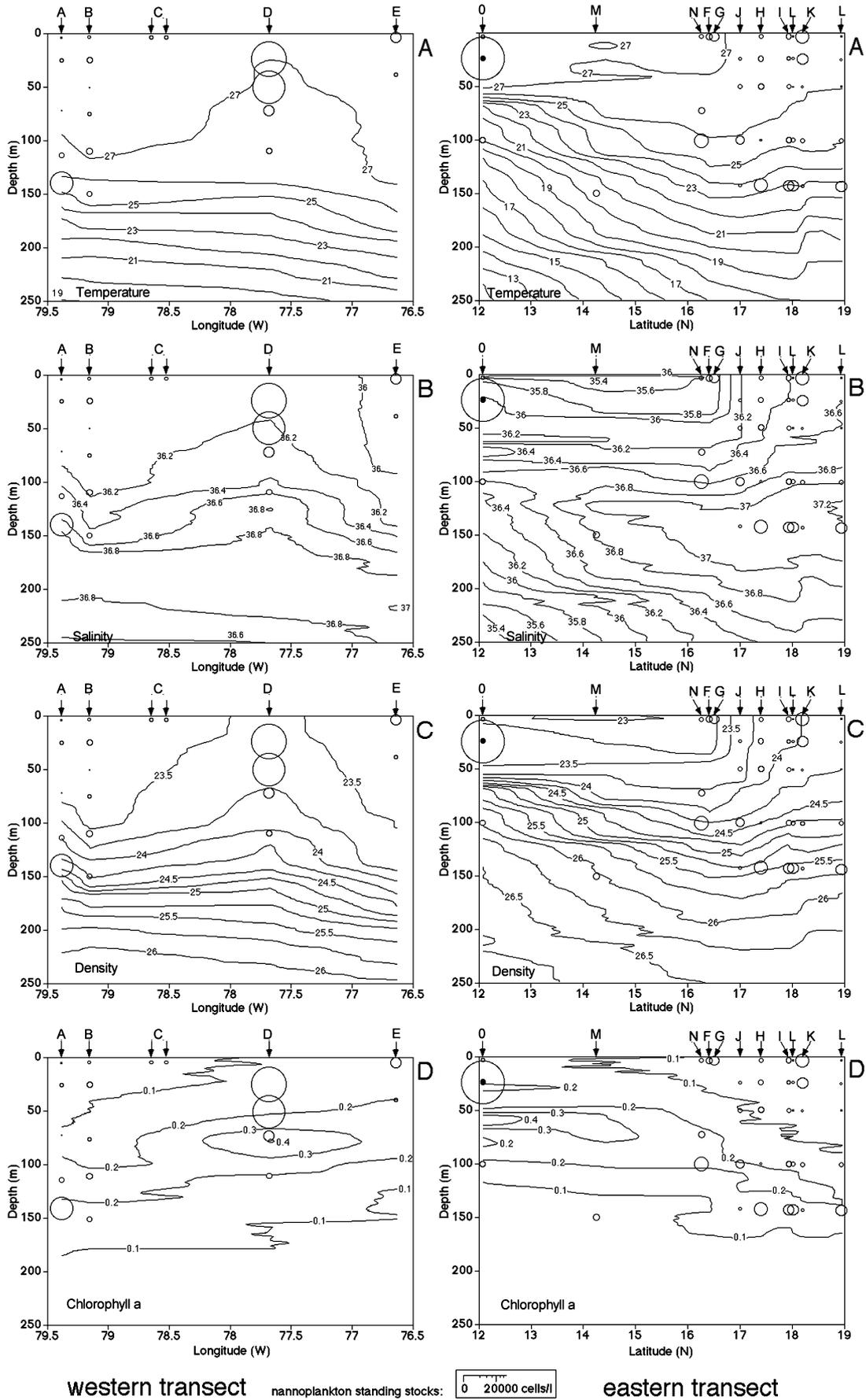
Hydrographic conditions (temperature, salinity, density and chlorophyll-a) during the cruise are presented in Fig. 2. The latitudinal excursions of the intertropical convergence zone (ITCZ) and associated precipitation in the Amazon Basin produce two major climatic and hydrographic seasons in the Caribbean. During summer and fall, runoff from the Orinoco and Amazon Rivers approaches the Caribbean Sea and leads to the formation of low-salinity lenses at the surface (e.g., Wüst 1964; Gordon 1967; Müller-Karger et al. 1988, 1989; Corredor and Morell 2001). These surface waters have increased nutrient and phytoplankton pigment concentrations (Froehlich et al. 1978; Müller-Karger et al. 1989; Bidigare et al. 1993; Corredor and Morell 2001).

*Meteor* cruise 35/1 approached the Caribbean in the winter/spring season when the trade winds prevail and the low-salinity lenses are restricted to the southeastern and southern parts of the Caribbean. This area is characterized by a relatively steep seasonal thermocline, raised isotherms, and a strong deep chlorophyll maximum associated with the seasonal thermocline. We refer to this area as the Granada Basin waters (stations M–O; Fig. 1).

