Primary production of phytoplankton at a frontal zone located at the northern slope of the Dogger Bank (North Sea) *

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Abstract. In July 1988 a survey was made in the Dogger Bank area of the North Sea. As a result of wind stress the area was found to be frequently well mixed. At the northerly slope a transition zone was observed between the stratified central North Sea and the well-mixed Dogger Bank area. Low nutrient concentrations were observed in surface waters; especially for nitrate ($<0.1~\mu M$). High concentrations of phosphate ($>0.5~\mu M$), nitrate ($>1~\mu M$), ammonium ($>2~\mu M$) and silicate ($>2~\mu M$) only prevailed below the thermocline. Chlorophyll a values were below $1~\mu g~l^{-1}$ near the surface. Enhanced values (up to $4~\mu g~l^{-1}$) were observed in the deeper layer at the transition zone and just below the thermocline at well-stratified locations. At the transition zone high specific C-fixation rates (up to 100 mg C mg^{-1} chl a d^{-1}) at the surface indicated the presence of enhanced productivity. The compensation depth for primary production was found to coincide with a specific C-fixation rate of 5 mg C mg^{-1} chl a d^{-1}. At greater depths, phytoplankton was only found where tidally induced vertical mixing allowed a regular exposure to higher light intensities. Storms resulted in a rapid redistribution of chlorophyll a and enhancement of the C-fixation rate in the upper layer of the water column.

Introduction

The Dogger Bank is part of the northern edge of the southern North Sea. In contrast with the central North Sea (with depths of hundreds of meters) the Dogger Bank is shallow with an average depth of 25 m. The Dogger Bank originates from the Saale or Riss glaciation when huge deposits of sand and gravel were left after the glaciers from Scandinavia and Scotland had disappeared. The Gulf stream and predominantly westerly winds push the water from the North Atlantic towards NW-Europe.

In combination with the tidal wave that enters the North Sea from the north and the south, and also by density differences due to the inflow of fresh water from the coasts and low-salinity water from the Baltic, the average water circulation through the North Sea is in an anti-clockwise direction (Eisma 1987). This implies that the northern slope of the Bank is more under the influence of Atlantic water whereas the southern slope is confronted more frequently with water from the southern North Sea. As a result of increased solar irradiance a large part of the North Sea becomes thermally stratified during spring. In this period enhanced primary production is observed in surface waters (e.g. Gieskes and Kraay 1980). Nutrients are accumulated in the phytoplankton and after sinking of particulates including phytoplankton into the lower layer, the upper layer is depleted. This biologically-mediated downward transport of nutrients together with the inflow of nutrient-rich bottom water and relatively nutrient-poor surface water from the Atlantic Ocean (Eisma 1987), leads to a typical vertical distribution of nutrients during summer. Primary production in the surface mixed layer is fuelled by regenerated nutrients excreted by zooplankton and by upward transport of nutrients from below the thermocline. As can be observed in other stratified marine environments (Epply and Renger 1988, Lande and Yentsch 1988), processes like diffusion, internal waves and wind-induced vertical mixing are likely to be driving forces in the upward transport of nutrients. Consequently, this entrainment of nutrients into the photic zone leads to enhanced primary production (new production).

Shallow areas like the coastal zones, the most southern part of the North Sea and the shallowest part of the Dogger Bank are not stratified during summer. Wind-stress and tidal currents are strong enough to cause mixing of the entire water column in these areas. Differences in water density caused by temperature and/or salinity result in fronts between water masses (Pingree 1978, Pingree and Griffiths 1978). Such fronts are common in the southern North Sea in a broad zone separating the main mass of the North Sea water from the lower salinity water
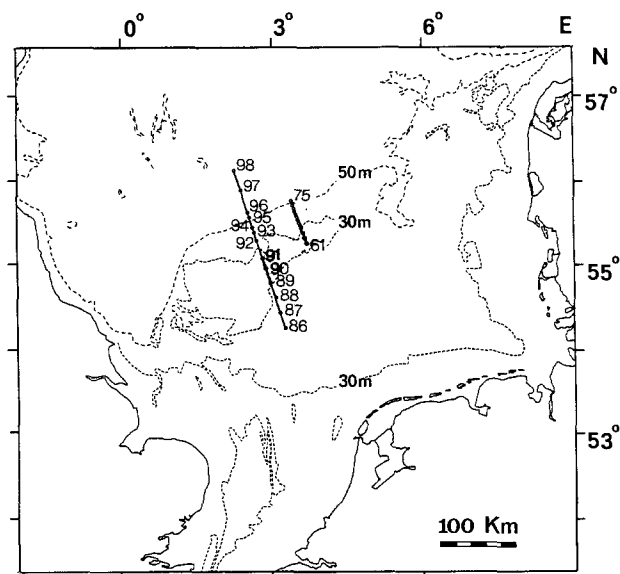
Fig. 1. Location of sampling stations at Transects 61/75 and 86/98 (60 km apart) of the Dogger Bank (shaded area). Depth in m; dashed lines: isolines

in the south, along the Norwegian coast, and on a smaller scale in river mouths and in coastal waters. Enhanced algal biomass has been observed frequently in these areas (e.g. Pingree et al. 1978, Creutzberg 1985). If this biological phenomenon is typical for transition zones between completely mixed and well-stratified areas, one would expect to find enhanced primary production in the Dogger Bank area at locations where such water masses meet. According to the geomorphology of the area such a transition zone should be present at the northern slope of the Dogger Bank. To what extent the hydrodynamical conditions in this transition zone could favour phytoplankton growth was studied along two different transects across the Dogger Bank (Fig. 1). Phytoplankton biomass and primary production were measured and related to chemical and physical properties of the water column at various stations.

