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Production and downward flux of organic matter and calcite in a North Sea bloom of the coccolithophore *Emiliania huxleyi*

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ABSTRACT: In July 1993, an extensive study was made of a large bloom of the coccolithophorid *Emiliania huxleyi* in the North Sea halfway between the Shetland Islands and Norway. Here we report on the hydrography, production and sedimentation of particulate organic carbon (POC) and calcite carbon (calcite-C) at 4 stations occupied for 24 h, 2 inside the bloom and 2 just outside. The coccolithophorid bloom was confined to North Sea waters, where a stable shallow mixed layer had been formed. Bloom development had entered the decaying phase, judged by the relatively low living cell number (maximally 1200 cells cm^{-3}), the high number of loose coccoliths (up to 350000 coccoliths cm^{-3}), and the fact that sedimentation of calcite-C exceeded production. In the top 15 m at the bloom stations, the mean daily production of coccoliths was 17 per cell. At the 2 stations outside the bloom, the dominant coccolithophore was a holococcolithophorid (up to 1400 cells cm^{-3}), with insignificant amounts of calcite produced per cell. At these stations, nutrients were present in non-limiting concentrations and production of POC was twice as high as at the bloom stations. In the bloom, mixed layer nitrate levels were below 0.2 µM. Faecal pellets collected in the sediment traps contained large numbers of coccoliths of *E. huxleyi*. Although the numbers of grazers at the 2 stations outside the bloom were not lower than those in the bloom, the volume of faecal matter sedimenting at 50 m was about 70 times lower. It is hypothesized that faecal pellets outside the bloom were so light in weight that they did not sink very far before degradation, whereas the pellets produced in the *E. huxleyi* bloom in general were exported rapidly due to their heavy load of calcite. This implies that recycling of materials in the mixed layer of this bloom is relatively low due to high downward flux rate. The ratio at which POC and calcite-C were sedimenting amounted to 1.3 on average for the 2 bloom stations at 50 m water depth.

KEY WORDS: *Emiliania huxleyi* · Coccoliths · Primary production · Calcification · Calcite dissolution · Sedimentation · Faecal pellets · North Sea

INTRODUCTION

The prymnesiophyte algal group of the coccolithophores comprises one of the main groups of calcifying organisms in the photic zone of the oceanic environment. Intracellularly, they form calcitic particles, the coccoliths, which after completion are extruded and incorporated in the so-called coccosphere. The coccolithophorid skeletal remains are transported downward mainly in the form of faecal matter and aggregates (Honjo 1976, 1978, 1980, Honjo & Roman 1978) and may contribute to up to 70% by weight to the total recent sediments covering the ocean floor above the calcite compensation depth (McIntyre & McIntyre 1971). It has been estimated that 0.8 gigatons of calcite carbon and 0.5 gigatons of organic carbon reach the ocean floor each year (Westbroek et al. 1993). This may show the importance of calcification as a regulatory mechanism in the global ocean carbon flux. Formation of $CaCO_3$ causes a lowering of both the alkalinity and the dissolved inorganic carbon (DIC) and an increase in CO_2 according to the following equation:

$$Ca^{2+} + 2HCO_3^- \longrightarrow CaCO_3 + CO_2 + H_2O$$

Apparently, calcification is a sink for bicarbonate and a source of CO_2 and, since this process mainly takes place in the sunlit part of the ocean, it tends to

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decrease the air to sea gradient of CO_2. This may cause a diminished influx of CO_2 into the sea or even an efflux of CO_2 from the sea to the atmosphere. On the other hand, primary production, which only slightly affects alkalinity, provides an increase in the air to sea gradient of CO_2. Coccolithophores also produce the gaseous compound dimethyl sulphide (DMS), which upon liberation into the atmosphere is oxidized to sulphate (cf. Charlson et al. 1987). Since this substance forms condensation nuclei for water vapour, cloud formation would be enhanced over areas with DMS production; the subsequent diminished solar irradiance may then act as a negative feedback mechanism for coccolithophorid growth and hence DMS production (Charlson et al. 1987).

In recent years much interest has been directed towards the study of the impact of coccolithophores on carbon and sulphur cycles in the global ocean and on world climate. To this purpose the Global Emiliania Modelling Initiative (GEM) was established, an international collaboration using the coccolithophore *Emiliania huxleyi* as a model organism (Westbroek et al. 1993). *E. huxleyi* is the dominant coccolithophorid species occurring world-wide in the ocean surface layer. It forms vast blooms of up to 1 million km^2 especially at mid-latitudes in summer and early autumn, as was revealed by satellite imagery affirmed, in a number of cases, by *in situ* observations (Holligan et al. 1983, 1989, 1993a, b, Groom & Holligan 1987, Ackleson et al. 1988, Brown & Yoder 1994a, b). The satellite detection of blooms is accomplished by the enhanced light reflectance of the surface waters due to the occurrence of loose coccoliths in numbers of up to 400000 cm^{-3}. The loose coccoliths may either be released by the living cell, by desintegration of whole coccospheres after cell lysis, or by zooplankton grazing of cells and subsequent desintegration of faecal matter. An extensive literature exists on the physiological and morphological characteristics of *E. huxleyi*, which is easy to cultivate under laboratory conditions (for references see Westbroek et al. 1993). Furthermore, the development of *E. huxleyi* blooms has been frequently monitored in mesocosms containing natural sea water to which varying amounts of nutrients were added (Bratbak et al. 1993, Egge 1993, Egge & Heimdal 1994). Blooms occurring in the natural environment have also been thoroughly studied including two on the continental shelf of the Gulf of Maine (Balch et al. 1991, 1992), one at the shelf edge (Holligan et al. 1983) and one in the open ocean (Holligan et al. 1993a). However, many questions still remain as to the success of this species and its impact on the carbon and sulphur cycles.

In the North Sea area many blooms of *Emiliania huxleyi* develop each year in summer, as revealed by satellite imagery (Holligan et al. 1989, 1993b). Yet, only occasionally have *in situ* observations of blooms occurring here been reported. In July 1993 a cruise, named BLOOM 93, with the Dutch research vessel 'Pelagia' was undertaken to monitor a large number of physical, chemical and biological parameters in such *E. huxleyi* shelf sea blooms. By means of satellite images the ship was guided to a highly light-reflecting area situated halfway between the Shetland Islands and Norway (see Fig. 1). Upon arrival the water appeared to have a whitish, turquoise coloration characteristic for *E. huxleyi* blooms (Holligan et al. 1993a) and microscopic inspection of water samples revealed, indeed, the presence of this species. In this report we focus on experiments performed at 4 stations occupied for 24 h, 2 of which were located inside the bloom and the other 2 outside, but in close proximity to the bloom. Here, we present (1) hydrographic data, (2) the calcite and particulate organic carbon (POC) production, and (3) the downward flux of particulate matter as measured with floating sediment traps. Our objectives were (1) to assess the growth conditions of an *E. huxleyi* bloom and (2) to quantify the impact of such a bloom on material fluxes, in particular that of carbon.

MATERIAL AND METHODS

Sampling stations. BLOOM 93 lasted from 28 June until 13 July 1993. Satellite images were recorded prior to and during the cruise by the Advanced Very High Resolution Radiometer (AVHRR) aboard the NOAA satellites. Image processing was done as in Groom & Holligan (1987). A total of 34 stations were sampled. At 4 main stations, Stns 7, 12, 15 and 19, *in situ* experiments were performed lasting for 24 h. In this study only the results obtained at these 4 stations are described. Stns 7 and 15, respectively occupied on 1/2 and 7/8 July, were located within the bloom; Stns 12 and 19, respectively occupied on 4/5 and 10/11 July, were situated outside the bloom (see Fig. 1).

Hydrography and (bio)chemical analyses. Vertical profiles of salinity, temperature and the beam attenuation coefficient at 530 nm were recorded. The first 2 parameters were measured with a CTD manufactured by Sea-Bird Electronics type SBE9+. The beam attenuation coefficient was measured with a transmissometer manufactured by Dansk Havteknik (Denmark) and was corrected for the beam attenuation in pure seawater. The light levels of the solar irradiance at various water depths were measured at the sun's zenith with a spherical photosynthetic active radiation (PAR) (400 to 700 nm) sensor.

At 04:00 h, water samples were collected using a rosette sampler with 10.5 l NOEX bottles (Technicap) from 2, 5, 10, 15, 25 (27 at Stn 7), 40 and 50 m for nutri-

ents, dissolved inorganic carbon (DIC), POC, calcite, calcium-ions, chlorophyll *a* (chl *a*), phaeopigments, phytoplankton cells and loose coccoliths and for the assessment of rates of photosynthesis and calcification. Phosphate, nitrate, nitrite, ammonium and silica concentrations were measured in water samples filtered through Acrodisc filters with pore diameter 0.2 µm (Gelman Sciences) by means of a Traacs 800 autoanalyzer. DIC was determined according to the coulometric method described in DOE (1991). POC was determined in material retained on 47 mm, pre-combusted Whatman GF/F glass fibre filters after filtration of 3.5 to 5 l of seawater sample. Filters were stored immediately at −50°C. In the laboratory, 12 circular punches, 4.2 mm in diameter, from each filter were placed in a small cup of tin foil and acidified with H_2SO_3 so as to volatilize the carbon present in the calcite. POC was analysed with a Carlo-Erba NA-1500 CHN analyser according to the Dumas combustion method. Calcite was measured in material retained on polycarbonate filters (Isopore) with pore diameter 0.8 µm after filtration of 0.3 to 1.0 l of seawater. While still in the fitration apparatus, filters were quickly rinsed twice with 5 ml of a 5 mM NH_4HCO_3 solution (pH 8) to remove all seawater. Prior to filtration, filters and equipment were washed in 6 N HCl and then carefully rinsed in a 5 mM NH_4HCO_3 solution (pH 8). Filters were stored at room temperature. In the laboratory they were transferred to plastic tubes containing 5 to 10 ml 0.1 N HCl (supra pure) solution. After 12 to 18 h the Ca-ion concentration was measured in the solution with a flame atomic absorption spectrometer (Perkin Elmer 2380). Ca-ion concentrations in the seawater were determined by flame atomic absorption spectrometry after a 100- to 200-fold dilution of the samples with demineralized water. Chl *a* and phaeopigments were determined fluorometrically according to the method described by Holm-Hansen et al. (1965).

Phytoplankton analysis. To measure concentrations of coccospheres and loose coccoliths 0.1 to 1.0 l samples were fixed in buffered formalin and carefully filtered through cellulose acetate filters with pore diameter 0.45 µm (HAWP Millipore filters). Filters were stored at −50°C. In the laboratory the filters were dried and mounted on microsope slides with the resin Canada balsam (Serva), by which treatment they become transparent. Coccospheres and loose coccoliths were counted by viewing the preparations under a microscope using crossed polarizers. In combination with fluorescence microscopy the coccospheres containing chlorophyll, the living cells, could be distinguished from empty coccospheres, the dead cells.

