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Dynamics of primary production as measured by the ISIS in situ technique

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Abstract

The ISIS *in situ* incubator was used to evaluate the dynamics of a phytoplankton bloom in the Kattegat in late October 1979. The nutrient status of the water column indicated a typical fall regenerative situation with relatively high concentrations of ammonium and phosphate and only low concentrations of nitrate. The photic zone was well mixed during the bloom due to preceding rough weather. Clear, sunny and calm conditions prevailed the day prior to and during the bloom. Primary production was measured at four depths and amounted to 90.4 mg C m^{-2} h^{-1} integrated from the surface to 12 m. The highest fixation rate occurred at 1 m depth and was 16.4 mg C m^{-3} h^{-1}. The productivity index was 3.7 mg C (mg chlorophyll a)$^{-1}$ h^{-1} at 1 m and 5.3 mg C (mg chlorophyll a)$^{-1}$ h^{-1} at 4 m depth. The light response relationship showed light saturation at about $3.8 \cdot 10^{23}$ quanta m^{-2} h^{-1}. It is concluded that primary production during this experiment was controlled by a combination of excess light energy and temperature but not by nutrient limitation.

Introduction

The last decade or so has seen an increased interest in relating phytoplankton primary production in a quantitative manner to environmental conditions, in the first place to light energy and inorganic nutrients. A large amount of work has been done with laboratory cultures in chemostats and other culturing devices under strictly controlled conditions (for recent references see e.g. BANNISTER 1979) which has led to the formulation of various useful (and sometimes not so useful!) models of primary production and plankton growth dynamics. The testing of such models in the field is the next step towards a comprehension of the mechanisms controlling production in the seas. Reports of such research are now appearing more and more frequently in the literature (EPPLEY et al. 1973, JITTS et al. 1976, HUNTSMAN and BARBER 1977, BIENFANG and GUNDERSEN 1977, MOREL 1978). The most comprehensive investigation along these lines in Scandinavian waters was made by GARGAS et al. (1978) in connection with the Danish Belt Project.

The present investigation examines primary production and the phytoplankton community in relation to light energy, nutrients, temperature and oxygen in the photic zone during an autumn bloom in the Kattegat in October 1979. In this work we have used the ISIS *in situ* incubator technique which will be described in more detail below. A more comprehensive report of this work will be published elsewhere (EKLUND et al. in preparation).

