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Blooms of the coccolithophore *Emiliania huxleyi* with respect to hydrography in the Gulf of Maine

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Abstract—We present results of oceanographic surveys of visually turbid blooms of the coccolithophore *Emiliania huxleyi* in the Gulf of Maine during the summers of 1988, 1989 and 1990. In each year, hydrographic stations within the blooms could be distinguished from non-bloom stations on a temperature–salinity diagram. In 1988 and 1989 the blooms were confined to the surface waters of the central western Gulf of Maine; *T–S* analyses showed they occurred in higher salinity surface waters at stations characterized by a well-defined upper mixed layer overriding a sharp pycnocline. Nutrients (not measured in 1988) were near depletion in the surface waters of both bloom and non-bloom stations in 1989, with surface phosphate being lower in the bloom waters (0.02–0.16 μM in the top 15 m) than in non-bloom waters (0.21–0.49 μM). Phosphate was not as low in the surface waters of the 1990 bloom. The bloom that year was much smaller in areal extent than in 1988 or 1989, and was limited to the northern part of the Great South Channel and western Georges Bank area of the Gulf of Maine. *T–S* analyses indicated significant mixing of different water masses in the area of the bloom in 1990, with the bloom being confined to those stations having less dense surface waters, of lower salinity, than the non-bloom stations. There also was evidence of a subsurface salinity minimum beneath the bloom waters in 1990. Blooms of *E. huxleyi* with surface expressions of visually turbid waters do not occur every year in the Gulf of Maine, and we discuss possible causative factors, specifically as related to the age or maturity of surface waters and macro- and micro-nutrient levels, that could facilitate bloom formation and which could vary between years.

INTRODUCTION

COCCOLITHOPHORES are phytoplankton of the Class Prymnesiophyceae whose cells are typically surrounded by several layers of calcium carbonate plates, the coccoliths. Coccolithophores are important in the cycling of carbon and sulfur, and affect the optical and heat-absorbing characteristics of surface waters during bloom events (HONJO, 1976; ACKLESON and HOLLIGAN, 1989; BALCH *et al.*, 1991). They are perhaps the most significant group of organisms with regard to: (a) fluxes of calcium carbonate to the deep waters and

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sediments of both the ocean basins and continental shelf seas; and (b) production of dimethyl sulfide (DMS), which is of primary importance to the global sulfur budget and perhaps climate (Holligan, 1992). The most common species is *E. huxleyi*, which is cosmopolitan in its distribution (Raymont, 1980) and commonly occurs in blooms during the summer in the subpolar regions of both the open North Atlantic ocean and continental shelf seas (Holligan *et al.*, 1983). The shedding of coccoliths into the surrounding waters during times of maximum growth rates sometimes results in visually turbid bloom phenomena, or "white water" as reported by Hardy (1956) for the North Sea. In particularly intense blooms, where densities of detached coccoliths exceed *ca.* 0.5×10^5 ml^{-1}, the strong backscattering of visible light enables detection of coccolithophore blooms by satellite remote sensing (Holligan *et al.*, 1983; Ackleson and Holligan, 1989; Groom and Holligan, 1987; Balch *et al.*, 1991). In general, the greatest densities of coccolithophores are reached at times of maximum water column stratification and nutrient depletion in the surface waters following the spring diatom bloom (Margalef, 1979; Balch *et al.*, 1991). Marshall (1984 a,b) and Marshall and Cohn (1983) reported that *E. huxleyi* is present year round in the Gulf of Maine, that it is more common away from shore in outer shelf waters, and that it is most abundant during the summer months. But the causes of visually turbid blooms in certain years are not known, and with our present level of understanding of such blooms in the Gulf of Maine, we cannot predict whether one is going to occur in any given year. We report here results of our studies of coccolithophore blooms in the Gulf of Maine in 1988, 1989 and 1990, relating the distributions of blooms to the hydrography of the area.

MATERIALS AND METHODS

Three research cruises were conducted in the Gulf of Maine during summer coccolithophore blooms: 9–12 July 1988 and 20–25 June 1989, both on the R.V. *ARGO-Maine*; and 6–13 July 1990 on the R.V. *Cape Hatteras* (Brown, 1988; Ackleson *et al.*, 1989, 1990; Kilpatrick, 1990). The primary focus of each of these cruises was not hydrography, but was related to the optical properties of coccolithophore blooms and calcification rates, and those results have been reported (Ackleson *et al.*, 1989, 1990; Balch *et al.*, 1991, 1992). The development of the coccolithophore bloom was monitored each year using visible satellite imagery of the surface water reflectance to reveal the locations of bloom waters and to guide the cruise tracks [AVHRR, Advanced Very High Resolution Radiometer, with channel 2 (725–1100 nm) subtracted from channel 1 (570–680 nm); Groom and Holligan, 1987; Ackleson and Holligan, 1989; Ackleson *et al.*, 1989]. Visible satellite images of the blooms, and thermal IR (AVHRR, channel 4, 10.2–11.3 μm) images of sea surface temperatures, for the 1988, 1989 and 1990 blooms, are shown in Figs 1–3, along with hydrographic station locations for each of the three cruises.

On the 1988 cruise, CTD casts were made at several stations inside and outside the bloom waters (Fig. 1) using a Neil Brown Smart CTD. Separate Niskin bottle casts were made to collect water samples for the determination of phytoplankton chlorophyll, determined fluorometrically (Parsons *et al.*, 1984), and for counts of coccolithophores and loose coccoliths (Brown, 1988). The same measurements were made again in 1989, except that the CTD was equipped with a Sea Tech *in situ* fluorometer and 25-cm path length transmissometer. Phytoplankton cell counts and gross identifications were performed on settled samples preserved in either non-acidic Lugols solution (5% by volume)

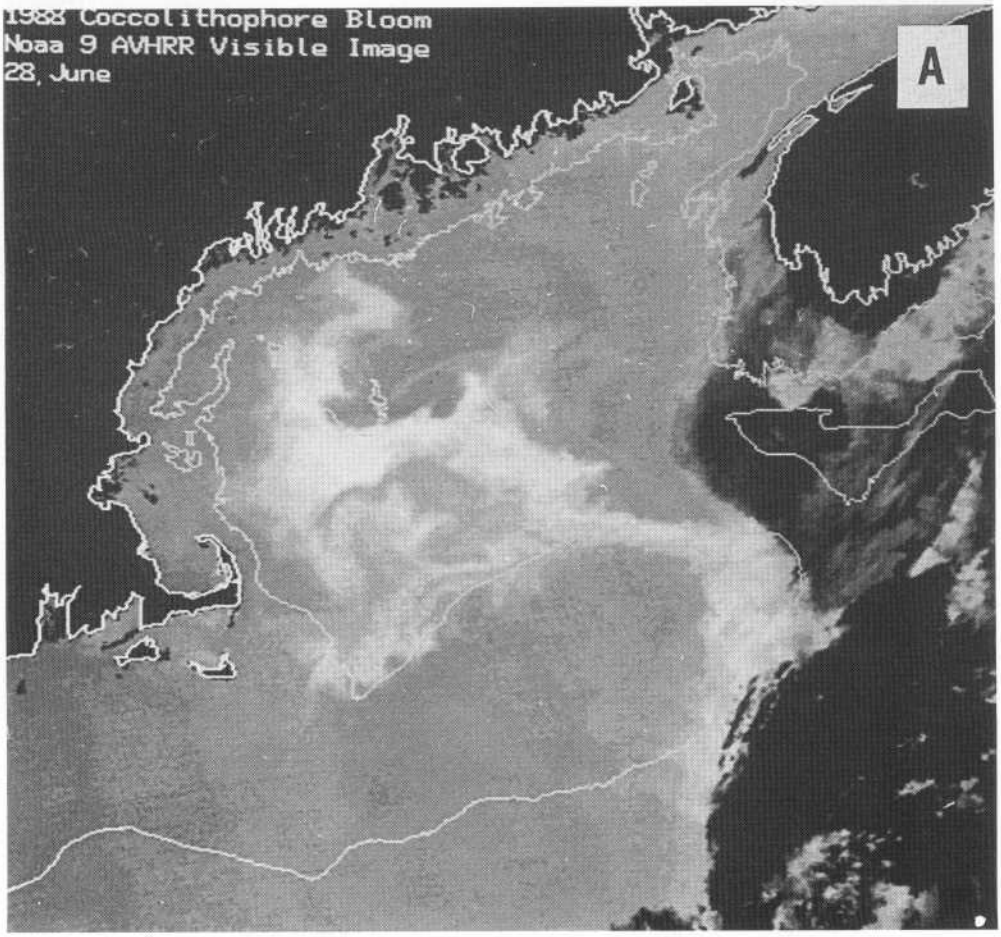

Fig. 1. (A) AVHRR image taken by NOAA-9 satellite on 28 June 1988 and processed as described in GROOM and HOLLIGAN (1987). The coccolithophore bloom waters are white. (B) Sea surface temperature for same image as in (A); the temperature scale is given. Colder waters are darker. The 100 m bottom depth contour is given in (A) and (B). (C) Hydrographic station locations in the Gulf of Maine for the R.V. *ARGO-Maine* cruise 9–12 July 1988; the 100 and 200 m bottom depth contours are given, as are features referred to in the text.

