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Biological and optical properties of mesoscale coccolithophore blooms in the Gulf of Maine

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Abstract

Two coccolithophore blooms in the Gulf of Maine were studied in 1988 and 1989. Each bloom was about 50,000 km^2 in area and confined to the top 20 m of the water column. Maximal cell concentrations were ~2,000 cells ml^{-1} and coccolith densities of 3×10^5 ml^{-1} were observed. The coccolith : cell ratio was highest in the bloom center (region of most intense reflectance) and lowest at the bloom periphery, an indication of varying organic vs. inorganic C production. Chlorophyll concentrations were generally low within the bloom and no relation could be observed between major nutrients and coccolithophore abundance. Backscattered light was profoundly affected by coccolith density and was slightly wavelength-dependent. We calculated total backscattering as well as backscattering (b_b) caused exclusively by coccoliths and derived the algorithm relating coccolith density to backscattering. Although cells were efficient light absorbers, coccoliths showed negligible light absorption. Diffuse attenuation was lowest in the green and blue-green part of the visible spectrum. At the center of the bloom, coccoliths contributed >75% of the backscattering signal and >50% of the beam attenuation signal. The most accurate way to estimate coccolith concentrations via remote sensing is to measure water-leaving radiance in the green wavebands.

The coccolithophore *Emiliania huxleyi* (Lohm) Hay et al. Mohler (class Prymnesiophyceae) is thought to be the most abundant calcifying organism on earth (Westbroek et al. 1985). Of all coccolithophore species, *E. huxleyi* is numerically dominant and can be found from tropical to subarctic regions of the Atlantic, extending into waters with temperatures <0°C off Spitsbergen. Furthermore it is the only coccolithophore species that is regularly abundant in neritic, continental shelf seas including the Gulf of Maine (Marshall 1984). The distributions of this species and others in the surface waters tend to match those in the sed-

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iments. Studies on the growth of a large number of clones of *E. huxleyi* indicate that populations from different water masses are genetically distinct (Brand 1982).

Ecological studies have shown that coccolithophores succeed diatoms in response to increasing stabilization and nutrient depletion of surface waters (Margalef 1978). Nitrate or silicate limitation appears to induce the replacement of diatoms by coccolithophores, and for this reason biomass (as Chl *a*) is typically low within coccolithophore blooms (Holligan et al. 1983; Balch et al. 1989). The slowing of diatom growth in subpolar regions may be induced by iron deficiency. This deficiency may also favor coccolithophores, which are known to maintain high growth rates in low-iron media (Brand et al. 1983).

The occurrence of coccolithophore blooms in the oceans has long been recognized as the main cause of "white-water" conditions (Brongersma-Saunders 1957). It is only with the availability of satellite visible-band images from LANDSAT, the CZCS (Coastal Zone Color Scanner), and the AVHRR (Advanced Very High Resolution Radiometer), however, that the scale and frequency of the blooms have been recognized (Holligan et al. 1983). In the temperate and subarctic regions of the North Atlantic extensive areas of high reflectivity (up to 25% of the light penetrating the sea surface) are seen each summer in both the open ocean and coastal or upwelling waters including the Gulf of Maine. Similar features have been observed off Nova Scotia, Chesapeake Bay, California, Japan, Argentina, and within North Atlantic warm-core rings.

The main cause of the high reflectance has been suggested, both on observational and theoretical grounds, to be backscattering by detached coccoliths as opposed to whole cells (Holligan et al. 1983; Bricaud and Morel 1986; Balch et al. 1989). In cases where water samples have been collected (NW European shelf, NE Atlantic, Gulf of Maine), the populations have been dominated by *E. huxleyi,* with cell and coccolith densities in the ranges 10^3–10^4 and 10^4–10^5 ml^{-1}, respectively. Other species have not been shown to produce such large numbers of detached plates under natural conditions, so that the features observed on satellite images are most likely attributable to *E. huxleyi.*

Apart from inherent ecological interest in the development and fate of large-scale, monospecific populations of phytoplankton, recent attention on the coccolithophores has focused on their role in global biogeochemical cycles. Coccolithophores represent a major component of pelagic calcareous sediments in world oceans. Such sediments are widely distributed in the North Atlantic where water depth is less than the lysocline depth for calcite (~4,600 m). The most abundant species in all recent deposits is *E. huxleyi,* especially at higher latitudes where warm-water species are absent. Studies with sediment traps have also demonstrated the importance of coccolithophores such as *E. huxleyi* in the downward flux of particulate biogenic material in the oceans (Honjo 1976).

Methods

The first survey was performed aboard the RV *Argo Maine* from 6 to 12 July 1988. The station grid was based on historical and real-time satellite imagery from the AVHRR aboard the NOAA-9 satellite. The technique of Groom and Holligan (1987) was used to process images. The ship survey consisted of 10 stations inside and outside the bloom. Chlorophyll concentrations were measured on GF/F filters according to Yentsch and Menzel (1963). Chlorophyll *c* was present, so calculation of pheopigments was problematic. Therefore, measurements were made with both 440- and 405-nm excitation (the latter allowing for correction of the pheopigment value; C. Yentsch and D. Phinney pers. comm.). Cell-count samples were preserved with both buffered Formalin and Lugol's iodine (5% by volume) and settled once ashore. Species enumeration was performed with an inverted microscope.

At each station, measurements were made of down and upwelling irradiance (E_d and E_u) at 440, 520, 550, and 680 nm with the irradiance meter described by Phinney and Yentsch (1991). Irradiance reflectance was calculated as the ratio of E_u:E_d. Diffuse attenuation (K_λ) was calculated as the nega-

tive slope of natural log-transformed irradiance vs. depth. Optical transmittance of particulate material on Whatman GF/F glass-fiber filters was measured continuously between 400 and 700 nm with the technique of Yentsch and Truper (1967). In situ beam attenuation was measured with a Sea Tech transmissometer (660 nm). Satellite-derived reflectance was calculated from AVHRR data according to Groom and Holligan (1987).

The second survey was carried out between 20 and 25 June 1989 aboard the RV *Argo Maine*. Chlorophyll and cell counts were performed as before (except that pheopigment values were slightly overestimated as no corrections for Chl *c* were made). Cell counts were performed on the ship with an Olympus BH2 epifluorescence microscope equipped with 490-nm excitation filter, 515-nm barrier filter, and 590-nm dichroic filter for Chl *a* fluorescence and 545-nm excitation, 590-nm barrier, and 580-nm dichroic filters for biliprotein fluorescence. Epifluorescence allowed enumeration of Chl-containing cells, and a polarizing filter was used to enumerate coccoliths. Replicate samples were also preserved with buffered Formalin and Lugol's solution for settling and enumeration ashore as described above. Samples for nutrient analyses were frozen at each station. Nitrate and nitrite, reactive phosphorus, and silicate were measured with a customized continuous-flow system derived from Whitledge et al. (1981).

Several optical measurements were made to assess the importance of coccoliths and associated cells to the optical properties of the water. The absorption of particulate material on glass-fiber filters was performed as described above. A Brice-Phoenix light scattering photometer (model 2000) was used to measure the volume scattering function of water samples at 436 and 546 nm for 0, 45, 90, and 135°. These data were then incorporated into the model of Gordon (1976) to calculate backscattering, b_b. Bubbling with CO_2 for 30 s dissolves the coccoliths present in the sample (Paasche 1962). Measurements of volume scattering function were performed before and after bubbling and the backscattering due to coccoliths (b_b') was calculated as the difference between unbubbled seawater (total b_b) and bubbled seawater (b_b due to noncalcite particles). The pH of the sample decreased to ~5.0 following the CO_2 bubbling, and microscopic examination revealed that the cells were still intact.