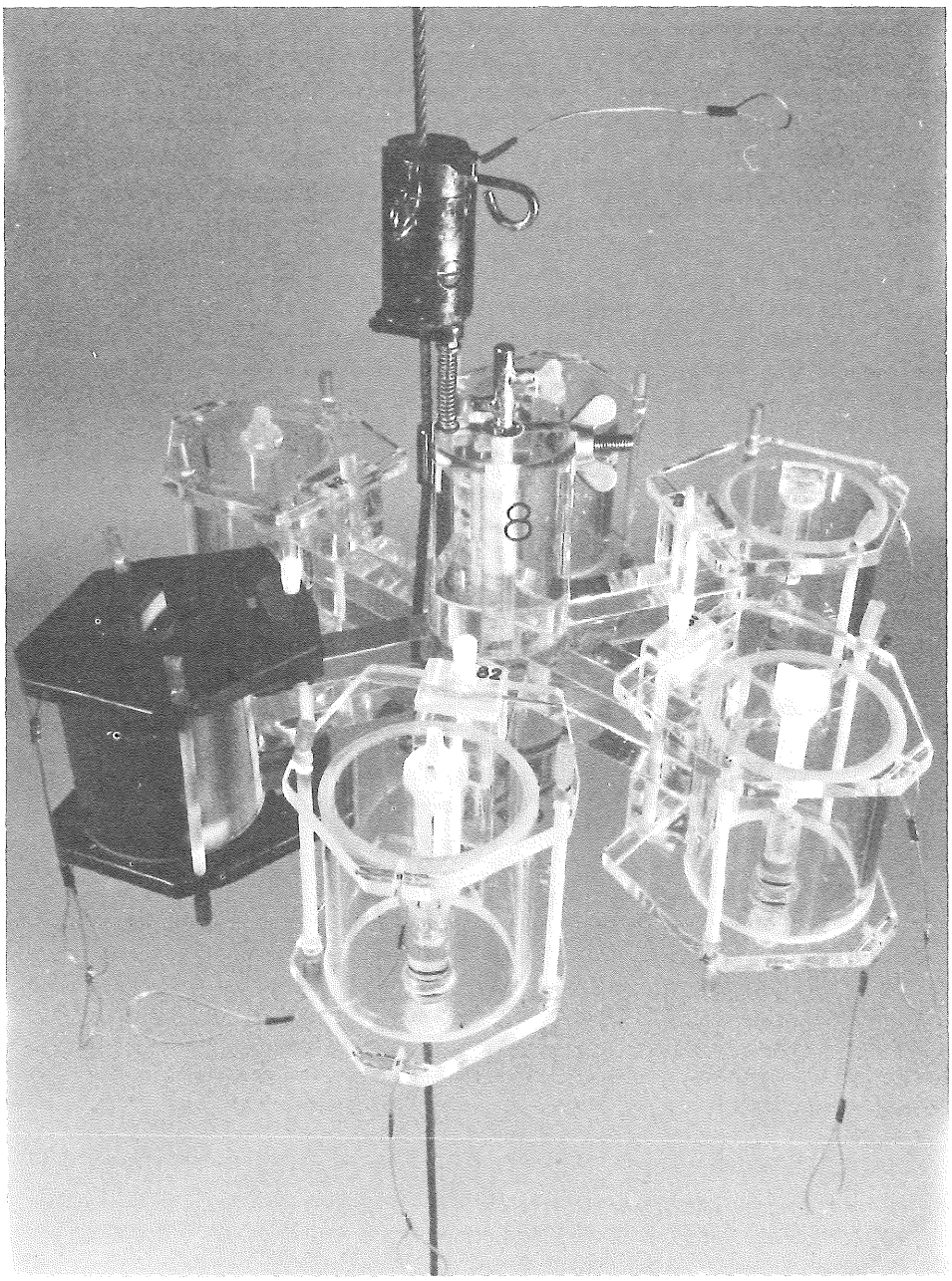

Figure 1
ISIS incubator with five transparent and one opaque bottles, closed position. Photo: J.-S. Selmer

Material and methods

The station was at 57°42'N, 11°04'E in the northern Kattegat with a water depth of 36 m. The weather conditions were good during the experiment with sunny skies, almost no

wind, and calm seas. The air temperature was from about zero in the early morning to less than 10 °C at mid-day. During the two weeks preceding the experiment a low pressure condition prevailed in the area with SW winds, 5–10 m sec^{-1}, rough seas and predominantly overcast skies and rain. The cruise was made onboard the Gothenburg University's R/V ,,Svanic''.

Primary production measurements

Primary production was measured by the *in situ* (ISIS) incubator method described by GUNDERSEN (1973). The incubators consist of five transparent plexiglass bottles and one opaque PVC bottle, each of 250 ml volume, mounted as a rosette around a central frame (Fig. 1). Four of the ISIS units were suspended in series at selected intervals along a piece of 4 mm hydrographic wire and suspended under a buoy during incubation 1 ml of ^{14}C Na-carbonate solution of 10 μCi specific activity was mixed into two transparent and the one opaque ISIS-bottles per depth. Incubation time was 1.5 h. After the ISIS units were retrieved the entire volume of the ^{14}C enriched bottles was rapidly filtered through 1.2 μm Sartorius membrane filters which were subsequently dissolved in Aquassure scintillation liquid (New England Nuclear) and counted on return to the laboratory in a Packard Tri-Carb liquid scintillation counter.

Light measurements

Surface irradiance (in mW cm^{-2}) was measured by means of a Kipp & Zonen pyranometer CCI, equipped with a spherical collector, throughout the entire day of the experiment with hourly printouts of accumulated effects. The wavelength range covered by the pyranometer was roughly 400–700 nm. The accumulated irradiance for each incubation period was calculated from the diel plots and recalculated in quantum units by assuming that 1 mW h^{-1} is equivalent to $4.23 \cdot 10^{18}$ quanta within the spectral range measured (MOREL 1978). Reflectance against the calm sea surface was estimated from the observed elevation of the sun and tables given by JERLOV (1968). The extinction coefficient of the water column was calculated from Secchi disc readings using the empirical relationship, $k_e = 2.1/T$, where T is the Secchi depth in meters. Under-water quantum flux was finally plotted from the surface irradiance data, I_0+, minus percentage reflectance to yield subsurface irradiance, I_0-, as quanta m^{-2} h^{-1}.

Phytoplankton and chlorophyll a samples were drawn from the transparent no. 4 ISIS bottle. The plankton samples were preserved with 0.4 % neutralized formalin for later counting by the UTERMÖHL (1958) inverted microscope technique and identification. Phytoplankton biomass (in mg C m^{-3}) was estimated by measuring the dominant species in the microscope and calculating the carbon contents according to STRATHMANN (1967). For the non-dominant species the average values of SMETACEK (1975) were used. The samples for chlorophyll a (150 ml) were filtered through Whatman GF/F filters, extracted with 90 % acetone and read in a Turner Model 111 fluorometer.

