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The phytoplankton spring bloom in the Baltic Sea in 1985, 1986: multitude of spatio-temporal scales

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Abstract—The spatio-temporal development of the phytoplankton spring bloom in the Baltic Sea for two consecutive years is analysed. Quasi-continuous, on-track measurements of particle concentration, fluorescence, temperature and salinity with a resolution of the spatial scales from ≈400 m to basin-wide were supplemented with quantitative samples of the phytoplankton abundance, pigments, and vertical CTD/fluorescence profiles. The improved spatial and temporal resolution allowed us to distinguish variability on different time and space scales. Year-to-year differences were found that include not only the timing of the bloom but also the size distribution of the plankton (composition of the phytoplankton assemblage). Contrary to conventional understanding, the bloom does not start due to the establishment of the vertical thermal stratification as the vertical density profile is controlled by the salinity stratification. The well-known massive diatom bloom is preceded by an initial growth of unidentified small-sized (1–4 μm) phytoplankton. As the bloom usually starts when the surface temperature is still below the temperature of maximum density (about 2.4°C for the salinity in the central Baltic), warming of the surface layer during that period has in fact a destabilizing effect on the stratification. The expansion of the bloom does not appear as a smooth, wave-like propulsion in the northeastern direction but rather as centripetal movements in the form of eddies and filaments from the more stratified coastal areas towards the center; hence, in the northern Baltic proper the progression is roughly in the southerly direction. The central eastern Gotland Basin with the least likelihood of vertical stratification in the photic layer is the last where the bloom commences. There the bloom starts in a mosaic of filaments and eddies that provide the vertical stability. The filaments with reduced salinity and increased temperature probably originate from the coastal areas and represent transformed coastal water.

INTRODUCTION

THE phytoplankton spring bloom in the Baltic Sea is ecologically the most dynamic event of the seasonal cycle as only in a few weeks most of the upper layer nutrients are consumed, followed by pulses of intense sedimentation of the newly produced material (JANSSON, 1978; BODUNGEN *et al.*, 1981; LARSSON *et al.*, 1986). The widespread understanding that the bloom in temperate and high latitude waters is initiated by the reduction of vertical mixing due to the onset of stratification was established long ago by classic studies (GRAN and BRAARUD, 1935; RILEY, 1942). In general, the relationship of the commencement of the bloom to the vertical stability (the ration between the thicknesses of the mixed and euphotic layers) has been demonstrated in the Baltic (KAISER and SCHULZ, 1978). In most of the studies, it has either implicitly or explicitly been assumed that the vertical stratification during the commencing spring bloom is provided by the onset of thermal stratification. The Baltic Sea is the world's largest brackish water

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estuary with the depths in the Baltic proper commonly between 50 and 120 m. The vertical density stratification is complicated by the addition of both the thermal and saline components. Depending on the actual salinity, the density maximum in the Baltic proper waters occurs near the temperature value 2.5°C (DIETRICH and KALLE, 1957). The influence of the thermal convection during the unstabilizing heating on the phytoplankton bloom is poorly known. With the aid of a numerical model SJÖBERG and WILMOT (1977) concluded that convection is possibly important for increasing the total production, although ACKEFORS and LINDAHL (1975) argue on the basis of empirical data that the spring bloom can commence only after the maximum density has been reached. Understanding of the spatial and temporal dynamics of the spring bloom has been grossly simplified due to the lack of data with adequate time and space resolution. Thus it has been a common understanding that the spring bloom in the Baltic is delayed, the further to the north the area is situated. In a comprehensive review of the Baltic biological oceanography HÄLLFORS and NIEMI (1981, p. 224) bluntly state that the bloom is regulated by the availability of light and the development of a thermal stratification, without even mentioning the influence of the saline stratification or the possible effects of the thermal convection during the heating phase.

Sea-surface temperatures and near-surface pigment images from satellite sensors (HORSTMANN *et al.*, 1986) show patterns in the spatial development of the spring bloom, notably large prominent areas with increased temperature and pigment levels that originate from the east coast of the Baltic proper. However, very little work has been done in the intercomparison of the satellite and *in situ* data.