Materials and methods

The two cruise tracks across the Dogger Bank (North Sea) are shown in Fig. 1. At all stations CTD-profiles (conductivity/temperature/depth) were made to provide information on temperature, salinity, light attenuation, turbidity and fluorescence. The transect between Stn 61 (55°16'N, 3°41'E) and Stn 75 (55°44'N, 3°20'E) was investigated twice (July 21 and 28, 1988) and the second transect, which was made within 24 h on August 1, started at Stn 86 (54°15'N, 3°15'E) and ended at Stn 98 (56°06'N, 2°13'E). Along this latter transect, water was taken with a rosette sampler at various depths for carbon-fixation (two depths), chlorophyll a (four depths) and nutrient measurements (every 5 m).

Incident solar irradiance was measured for 4 wk on board ship, using a Kipp Solarimeter. From the average daily irradiance the photosynthetically available radiation (PAR) was calculated assuming PAR to be 45% of the total irradiance and expressed as $J m^{-2} s^{-1}$ (Luning 1981). Light reflection at the sea surface was assumed to be 3% of the total irradiance (Vermij 1987). The underwater attenuation coefficient (K_d, m^{-1}) was calculated from under-

water quantum measurements and fitted according to the Lambert-Beer law. At some stations K_d was found to vary with depth (data not shown). At stations where sampling occurred during the night, K_d was estimated from turbidity measurements.

Dissolved nutrients were determined on a TRAACS 800 auto-analyser according to the procedures given in Strickland and Parsons (1972). Ammonium, nitrite and nitrate were analysed within 1 mo (storage at –30°C). Silicate and phosphate were analysed immediately after sampling.

Samples for chlorophyll a analysis were collected by filtration (Whatman GF/C), immediately frozen, and stored in the dark at –30°C until analysis according to Holm-Hansen et al. (1965).

For the identification of phytoplankton species 500 ml samples were taken and preserved with Lugol. Counting was performed after concentration by sedimentation according to Utermöhl (1958).

Carbon fixation was estimated using the 14-C technique. Water samples were taken from two different depths (5 m below the surface and at the fluorescence maximum) and subdivided in 50 ml subsamples. Prior to incubation 5 μCi NaH^{14}CO$_3$ (Amersham) was added to subsamples in an irradiance gradient incubator at in situ temperatures. The incubator was illuminated with an Osram metal-logen HMI 1200 W lamp, the spectrum of which closely resembles that of natural sunlight (Colijn 1983). Different irradiances were achieved using neutral density filters (Lee, Andover, England). The side walls of the incubation vessels (tissue culture bottles; Greiner, Solingen, West Germany) were covered with black tape to ensure illumination exclusively from the front side. It was concluded, from previous tests, that this precaution improved the reproducibility of P/I (photosynthesis/irradiance) measurements. Irradiances were measured prior to every incubation using a Licor underwater Quantum sensor LI-192 SA. Calculation of the average irradiance of each vessel was based on in- and outcoming irradiance which was measured for each incubation series. For the measurement of one P/I relationship at least five different irradiances (ranging from 50 to 3000 μE m^{-2} s^{-1}) were used. After incubation for 2 h samples were filtered (Sartorius SM 11 306, 0.45 μm) with a gentle filtration pressure (<100 mmHg). Filters were acid fumed for at least 5 min and counted in a liquid scintillation counter after addition of 10 ml Instagel II (Packard Instrument Company USA). Calculation of C-fixation rates was based on the initial concentration of label added. A value of 24.5 mg C l^{-1} for the total inorganic carbon concentration, based on earlier measurements, was used (G. W. Kraay personal communication). Filter absorbtion was found to be negligible. Dark values, never exceeding 5% of the maximum photosynthesis rate, were not subtracted from light values (Mortain-Bertrand et al. 1988).

P/I-curves were fitted according to the following equation (Platt et al. 1980):

$$P = P_{max} \left[1 - e(-\alpha I/P_{max})\right] \times e(-\beta I/P_{max}) \tag{1}$$

where P_{max} is the maximum carbon fixation rate at saturating irradiance (mg C m^{-3} h^{-1}), I is the average irradiance in the incubation vessel (μE m^{-2} s^{-1}), α the initial slope [mg C h^{-1} (μE m^{-2} s^{-1})$^{-1}$], and β the photo-inhibition constant (same units as α). For the fitting procedure, algorithm E04FDF from the library of numerical algorithms group (NAG) was used which enabled a simultaneous and independent estimate of the parameters (Gill and Murray 1978). Daily C-fixation profiles were calculated from the incident solar irradiance, the underwater irradiance attenuation, the measured P/I relationship, and corrected for the vertical distribution of phytoplankton as indicated by the fluorescence measurements. For this calculation and for the calculation of the vertical distribution of C-fixation at different stations the daily irradiance was averaged over 4 wk. This approach allowed us to calculate production under typical summer conditions and to compare measurements from Stn 68 which had been performed on different days.

The described incubator method to estimate C-fixation rates throughout the entire water column was found to deviate less than 10% from in situ measurements which had been performed during this cruise (data will be published elsewhere).

Results

Meteorological conditions varied during the cruise. South-westerly winds dominated with occasional speeds of up to 20 m s^{-1}. The total daily irradiance (TDI) varied from 2694 to 25414 kJ m^{-2}. The week before Transect 61/75 was visited, it was dominated by weak westerly winds (average speed 5 m s^{-1}) and relatively low TDI (a 13000 kJ m^{-2}). The water temperature on the Dogger Bank (Fig. 2A, Stns 61 to 63) gradually varied from 14.6° at the surface to 14.3 °C at the bottom. Thermal stratification was much more pronounced at the northerly stations (70 to 75, Fig. 2A) with the thermocline at 27 m. A transition zone of ca 25 km was observed between stratified and almost completely mixed waters. In this area (Stns 67 to 70), stratification was less severe (delta temperature was <5 °C). The position of the thermocline was more or less related to the bottom profile: at shallower locations (Stns 67 and 68) the thermocline was elevated to 20 m.