Attenuation of light through seawater as a function of wavelength was measured onboard ship with a modified Beckman DU-2 scanning spectrophotometer. The device was modified to accept a 50-cm quartz cuvette with 7.5-mm entrance window. The light beam had a divergence of <3°. The field of view of the detector was restricted to the end of the cuvette by a mask around the cuvette. We performed scans from 400 to 700 nm before and after bubbling with CO_2 to evaluate the attenuation due to coccoliths. Besides the shipboard attenuation measurements, we also measured in situ beam attenuation with a Sea Tech transmissometer (660 nm) and a spectral transmissometer (440, 490, 520, 550, and 670 nm) described by Petzold and Austin (1968). A Biospherical Instruments MER-1032 was used to measure downwelling irradiance (410, 441, 488, 532, 550, 589, 633, 656, 671, and 694 nm), upwelling irradiance (410, 441, 488, 520, 589, 633, and 671 nm), upwelling radiance (410, 441, 488, 520, 550, 589, 710 nm), scalar irradiance (PAR), and upwelling natural fluorescence. Irradiance reflectance was calculated from the MER-1032 data as the ratio of upwelled radiance to downwelled irradiance. Volume scattering phase functions were measured in situ at five wavelengths (440, 490, 520, 610, and 670 nm) with the general angle scattering meter (GASM; Petzold 1972). Measurements of volume scattering were made continuously from 10° to 170°. Satellite-derived reflectance was calculated as previously described.

Results

Field data—Dense blooms of coccolithophores were observed in the 1988 and 1989 field seasons. (Figs. 1A and 2A). In both cases, high-reflectance water covered much of Wilkinson Basin, extending around the northern flank of Georges Bank through the northeast channel (south of Browns Bank), then south along the eastern side of Georges

Bank. The 1988 bloom was slightly larger than the 1989 bloom, although both covered ~50,000 km^2.

There was pronounced hydrographic variability in the Gulf of Maine during the blooms (Figs. 1B and 2B). During the 1989 event, vertical temperature profiles from north of the bloom (station 9) were characterized by 11°C surface water, with a steep 3° thermocline at 10 m followed by a decrease of 1°C down to 75 m, where another thermocline was observed. Within the bloom, the surface mixed layer was at 14°C and 10 m deep, with a gradual decrease in temperature to 6.5°C at 40 m where a pronounced thermocline was encountered. Below this thermocline, the water was isothermal at ~4.5°C to 110 m.

Surface gradients of temperature and beam attenuation at 660 nm for the transects between Georges Bank and Boothbay Harbor in 1988 and 1989 (Fig. 3) showed the colder, well-mixed waters of Georges Bank and the warmer waters over Wilkinson basin. Higher values of beam attenuation were associated with the warmer waters in the middle of the basin.

During blooms in both years surface chlorophyll concentrations were usually 0.5–1.0 μg liter^{-1} within the bloom and higher outside of it (Figs. 4 and 5). Coccolith concentrations approached 0.75–3.0 $\times$ 10^5 ml^{-1}, and cell concentrations were typically 1,000–2,000 ml^{-1}. (Note that the counts of coccoliths were quite different between 1988 and 1989. This difference was probably real because the coccoliths are easy to count under polarized light and preservation techniques were identical.) It is readily apparent (Figs. 6 and 7) that *E. huxleyi* was confined to the top 20 m of the water column and that beam attenuation and coccolith concentrations covaried.

Nutrient concentrations were always low within the coccolithophore bloom. Nitrate was detectable at ~0.2–0.4 μM in the top 15 m (Fig. 7B). Silicate was at concentrations of 0.3–0.5 μM. A clear subsurface NH_4^+ peak was observed between 20 and 50 m; NO_2^- remained low or undetectable.

Optical features—The blooms markedly altered the photic regime of these waters, in particular, beam attenuation was very high (Table 1). Diffuse attenuation was least in the blue-green and green portions of the visible spectrum. Values of in situ beam attenuation in the blue-green approached 2 m^{-1} during the 1989 cruise. Spectral reflectance values were also high, especially in the blue-green wavelengths. Reflectance values of 7 and 39% were observed at these two stations.

The spectrophotometer measurement of attenuation (with a 50-cm cuvette) was also somewhat wavelength-dependent for raw seawater suspensions, higher in the blue than the green part of the spectrum. Attenuation due to just coccoliths (C_c; calculated as a difference spectrum) was highest in the blue and often represented over half of the total attenuation in the visible part of the spectrum (Fig. 8). For the deeper samples where no coccoliths were observed, there was no difference in attenuation before and after bubbling with CO_2. These shipboard attenuation estimates (made with a spectrophotometer) were ~40% lower than the in situ attenuation values from the spectral beam transmissometer at comparable wavelengths. Probable sources of error in this measurement include internal reflections from the cuvette wall, acceptance of light piped down the cuvette wall, and acceptance of multiply scattered light. Nevertheless, these results are valuable as qualitative measures of the importance of coccoliths on the beam attenuation of the samples.

This change could have been due to either absorption or scattering by the coccoliths. To examine coccolith absorption, we filtered seawater suspensions onto glass-fiber filters before or after dissolving the coccoliths. Particulate absorption was not affected by their presence (Fig. 9). Spectral scans of light transmittance through a glass-fiber filter containing bloom particulate material showed typical absorption profiles of coccolithophores (Haxo 1985): pronounced Chl *a* absorption at 440 nm with a broad shoulder at 465 nm due to accessory pigments and a peak at 674 nm due to Chl *a*. The spectral scan of transmittance was identical for samples without coccoliths.

Light scattering was most likely the cause of the high beam attenuation and diffuse attenuation coefficients in the bloom (as de-