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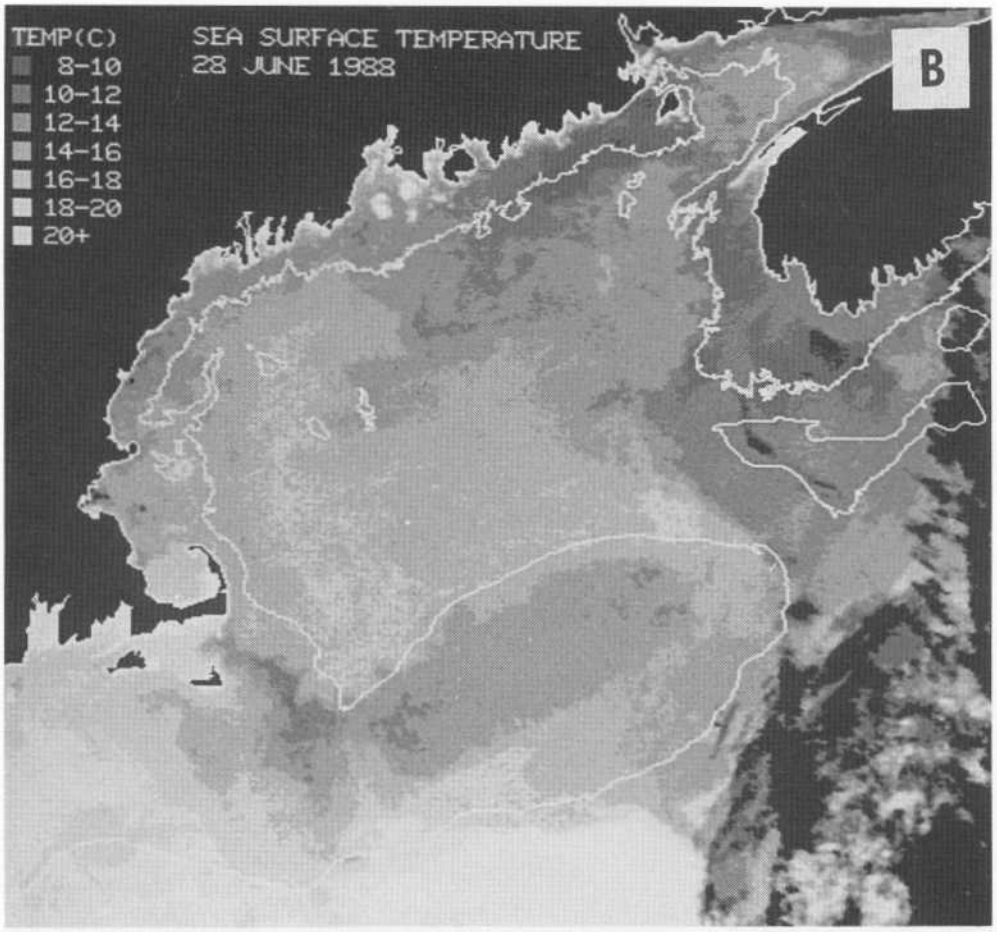

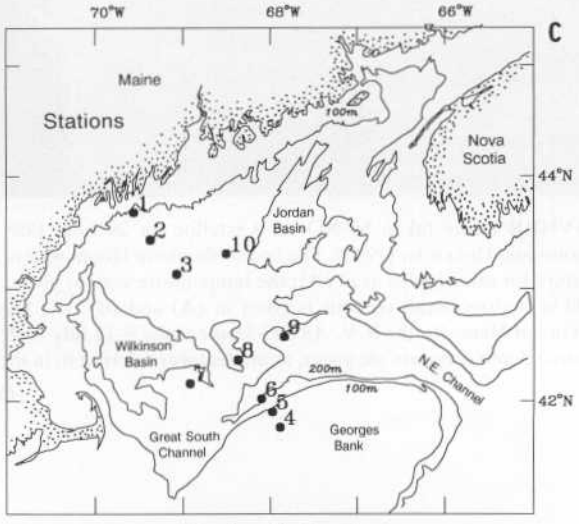

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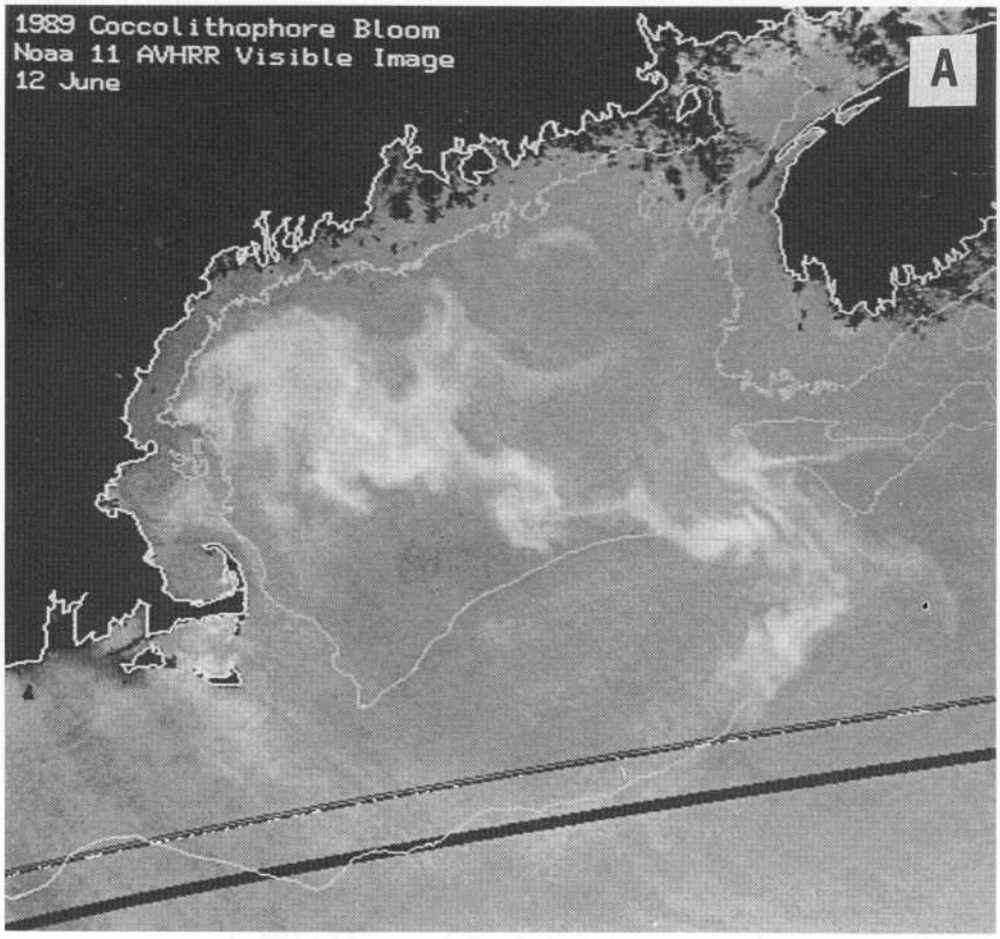

Fig. 2. (A) AVHRR image taken by NOAA-9 satellite on 12 June 1989 and processed as in Fig. 1. The coccolithophore bloom waters are white. (B) Sea surface temperatures for same image as in (A); the temperature scale is given. Colder waters are darker. The 100m bottom depth contour is given in (A) and (B). (C) Hydrographic station locations in the Gulf of Maine for the R.V. *ARGO-Maine* cruise 20–25 June 1989; the 100 and 200 m bottom depth contours are given, as are features referred to in the text.

