Evaluation of measurements and calculation of primary production in the Dogger Bank area (North Sea) in summer 1988[*]

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ABSTRACT: Primary production was measured during a survey in the Dogger Bank area, where both stratified and non-stratified conditions existed in July–August 1988. Daily primary production was calculated, based on ^{14}C-fixation rates in an incubator with an artificial light source, depth profiles of in situ irradiance, and vertically heterogeneous phytoplankton distributions. Values ranged among stations from 300 to 2200 mg C m^{-2} d^{-1}. Average primary production in the Dogger Bank area was estimated at 1.2 g C m^{-2} d^{-1}. Variation in cloudiness affected primary production by a factor of 4.5. Calculations based on surface samples alone showed an average areal primary production underestimate of 17 %. After correction for the uneven vertical biomass distribution, primary production was still underestimated by 12 % as a result of photoadaptation. Especially below 30 m, I_k was reduced from 310 to 174 μE m^{-2} s^{-1}, demonstrating the presence of shade-adapted phytoplankton at the thermocline. Calculated daily primary production rates based on in situ incubations and on incubator measurements deviated by only 5 %. Light quality did not have a significant effect on water column productivity. Size-dependent primary production based on post-incubation filtration onto 5 μm filters showed that, on average, 84 % of total primary production was in the > 5 μm fraction.

INTRODUCTION

The importance of a reliable estimate of primary production in the North Sea has been recognized by various authors (Steele 1974, Jones 1984). From a literature survey on the references database 'Biosis Previews' 1969–1989 it can be concluded that only a limited amount of data has been published during the past 20 yr. Most plankton studies of this period (Fig. 1) were restricted to coastal zones such as the English coast ((2) & (3), Ochocki et al. 1973), the Belgian coastal zone ((4), Lancelot & Billen 1984) and the Dutch and German coastal zones ((5), Mommaerts 1973; (6), Veldhuis et al. 1986; (7), Gieskes & Kraay 1977; (8), Cadée 1986; (11), Colijn et al. 1990). Along the German coast (Sylt) primary production measurements were reported by Asmus & Asmus 1985 (12). Offshore studies are even more scarce ((1), Gieskes & Kraay 1980; (9), Gieskes & Kraay 1984, Tijssen & Wetsteyn 1984). The lack of sufficient year-round data and the unequal attention

that has been paid to the different hydrographic regimes in the North Sea (indicated by the dotted lines in Fig. 1) preclude the calculation of a reliable primary production estimate. This lack of data is mainly due to the size of the North Sea and the unfavourable weather during autumn and winter. Moreover, a preference for coastal zone studies is stimulated by the frequent recognition of eutrophication effects in coastal regions.

The main purpose of this study was to evaluate a simple and fast method which could enable monitoring of primary production over large areas over a short period of time. The measurements were made during July 1988 in the Dogger Bank area. No measurements on primary production had been made in this area previously. Estimation of primary production from ^{14}C-incubation data yields a value somewhere between gross and net production (Peterson 1980).