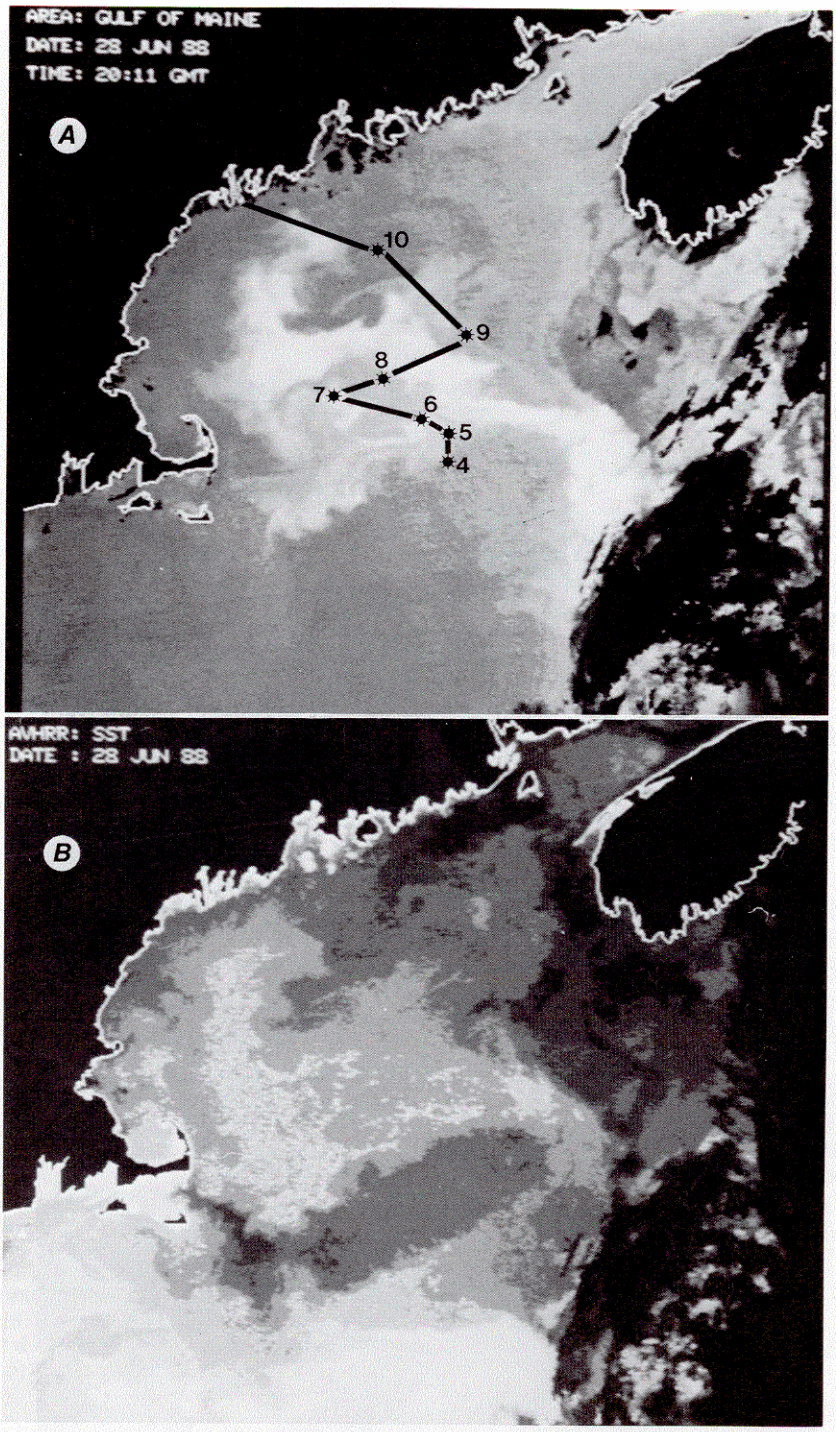

Fig. 1. A. NOAA-9 AVHRR image of bloom of *Emiliania huxleyi* in the Gulf of Maine, 28 June 1988. This image was processed according to Grooms and Holligan (1987). The center of the bloom was at ~43°N, 68°W. Reflectance values were measured from the ship at the designated location and were ~7% at 520 nm (*see Table 1*). The ship track is also shown. B. Surface temperature image for the same overpass shown in panel A. Dark areas represent cold water.

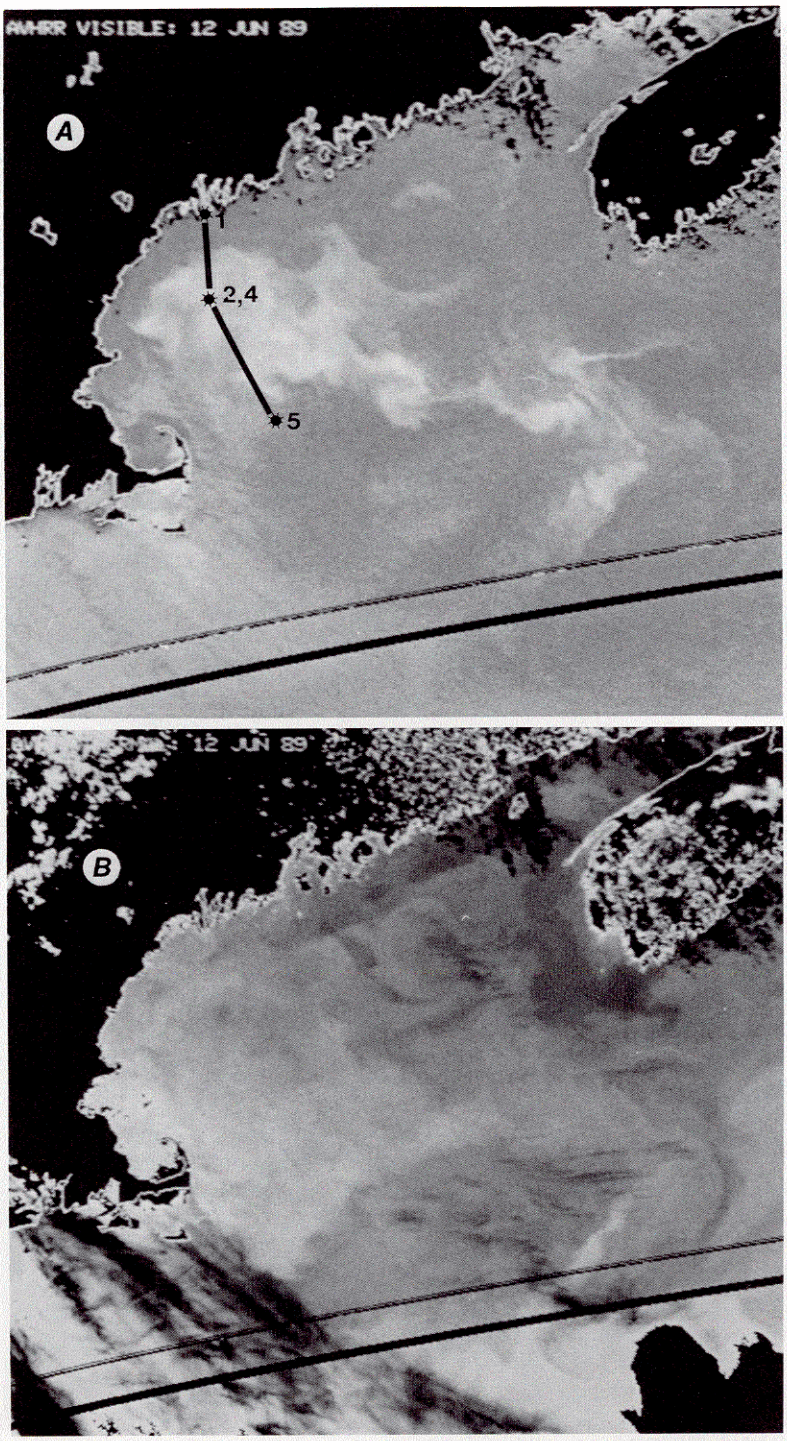

Fig. 2. A. NOAA-9 AVHRR image, 12 June 1989, processed as in Fig. 1, showing a high-reflectance coccolithophore bloom. This bloom penetrated farther into Massachusetts Bay than the 1988 bloom. Note sharp fronts between the stratified waters of the bloom and mixed waters north of it. Reflectance values at the designated location were ~38% at 520 nm (*see Table 1*). The ship track is shown on this image, with station numbers indicated. B. Surface temperature image for the same overpass shown in panel A. Dark areas represent cold water.

