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Growth and sedimentation of the phytoplankton spring bloom in the Bornholm Sea (Baltic Sea)*

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Abstract

Results obtained from short-term (8 h to 24 h intervals) measurements of physical, chemical and biological properties of the 70 m water column from an anchor station in the Bornholm Sea over a 10-day period are presented and discussed. Phytoplankton biomass concentration and production rates indicated that the spring bloom was in progress in this period. The onset of the spring bloom occurred prior to the advent of thermal stratification. Peak growth rates, accompanied by nutrient depletion and biomass accumulation in surface layers, were concomitant with calm weather and a cloudless sky after which a part of the population was observed to sink out of the water column unimpeded by the permanent halocline. Maximum sinking rates of the dominant species, *Skeletonema costatum*, ranged between 30 to 50 m per day during this event. The development of the spring bloom apparently takes place in a series of events during which periods of low production alternate with periods of high production and rapid sedimentation of parts of the population.

Introduction

In boreal regions, the spring bloom of phytoplankton is an outstanding event in the annual cycle of primary production. Increasing solar radiation in the spring is one of the major factors initiating commencement of the spring bloom which is eventually terminated by the exhaustion of available nutrients. The spring bloom thus represents the transition from light-controlled to nutrient-controlled phytoplankton production in the surface layers.

The development of the spring bloom is largely dependent on seasonal changes in physical factors of the environment, particularly light intensity in the water column and the depth of the mixed layer (SVERDRUP 1952). These gradual seasonal trends can be reversed for short periods by changing weather conditions (e.g. cloudiness, storms), which considerably affect the development of the spring bloom.

In this paper, data obtained over a 10-day period from an anchor station during spring bloom development is presented and discussed (Fig. 1). This investigation, carried out in the Bornholm Sea on board RV "Meteor", was part of the multidisciplinary exercise BALTIC 75.

The Bornholm Sea is one of a series of basins in the southern Baltic Sea with an average water depth of 80 m and sills of 45 m and 60 m depth to the west and east

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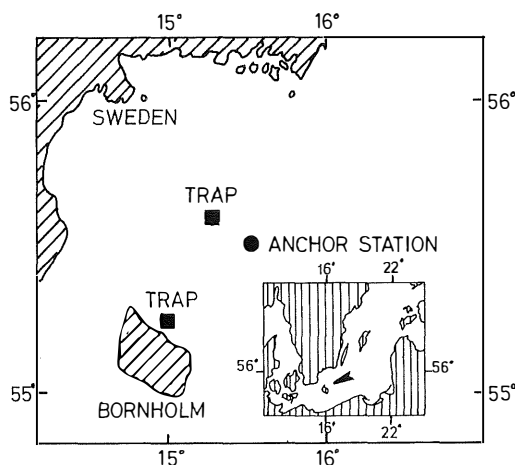


Figure 1

Location of the anchor station in the Bornholm Sea and position of the sediment traps of SME-TACEK *et al.* (1978).

respectively. The water column is stratified by a permanent halocline at a depth of about 50 m (GRASSHOFF 1975). A seasonal thermocline develops at about 30 m in April/May.

Material and methods

Hydrographic profiles were obtained using a CTD-system (conductivity, temperature, depth) by Howaldt (Bathysonde). The data were made available to us by W. Horn.

Nutrient concentrations were measured by K. Grasshoff, H. Johannsen and A. Wenck using an autoanalyzer and the procedures described by GRASSHOFF (1976).

Samples for primary production were taken from 100, 50, 25, 10 and 1 % light depths. Production was estimated by the ^{14}C -method using the *in situ* simulated technique in collaboration with the International ^{14}C Agency, Denmark. Sets of samples were incubated from sunrise to noon, sunrise to sunset, noon to sunset. A fourth set was exposed to 70 % of surface light from sunrise to sunset and will be referred to as 'optimal production' in the following.