In this paper, we analyse a large set of horizontal near-surface measurements of particle size fractions, chlorophyll fluorescence and the associated data collected on two consecutive years during the spring bloom season in the Baltic Sea. We attempt to partition the multitude of patterns observed into different time and space scales. We provide evidence that a certain vertical stability needed to trigger the commencement of the spring bloom is commonly caused not by local heating of the water column but by lateral advection of lower-density water. This can be expected in any brackish water basin where the water masses are formed as a result of complicated horizontal stirring and vertical mixing processes. On the contrary to the common understanding, the onset of thermal stratification caused by the local heating may be a terminating rather than the initiating factor as it separates the upper layer plankton from the deeper water nutrient supply.

METHODS AND DATA

Most of the observations that will be discussed were made from R.V. *Arnold Veimer* in the "along-track" mode while the ship was steaming along a straight course at a constant speed from 6 to 12 kn. Underway shipboard measurements of particle concentrations, *in vivo* fluorescence, temperature and salinity were obtained from a depth of 5 m. The "flow-through" system contained a bubble trap and a reservoir tank to maintain a relatively constant flow rate necessary to obtain the particle concentrations from an online Hiac-Royco PC-320 particle size analyser (PUGH, 1978). The counter included two sensors (CMH-60 and E-1000) that enabled us to register particles with the equivalent spherical diameter from 1 to 1000 µm in 12 size classes (Table 1). The channel settings of the counter were held constant throughout the study and the concentration in the respective size fractions will be designated as Ch1 to Ch12. The usual way of representing

Table 1. *Channel settings for the Hiac-Royco Model PC-320 particle counter in equivalent spherical diameters*

Sensor	Channel	Diameter range (μm)
CMH-60	1	1–2
	2	2–4
	3	4–6
	4	6–10
	5	10–20
	6	20–60
E-1000	7	28–42
	8	42–73
	9	73–105
	10	105–163
	11	163–305
	12	305–1000

particle data is to express them as volume concentrations (ppm), but as the particles can be seldom considered spherical, the conversion of the surface area measured by the counter to volume has not been pursued. Moreover, the activity of organisms is roughly proportional to their surface area and not to the volume (PLATT and DENMAN, 1978). Hence, as a measure of the integral particle concentration we use the total particle surface area in the range 1–1000 μm that was calculated by multiplying the channel count to the average area and summing over all the size groups. As a measure of the relative importance of different size fractions, the ratio of a size fraction's surface area to the total surface area (in percent) is used.

In vivo fluorescence of the chlorophyll pigments were measured from the same water with a Turner Designs 10-005R flow-through fluorometer. Mixing in the pumping system and collecting the particle counts over a time interval (10 s) needed to get a representative number of particles in each size group acted as a low-pass spatial filter.

Simultaneously, data on the water temperature, conductivity (both from 5 m depth) and wind velocity were recorded by the ship's automatic weather station. Although accurate calibrations of salinity were occasionally made with a salinometer, the salinity calculated from the weather station records is only considered as a relative measure of salinity and no absolute values will be inferred.

The time interval between the registration of integrated particle counts as well as fluorescence, temperature and conductivity was set at 1 min. Depending on the ship speed the spatial sampling interval varied from about 200 to 400 m.

Vertical profiles of the water column were obtained with a complex of a Neil Brown CTD, a submersible "EOS" fluorometer (Elektro-Optik Suarez, F.R.G.), and a rosette sampler.

Data from both fluorometers were calibrated against extracted chlorophyll *a* of the water samples either from the rosette or from the flow-through water. Chlorophyll extraction and photometric analyses (using the Jeffrey–Humphrey equations) were made according to the recommendations by EDLER (1979). The obtained good correlation coefficients (r = 0.884 and 0.986 for the flow-through data of 1985 and 1986, respectively) prove that in the majority of cases the bivariate regressions can be reliably used to infer the Chl *a* concentration.

Figure 1 shows the locations of the main study areas. The along-track measurements (transects) were made along straight lines between the stations. The study period