Two days after these observations the wind speed increased. A south-westerly storm occurred and continued for 3 d (10 to 20 m s^{-1}); the same transect was then investigated again. The surface temperature had declined several tenths of degrees (Fig. 2C). On the Dogger Bank (Stns 61 and 63) the temperature difference between surface and bottom water was reduced to 0.2 °C. In the transition zone (Stns 65 to 70) the decrease in temperature with depth had become less-severe. At the well-stratified locations, i.e. the northerly stations, the thermocline was found at greater depth. The impact of the storm is illustrated by the observation that at all stations the vertical temperature gradient within the upper 25 m was reduced to 0.2 °C (Fig. 2C).

Before the storm, fluorescence distribution (as a semi-quantitative indicator of algal distribution) showed a pattern which was comparable with the thermal distribution of the water column (Fig. 2B). In surface waters, fluorescence was low and evenly distributed along the transect. High fluorescence was found near the bottom at the stations located at the transition zone. In the strongly stratified area a clearly defined fluorescence maximum existed with values of 40 (arbitrary units) or more. At the surface, values lower than 10 were observed. Chlorophyll *a* measurements at Stn 75 showed a maximum concentration of 3.2 μg l^{-1} at 1 m below the thermocline.

Fluorescence distribution had changed after the storm (Fig. 2D). At the transition zone enhanced fluorescence values were observed near the bottom over a distance of 16 km from the transect. At well-stratified locations only a weak fluorescence maximum, compared to before the storm was observed. Microscopic observations demonstrated the presence of resuspended benthic diatoms at 5 m for stations located in the shallowest part of the Dogger Bank (25 m depth). The differences between Fig. 2 B and D illustrate the temporal changes in the distribution of phytoplankton. Before the storm, the phytoplankton at 5 m at Stn 68 was dominated by small flagellates (diameter 10 μm) and *Ceratium furca*. At 30 m the population was dominated by *Rhizoselenia stolterfolthii*, *Chaetoceros curvisetum* and *Ceratium furca*. After the
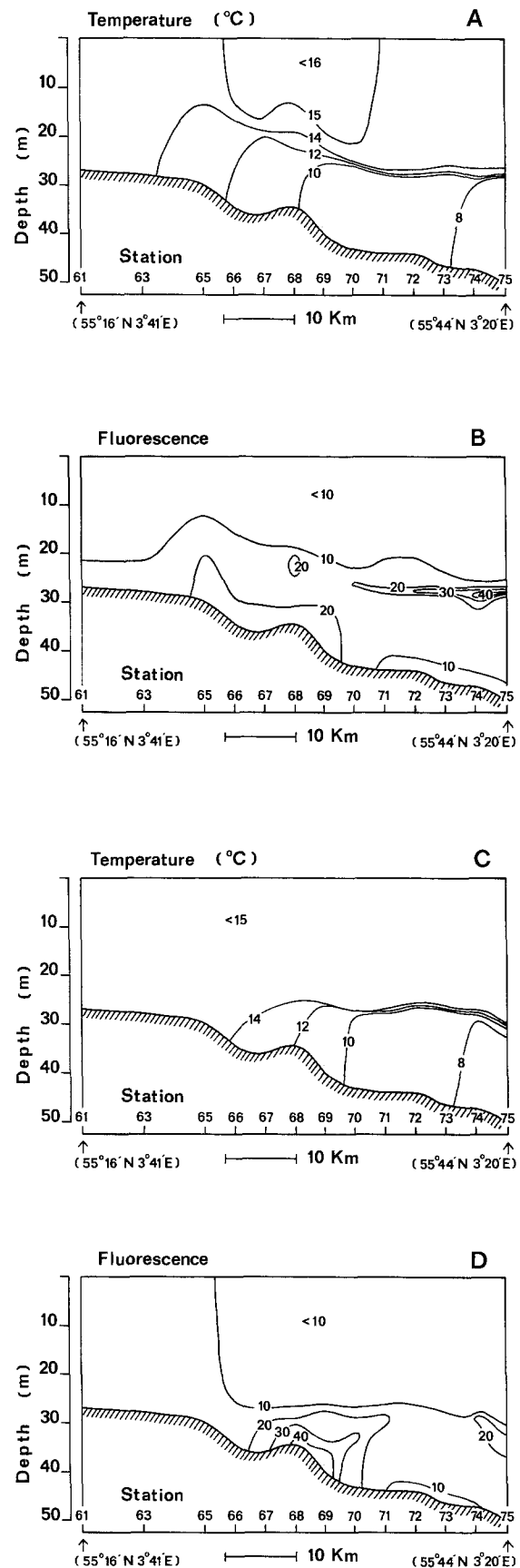

Fig. 2. Temperature (isolines in °C) and fluorescence distribution (relative isolines based on linear scale) on July 22 1988 before a storm event (A and B) and on July 24 after a storm event (C and D) in 1988. Shaded zone indicates sea floor profile

storm, these species were also present in significant numbers (more than 1000 ind. l^{-1}) at 5 m. At 30 m, the previous dominant species had decreased in number whereas a penate diatom (400 000 ind. l^{-1}) suddenly dominated the population.