Discrete samples from 12 depths (including the light depths) down to 70 m were taken for chlorophyll a (Chl a), particulate organic carbon and nitrogen (POC and PON respectively) at 8 h intervals and for plankton counts at noon. Samples for Chl a were homogenized and then treated as recommended by UNESCO (1966). POC and PON were determined on precombusted Whatman GF/C filters using a CHN-Analyzer (Hewlett-Packard, 185B). Phytoplankton carbon (PPC) was derived by multiplying cell counts obtained with an inverted microscope with carbon conversion factors given by SMETACEK (1975).

Zooplankton was sampled by vertical bottom-to-surface hauls with a 100 μm Apstein net at noon each day.

Results

Hydrography

The water column was initially well mixed to the depth of the permanent halocline between 50 and 55 m with temperatures ranging from 3.9 to 4.2°C in the mixed layer

(Fig. 2) and salinity between 7.95 and 8.05‰. In the subhalocline layer temperature and salinity ranged between 5.0 and 8.9 °C and 10.5 and 14.7‰ respectively. Daily average wind speeds (Fig. 2) varied from 6 to 14 kn, the range of actual values extended from 0 to 30 kn. A violent storm on the 14 and 15 April delayed commencement of the investigation and winds slackened with occasional interruptions up to 20 April. The calmest period was from 21 to 23 April which coincided with a cloudless sky, and a concomitant decrease in the depth of mixing was reflected in increasing temperatures in the surface layer (Fig. 2). Wind speed increased on 24 April and the depth of the mixed layer increased, as shown by the depression in the 4.5 °C isoline in Fig. 2. However, typical stable thermal stratification above the permanent halocline was not established before mid-May (KIELMANN, pers. comm.). Further aspects of the hydrography of the investigation area are given by SMETACEK et al. (1978). The authors state that neither the subhalocline water nor the water column of the mixed layer was exposed to sudden advection of water from distant areas throughout the investigation period.

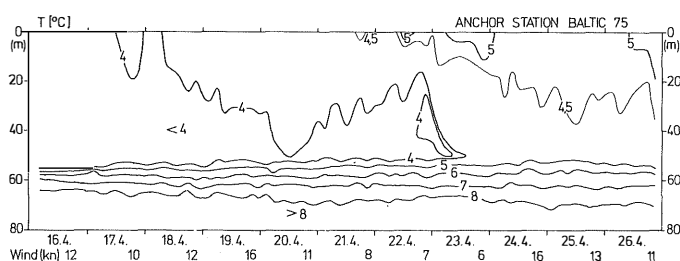


Figure 2

Isotherms during the investigation period. Average daily wind speeds in knots are given at the bottom of the figure.

The 1 % light depth, calculated from Secchi readings, was most commonly at 24 m and rose for 2 days to 20 m following an increase in phytoplankton biomass after 22 April (Fig. 4b).

Nutrients

Nutrient concentrations in the mixed layer during the first half of the investigation were approximately $1.5 \mu\text{gat NO}_3\text{-N l}^{-1}$, $0.4 \mu\text{gat PO}_4\text{-P l}^{-1}$ (Fig. 3a, b) and $15 \mu\text{gat SiO}_4\text{-Si l}^{-1}$. These values are considerably lower than normal winter concentrations for the study area (GRASSHOFF 1975, SCHULZ et al. 1978), indicating that nutrient uptake due to phytoplankton growth had occurred before 17 April. A substantial decline in nutrient concentrations was observed after 20 April, and, by 21 April, nitrate values were below $0.1 \mu\text{gat l}^{-1}$. Lowest recorded values for phosphate and silicate were 0.2 and $8.5 \mu\text{gat l}^{-1}$ respectively, indicating that neither of these elements played a role in limiting phytoplankton growth. Ammonia was not measured but, as this form of nitrogen is taken up more rapidly than nitrate, it can be safely assumed that little, if any, ammonia was available and that nitrogen was indeed the limiting nutrient for phytoplankton growth during the period of investigation.