Scanning electron microscopical studies have revealed that at least 4 coccolith morphotypes are present within the *Emiliania huxleyi*-complex (Young & Westbroek 1991). With antibodies raised against the polysaccharides present in the coccoliths the identification of 2 of these types, types A and B, could also be performed by light microscopy (Van Bleijswijk et al. 1991). Using the same antibodies we have made immunoassays according to the procedure described below. Water samples of 250 ml to 1 l were fixed in buffered formalin and then filtered through Sudan Black stained, 47 mm polycarbonate filters with 0.8 µm pore size. The filters were stored at −50°C. In the laboratory filters were dried and cut into square pieces of about 1 cm^2. These filter pieces were exposed to about 1 ml of the various reactants and rinsing fluids used and transferred from one fluid to the next with a pair of tweezers. The composition and sequence of application of the fluids was as follows: Filtered seawater with 0.05% Tween (several minutes); filtered seawater containing 0.05% Tween, 1% newborn calf serum and the antibody (1 h, 4°C in the dark); filtered seawater with 0.05% Tween (3 times for several minutes); filtered seawater containing 0.05% Tween, 1% newborn calf serum and the fluorescent label swine anti-rabbit FITC (30 min, 4°C in the dark); filtered seawater with 0.05% Tween (2 times for several minutes); filtered seawater (several minutes). The filters were then dried and mounted on microscope slides with immersion oil and viewed in a fluorescence microscope.

By means of a flow-cytometer (EPICS CS), installed on board, algal groups present in 0.5 ml untreated samples were counted and classified according to their size. The excitation wavelength used was 488 nm (Veldhuis & Kraay 1990).

Some phytoplankton material sampled in the water column and also material collected in sediment traps (see below), that were mounted on either HAWP Millipore filters or polycarbonate filters prepared for light microscopical inspection, were also viewed in the scanning electron microscope. Small pieces of filter were mounted on aluminium stubs, coated with a thin layer of gold and examined in a Jeol 6400 at 25 kV.

Particulate carbon production and calcite dissolution. The production of POC and calcite was measured with the radioactive isotopes ^{14}C and ^{45}Ca, respectively. Duplicate samples, contained in 60 ml Nalgene bottles, were spiked with 222–259 kBq $NaH^{14}CO_3$ or 296–481 kBq $^{45}CaCl_2$ and incubated in the open sea at their depth of collection. These *in situ* incubations were terminated after 24 h. Another set of samples, also contained in 60 ml Nalgene bottles, were wrapped in black plastic foil after labeling and stored for 24 h at *in situ* temperature. Assuming that dark-uptake of label did not occur, these samples were used to correct uptake rates for adsorption of radionuclides to particulate matter and for ion-exchange effects. After incubation, ^{14}C-labeled samples were carefully filtered

through Whatmann GF/F filters at vacuum pressures below 0.2 bar, so as to avoid breakage of the cells. To remove excess label the GF/F filters were acidified with fuming HCl for several minutes and dried at 60°C for several hours. After that, each filter was transferred to a scintillation vial to which, subsequently, was added 9 ml of the scintillation fluid Instagel. After incubation, the ^{45}Ca-labeled samples were suction-filtered through polycarbonate filters with 0.8 µm pore size. While still in the filtration apparatus the filter was washed 3 times with 30 ml filtered sea water in order to remove excess label. The filter was then transferred to a scintillation vial and subsequently soaked in 1 ml 0.1 N HCl to dissolve the calcite retained. Then 18 ml Instagel was added. The type of filter used is of paramount importance in these experiments. Laboratory testing revealed that GF/F filters were superior to polycarbonate filters in causing the least damage to cells, while radioactive bicarbonate could still completely be removed from the GF/F filters by the acidifying and drying procedure described above. Excess radioactive $CaCl_2$ can only be removed by thorough washing of the filters. In this process cells may easily break causing loss of the intracellular pool of labeled calcium other than coccoliths. Laboratory testing showed that excess ^{45}Ca could completely be removed from polycarbonate filters; the GF/F filters performed poorly in this respect. In order to determine the total amount of label added, 0.1 ml sea water samples were taken from a selected number of spiked bottles. Samples were put in a scintillation vial and mixed with 9 ml Instagel. The radioactivity was measured in a Wallac-LKB liquid scintillation analyzer, type 1909 Rackbeta. Quenching was corrected using the channels ratio method. The measured concentrations of DIC and Ca-ions were used to assess the specific activities of the respective labels.

One experiment was performed to determine calcite dissolution. Nine samples collected from 5 m depth at a station located within the *Emiliania huxleyi* bloom were spiked with 444 kBq $^{45}CaCl_2$ and were then incubated on deck. The incubator was kept at ambient sea water temperature. After 75 h the samples were wrapped in black plastic foil and placed back in the incubator. Radioactivity in the particulate fraction was measured after 4, 8, 24 and 48 h of dark incubation according to the procedure described above. One sample collected at the same site and depth and spiked with a similar amount of tracer was immediately incubated in the dark at ambient sea water temperature at the onset of the experiment. This sample was processed at the end of the experiment and was used to correct for adsorption and ion-exchange effects.

Sediment traps. The sediment traps used were 65 cm high funnels with a maximum width of 40 cm steeply tapering towards a removable sampling bottle. The cir-

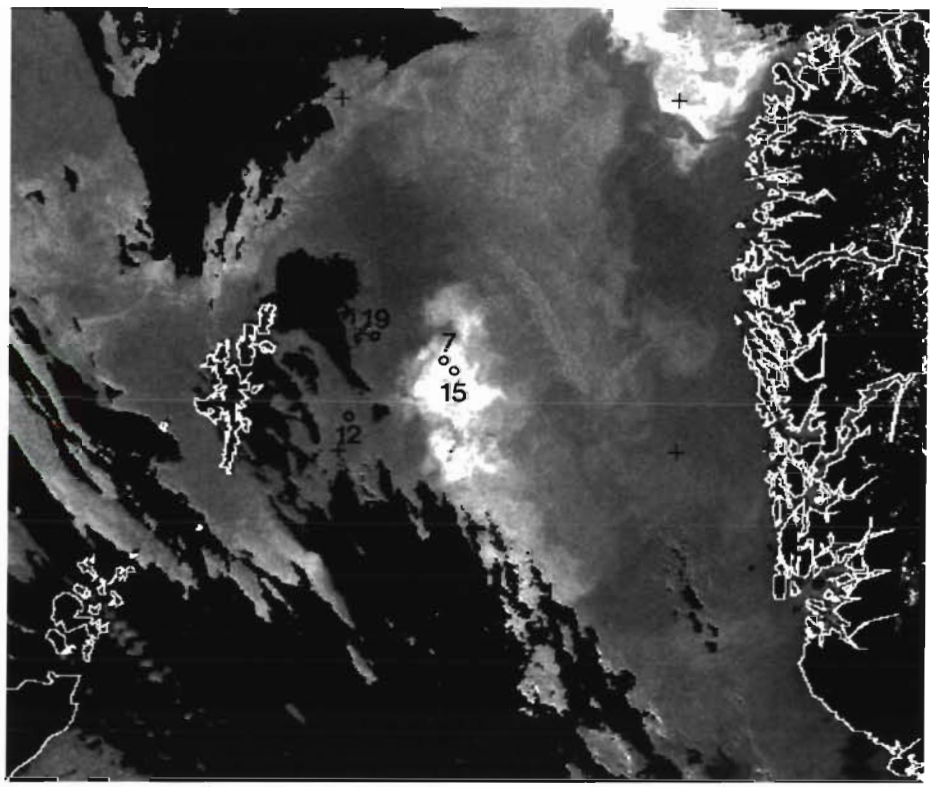

Fig. 1. AVHRR visible band image recorded on 27 June 1993 covering an area of the northern North Sea and adjacent Atlantic Ocean between 58° N (lower edge of image) and 62° 30' N and between 4° W and 7° E. The high reflectance waters (lighter shades) off the east coast of Shetland demarcate the studied *Emiliania huxleyi* bloom. The positions of the 4 *in situ* stations are indicated. Land and clouds are masked in black

cular catchment area had a diameter of 20 cm and contained a 1 × 1 × 5 cm deep grid. A valve above the bottle could be closed after recovery of the trap so as to avoid loss of sedimented material: without a valve the traps vigourously empty upon detachment of the bottle. These 'Kiel-type' traps (Zeitzschel et al. 1978) were deployed in duplicate during 24 h in the mixed layer at a depth of 10 m and below the mixed layer at 50 m depth. They were freely drifting and attached to a buoy equipped with a flash light and a radio beacon. To the bottle of one of the traps at each depth 50 ml of a solution containing 18% formalin buffered with 20% hexamine was added to stop microbial and zooplankton activity. After collection, the trapped material was transferred to plastic containers, fixed in buffered formalin and stored at room temperature.

Caught zooplankton were identified and counted using a binocular microscope. Subsamples of the trapped material were filtered through cellulose acetate filters with pore diameter 0.45 µm (HAWP Millipore filters), dried and mounted on microsope slides with Canada balsam. By this treatment they become suitable for microscopical investigation using transmitted light. The length and width of faecal pellets were measured and their volume calculated assuming that they were cylindrical or spherical in shape. POC and calcite were measured in material trapped by the poisoned and non-poisoned traps deployed at 50 m depth in the stations situated in the *Emiliania huxleyi* bloom (Stns 7 and 15). Subsamples were filtered over precombusted Whatman GF/F filters. From the material retained by the filters all zooplankters were removed, which include copepods, gastropods, pelecypods and Foraminifera. Each filter was then transferred to an ampoule to which subsequently 4 ml 3% phosphoric acid was added. All CO_2 escaping from the ampoule was measured in an infrared analyzer, 0524B Total Carbon System (Oceanography International Corporation, Cadée 1986). The result gives a measure of the total amount of detrital calcite-C retained on the filter. Next, in order to also measure the POC content, 200 mg potassium persulphate was added to the same ampoule. After sealing and autoclaving, the ampoule was broken. All CO_2 derived from the oxidation of organic matter was measured in the same infrared analyzer. Filters over which filtered seawater (0.2 µm) was filtered were used as blanks.