The day after these observations were made, a second westerly storm occurred with an average wind speed of 20 m s^{-1} for 24 h. The water column at Stn 68, originally slightly stratified (Fig. 2C), was found to be completely mixed with respect to temperature distribution (data not shown). The average density (t) of the entire water column had increased slightly (from 26.089 to 26.200). Turbidity and chlorophyll a only slightly increased with depth. Chlorophyll a at the surface had increased from 0.3 to 0.8 μg l^{-1} whilst at 30 m a decrease from 4.7 to 1 μg l^{-1} was observed. Also, the C-fixation profile had changed dramatically (Fig. 3). The original deep production maximum, coinciding with a fluorescence maximum near the bottom, had disappeared. Surface production values were enhanced an order of magnitude. Note that these differences are not the result of daily variations in PAR since both production profiles were calculated using the same incident irradiance values (see also Material and methods). Specific production was found to be enhanced from 16.7 to 56 mg C mg^{-1} chl a d^{-1} at 5 m. Near the bottom (32 m) specific production was unchanged: 4.3 mg C mg^{-1} chl a d^{-1}.

Mixing of the water column was simulated experimentally by the incubation of several mixtures (different ratios) of a water sample taken at 25 m depth from Stn 65 and a surface water sample (5 m) from Stn 62. Incubation for 24 h at 50% surface irradiance showed remarkable effects on the chlorophyll a concentration (Fig. 4). Exposure of phytoplankton from deeper water to higher light intensities resulted in a doubling of chlorophyll a within 24 h. On the other hand, mixtures mainly composed of surface water tended to experience a decrease in the chlorophyll a concentration of the population. Initial concentrations (in μM) of dissolved ammonium, nitrate, silicate and phosphate were respectively 1.5, <0.01, 1.1 and 0.25 in the surface sample, and 1.6, 0.46, 1.3 and 0.47 in the 25 m sample.

Sixty kilometers to the west of Transect 61/75 a second Dogger Bank transect (86/98) was studied. Based on t distribution (Fig. 5A), mainly caused by differences in temperature rather than salinity, stratification was shown at the northern and southern edges of Dogger Bank and the thermocline was observed at 30 m. At the shallowest stations the water density was equally vertically homogeneous. In addition, the vertical distribution of chlorophyll and photosynthetic parameters was found to be homogeneous at Stns 89 and 90, which indicates complete vertical mixing at sites on the top of Dogger Bank.

Fig. 5B shows the penetration of light along the transect. Deepest penetration was found at the northerly stations where 1% of incident irradiance was still present at 55 m. At the shallower, well-mixed and slightly stratified locations light penetrated all the way to the bottom. Only at well-stratified locations was the compensation point for primary production (taken as 1% of TDI) located in the water column.
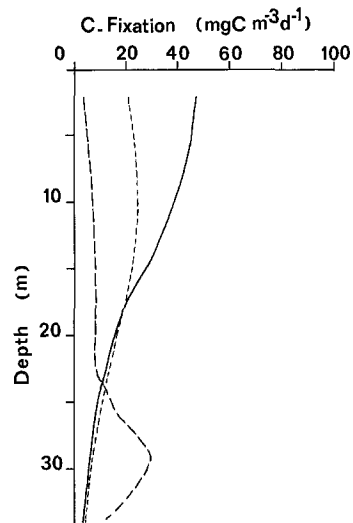

Fig. 3. Vertical distribution of C-fixation rate at Stn 68 measured before (– – – –) and after a storm event (———); and calculated C-fixation rate as a result of complete mixing of the initial water column due to wind stress (- - - - - -) based on complete redistribution of biomass and photosynthesis parameters along the entire water column
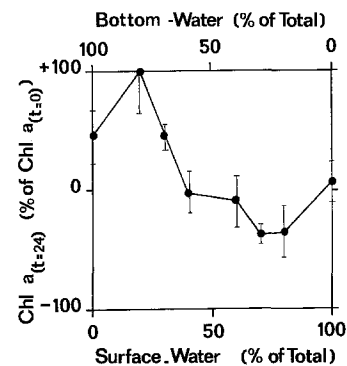

Fig. 4. Effects of a 24 h incubation at 50% incident irradiance on the chlorophyll a concentration of different mixtures of samples from 25 m at Stn 65 ("bottom" water) and 5 m at Stn 62 ("surface" water). Values indicate percentage increase/decrease