After 22 April, nutrient profiles in the mixed layer indicate a distinct alternation of nutrient depletion in the euphotic zone and upward mixing from the disphotic zone for all nutrients (Fig. 3a, b). Nutrient depletion and upward mixing corresponded with increasing phytoplankton growth and higher wind speeds respectively (Fig. 4a and 2).

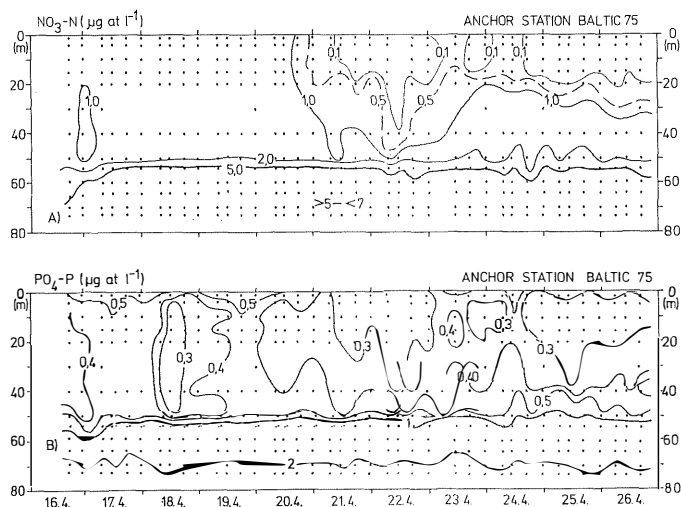


Figure 3
Nitrate (a) and phosphate (b) vertical distribution at the anchor station.

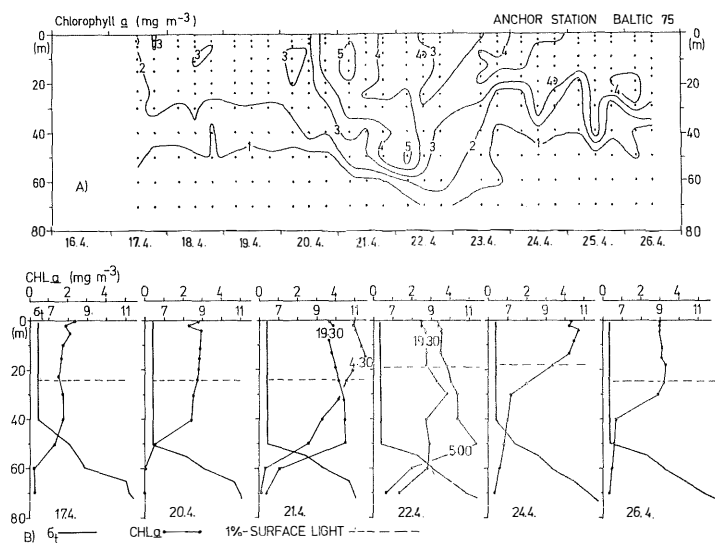


Figure 4
Chlorophyll distribution in the water column (a). Selected vertical profiles of density and chlorophyll (b). The dashed line indicates the 1 % light depth, the time of measurement is given in the profiles from 21 and 22 April.

Chlorophyll a

Before the beginning of the spring bloom, chlorophyll concentrations of less than $1 \text{ mg} \cdot \text{m}^{-3}$ are reported from the Bornholm Sea (KAISER and SCHULZ 1978). The higher concentrations of 2 to $3 \text{ mg} \cdot \text{m}^{-3}$ also indicated the commencement of phytoplankton growth before 17 April. From 17 to 20 April, the chlorophyll content was more or less evenly distributed throughout the mixed layer (Fig. 4a). A distinct accumulation of chlorophyll in the euphotic zone took place from 20 to 21 April, immediately followed by higher values in the disphotic and subhalocline layer on 21 and 22 April. Thereafter chlorophyll again accumulated in the euphotic zone.