RESULTS

Hydrographic data

Fig. 1 is a NOAA satellite image of the northern North Sea and adjacent Atlantic Ocean recorded in the period that RV 'Pelagia' visited the area. The high reflectance of the waters off the east coast of Shetland is the result of bloom development of the coccolithophorid *Emiliania huxleyi*: the large numbers of loose coccoliths formed during this development cause a relatively high backscatter of the incoming radiation. The position of the four 24 h stations are indicated in the figure. Stns 7 and 15 were located inside the bloom and Stns 12 and 19 outside of it. The water depths at these stations ranged between 134 and 145 m. The beam attenuation coefficient c530 (corrected for the attenuation in pure sea water) was highest in the top layer of the coccolithophore-rich waters being about 1.5 and 1.0 m^{-1} at Stns 7 and 15, respectively (Fig. 2A). Between 20 and 40 m, the beam attenuation coefficients rapidly declined and minimal values of about 0.05 m^{-1} were reached at 60 m water depth. Since the transparency of the water in these 2 stations is predominantly determined by the presence of detached coccoliths, the profiles show that the bulk of these particles is located in the top 30 m of the water column (see also below). At the other 2 stations, beam attenuation coefficients were also maximal in the top layer of

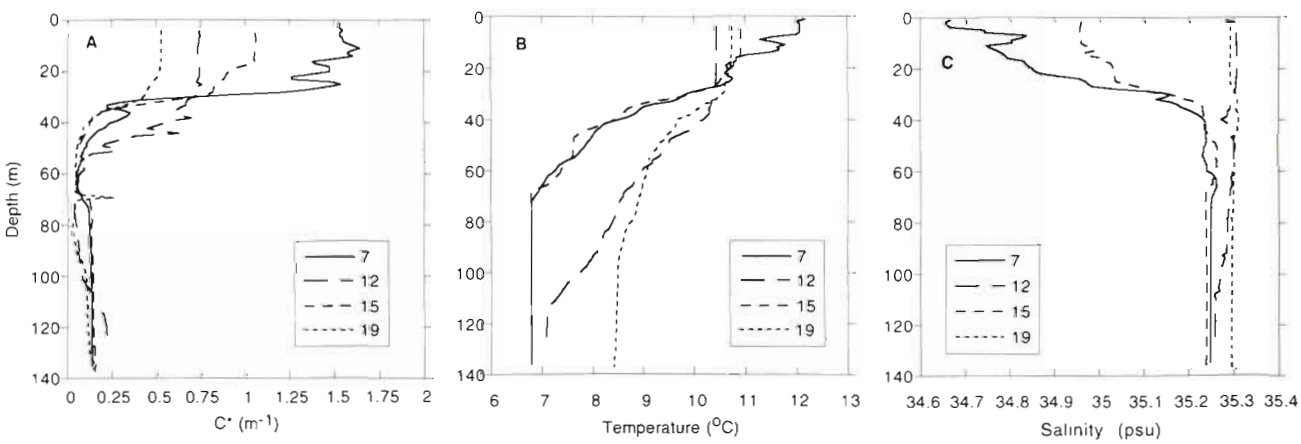

Fig. 2. (A) Light transmission profiles, recorded at 553 nm, (B) temperature profiles and (C) salinity profiles at Stns 7, 12, 15 and 19

the water column, reaching values of 0.7 and 0.5 m^{-1} at Stns 12 and 19, respectively, and declined below 20 m to minimal values of about 0.05 m^{-1} at 60 m. The lower transparency in the top layer at Stn 12, as compared to the transparency at Stn 19, is caused by the fact that here both the content of detached coccoliths and chl *a* were higher than at Stn 19 (see below). The 1% isolumen for the PAR was situated at 16, 31 and 14 m water depth at Stns 7, 12 and 15, respectively. No PAR measurements were performed at Stn 19.

The temperature and salinity profiles recorded were very similar for Stns 7 and 15 (Fig. 2B, C): (1) the bottom of the thermocline was at about 70 m, (2) the temperature of the bottom layer was 6.8°C, (3) in the top 40 m of the water column a halocline had formed, and (4) below the halocline salinity remained rather constant at about 35.25 psu. The profiles at these stations differed in that at Stn 7 temperatures in the mixed layer were higher and salinities in the halocline were lower. The temperature and salinity profiles of Stns 12 and 19 showed considerable similarity in the first 60 m of the water column. Below that depth both temperature and salinity at Stn 12 started to deviate from those of Stn 19, reaching values in the bottom layer that were very close to those measured at Stns 7 and 15. At Stn 19 the temperature of the water below the thermocline was about 8.4°C and the salinity values over the total water column showed a very narrow range of only 35.29 to 35.30 psu.

The low salinity layer at Stns 7 and 15 is established through the input of river water into the North Sea basin after the storm season. During winter North Sea waters are completely mixed at these sites (Otto et al. 1990). No fresh water input is apparent at Stns 12 and 19. The salinity in the upper water layer at Stn 12 is similar to that at Stn 19, whereas both salinity and temperature in the bottom layer at Stn 12 are similar to those at Stns 7 and 15. These observations clearly indicate that Stn 12 is positioned within the frontal system where Atlantic and North Sea waters meet. The waters at Stn 19 have an Atlantic signature.

The profiles for the phosphate (P) concentrations at Stns 7 and 15 show considerable similarity (Fig. 3A). Concentrations were lowest in the mixed layer, viz. about 0.1 µM, increased rapidly in the thermocline and remained more or less constant in the bottom layer at values of about 1.0 µM. The phosphate profile in the 'Atlantic' Stn 19 has a similar sigmoidal form, but the values only varied from 0.3 µM in the mixed layer to 0.85 µM in the bottom layer. At Stn 12, the mixed layer concentrations of phosphate were intermediate between those of Stns 7 and 15 on the one hand and Stn 19 on the other. In the lower half of the thermocline concentrations were similar to those at Stn 19 and in the bottom layer a value was measured comparable to those found at Stns 7 and 15, which may again indicate that this layer has a North Sea signature.

The depth profiles for the nitrate concentrations are almost identical in shape to those of the phosphate concentrations (Fig. 3B). The mean values in the mixed layer at Stns 7 and 15 were 0.08 and 0.15 µM, respectively, and at Stns 12 and 19 were 1.48 and 3.93 µM, respectively. In the bottom layer nitrate concentrations were lowest at Stn 19. In the mixed layer ammonium concentrations were generally higher at Stns 7 and 15 as compared to those at Stns 12 and 19 (Fig. 3C). Maximum concentrations were attained in the thermocline layer and were especially prominent at Stns 7 and 15. This maximum is caused by the combined effect of remineralization of organic N-compounds in the top 60 m of the water column and the incorporation of ammonium again into organic compounds by the autotrophic biota in the mixed layer.

The N/P ratios below the mixed layer at all 4 stations ranged between 13 and 15. In the mixed layer at Stns 12 and 19 these ratios were similar to those measured in the water column below. In the coccolithophore-rich mixed layer at Stns 7 and 15, the N/P ratios ranged

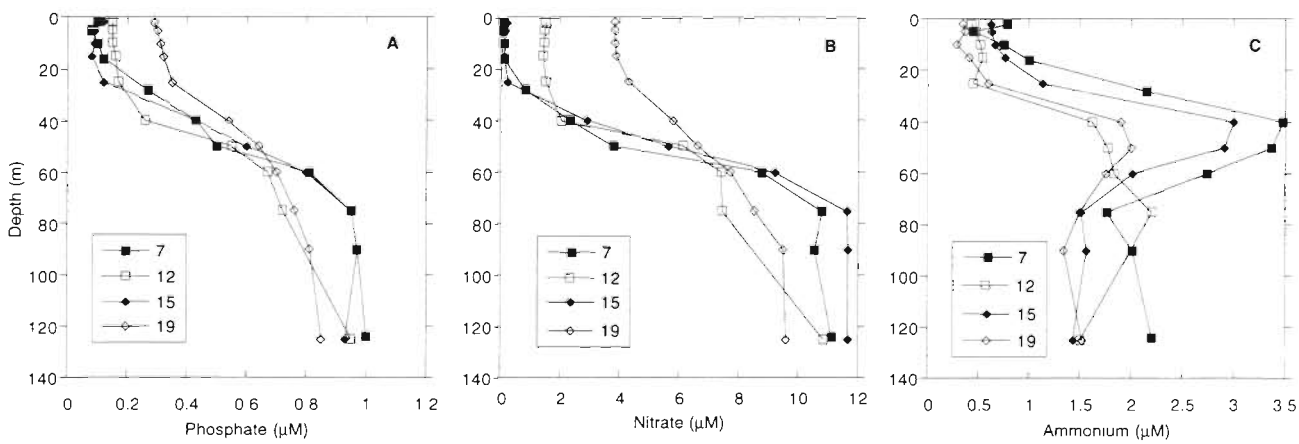

Fig. 3. (A) Phosphate, (B) nitrate and (C) ammonium concentrations at Stns 7, 12, 15 and 19

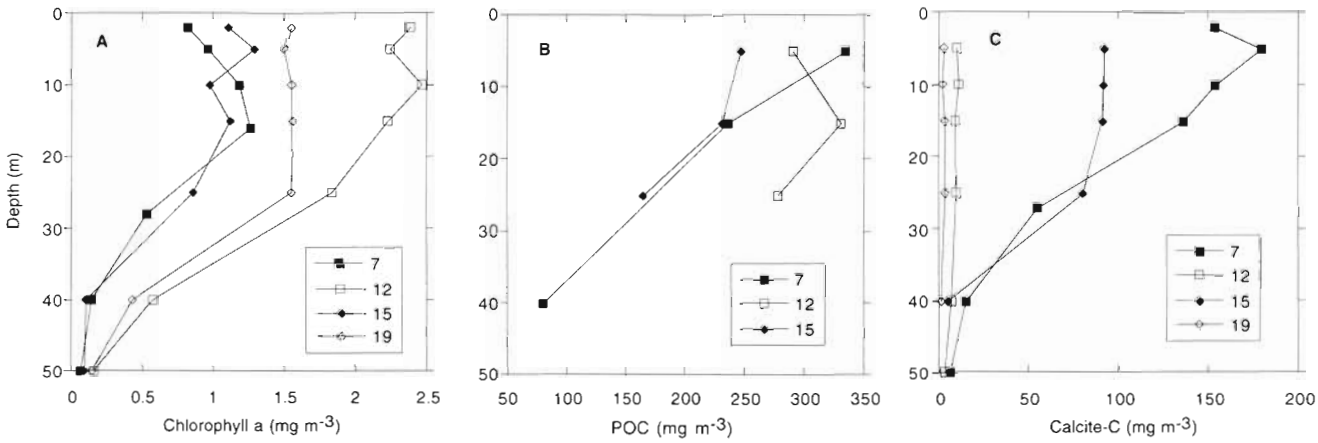

Fig. 4. (A) Chlorophyll *a*, (B) POC and (C) calcite-C concentrations at Stns 7, 12, 15 and 19

between 6 and 11. No data were collected on the concentrations of the dissolverd organic nitrogen and phosphorus compounds.

