

WHITE WATERS OF THE GULF OF MAINE

By S. Ackleson, W.M. Balch and P.M. Holligan

Blooms of the coccolithophore *Emiliana huxleyi* constitute a natural laboratory for optical, physical, and biogeochemical studies in the oceans.

FOR more than 100 years plankton biologists and marine geologists have been well aware that coccolithophores, a group of phytoplankton that produce external calcium carbonate plates or coccoliths (see figure on Table of Contents page), are widespread and abundant in the oceans (see Brongersma-Sanders, 1957; Bramlette, 1958). At high concentrations of cells and detached coccoliths, the water appears milky white in color, primarily due to light scatter from the coccoliths. Sightings of "white water" have been reported for virtually all of the world's oceans. Yet, only recently using ocean satellite remote sensing have we begun to fully appreciate the magnitude of the spatial and temporal scales of coccolithophore blooms (Holligan *et al.*, 1983) and the possible effects upon the optical, thermal and biogeochemical properties of surface ocean waters.

Extensive areas of high reflectivity in both oceanic and offshore coastal waters have been observed on visible-band images collected by a variety of satellite sensors — the CZCS (Coastal Zone Color Scanner) on Nimbus-7, the Landsat MSS (Multispectral Scanner) series, and the AVHRR (Advanced Very High Resolution Radiometer) on the NOAA series (Gower *et al.*, 1980; Holligan *et al.*, 1983; Groom & Holligan, 1987). Analyses of water samples have shown the cause of the high reflectance to be backscattering of light by cells and coccoliths of *Emiliana huxleyi* at typical maximum densities of about 5×10^3 and 10^5ml^{-1} respectively. This species has a world-wide distribution and is the only coccolithophore known so far to shed such large numbers of coccoliths under natural conditions. The coccoliths, as opposed to the cells, are thought to be the main cause of the backscattering (Bricaud & Morel, 1986).

Our knowledge of the occurrence of surface blooms of *E. huxleyi* is largely based on studies of the North Atlantic. A thorough search of satellite image archives indicates that they are found most frequently,

both in oceanic and offshore coastal waters, at mid-latitudes (45-65°N) during spring and summer (Holligan & Groom, 1986) and close to upwelling regions (Dupouy & Demarcq, 1987), with surface water temperatures in the general range 8-15°C. Comparable information for other oceans, such as the North Pacific (Fukushima *et al.*, 1987) remains incomplete.

Attempts to interpret ocean satellite imagery serve to emphasize our lack of understanding of the ecology of *E. huxleyi*. Patches of high coccolith concentration appearing in sequential satellite images may be treated as natural Lagrangian tracers, highlighting eddy structures and frontal boundaries that characterize the complex dynamic processes occurring in the surface mixed layer (Gower *et al.*, 1980). At the physiological level, there is still no clear understanding of why the cells produce and shed coccoliths, although various theories concerning flotation, light conditions for photosynthesis, and the maintenance of internal CO₂ concentrations have been proposed (Klaveness and Paasche, 1979; Westbroek *et al.*, 1983). In addition, there is no firm ecological basis for explaining the distribution of *E. huxleyi* blooms, which tend to be monospecific, in terms of competition with other species for light and nutrients, and of mortality due to sinking and grazing.

What is known about coccolithophores is that sinking coccoliths form a major component of the downward flux of particulate biogenic material (Honjo, 1976) and of the calcite found in marine sediments (Bramlette, 1958); furthermore, they produce large quantities of volatile organic sulfur compounds which eventually pass to the atmosphere (Andreae, 1986; Turner *et al.*, 1988). These factors, coupled with their ubiquitous nature, serves to emphasize the potentially important role of coccolithophores in global geochemical cycles.

The Application of AVHRR Imagery

The visible band of AVHRR imagery (channel 1, 0.58-0.68µm) seems unlikely to be useful as an oceanographic instrument because the radiometric sensitivity is low. Most ocean water, for which the volume reflectance is unaffected by bottom reflectance, appears homogeneous and dark. Subtle variations in volume reflectance of a few percent, which

S. Ackleson, *Bigelow Laboratory for Ocean Sciences, McKown Point, West Boothbay Harbor, Maine 04575*; W.M. Balch, *School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149*; P.M. Holligan, *Bigelow Laboratory for Ocean Sciences, McKown Point, West Boothbay Harbor, Maine 04575*.