More details of the chlorophyll distribution are given in the selected vertical profiles (Fig. 4b). For the first 4 days, the distribution in the mixed layer was homogeneous. By the morning of 21 April, the chlorophyll content in the water column had doubled to $233 \text{ mg} \cdot \text{m}^{-2}$. In the night of the same day $230 \text{ mg} \cdot \text{m}^{-2}$ was measured, and the maximum recorded production of 2 gC m^{-2} was recorded on that day. The depth distribution of chlorophyll, however, changed markedly. Maximum levels were found within the euphotic zone at 4.30 hrs., but around the depth of the halocline at 19.30 hrs. The next day, 22 April, an even more distinct maximum was measured in the disphotic zone concomitant with increased levels below the halocline. By night more chlorophyll had sunk below the halocline and a general decrease in the entire water column was found. From 23 April onward the chlorophyll content below the euphotic zone declined sharply in the absence of any corresponding gradient in density.

Phytoplankton

Skeletonema costatum accounted for 40 % of the total phytoplankton carbon (PPC) in the initial period and for 60 % in the last days (Fig. 5a, b; Table 1). Another important contributor to PPC was the photoautotrophic ciliate *Mesodinium rubrum* (10 to 40 % of PPC). Other centric diatoms such as *Thalassiosira* sp. and *Chaetoceros danicus* accounted for most of the remainder. Initially PPC was 2 to 3 gC m^{-2} , during the maximum 7.8 gC m^{-2} , and in the last days 5 to 6 gC m^{-2} . The vertical PPC distribution basically followed that of the chlorophyll. After doubling of PPC in the euphotic zone on 21 April, rapidly increasing levels were recorded in the disphotic and subhalocline layer. Below the halocline 59 mg PPC m^{-3} was found on 24 April.

Table 1

Percentage contribution to total phytoplankton carbon by the dominant species *Skeletonema costatum* and *Mesodinium rubrum*. Other diatoms are grouped under the third column; flagellates, largely nanoflagellates, constituted the remainder.

Date	<i>S. costatum</i>	<i>M. rubrum</i>	other diatoms
17.4.75	49	27	12
18.4.75	33	39	17
19.4.75	43	28	19
20.4.75	47	39	10
21.4.75	64	13	9
22.4.75	61	10	12
23.4.75	64	19	7
24.4.75	47	29	8
25.4.75	62	19	7
26.4.75	64	19	9

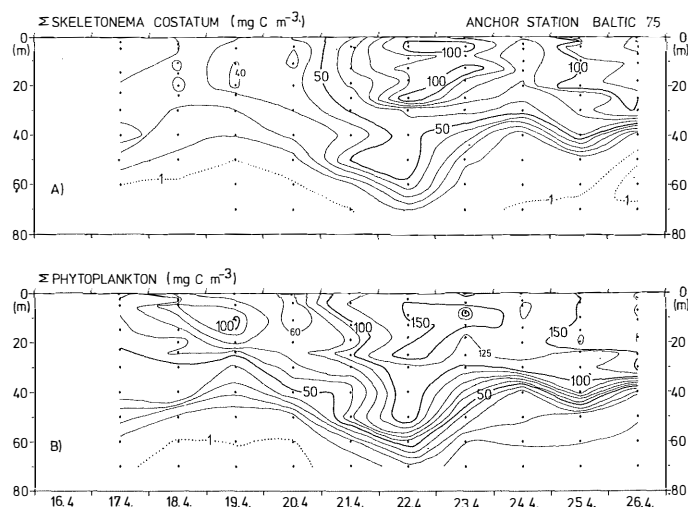


Figure 5

Vertical distribution of the dominant phytoplankton species *Skeletonema costatum* (a) and total phytoplankton biomass (b) in mg C m^{-3} .