Si concentrations were only measured at Stns 7 and 12. In the mixed layer the average concentration amounted to 0.6 µM in the 2 stations. In the thermocline layer concentrations rapidly increased to values of 5 to 7 µM in the bottom layer (data not shown).

The chl *a* concentrations in the coccolithophore-rich mixed layer at Stns 7 and 15 were on average about twice as low as at Stn 12 and about 1.5 times as low as at Stn 19 (Fig. 4A). The mean chl *a*/phaeopigment ratios measured in the mixed layer at Stns 7 and 15 were 4.6 and 5.4, respectively. At Stns 12 and 19 these ratios were about 1.5 times higher amounting to 7.4 and 7.8, respectively. At Stns 7, 12 and 15 only a limited number of samples were analysed for POC and particulate organic nitrogen (PON) content (Fig. 4B). In the stations located in the *Emiliania huxleyi* bloom a maximum POC content of 334 mg POC m^{-3} was measured. Here, POC levels declined to less than 100 mg POC m^{-3} at 40 m depth. Similar values were also measured at Stn 4, which was also situated inside the *E. huxleyi* bloom. Outside the *E. huxleyi* bloom maximum POC levels were similar to those inside the bloom. Due to lack of data, a clear trend of POC concentrations with depth could not be assessed in the area outside the bloom. The POC/PON ratios in the mixed layer waters at Stns 7, 12 and 15 were 7.7, 6.7 and 6.8, respectively. In the top 15 m in the coccolithophore-rich waters of Stns 7 and 15, the mean calcite-C concentration amounted to 155 and 92 mg m^{-3}, respectively; below the mixed layer concentrations declined (Fig. 4C). At 50 m depth at Stn 7, e.g. calcite-C content was only 6 mg m^{-3}. At Stns 12 and 19 the mean calcite-C concentrations in the mixed layer were 10 mg m^{-3} and 3 mg m^{-3}, respectively; at 50 m water depth calcite-C concentrations were about 3 times lower.

Coccolithophores and other algal species

The phytoplankton cells in the 4 stations were rather small with maximum diameters of about 6 µm. Cell numbers and biodiversity of the phytoplankton community were larger at Stns 12 and 19, the 2 Atlantic stations. The most conspicuous differences were the occurrence of large numbers of a holococcolithophorid species and a small pennate diatom species at Stns 12 and 19, which were absent at Stns 7 and 15. Also, flow-cytometric analysis of sea water samples revealed the presence of a group of eukaryotes with a diameter of about 2 to 2.5 µm in the former 2 stations, which were not detected in the latter 2. Cyanobacteria were an important constituent at all 4 stations. By flow-cytometry up to 35000 cells cm^{-3} were counted in the mixed layer at Stns 7 and 15, and about 50000 and 60000 cells cm^{-3} in the mixed layer at Stns 12 and 19, respectively. The immunofluorescence staining technique enabled us to distinguish between 2 morphotypes of *Emiliania huxleyi* by using fluorescence microscopy. It appeared that type A was the dominant morphotype. Type B was absent from Stn 19 and in the other 3 stations relatively low numbers of loose coccoliths of this type were found and only sporadically a whole coccosphere.

In the high reflectance waters, *Emiliania huxleyi* was the dominant coccolithophore. At Stn 7 living cell numbers showed a sharp maximum of about 1200 cells cm^{-3} at 10 m depth (Fig. 5A). The number of empty coccospheres (cells without detectable traces of chlorophyll) were about equally abundant in the top 30 m of the water column in this station amounting to about 600 specimens cm^{-3} (Fig. 5B). Here, the number of living cells exceeded the number of empty coccospheres by a factor of 1.5 on average. In the other station located in high reflectance waters (Stn 15) the total number of cells (living and dead) were quite similar to that found at Stn 7. However, only about 20% of these

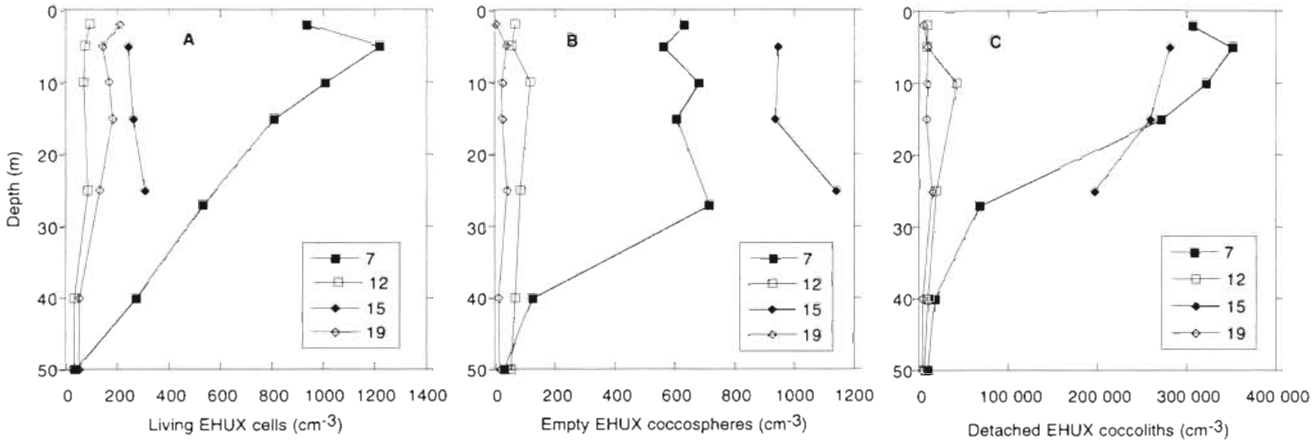

Fig. 5. *Emiliania huxleyi* (EHUX). Numbers of (A) living cells, (B) empty coccospheres and (C) loose coccoliths at Stns 7, 12, 15 and 19

cells were alive (Fig. 5A, B). Within the *E. huxleyi* bloom 2 other heterococcolithophorid species were detected by using scanning electron microscopy. They only occurred in subordinate numbers and were identified as *Syracosphaera pulchra* and *Algirosphaera* sp.

At the 2 stations outside the *Emiliania huxleyi* bloom, the *E. huxleyi* cell numbers, i.e. living cells and empty coccospheres, amounted to about 200 cells cm^{-3} in the top 25 m of the water column in both stations (Fig. 5). At Stn 19 the viability of the *E. huxleyi* population was high with 3 to 50 times as many living cells as empty coccospheres. At Stn 12 living and dead *E. huxleyi* cells were present in about equal numbers. The dominant coccolithophore in these 2 stations was a holococcolithophore with a maximal count of about 1400 cells cm^{-3} at 5 m depth at Stn 19. Because of the low birefringence of their coccoliths they were not detected on the HAWP Millipore filters. However, due to the fact that their coccoliths showed a positive reaction with the antibody raised against the coccolith polysaccharide of *E. huxleyi* type A cells, this species could be distinguished and counted in the samples prepared for the immuno-assays. Subsequent scanning electron microscopy revealed that we dealt with an unknown species that can be classified as belonging to the genus *Anthosphaera*. The coccosphere is about 4 µm in diameter and is composed of about 100 calyptroform ordinary holococcoliths and several fragarioform stomatal holococcoliths (cf. Kleijne 1991). A detailed description of this new, bloom-forming species will be published elsewhere.

Highest numbers of detached coccoliths were encountered in mixed layer waters of Stn 7 with a maximum of over 350000 specimens cm^{-3}; beneath the mixed layer in this station numbers rapidly declined to less than 10000 cm^{-3} at 50 m (Fig. 5C). At Stn 15, similar coccolith numbers were found in the mixed layer with a maximum of 281000 cm^{-3} at 5 m. In the mixed layer waters of Stns 12 and 19 coccolith numbers amounted to about 20000 and 10000 cm^{-3} on average, respectively. At 5 m water depth, the loose coccolith/coccosphere ratio was about 200 at Stns 7 and 15 and about 60 at Stns 12 and 19. There was a strong correlation between the concentration of detached coccoliths and the concentration of calcite-C as revealed by linear regression analysis of all data ($R^2 = 0.951$, n = 23). However, no proper estimate could be made of the amount of calcite-C per coccolith: at Stns 7 and 15, the attached coccoliths were incorporated in multilayered coccospheres and aggregates and no reliable counts could be obtained of the number of coccoliths present in them; at Stns 12 and 19 other coccolithophorid species contributed to a large extent to the measured calcite concentrations.

Production of POC and calcite-C

Photosynthetic rates were maximal in the upper 5 m of the water column amounting to about 80 and 60 mg POC m^{-3} d^{-1} in the low reflectance waters of Stns 12 and 19, respectively, and to about 40 mg POC m^{-3} d^{-1} at the 2 stations located in the *Emiliania huxleyi* bloom (Fig. 6A). The rates gradually decreased with depth reaching values less than 2 mg POC m^{-3} d^{-1} below 25 m at the latter 2 stations and below 40 m at the other 2 stations. The total daily production of POC was about 2 times higher in the low attenuation waters as compared to that in the high attenuation waters with a maximum of 1329.5 mg POC m^{-2} d^{-1} at Stn 12 (Table 1). The differences in productivities are largely related to differences in both chl *a* content and transparency of the waters at the respective stations (see Figs. 2A & 4A). The production of POC per unit chl *a* at the 4 *in situ* stations is illustrated in Fig 6B. In the top 5 m of the water column there was not much difference

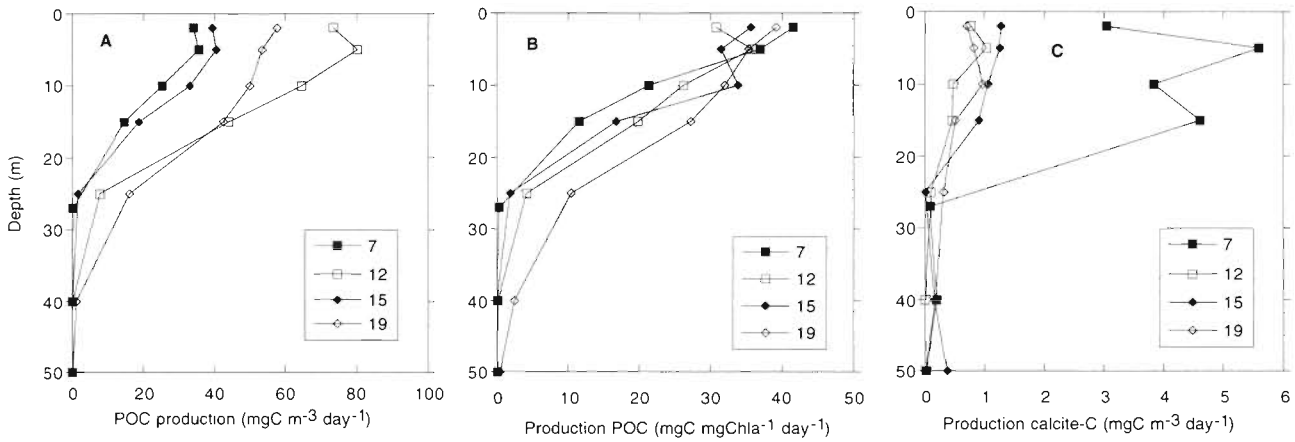

Fig. 6. (A) Production of POC, (B) production of POC per unit chlorophyll *a* and (C) production of calcite-C at Stns 7, 12, 15 and 19

in chlorophyll performance among the stations with mean values ranging between 33 and 39 mg POC mg^{-1} chl *a* d^{-1}. With increasing depths the performance of chlorophyll declines at a rate that is largest at Stn 7 and smallest at Stn 19. This phenomenon is related to the transparency of the water in the mixed layer, which was minimal at Stn 7 and maximal at Stn 19 (Fig. 2A).