The phytoplankton in the North Sea is distributed very heterogeneously due to variations in physical and chemical factors (Braarud et al. 1953, Gieskes & Kraay 1977, Creutzberg 1985). Consequently, spatial variation in primary production was to be expected. To collect as much data as possible, preference was given
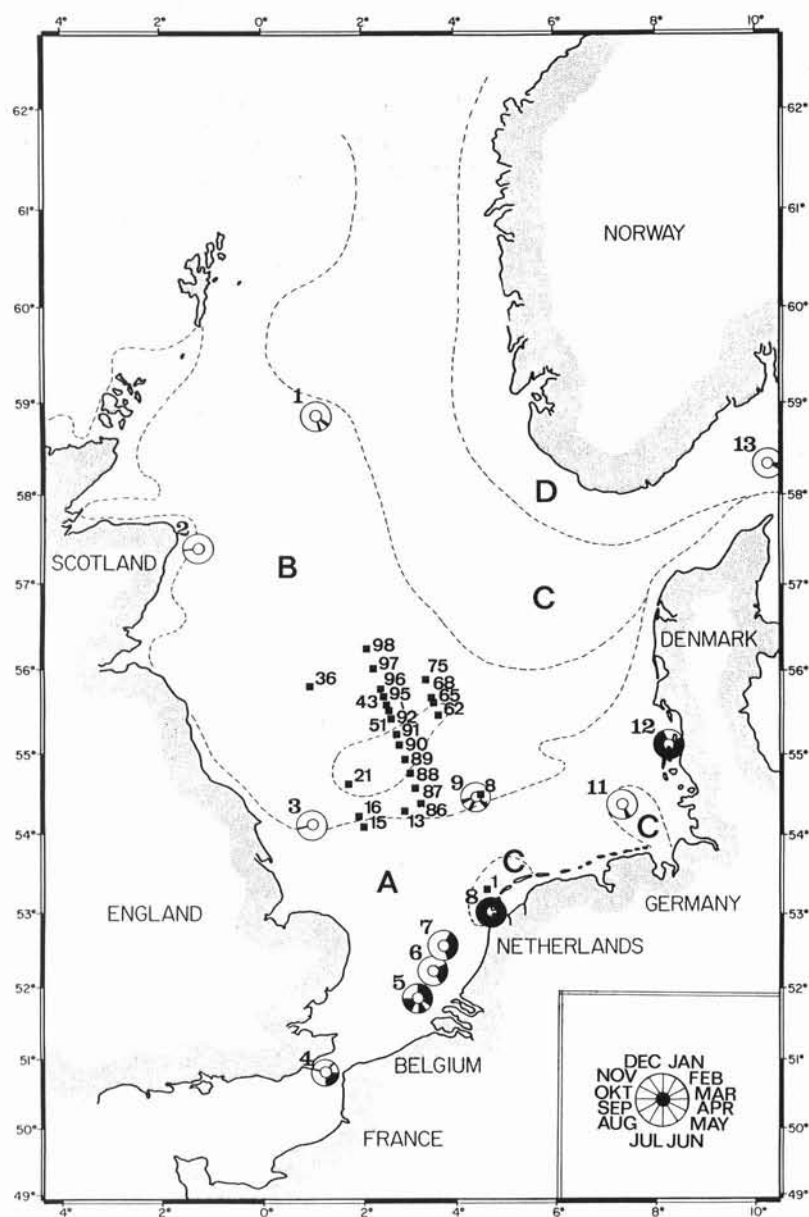
Fig. 1. Locations of published primary production studies (references in text). Black shading in rings indicates measuring period. (■) Sampling stations of present study. Dotted lines indicate borders between different water regimes after Dietrich (1950): (A) homohaline and homothermal throughout the whole year; (B) seasonal thermal stratification in homohaline water; (C) seasonal thermal stratification and permanent (weak) haline stratification; (D) permanent strong haline stratification

to short-term (i.e. 2 h) ^{14}C-incubations. Production profiles were estimated from production-irradiance (P-I) relationships and the vertical distribution of fluorescence and irradiance. These profiles were compared with in situ incubations. Also, the effect of spectral distribution on daily primary production estimates and the relative importance of primary producers smaller than 5 μm was studied.

MATERIAL AND METHODS

The sampling locations are shown in Fig. 1. At some stations more than one production profile was measured within 24 h to obtain insight into possible diel changes in

photosynthetic characteristics of watermasses drifting past the ship. A S-N transect over the Dogger Bank was completed within 1 d. These stations included a completely mixed situation (Stns 89 & 90) and 2 stratified situations (Stns 86 to 88 & 91 to 98). Samples for the determination of ^{14}C-fixation rates were taken from at least 2 depths: at 5 m and at the chlorophyll fluorescence maximum around the thermocline, if present. Where fluorescence was homogeneously distributed the second sample was taken at 5 m above the sea floor. In 1988, our Niskin sampler was equipped with a rubber cord. Its inhibitory effect on carbon fixation measurements has been reported recently (Williams & Robertson 1989) for oligotrophic phytoplankton during long-term (> 6 h) incubations. In our study much shorter incuba-