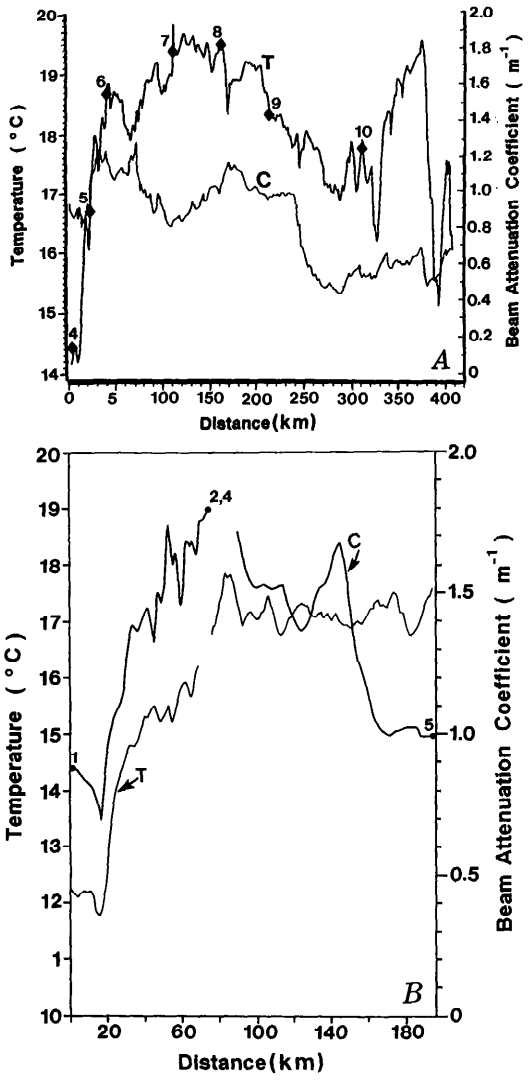

Fig. 3. Surface transects of temperature (T) and beam attenuation (c, 660 nm) for the cruise tracks through Wilkinson Basin. A. July 1988 transect crossed the coccolithophore bloom midway across the basin (observed as dramatic increases in beam attenuation along with warmer water). The ship track is shown in Fig. 1A. B. Same as in panel A except that this transect was made in 1989 and was along the western edge of Wilkinson Basin. First leg of transect (between stations 1 and 2) was 2 d earlier than the second leg (between stations 4 and 5). The ship track is shown in Fig. 2A.

rived from shipboard and in situ measurements). About 80% of the backscattered light was due to coccoliths, with the remaining scattering due to *E. huxleyi* cells, other particulate matter, and water (Fig. 10B, C). Total backscattered light (b_b) was slightly wavelength-dependent for *E. huxleyi*-coccolith suspensions (Fig. 10A) as well as just coccolith suspensions (b_b'; data not shown). The values of b_b were typically 1.2 times higher at 436 nm than at 546, while coccolith light scattering, b_b', was 1.4 times higher at 436 nm than at 546. Coccolith backscattering in the blue and green increased approximately linearly with coccolith concentration up to ~150,000 coccoliths ml^{-1}. A second-order polynomial was fitted to these data (Fig. 11A, B: $Y = 3.24 \times 10^{-3} + 1.41 \times 10 \times^{-7} X - 5.27 \times 10^{-14} X^2$ at 436 nm, $r^2 = 0.85$; $Y = 1.28 \times 10^{-3} + 1.29 \times 10^{-7} X - 8.41 \times 10^{-14} X^2$ at 546 nm, $r^2 = 0.85$).

The scattering function, when normalized to one at 90°, had a characteristic shape independent of wavelength for all the measurements in the bloom. This measured scattering function is compared in Fig. 12 with that of Petzold's (1972) turbid-water scattering function. The shapes of these scattering functions are similar with the coccolithophore function being even more featureless in the backward direction (scattering angle >90°).

Discussion

The satellite images (Figs. 1, 2) depict mesoscale features on comparable size scales to the blooms previously observed by Holligan et al. (1983) in the Celtic Sea. These images also suggest that the blooms are occurring in stratified water in the Gulf of Maine, where surface temperatures are between 14° and 17°C. The inshore boundaries of the 1988 and 1989 blooms abruptly ended near the 100-m isobath, possibly at the boundary between tidally mixed and stratified waters. A more complete series of images (Ackleson et al. 1988) showed that the high-reflectance feature was detectable for ~2–3 weeks.

The chlorophyll distributions shown in Figs. 4 and 5 suggest that the term "bloom" is somewhat of a misnomer for the coccolithophore populations in the Gulf of Maine. Although the presence of *E. huxleyi* discolored the surface waters, the areas of highest abundance had surface chlorophyll concentrations of only 0.5–0.8 mg m^{-3}. A C:Chl

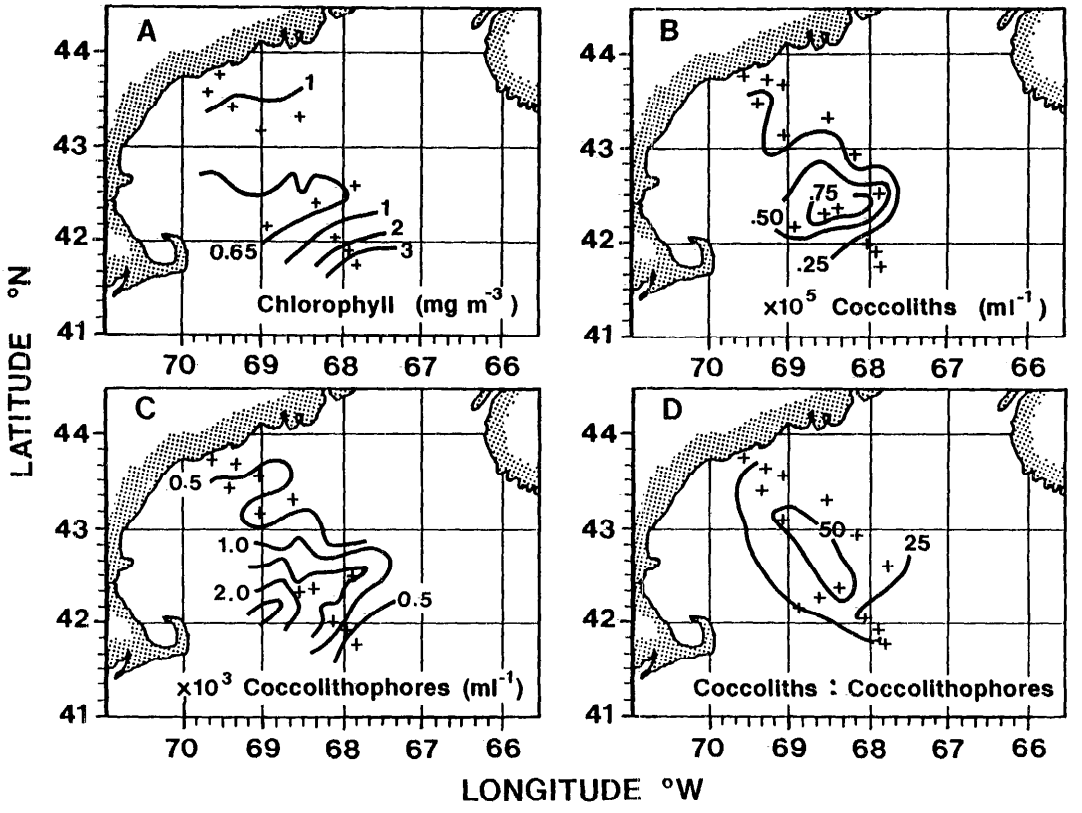

Fig. 4. A. Map of the Gulf of Maine showing contours of Chl *a* within the coccolithophore bloom of 1988. Station locations—+. B. Contours of coccolith concentration. C. Contours of coccolithophore cell concentration. D. Contours of the ratio of detached coccoliths per coccolithophore.

ratio of 50 would suggest that particulate biomass attributable to coccolithophores was only 25–40 μg C liter^{-1}—low for this region. Chlorophyll concentrations were up to 10 times higher outside the bloom in the tidally mixed coastal waters to the north and over Georges Bank. Moreover, cell concentrations rarely exceeded 2,000 cells ml^{-1}, which—using the volume–carbon conversion of Strathmann (1967)—represents an equally low C-specific biomass. The pigment and cell count data demonstrated an important aspect of coccolithophores: at very low concentrations or biomass, they can alter markedly the optical properties of the surface ocean by producing coccoliths.