The northeastern Caribbean and the Anegada Passage (Fig. 1) are characterized by a smooth “subtropi-

**Fig. 1** Map showing locations of sampling stations (A–O) in the Caribbean Sea. Stations A–C Northern Caribbean waters, D–G Pedro Bank waters, H–L Atlantic surface waters, M–O Granada waters





**Fig. 2A–D** Coccolithophore abundances (*circles*) and physical/biological parameters (*contours*) encountered during RV *Meteor* cruise 35/1 in the eastern Caribbean (Barbados–Anegada Passage–Puerto Rico). *Circles* indicate the depths at which nanoplankton samples were obtained with a rosette water sampler, and the size of the circles represent coccolithophore abundances (cells  $\text{l}^{-1}$ ). Panels are divided into western section (*left panels* shown by longitude; stations A–E) and eastern section (*right panels* shown by latitude; stations H–O). **A** Temperature ( $^{\circ}\text{C}$ ), **B** salinity (psu), **C** density ( $\text{kg m}^{-3}$ ), **D** chlorophyll-a ( $\mu\text{g l}^{-1}$ ) derived from fluorescence. For location of stations, see map in Fig. 1

cal” seasonal thermocline and oligotrophic conditions with a deep and broad chlorophyll maximum (Fig. 2, right panels). The lower salinity of the surface waters relative to most parts of the tropical Atlantic derives, in part, from the dilution by Amazon River water (Moore and Todd 1993). This water, however, has a long residence time and is depleted in nutrients. We refer to this oligotrophic area as the Atlantic surface waters (stations H–L).

Northern Caribbean waters (Fig. 2, left panels; Fig. 1, stations A–C) experience deep mixing induced by the trade winds primarily in winter and spring. This produces a deep mixed layer and a gradual change in water density with depth below the mixed layer. The strong differences in mixed layer depths between the northeastern Atlantic waters and the northern Caribbean waters can be assigned to the fetch of the trade winds which blow in a NE–SW direction. The chlorophyll concentrations suggest oligotrophic conditions in the northern Caribbean waters.

Pedro Bank waters (stations D–G) derive from interaction with this shallow carbonate platform, resulting in localized upwelling and increased plankton biomass. The upwelling water derives from a depth of between 100 and 150 m, which coincides with the mixed layer depth in this area during RV *Meteor* cruise 35/1.

## Materials and methods

The samples were retrieved from 15 different stations (A–O; stations C1 and C2 combined) during cruise 35/1 of the RV *Meteor* between 18 April and 15 May 1996 (Barbados–Ponce; Fig. 1, Table 1). Temperature, salinity, and fluorescence depth profiles were measured with a portable CTD at plankton sampling sites to determine water structure and chlorophyll-a concentrations. A rosette water sampler equipped with 10-l Niskin bottles was deployed to collect ocean water. Usually five bottles were taken from 3, 25, 50, 100, and 140 m (Table 1). The lowermost samples were taken at or near the fluorescence peak (Fig. 2D). At three of the stations (C, F, G), only surface samples were obtainable with the ship’s independent water-pump system which consists of a continuous-flow seawater intake system and is kept very clean for scientific use only. In all, 48 water samples were

filtered. On average, 6 l (4–7 l) was filtered through 0.8- $\mu\text{m}$ , 47-mm-diameter cellulose Millipore filters at low vacuum (5 psi) and washed thoroughly with de-ionized water (pH 7). Afterwards, the filters were air-dried. Coccolithophore abundances (Table 1, upper lines) were counted by examining a 16- $\text{mm}^2$  area on the filter (equivalent to a minimum of 10-ml water throughput) with cross nicols of a polarizing microscope at 1,250 $\times$  magnification. Isolated coccoliths were neglected. For five of the 48 samples, the number of liters filtered was not recorded and abundance counts were impossible (Table 1, marked with x). For species identification a rectangular portion (0.5  $\text{cm}^2$ ) of the filter was coated with gold–palladium and placed on a stub for viewing with a Zeiss digital scanning electron microscope 850 (Gothenburg University) and Zeiss 950 (BAH-List).

## Results

### Abundance

Coccolithophore abundances for the 48 filters (Table 1) examined by polarizing microscope ranged between  $10^1$  and  $10^4$  cells  $\text{l}^{-1}$ . The mean abundance for all filter samples was 2,700 cells  $\text{l}^{-1}$ . The highest values ( $10^4$  cells  $\text{l}^{-1}$ ) occurred at two stations, D (Pedro Bank 25 and 50 m) and O (Granada Basin 25 m; Table 1).

We combined samples into three depth zones: the upper photic zone (3–25 m), middle photic zone (40–110 m), and deep photic zone (140–150 m), based on results of this cruise and previous work by Okada and Honjo (1973), Winter et al. (1994), and Jordan and Chamberlain (1997). The upper photic zone had a mean abundance of 3,875 cells  $\text{l}^{-1}$ , the middle photic zone of 1,668 cells  $\text{l}^{-1}$ , and the deep photic zone of 2,171 cells  $\text{l}^{-1}$ . With the exception of stations D and O, there was no significant difference between abundances of the three photic zones because the standard deviations generally overlapped (data not shown). Also, there was no marked difference in coccolithophore abundances between the western and eastern parts of the transect. Half of the stations ( $n=7$ ) with samples collected from 140–150 m water depths showed abundance peaks at these deepest sampling depths.