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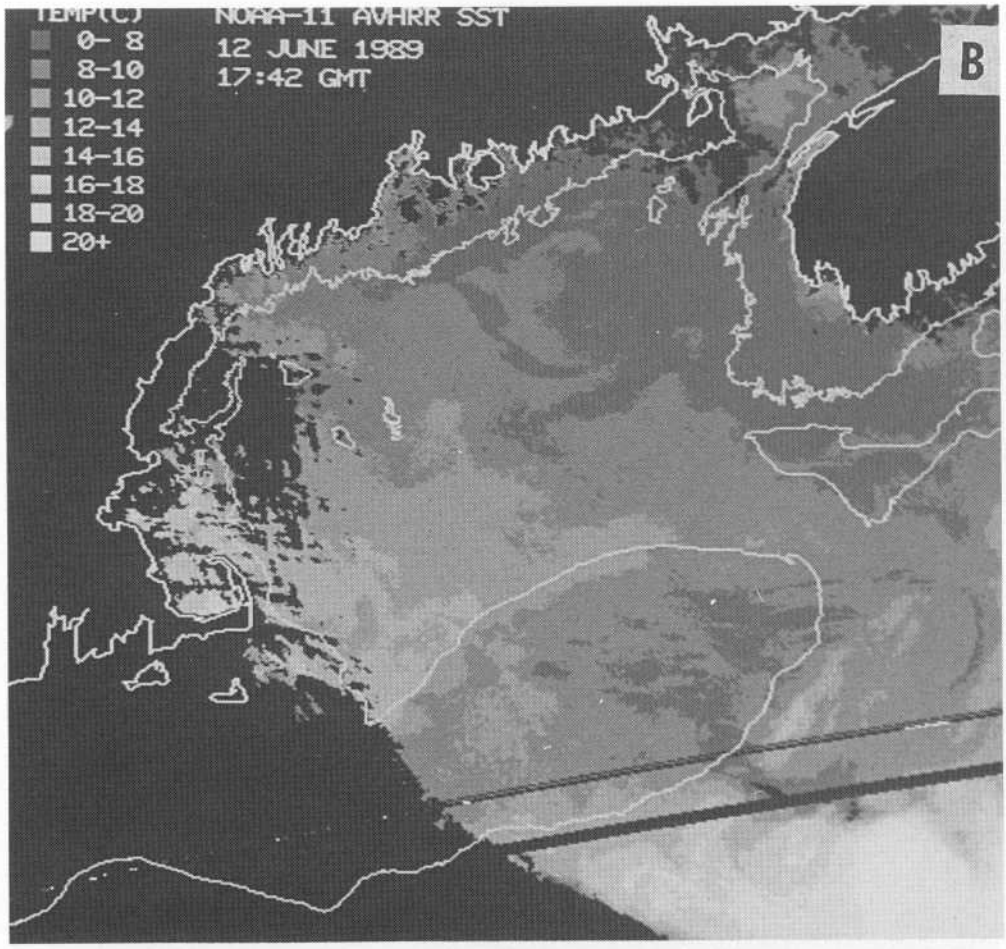

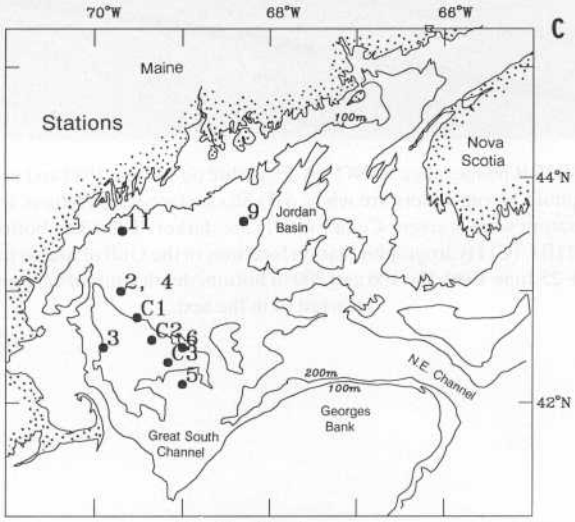

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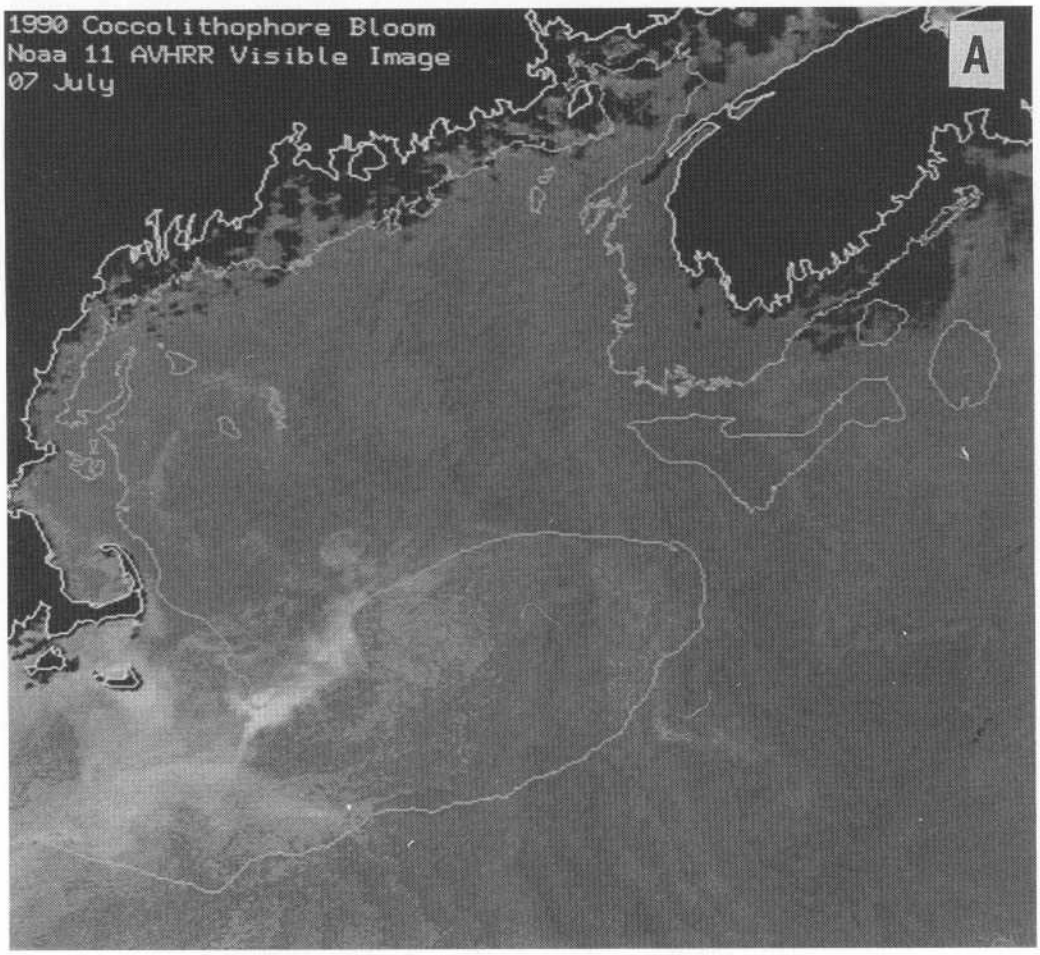

Fig. 3. (A) AVHRR image taken by NOAA-11 satellite on 7 July 1990 and processed as in Fig. 1. The coccolithophore bloom waters are white. (B) Sea surface temperature for same image as in (A); the temperature scale is given. Colder waters are darker. The 100 m bottom depth contour is given in (A) and (B). (C) Hydrographic station locations for the R. V. *Cape Hatteras* 6–13 July 1990; the 100 and 200 m bottom depth contours are given, as are features referred to in the text.

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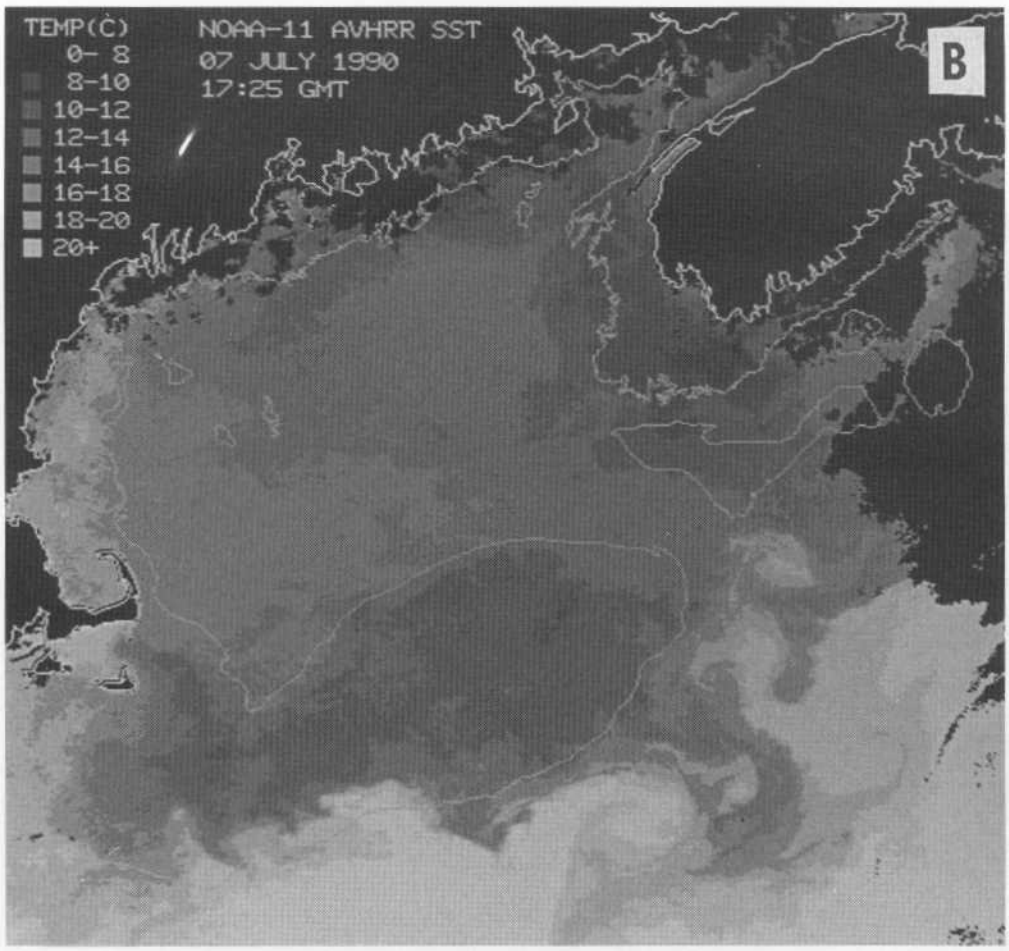