The highest calcite-C production was recorded at Stn 7. Here, the daily production ranged between 3.0 and 5.6 mg calcite-C m^{-3} in the upper 15 m of the water column; below 27 m daily productions were less than 0.2 mg calcite-C m^{-3} (Fig. 6C). At the other 3 stations, the highest productions were close to 1 mg calcite-C m^{-3} d^{-1}. The integrated daily production of calcite-C at Stn 7 was 4 to 7 times higher than at the other 3 stations (Table 1). At Stn 7, the total production of calcite-C amounted to 18% of that of the total production of POC; in the other 3 stations the calcite-C production relative to POC production only ranged between 1 and 3% (Table 1).

Coccolithophores were the only calcifying organisms detected in the water samples in which the production measurements were performed. At Stns 7 and 15 this group consisted almost exclusively of the species *Emiliania huxleyi*, so that the daily production of calcite per *E. huxleyi* cell could be calculated. It appeared that the coccolith production in the top 15 m of the water column ranged between 12.5 and 21.9 coccoliths $cell^{-1}$ d^{-1} and that somewhere between 15 and 27 m coccoliths production decreased to below 1.0 $cell^{-1}$ d^{-1} at Stn 7 and to zero at Stn 15 (Table 2). The daily coccolith production per *E. huxleyi* cell integrated over the top 15 and 25 m of the water column was 15.9 and 15.6, respectively, at Stn 7 and 17.8 and 12.7, respectively, at Stn 15. We have also calculated the amount of calcite-C produced per coccolithophorid cell in the 5 and 15 m samples at Stn 19. The production appeared to be about 0.50 pg calcite-C $cell^{-1}$ d^{-1}. This shows that the calcite-C production in the holococcolithophorid species, which dominated the coccolithophorid phytoplankton in these samples, was far less than that in *E. huxleyi*.

Table 1. Integrated production of POC and calcite-C and calcite-C/POC production ratios at Stns 7, 12, 15 and 19

Station	POC (mg m^{-2} d^{-1})	Calcite-C (mg m^{-2} d^{-1})	Calc-C/POC
7 (1 July)	514.2	94.6	0.18
15 (7 July)	626.7	21.4	0.03
12 (4 July)	1329.5	13.8	0.01
19 (10 July)	1201.6	20.4	0.02

Table 2. *Emiliania huxleyi*. Numbers of living cells and daily production of calcite-C and coccoliths per cell at Stns 7 and 15

Depth (m)	Living EHUX (cells ml^{-1})	Calcite-C $cell^{-1}$ d^{-1} (pg)	Coccoliths[a] $cell^{-1}$ d^{-1}
Stn 7 (1 July)			
2	935	3.25	12.49
5	1219	4.59	17.65
10	1007	3.81	14.64
15	809	5.70	21.91
27	532	0.15	0.57
40	271	0.71	2.72
50	37	0.46	1.78
Stn 15 (7 July)			
5	240	5.19	19.96
15	260	3.44	13.25
25	305	0.00	0.00

[a]It is assumed that 1 coccolith of *E. huxleyi* contains 0.26 pg calcite-C. This was calculated to be the average amount of calcite-C per coccolith in an *E. huxleyi* bloom in the Gulf of Maine, USA (Balch et al. 1992)

Dissolution of calcite

One experiment was also performed to measure the dissolution of $CaCO_3$. For this purpose, water samples containing *Emiliania huxleyi* cells in concentrations of several hundreds per cm^3 were spiked with $^{45}CaCl_2$ and incubated at ambient sea water temperature in an open deck incubator. After 75 h the water samples were wrapped in black plastic foil to stop coccolith formation. The concentration of radioactively labelled $CaCO_3$ was measured after 4, 8, 24 and 48 h of incubation in the dark (Table 3). Since the mean values did not show a decreasing trend in the course of time, the conclusion must be that at least during 48 h no dissolution of labelled $CaCO_3$ took place in these samples.

Several phytoplankton samples were also viewed in the electron microscope to look for effects of calcite dissolution. Most coccospheres and free coccoliths sampled from within the *Emiliania huxleyi* bloom showed a fresh and solid appearance. However, also whole coccospheres were detected which were composed of coccoliths with incomplete and disjoined crystal elements (Fig. 7). It is possible that this aberrant appearance of cells is caused by dissolution of the coccoliths, implying that dissolution is a selective process (see 'Discussion').

Table 3. Concentrations of radioactively labelled calcite after 4, 8, 24 and 48 h of incubation in the dark. Spiked calcite was allowed to be formed during a light incubation period of 75 h

Duration of dark incubation (h)	Labelled calcite (mg m^{-3}) Mean	SD	n
4	57.59	1.89	2
8	51.93	0.23	2
24	59.10	0.35	2
48	54.82	2.53	3

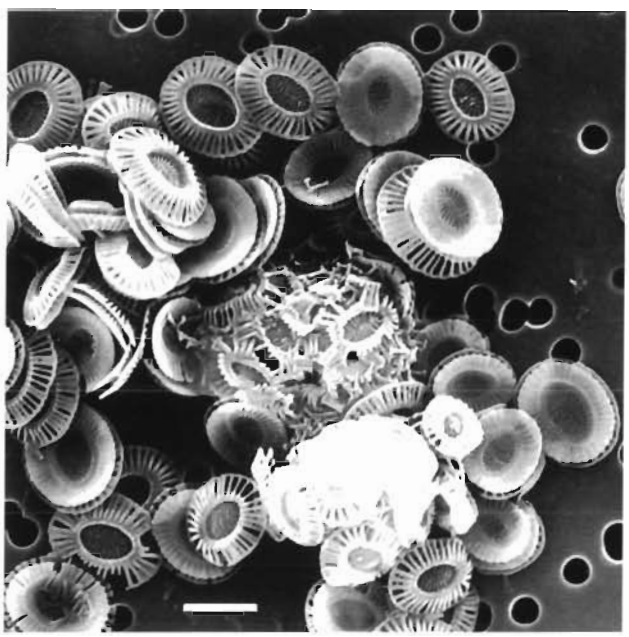

Fig. 7 *Emiliania huxleyi*. Scanning electron micrograph of deteriorated coccosphere (centre) surrounded by undamaged detached coccoliths and a whole coccosphere (bottom). Plankton sample collected at Stn 15 from 5 m depth. Scale bar = 2 µm

Sediment traps

At each of the 4 *in situ* stations 4 sediment traps were deployed, viz. 2 at 10 m and 2 at 50 m depth. At each depth one of the traps was poisoned with formalin. It should be borne in mind that formalin kills all life forms preventing (1) the decomposition and consumption of sedimented material by heterotrophic organisms including microbes (e.g. Honjo & Roman 1978, Azam et al. 1983, Gowing & Silver 1983, Ducklow et al. 1985) and mesozooplankters (e.g. Lampitt et al. 1990, Noji et al. 1991) and (2) production, inside the trap, of faecal material, which otherwise would have been measured as sedimented matter (Lee et al. 1988). The most important mesozooplankton groups caught in the traps were copepods, gastropods and pelecypods. Their numbers are listed in Table 4. Echinoderm larvae, bryozoans and polychaetes were also encountered, but since they were often absent or occurred only in subordinate numbers, they are not listed here. In general, there is a large difference in copepod numbers between the poisoned and non-poisoned traps at both 10 and 50 m water depth with the highest numbers being always present in the poisoned trap. In our opinion this shows that during the deployment copepods actively swim into and out of the traps, but that many of those entering the poisoned traps get killed by the formalin and become trapped. Indeed, most of the copepod specimens had a fresh and undamaged appearance and hardly any debris of copepod remains was encountered.

The shallowest poisoned trap at each site always contained the largest number of copepods. This is probably due to the fact that the copepod population at 10 m depth is more abundant than that at 50 m. Stn 19 ranked first in copepod abundance, followed by Stns 7, 15 and 12. The following 5 copepod genera were identified. *Calanus*, *Metridia*, *Oithona*, *Pseudocalanus* and *Temora*. *Calanus* was dominant in all the traps, except in those deployed at 10 m at Stns 12 and 19. At this depth at Stn 12 *Oithona* was most abundant, while the copepods found in the shallow trap at Stn 19 consisted for about 90% of *Pseudocalanus*, a genus that was rare or absent in all the other traps. *Temora* and *Metridia*

Table 4. Numbers of copepods, gastropods and pelecypods and flux of faecal pellets in poisoned and non-poisoned sediment traps deployed at 10 and 50 m at Stns 7, 12, 15 and 19

Station	Depth (m)	Poisoned	Copepoda	Gastropoda	Pelecypoda	Flux of faecal pellets ($mm^3 m^{-2} d^{-1}$)
7	10	Yes	1280	572	344	258.7
7	10	No	28	152	104	128.3
7	50	Yes	16	0	64	1773.5
7	50	No	8	32	72	4210.6
15	10	Yes	464	40	60	292.7
15	10	No	64	28	88	260.7
15	50	Yes	204	4	4	727.6
15	50	No	4	8	8	1043.5
12	10	Yes	84	36	524	18.9
12	10	No	32	60	424	51.1
12	50	Yes	60	0	60	17.3
12	50	No	4	7	8	56.5
19	10	Yes	9696	896	160	11.0
19	10	No	2752	1328	136	3.1
19	50	Yes	1072	2056	3792	13.3
19	50	No	28	196	1840	22.0

were only found in the poisoned traps at Stn 19, the former in the shallow trap and the latter in the deep trap. In both cases their numbers were very low.