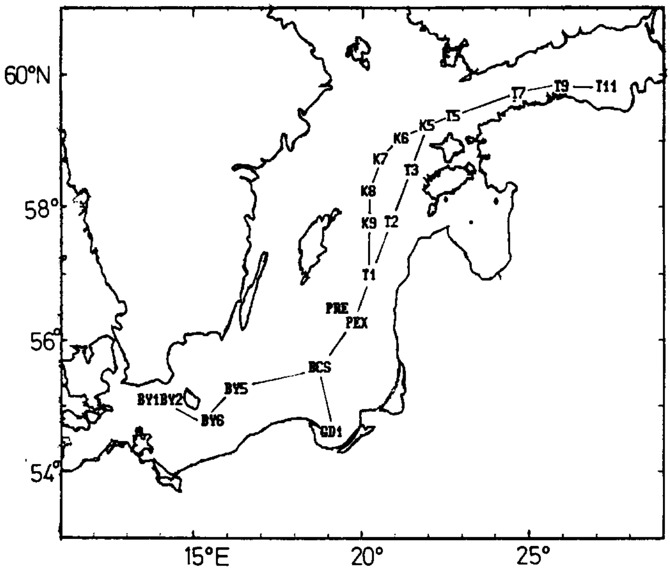

Fig. 1. Map of the Baltic Sea showing stations and study areas. The PrePEX'85 (PRE) and PEX'86 (PEX) were international experiments carried out under the auspices of ICES. The horizontal transects were made in between the stations or repeatedly on study areas.

extended from 17 April to 29 May in 1985 and from 18 April to 21 May in 1986. In both years most of the measurements in the middle of the study period were made in the central part of the eastern Gotland Basin. In 1985 the first four surveys were part of the PrePEX exercise and in 1986 most of the measurements were related to the international patchiness experiment (PEX'86) conducted under the auspices of ICES (ICES, 1989).

RESULTS

Some examples of how the bloom starts?

Example 1 is from the prebloom measurements that were made as part of the PrePEX study. Figures 2 and 3 show the results of two consecutive surveys on the same transect. On 19 April 1985 significant phytoplankton patchiness had evolved in spite of the apparently homogeneous surface temperature (from 1.5 to 1.7°C) and salinity. The temperature was clearly below the temperature of maximum density (2.4°C); hence, at equal salinity higher temperature at the surface would mean hydrostatic instability. The patches were most significant for the 2–5 μm size fraction that also exhibited the best correlation with chlorophyll. The same patchy structure was present in the 1–2 μm fraction but less so in the larger fractions. The small size fractions (1–10 μm) made up about 70% of the total particle surface area and obviously contained most of the chlorophyll. The usually dominant Ch7 and Ch8 fractions were very low and did not show any correlation with the chlorophyll concentration. The evolving initial phytoplankton growth was clearly associated with the vertical structure of the water column. The deep-mixed stations with the density jump below the 40-m depth had very low pigment and phytoplankton concentrations and resembled typical winter water. The slight salinity-caused density jump shallower than 40 m was definitely the factor restricting vertical mixing and triggering the spring bloom. On the next day, 20 April (Fig. 3), the water temperature had slightly increased, ranging from 1.4 to 1.8°C, and the surface