Oxygen and carbonate alkalinity were determind in samples drawn from ISIS bottle no. 5. Oxygen was titrated according to Winkler. Alkalinity would normally have been titrated according to Gripenberg's back titration method (GRASSHOFF 1976) but as the analysis could not be carried out during this cruise a carbonate alkalinity value of 2.2 mM, about the average for these waters, was used in the calculation of carbon fixation.

Nutrient samples for phosphate, ammonium, nitrate and nitrite were taken from ISIS bottle no. 6. Standard methods were used for the analysis of these nutrients (CARLBERG 1972, GRASSHOFF 1976), which were all carried out on board.

Temperature and salinity were recorded with a STD-system built and calibrated in the Department of Oceanography, Gothenburg University.

Results and discussion

The water environment

The light conditions during the experiment are summarized in Table 1. The ISIS incubators were suspended at 1, 4, 8 and 12 m depth which correspond to 76, 33, 11 and 4 % respectively of the sub-surface light energy (I_0-).

Table 1

Light and optical conditions

Secchi depth, m	7.0
Extinction coefficient, k_e	0.30
Irrandiance (400–700 nm) at sea surface (I_0+) during incubation, quanta · 10^{22} m^{-2} h^{-1}	146
Average sun height, s°	21
Reflectance against sea surface, ϱ_s %	15
Subsurface irradiance (I_0-), quanta · 10^{22} m^{-2} h^{-1}	124
1% I_0-, m	13

There was no halocline or thermocline within the photic zone indicating that the water in general was well mixed during the experiments, presumably due to the preceding rough weather.

The nutrient status of the water column was typical of an autumn regenerative activity with relative high concentrations of phosphate, ammonium and nitrite but with nitrate still in the process of being formed (Table 2). N/P ratios indicated a relative abundance of phosphate over inorganic nitrogen. The organic dissolved and particulate fractions were not analyzed.

Table 2

Hydrography and nutrients

Depth m	Temp. °C	S ‰	σ_T	PO_4^{3-}	NH_4^+	NO_2^-	NO_3^-	ΣN_i	N/P
						µmol l^{-1}			
1	10.6	30.2	23.1	0.16	0.31	0.17	0.32	0.80	5.1
4	10.6	30.2	23.1	0.20	0.45	0.18	0.41	1.04	5.3
8	11.2	30.6	23.3	0.32	1.70	0.12	0.75	2.57	8.0
12	11.4	30.6	23.3	0.33	1.81	0.12	0.82	2.75	8.3

The oxygen concentration was close to saturation in the upper water column and did not go below 93 % saturation at the bottom of the photic zone.

The phytoplankton

The phytoplankton population during the experiment was dominated by diatoms (Table 3) with *Cerataulina pelagica*, various *Chaetoceros* species and *Skeletonema costatum* as predominant organisms. Among the dinoflagellates *Prorocentrum micans* occured in large numbers. The total number of species did not differ much in the upper part of the water column but the populations was less varied in the deepest part. Diversity indices (calculated according to MARGALEF 1951) seemed relatively low for a typical ''bloom'' (Table 3).

Table 3

Phytoplankton population composition

	Numbers of cells l^{-1}			
	1 m	4 m	8 m	12 m
Diatoms	372 580	177 800	3 760	4 100
Dinoflagellates	28 060	2 640	2 140	360
Other groups	16 000	4 320	6 520	5 940
Total	416 640	184 760	12 420	10 400
Total number of species	35	31	31	16
Diversity index	2.63	2.47	3.18	1.62

On a carbon basis the diatom *C. pelagica* was predominant and accounted for 60 % of the total biomass at 1 and 4 m (Table 4).

Table 4

Phytoplankton biomass

	mg C m^{-3}			
	1 m	4 m	8 m	12 m
Diatoms	126	57	1	$\approx$ 0
Dinoflagellates	48	11	7	2
Other groups	$\approx$ 0	0	0	0
Total	174	68	8	2

Chlorophyll a

The chlorophyll distribution in the water volumn was, as expected, similar to the phytoplankton biomass and numerical distribution with 4.48 mg chlorophyll a m^{-3} as the highest value at 1 m depth (Table 5). If calculated as the amount of chlorophyll present per organism the concentration increased sharply with depth (Table 5). This was not surprising as it is a common phenomenon that the rate of chlorophyll a biosynthesis is inversely related to the amount of photosynthetically available light energy. However, we have not by searching the literature been able to find data on

chlorophyll a per cell as a function of optical depth in natural waters. Therefore, our data are presented with some reservation.