tion times (2 h) were used. P-I relationships were measured in an incubator at 5 irradiances, ranging from about 2500 to 25 $\mu E\,m^{-2}\,s^{-1}$, for 2 h after the addition of 5 $\mu Ci\,NaH^{14}CO_3$ (Carrierfree, Amersham, USA) to 50 ml subsamples. The incubator was illuminated with an Osram metallogen HMI 1200 W lamp (Colijn 1983). Different irradiances were achieved by neutral density filters (Lee, Andover, England) covering the polystyrene tissue culture bottles (Greiner, Solingen, Germany). Prior to every incubation, incubator irradiances were measured with a Licor underwater Quantum sensor LI-192 SA. From these measurements the irradiance was calculated for each bottle. After incubation the samples were filtered onto Sartorius membrane filters (SM 11306, 0.45 μm) at reduced differential pressure (< 100 mm Hg). Filters were then acid-fumed for at least 5 min and counted in a liquid scintillation counter after addition of 10 ml Instagel (Packard, USA). The incubation bottles were cleaned with and left in Whatman GF/F filtered surface seawater between experiments. Prior to use they were flushed with at least 3 times their volume of the seawater sample. A separate series of bottles was used for surface samples which were expected to have low nutrient concentrations in order to avoid any possible contamination with nutrients. Calculation of C-fixation rates was based on the initial amount of label added, whereas a constant value of 24 mg C l^{-1} for total inorganic carbon was assumed. Dark uptake values were not subtracted from light values (Mortain-Bertrand et al. 1988). In general dark values did not exceed 5 % of the P_{max} value. P-I curves were fitted according to Platt et al. 1980 (cf. Colijn 1983) using the procedure algorithm EO4FDF from the library of Numerical Algorithms Group (NAG) (Anonymous 1987) which enabled a simultaneous and independent estimate (Gill & Murray 1978) of the maximum photosynthetic rate (P_{max}), the affinity of photosynthesis for light (α), the inhibition constant (β) and I_k (the ratio between P_{max} and α). During the whole period incident solar irradiance was measured on board using a Kipp solarimeter. From the average daily irradiance the photosynthetically active radiation (PAR) was calculated assuming PAR to be 45 % of the total irradiance, expressed as J $m^{-2}\,s^{-1}$ (Lüning 1981). Light reflection at the sea surface was assumed to be 3 % of total irradiance (Jerlov 1968). The underwater attenuation coefficient (K_d in m^{-1}) was calculated from underwater quantum measurements and fitted according to the Lambert-Beer law. At some stations K_d was found to vary with depth. At stations where sampling occurred during the night K_d was estimated from turbidity measurements using a relationship between light attenuation and turbidity established during the cruise. To optimize an estimated production profile the watercolumn was divided in 2 to 4 segments, depending on the variation in vertical

fluorescence distribution, in such a way that each water sample represented the entire segment. Fluorescence profiles were used to correct the calculated production profiles for a non-homogeneous distribution of algal biomass within each segment. At 2 stations an extensive comparison of in situ and incubator measurements could be achieved over a whole day.

Chlorophyll concentrations were determined by fluorometry on acetone extracts of particulate matter collected on Whatman GF/C filters and standardized against commercially available chlorophyll a (isolated from spinach; Sigma, USA).

At a few stations post-incubation filtration (cellulose nitrate filters; Sartorius, Germany) was performed to compare primary production in the > 5 μm with the small fraction between 0.45 and 5 μm.

At 2 stations (68 and 75) 24 h studies were performed: sampling at a time interval of about 6 h should give insight into possible diel variation of photosynthetic characteristics per se and within watermasses drifting past the ship.

The effect of light quality was checked on depth samples from 3 stations: 51, 62 and 75. Incubations were performed in series with neutral density filters and series equipped with 2 different cuvettes containing separated solutions of $FeCl_3$ and $CuSO_4$ with a known specific absorption spectrum (measured with a spectrophotometer). The concentration of these solutions was calculated, using a special designed computer program, in such a way that the combination of both liquid filters allowed an optimum approximation of the in situ spectral light distribution. The in situ spectral light distribution at the sampling depth was measured using a spectral irradiance meter (Spitzer & Wernand 1986).

RESULTS

Information on the sampling stations is presented in Table 1. In agreement with earlier reports on offshore areas (Gieskes & Kraay 1984, Creutzberg 1985) summer chlorophyll a values in the surface layers were low: mean 0.65 $\mu g\,l^{-1}$. Only the coastal station (Stn 1) showed a very high value. The stratified stations showed a deep chlorophyll a maximum with 5- to 10-fold higher values compared to the surface concentration. This maximum was present at the thermocline where the nitrogen-depleted, warmer upper layer (15 $\pm$ 1 °C) was separated from the nutrient-rich, cold lower layer (6 to 8 °C). More detailed information on nutrient levels and temperature distribution is presented elsewhere (Riegman et al. 1990).