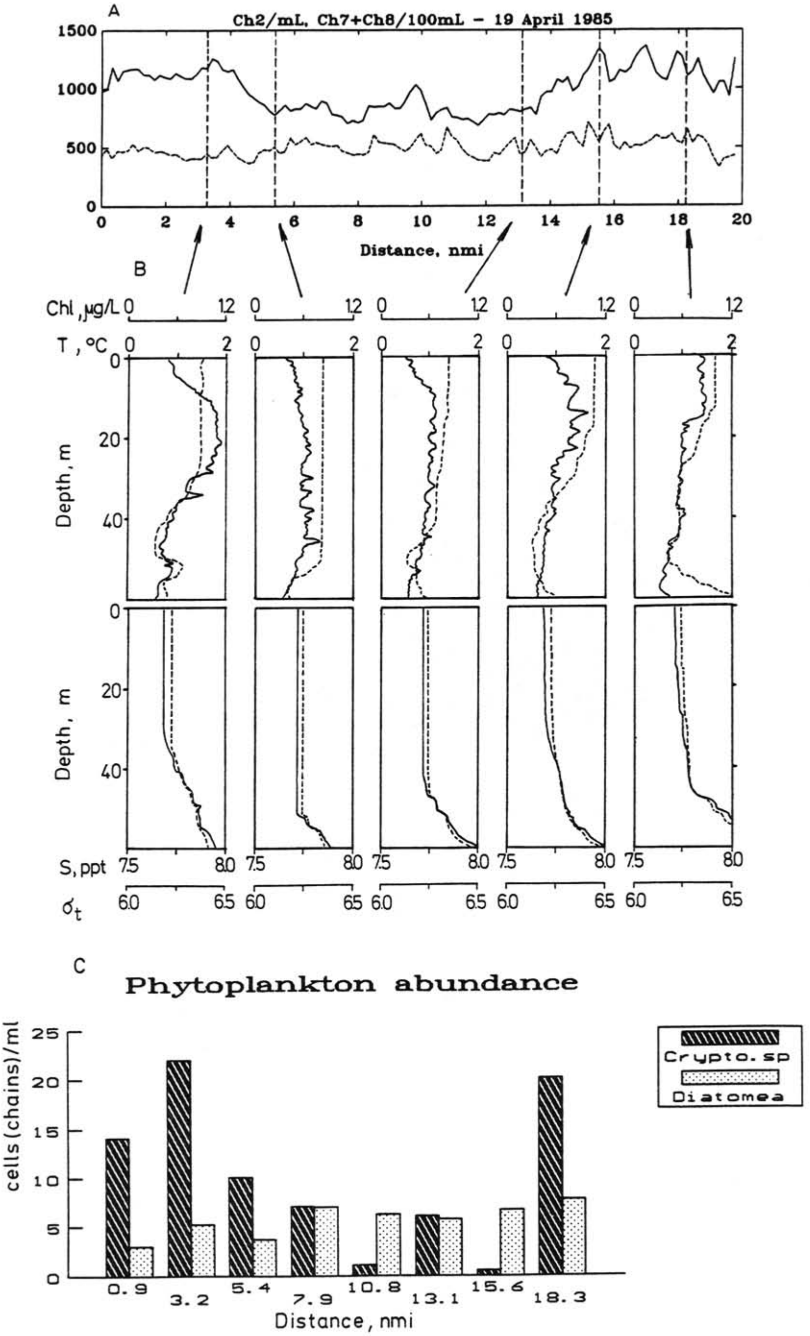

Fig. 2. The initial phytoplankton growth phase on 19 April 1985 on the PrePEX area. (A) Horizontal distributions of the 2–4 µm (Ch2) and 28–73 µm (Ch7+Ch8, dashed line) fractions expressed as particles per 1 ml (Ch2 ml^{-1}) or 100 ml (CH7+Ch8/100 ml). (B) Examples of the vertical profiles of (upper panel) chlorophyll *a* concentration (continuous line) and temperature (dashed), and (lower panel) salinity (continuous line) and density (sigma-*t*, dashed). (C) Abundance of the two characteristic phytoplankton groups: *Cryptomonadales* and *Diatomea*.