Gastropod and pelecypod numbers greatly differed among the non-poisoned and poisoned traps deployed at the same depth in each station, as was observed for the number of copepods. But contrary to what was found for the copepods, the highest numbers of gastropods and pelecypods were not always found in the poisoned traps. In fact the highest numbers in these traps were met in exactly half of the studied cases. We think that the large differences in gastropod and pelecypod numbers among paired traps largely arose through distortion of the hydrodynamical conditions induced by the trap system itself, resulting in a dissimilar performance of the traps (see 'Discussion'). This implies that the effect of the use of poison in assessing material fluxes cannot reliably be studied. For that reason, the average value of the flux rates measured separately in the paired non-poisoned and poisoned traps is considered to represent the best approximate for the real flux rates occurring at the site and depth of trap deployment.

Other important components found in the trap samples were round, oval or cylindrical pellets with a smooth and sharp outline, and aggregates having a jagged outline and irregular shape. The cylindrical material was most abundant and was very likely produced by copepods (cf. Martens 1978), which were the most prolific grazers as judged from the trap content. However, identification was problematic due to the fact that in most cases the cylinders occurred in fragmented form. The origin of the round and oval pellets is unknown, but for convenience they will be classified together with the cylindrical pellets as faecal pellets. The irregular-shaped aggregates may have had a mixed origin or represented faecal pellets in a much desintegrated form. Faecal pellets and other aggregates were most abundant in the stations located in the *Emiliania huxleyi* bloom (Stns 7 and 15). At these stations, they almost exclusively consisted of the skeletal remains of *E. huxleyi*. Coccoliths always formed an integral part of faecal pellets and aggregates found in the other 2 stations also, but often to a much lesser degree. The oval and round pellets consisted of a dense packing of free coccoliths and whole coccospheres; these components always had a fresh and undamaged appearance (Fig. 8). In the cylindrical-shaped pellets the coccoliths were mostly fragmented; whole coccospheres were not detected in them (Fig. 9).

In all traps the frequency distribution of the faecal pellet volumes had a positive skewness, as is shown in the percentile plot of Fig. 10. The median values ranged between 45000 and 404000 μm^3. The aspect ratios of the faecal pellets showed similar frequency distributions with the median values ranging between 1.3 and 5.8. In other words, the majority of the trapped faecal pellets were relatively small and short. The positive skewnesses of the frequency distributions of both the aspect ratio and the volume of the faecal pellets may indicate that they were subjected to desintegration during settling causing their mean to shift to lower values. The faecal pellet volumes had a normal distribution, when values were log-transformed. To test the

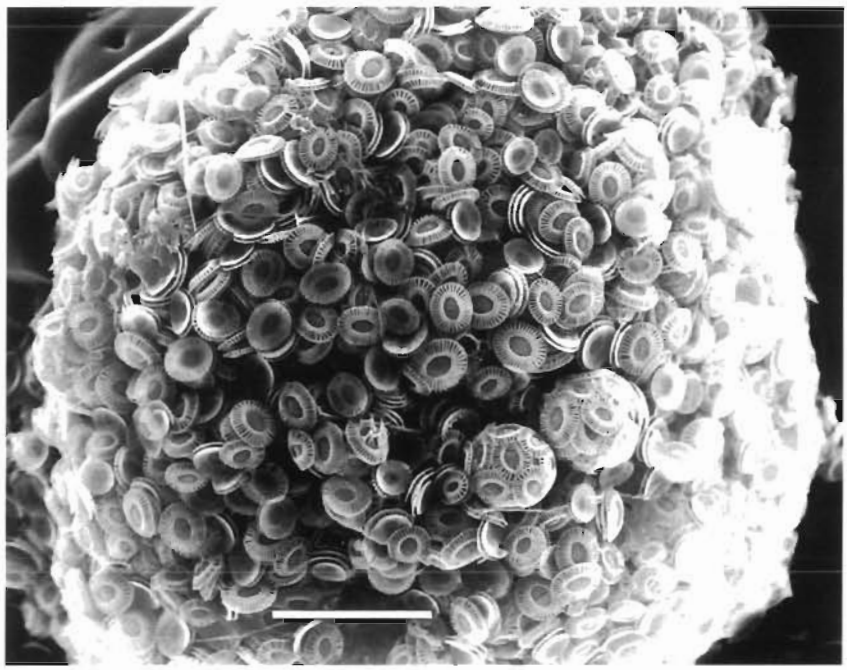

Fig. 8. Scanning electron micrograph of round pellet largely consisting of detached coccoliths and whole coccospheres of *Emiliania huxleyi*. Sample collected in sediment trap deployed at 10 m water depth at Stn 15. Scale bar = 10 µm

effect of poisoning and of depth and position (within and outside bloom) of trap deployment on the mean volumes a 3-way analysis of variance was performed on the log-transformed data. It appeared that the mean faecal pellet volumes were (1) larger in the non-poisoned than in the poisoned traps ($p < 0.01$), (2) larger in the non-poisoned, deep traps than in the non-poisoned, shallow traps ($p < 0.05$) and (3) not significantly different in the bloom and non-bloom stations (compare also Fig. 10). The fact that the mean faecal pellet volume was larger in the non-poisoned traps is likely the result of the production of fresh faecal matter by grazers dwelling in the trap during deployment, an effect that was apparently larger in the traps at 50 m than at 10 m.

The flux rates of faecal material caught in the traps are listed in Table 4. These data also show, as for the pelecypod and gastropod numbers, that the performances of the paired traps differ markedly among one another (see 'Discussion'). The largest drain of faecal

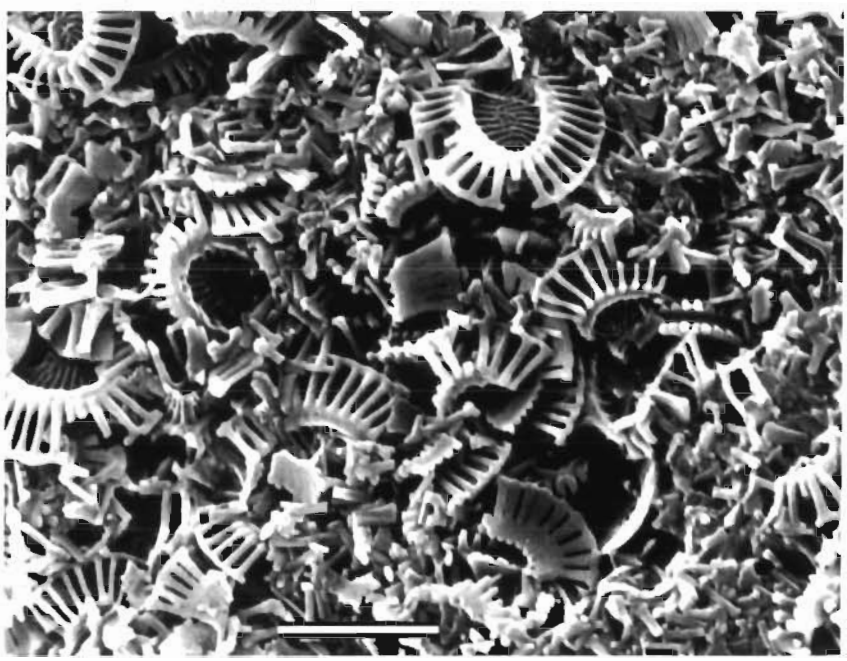

Fig. 9. Scanning electron micrograph showing detail of content of cylindrical pellet. Only skeletal remains of *Emiliania huxleyi* are visible. Sample collected in sediment trap deployed at 50 m water depth at Stn 7. Scale bar = 2 µm

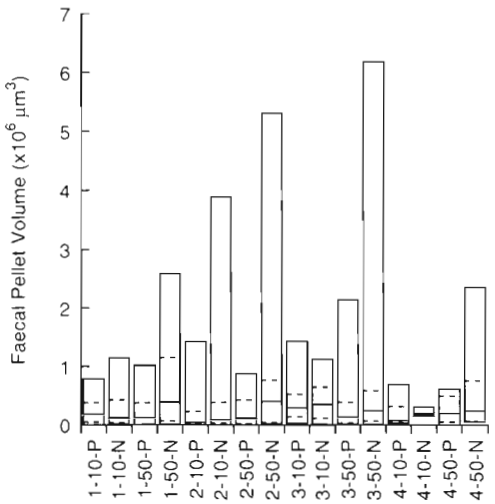

Fig. 10. Frequency distribution of the volumes of the faecal pellets caught in the 16 sediment traps deployed. The lower and upper ends of each box represent the 5% and 95% abundances, respectively. (——) median level; (- - - - -) 25% and 75% percentiles. The traps are coded as follows: the first number is the site (1: Stn 7, 2: Stn 12, 3: Stn 15, 4: Stn 19); the second number is depth in m; P: poisoned; N: non-poisoned

material occurred at Stns 7 and 15 located in the *Emiliania huxleyi* bloom. At Stn 7, the mean flux at 10 m amounted to 193.5 mm^3 m^{-2} d^{-1}, which is 70% of the mean flux measured at 10 m at Stn 15. The mean flux at 50 m at Stn 7 was 2992.1 mm^3 m^{-2} d^{-1}, which is 338% of the mean flux registered at Stn 15 at the corresponding depth. The mean fluxes calculated for both the poisoned and non-poisoned traps at Stns 7 and 15 were 3 to 15 times higher in the deep traps than in the shallow ones showing that the production was much larger in the upper 50 m than in the upper 10 m of the water column. The fluxes of faecal pellets at Stns 12 and 19 were insignificant compared to those of Stns 7 and 15. Also the fluxes measured at 10 and 50 m in each of these stations showed hardly or no difference. This is very remarkable given the fact that, especially at Stn 19, the standing stocks of copepods, gastropods and pelecypods were presumably very high relative to those found at Stns 7 and 15, as judged by the number of trapped specimens at these stations.

We have also measured the fluxes of POC and calcite-C at 50 m water depth at the stations situated in the *Emiliania huxleyi* bloom. For this purpose, the analysis was done on small subsamples from which all zooplankton specimens were carefully removed. Again, the large differences in content among the traps of the same depth are conspicuous (Table 5). The fluxes of calcite-C and POC at Stn 7 were 4 to 5 times as large on average as those at Stn 15. The calcite-C/POC ratios in the 2 poisoned traps were close to 0.5, whereas the ratios in the non-poisoned traps were larger than 1. Obviously, compared to the non-poisoned traps, relatively more POC than calcite-C is caught in the poisoned traps.

The daily removal of calcite-C, as fraction of its standing stock, from the top layer by sedimentation amounted to 6.3% and 1.7% at Stns 7 and 15, respectively (Table 6). The corresponding values for POC were about 2 times less. The amount of calcite-C transported per day out of the upper 50 m was more than 2 times higher than the daily calcite-C production in this layer at both Stns 7 and 15. It shows that the *Emiliania huxleyi* population was in its declining phase. On the other hand, daily POC production was in excess of the daily POC flux indicating that *E. huxleyi* contributed only little to total primary production.