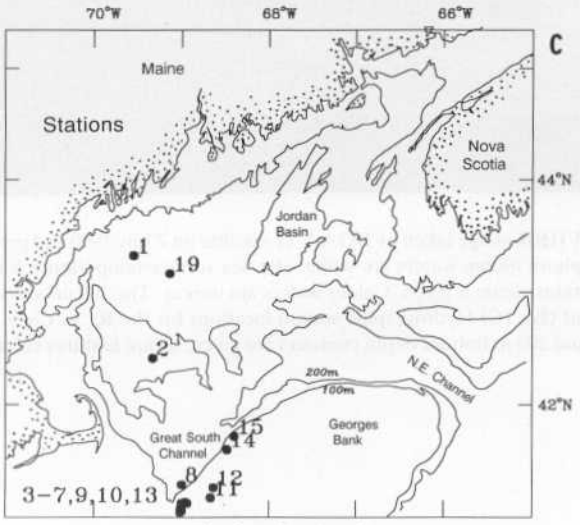

Fig. 3. *Continued*

or in 0.5% buffered formalin, to prevent coccolith dissolution, and enumerated with an inverted microscope ashore. A number of samples were analyzed for inorganic nutrient concentrations using standard autoanalyzer techniques. Stations were again sampled both inside and outside the bloom waters in 1989 (Fig. 2). In 1990 we used the ship's (R.V. *Cape Hatteras*) Neil Brown Smart CTD and rosette water bottle sampler, equipped with a Sea Tech *in situ* fluorometer and transmissometer. Profiles were made at stations in the immediate vicinity of the coccolithophore bloom in 1990, which was confined to a much smaller area of the Gulf (Fig. 3). Phytoplankton chlorophyll and inorganic nutrients were determined as in 1989. Phytoplankton counts were made using both settled counts and using size fractionated samples (8, 3 and 0.2 μm) and epifluorescence microscopy (SHAPIRO and HAUGEN, 1988). Coccolith enumeration was performed using a polarizing filter (BALCH *et al.*, 1991). Concentrations of particulate calcium carbonate in the water column were determined in 1990 by filtering replicate 500 ml samples onto a GF/F glass fiber filter, freezing the filters, and then analyzing for carbon content before and after acidification with HCl fumes in order to drive off the carbonate. Carbon content was analyzed using a Control Equipment Model 240-XA CHN Analyzer.

RESULTS

General

The coccolithophore blooms in 1988 and 1989 were intense enough to be detected in visible satellite imagery and covered broad expanses of the Gulf of Maine (Figs 1 and 2). The bloom in 1990 was much smaller in areal extent than the previous two years and was limited to the Great South Channel and western Georges Bank area (Fig. 3).

Comparisons of the bloom distributions with the satellite images of sea surface temperatures in 1988 and 1989 reveal that the blooms were restricted to the more offshore waters of the western half of the Gulf of Maine (Figs 1 and 2). The blooms were not visible in coastal waters or the more tidally energetic waters of the southwest Nova Scotian shelf and Georges Bank. They also appeared to be excluded from those offshore waters in the western Gulf that originate from the eastern Maine coastal current/plume system (TOWNSEND *et al.*, 1987). This plume system consists of cold, tidally mixed waters emanating from the northeastern Gulf and is clearly visible in the 1988 thermal IR satellite image of sea surface temperature as a band of colder water extending from the eastern Maine coast out across the Gulf of Maine (Fig. 1). The plume feature is more coastally oriented in 1989, with perhaps a remnant filament of cooler plume water extending across the central Gulf (Fig. 2). In both 1988 and 1989 there was evidence of export of surface bloom waters, rich in coccoliths, out of the Gulf of Maine; the high reflectance bloom waters can be traced along with the clockwise flow around Georges Bank (FLAGG, 1987) and to the continental slope (Figs 1 and 2).

The distribution of bloom waters in 1990, which were confined to the Great South Channel and western Georges Bank area of the Gulf, do not appear to be as easily related to the hydrography, based on the satellite image of sea surface temperature, as in the previous 2 years (Fig. 3). The bloom occupied an area in the vicinity of the northern end of the Great South Channel, between the warmer surface waters of the western Gulf of Maine, and the shallower, tidally well-mixed waters on Georges Bank.

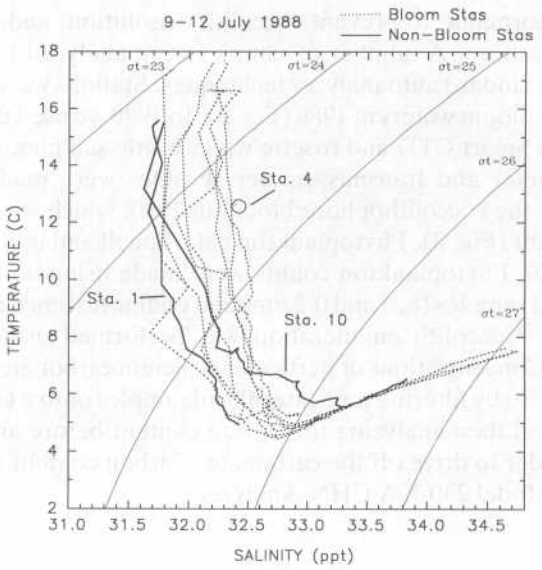

Fig. 4. Temperature–salinity diagram for CTD stations during the 1988 cruise. Data were depth-averaged over 1-m intervals. The stations occupied inside the coccolithophore-rich waters are labelled Bloom Stas, while stations occupied outside the coccolithophore-rich waters are labelled Non-Bloom Stas. Stations 2, 3, 5, 6, 7, 8 and 9 were inside the bloom [Fig. 1(A)]; Stations 1, 4 and 10 were outside the bloom. Station 1 is a shallow station off the Maine coast and Sta. 10 is an offshore station exhibiting characteristics of the eastern Maine coastal current/plume system. Station 4 was on the tidally well-mixed Georges Bank and had uniform temperature and salinity from top to bottom; all the *T–S* data points are within the circled point.

The 1988 *bloom*

Estimates of *Emiliania huxleyi* coccolith densities in the surface waters of the 1988 bloom reached 130,000 ml^{-1} at Stas 2 and 8, and *E. huxleyi* cell densities reached 2400 ml^{-1} at Sta. 7 (BROWN, 1988; ACKLESON and HOLLIGAN, 1989; BALCH *et al.*, 1991). The bloom began in mid-June, lasted into mid-July, and was limited to the deeper, vertically well-stratified waters of the central Gulf of Maine, covering an area of some 25,000 km^2 (Fig. 1). Concentrations of phytoplankton chlorophyll *a* were uniformly lower in the bloom waters ($<1\ \mu g\ l^{-1}$) than outside the bloom. There was a subsurface chlorophyll maximum beneath the coccolithophore-rich surface water layer ($1.7\ \mu g\ l^{-1}$ at 20m at Sta. 8 vs $0.6\ \mu g\ l^{-1}$ at the surface). The species composition of this maximum was not determined, although the coccolithophore cell maximum was recorded at this depth.

The temperature–salinity diagram for the stations sampled in 1988, which includes stations in the bloom waters as well as stations where no surface bloom was evident, is given in Fig. 4. The deep water stations plotted in Figure 4 show the characteristic *T–S* relations for the three prominent water masses in the offshore Gulf of Maine (HOPKINS and GARFIELD, 1979): Surface Water, Intermediate Water and Bottom Water. The Surface Water layer is formed each year as the upper water column warms and caps off the colder Intermediate Water layer just beneath. Intermediate Water results from the cooling of the upper water column the previous winter, and is identified as a temperature minimum layer which can persist throughout the summer. The Bottom Water layer represents the warmer,

saltier water of Slope Water origin, which enters the Gulf of Maine through the Northeast Channel. The *T–S* relations for stations at which *E. huxleyi* was blooming (Stas 2, 3, 5, 9) were, in general, somewhat vertical and inclined with respect to their intersection with lines of constant sigma-*t* as shown in Fig. 4. In contrast to the bloom stations, Sta. 1 (a near-shore station) and Sta. 10 in Fig. 4 have fresher surface waters. Station 4, a non-bloom station, was on Georges Bank, and had uniform temperature and salinity from top to bottom as a result of tidal mixing. Station 10 (non-bloom station) has a greater relative increase in salinity with depth than for any of the bloom stations. The relative change in density with increasing depth in the upper water column was greater at the two non-bloom Stas 1 and 10, with their *T–S* plots being slightly more perpendicular to the lines of constant sigma-*t*, and thus, denser water was nearer the surface at these two non-bloom stations than at the bloom stations. In general, the surface waters at the bloom stations had higher salinities than surface waters at the non-bloom stations, yet the surface densities covered a similar range for both groups of stations. Based on these limited *T–S* observations, we would suggest that *E. huxleyi* was more abundant at those surface waters in the Gulf that exhibited a more clearly defined upper mixed layer, overriding a sharp pycnocline. Coccolithophores were not blooming at stations where denser waters, perhaps of a more immediate, deeper origin, were upwelling, or where there were fresher surface waters of more coastal origin. Thus, it would appear that upwelling waters and fresher coastal waters either prevented *E. huxleyi* from blooming, or lacked some factor necessary to initiate a bloom. The bloom occurred only where there was a better developed upper mixed layer, which might have served to better isolate near surface waters from the more nutrient-rich deeper waters.