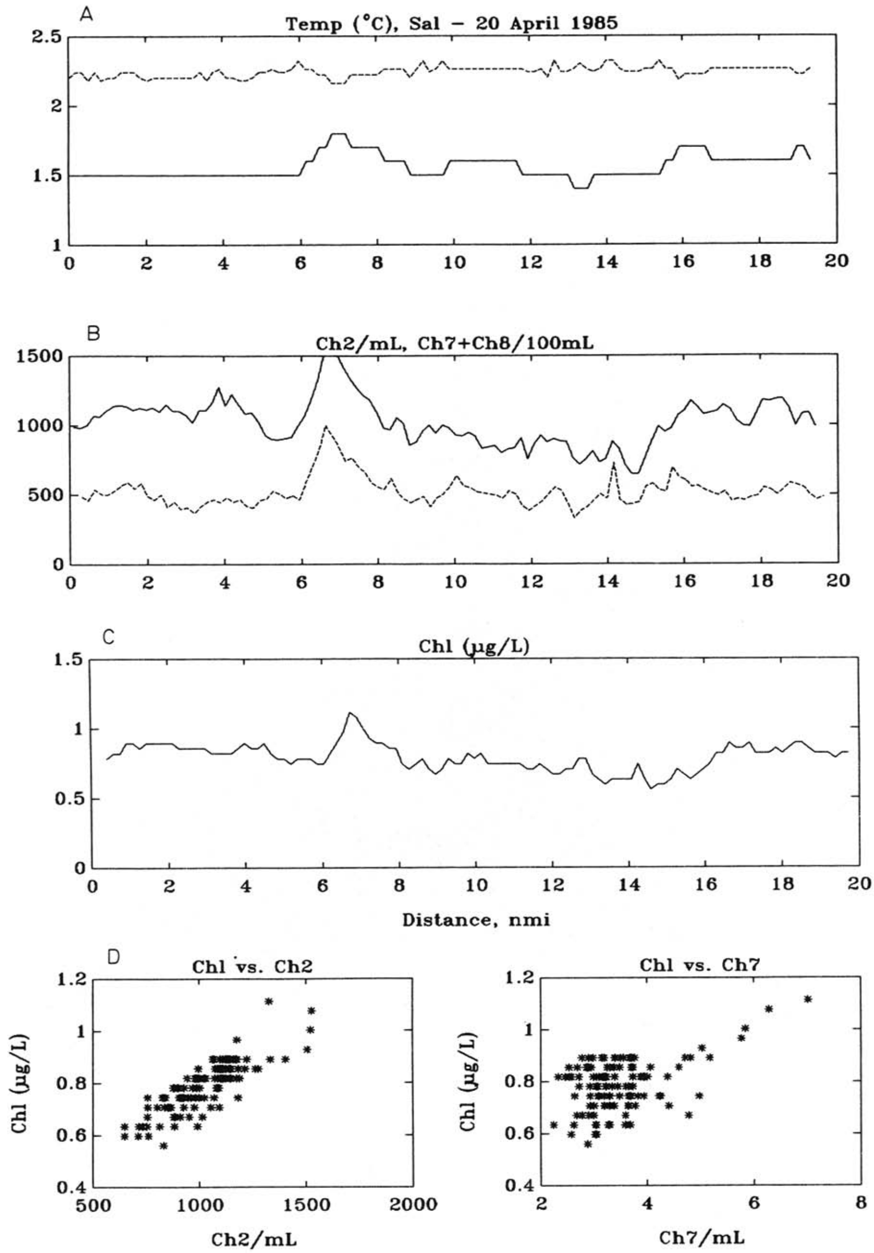

Fig. 3. Horizontal distributions on the PrePEX area on 20 April 1985. (A) Temperature and salinity (relative units, dashed). (B) Ch2 (per ml), combined Ch7 and Ch8 (per 100 ml, dashed). (C) Chlorophyll *a*. (D) Relationships of chlorophyll *a* with Ch2 and Ch7.

salinity appeared inversely correlated with the water temperature. The small size fractions had been further increased in numbers and were highly dominant. The Ch7–Ch8 fraction representing diatoms was still very low but showed initial growth in a definite patch. Neglecting the few higher values from the patch, the correlations of Ch7 and Ch8 with chlorophyll were still insignificant (Fig. 3D).

It appears that we had followed the initial growth phase of the Baltic phytoplankton before the outbreak of the well-known diatom bloom. The initial phytoplankton patches consisted mostly of unidentified, very small (1–4 μm) chlorophyll-containing organisms. The Ch4–Ch5 size fraction was also very important with 35% of the total particle surface area and, as determined microscopically, represented mostly small monads of the *Cryptomonas* species (Fig. 2C) with the average size of 15 × 7 μm (length × width).

Example 2 is a long section along the axis of the Baltic Sea on 17–19 April 1986 (Fig. 4). Bloom values were observed across the whole northern Baltic proper and still prebloom winter values dominated large areas of the central Baltic. At least eight individual features in the form of filaments with lower salinity, higher temperature and drastically increased phytoplankton concentration can be seen in the southern half of the section (Fig. 4D,E). The water temperature in the filaments was definitely below the temperature of maximum density. At this temperature surface warming would promote vertical instability and thermal convection, if not countered by increased salinity. Therefore, it is the salinity that is providing stable stratification and enables the commencement of the bloom. Although the nutrients were certainly not limiting at the time (Fig. 4C), a significant amount of them had been used up at stations with high phytoplankton values. As seen in Fig. 4B, areas in the Baltic proper with the prebloom water correspond to deeply mixed water with almost no stratification in the upper 60 m, whereas in the more stratified areas the bloom had started. The distribution of phytoplankton species shows a relatively uniform distribution of *Cryptomonas* spp., the dominance of the diatoms in the waters with a more advanced stage, and the occurrence of very high peak values of the *Pyramimonas* sp. in the initial bloom stations (Fig. 4G). The stage of the spring bloom is well depicted by the changing share of different size fractions (Fig. 4F): the relative proportions of the Ch7 and Ch2 fractions are reversed. The proportion of Ch7 in the total particle surface area (Ch7%) was increased up to 60% in the peak bloom values and was below the respective Ch2% value in the prebloom water.