The vertical attenuation coefficient varied between 0.06 and 0.15 m^{-1} (Stn 1: 0.41 m^{-1}) with an average of

Table 1. Compilation of data from all primary production stations. Attenuation coefficient K_d in m^{-1}. The presence of stratification was concluded from the vertical temperature distribution. Values from subsurface samples (5 m) are given for chlorophyll a ($\mu g\ l^{-1}$); P_{max} (mg C $m^{-3}\ h^{-1}$) and α (mg C $m^{-3}\ h^{-1}\ [\mu E\ m^{-2}\ s^{-1}]^{-1}$). Primary production (PP) in g C $m^{-2}\ d^{-1}$ is calculated for a 'standard' day

Date (1988)	Station	Time (h)	Depth (m)	Stratification	K_d	Chl a	P_{max}	α	PP
14 Jul	1	12:00	22	+	0.41	13.01	76.1	0.124	1.76
15 Jul	8a	12:00	45	+	0.07	0.46	7.3	0.016	1.38
6 Aug	8b	12:00	45	–	0.12	2.10	36.6	0.084	3.49
16 Jul	13	12:00	44	+	0.07	0.93	8.1	0.017	1.36
5 Aug	15a	6:00	32	–	0.15	1.9	17.0	0.042	1.80
5 Aug	15b	13:00	32	–	0.15	1.2	13.2	0.045	2.04
17 Jul	16	12:00	77	+	0.08	0.61	3.4	0.023	1.45
18 Jul	21a	12:00	27	–	0.13	0.90	3.7	0.017	1.69
4 Aug	21b	12:00	27	–	0.12	0.43	10.3	0.042	0.89
19 Jul	36	12:00	77	+	0.07	nd	3.2	0.012	1.40
3 Aug	43a	6:00	50	+	0.08	0.26	6.8	0.017	1.60
3 Aug	43b	13:00	50	+	0.08	0.24	8.6	0.020	1.69
20 Jul	51	12:00	34	+	0.06	0.24	3.2	0.009	0.85
21 Jul	62	12:00	27	+	0.10	0.13	6.6	0.020	0.97
21 Jul	65	16:00	30	+	0.11	0.59	6.4	0.019	1.00
28 Jul	68a	00:00	33	+	0.13	0.30	2.7	0.016	0.37
30 Jul	68b	12:00	33	+	0.13	0.74	7.6	0.028	1.49
30 Jul	68c	16:00	33	+	0.13	0.48	6.8	0.037	2.64
30 Jul	68d	24:00	33	+	0.13	0.81	3.9	0.034	0.89
27 Jul	75a	8:00	50	+	0.08	0.24	4.6	0.025	1.28
27 Jul	75b	13:30	50	+	0.08	0.20	2.8	0.015	0.71
27 Jul	75c	19:00	50	+	0.08	0.19	3.9	0.012	0.42
27 Jul	75d	24:00	50	+	0.08	0.17	2.4	0.022	0.87
22 Jul	75e	00:00	50	+	0.08	0.44	6.4	0.022	0.81
31 Jul	86	24:00	41	+	0.08	0.56	3.8	0.026	1.26
1 Aug	87	2:00	41	+	0.12	1.60	7.8	0.049	1.60
1 Aug	88	4:00	34	+	0.12	0.97	3.9	0.027	0.89
1 Aug	89	6:00	22	–	0.13	1.59	12.2	0.070	2.03
1 Aug	90	8:00	22	–	0.15	0.79	7.3	0.031	0.86
1 Aug	91	10:00	27	+	0.15	0.88	7.7	0.040	1.48
1 Aug	92	12:00	32	+	0.10	0.33	6.1	0.020	1.27
1 Aug	93	14:00	36	+	0.08	0.4	3.6	0.012	1.22
1 Aug	94	16:00	38	+	0.08	0.45	6.6	0.018	1.17
1 Aug	95	18:00	54	+	0.09	0.50	13.4	0.012	1.03
1 Aug	96	20:00	69	+	0.10	0.66	10.7	0.019	1.12
1 Aug	97	22:00	82	+	0.08	0.41	2.8	0.013	0.79
1 Aug	98	24:00	84	+	0.07	0.17	1.1	0.008	0.33

nd: not determined

$0.10\ m^{-1}$. Total daily irradiance (TDI) ranged from 2694 kJ m^{-2} to 25 414 kJ m^{-2}. Over the whole survey period the average value of TDI was 15 760 kJ m^{-2}. This is referred to as the 'standard' day.