### Diversity

Sixty-seven species were identified from a total of 3,035 specimens examined from the 48 filters observed by SEM (Appendix). The average number of species in the water column per station was 19. The highest number of species (42) was recorded at station D, followed by stations K (31), N (26) and I (21). The highest number of species at any given water depth (Table 1) occurred at station D (32 at 50 m, and 23 at 25 m). There was no

difference in species diversity between the western and eastern parts.

### Distribution

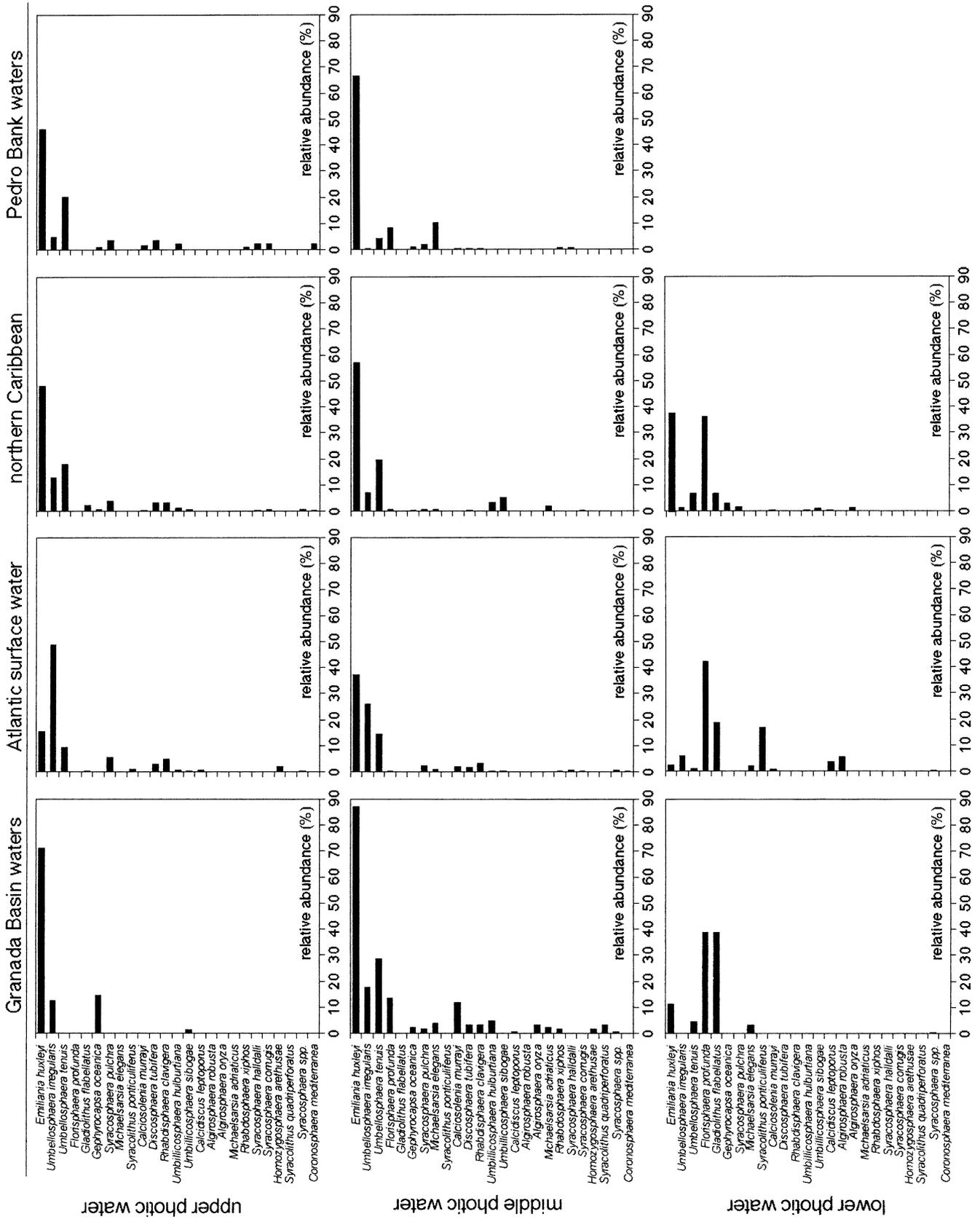
The vertical and horizontal percent distribution of coccolithophores sorted according to the 25 most abundant species is presented in Fig. 3. Eight species

**Fig. 3** Relative abundances of coccolithophore species (above 2%) in the four oceanographic provinces encountered during *Meteor* cruise 35/1 at deep, intermediate and shallow depths. Note the dominance of *E. huxleyi* in shallow waters, except in the Atlantic waters where *U. irregularis* is the most abundant species. Variation in the dominance of *E. huxleyi* and species of *Umbellosphaera* at intermediate depths are also characteristic for the oceanographic provinces. In deep surface waters the abundance of *Florisphaera* is expected, except for abundant *E. huxleyi* in northern Caribbean waters