Vertical profiles of temperature, salinity and density (sigma-*t*) at a bloom station (Sta. 2) and non-bloom station (Sta. 10) are given in Fig. 5, illustrating the better-defined upper mixed layer in the top 10–15 m at the bloom station. The upper mixed layer at Sta. 10 is thinner (<5 m) and fresher.

The 1989 *bloom*

The 1989 coccolithophore bloom began in mid-June and disappeared from visible satellite images in mid–late July (Fig. 2). The bloom was, as in 1988, quite intense, with beam attenuation coefficients in excess of 1.8 and secchi disk depths less than 3 m (Ackleson *et al.*, 1989; Balch *et al.*, 1991) in what normally is relatively clear, low-productivity waters in summer (Townsend *et al.*, 1987). The densities of coccoliths exceeded 300,000 ml^{-1} and densities of *E. huxleyi* cells exceeded 1500 ml^{-1} during the peak of the bloom (Ackleson *et al.*, 1989; Balch *et al.*, 1991); the greatest densities of cells and loose coccoliths were confined to the surface waters above the thermocline (the upper 15–25 m) as reflected in the transmissometer tracings (Fig. 6).

The temperature–salinity relationships for bloom vs non-bloom stations in 1989 were similar in general trends to those from the previous year (Figs 7 and 8). Stations exhibiting the bloom in 1989 had slightly different *T–S* relationships than the non-bloom stations, and again, it appears that *E. huxleyi* may have been limited to those surface waters exhibiting a slightly more vertical *T–S* plot, indicating a better-defined surface mixed layer and less of a change in density with increasing depth in the upper water column. There was a greater density change with depth near the surface at the non-blooming stations, suggestive of deeper, upwelling waters reaching closer to the surface. Linear regression analysis of the

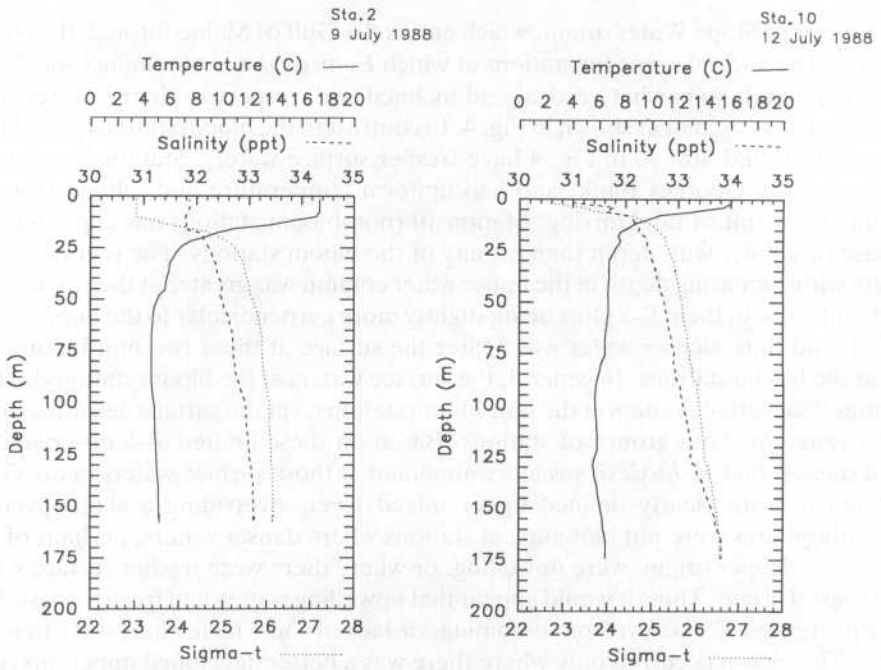

Fig. 5. 1988. Vertical profiles of temperature (°C), salinity (ppt), and density (sigma-t) for Sta. 2, which was in the coccolithophore bloom, and Sta. 10, which was outside the bloom waters (Fig. 1). Data are depth-averaged over 1-m intervals.

T–S data from the surface to the depth of 25.25 σ_t (selected in order to avoid bias in data density at depth; Fig. 7) revealed that the means of the slopes of bloom and non-bloom stations were statistically different at the 0.05 level (Fig. 8). Two of the four non-bloom stations plotted in Fig. 7 have warmer surface waters than any of the bloom stations, while the other two non-bloom stations had colder surface water temperatures. Thus, the bloom itself did not appear to be related to the surface water temperature. The surface waters at the non-bloom stations tended to have lower salinities.

Vertical profiles of temperature, salinity, density, chlorophyll fluorescence and light transmission are presented in Fig. 6 for a station inside the bloom waters (Sta. 3) and one outside the bloom (Sta. 9). Station 3 had a near-surface mixed layer of about 8 m, with a second thermocline at about 15 m; there was a sharp pycnocline, with a $\Delta\sigma_t$ of about 1.0 kg m^{-3} m^{-1} between 14 and 16 m. Surface salinity was between 31.8 and 32.1 ppt. Station 9, a non-bloom station, had only a very shallow surface mixed layer of *ca* 5 m; the salinities in the surface layer were >32 ppt.

The vertical distribution of phytoplankton chlorophyll, as reflected in the fluorescence traces in Fig. 6, reached a peak at 18 m at the bloom Sta. 3, which was just beneath the pycnocline and the light transmission minimum. Coccolithophores were the dominant phtyoplankton at the depth of chlorophyll maximum, although dinoflagellates and a mixture of photosynthetic flagellates were also present in significant numbers. Percentage light transmission was low in the surface waters of Sta. 3, dropping to about 60% at 15 m. Chlorophyll fluorescence maximum exceeded 10 μg l^{-1} at 10 m at Sta. 9 (the result of diatoms in the high-nutrient coastal current/plume waters). Despite the high chlorophyll

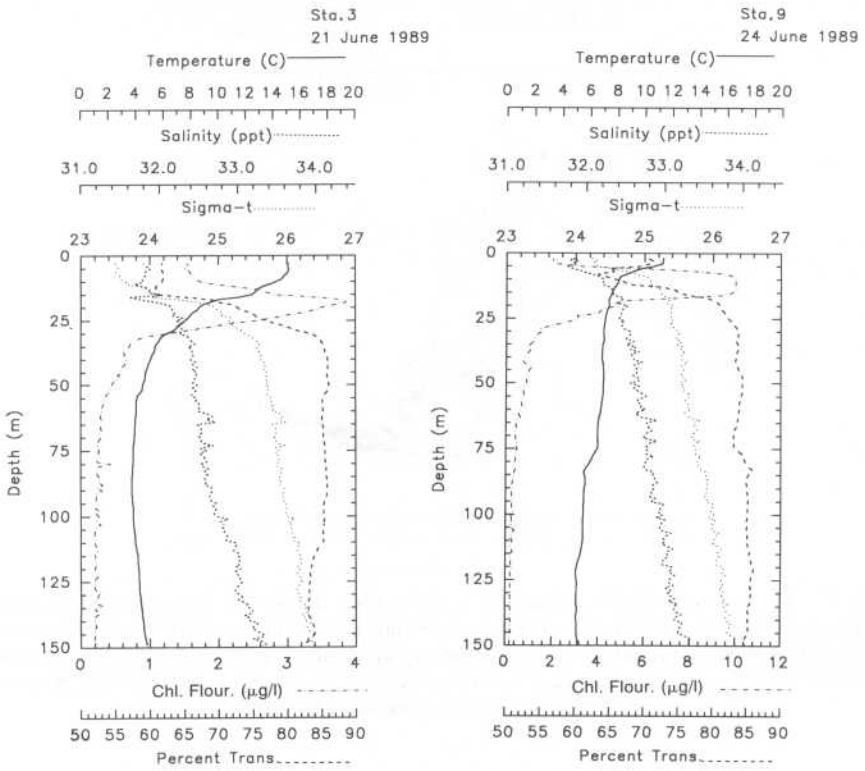

Fig. 6. 1989. Vertical profiles of temperature (°C), salinity (ppt), density (sigma-t), phytoplankton chlorophyll fluorescence ($\mu g\, l^{-1}$) and percentage light transmission for Sta. 3, which was in the coccolithophore bloom, and Sta. 9, which was outside the bloom waters (Fig. 2). Data are depth-averaged over 1-m intervals.

fluorescence at Sta. 9, the light transmission did not drop below 63%, which illustrates the significance of the coccolithophore bloom in light attenuation.