The ratios of coccoliths to coccolithophores were highest in the center of the bloom and lowest at its periphery. Further, the areas where cell concentrations were highest were not the areas where coccoliths were most abundant. These results suggest that the areas of high reflectance observed by the satellite were the older parts of the bloom where the cells were not actively growing. That is, they were directing more of their C budgets into calcite than organic growth while the regions near the bloom edge were directing more C into organic growth than calcite. In both years, *E. huxleyi* abundance was highest at the southern edge of the bloom near Massachusetts Bay.

The amount of C as calcite in this coccolithophore bloom can be estimated from the satellite images together with the coccolith counts. If we assume a bloom area of 50,000 km^2, a bloom depth of 20 m, an average coccolith concentration of 2.5 × 10^5 coccoliths ml^{-1}, and an average weight of C per coccolith of 2.0 pg (Paasche 1962), the calcite C of the bloom represented 50,000 t.

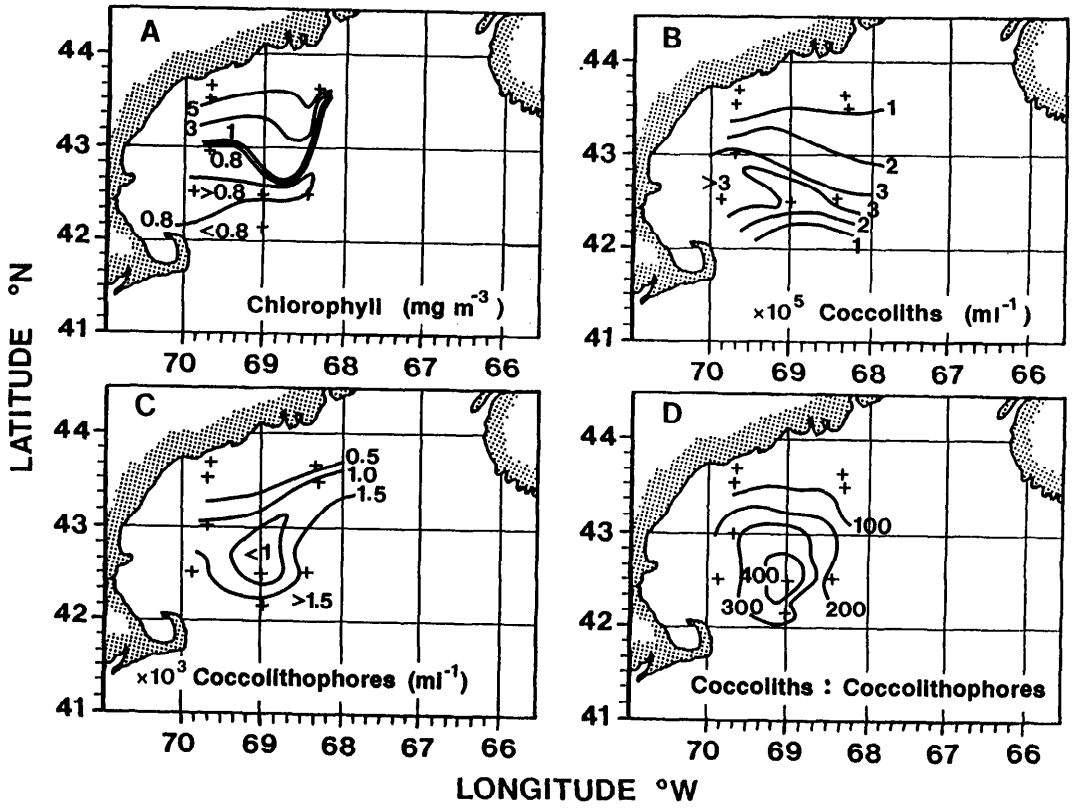

Fig. 5. As Fig. 4, but for 1989 coccolithophore bloom.

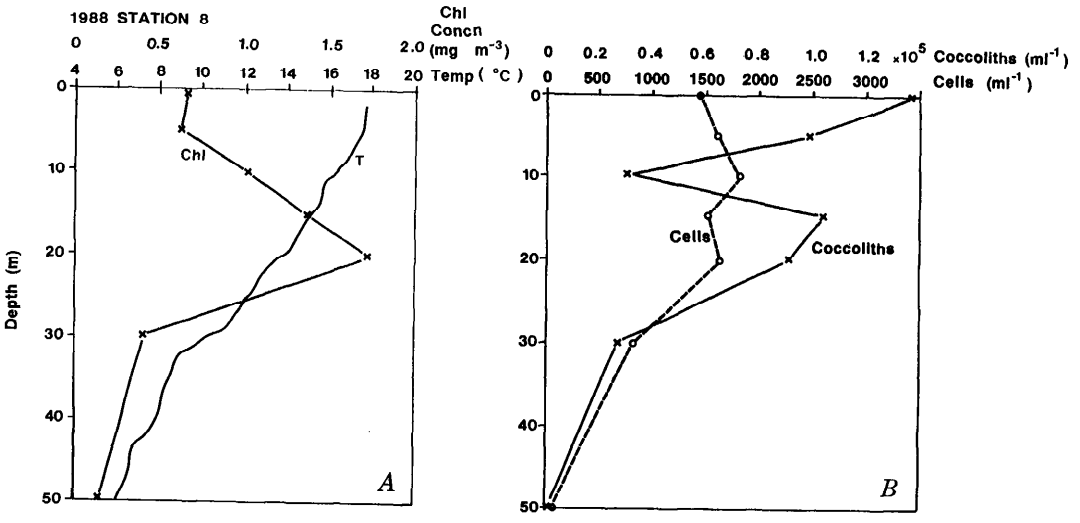

Fig. 6. A. Vertical profiles of temperature (T) and chlorophyll at station 8 from the 1988 cruise. B. Vertical profiles of coccolithophore and coccolith concentration at the same station.

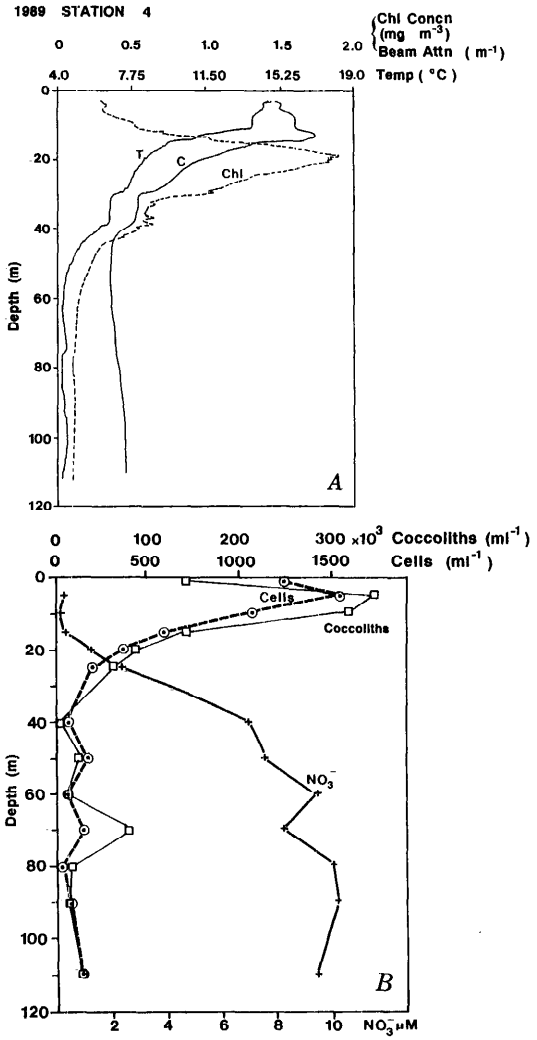

Fig. 7. Vertical profiles for station 4 during the 1989 cruise. Same parameters shown as in Fig. 6 except that beam attenuation (*c*, 660 nm) is also shown in panel A and nitrate concentration is also shown in panel B.