**Table 1** Coccolithophore water sampling locations as well as species/specimen count information taken during Caribbean cruise M35/1

Province	Geographic coordinates, date of sampling, RV <i>Meteor</i> cruise no.		Station	Sample depths (m) <sup>a</sup>										Water column totals	
	N	W		Upper		Middle				Lower					
				3	25	40	50	70	75	100	110	140	150		
Northern Caribbean	16.54.81	79.54.88	A	x	223			x			433	9,076		9,732	
	5 May 1996				<i>44</i>	<i>8</i>			<i>4</i>		<i>120</i>	<i>101</i>		277	
	M35037				<i>3</i>	<i>4</i>			<i>4</i>		<i>8</i>	<i>8</i>		12	
	17.38.6	79.08.998	B		115	583	x			198		674		374	1,944
	12 May 1996				<i>28</i>	<i>104</i>		<i>127</i>		<i>0</i>		<i>150</i>		<i>112</i>	<i>521</i>
	M35043				<i>6</i>	<i>11</i>		<i>8</i>		<i>0</i>		<i>9</i>		<i>9</i>	<i>18</i>
	16.32.084	78.46.554	C		170										170
14 May 1996				<i>46</i>										46	
Pump				<i>12</i>										12	
Pedro Bank	16.34.389	77.40.802	D		22,613		19,968	2,363						44,944	
	15 May 1996				<i>257</i>		<i>355</i>	<i>18</i>						<i>630</i>	
	M35052				<i>23</i>		<i>32</i>	<i>4</i>						42	
	16.32.14	76.37.79	E	1,936		214								2,150	
	15 May 1996			<i>32</i>		<i>10</i>								42	
	M35054			<i>8</i>		<i>4</i>								10	
	16.30.594	75.36.079	F	726										726	
13 May 1996			<i>182</i>										<i>182</i>		
Pump			<i>22</i>										<i>22</i>		
Atlantic surface	16.44.674	73.16.283	G	1,602										1,602	
	12 May 1996			<i>187</i>										<i>187</i>	
	Pump			<i>22</i>										<i>22</i>	
	17.40.34	65.26.113	H	263	415		550			61		3,072		4,361	
	1 May 1996			<i>52</i>	<i>52</i>		<i>56</i>			<i>56</i>		<i>22</i>		<i>238</i>	
	M35021			<i>8</i>	<i>10</i>		<i>10</i>			<i>7</i>		<i>5</i>		<i>21</i>	
	17.55.014	65.02.092	I	415	207		279		66			1,919		2,886	
28 April 1996			<i>19</i>	<i>23</i>		<i>86</i>		<i>16</i>			<i>8</i>		<i>152</i>		
M35017			<i>4</i>	<i>10</i>		<i>10</i>		<i>1</i>			<i>2</i>		<i>21</i>		
Granada	17.02.57	65.00.12	J		130		316			1,383		156		1,985	
	2 May 1996				<i>20</i>		<i>68</i>			<i>77</i>		<i>1</i>		<i>166</i>	
	M35024				<i>6</i>		<i>8</i>			<i>12</i>		<i>1</i>		<i>18</i>	
	18.18.1	63.58.08	K	3,184	2,011		61				279	170		5,705	
	25 April 1996			<i>63</i>	<i>101</i>		<i>36</i>				<i>18</i>	<i>3</i>		<i>221</i>	
	M35012			<i>11</i>	<i>11</i>		<i>18</i>				<i>4</i>	<i>3</i>		<i>31</i>	
	19.02.98	63.38.57	L	x	76		x			250		1,936		2,262	
24 April 1996			<i>6</i>	<i>10</i>		<i>27</i>			<i>25</i>		<i>25</i>		<i>93</i>		
M3509/16			<i>2</i>	<i>3</i>		<i>9</i>			<i>7</i>		<i>7</i>		<i>21</i>		
Granada	14.24.792	61.37.684	M										666	666	
	21 April 1996												<i>18</i>	<i>18</i>	
	M35004												<i>5</i>	<i>5</i>	
	16.25.061	62.27.214	N	303			782			3,509				4,594	
	22 April 1996			<i>4</i>			<i>60</i>			<i>125</i>				<i>189</i>	
	M35006			<i>2</i>			<i>14</i>			<i>18</i>				<i>26</i>	
11.45.58	61.25.07	O	242	33,824									34,066		
19 April 1996			<i>300</i>	<i>73</i>									<i>373</i>		
M35001			<i>8</i>	<i>4</i>									<i>6</i>		

<sup>a</sup>Sample depths: first line, abundances (cells l<sup>-1</sup>); second line (italics), specimens counted; third line, species; x, no abundance counts possible; station B (75 m), no cells were identified by SEM but abundance counts were possible by light microscope



comprised about 82% of all those identified in the Caribbean, these being (in order of importance) *E. huxleyi*, *Umbellosphaera irregularis*, *Umbellosphaera tenuis*, *Florisphaera profunda*, *Gladiolithus flabellatus*, *Rhabdosphaera clavigera*, *Syracosphaera pulchra*, and *Gephyrocapsa oceanica*. The most dominant species by far on all the filters observed was *E. huxleyi* (mean = 43%) (Fig. 3).