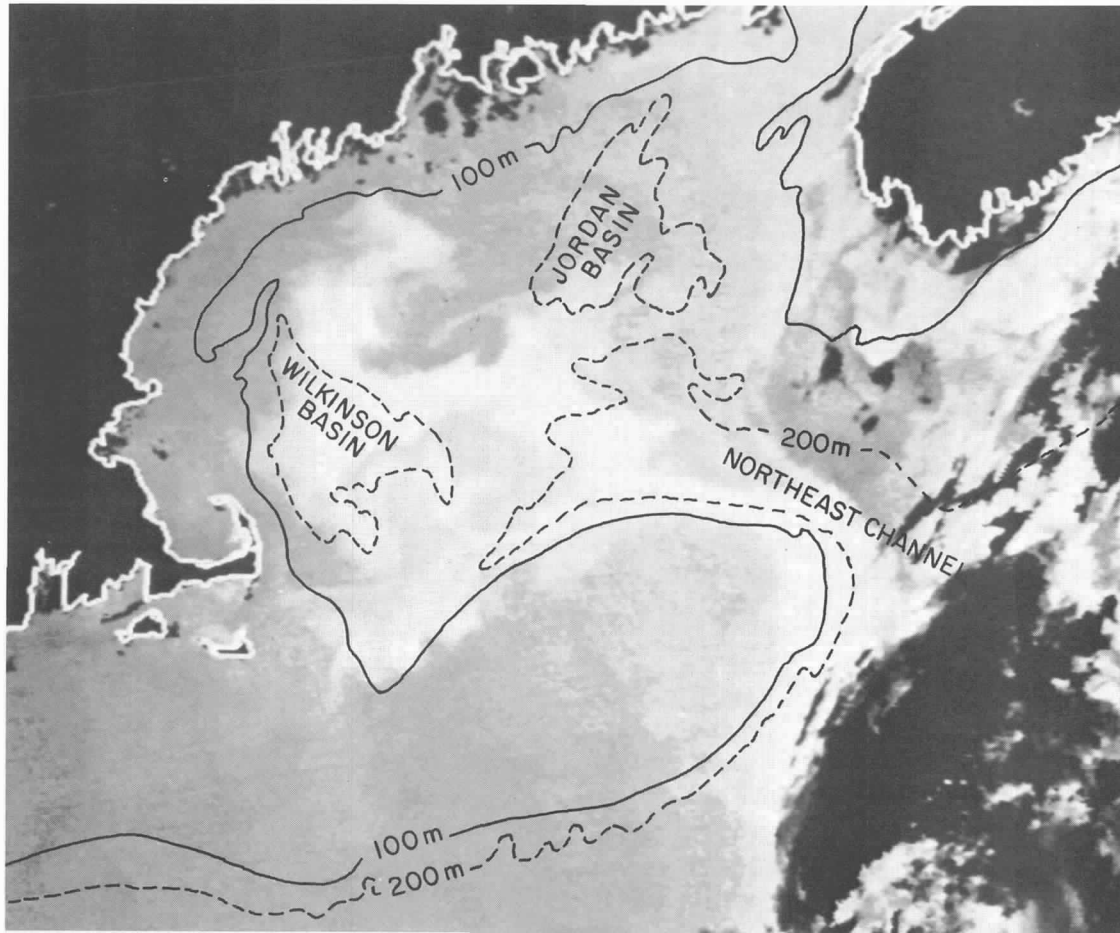


Figure 1: AVHRR visible-band image (channel 1, 0.58-0.68 μm) of the Gulf of Maine, collected June 28, 1988. Black areas are either land (Cape Cod appears in the lower left and Nova Scotia in the upper right) or clouds (as in the lower right). An extensive

coccolithophore bloom (lighter shades of gray) appears in the southwestern portion of the gulf and extends eastward into the North Atlantic.