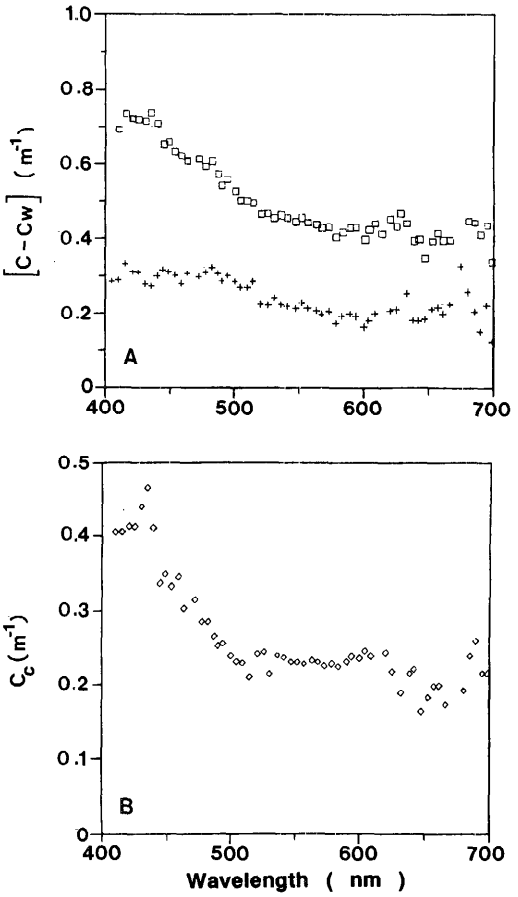

Fig. 8. A. Attenuation by suspended material (with water attenuation subtracted out) as a function of wavelength at station 10 at 15 m (1989 bloom). Cell concentration was 6.68×10^2 cells ml^{-1}; coccolith concentration was 1.51×10^5 ml^{-1}. *See text for details of measurement.* Upper symbols represent attenuation by raw seawater. Lower symbols represent attenuation by same sample following dissolution of coccoliths by bubbling with CO_2. B. Difference spectrum between two measurements shown in panel A, which represents attenuation due to coccoliths (C_c).

There was not a tight relationship between either coccolith or coccolithophore abundance and nutrient concentrations. It can be said only that coccolith concentrations were inversely related to ammonium, nitrate, nitrite, phosphate, and silicate concentrations (similar to the observations of Bauman et al. 1978, except they discussed only nitrogenous nutrients). The nutrient that explained the most variance in the coccolith distribution was phosphate. At concentrations >0.5 µM phosphate, coccolith concentrations never exceeded 50,000 cells ml^{-1}. Perhaps calcification rates were inhibited at high phosphate concentrations. No relation could be observed, however, between coccolith : cell ratios as a function of either absolute nutrient concentrations or ratios of the major nutrients measured here. Paasche (1968 and reference therein) suggested that coccolithophores can utilize dissolved organic N in lieu of inorganic N sources, which might explain their ability

Table 1. Typical optical parameters measured at two stations during 1988 and 1989 coccolithophore blooms in the Gulf of Maine. These parameters include the diffuse downwelling irradiance attenuation coefficient (K_λ; m^{-1}), in situ beam attenuation (c_λ; m^{-1}) in-water irradiance reflectance (R_λ), satellite-derived irradiance reflectance (R_λ satellite), particulate absorption ($a_{p\lambda}$; m^{-1}) and backscattering ($b_{b\lambda}$; m^{-1}). Chlorophyll *a* concentrations at these depths were 1.0 and 0.96 μg liter^{-1} for stations 8 and 4. The cell and coccolith counts were 1,798 cells ml^{-1} and 1.29×10^5 coccoliths ml^{-1} for station 8 at 10 m and 1,070 cells ml^{-1} and 3.19×10^5 coccoliths ml^{-1} for station 4 at 10 m.

	Wavelength (nm)							
	410	440	490	520	550	589	633	671
				Station 8, 1988				
K_λ (10 m)		0.321		0.241	0.236*			0.544
c_λ (10 m)								1.0†
R_λ (0 m)		0.051		0.069	0.067			0.009
R_λ satellite (0 m)							0.016‡	
$a_{p\lambda}$ (10 m)	0.097	0.101	0.072§	0.036	0.021	0.016	0.014	0.032
				Station 4, 1989				
K_λ (10 m)	0.356	0.310	0.232	0.211	0.206	0.260	0.459	0.472
c_λ (10 m)			2.09		1.93			
R_λ (0 m)	0.225	0.268	0.389	0.376	0.328			
R_λ satellite (0 m)							0.010‡	
$a_{p\lambda}$ (10 m)	0.159	0.171	0.107	0.056	0.034	0.023	0.027	0.058†
$b_{b\lambda}$ (10 m)		0.059‖			0.055#			

* Actual measurement made at 560 nm.
† Actual measurement made at 660 nm.
‡ Broadband measurements made from AVHRR channel 1 (580–680 nm).
§ Actual measurement made at 480 nm.
‖ Actual measurement at 436 nm.
Actual measurement at 546 nm.

to survive in stratified, low-nutrient regimes. It is important that future work concentrate on other micronutrients that may affect growth of this organism.

Vertical profiles in the bloom showed a clear chlorophyll fluorescence maximum and extracted pigment maximum at the base of the surface mixed layer near 20 m. Coccolithophores, however, probably contributed less biomass than the other algal groups.

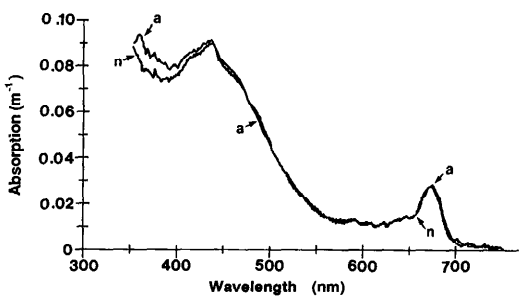

Fig. 9. Particulate absorption spectrum (m^{-1}) from station 8 at 5 m. Data represent two scans, one of a glass-fiber filter through which raw coccolithophore bloom water was passed (curve n) and an identical filter through which bloom water was passed following dissolution of coccoliths (curve a).

The microscope cell counts revealed cyanobacteria (2–7 × 10^4 cells ml^{-1}), dinoflagellates (100–200 cells ml^{-1}), flagellates (50–200 cells ml^{-1}), and cryptomonads (200–500 cells ml^{-1}). It is also possible that fluorescence and pigment per cell increased in the pigment maximum without a commensurate change in biomass. We can only speculate from the cell counts as to which species contributed the most biomass in the deep populations. Lack of coccoliths below 20 m was also demonstrated by the lack of change in attenuation and backscattering of water samples after bubbling with CO_2.