Primary production

The vertical distribution of primary production is shown in Table 5 and was considerable in the upper part of the water column. The integrated hourly production was 90.4 mg C m^{-2}. The photosynthetically effective day lenght during the experiment, which was conducted on October 23, was 10 hours. Since three other experiments not(reported here) were carried out on the same and the previous day at various hours of the day, diel production rate curves between 0700 and 1700 hours could by plotted and an approximate daily production of 590 mg C m^{-2} calculated. For comparison, STEEMANN NIELSEN (1964) found an October average of some 290 mg C m^{-2} d^{-1} from a seven-year long series and GARGAS et al. (1978) reported averages of about 130–215 mg C m^{-2} d^{-1}, both from the same area. Considering the excellent light conditions during our experiment the higher value seems reasonable.

Table 5

Primary production (P), chlorophyll a, and productivity index (P.I.)

Depth m	A P	A Chl a	A P.I.	B P	B Chl a	C P/C
1	16.35	4.38	3.7	3.9	1.1	0.09
4	12.32	2.34	5.3	6.7	1.3	0.18
8	1.38	0.77	1.8	11.1	6.2	0.17
12	0.46	0.89	0.5	4.4	8.6	0.23

A. Total production
P = mg C · m^{-3} · h^{-1}
Chl a = mg · m^{-3}
P.I. = mg C · (mg Chl a^{-1} · h^{-1}

B. Production per organism
P = µg C · 10^{-5} · $organism^{-1}$ · h^{-1}
Chl a = µg · 10^{-5} · $organism^{-1}$

C. Production per unit biomass (C)
P/C = mg C fixed · mg C biomass · h^{-1}

Productivity indices

The productivity index (assimilation number) shows its highest value, 5.3 mg C (mg chl. a)$^{-1}$ h^{-1}, at 4 m (Table 5, column A). If primary production, however, is related to unit biomass (as cell carbon) a different distribution pattern results with the lowest value at 1 m and a slight increase below (Table 5, column C). As the amount of chlorophyll a per organism (Table 5, column B) increases with depth this result is not surprising.

Primary production versus irradiance

Fig. 2 shows a plot of primary production as a function of available quanta at the four depths of the experiment. In the lower linear portion of the curve production clearly is light-controlled. Light saturation occurs at 3.8 · 10^{23} quanta m^{-2} h^{-1}. Similar light

saturation values in natural population have been reported by STEEMANN NIELSEN (1937) and BERGE (1957). The first author found an I_{sat} value of about $2 \cdot 10^{23}$ quanta $m^{-2} \cdot h^{-1}$ (= 0.03 ly min^{-1}) in the Sound off Helsingør, Denmark, and the latter about $4 \cdot 10^{23}$ quanta m^{-2} h^{-1} near Bergen, Norway.

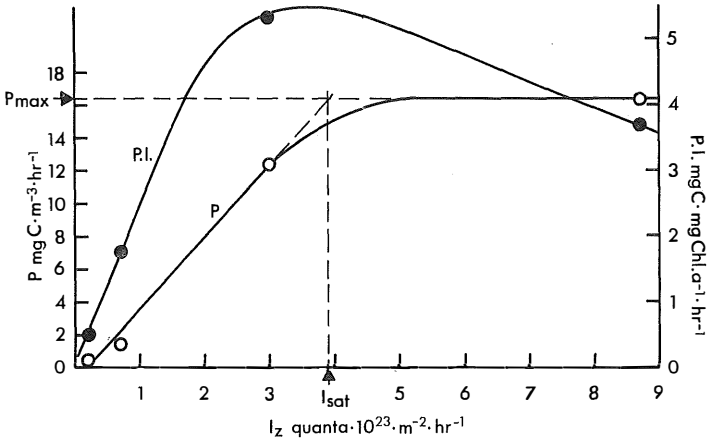

Figure 2
Primary production (P) and productivity index (P.I.) versus irradiance (I)

When productivity index is plotted against quanta the resultat curve seems to indicate a light inhibiting effect above 4 m. It is quite possible that a similar effect would have been seen even in the P vs. I plot if more observation depths had been available between 1 and 4 m.