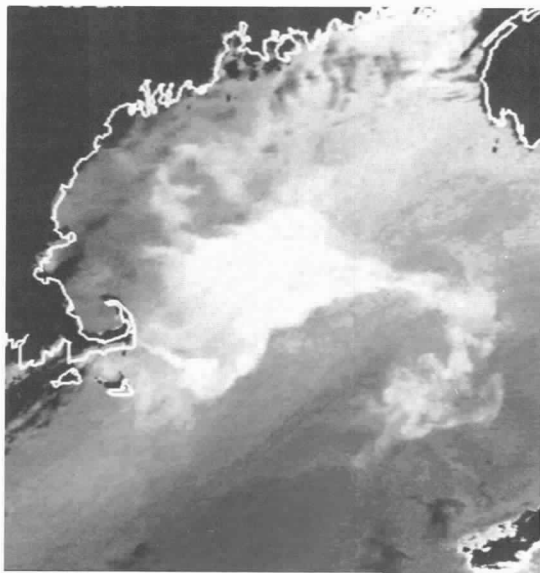


Figure 2: AVHRR visible-band image of the Gulf of Maine, collected July 7, 1988, showing changes in coccolithophore bloom distribution since June 28 (Fig. 1).

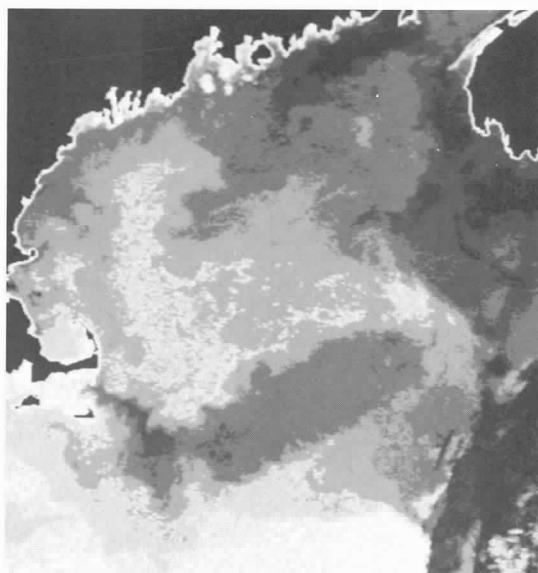


Figure 3: AVHRR thermal-band image (channel 4, 10.3-11.3 μm) of the Gulf of Maine, collected June 28, 1988. Warm surface water (14-18°, lighter shades of gray) occupies areas dominated by coccolithophores within the southwestern portion of the gulf, while colder waters occupy the northern and eastern portions of the gulf and identify the tidally mixed waters along the coast of eastern Maine and Nova Scotia and over Georges Bank.

are typical of most marine phytoplankton blooms and show up quite readily in CZCS imagery, are lost in the coarse AVHRR quantization procedure. Coccolithophore blooms, however, are optically very different from other marine phytoplankton blooms, primarily due to the scattering properties and high concentrations of detached coccoliths. In the absence of coccolithophores, volume reflectance is usually on the order of 2-3 percent. By comparison, inside a bloom, volume reflectance may exceed 20 percent (Groom and Holligan, 1987). With an order-of-magnitude increase in volume reflectance, coccolithophore blooms appear in the AVHRR visible band as bright areas while other areas appear dark.

The thermal band of AVHRR imagery (channel 4, 10.3-11.3 μm) is capable of measuring sea surface temperature to within 0.2°C. Coccolithophore blooms are frequently accompanied by an increase in sea surface temperature, although the connection between the coccolithophore concentration and local heating is not completely understood. Local heating in the presence of phytoplankton where absorption by chlorophyll is the dominant optical process has been addressed by several researchers (Lewis *et al.*, 1983; Lewis and Platt, 1987; Siegel and Dickey, 1987; Morel, 1988), but the added effect of multiple scattering within a coccolithophore bloom has yet to be demonstrated.

A 1988 Bloom of *E. huxleyi*

E. huxleyi is a well recognized component of the summer flora in seasonally stratified water of the Gulf of Maine (Gran & Braarud, 1935). Inspection of historical CZCS and AVHRR archives shows that patches of water with high reflectance consistently appear in June and July each year, although the location and spatial scales of these blooms are variable. In some years, even small blooms are difficult to detect, while in other years, a single bloom may encompass more than half of the Gulf of Maine surface waters.