Nutrient concentrations (Fig. 6), measured along Transect 86/98 followed a patchy distribution in the upper layer; for example, ammonium concentrations varied along Transect 86/98 between 1 and 2.0 μM in the upper layer. Higher values occurred in the lower layer at well-stratified locations (Stns 96, 97 and 98). At first sight, the nitrate distribution appeared to be inversely correlated with chlorophyll a concentrations. In comparison with the distribution of the other nutrients, surface values were generally low (<0.1 μM). At stratified locations, nitrate could increase up to 6 μM in the cold subthermocline layer. Silicate was only depleted in surface waters of a few locations (Stns 89, 97 and 98), and was present in high concentrations below the thermocline and at the surface of Stn 95. Phosphate varied from 0.11 to 1 μM, was distributed irregularly, and exhibited no correlation with chlorophyll a. At stratified stations phosphate was
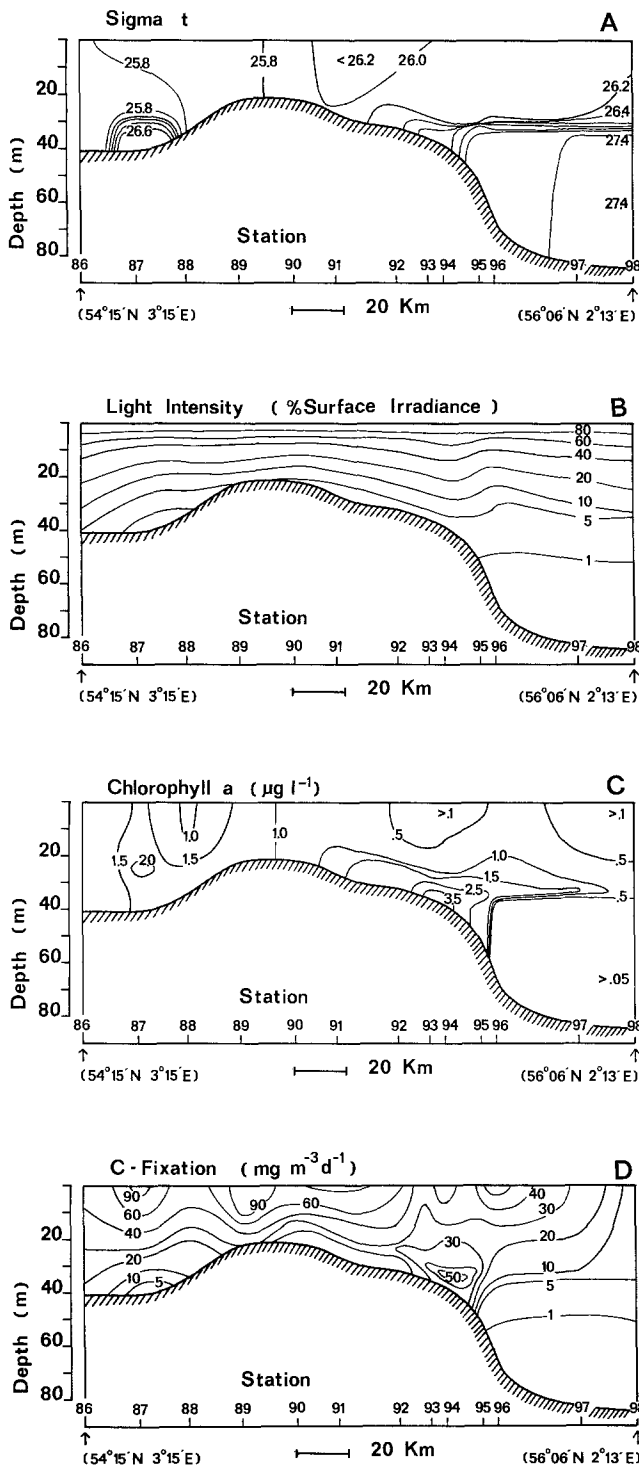
Fig. 5. Vertical distribution of Sigma t density (A), irradiance (B). chlorophyll a (C) and C-fixation rate (D) along Transect 86/98. Units of isolines are given on top of each graph. Shaded zone indicates sea floor profile
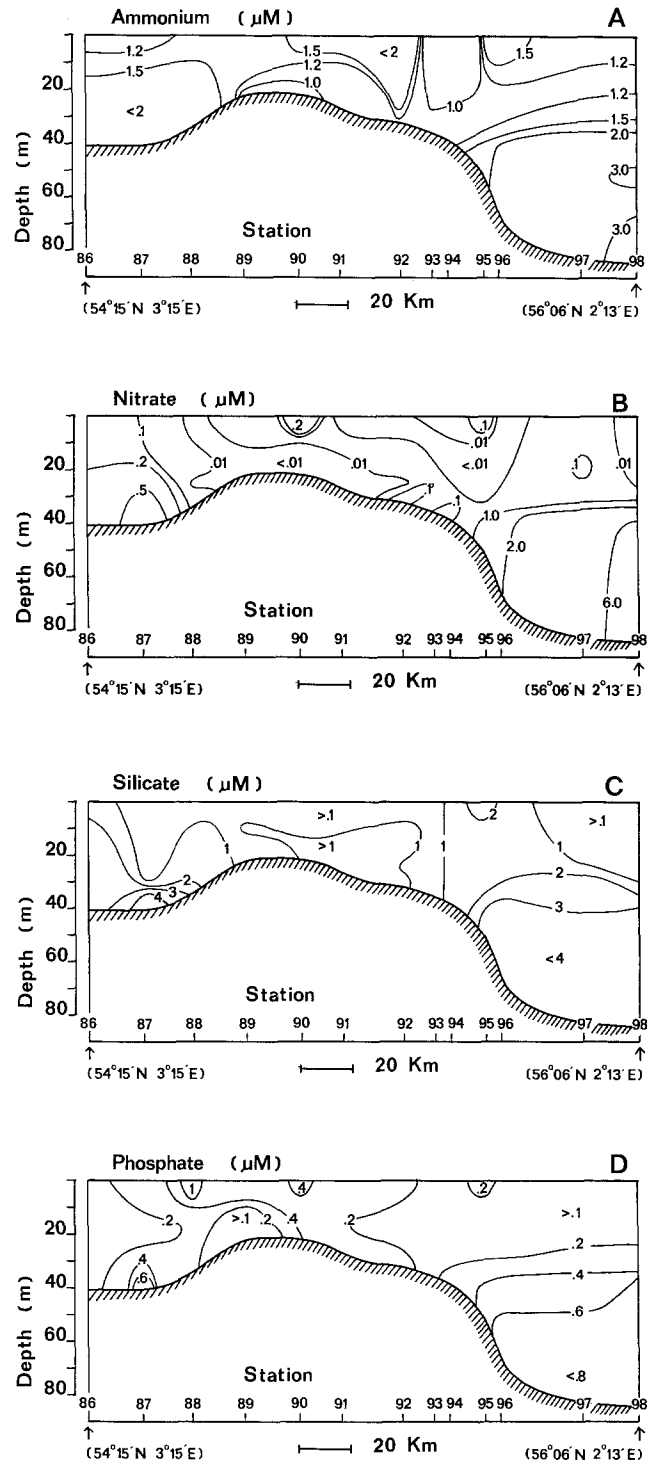
Fig. 6. Vertical distribution of dissolved nutrients (A: ammonium; B: nitrate; C: silicate; D: phosphate all in μM) along Transect 86/98. Units of isolines are given on top of each graph. Shaded zone indicates sea floor profile

slightly enhanced, up to values of 0.7 μM in the lower layer (Stns 87, 97 and 98).