Primary production versus inorganic nutrients and temperature

The flattening of the P vs. I curve at irradiances above light saturation could be a result of light inhibition but other limiting factors may have played a role as well, for example availability of nutrients, or temperature. As seen in Table 2 phosphate as well as ammonium and nitrate were present at 1 and 4 m at concentrations which seem fully adequate for optimal growth of the size of phytoplankton population present. Unless some nutrient not analyzed, e.g. iron or silicate, were depleted and could have controlled production we do not believe that the flattening of the P vs. I curve above the light saturation point was a result of nutrient limitation.

The effect of temperature on primary production is more difficult to evaluate. During the 4–6 weeks preceding the experiment the water temperature in the area had dropped from about 18 to 11°C. It is known that the photosynthetic rate in natural populations as well as in pure cultures of phytoplankton is temperature dependent and that this effect is more pronounced the higher the irradiance, within certain limits (ARUGA 1965, EPPLEY 1972). We therefore find it plausible to conclude that the ''bloom''–like phytoplankton activity during this October day in Kattegat was triggered by a period of bright and calm weather and increasing nutrients in the water but that primary production was controlled in the upper part of the photic zone by a combination of excess light energy and a low temperature.

References

ARUGA, Y., 1965. Ecological studies of photosynthesis and matter production of phytoplankton. I Seasonal changes in photosynthesis of natural phytoplankton. Bot. Mag. (Tokyo) **78**, 280–288.

BANNISTER, T.T., 1979. Quantitative description of steady state, nutrient-saturated algal growth, including adaptation. Limnol. Oceanogr. **24**, 76–96.

BERGE, G., 1957. The primary production in the Norwegian Sea, June 1954, as measured by an adapted ^{14}C-technique. Paper presented at a Symposium of ICES, Bergen 1957.

BIENFANG, P. and K. GUNDERSEN, 1977. Light effects on nutrient-limited, oceanic primary production. Mar. Biol. **43**, 187–199.

CARLBERG, S. R., 1972. New Baltic Manual. ICES Coop. Res. Rept. Ser. A, no. **29**.

EPPLEY, R. W., 1972. Temperature and phytoplankton growth in the sea. Fish. Bull. **70**, 1063–1085.

EPPLEY, R. W., E. H. RENGER, E. L. VENRICK, and M. M. MULLIN, 1973. A study of plankton dynamics and nutrient cycling in the central gyre of the North Pacific Ocean. Limnol. Oceanogr. **18**, 534–551.

GARGAS, E., G. ÆRTEBJERG NIELSEN and S. MORTENSEN, 1978. Phytoplankton production, chlorophyll a and nutrients in the open Danish waters 1975–77. The Belt Project. Nat. Agency of Environ. Protect., Denmark. Special Report. 42 + 61 pp.

GRASSHOFF, K., 1976. Methods of seawater analysis. Verlag Chemie, Weinheim, New York.

GUNDERSEN, K., 1973. *In situ* determination of primary production by means of a new incubator ISIS. Helgoländer wiss. Meeresunters. **24**, 465–475.

HUNTSMAN, S. A. and R. T. BARBER, 1977. Primary production off northwest Africa: the relationship to wind and nutrient conditions. Deep-Sea Res. **24**, 25–33.

JERLOV, N. G., 1968. Optical oceanography. Elsevier Publ. Comp., Amsterdam. 194 pp.

JITTS, H. R., A. MOREL and Y. SAIJO, 1976. The relation of oceanic primary production to available photosynthetic irradiance. Aust. J. Mar. Freshwater Res. **27**, 441–454.

MARGALEF, D. R., 1951. Diversidad de especies en les communidades naturales. Publ. Inst. Biol. apl. (Barcelona) **9**, 5–27.

MOREL, A., 1978. Available, usable, and stored radiant energy in relation to marine photosynthesis. Deep-Sea Res. **25**, 673–688.

SMETACEK, V., 1975. Die Sukzession des Phytoplanktons in der westlichen Kieler Bucht. Diss. Univ. Kiel.

STEEMANN NIELSEN, E., 1937. The annual amount of organic matter produced by the phytoplankton in the Sound off Helsingør. Medd. Dan. Fisker. Havunders. Ser. Plankton **3**.

STEEMANN NIELSEN, E., 1964. Investigations of the rate of primary production at two Danish light ships in the transition area between the North Sea and the Baltic. Medd. Dan. Fisker. Havunders. N.S. **4**, 31–77.

STRATHMANN, R. R., 1967. Estimating the carbon content of phytoplankton from cell volume or plasma volume. Limnol. Oceanogr. **12**, 411–418.

UTERMÖHL, H., 1958. Zur Vervollkommnung der quantitativen Phytoplanktonmethodik. Mitt. int. Ver. theor. angew. Limnol. **9**, 1–38.