Daily primary production (in g C $m^{-2}\ d^{-1}$) was calculated for the actual (A) daily irradiance (irradiance of sampling day), but also for the average (B) irradiance during the survey period (an average summer period, the 'standard' day), and – to check daily variability due to irradiance differences – for the days with maximal (C) and minimal (D) irradiance. Actual daily primary production ranged from 0.3 to well over 2.0 g C m^{-2}; primary production on the 'standard' day (B) ranged from 0.4 to over 3 g C m^{-2}. Method C gave results

ranging from 0.4 to 4.5 g C m^{-2} whereas Method D gave very low productivities ranging from 0.1 to 1.3 g C m^{-2}. Average values over 37 measurements were 1.16, 1.29, 1.68 and 0.37 for Methods A, B, C, and D, respectively. This underlines the preponderant influence of irradiance on long-term primary production. In stratified waters an average value of 1.06 g C $m^{-2}\ d^{-1}$ at an average chlorophyll a subsurface concentration of 0.50 $\mu g\ l^{-1}$ was found. In completely mixed waters these values were higher, viz. 1.49 g C $m^{-2}\ d^{-1}$ and 1.27 μg chl $a\ l^{-1}$ (coastal Stn 1 was excluded from the calculation). Clearly the differences in chlorophyll a concentration were less strongly reflected in the daily primary production. In both types of watermasses a
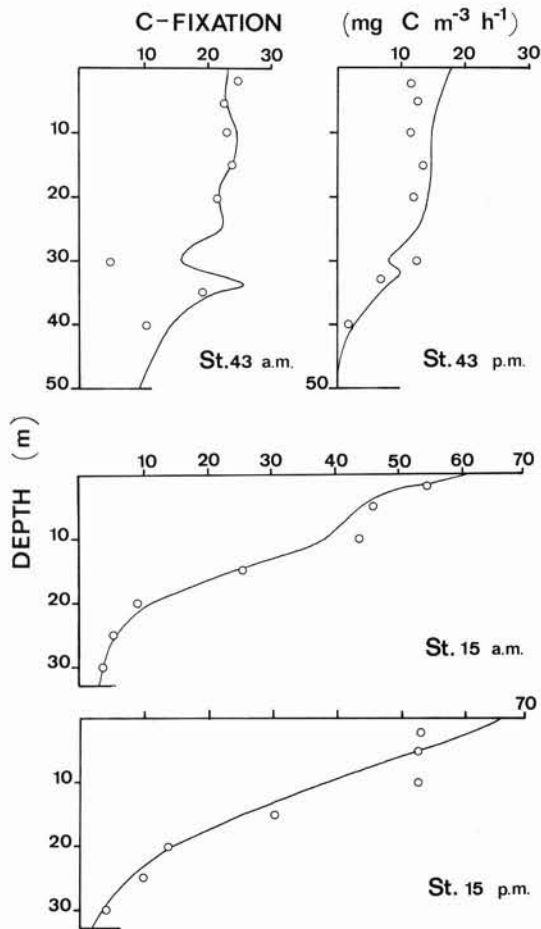
Fig. 2. Vertical distribution of primary production at the well-mixed Stn 15 and at the stratified Stn 43. Incubator method A (———) was compared with in situ measurements (○) from 6:00 to 13:00 h ('a.m.') and from 13:00 to 20:00 h ('p.m.')

Table 2. Average values and standard deviation of photosynthetic parameters from samples taken between 0 and 15 m, 15 to 30 m, and > 30 m at the various sampling stations. P^b_{max} in mg C (mg chl a)$^{-1}$ h^{-1}; α^b in µg C (mg chl a)$^{-1}$ h^{-1} (µE m^{-2} s^{-1})$^{-1}$ and I_k in µE m^{-2} s^{-1}. Number of samples in brackets

Depth category	P^b_{max}	α^b	I_k
0–15 m	13.8 ± 11 (36)	46.4 ± 23 (37)	297
15–30 m	13.6 ± 10 (25)	42.0 ± 25 (29)	323
> 30 m	5.9 ± 3.4 (28)	34.0 ± 12 (29)	174
0–30 m < 5 µm	1.5 ± 0.7 (7)	8.2 ± 3.8 (7)	183

calculations primary production is overestimated by ca 25 %. At 2 stations, 2 consecutive half-day in situ incubations were performed with samples suspended from a drift buoy (Fig. 2). For all 4 incubations we observed good agreement between values calculated from P-I relations and those measured in situ, with no consistent deviation for one method or the other. On average the total column production estimated from the incubator method was 5 % higher than the estimate from the in situ incubations.