The nutrient concentrations at Stas 3, 4 and 9 are given in Fig. 9. Each nutrient, with the possible exception of silica, was generally depleted in the surface layer at each of the three stations. Phosphate was very low at the two bloom stations (3 and 4) as compared with Sta. 9; surface phosphate was 0.02–0.16 μM in the top 15 m at Stas 3 and 4, while it was more than twice as high, ranging from 0.21 to 0.49 μM at Sta. 9. Also, the nutricline was shallower at Sta. 9 and began at about 10 m, as would be expected given the shallow pycnocline (Fig. 6).

The 1990 *bloom*

The bloom in 1990 was, as in the previous 2 years, a bloom of *E. huxleyi*. Unlike the previous two summers, however, the 1990 bloom was relatively small ($\approx$1800 km^2) and was confined to the Great South Channel and western Georges Bank areas of the Gulf of Maine, as determined from satellite imagery (Fig. 3). Also in contrast to previous years, phtyoplankton chlorophyll *a* concentrations were high (2–4 $\mu g\, l^{-1}$; KILPATRICK, 1990), as is

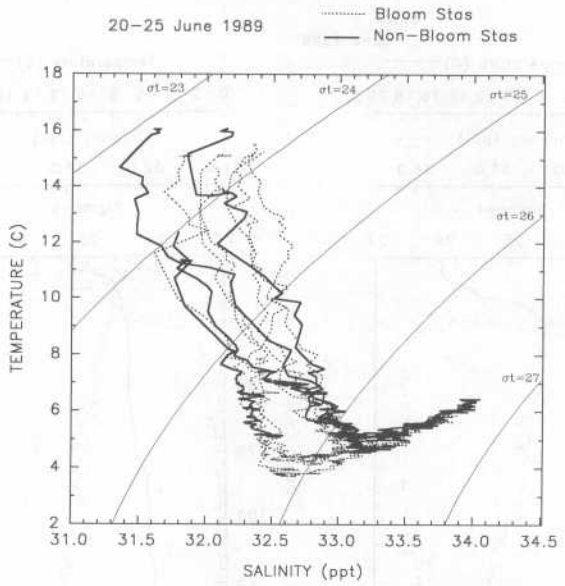

Fig. 7. Temperature–salinity diagram for CTD stations during the 1989 cruise. Data were depth-averaged over 1-m intervals. The stations occupied inside the coccolithophore-rich waters are labelled Bloom Stas, while stations occupied outside the coccolithophore-rich waters are labelled Non-Bloom Stas. Sections 2, 3, 4, 6, C1 and C2 were inside the bloom [Fig. 2(A)]; Stations C3, 5, 9 and 11 were outside the bloom.

common for this productive part of the Gulf of Maine. The chlorophyll could be attributed equally to coccolithophores and other species. Coccolithophores represented only about 50% of the total number of cells present inside the bloom. The other half was composed mainly of phytoflagellates, mostly of the genera *Pyramimonas* and *Tetraselmis*. The abundance of these phytoflagellates remained fairly constant inside and outside the bloom area. Particulate calcite concentrations in the bloom were 1.3–1.9 g $CaCO_3$ m^{-3}, and *E. huxleyi* cell concentrations were $>10^6$ cells l^{-1}. These cell concentrations, as well as those from the previous two summers, are much greater than those reported in the open ocean (10^4–10^5 cells l^{-1}; MITCHELL-INNES and WINTER, 1987; HONJO, 1976). Our estimate of the vertically integrated calcite content in the surface mixed layer, the top 15m within which the bloom appeared to be contained, was about 25 g $CaCO_3$ m^{-2}. Outside of the bloom and beneath the surface mixed layer, calcite concentrations decreased to <0.5 g m^{-3}. This integrated calcite content is roughly equivalent to that reported for a bloom on the northwest European continental shelf (40 g m^{-2}, HOLLIGAN *et al.*, 1983).

The temperature–salinity relationships of bloom and non-bloom stations in 1990 are given in Fig. 10. Three general *T–S* relations can be discerned: The first type includes the shallower stations inside the bloom and in the area of the Great South Channel (Fig. 3); these stations have low surface salinities and a subsurface salinity minimum (Stas 3–10 and 13). The second type includes deeper stations (the non-bloom Stas 1, 2, 11 and 19) which have higher surface salinities, somewhat cooler surface temperatures, and have the densest surface waters of any sampled. There is no overlap of water types one and two on the *T–S* diagram. The third type is probably a mixture of the first two, with warmer near-

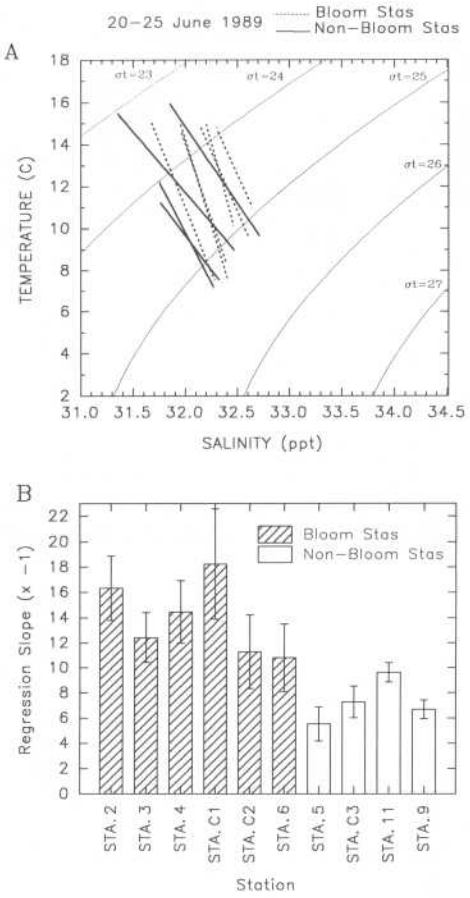

Fig. 8. Fitted linear regression lines of temperature versus salinity for the 1989 bloom and non-bloom station *T–S* data in Fig. 7. Only *T–S* data corresponding to less than 25.25 sigma-*t* units were used in the regressions, in order to represent the hydrographic structure in only the upper water column, and to eliminate excess weighting by greater data density at higher sigma-*t* values. The R^2 values were significant for each. (B) Bar graph of the slopes ($\times -1$) of regression lines for bloom and non-bloom stations in (A). The error bars correspond to plus/minus one standard error. The means of the slopes of the bloom and non-bloom stations were significantly different at the 0.05 level.

surface waters of low salinity, and intermediate-depth salinities that increase quickly with depth, eventually overlapping with deep water characteristics of the type two (non-bloom) stations. The type three stations also were bloom stations (Stas 12, 14 and 15). The waters in which *E. huxleyi* was blooming likely originated from the advection of lower salinity surface waters from the Great South Channel area to the northeast and around the northern edge of Georges Bank (see locations of Stas 12, 14 and 15 in Fig. 3). The *E. huxleyi* bloom was apparently limited to the surface waters of only those stations with low density surface waters (with salinities less than *ca* 32 ppt). We suspect, however, that salinity was not the controlling factor determining the distribution of *E. huxleyi* in 1990; if it were, the 1990 results would be in direct contrast to the results from 1988 and 1989.

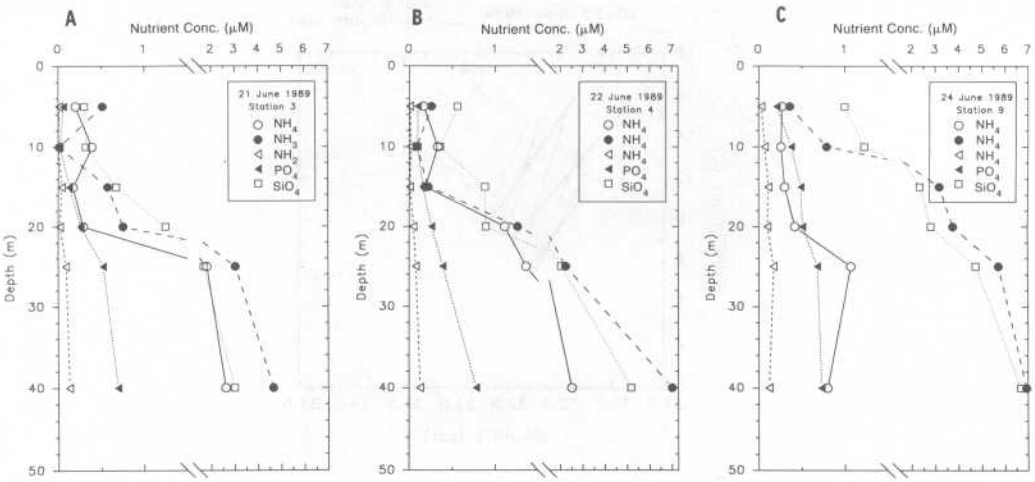

Fig. 9. 1989. Vertical distributions of inorganic nutrients at Stas 3 and 4, which were inside the bloom waters, and Sta. 9, which was outside the bloom (Fig. 2).