Figure 1 shows an AVHRR channel 1 (0.58-0.68 μm) image of the Gulf of Maine collected at 1411 local time on June 28, 1988. The data were subsampled from the larger AVHRR scene and geometrically corrected to form a full resolution (1.1km) 512 X 512-pixel image of the Gulf of Maine and adjacent North Atlantic. In addition, a simple atmospheric correction was applied by subtracting channel 2 (0.725-1.0 μm) from channel 1, on the assumption that the channel 2 water signal is zero and therefore attributable to the atmosphere. Land and clouds appear black, while water appears as various shades of gray.

An extensive coccolithophore bloom (light grey) is shown occupying most of the southwestern portion of the gulf (centered over Wilkinson Basin). The boundary between the bloom and relatively clear water (dark areas) is characterized by complex filament and eddy structures. The clear waters along the coast and over Georges Bank correspond to regions of relatively strong tidal mixing. The edge of the

plume adjacent to Georges Bank closely follows the 100m contour, except that it cuts across the northern flank close to the 60m isobath. This feature is indicative of the flow of surface water out of the gulf southwest along the shelf break and is consistent with the general circulation of surface water within the Gulf of Maine (Brooks, 1985).

The bloom is most reflective along its northern boundary, presumably due to higher concentrations of detached coccoliths. By July 7, 1988, AVHRR imagery (Fig. 2, p. 19) revealed that the most intense portion of the bloom in terms of reflectance had shifted to the area east of Cape Cod, although the general shape of the bloom remained similar. Small scale structures along the boundaries changed significantly, including the dissipation of an intense linear feature that was parallel to the coastline on June 28. The complex eddy structures east of Georges Bank indicate strong horizontal shear, apparently associated with a clockwise circulation around the bank.

AVHRR thermal imagery from June 28, 1988, (Fig. 3, p. 19) indicates that sea surface temperature (SST) is highly correlated with water reflectance (Fig. 1, p. 19). SST within the bloom is about 5° warmer than surrounding water areas. In addition, the rate of increase in SST is greater inside the bloom than outside it. Between June 28 and July 7, bloom areas increased in SST at a rate of about .32°C d⁻¹. In contrast, SST in Jordan Basin, which tends to be similar in vertical thermal structure to Wilkinson Basin in the absence of a coccolithophore bloom, increased at a rate of .06°C d⁻¹. Are the coccolithophores affecting SST and if so, to what extent?

Field measurements collected from the R/V *ARGO Maine* between July 9 and 12, 1988, indicate that the transition from clear to turbid water corresponded to the boundary between mixed diatom-flagellate phytoplankton communities to one almost totally composed of *E. huxleyi* (Fig. 4, p. 21). Secchi disk depths ranged from 8-12m outside the bloom to 3-6m within the bloom. The maximum densities of cells and detached coccoliths were about 3.5x10³ and 1.2x10⁵ ml⁻¹ respectively at the surface, with concentrations of chlorophyll-a as high as 1.5 mg m⁻³. For a 20m surface mixed layer, the estimated standing crops of coccoliths were as high as 4 x 10¹² m⁻², with somewhat less than half attached to cells. The maximum rate of coccolith production under optimal conditions of illumination is probably about 20 cell⁻¹d⁻¹ (Paasche, 1962) which, for the observed ranges in cell-to-detached lith ratios, gives a production time for the detached coccoliths of 3-10 days, depending on ambient light levels. This time scale represents a first order estimate of the rate at which free coccoliths are accumulated in surface water and/or are lost to deep water via fecal pellets and direct sinking. The estimated quantities of calcium carbonate in the surface mixed layer, based on the conversion of 0.6 pg C lith⁻¹ (Holligan *et al.*, 1983), are as high as 20g m⁻².

Inside a bloom, volume reflectance may exceed 20 percent.