Because the common approach (cf. below) of counting 300 specimens per station was not possible given the low abundances, our strategy was to combine stations according to the four surface water masses (Granada Basin, Atlantic surface, northern Caribbean surface, and Pedro Bank waters). Here we describe the salient features of the resulting distribution patterns. *E. huxleyi* was found at all depths in this study. It was the most abundant species at nearly all stations, except for the Atlantic surface waters in the lower photic zone. At this location *F. profunda* and *Gladiolithus flabellata* dominated. Highest species richness occurred in the Pedro Bank samples at upper and middle depths. *U. tenuis* and *U. irregularis* were evenly distributed in the upper and middle photic zones at all stations, except for the upper photic zones of the Granada Basin waters where *U. tenuis* was nearly absent (Fig. 3) and replaced by *G. oceanica*. Of interest is the presence of *Calciosolenia murrayi* in middle photic waters throughout the study area, except in those of the northern Caribbean waters, and also various occurrences of *Syracolithus ponticuliferus* in the deeper photic zone of the Atlantic surface waters (cf. not among the top 25 but in the top 30 species).

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## Discussion

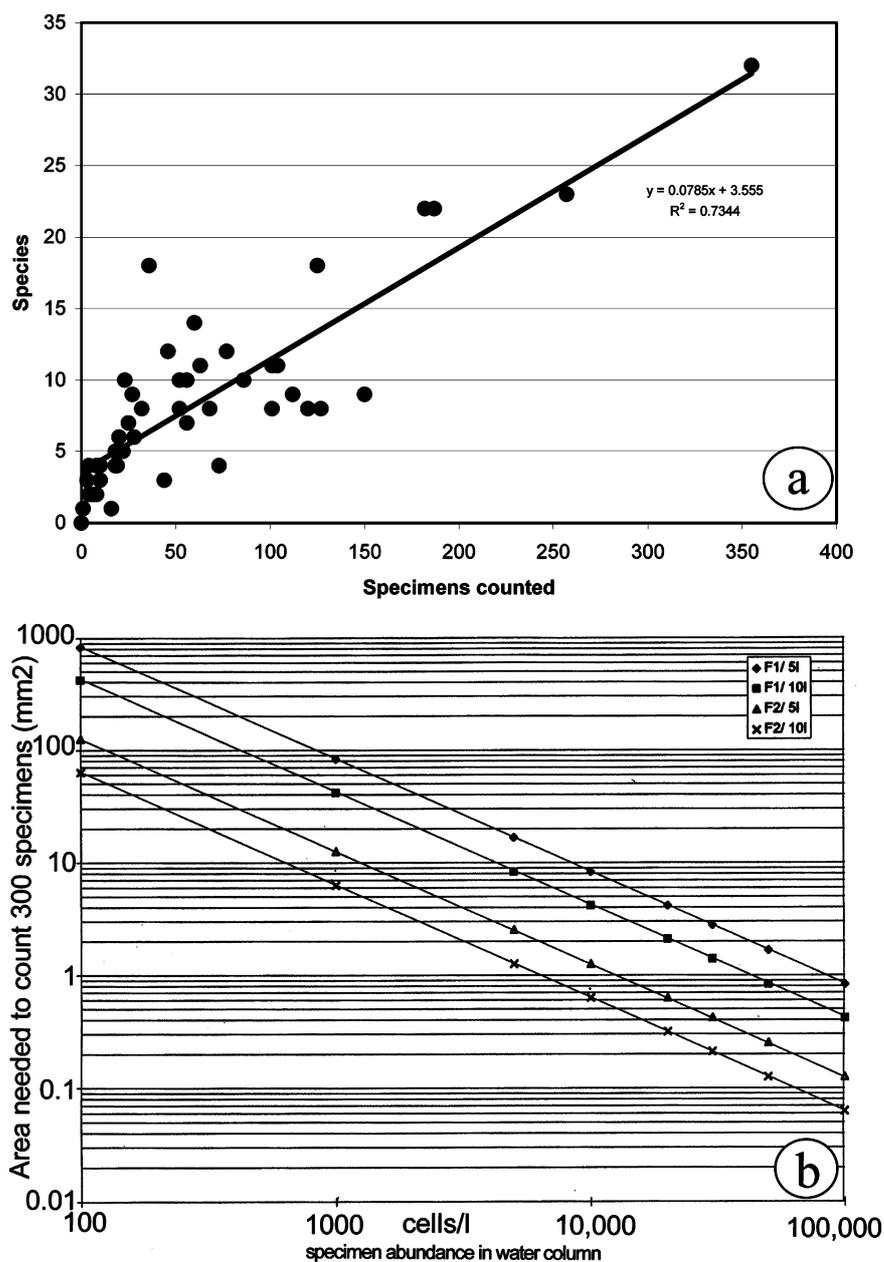
The results of the present study show that average coccolithophore abundance ( $10^3$  cells  $l^{-1}$ ) was fairly low and ranged from 0 to  $10^4$  cells  $l^{-1}$ . These values are representative of coccolithophore abundance in nutrient-poor gyres and oligotrophic seas (Winter et al. 1994). Earlier investigations in the Caribbean Sea (Thronsen 1972; Jordan and Winter 2000) revealed very similar abundance ranges. At some sites in this study coccolithophores were very rare to absent. Other workers have also reported the near-complete absence of coccolithophores in similar settings, for example, the Central North Pacific Gyre and Bermuda (Cortés 1997; Haidar et al. 2000). In fact, productivity has been difficult to measure in subtropical waters because of the highly fluctuating production and dispersion of phytoplankton in oligotrophic waters (Taguchi et al. 1988).