The part of the transect with the most drastic filament near 40 nmi (see Fig. 4E) is zoomed out in Fig. 4H. The difference in temperature with the surrounding water is only 0.3°C (1.7°C in the maximum vs 1.4°C outside). The two closely spaced maxima are clearly different in their plankton size structure. Whereas most of the fractions peak together with Ch7 in the southern patch, Ch2 reached its maximum in the northern patch. It is tempting to associate the two separate maxima with different stages of the bloom (i.e. more advanced stage in the southern patch). It is even more tempting to associate some of the temperature increase with the increased absorption due to the higher plankton concentration.

It appears that the bloom in the central parts of the eastern Gotland Basin starts as a mosaic of individual patches that provide vertical stability in the photic layer. The filaments probably originate from plumes of transformed coastal waters with salinity deficiency. The plumes, eddies and filaments can be seen as sea-surface temperature and pigment anomalies on many spring-time satellite images (Horstmann *et al.*, 1986). As we do not have information on the life history of the filaments, it is not clear how much of

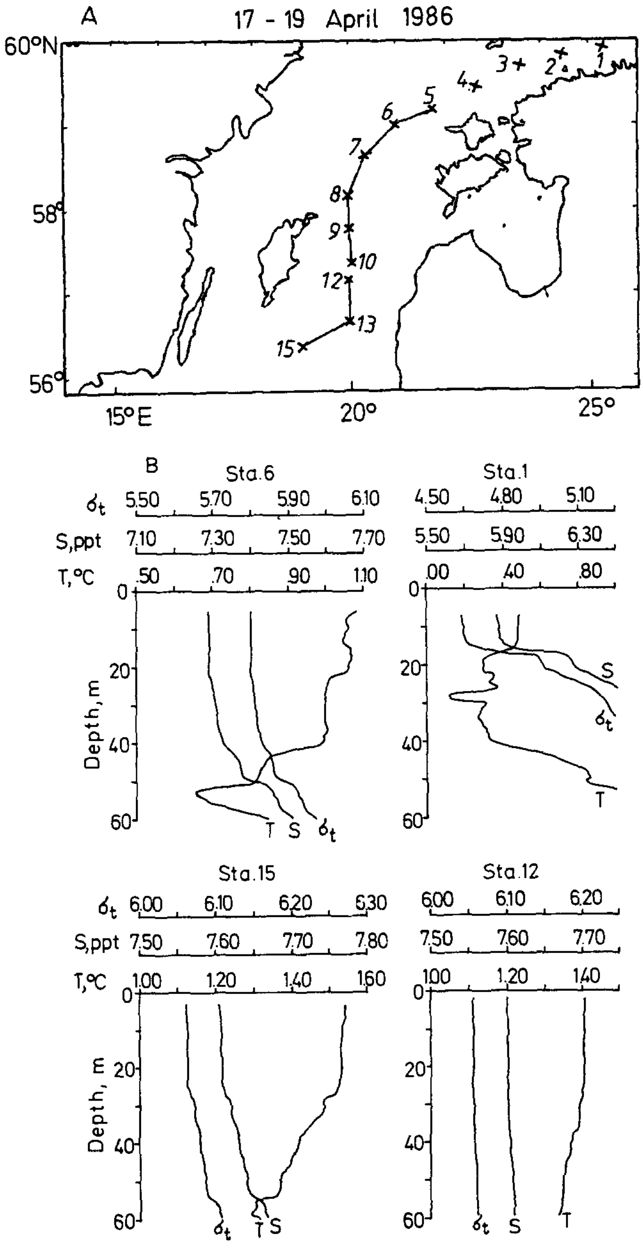
A
17 - 19 April 1986
60°N
58°
56°
15°E
20°
25°
1
2
3
4
5
6
7
8
9
10
12
13
15
B
Sta.6
σt 5.50 5.70 5.90 6.10
S,ppt 7.10 7.30 7.50 7.70
T,°C .50 .70 .90 1.10
Depth, m
0
20
40
60
T S σt
Sta.1
4.50 4.80 5.10
5.50 5.90 6.30
.00 .40 .80
S
σt
T
Sta.15
σt 6.00 6.10 6.20 6.30
S,ppt 7.50 7.60 7.70 7.80
T,°C 1.00 1.20 1.40 1.60
σt T S
Sta.12
6.00 6.10 6.20
7.50 7.60 7.70
1.00 1.20 1.40
σt S T

Fig. 4A, B.