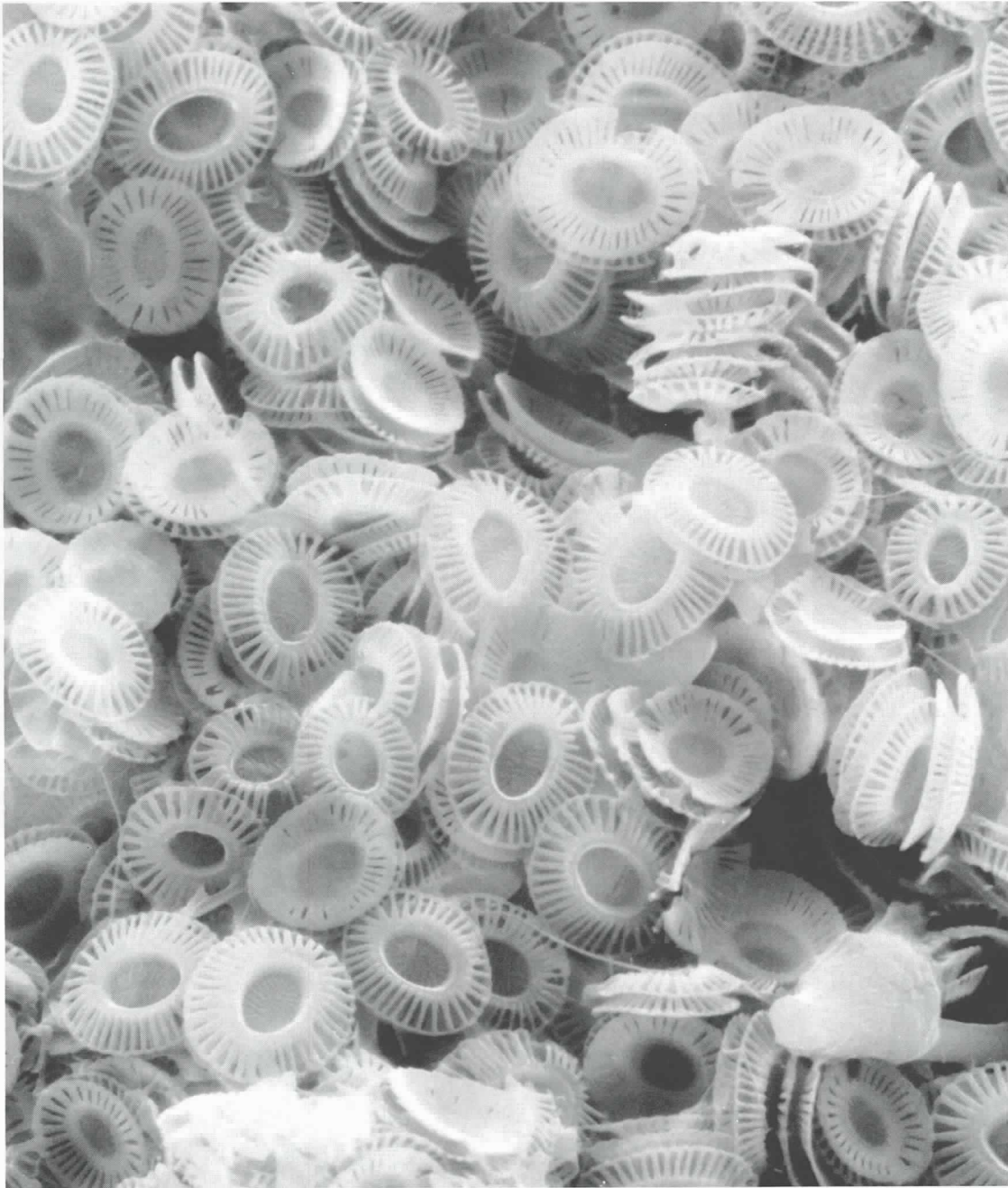


Figure 4: Scanning electron micrograph of detached coccoliths of *Emiliana huxleyi* from a surface water sample collected in the Gulf of Maine on July 11, 1988. The calcium carbonate plates

measure approximately $2\mu\text{m}$ wide by $4\mu\text{m}$ long. (Photo courtesy of Charles K. Paull, University of North Carolina.)