Primary production

Primary production levels ranged between 0.65 and $0.99 \text{ g C m}^{-2} \text{ d}^{-1}$ in the initial period. Similar values were recorded in spring blooms from the Baltic Sea (SCHULZ et al. 1978, RENK et al. 1975). Most of the production took place in the upper 6 m, as can be seen from Fig. 6a. Maximum production was measured on 21 April with $2.4 \text{ g C m}^{-2} \text{ d}^{-1}$. After this, production declined but remained at a fairly high level of about $1 \text{ g C m}^{-2} \text{ d}^{-1}$. In the last 2 days, production increased again to $1.9 \text{ g C m}^{-2} \text{ d}^{-1}$ as higher rates were recorded throughout the euphotic zone and even at the 1% light level, $60 \text{ mg C m}^{-3} \text{ d}^{-1}$ was measured. The total production over the 10 day period was 12.6 g C m^{-2} .

The results obtained from different incubation times have been compared in Fig. 6b, from which the following points of interest are evident: a. Production rates recorded during forenoon and afternoon of the same day are very similar with only 2 exceptions on 22 and 24 April; b. Some variation can be seen between results obtained from sunrise to sunset incubation (column 3) and those representing the sum of sunrise to noon and noon to sunset incubation (T-bars), although a consistent trend is absent; c. Optimal production rates are higher than simulated *in situ* rates up to 21 April, the discrepancy being much less or reversed thereafter.

Zooplankton

Zooplankton biomass was fairly constant throughout the investigation period and ranged between 0.40 and 0.45 g C m^{-2} . The main constituent was *Pseudocalanus elongatus* together with its young stages.

Discussion

It is apparent from the results that different stages of the spring bloom were encountered at the fixed station in this investigation. The observed changes in biomass and depth distribution of the phytoplankton point to a temporal sequence of

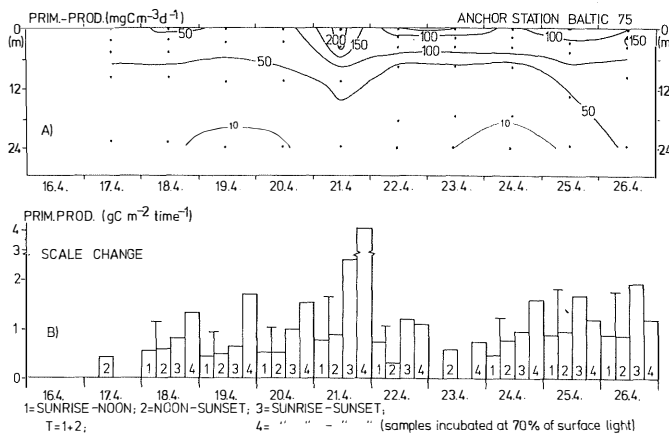


Figure 6

Vertical distribution of phytoplankton primary production (incubation from sunrise to sunset) from simulated *in situ* measurements (a). Histograms of daily production (gC m^{-2}) for different incubation times at simulated *in situ* and optimal light conditions (70 % of surface light) (b). Column 1: sunrise-noon incubation, column 2: noon-sunset incubation, column 3: sunrise to sunset incubation, column 4: optimal production from sunrise to sunset incubation. T-bars indicate the sum of 1 and 2).

events in bloom development governed by weather conditions. Before integrating the observations into a consistent picture of the growth and maturity of the bloom, it is important to consider the role of horizontal advection and the possible extent of spatial heterogeneity in determining the sequence of events.

The anchor station was situated in the middle of the Bornholm Sea which is a region of eddy formation generated by the interaction of wind stress and bottom topography (SMETACEK et al. 1978). SMETACEK et al. state that large scale addition of water masses from distant areas to the Bornholm Sea is a slow process because of its circulation patterns. Their arguments are based on data collected during BALTIC 75. Thus, because of the long residence time of water in the Bornholm Sea, one can assume that the water mass under observation during the 10 day period had experienced much the same irradiation and weather conditions. As plankton growth is most sensitive to the physical environment during this season, it is unlikely that spatial variations within such a homogeneous environment could account for the rapid changes in biomass and its depth distribution between 20 and 23 April. The fact that the observed changes in biological parameters of the water column could be attributed to the variations in local weather conditions proves that the results actually reflected a temporal sequence in spring bloom development that probably occurred in a wider area of the Bornholm Sea.