Table 5. Fluxes of calcite-C and POC in the poisoned and non-poisoned traps deployed at 50 meter at Stns 7 and 15

Stn	Poisoned	Flux calcite-C (mg m^{-2} d^{-1})			Flux POC (mg m^{-2} d^{-1})			Flux calc-C/ Flux POC
		Mean	SD	n	Mean	SD	n	
7	Yes	153.60	3.61	4	241.88	15.78	3	0.64
7	No	356.40	18.69	4	325.24	22.87	4	1.10
15	Yes	58.52	3.61	4	113.91	17.67	3	0.51
15	No	38.34	0.51	4	28.52	2.66	4	1.34

Table 6. Summary of standing stocks, productions and fluxes of calcite-C and POC in the upper 50 m of the water column at Stns 7 and 15

	St. stock (mg m^{-2})	Production (mg m^{-2} d^{-1})	Flux[a] (mg m^{-2} d^{-1})	Flux/St. stock (%)	Flux/Prod. (%)
Calcite-C					
Stn 7	4047.9	94.6	255.0	6.3	269.6
Stn 15	2921.0	21.4	48.4	1.7	226.3
POC					
Stn 7	9063.8	514.2	283.6	3.1	55.1
Stn 15	7731.3	626.7	71.2	0.9	11.4

[a]Mean value of poisoned and non-poisoned traps

DISCUSSION

Development of the Shetland bloom

The large continental shelf *Emiliania huxleyi* bloom investigated here was confined to water derived from the North Sea, as was demonstrated in vertical profiles of salinity, temperature and nutrients. Almost every year dense blooms of *E. huxleyi* develop in the Norwegian fjords (Berge 1962) starting with populations living at rather low salinities (Kristiansen et al. 1994). In 1993 satellite images of the North Sea area revealed that the first signs of blooms were apparent by the beginning of June in the fjord systems in southwest Norway. Shortly after that extensive blooms were recorded in the adjacent Norwegian current; by the end of June the bloom east of Shetland, which we have studied, was registered in the visible band images (Van der Wal et al. unpubl.). This westward displacement of the blooming phase of *E. huxleyi* is possibly related to the spread of low saline runoff waters, which may have facilitated the forming of a stable shallow mixed layer, a condition that appears to be a prerequisite for the prolific growth of *E. huxleyi* (Berge 1962, Balch et al. 1991, Holligan et al. 1993a, b, this study).

We have shown that in the *Emiliania huxleyi* bloom the flux of calcite-C exceeds the production of calcite-C by a factor of more than 2. This is a clear indication that at the studied sites the bloom was already past its culmination. This is also apparent from the relatively high photosynthesis/calcification ratios of 5.4 and 29.3 measured in the productive layer at Stns 7 and 15, respectively: in culminating *E. huxleyi* blooms induced to grow in mesocosms, this ratio was below 2 (Van der Wal et al. 1994). In general, high concentrations of loose coccoliths on the one hand and low cell numbers on the other indicate that such blooms have entered into their decaying phase.

The results of the sediment traps demonstrated that the drain of matter from the productive layer inside the bloom was much larger than outside the bloom. We assume that this is caused by the higher recycling rate of faecal matter outside the bloom (see below). This implies that in blooms of *Emiliania huxleyi* nutrients may rapidly be exhausted, whereas outside such blooms substantial remineralization of nutrients in the productive layer may account for a prolonged sustenance of large phytoplankton populations. Indeed, nitrate concentrations in the *E. huxleyi* bloom were very low as compared to those in the waters adjacent to the bloom. Furthermore, there was hardly any or no peak of ammonium below the mixed layer at the 2 stations outside the bloom contrary to what was found at the other 2 stations. This may show that, outside the bloom, regeneration of N-compounds was confined to the mixed layer to a large extent. The rapid drawdown of nutrients from the mixed layer undoubtedly has a strong impact on the phytoplankton composition and, consequently, on the development of the *E. huxleyi* bloom. It is thought that the increasingly lower nutrient levels result in the gradual disappearance of species, until finally those species survive which have the highest competitive strength at low nutrient levels. Due to its low nutrient requirements (Eppley et al. 1969) *E. huxleyi* may endure these conditions for a very long time, so that a rather pure bloom of this species may be formed. However, the positive feedback of the success of this species on the further removal of nutrients finally makes conditions for this species also unbearable.

The phytoplankton present in the decaying *Emiliania huxleyi* bloom studied here appeared to be nitrogen limited, as was shown in short bioassays in which the ratio of the intracellular glutamine/glutamate ratio before and after a pulse of ammonium was used as an index for nitrogen limitation (Flynn 1990, Willem Stolte pers.comm.). Possibly, nitrogen limitation may have been the prime cause for the bloom's decline. In the summer of 1989 an *E. huxleyi* bloom was studied in the Gulf of Maine, USA, which resembled the Shetland bloom in many respects including coccosphere and loose coccolith number and concentrations of nutrients and chlorophyll (Balch et al. 1992). Nutrient enrichment experiments showed that there both calcification and primary production were nitrate limited. Likewise, mesocosm experiments have shown that nutrient depletion may cause the decline of *E. huxleyi* blooms (Bratbak et al. 1993, Egge & Heimdal 1994). Another cause for a bloom to decay is by the infection of *E. huxleyi* cells by virus particles, as was also demonstrated in mesocosm experiments (Bratbak et al. 1993). In an *E. huxleyi* bloom occurring south of Iceland in June 1991, nutrient levels did not attain limiting levels and viruses were not observed to have infected the cells (Holligan et al. 1993a). Possibly, light level was the limiting factor here: the beam attenuation coefficients at 532 nm in the high reflectance waters of the Iceland bloom were about 2 times higher than in the high reflectance waters in the Shetland bloom (Holligan et al. 1993a, this study).

Production

The calcite-C production per cell in *Emiliania huxleyi* blooms has been monitored in two 4 m deep mesocosms in spring 1992 in Bergen, Norway (Van der Wal et al. 1994). It appeared that this production was similar in all stages of bloom development amounting to average values of 3.82 and 4.22 pg calcite-C $cell^{-1}$ d^{-1}.

These values are similar to those measured in the top 15 m at Stns 7 and 15 (Table 2) and also similar to the maximum rate measured in an *E. huxleyi* bloom occurring in the Samnangerford, Norway (Kristiansen et al. 1994). In an *E. huxleyi* bloom occurring south of Iceland in the summer of 1991 Fernandez et al. (1993) measured a cell-specific calcification rate that was about twice as low.

In mesocosm studies of *Emiliania huxleyi* blooms it was shown that the loose coccolith/coccosphere ratios were below 30 in the initial stages and rapidly increased to between 50 and 200 a few days after the bloom had reached its peak (Van Bleijswijk et al. 1994a). By this criterium also the Shetland bloom is shown to be in a late developmental stage. It was suggested that the Iceland bloom had also entered into its final stage by Holligan et al. (1993a). Yet, the loose coccolith/coccosphere ratio did not exceed 40 (Fernandez et al. 1993). Coccoliths in the coccosphere are embedded in a polysaccharide-containing organic substance (see e.g. Van der Wal et al. 1983), which may act as a glue to hold the coccoliths together. It is possible that in the Iceland bloom the stickiness of coccoliths was enhanced preventing (1) the easy release of coccoliths from calcifying cells and (2) the ready desintegration of empty coccospheres. Also, aggregate formation of loose coccoliths may have been much enhanced in the Iceland area due to microturbulence conditions that were different from those prevalent in the shelf sea bloom.

We have shown that the calcification rates per *Emiliania huxleyi* cell at Stns 7 and 15 were very high in the upper 15 m of the water column and that a steep decrease occurred in coccolith production between 15 and 25 m. Taking into consideration that the 1% light level for PAR was situated at about 15 m, these results may show that coccolith formation is saturated at very low irradiances. On the other hand, photosynthesis was saturated at much higher light levels, as judged from the gradual decrease of organic carbon production per unit chl *a* with depth. It should be stated here that the values of the calcification rates presented have already been corrected for the coccolith formation in the dark. Therefore, the alternative explanation can be excluded that the *E. huxleyi* cells in the mixed layer would have drawn from an intracellular energy reservoir large enough to sustain coccolith formation, while the cells below this layer would have exhausted their intracellular energy supplies, as a result of a prolonged deprivation of light. It has been shown in both long-term (Van Bleijswijk et al. 1994b) and short-term experiments (Balch et al. 1992, Fernandez et al. 1993) that calcite production in *E. huxleyi* may, indeed, become saturated at very low irradiances. However, various short-term experiments have also been conducted yielding the opposite result of calcite productions being saturated at very high irradiances (Paasche 1964, Balch et al. 1992, Fernandez et al. 1993, Nimer & Merrett 1993). This discrepancy may be inherent to short-term experiments in which cells are not allowed to adapt to changing conditions. The low light saturation level for coccolith formation in the Shetland bloom is in agreement with the model presented by Balch et al. (1992).

At Stn 7 highest calcification rates were measured. Here the integrated calcite-C production amounted to 18% of the integrated POC production. This value is comparable to that calculated for the *in situ* station with maximal calcification in the Iceland bloom (Fernandez et al. 1993). In *Emiliania huxleyi* blooms induced to grow in mesocosms the calcite-C/POC production ratios rose to over 0.5 when the blooms were close to their culmination (Van der Wal et al. 1994). These values were measured at 2 m water depth. At the corresponding depth at Stn 7 the calcite-C/POC production ratio was about 5 times lower, which indicates that even at this station the Shetland bloom had developed into its post-culmination stages.

In this study we have shown that in radio-tracer experiments coccoliths did not dissolve within up to 5 d after their formation (Table 3). On board experiments were also performed to determine dissolution of $CaCO_3$ in the *Emiliania huxleyi* bloom by measuring the standing stock of $CaCO_3$ in sea water samples that had been incubated in the dark for 0, 24 and 28 h. It appeared that the $CaCO_3$ standing stocks might diminish by up to 25% within 24 h of dark incubation (Buitenhuis et al. unpubl.). The conclusion that can be drawn from these results is that dissolution of $CaCO_3$ only occurs in old coccoliths and that freshly formed coccoliths, i.e. coccoliths that are at least younger than 5 d (the maximal duration of the experiment), are not affected. In mesocosm blooms of *E. huxleyi* it was demonstrated that dissolution of $CaCO_3$ started only after the culmination of the bloom with a rate of about 5% of the $CaCO_3$ standing stock per day, a phenomenon that was assessed by comparing the $CaCO_3$ standing stock and the cumulative amount of $CaCO_3$ produced (Van der Wal et al. 1994). This may show that dissolution is related to the bloom's decay in such a manner that dissolution only affects the coccoliths in decaying cells. This view is consistent with the finding that freshly formed coccoliths are not liable to dissolution, because these coccoliths are most likely still incorporated in the coccospheres of viable, calcifying cells. At macro-environmental level no clues are apparent as to the causes of calcite dissolution. We think, therefore, that each decaying *E. huxleyi* cell is a micro-environment in which CO_2 concentrations are enhanced through either the inorganic decomposition

of organic material, or the heterotrophic activity of microbial organisms causing the coccolith-calcite to dissolve. Such a selective dissolution of coccolith calcite is in agreement with our scanning electron microscope (SEM) observations of the co-occurrence of fresh-looking and deteriorated coccospheres (Fig. 7).