Future Work

There is no evidence to suggest that blooms of *E. huxleyi* in the Gulf of Maine are a new phenomenon. Satellite images from 1983 show coccoliths throughout the eastern as well as the western basins over a period of several weeks (J. Campbell, unpublished), but that bloom was not reported at the time. We assume that such events have occurred in the past without coming to the attention of plankton biologists. Although different clones of *E. huxleyi* are known to be genetically distinct in terms of their growth characteristics (Brand, 1982), the effects of light and nutrients on calcification by this species are

poorly understood (Klaveness & Paasche, 1979). Particularly intriguing is the hypothesis that iron limitation in surface ocean waters (Martin & Fitzwater, 1988) may lead to phytoplankton communities dominated by *E. huxleyi* and other coccolithophore species that grow well at low ambient concentrations of iron (Brand *et al.*, 1983). Nutrient levels affect the ratio of carbon incorporation into calcite and organic material (Bauman *et al.*, 1978), although experiments on the partitioning of carbon by *E. huxleyi* under nutrient conditions comparable to those in ocean waters have yet to be carried out.

An understanding of the control of growth and

calcification by *E. huxleyi*, including the shedding of coccoliths, is relevant to a wide range of biogeochemical and optical problems in the oceans. In relation to the carbon cycle, any change in the relative or absolute rate of calcification by coccolithophores will affect CO₂ fluxes between the ocean and the atmosphere due to the reaction



which tends to increase pCO₂ when calcite is formed. For this reason changes in coccolithophore production associated with glacial/interglacial variations in surface water temperature or in the availability of iron are likely to have had a significant effect on atmospheric CO₂ levels (Dymond & Lyle, 1985; Sarmiento *et al.*, 1988).

Also it has been postulated that the release and oxidation in the atmosphere of phytoplankton dimethylsulfide (DMS) is the main source of cloud condensation nuclei over the oceans (Charlson *et al.*, 1987). Such an effect would directly influence sea surface radiation and act as a feedback mechanism on phytoplankton photosynthesis, calcification and DMS production. The implications of interactions of this type between the carbon and sulfur cycles have yet to be explored.

A further consideration is the effect of coccolith-induced multiple scattering on the radiation budget for the surface mixed layer. It is likely that high concentrations of coccoliths increase the path length of light per unit depth due to multiple scattering which would increase the rate of absorption by both water and coccolithophore cells. One consequence might be that increased light absorption within the near surface waters will translate into increased heating and, therefore, increased stratification. Multiple scattering within the near surface water means that not only will more light be reflected out of the water but less light will be available to penetrate beneath the surface layer occupied by the coccolithophores. In essence, coccolithophores, by creating a stable surface scattering layer, could significantly impact the survival of the subsurface chlorophyll maximum and structure of the seasonal thermocline.

References

- Andreae, M. O., 1986: The ocean as a source of atmospheric sulfur compounds. In *The Role of Air-Sea Exchange in Geochemical Cycling*, P. Buat-Menard [ed.], 331-362.
- Bauman, F.G., H.D. Isenberg and J. Gennaro, 1978: The inverse relationship between nutrient nitrogen concentration and coccolith calcification in cultures of the coccolithophorid *Hymenomonas* sp. *J. Protozool.*, 25, 253-256.
- Brand, L.E., 1982: Genetic variability and spatial patterns of genetic differentiation in the reproductive rates of the marine coccolithophores *Emiliania huxleyi* and *Gephyrocapsa oceanica*. *Limnol. Oceanogr.*, 27, 236-245.
- Brand, L.E., W.G. Sunda and R.R.L. Guillard, 1983: Limitation of marine phytoplankton reproductive rates by zinc, manganese and iron. *Limnol. Oceanogr.*, 28, 1182-1198.