The number of species identified (67; Appendix) is higher than that found by Thronsen (1972) during May in the Caribbean (48 species) but not as high as the 104 taxa identified from January to May 1995 by Jordan and Winter (2000) and Jordan et al. (2000) who

counted 25,000 specimens. The number of species identified per sample in the present study seems clearly to be a near-linear function ( $r^2=0.73$ ) of the total number of specimens per filter counted (Fig. 4a). As is well known, however, the linear function would eventually become asymptotic had enough specimens been counted (Preston 1962), assuming that each station is part of the same community. Counting 300 specimens per sample has become common practice and seems to be the optimal number for a statistically significant representation of the assemblage (Pielou 1966). Counting less than 300 specimens can underestimate species diversity. Nevertheless, when coccolithophore abundances are low, as in the Caribbean Sea, counting 300 specimens on a filter can be very time consuming and may not add substantially to information on diversity. Figure 4b shows that the filter area needed to count 300 specimens is primarily a logarithmic function of specimen abundance in the water column. At abundance levels encountered in this study ( $10^3$  cells  $l^{-1}$ ), using F1 filters (36 mm) and 6 l water, one would need to scan an area of approximately 60 mm<sup>2</sup> to count 300 specimens. Decreasing filter size or increasing the water volume filtered can reduce the filter area required to count 300 specimens by an order of magnitude. Unfortunately, this was not possible for this study because the filters on board were standardized and ocean water was in keen demand by other investigators. In most cases not more than 100 coccolithophore specimens were identified. Using the diversity measurement (Simberloff 1972), it is possible to determine the sample size for any degree of accuracy in estimating species presence. Nevertheless, by counting less than the recommended 300 specimens, the relative percent abundance of the dominant species (usually of most interest) will not change significantly (Kenneth 1982).

In this study, we encountered four oceanic provinces (i.e., Granada Basin waters, Atlantic waters, northern Caribbean waters, and Pedro Bank waters) with differing nutrient and physical parameters. Overall, the distributions of the commonly observed species, *E. huxleyi*, *U. irregularis*, *U. tenuis*, and *F. profunda*, are influenced by the four water masses. The difference in the coccolithophore assemblages between the western (Pedro Bank and northern Caribbean surface waters) and eastern (Atlantic and Granada surface waters) parts of the Caribbean transect is due mainly to the abundance of *E. huxleyi* and *Umbellosphaera* spp. In general, *E. huxleyi* dominated the western stations whereas *Umbellosphaera* spp. were more abundant in the east. This is most likely a result of the higher nutrient levels in the western part and the more open ocean conditions. Because oceanic species like *U. irregularis* do not increase in number during nutrient enrichment (Hulburt 1983), the difference in horizontal distribution seems to be mainly a function of *E. huxleyi*. Under slightly more eutrophic conditions, *E. huxleyi* outcompetes strongly oligotrophic

**Fig. 4 a** Graph showing the relationship between the number of specimens counted and the number of species identified (see text for further discussion). **b** Filter area needed to count 300 specimens vs. specimen abundance for four different scenarios: *circles* 5 l water filtered through an F1 filter (12 mm); *squares* 10 l water filtered through an F1 filter (12 mm), *triangles* 5 l water filtered through an F2 filter (36 mm), *crosses* 10 l water filtered through an F2 filter (36 mm)



umbelliform coccolithophores. In the deeper photic zone, the floriform coccolithophores made up only 40% in the west but clearly predominated (>80%) in the east.

The order of magnitude higher coccolithophore abundances, especially at 25-m water depth (station O) in the Granada waters, were probably due to the influences of increased nutrient supply. These sites in the Granada Basin are under the influence of Orinoco and Amazon river runoff which is enriched in nutrients (Froehlich et al. 1978). The high number of *G. oceanica* (>25%) in the Granada upper photic waters is also evidence of the high nutrient conditions in the Granada Basin. *G. oceanica* has been reported as an upwelling species (see Winter et al. 1994, p. 40 for

references) which blooms at a lower salinity than *E. huxleyi* (Kleijne et al. 1989). In the neritic Gulf of Panama it was also found to be the dominant species (Smayda 1966; Thronsen 1972). In the oligotrophic Caribbean, it has been only rarely observed (Thronsen 1972).

The northern Caribbean surface water assemblages are typical for oligotrophic waters (Okada and Honjo 1975). The close vicinity of the Pedro Bank may be the reason for the high coccolithophore abundances observed in Pedro Bank waters. The shallow Pedro Bank (water depth approx. 20 m) is a source of productivity through upwelling in the upper 120 m of the water column. This is reflected by relatively high chlorophyll-a concentrations at this site (Fig. 2). Compared with

other upwelling regions, however, the coccolithophore abundances at this location are not very high (Winter et al. 1994).