In Table 2 the physiological parameters (P^b_{max}, α^b and I_k) obtained from the fits of the P-I curves are summarized. These data show that P^b_{max} and I_k are fairly constant within the upper 30 m of the water column but decrease in the samples taken at greater depth. This decrease is due to photoadaptation to low irradiance in the deeper layers, but is probably also due to a different species composition in the subthermocline layers, with a dominance of *Ceratium* spp. (unpubl.). Obviously the < 5 µm fraction is low-light adapted, but aberrant in its physiology because of its reduced P^b_{max}. Also its photosynthetic efficiency (α^b) is 5 times lower than that of the total fraction.

At 3 stations the effect of the spectral distribution of light on photosynthesis was studied. Incubation with white light resulted in almost a doubling of the P_{max} values and a reduction of the photosynthetic efficiency (α) compared to incubation with blue-green light (Table 3). At these sampling depths non-saturating irradiances prevail. Therefore, the reduction of α induced by the use of neutral density instead of coloured filters would have the largest impact on photosynthesis estimation. However, it appeared that the impact on the estimates of total primary production of the entire water column was negligible (Table 3). This was mainly because most of the primary production occurred in the upper part of the photic zone.

The results of post-incubation filtration into 2 fractions are summarized in Table 4. On average 84 % of the daily primary production was found in the > 5 µm fraction. Stns 36 and 75 showed the highest contribu-

'standard day' primary production of > 1 g C m^{-2} d^{-1} could be reached easily. Subsequently, 3 other methods were used to calculate daily primary production with the following assumptions: in Method E, calculation was based on incubation of the surface sample only (instead of a second sample from the thermocline), but with a biomass correction by means of the fluorescence profiles; in Method F, the same procedure was followed but without a biomass correction; and finally, to study the effect of inhibition (Method G), the inhibition factor (β) in Platt's formulation was set to zero. The results of these calculations (using the irradiance of a 'standard' day) showed that the average values from Methods E, F and G were respectively 1.13, 1.07 and 1.59 g C m^{-2} d^{-1}. These results imply that primary production values based on incubation of surface samples only and without a biomass correction would underestimate total water column production by 10 to 20 % in these waters during this time. If light inhibition is not incorporated in the

Table 3. Effect of light quality on photosynthetic parameters (same units as in Table 2) and estimated primary production of the water column (in g C m^{-2} d^{-1})

Station	Sampling depth (m)	'White' light			'Blue-green' light		
		P^b_{max}	α^b	PP	P^b_{max}	α^b	PP
51	26	13.1	28.2	0.85	7.0	31.3	0.87
62	24	32.7	139.0	0.97	17.1	183.2	0.99
75e	28	3.9	23.8	0.79	2.3	37.9	0.80

tion of the < 5 μm fraction; both these stations are in the stratified region of the surveyed area. The completely mixed stations (8b, 13 and 21) showed the lowest contribution of the < 5 μm fraction in the daily primary production.

DISCUSSION

Small-scale patchiness of phytoplankton distribution and productivity was illustrated by the strong fluctuations observed at a single station within 24 h (Stns 68a–d and 75a–d; Table 1). This patchiness, created by, among other things, the complex hydrodynamics of the area and the irregular occurrence of wind mixing, emphasizes the need for a measurement technique that allows a high frequency of sampling. The in situ method is probably the most reliable and realistic method of incubation (Jitts 1963, Sorokin & Konovalova 1973) but has very limited practical applicability for sea-going survey operations. The alternative method, where samples are incubated in a gradient of natural sunlight in deck boxes on board ship (simulated in situ method; originally described by Steemann Nielsen in 1957) is widely used in marine primary production

Table 4. Size-dependent daily primary production based on postincubation filtration over 5.0 and 0.45 μm filters as % of total daily column primary production