Chlorophyll a was found to be more or less evenly distributed and present in low concentrations (0.2 to 1.6 $\mu g\ l^{-1}$) in surface waters (Fig. 5C). Values of up to 3.5 $\mu g\ l^{-1}$ coincided with density gradients (Fig. 5A) in the transition zone of the northern slope.

C-fixation rates (Fig. 5D) in surface waters varied greatly. C-fixation was low at Stn 98 (7 mg C m^{-3} d^{-1}; the most northern). On Dogger Bank (Stn 89) the highest fixation rate was observed (150 mg C m^{-3} d^{-1}). Also, at greater depths C-fixation was enhanced at the transition zone (Stns 92 to 96), this deep production maximum extended a distance of ca 30 km across the northern slope.

Discussion

In addition to earlier reports (Gieskes and Kraay 1984, Creutzberg 1985, Owens et al. (1990) this study shows the presence of enhanced algal biomass well below 10 m. A subsurface phytoplankton bloom at the northern slope of Dogger Bank was observed in May 1948 by Braarud et al. (1953). *Rhizoselenia* spp. and *Exuviaella baltica* were the most dominant species; they also reported the presence of *Ceratium furca*, *C. fusus* and *C. tripos*. Forty years later, a similar distribution in algal biomass and species composition (with the exception of *E. baltica*, which was present in low numbers) was found. It appears that the local environmental conditions favour the occurrence of bloom formation at the subsurface.

Expression of C-fixation as a rate per unit of biomass yields the specific activity of the phytoplankton (Fig. 7). The use of chlorophyll a as an indicator of algal biomass is questionable since chlorophyll a quota are affected by environmental conditions and species composition. However, no other data on phytoplankton biomass are available. In the upper layer the highest specific C-fixation rates were found at stations in the transition zone (Stns 91 to 96). Comparison of the values observed at a depth where 10% of the incident irradiance was available (Fig. 5C) shows that at these (greater) depths (ca 30 m) the highest specific production rates (Fig. 7) also prevailed in the transition zone. This indicates that these enhanced chlorophyll a concentrations might be the result of locally enhanced growth. Additional mechanisms of convergence cannot be ruled out since no current velocities have been measured. Oxygen consumption rates of the sediments at the transition zone were comparable to rates measured at stations on Dogger Bank (A. Cramer personal communication). Hence the enhanced biomass of nutrient-limited phytoplankton is assumed to be related to the hydrodynamical conditions leading to an enhanced availability of nutrients, rather than nutrient release from the sediments.

Low chlorophyll a values were found deeper than 35 m at Stns 96, 97 and 98 (Fig. 5C). At 35 m the specific C-fixation rate was 5 mg C mg^{-1} chl a d^{-1} (Fig. 7). Respiration of the <200 μm fraction (measured at various

stations and below the thermocline) yielded a value of 5.5 ± 3 mg C mg^{-1} chl a d^{-1} (data not shown), assuming that the main activity can be attributed to phytoplankton. Recalculation of data on light-limited cultures (Falkowski et al. 1985, Langdon 1987) leads to a comparable value. They reported (species-dependent) specific C-fixation rates which varied between 0.6 and 9.7 mg C mg^{-1} chl a d^{-1} with an average value of 4.7 ± 3.1 ($\pm$SD, $n = 6$). This respiration activity would indicate that below 35 m more carbon is respired for maintenance purposes than can be fixed during the light-period. Under these conditions survival of phytoplankton at deeper layers is possible if higher light intensities prevail or if a frequent upward transport (due to tidal mixing) occurs. Obviously, the latter was the case at Stns 87 and 95 where high chlorophyll a values were found well below the depth at which 5 mg C mg^{-1} chl a d^{-1} could be fixed. In conclusion, this phytoplankton can only persist if they are regularly exposed to higher irradiances such that an average specific carbon fixation rate of ca 5 mg C mg^{-1} chl a d^{-1} is attained. Note, at most stations this minimum C-fixation rate did not coincide with the 1% surface irradiance isoline (Fig. 5B). Under well-stratified conditions, which prevail during the summer in the central North Sea, a minimal value of 5% incident irradiance appears to be more likely. At shallower locations, processes like tidal-mixing and wind mixing should be taken into consideration when algal distribution is related to the underwater distribution of light. Such processes are not easy to quantify. Furthermore the quantitative value of the percentage of incident irradiance is not a constant but has a fluctuating value due to variation in cloudiness and time of the day. For these reasons a minimum specific carbon fixation rate of ca 5 mg C mg^{-1} chl a d^{-1} (as a lower limit for the survival of light-limited phytoplankton) seems more likely.

The relatively high ammonium levels might be a result of sample treatment. Freezing and thawing of water samples before analyses results in higher ammonium values (W. Helder personal communication). In surface layers across the Dogger Bank nitrate concentrations were low. This observation is in agreement with the findings of Owens et al. (1990), who in addition found a close relationship between low nitrate levels and primary production of phytoplankton >5 μm, indicating N-limited growth of this fraction of the population. It was assumed that nitrogen limited growth during the period of our investigation. According to the vertical distribution of nitrate at Stns 95 to 98, one can expect N-limitation to become less pronounced at greater depth, since less light and a higher nitrate concentration were present. Phytoplankton grown under low-light conditions contain a surplus of nutrients due to luxury uptake (Davis 1976, Falkowski 1980, Rhee and Gotham 1981, Riegman and Mur 1985). Severely nutrient-limited phytoplankton possesses a surplus of energy in the form of carbohydrates (Kuhl 1974, Riegman et al. 1985, Kromkamp 1987) and/or lipids (Kuhl 1974). Wind mixing induces a rapid transport of phytoplankton along the contra-directional vertical gradients of nutrient and light availability. Phytoplankton grown at low light and transported upwards
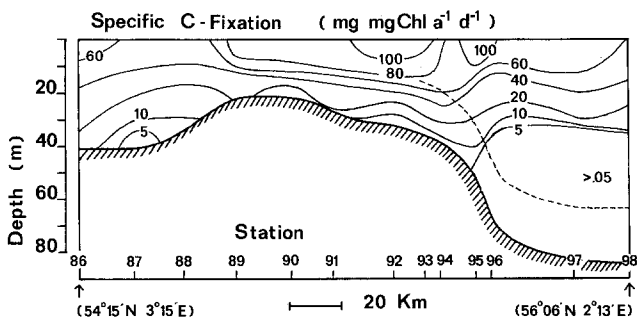