The deep photic zone is populated mainly by floriform coccolithophores which live within or below the thermocline under low light and temperature conditions. High abundances of coccolithophores were found directly below the deep chlorophyll maximum (DCM), consisting mainly of *F. profunda* and *G. flabellatus*. It is usually not recognized that substantial biomass production occurs in deeper waters, especially in models which rely on satellite image analysis. In eutrophic waters light attenuation is low mostly due to the high abundance of plankton and aggregates in the shallow mixed layer. The autotrophic community in eutrophic waters is limited to the mixed layer, unlike oligotrophic communities where photosynthetically available radiation is available for photosynthesis at greater depths.

These floriform coccolithophores are unique in that they are adapted to the high nitrate and low light levels (Cortés 1997) associated with the deeper photic zone below the DCM. This also means they do not have to compete with the DCM flora. Their coccoliths seem to be especially arranged to take advantage of the high refractive index of calcite by forming an inverted bowl which refracts light into the cell (Gartner and Bukry 1969), and their coccospheres are particularly large relative to the cell size. In addition, floriform coccolithophores probably are motile (Young 1994), which may allow them to move vertically in the water in search of optimal depth light/nutrient conditions. It is interesting in this regard to note that in a study of primary productivity in the Caribbean, Taguchi et al. (1988) found that most  $^{14}\text{C}$  uptake occurred at the chlorophyll maximum and at night time, which may be a result of heterotrophy at these depths.

Exclusive surface monitoring of phytoplankton will result in underestimation of coccolithophore abundances in the photic zone. Although light is obviously a limiting factor for coccolithophores within the water column, the absolute lower limit where coccolithophores live in the water column is unknown and needs to be investigated further. In warm oligotrophic waters the nutrient-level is usually the limiting factor for plankton (Brand 1994). In tropical sediments *Florisphaera* specimens are often difficult to detect but constitute the greatest percentage of coccoliths (e.g., Okada 1983; Molino and McIntyre 1990; Tanaka 1991).

The vertical distribution of coccolithophores in the Caribbean in this study seems to be typical for tropical-subtropical regions (Okada and Honjo 1973). In the upper and middle photic zones placolith-bearing and umbelliform coccolithophores dominate. Usually *E. huxleyi* is the most important species, followed by *U. irregularis* and *U. tenuis*. *E. huxleyi* seems to thrive at high light levels (Nanninga and

Tyrrell 1996) because it has a lack of photoinhibition at intensive light levels (up to at least  $1,000 \text{ Ein m}^{-2} \text{ s}^{-1}$ ). Furthermore, there is an enhanced level of photoadaptation (Lewis et al. 1984), and *E. huxleyi* also has an exceptionally high P uptake rate (Riegman et al. 2000). *Umbellosphaera* spp. are well adapted to oligotrophic, nutrient-depleted waters and are usually found in subtropical latitudes ( $10\text{--}30^\circ\text{N}$ ) between 0- and 100-m depths (Okada and Honjo 1973). Their absence in high-latitude, oligotrophic waters implies that they tolerate neither low temperatures nor low light levels (Young 1994, p. 75). This may be the reason for their minor role in the deep photic assemblage. Our results concur with the coccolithophore ecology and functional morphology strategy developed by Brand (1994), Young (1994), and Winter et al. (1994). This approach suggests that coccolithophore distribution is basically controlled by water masses, and species-specific r-K strategies whereby K-selected species, such as *Umbellosphaera*, easily adapt to stable but difficult environments whereas r-selected species, such as *E. huxleyi*, can rapidly exploit resources. In the deep photic zone the floriform coccolithophores dominate because of the special adaptations mentioned above.

Up to now there are about 200 species of heterococcolithophore and holococcolithophore species described (Jordan and Green 1994; Jordan et al. 2000). There is increasing evidence, however, that at least some holococcolithophore taxa are life-cycle stages – perhaps the haploid stage – of heterococcolithophore taxa (Cros et al. 2000). This will reduce the number of valid taxa. Consistent with the findings of Young (1994), we observed high abundances (20% of the assemblage) of the holococcolithophore *S. ponticuliferus* in the deep surface waters of the Atlantic, together with floriform species. Perhaps this species is a life-cycle stage of a common heterococcolithophore? Cros et al. (2000) showed (1) that *Syracolithus catilliferus* is a life-cycle stage of *Helicosphaera carteri*, and (2) that *S. catilliferus* and *Syracolithus confusus* are variants of the same species. The very similar “species” *Syracolithus dalmaticus* and *Syracolithus schilleri* are very probably also produced by *Helicosphaera*. Conversely, *Syracolithus quadriperforatus*, *Syracolithus bicorium* and *Syracolithus* sp. B (Kleijne) are all very different (two-layered wall structure with totally different crystallographic orientation). As *S. ponticuliferus* shows the same structure as *S. catilliferus*, it is reasonable to assume that it is formed either by a *Helicosphaera* sp. or (if somewhat different) maybe by *Pontosphaera/Scyphosphaera*.