Sedimentation

We have shown that often large differences were observed in the numbers of caught pelecypods and gastropods, and in the amount of caught faecal material, POC and calcite-C among the traps that formed a paired system. In our opinion these differences largely arose through distortion of the hydrodynamical conditions induced by this system itself, as will be explained in the following. The double trap system probably attained an orientation parallel to the current in the water, so that one of the traps had an upstream position with respect to the other one. In that situation the upstream trap might have produced so much turbulence around the funnel opening of the downstream trap that the downward flux of particulate matter into this trap was strongly influenced (e.g. Honjo 1978). We think that this problem would not have occurred, if a shield or rudder (e.g. Gundersen 1991) was attached to the double trap system. In that case the system might have oriented itself transverse to the current, so that the traps would have met similar hydrodynamical conditions. Due to the dissimilar performance of the traps, the effect of the use of poison in assessing material flux rates could not reliably be studied.

We have found that the fluxes of faecal pellets at Stns 12 and 19 were insignificant compared to those at Stns 7 and 15, despite the fact that, especially at Stn 19, the standing stocks of copepods, gastropods and pelecypods were presumably very high relative to those found at Stns 7 and 15, as judged by the number of trapped specimens at these stations (Table 4). We offer the following explanation to this phenomenon. Inside the *Emiliania huxleyi* bloom mesozooplankters consume large amounts of coccoliths. These particles have a high specific weight and, hence, their ingestion would lead to a higher sedimentation rate of the faecal pellets produced. In contrast, in waters outside the *E. huxleyi* bloom the residence time of faecal material in the top 10 and 50 m of the water column is relatively high, because of the lower sedimentation rate. Biological activity is an important mechanism in the recycling of faecal material. There is growing evidence that the consumption and desintegration is largely accomplished by microbial organisms (Honjo & Roman 1978, Turner 1979, Gowing & Silver 1983, Jacobson & Azam 1984, Ducklow et al. 1985) and meso- and macrozooplankton (Paffenhöfer & Strickland 1970, Smetacek 1980, Lampitt et al. 1990, Noji 1991, Noji et al. 1991). Lower sedimentation rates would then lead to a higher degree of consumption and desintegration of faecal pellets by bacteria and coprophagous organisms. Moreover, in the process, faecal pellets become smaller and less compact resulting in even lower sedimentation rates (Noji et al. 1991). In short, the downward transport of faecal material in the *E. huxleyi* bloom was greatly enhanced due to the ballasting effect of the coccoliths.

Similar to our findings, Voss (1991) observed that changes in the diet of copepods, in response to changes in the phytoplankton composition, could lead to increased sedimentation rates of particulate matter from the productive surface layer. Rapid recycling in combination with low sinking rates of faecal matter in the euphotic zone have also been inferred from various other field studies, whether conducted in fresh water lakes, shelf seas or the open ocean (Ferrante & Parker 1977, Smetacek 1980, Krause 1981, Alldredge et al. 1987, Bathmann et al. 1987, Cadée et al. 1992, Gonzalez et al. 1993). The importance of coccoliths as a ballasting material in accellerated downward transport has also been revealed in several other field studies. Honjo (1978, 1980) found that all faecal pellets definitely originating from the productive layer ('green' faecal pellets) that were trapped at meso- and bathypelagic depths at various sites in the Atlantic and Pacific Oceans were loaded with coccolithophorid calcite remains. Also, long-term sediment trap studies have revealed that coccolithophorid blooms were associated with increased material fluxes. In the Panama Basin in June through July 1980 a bloom of the coccolithophorid *Umbilicosphaera sibogae* caused a material flux that was up to 2 orders of magnitude larger than the usual fluxes measured in that year (Honjo 1982). Knappertsbusch & Brummer (in press) have found that faecal matter stuffed with the coccolithophorid remains of *Syracosphaera pulchra* were associated with enhanced material fluxes in the open ocean. From the differences in arrival times of the spikes at the various depths of trap deployment the average sinking velocity of the particles was estimated to be about 150 m d^{-1}.

Sinking rates of particles are dependent on their specific weight, shape and size. With respect to faecal pellets it has been demonstrated that (1) the density of faecal pellets is positively related to sinking rate (Bienfang 1980, Voss 1991, Cadée et al. 1992); (2) round and oval pellets have relatively higher settling velocities than cylindrical ones due to lower form resistance to sinking (Cadée et al. 1992); (3) large pellets settle more quickly than smaller ones (Cadée 1986, Cadée et al. 1992). Alldredge et al. (1987) and Cadée et al. (1992) have demonstrated that faecal pellets, that did not sink

out from the mixed layer, settled at several tens to hundreds of meters per day in laboratory experiments. Other laboratory experiments have also invariably shown high sedimentation rates of faecal material (for references see Cadée et al. 1992, Harris 1994). Obviously, these experiments do not mimick the conditions in the natural environment. In nature settling velocities may be reduced by (1) microbial gas development in faecal material, as suggested by Krause (1981); (2) fragmentation (coprorhexy) and 'loosening' (coprochaly) of pellets due to meso- and macrozooplankton activity (Lampitt et al. 1990, Noji 1991, Noji et al. 1991); or (3) turbulence and density discontinuity layers not present in the laboratory settling tubes, as suggested by Cadée et al. (1992).

The calcite-C flux measured in the *Emiliania huxleyi* bloom ranged between 38 and 356 mg C m^{-2} d^{-1} with an average of 152 mg C m^{-2} d^{-1}; the flux of POC ranged between 29 and 325 mg C m^{-2} d^{-1} with an average of 177 mg C m^{-2} d^{-1}. Fluxes of particulate carbon were also determined in the above-mentioned *Umbilicosphaera sibogae* bloom occurring in the open ocean. Here, the calcite-C and organic carbon fluxes in the shallowest trap (890 m) were 191 and 25 mg C m^{-2} d^{-1}, respectively, averaged over a period of 2 mo (Honjo 1982). Thus, calcite-C fluxes in the 2 blooms were similar. The lower POC fluxes measured in the relatively deep trap in the open ocean station is probably the result of the rapid remineralization of POC in the upper few hundred meters of the water column. Carbon fluxes in a non-coccolithophorid bloom, the colonial microflagellate *Corymbellus aureus*, have been measured on Fladen Ground, about 100 miles south of the area investigated here, using the same type of free-floating traps (Cadée 1985, 1986). The highest flux recorded was 43.7 mg C m^{-2} d^{-1} occurring when the bloom was declining. This value is low compared to the POC flux measured in the *E. huxleyi* bloom. The accelerated transport of POC in coccolithophorid blooms is probably accomplished by the packaging of organic matter in fast sinking coccolith-laden particles (see also Honjo 1978). An additional mechanism to explain the enhanced material fluxes may be related to the consumption of large amounts of coccoliths by mesozooplankters. Since these particles are not nutritious, all ingested coccoliths end up in faecal pellets, which at unchanged ingestion rates would lead to higher rates of defaecation. Harris (1994) has calculated the flux of calcite-C mediated by 2 common copepod species in a shelf-break bloom and an oceanic bloom of *E. huxleyi* based on actual field abundances and laboratory experiments on the egestion rates of calcite-C by these copepods fed exclusively with *E. huxleyi* cells. The flux in the shelf-break bloom was in the lower range of values measured in the Shetland bloom; the flux in the oceanic bloom was insignificant due to the low abundance of copepods.

We have found that at Stns 7 and 15 the calcite-C/POC ratios in the poisoned traps were much lower than in the non-poisoned traps (Table 5). Obviously, compared to the non-poisoned traps, relatively more POC than calcite-C is caught in the poisoned traps. It is possible that the amount of POC sedimented in the non-poisoned trap is reduced by biological induced remineralization of POC during deployment (heterotrophy of microbes and mesozooplankters). Alternatively, the amount of POC found in the poisoned trap may give rise to an overestimation of the flux as a result of the presence of the preservative formalin: Formalin may have been diffused into the funnel of the trap where it would have caused the aggregation of organic matter, which subsequently was rapidly deposited in the sampling bottle of the trap. Artifacts may also have been introduced due to precipitation of the hexamine buffer or the formalin (Gundersen 1991). Thus, both the POC values of the poisoned and non-poisoned traps may not be very reliable. Nevertheless, the similarity of the calcite-C/POC flux ratios among the 2 stations strongly indicates that POC and calcite-C are transported with the same vehicle.

Probably as a result of the accellerated downward transport of materials out of the mixed layer nutrients were almost exhausted (this study) in this layer and surface DIC levels were about 10 µmol kg^{-1} lower compared to the levels found immediately outside the bloom (Buitenhuis et al. unpubl.). The ratio at which POC and calcite-C are exported from the mixed layer effect the relative abundances of the components of the carbonate system. For instance, preliminary results of a numerical model study of *Emiliania huxleyi* blooms showed that the fCO_2 in the final stages of the bloom is lowered compared to the fugacity in the pre-bloom phase due to the fact that together with calcite-C also POC is exported from the mixed layer. If only calcite-C had been exported, fCO_2 would have risen above the pre-bloom levels in the final stage.

We have found that in the cylindrical-shaped pellets coccoliths were mostly fragmented (Fig. 9). This may have been due to (1) the feeding habits of the grazing organism causing mechanical wear of the coccoliths and/or (2) the combination of mechanical wear and weakening of the calcite through dissolution occuring in the gut of the grazer. According to Harris (1994) calcite may dissolve in the digestive tract of copepods. Contrary to the cylindrical pellets the oval and round pellets found in the traps were all composed of undamaged coccoliths and coccospheres (Fig. 8). They may represent faeces of a zooplankter different from those producing the cylindrical-shaped pellets. On the other hand, they may not be faeces at all, but aggregates

similar to the macroaggregates of whole *Emiliania huxleyi* cells described by Cadée (1985). It is unknown how these macroaggregates are formed. Knowledge of the conditions regulating their formation is important, since these particles may contribute considerably to the downward flux of POC and calcite.

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