The production of coccoliths appeared to be highest in the well-illuminated surface mixed layer. This pattern is consistent with the fact that *E. huxleyi,* unlike other algal groups, can grow at extremely low levels of major nutrients (Brand et al. 1983). Combined with the ability of coccolithophores to increase light scattering by producing coccoliths, tolerance of low nutrients may allow them to outcompete deeper algal species. The coccolith suspension would restrict the visible radiation to the surface layer due to increased scattering. The euphotic

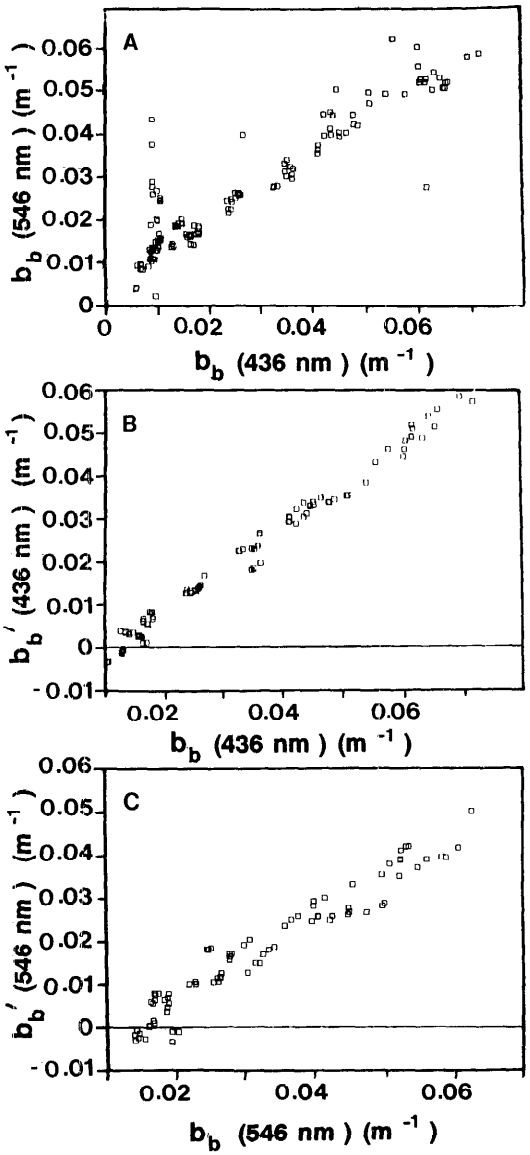

Fig. 10. A. Total backscattering at 546 nm vs. total backscattering at 436 nm. Backscattering calculated as described in text. B. Backscattering due only to coccoliths (b_b') at 436 nm vs. total backscattering at 436 nm. C. As panel B, except at 546 nm.

zone (depth of 1% surface PAR) would have decreased from ~45 m (during nonbloom periods) to 20 m during a bloom. Thus, for cells below the upper 20 m, the chance of a photon capture event would decrease with the increase in coccoliths and the deeper Chl-maximum assemblage would be deprived of photosynthetically utilizable radiation. Shallowing the euphotic zone might also allow more nutrient-rich water to diffuse above the Chl-maximum populations because NO_3^- assimilation is usually light-dependent (MacIsaac and Dugdale 1972).

Profiles of downwelling and upwelling irradiance at 440, 520, 550, and 670 nm showed that blue-green and green light penetrated deepest (Table 1). Moreover, beam attenuation due to coccoliths was higher in the blue than in the green wavelengths (Fig. 8B). The observations of greater values of K and c in the blue than in the green likely was due to two factors, wavelength-dependent scattering by the coccoliths (backscattering was, on average 1.4 times higher in the blue than in the green) and wavelength-dependent coccolithophore absorption (about five times higher in the blue than in the green; *see particulate absorption values in Table 1*). Absorption due to coccoliths was negligible since particle light absorbance was identical with and without coccoliths (Fig. 9), in agreement with the expectations of Gordon et al. (1988). Wavelength-dependent backscatter was probably due to the small size of coccoliths (1-mm diam, 250 nm thick), close to the wavelengths of blue and green light (Balch et al. 1989).

The optical properties changed, not only as a function of depth, but also spatially throughout the bloom, due to variation in coccolith backscattering and cell absorption. Figure 11A, B shows b_b' as a function of coccolith abundance. The least-squares fit to these data showed increasing b_b' at increasing concentrations of coccoliths. The relationship used here was a second-order polynomial (although, given the variance in the data, these lines are not significantly different from straight lines).

Irradiance reflectance just below the sea surface (R) is related to backscattering (b_b), absorption (a), and the downwelling irradiance attenuation coefficient, K (using the approximation $K = a + b_b$) by the simple relation given by Gordon et al. (1988; with their value of the distribution function, $Q = \pi$, for a given wavelength):