Growth of the spring bloom had commenced before 17 April, prior to the development of stable thermal stratification in the mixed layer. Apparently, the critical depth had receded below the halocline level as a result of the seasonal increase in irradiation. The diatom population was fairly evenly distributed in the 50 m of the mixed layer. Up to 20 April, biomass build up was relatively slow and occurred in the entire mixed layer. This is because significant production was restricted to the upper 10 m. The entire population, however, was continuously dispersed in the 50 m water column down to

the halocline as the strong winds maintained the depth of mixing down to that depth. The decrease in wind speed on 20 April led to the next stage of this spring bloom – a period of high production and rapid sedimentation of the phytoplankton that lasted up to 23 April.

Due to the calm weather the depth of mixing decreased. Hence, residence time of phytoplankton cells in the upper 10 m was prolonged, which led to accumulation of the newly produced biomass within this layer, as shown by the dramatic change in all parameters during 21 April. Nutrient concentrations and much higher optimal production in comparison to the *in situ* simulated values indicate clearly that phytoplankton up to this date was light controlled. On 22 April, however, nitrate concentrations in the euphotic zone were below $0.1 \mu\text{gat}\cdot\text{l}^{-1}$ and *in situ* and optimal production levels were similar. Evidently, the nitrogen supply rather than light now controlled phytoplankton growth. This resulted in nitrogen deficiency of the cells as indicated by the sudden increase in POC/chlorophyll and POC/PON ratios in the water column (Table 2). The high forenoon/afternoon production ratio of this day is due to the much lower biomass levels in the afternoon as compared to the forenoon. This is also indicated by comparatively low variation in assimilation numbers during this period (Table 2).

Table 2

Temporal changes in growth dynamics and composition of particulate material expressed as ratios of different parameters (POC, PON: particulate organic carbon and nitrogen; PPC : phytoplankton carbon; Chl a : chlorophyll a; assimilation number : $\text{mg C}/\text{mg Chl a m}^{-2} \text{h}^{-1}$. Ratios are calculated from integrated values for the euphotic zone).

Date	POC/PON	PPC/Chl a	Assimilation number	Daily Production/Optimal Production	Forenoon/Afternoon Production
17. 4. 75	7.5	29	1.6	–	–
18. 4. 75	6.5	25	1.3	0.6	0.95
19. 4. 75	7.4	32	0.8	0.4	0.91
20. 4. 75	6.4	25	1.1	0.6	1.00
21. 4. 75	6.9	23	1.6	0.6	0.88
22. 4. 75	8.5	46	1.5	1.1	2.30
23. 4. 75	6.4	38	1.5	0.8	–
24. 4. 75	6.8	33	1.0	0.7	0.62
25. 4. 75	6.9	41	1.9	1.4	0.93
26. 4. 75	7.7	53	1.8	1.6	1.03

The biomass that had accumulated in the upper layers during 21 April dispersed in the water column and a new accumulation appeared at the halocline level on 22 April. Nutrients declined concomitantly. We attribute this vertical movement to a sinking out of a part of the population rather than to downward mixing for the following reasons:

- a. The sea surface was very calm on 22 and 23 April and a temperature gradient in the near surface region appeared for the first time on these days.

b. The population apparently continued its descent through the halocline as a considerable amount of phytoplankton cells suddenly appeared in this stagnating layer of water. There is no explanation other than sinking to account for the presence of such large numbers of cells below the halocline.

c. Both decreasing turbulence levels and nutrient deficiency are known to greatly increase sinking rates of diatom cells (TITMAN and KILHAM 1976, ANDERSON and SWEENEY 1978, MARGALEF 1978). Such nutrient-deficient cells take up dissolved nutrients from the environment even in the dark (YENTSCH et al. 1977), which would explain why nutrients decreased in the entire water column above the halocline.