Fig. 7. Specific C-fixation rates along Transect 86/98 at various depths. The impact of tidal mixing, estimated (see Discussion) from temperature distribution (Fig. 2A, 2C), being restricted to the lowest 20 m of the water column at the northern slope of the Dogger Bank (- - - - -). Isolines in mg C mg^{-1} Chl $a \cdot$ d^{-1}. Shaded zone indicates sea floor profile

will increase in growth rate (Fig. 3) and biomass (Fig. 4). Nutrient-limited phytoplankton transported downwards will take up nutrients that become available from deeper layers due to tidal mixing and consequently a build-up of biomass is triggered (Fig. 2D). In other words, as a result of luxury uptake of nutrients in deep waters and (light) energy at the surface, a storm event leads to a net transport of nutrients upwards and (light) energy downwards, effecting an increase in biomass. The upwardly transported phytoplankton, especially, is able to increase its growth rate since higher irradiances prevail at the surface.

In shallow waters where phytoplankton is mixed throughout the entire water column, no vertical differentation in growth-rate limiting factors will occur. In deep well-stratified waters the lower layer with light-limited phytoplankton will tend not to mix with the upper layer, since tidal mixing predominantly takes place near the bottom. Wind-induced turbulence will, therefore, only reach the lower layer under exceptionally high wind stress. When wind mixing is excluded, for instance after a period of calm weather, the impact of tidal mixing can be estimated. For example Fig. 2A shows a steep temperature gradient at the thermocline (Stns 71 to 75), at shallower stations (Stns 66 to 70) the thermocline became broad-indicating the mixing of warm surface-water and cold deeper-water. Assuming that the observed temperature distribution was mainly the result of tidal mixing rather than horizontal advection, it can be concluded that tidal mixing was mainly restricted to the lowest 20 m of the water column. Since tidal currents do not differ much among various locations of the northern slope of Dogger Bank (Anonymous 1963), the same value (20 m) was assumed for stations at Transect 86/98. In the transition zone, tidal mixing forces the exchange of nutrients and phytoplankton between the two layers. During a period of calm weather, the deep chlorophyll maximum is established (Fig. 5C). Since the thermocline is elevated to a lower depth (Figs. 2 and 5A) even a small storm event will accelerate the net upward transport of nutrients and phytoplankton. If this explanation is correct, wind-induced algal blooms are to be expected along transitional frontal regions between well-mixed waters and well-stratified waters.

Besides a rapid vertical redistribution, an additional effect of a storm is the resuspension of benthic phytoplankton at shallow locations. The large number of penate diatoms present in the lower part of the water column at Stn 68 the day after a storm (Fig. 2D) suggests that resuspension and sedimentation due to the presence or absence of wind mixing might be an important factor in the productivity of benthic phytoplankton in the Dogger Bank area. However, more detailed observations on the distribution of benthic diatoms in the sediments and the overlying water should be made to estimate the impact of a storm event on benthic phytoplankton.

It has earlier been recognized (Sverdrup 1953, Pingree et al. 1978) that temporal changes in phytoplankton distribution can be remarkable within a period of a few days. Besides horizontal advection and wind-induced mixing (Fig. 2) phytoplankton growth also can induce

variations in chlorophyll a at a certain sampling station within a period of 24 h as a result of changing environmental conditions (Fig. 4). Features like nutrient distribution, chlorophyll a distribution and primary production are not only subject to actual processes at the time of sampling, but factors often mirror events which have occurred during the period prior to sampling. For this reason data on wind and daily irradiance should be taken into account when phytoplankton activity and distribution are studied.

Algal blooms, as indicated by enhanced chlorophyll concentrations, during the summer in the North Sea have been observed at different transitional frontal regions like Flamborough Head (Pingree et al. 1978), the southern margin (Creutzberg 1985) and the eastern margin (Owens et al. in press). In contrast with the Ushant front (Holligan et al. 1984) phytoplankton in the mixed side of the Dogger front was not light-limited but nitrogen-limited. As emphasized by Loder and Platt (1985), enhanced primary production at fronts might be the result of mixing between two water masses both deficient in complementary nutrients. At the northern slope of Dogger Bank, nitrogen entrainment of the photic zone, stimulating the growth of nitrogen-limited phytoplankton, seems to be the key factor. Intermittence of the physical forces determines to what extent enhanced algal biomasses can be observed at the Dogger front.