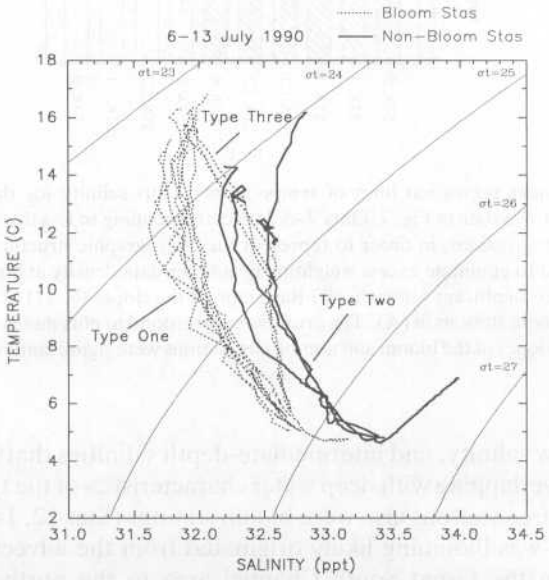

Fig. 10. Temperature–salinity diagram for CTD stations during the 1990 cruise. Data were depth-averaged over 1-m intervals. The stations occupied inside the coccolithophore-rich waters are labelled "Bloom Stas", while stations occupied outside the coccolithophore-rich waters are labelled "Non-Bloom Stas". Three types of water masses can be distinguished: Type one included the bloom Stas 3, 4, 5, 6, 7, 9, 10 and 13; type two stations included non-bloom Stas 1, 2, 11 and 19; type three stations included the bloom Stas 12, 14 and 15.

Vertical profiles of temperature, salinity, density, chlorophyll fluorescence and light transmission for bloom and non-bloom stations are given in Fig. 11. The profiles for Stas 3–5, from among the cluster of bloom stations in the northern end of the Great South Channel (Fig. 3), show quite a bit of variability for stations so close to one another. There is generally fresher water in the upper 20 m, where the bloom is confined, while there is no well-defined surface mixed layer, except in the upper 2–4 m. Each of the bloom stations exhibited a salinity minimum between 5 and 15 m, which could not be ascribed to CTD salinity spiking in the thermocline. The salinity minima at depth could signal a horizontal mixing of surface water masses. Further evidence of horizontal mixing of water masses is seen in the different temperature profiles for Stas 3–5, which were all within 1 or 2 miles of one another (Fig. 3). Station 3 exhibited a stepped thermocline, with four distinguishable mixed layers, while Sta. 4 suggests a smoothing of those layers. Station 5 illustrates more of a single upper mixed layer. The non-bloom stations in Fig. 11 (Stas 2 and 19) have higher surface salinities (>32.1 ppt), which is the only feature distinguishing them from the bloom stations.

The phtyoplankton chlorophyll, as indicated by the fluorescence traces in Fig. 11, was quite high in the subsurface chlorophyll maximum at 10–12 m at Stas 3–5 (up to 4 $\mu g\, l^{-1}$). Again, as in the 1989 bloom, the transmission minimum was shallower than the chlorophyll maximum, and was lower than in 1989, dropping to 51% at 9 m at Sta. 4. At Sta. 2, a non-bloom station, there was also a large subsurface chlorophyll maximum (about 4 $\mu g\, l^{-1}$ at 26 m), but the light transmission did not drop below 74%.

The vertical distributions of nutrients at Stas 2 and 3, shown as examples of the non-bloom and bloom stations, respectively, each showed depletions in the near surface waters (Fig. 12), but nutrients increased with depth nearer the surface at the bloom station (Sta. 3). The phosphate concentrations were similar at each station sampled in 1990; there were no clear indications that phosphate was lower in the bloom waters as had been the case in 1989. Given the complicated nature of mixing inside the bloom waters, it is difficult to draw any generalizations about the nutrient distributions, other than to suggest an influx into the bloom area from horizontal mixing and upwelling.

DISCUSSION

It is well documented that *E. huxleyi* is a major component of the phytoplankton community in the Gulf of Maine (Gran and Braarud, 1935; Marshall, 1984a,b; Marshall and Cohn, 1983). However, intense bloom phenomena with surface manifestations of white water, as are visible in satellite images, are not regular events, and our results would suggest that they may be related to subtle, interannual variability in the hydrography of the Gulf of Maine. Though blooms occurred in each of the 3 years of our study (1988–1990), they do not occur every year in the Gulf of Maine, nor are they predictable. Examination of available satellite imagery from 1979 to 1992 showed that blooms occurred in the Gulf in 1983, and again in 1988, 1989 and 1990. There was no surface manifestation of a bloom in the summers of 1991 and 1992, though *E. huxleyi* was an abundant component of the phytoplankton assemblage (unpublished). We observed that in each of the 3 years of this study in which blooms occurred, they were confined to water masses that could be distinguished from non-bloom waters on a *T–S* diagram. This suggests some unique water mass trait that favored, or allowed, a bloom to form. In 1988, the *T–S* relations for stations at which *E. huxleyi* bloomed suggest that blooms occurred in

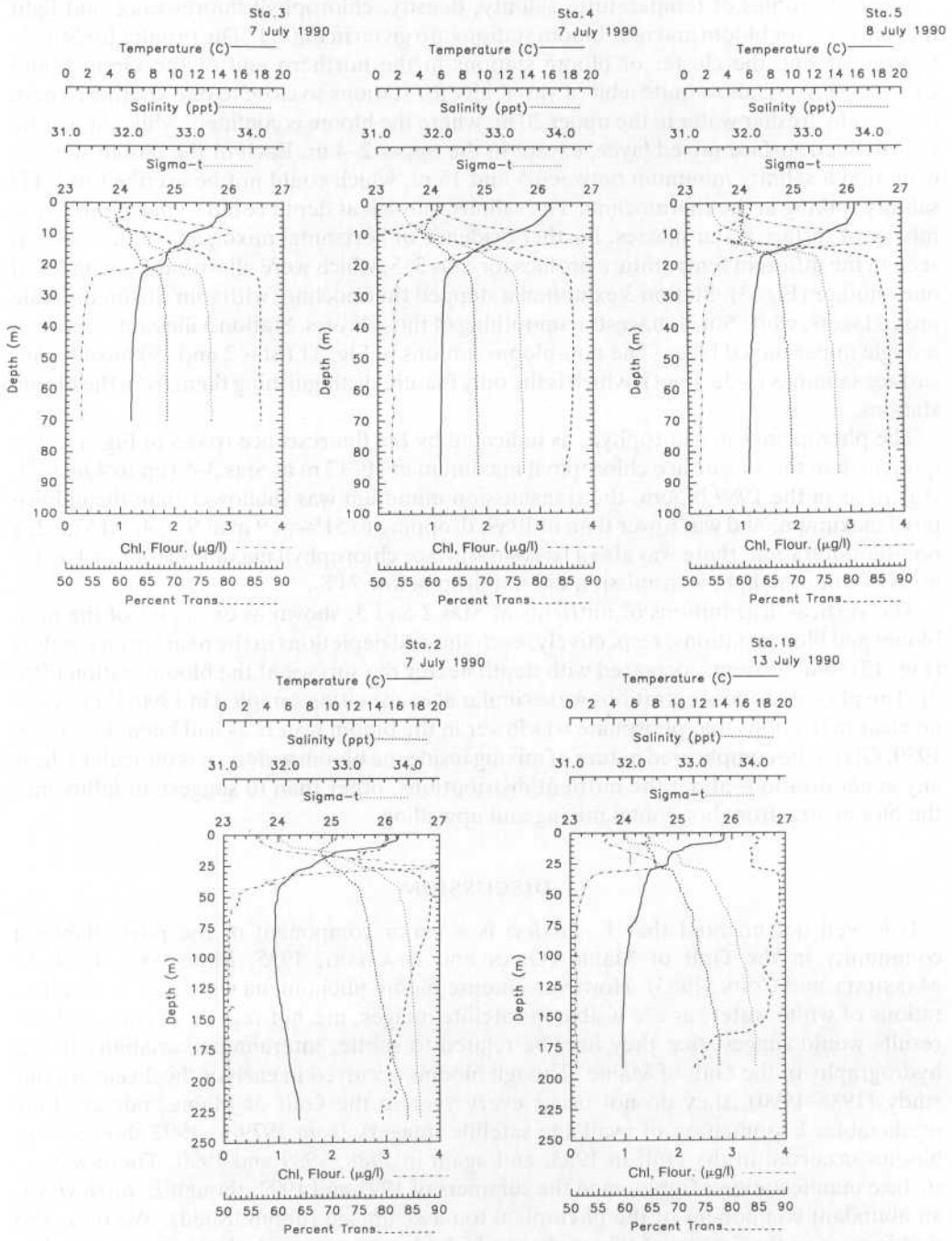

Fig. 11. 1990. Vertical profiles of temperature (°C), salinity (ppt), density (sigma-*t*), phytoplankton chlorophyll fluorescence ($\mu g\ l^{-1}$), and percentage light transmission for Stas 3, 4 and 5, which were in the coccolithophore bloom, and Stas 2 and 19, which were outside the bloom waters (Fig. 3). Data are depth-averaged over 1-m intervals.