- Bricaud, A. and A. Morel, 1986: Light attenuation and scattering by phyto-planktonic cells: a theoretical modelling. *Appl. Optics*, 25, 571-580.
- Bramlette, M. N., 1958: Significance of coccolithophorids in calcium carbonate deposition. *Bull. Geol. Soc. Am.*, 69, 121-126.
- Brongersma-Saunders, M., 1957: Mass mortality in the sea. *Mem. Geol. Soc. Am.*, 67, 941-1010.
- Brooks, D.A., 1985: Vernal circulation in the Gulf of Maine. *J. Geophys. Res.*, 90, 4687-4705.
- Charlson, R. J., J. E. Lovelock, M. O. Andreae and S. G. Warren, 1987: Oceanic phytoplankton, atmospheric sulphur, cloud albedo and climate. *Nature*, 326, 655-661.
- Dupouy, C. and H. Demareq, 1987: CZCS as an aid for understanding modalities of the phytoplankton productivity during upwelling off Senegal. *Adv. Space Res.*, 7, 63-71.
- Dymond, J. and M. Lyle, 1985: Flux comparisons between sediments and sediment traps in the eastern tropical Pacific: implications for atmospheric CO₂ variations during the Pleistocene. *Limnol. Oceanogr.*, 30, 699-712.
- Fukushima, H., K. Hiramatsu and Y. Sugimori, 1987: CZCS-derived pigment concentration fields in Japanese coastal area. *Adv. Space Res.*, 7, 79-82.
- Gower, J. F. R., K. L. Denman and R. J. Holyer, 1980: Phytoplankton patchiness indicates the fluctuation spectrum of mesoscale oceanic structure. *Nature*, 288, 157-159.
- Gran, H. H. and T. Braarud, 1935: A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine [including observations on hydrography, chemistry and turbidity]. *J. Biol. Bd. Can.*, 1, 279-467.
- Groom, S. B. and P. M. Holligan, 1987: Remote sensing of coccolithophore blooms. *Adv. Space Res.*, 7, 73-78.
- Holligan, P. M. and S. B. Groom, 1986: Phytoplankton distributions along the shelf break. *Proc. R. Soc. Edinb.*, 88B, 239-263.
- Holligan, P. M., M. Viollier, D. S. Harbour, P. Camus and M. Champagne-Philippe, 1983: Satellite and ship studies of coccolithophore production along a continental shelf edge. *Nature*, 304, 339-342.
- Honjo, S., 1976: Coccoliths: Production, transportation and sedimentation. *Mar. Micropaleontol.*, 1, 65-79.
- Klavness, D. and E. Paasche, 1979: Physiology of coccolithophorids. In *Biochemistry and Physiology of Protozoa* (2nd Ed.), Vol. 1. Eds. Levandowski, M., Huntner, S. H. Acad. Press, 191-213.
- Lewis, M.R., J.J. Cullen and T. Platt, 1983: Phytoplankton and thermal structure in the upper ocean: consequences of nonuniformity in chlorophyll profile. *J. Geo. Res.*, 88(C4), 2565-2570.
- Lewis, M.R. and T.C. Platt, 1987: Remote observations of ocean color for prediction of upper ocean heating rates. *Adv. Sp. Res.*, 7(2), (2)127-(2)130.
- Martin, J.H. and S.E. Fitzwater, 1988: Iron deficiency limits phytoplankton growth in the north-east Pacific subarctic. *Nature*, 331, 341-343.
- Morel, A., 1988: Optical modeling of the upper ocean in relation to its biogeochemical matter content (case I waters). *J. Geo. Res.*, 93(C9), 10,749-10,768.
- Paasche, E., 1962: Coccolith formation. *Nature*, 193, 1094-1095.
- Sarmiento, J.L., J.R. Toggweiler and R. Najjar, 1988: Ocean carbon-cycle dynamics and atmospheric pCO₂. *Phil. Trans. R. Soc. Lond. A* 325, 3-21.
- Siegel, D.A. and T.D. Dickey, 1987: On the parameterization of irradiance for open ocean photoprocesses. *J. Geo. Res.*, 92(C13), 14,648-14,662.
- Turner, S. M., G. Malin, P. S. Liss, D. S. Harbour and P. M. Holligan, 1988: The seasonal variation of dimethyl sulfide and dimethylsulfoniopropionate concentrations in nearshore waters. *Limnol. Oceanogr.*, 33, 364-375.
- Westbroek, P., E.W. de Jong, P. van der Wal, T. Borman, J.P.M. de Vrind, P.E. van Emburg and L. Bosch, 1983: Calcification in Coccolithophoridae - wasteful or functional? In: *Environmental Biogeochemistry*, Ecol. Bull. (Stockholm) 35, R. Hallberg (Ed.), 291-299.