$$R = 0.35b_b/K = 0.35b_b/(a + b_b). \quad (1)$$

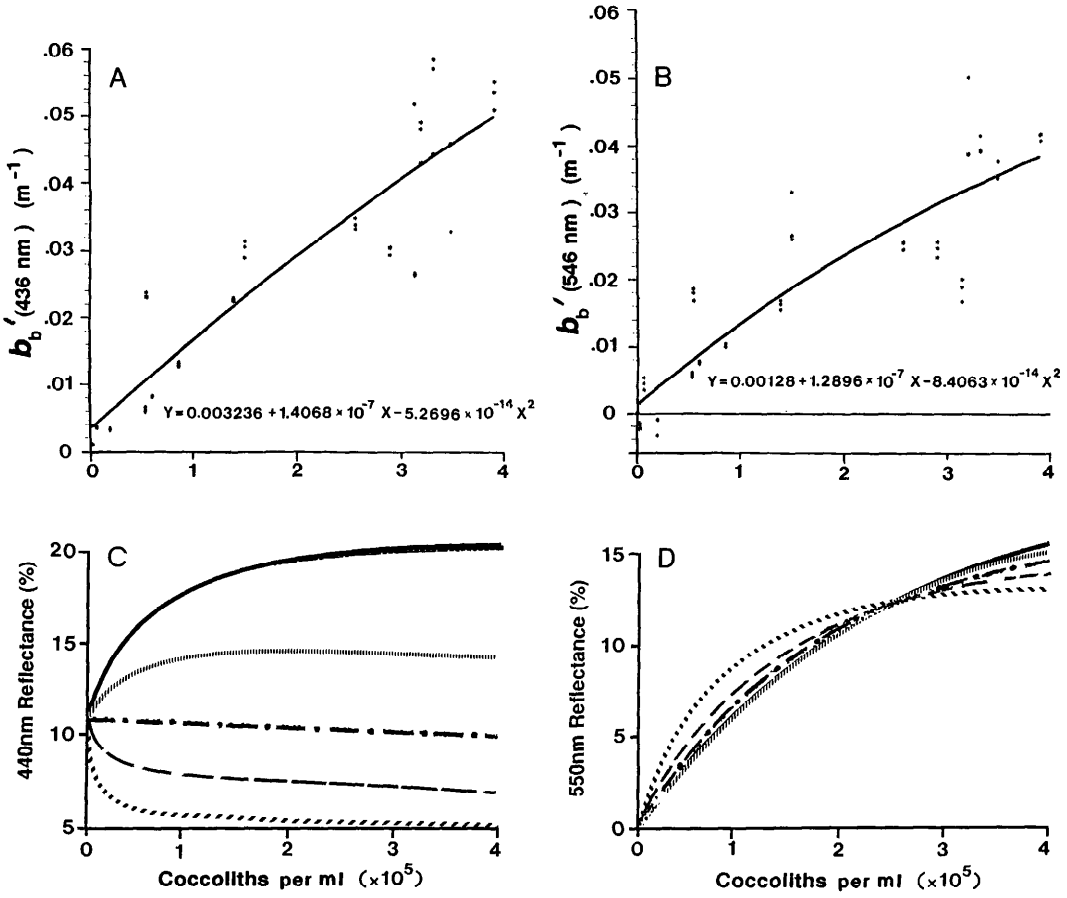

Fig. 11. A. Coccolith backscattering at 436 nm vs. coccolith concentration; 85% of the residual variance about the mean is explained by the equation shown. B. As panel A, but with 546-nm light. The equation represents a best-fit polynomial to the data (80% of the residuals about the mean is explained by it). For the coccolith concentrations shown here, however, the polynomial fit is not significantly better than a linear fit. C. Results of reflectance model (Eq. 2) for blue light (436 nm). Different lines represent different ratios of coccoliths to cells: hatched line, 20 coccoliths cell^{-1}; dashed line, 50 coccoliths cell^{-1}; dash-dot line, 100 coccoliths cell^{-1}; striped line, 200 coccoliths cell^{-1}; solid line, 400 coccoliths cell^{-1}; line for 1,000 coccoliths cell^{-1} is covered by the solid line. D. As panel C, but for green (546 nm) light.

Although applicable to typical ocean conditions, Eq. 1 is not suitable in a coccolithophore bloom, where multiple scattering may occur; the expanded form of the equation is more appropriate as given in Eq. 2 (*see* Gordon et al. 1975):

$$R = 0.3244X + 0.1425X^2 + 0.1308X^3 \quad (2)$$

where X is equal to $b_b/(a + b_b)$. As coccolith abundance increases, light scattering will increase due to cells and coccoliths, while absorption will increase due to cells only (the coccoliths themselves having negligible absorption, *see Fig. 9*). Increased absorption will tend to reduce reflectance. On the other hand, as b_b increases, the quotient $b_b/(a + b_b)$ will tend toward unity (increasing R) if $b_b >> a$. As shown in Table 1, b_b was $>a$ at 550 nm, thus the quotient $b_b/(a + b_b)$ should have been <1. In the blue wavelengths, a is likely to be $>b_b$, significantly reducing reflectance.

To understand the interaction of absorption and backscattering, we examined Eq. 2 for different coccolith : cell ratios and wave-

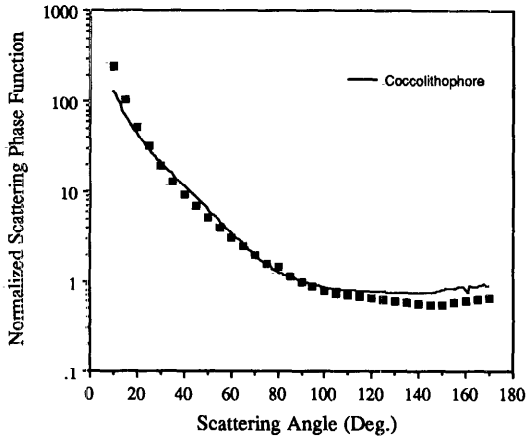

Fig. 12. Light scattering phase function at 520 nm measured with GASM at station 10 at 3 m during 1989 survey (solid line). The phase function was normalized to its value at 90°. For comparison, a Petzold (1972) turbid-water phase function normalized at 90° is also shown (■).

lengths by first calculating backscattering and absorption from cell-specific values and cell abundance (N_c). Total backscatter (b_b) was calculated as

$$b_b = (b_b') + (b_b^*{}_c \times N_c) + b_{bw} \quad (3)$$

where b_b' was the coccolith backscattering calculated from the coccolith counts and the polynomial relations from Fig. 11A, B. Cell-specific backscattering ($b_b^*{}_c$) was calculated from the backscatter measurements of CO_2-bubbled samples after removal of the scattering due to water (using data from station 4 at 20 m, 1989; $b_b^*{}_c = 2.18 \times 10^{-11}$ m^2 cell^{-1} at 436 nm and 0.54×10^{-11} at 546 nm). Such cell-specific backscattering values were representative only of unplated cells because all coccoliths were dissolved after the CO_2 treatment. Backscattering due to water (b_{bw}) was included in the total backscatter calculation.

Total absorption (a) was calculated as

$$a = (a^*{}_c \times N_c) + a_w \quad (4)$$

where cell concentration was multiplied by a cell-specific absorption coefficient value ($a^*{}_c = 5.62 \times 10^{-11}$ m^2 cell^{-1} at 436 nm and 1.17×10^{-11} at 550 nm) calculated from 1988 cell counts and particulate absorption measurements.

The results for the blue wavelengths (Fig. 11C) showed that at coccolith : cell ratios >100, the predicted reflectance increased as coccolith concentration increased. At lower ratios, particulate absorption of chlorophyll dominated, and reflectance values decreased as the coccolith concentration increased. This result suggests that when most coccoliths are attached to cells, with few detached coccoliths, then reasonable pigment data can be retrieved by satellite. In the green wavelengths, chlorophyll absorption did not dominate as much as for blue light, and reflectance increased in a curvilinear fashion, albeit saturating at a lower reflectance for the lower coccolith : cell ratios. This calculation suggests that in the blue wavelengths, coccolithophore blooms would not become visible to satellites until they were in advanced stages of growth, with high ratios of coccoliths to cells. Moreover, in the green wavelengths (Fig. 11D), an increase in coccolith concentration is universally associated with an increase in reflectance. Quantification of coccolith concentrations via satellite-derived reflectance will therefore be easier in the green wavelengths, but there will still be problems due to varying coccolith : cell ratios and the fact that increases in coccolith concentration are not necessarily accompanied by similar increases in reflectance.

Holligan et al. (1983) showed that reflectance was a logarithmic function of cell concentration. This empirical relation does not necessarily mean that the cells were the particles causing the high reflectance. Our data and model calculations suggest that the coccoliths do the bulk of the light scattering in *E. huxleyi* blooms but that the reflectance is more likely a function of coccoliths *and* cells. Any correlation in abundance between reflectance and cell concentration is likely due to the correlation in abundance between cells and coccoliths. Variability about the least-squares lines of Fig. 11A, B was likely due to backscattering of other calcified particles or, more importantly, backscattering of plated coccolithophore assemblages vs. naked coccolithophore assemblages (with coccoliths completely detached in the water). We did not quantify these groups during the cruises because preservation of the cells affects coccolith detachment.

It is clear from these data that coccolithophore blooms can represent a significant mesoscale perturbation to the pelagic optical environment of the Gulf of Maine. The fact that an algal group with such a low biomass (<1 μg Chl liter^{-1}) can dramatically alter the optical properties of the water column is noteworthy. Virtually nothing is known about how important *E. huxleyi* is to the optical properties of more typical mixed assemblages of phytoplankton. Three unresolved issues remain key to our understanding the ecology of *E. huxleyi*: its life history strategies, factors responsible for bloom induction, and the competitive impact of *E. huxleyi* blooms on subsurface algal growth. Resolution of these problems will go far toward explaining the spatial and temporal variability of this ubiquitous phytoplankton species.

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