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## Conclusions

The coccolithophore abundance in the Caribbean is low and varies in the range  $0\text{--}10^4 \text{ cells l}^{-1}$ . In all, 67 species were identified of which four are dominant: *E.*

*huxleyi*, *U. irregularis*, *U. tenuis*, and *F. profunda*. These species are typical for oligotrophic waters. Significant information on the relative percent abundance of dominant species can be obtained by counting less than 300 specimens per sample. This reduces the need to scan large filter areas for samples taken in oligotrophic areas with low standing stocks of coccolithophores. The coccolithophore assemblages in the four oceanographic provinces differ in their species composition and abundance, and the dominant species. There is a relatively high abundance of coccolithophores in the lower photic zone, and total absence of coccolithophores at some locations. This pattern needs to be considered in models of ocean carbon budgets and ground-truthing of satellite-derived data. *F. profunda* occurs just below the deep chlorophyll-a maximum at the top of the nitrate nutricline.

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## Appendix

Species list according to Jordan and Kleijne (1994) except where references are given

*Acanthoica quattrosipina* Lohmann  
*Algirosphaera oryza* Schlauder  
*Algirosphaera robusta* (Lohmann) Norris  
*Alisphaera unicornis* Okada and McIntyre  
*Anacanthoica acanthos* (Schiller) Deflandre  
*Anacanthoica cidaris* (Schlauder) Kleijne  
*Calcidiscus leptoporus* (Murray & Blackman) Loeblich and Tappan  
*Calciopappus caudatus* Gaarder and Ramsfjell  
*Calciosolenia murrayi* Gran  
*Calyptrolithina multipora* (Gaarder) Norris  
*Calyptrosphaera oblonga* Lohmann  
*Ceratolithus cristatus* Kamptner  
*Corisphaera* sp. type A (in Kleijne 1961)  
*Corisphaera gracilis* Kamptner  
*Corisphaera tyrrheniensis* Kleijne  
*Coronosphaera binodata* (Kamptner) Gaarder  
*Coronosphaera mediterranea* (Lohmann) Gaarder  
*Daktylethra pirus* (Kamptner) Norris  
*Discosphaera tubifera* (Murray & Blackman) Ostefeld  
*Emiliania huxleyi* (Lohmann) Hay & Mohler  
*Florisphaera profunda* Okada & Honjo var. *profunda*  
*Flosculosphaera calceolariopsis* Jordan & Kleijne  
*Gephyrocapsa muelleriae* Bréhéret  
*Gephyrocapsa oceanica* Kamptner

*Gladiolithus flabellatus* (Halldal & Markali) Jordan and Chamberlain (1993)

*Gliscolithus amitakareniae* Norris

*Hayaster perplexus* (Bramlette & Riedel) Bukry

*Helicosphaera pavementum* Okada & McIntyre

*Helicosphaera carteri* (Wallich) Kamptner var. *carteri*

*Helladosphaera cornifera* (Schiller) Kamptner

*Homozygosphaera triarcha* Halldal & Markali

*Homozygosphaera arethusae* (Kamptner) Kleijne

*Michaelsarsia adriaticus* (Schiller) Manton et al.

*Michaelsarsia elegans* Gran emend. Manton et al.

*Neosphaera coccolithomorpha* Lecal-Schlauder

*Ophiaster hydroideus* (Lohmann) Lohmann emend. Manton & Oates

*Ophiaster reductus* Manton & Oates

*Periphylophora mirabilis* (Schiller) Kamptner

*Poricalyptra isselii* (Borsetti & Cati) Kleijne

*Poritectolithus maximus* Kleijne

*Poritectolithus poritectus* (Heimdal) Kleijne

*Rhabdosphaera clavigera* Murray & Blackman var. *clavigera*

*Rhabdosphaera xiphos* (Deflandre & Fert) Norris

*Syracolithus catilliferus* (Kamptner) Deflandre

*Syracolithus ponticuliferus* (Kamptner) Kleijne & Jordan

*Syracolithus quadriperforatus* (Kamptner) Gaarder

*Syracolithus schilleri* (Kamptner) Loeblich and Tappan

*Syracosphaera anthos* (Lohmann) Jordan and Young

*Syracosphaera corolla* Lecal

*Syracosphaera corrugis* Okada & McIntyre

*Syracosphaera epigrosa* Okada & McIntyre

*Syracosphaera exigua* Okada & McIntyre

*Syracosphaera halldalii* Gaarder

*Syracosphaera lamina* Lecal-Schlauder

*Syracosphaera molischii* Schiller

*Syracosphaera nodosa* Kamptner

*Syracosphaera orbiculus* Okada & McIntyre

*Syracosphaera ossa* (Lecal) Loeblich and Tappan

*Syracosphaera pirus* Halldal and Markali

*Syracosphaera prolongata* Gran ex Lohmann

*Syracosphaera pulchra* Lohmann

*Syracosphaera rotula* Okada & McIntyre

*Umbellosphaera irregularis* Paasche

*Umbellosphaera tenuis* (Kamptner) Paasche

*Umbilicosphaera hulburtiana* Gaarder

*Umbilicosphaera sibogae* var. *foliosa* (Kamptner) Okada & McIntyre

*Zygosphaera hellenica* Kamptner

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