Literature cited

Anonymous (1963). Atlas der Gezeitenströme für die Nordsee, den Kanal und die Britischen Gewässer. Deutsches Hydrografisches Institut, Hamburg

Braarud, T., Ringdal Gaarder, K., Grontved, J. (1953). The phytoplankton of the North Sea and adjacent waters in May 1948. J. Cons. perm. int. Explor. Mer 13: 5–89

Colijn, F. (1983). Primary production in the Ems Dollard Estuary. Thesis, University of Groningen, Groningen

Creutzberg, F. (1985). A persistent chlorophyll a maximum coinciding with an enriched benthic zone. Proc. 19th Eur. mar. Biol. Symp., p. 97–108 [Gibbs P. E. (ed.) Cambridge University Press, Cambridge]

Davies, C. O. (1976). Continuous culture of marine diatoms under silicate limitation. 2. Effects of light intensity on growth and nutrient uptake of *Skeletonema costatum.* J. Phycol. 12: 291–300

Eisma, D. (1987). The North Sea: an overview. Phil. Trans. R. Soc. (Ser. B) 316: 461–485

Eppley, R. W., Renger, E. H. (1988). Nanomolar increase in the surface layer nitrate concentration following a small wind event. Deep Sea Res. 35(7): 1119–1125

Falkowski, P. G. (1980). Light-shade adaptation in marine phytoplankton. In: Falkowski P. G. (ed.). Primary Productivity in the Sea. Plenum Press, New York, p. 99–120

Falkowski, P. G., Dubinski, Z., Wyman, K. (1985). Growth-irradiance relationships in phytoplankton. Limnol. Oceanogr. 30: 311–321

Gieskes, W. W. C., Kraay, G. W. (1980). Primary productivity and phytoplankton pigment measurements in the northern North Sea during FLEX '76. "Meteor" ForschErgebn. A-22: 105–112

Gieskes, W. W. C., Kraay, G. W. (1984). Phytoplankton, its pigments, and primary production at a central North Sea station in May, July and September 1981. Neth. J. Sea Res. 18(1/2): 51–70

Gill, P. E., Murray, W. (1978). Algorithms for the solution of nonlinear squares problem. Soc. ind. appl. Math. J. num. Anal. 15: 977–992

Holligan, P. M., LeB. Williams, P. J., Purdie, D., Harris, R. P. (1984). Photosynthesis, respiration and nitrogen supply of plankton populations in stratified, frontal and tidally mixed shelf waters. Mar. Ecol. Prog. Ser. 17: 201–213

Holm-Hansen, O., Lorenzen, C. L., Holmes, R. W., Strickland, J. D. H. (1965). Fluorometric determination of chlorophyll. J. Cons. perm. int. Explor. Mer 30: 3–15

Kromkamp, J. (1987). Formation and functional significance of storage products in cyanobacteria. N. Z. J mar. Freshwat. Res. 21: 457–465

Kuhl, A. (1974). Phosphorus. In: W. D. P. Stewart (ed.). Algal Physiology and Biochemistry. Bot. Monogr. 10: 636–655

Lande, R., Yentsch, C. S: (1988). Internal waves, primary production and the compensation depth of marine phytoplankton. J. Plankton Res. 10(3): 565–571

Langdon, C. (1987). On the causes of interspecific differences in the growth-irradiance relationship for phytoplankton. J. Plankton Res. 9(3): 459–483

Loder, J. W., Platt, T. (1985). Physical controls on phytoplankton production at tidal fronts. Proc. 19th Eur. mar. Biol. Symp., p. 3–21 [Gibbs P. E. (ed.) Cambridge University Press, Cambridge]

Luning, K. (1981). Light. In: Lobban, C. S., Wynne, M. J. (eds.). The biology of seaweeds. Bot. Monogr. 17: 326–355

Mortain-Bertrand, A., Descolas-Gros, C., Jupin, H. (1988). Pathway of dark inorganic carbon fixation in two species of di-

atoms: influence of light regime and regulator factors on diel variations. J. Plankton Res. 10: 199–217

Owens, N. J. P., Woodward, E. M. S., Aiken, J., Bellan, I. E., Rees, A. P. (1990). Primary production and nitrogen assimilation in the North Sea during July 1987. Neth. J. Sea Res. 25: 143–155

Pingree, R. D. (1978). Mixing and stabilisation of phytoplankton distributions on the northwest European continental shelf. In: Steele, J. H. (ed.). Spatial pattern in plankton communities, Vol. 3, Plenum Press, New York, p. 181–200

Pingree, R. D., Griffiths, D. H. (1978). Tidal fronts on the shelf areas around the British Isles. J. geophys. Res. 83: 4615–4622

Pingree, R. D., Holligan, P. M., Mardell, G. T. (1978). The effects of vertical stability on phytoplankton distributions in the summer on the northwest European Shelf. Deep Sea Res. 25: 1011–1028

Rhee, G.-Y., Gotham, I. J. (1981). The effect of environmental factors on phytoplankton growth: Light and the interactions of light with nitrate limitation. Limnol. Oceanogr. 26: 649–659

Riegman, R., Mur, L. R. (1985). Effects of photoperiodicity and light irradiance on phosphate-limited Oscillatoria agardhii in chemostat cultures: II. Phosphate uptake and growth. Arch. Microbiol. 142: 72–76

Riegman, R., Rutgers, M., Mur, L. R. (1985). Effects of photoperiodicity and light irradiance on phosphate-limited Oscillatoria agardhii in chemostat cultures: I. Photosynthesis and carbohydrate storage. Arch. Microbiol. 142: 66–71

Strickland, J. D., Parsons, T. R. (1972). A practical handbook of sea water analyses. Bull. Fish. Res. Bd Can. 167: 1–311

Sverdrup, H. U. (1953). On conditions on the vernal blooming of phytoplankton. J. Cons. perm. int. Explor. Mer 18: 287–295

Utermöhl, H. (1958). Vervollkommung der quantitativen Phytoplankton-Methodik. Mitt. int. Verein. theor. angew. Limnol. 9: 1–38

Vermij, S. G. (1987). Analyses of algal growth in Lake Maarsseveen by means of mathemathical modelling. Thesis, University of Amsterdam, Amsterdam