Apparently, the phytoplankton cells of the population that suffered most from nutrient deficiency were the ones that settled out. It is reasonable to assume that these were mainly the cells that divided on 22 April, i.e. cells from the euphotic zone rather than from deeper layers. This would give sinking rates for *Skeletonema costatum* cells in the order of 30 to 50 m per day which is well above the maximum sinking rates of 8 m per day reported by SMAYDA and BOLEYN (1966). SMAYDA (1970) gives maximum rates for living phytoplankton of 30 m per day but suggests that, under certain circumstances, much higher sinking rates are possible. Our data show that these higher sinking rates do indeed occur for short periods of time. If this is true, it will necessitate a reassessment of the possible role of sedimentation in eliminating phytoplankton cells from the euphotic zone. That cells did indeed settle through the subhalocline layer after rapid passage of the density barrier posed by the halocline itself was proven beyond doubt by the large quantity of 'fresh' phytoplankton cells collected in traps deployed in the subhalocline water during BALTIC 75 (SMETACEK et al. 1978).

A rough estimate of the quantity of phytoplankton that sedimented during this period can be gained by subtracting the integrated biomass value recorded in the water column between compensation depth and bottom (30 to 70 m) after the sedimentation event i.e. 23 April, from the maximum recorded on 22 April. This gives a figure of 2 g PPC m⁻² and 105 mg Chl a m⁻² input to the bottom. The PPC/Chl a ratio of this material was 52 which is approximately double the average values of suspended cells before the event. Higher PPC/Chl a levels are a sign of increasing nutrient deficiency (SMETACEK and HENDRIKSON 1979) and this observation would substantiate the arguments on nutrient deficiency having precipitated the sedimentation event. Another estimate of the quantity of organic carbon that settled out on 22 April can be derived from a comparison of biomass and production rates of 21 and 22 April. This figure of 1.6 gC m⁻² is in reasonable agreement with the first estimate.

The chlorophyll values in the subhalocline water returned to their original low levels. Although the weather remained calm on 23 April, no additional sinking was observed and production was low on this day.

Increasing wind speeds on 24 April led to renewed homogenisation in the upper layers evidenced by the downward transport of heat and the upward transport of nutrients. Production levels increased and the nutrient input again was reflected in the higher optimal production values in comparison to values from *in situ* simulated conditions. Nitrate, after this, was again depleted in the upper 20 m and increasing biomass levels were observed during the last 2 days of the investigation period. It is likely that renewed nutrient depletion led to a new sedimentation event after 26 April, as the C/N and PPC/Chl a ratios had risen to similar levels as observed on 22 April when the first rapid sedimentation occurred. This assumption is also supported by sediment trap results from the vicinity where large quantities of phytoplankton cells were collected in subhalocline water as late as the second week of May (SMETACEK et al. 1978).

The above interpretation of the results leads to some interesting implications regarding the dynamics of spring phytoplankton growth that should be of some general importance. For one thing, the decisive influence of weather in shaping day to day events is clearly demonstrated. The depth of mixing apparently changes with wind speed in the unstratified upper layer as indicated by the phytoplankton distribution in the water column. RYTHER and HULBURT (1960) have shown that the vertical distribution of phytoplankton can be independent of density and dissolved properties in the same water column. Such vertical inhomogeneity can be the result of growth in surface layers and downward mixing of the daily increment to a depth depending on the daily variations of physical factors. Processes such as sinking and vertical migration of motile organisms can also determine the position of plankton in the water column within a certain range of vertical mixing intensity. The distribution of the ciliate, *Mesodinium rubrum*, which is known to be a motile organism (LINDHOLM 1981) was much more restricted to the upper 10 m than the diatoms. LÄNNERGREN (1979) has shown that even diatoms can achieve positive buoyancy during spring bloom growth. This would enable them to maintain a desired depth, again within a certain turbulence range. One can conclude that phytoplankton cells, because of the great variation in sinking rates of at least a factor of 4 (TITMAN and KILHAM 1976) exercise control over their position in the water column to an extent greater than widely appreciated at present.