Station	% of total primary production	
	> 5 μm	< 5 μm
1	88	12
8	96	4
8a	84	16
13	91	9
16	88	12
21a	82	16
21b	86	14
36	73	27
51	80	20
62	84	16
65	84	16
75e	77	23
Average	84	16

studies. This method is less suitable for the North Sea because of the strong fluctuations in weather conditions. Variation in cloudiness affects the primary production dramatically. Comparison between fully clouded conditions (calculation Method D) and unclouded wheather (calculation Method C) shows primary production to vary by a factor 4.5 due to incident irradiance alone. This implies that variations in cloudiness during a cruise will introduce artificial differences in the productivity of different areas, if weather conditions change dramatically during the period of the cruise. After a longer period (i.e. several days or longer) of continuous bad weather, these artificial differences might become less severe due to photoadaptation or selection towards shade-adapted species. Our study shows that an artificial light source should be used when the main purpose of primary production measurements is to compare the productivity of different areas. The measurement capacity of the present method could be doubled if only surface samples were taken. On the other hand an underestimate of 12 % was made if only P-I relationships of surface samples were used to calculate the column productivity but with a correction for non-homogeneous plankton distribution on the basis of fluorescence profiles. The underestimation is mainly due to the optimalisation of the photosynthesis parameters (photoadaptation) of phytoplankton at greater depth (Table 2). Especially in stratified areas with a deep chlorophyll maximum, the omission of the correction for non-homogeneous phytoplankton distribution will lead to serious underestimation. For the stratified locations around the Dogger Bank this underestimation was 18 %.

On-deck incubations with varying irradiance do not permit the calculation of photosynthetic parameters. The present method has the advantage of allowing both the incorporation of total daily irradiance and information on photosynthetic parameters. The latter can be used for modelling purposes (Harrison et al. 1985, Smith et al. 1987) and, especially in combination with remote sensing data, would enable a more synoptic estimate to be made (Platt et al. 1988).

When samples are taken at different depths, P_{max} and α can provide information on the vertical stability of the water column (Cullen & Lewis 1988). During the cruise

2 storms occurred successively (maximum wind speed 25 m s^{-1} for at least 48 h). Changes in temperature profiles indicated enhancement of the mixing depth from 20 m to about 30 m. The effect is reflected in the results presented in Table 2: on average samples taken between 15 and 30 m depth did not deviate significantly from the surface samples with respect to P_{max} and α. At greater depths shade-adapted phytoplankton was present, as can be concluded from their lower I_k values. The presented P_{max} values fall in the upper range of former published data on marine phytoplankton (Eppley 1972). This can be attributed to the fitting procedure ('Material and Methods'). The equation of Platt et al. (1980) implicitly assumes that photoinhibition also occurs at a light intensity where production is at a maximum. This explains the difference between the actual measured P_{max} values (being on average 43 % lower) and the calculated P_{max} values (presented in Tables 2 & 3).

At all 3 stations a stimulating effect of blue-green light on photosynthesis was observed. A higher photosynthetic efficiency under blue-green light has been reported for a large number of species (Wallen & Geen 1971, Glover et al. 1987, Prézelin et al. 1989). However, in samples from the Sargasso Sea, Prézelin et al. (1989) observed no such effect on P_{max}. With respect to the Sargasso Sea, where the average depth of the euphotic zone was 140 m, Prézelin et al. showed that the daily integrated water-column primary production would be 6 to 13 % higher with blue-green light instead of white light estimates. Around the Dogger Bank the average depth of the euphotic zone (1 % level) was much less: 46 m. The use of neutral density filters resulted in a maximal underestimation of the daily column production of 2 %. Apparently, the use of neutral density filters will not lead to serious underestimation in waters with a relative shallow euphotic zone.

Our limited number of experiments on the size distribution of primary producers shows that earlier observations in the central North Sea (Owens et al. 1990), which showed the preponderance of primary production in the very small fraction, could not be confirmed. Therefore, generalisations about the importance of size distribution for primary production studies and food-web studies are not yet possible. Long-term or annual time series are needed.

A comparison of our daily primary production data with other data for the same area is hampered by the lack of a consistent data set. Typical summer values are 0.065 g C m^{-2} d^{-1} for the northern North Sea (Gieskes & Kraay 1980) and 0.7 g C m^{-2} d^{-1} for the Belgian and Dutch coastal area (Mommaerts 1973, Gieskes & Kraay 1975, Lancelot & Billen 1984). The value for the Dogger Bank area (1.2 g m^{-2} d^{-1}) is close to the value observed for the Oyster Ground, south-

east of Dogger Bank (1.0 g m^{-2} d^{-1}; Tijssen & Wetsteyn 1984) which suggests that the southern part of the North Sea, up to the northern edge of the Dogger Bank, is characterised by relatively high primary production values during the summer.

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This article was submitted to the editor