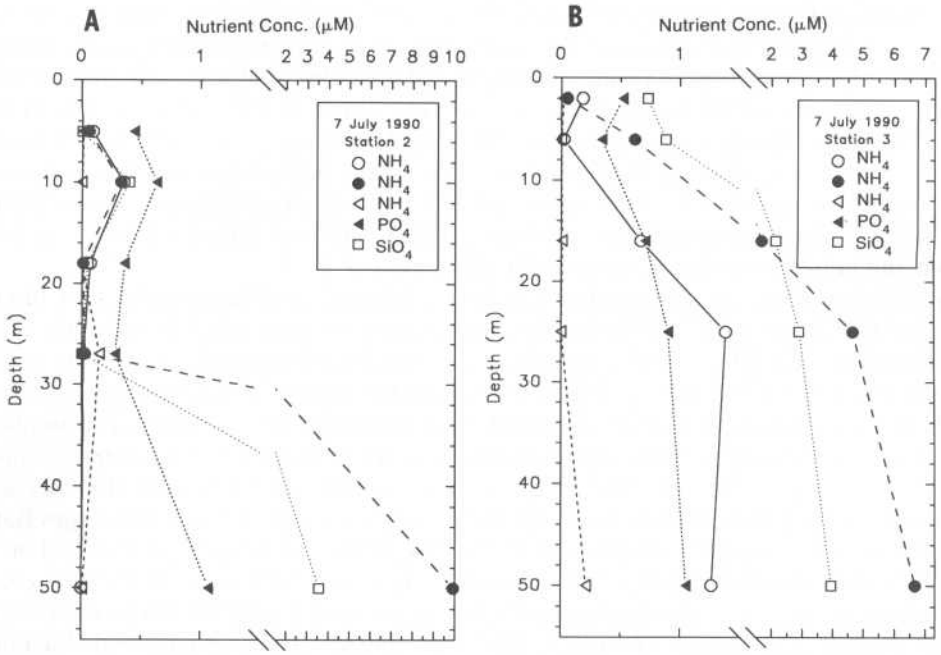

Fig. 12. 1990. Vertical distributions of inorganic nutrients at Sta. 3, which was inside the bloom waters, and Sta. 2, which was outside the bloom (Fig. 3).

surface waters in the Gulf that exhibited a well-defined upper mixed layer, overriding a sharp pycnocline. The bloom did not occur at stations with either upwelling waters or more coastal, fresher waters near the surface. We suggest that the blooms may have been confined that year to older, more mature (well-stratified), but non-coastal, surface waters. The *T–S* relationships in 1989 were similar to 1988 in that the bloom occurred at stations with a better-defined surface mixed layer, as revealed by statistically significant differences in the upper water column *T–S* regression slopes of bloom and non-bloom stations. The situation was complicated in 1990, when the bloom was confined to a relatively small area of the Gulf. The bloom that year was apparently limited to surface waters with lower salinities (in contrast to the 1988 and 1989 blooms), including those stations having a salinity minimum at 5–15 m. The bloom in 1990 was not adjacent to the coast and an immediate source of fresh water and hence the presence of low salinity surface waters in this part of the Gulf, some 100 miles from the nearest major river system, would suggest that the bloom water mass, as in previous years, was relatively "old". The general counter-clockwise circulation in the Gulf of Maine is known to transport coastal waters to this part of the Gulf, and around the northern edge of Georges Bank (Brooks, 1985).

Mitchell-Innes and Winter (1987) described high densities of *E. huxleyi* (2300 cells ml^{-1}), similar to the densities we encountered in the Gulf of Maine, in an upwelling plume off South Africa in what they characterized as mature waters. They noted that the coccolithophores reached their highest densities at the downstream end of the upwelling plume, following a bloom of diatoms and depletion of surface nutrients, although they did not report actual nutrient levels. Reigman *et al.* (1992) demonstrated in laboratory

experiments with mixed phytoplankton cultures that *E. huxleyi* outcompeted diatoms and *Phaeocystis* at higher N:P ratios, suggesting that *E. huxleyi* was a good competitor under P limitation. This experimental result is similar to our field observations for the 1989 bloom, where we found that the levels of phosphate were lowest in the surface waters of the coccolithophore bloom, ranging from 0.02 to 0.16 μM in the top 15 m, vs 0.21 to 0.49 μM over the top 15 m at the non-bloom station. Though the phosphate concentrations were lower in the bloom waters, the N:P ratios were not different (ranging from 5.9 to 6.4 for the top 20 m at bloom and non-bloom stations in 1989), although they were lower, in both bloom and non-bloom waters, than the Redfield ratio of 16.

In 1990 phosphate was similarly low but there were no clear differences between bloom and non-bloom waters (0.3–0.8 μM in bloom and non-bloom waters). The N:P ratio at the non-bloom Sta. 2 in 1990 was 0.6 and at the bloom Sta. 3 was 2.1, consistent with the results of Reigman *et al.* (1992). We must be careful, however, not to draw conclusions from the 1990 bloom, which occurred in an area of horizontal mixing of water masses. The bloom in 1990 may have developed in waters emanating from western Gulf of Maine coastal water which was advected to the south as part of a coastal current system (Franks and Anderson, 1992), around Cape Cod, and out to the Great South Channel–Georges Bank area. Low salinity waters are known to follow this pathway around Cape Cod and on to Georges Bank (Brooks, 1985). The relatively long transit time (several months) could allow these surface waters to age, or mature, as suggested by Mitchell-Innes and Winter (1987), perhaps altering macro-nutrient (and micro-nutrient) levels which might facilitate a bloom of *E. huxleyi*. The mixing of water masses in the area of the 1990 bloom obscured nutrient signatures and contributed to the diverse phytoplankton and zooplankton assemblages there (unpublished). It is not clear to us why the *E. huxleyi* bloom did not occur in other parts of the Gulf in 1990.

Alterations in macro- and micro-nutrient ratios may be at the crux of understanding the episodic nature of coccolithophore blooms in the Gulf of Maine. Brand *et al.* (1983) showed that *E. huxleyi* grows well at low levels of the trace metal micro-nutrients iron, manganese or zinc. More recently, Brand (1991) demonstrated that clones of *E. huxleyi*, including coastal isolates, were not limited by even 10^{-10} M levels of iron, nor did they exhibit any growth response to increasing levels of iron up to 10^{-7} M. Trace metals in sea water are of terrigenous origin, and it follows that more mature, older waters in the Gulf of Maine, such as those waters away from immediate coastal freshwater influences, or away from upwelling of waters in contact with the bottom, would have lower concentrations of trace metals. Wells *et al.* (1991) measured levels of available iron in the Gulf of Maine during the 1988 bloom, and found an order of magnitude higher levels in coastal waters and vertically well-mixed waters. Our observations of *E. huxleyi* blooms in 1988 and 1989, which were apparently confined to offshore waters that were isolated from direct coastal influences or from upwelling of deep waters (as indicated by a sharp pycnocline), as in tidally mixed areas, might relate to iron concentrations. Our observations of *E. huxleyi* blooms in fresher surface waters in 1990 would appear to be in contradiction, unless these fresher offshore waters were sufficiently aged as to have been depleted in micro-nutrients. Given a situation of both low micro- and macro-nutrient levels, *E. huxleyi* might outcompete other neritic phytoplankton species.

Interannual variability in the horizontal and vertical circulation in the Gulf of Maine could lead to years when conditions for bloom formation are better than others with respect to micro- and macro-nutrient levels in surface waters. Changes in freshwater

runoff from as far away as the Gulf of St. Lawrence can have a measurable effect on the hydrography of the Gulf of Maine (SUTCLIFFE, 1978). Slope water influxes through the Northeast Channel represent the ultimate source of most of the inorganic macro-nutrients required for planktonic production in the Gulf of Maine (TOWNSEND *et al.*, 1987; TOWNSEND, 1991). These fluxes into the Gulf of Maine are highly variable (RAMP *et al.*, 1985), as are their trajectories through the Gulf (BROOKS and TOWNSEND, 1989), and these dynamic processes may impart interannual effects on plankton dynamics in the Gulf (TOWNSEND and SPINRAD, 1986).

In conclusion, we believe that our results provide evidence that the hypothesis presented by MITCHELL-INNES and WINTER (1987) is plausible for *E. huxleyi* bloom formation. "Mature waters" or water masses with histories resulting in depletion or alterations in macro- and micro-nutrient levels could provide the right sets of conditions to facilitate bloom formation; however, we cannot eliminate other factors, such as changes in grazing pressures. Advances in our understanding of complicated natural phenomena such as coccolithophore blooms must await an even greater level of understanding of the basic oceanography of coastal regions.

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