If phytoplankton cells are indeed constantly being mixed downward indefinitely in the absence of stratification, which is a basic assumption of the Sverdrup model, some sort of a stratification will be necessary before the spring bloom can start. If, however, mixing only occurs to a certain depth such as the bottom in shallow areas or to a shallow permanent halocline, the advent of the spring bloom will be determined by the seasonal increase in irradiation independent of any thermal stabilisation of the mixed layer. In the 20 m Kiel Bight for instance, the spring bloom occurs in March and stormy weather can delay it up to early April, but not later (SMETACEK and HENDRIKSON 1979). In this shallow region, growth and sedimentation of the bloom takes place rapidly, and as little as 10 days sometimes separate the advent and the disappearance of the bloom. Nutrients are totally stripped from the water column during this process and sedimentation is one short intense event (SMETACEK 1980, PEINERT 1981, POLLEHNE 1981).

Growth and sedimentation of the spring bloom becomes increasingly complex with progressively greater depth of mixing. Thus, in the Bornholm Sea, which is in the same latitude as Kiel Bight, the spring bloom starts in mid-April and lasts well into May. KAISER and SCHULZ (1978) state that thermal stratification in the Bornholm Sea is essential for the commencement of the spring bloom. Our results do not corroborate their statement and show instead that the depth of the mixed layer varies with atmospheric conditions even in unstratified water bodies. It can extend to the pycnocline or to the bottom during convective mixing, but is more restricted when the mixing is wind-induced. Thus, even in deeper areas, it would seem that increasing solar radiation and the concomitant deepening of the critical depth combined with increasing day length is a more decisive factor in initiating phytoplankton biomass build up than a lessening of wind-induced vertical mixing.

Intermittent vertical mixing due to changes in wind speed apparently leads to successive stages of biomass accumulation and dispersal with sedimentation events following calm periods during the later stages. The upward transport of nutrients into surface layers during this process leads to utilization of nutrients from a much greater water column than merely the euphotic zone. The spring bloom is ultimately terminated

by the development of thermal stratification (which occurred in the Bornholm Sea in mid-May) and the resultant barrier to upward transport of dissolved nutrients. One can presume that year to year variation in biomass production will depend not only on the initial nutrient concentrations but also on the pattern of thermocline development, i.e. the number and the intensity of mixing events between the start of biomass build up and eventual establishment of the thermocline. Sedimentation rates and their temporal sequence will also be determined by the same process and this in turn can be expected to affect the benthos. During the investigation period, zooplankton biomass was generally less than 10 % of phytoplankton biomass. The role of metazooplankton in influencing the course of the spring bloom is apparently a minor one in the Bornholm Sea as biomass of this pelagic component was low and not influenced by phytoplankton biomass build up.

Conclusions

1. In the Bornholm Sea the advent and development of the spring bloom is independent of the presence of a thermocline.
2. Development of the spring bloom takes place in a series of events whereby periods of low growth alternate with periods of enhanced growth and sedimentation.
3. Sedimentation of phytoplankton does not occur as a steady loss but rather as distinct events where a part of the population rapidly sediments out *en masse*. An appreciable portion of biomass produced by the spring bloom is eventually utilised by the benthos or accumulates on the bottom in anaerobic areas such as the Bornholm Basin.
4. The establishment of the thermocline eventually terminates the spring bloom by cutting off nutrient input in the euphotic zone via vertical mixing.

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