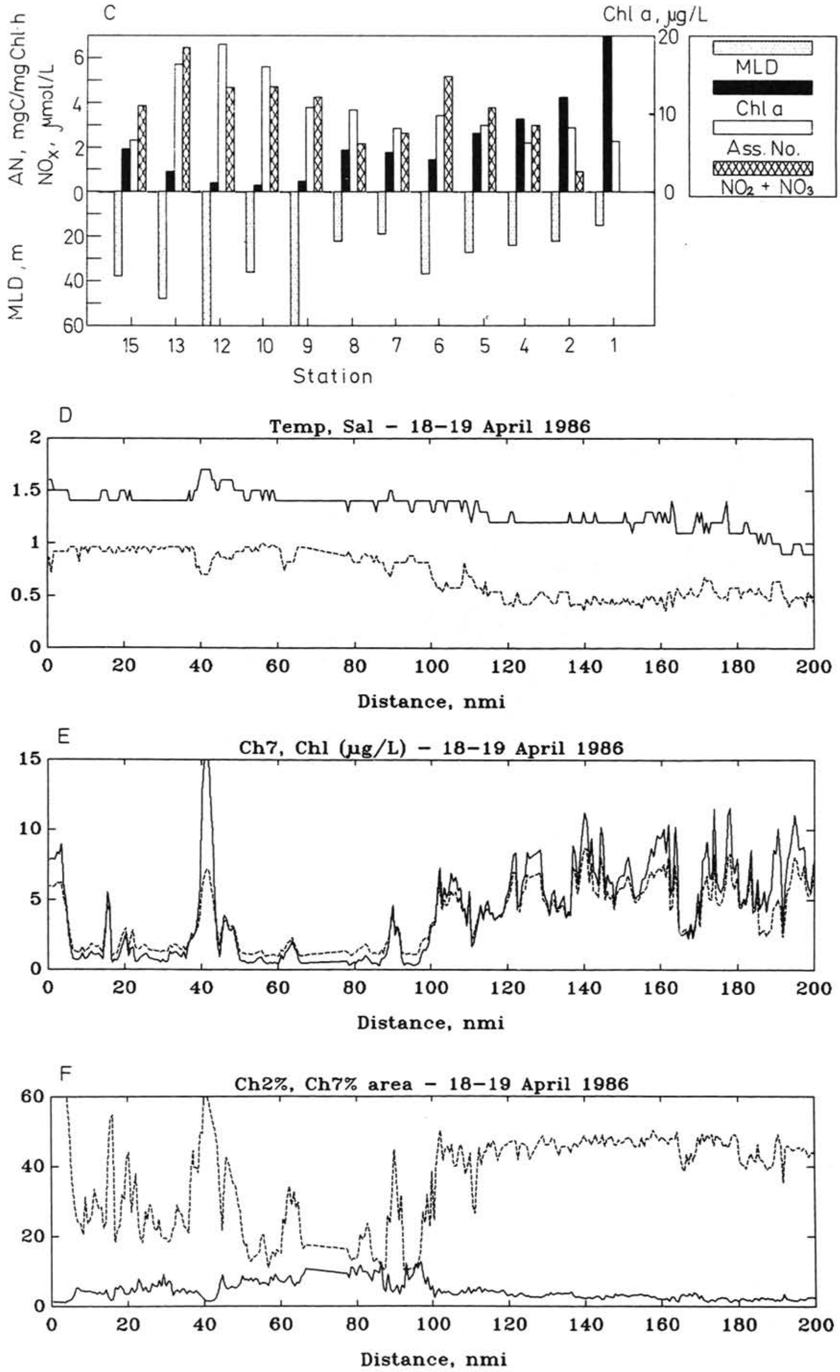
C
AN, mgC/mgChl·h
NOx, µmol/L
MLD, m
Chl a, µg/L
0
2
4
6
20
40
60
10
20
15 13 12 10 9 8 7 6 5 4 2 1
Station
MLD
Chl a
Ass. No.
NO2 + NO3
D
Temp, Sal – 18–19 April 1986
0
0.5
1
1.5
2
0 20 40 60 80 100 120 140 160 180 200
Distance, nmi
E
Ch7, Chl (µg/L) – 18–19 April 1986
0
5
10
15
0 20 40 60 80 100 120 140 160 180 200
Distance, nmi
F
Ch2%, Ch7% area – 18–19 April 1986
0
20
40
60
0 20 40 60 80 100 120 140 160 180 200
Distance, nmi

Fig. 4C, D, E, F.

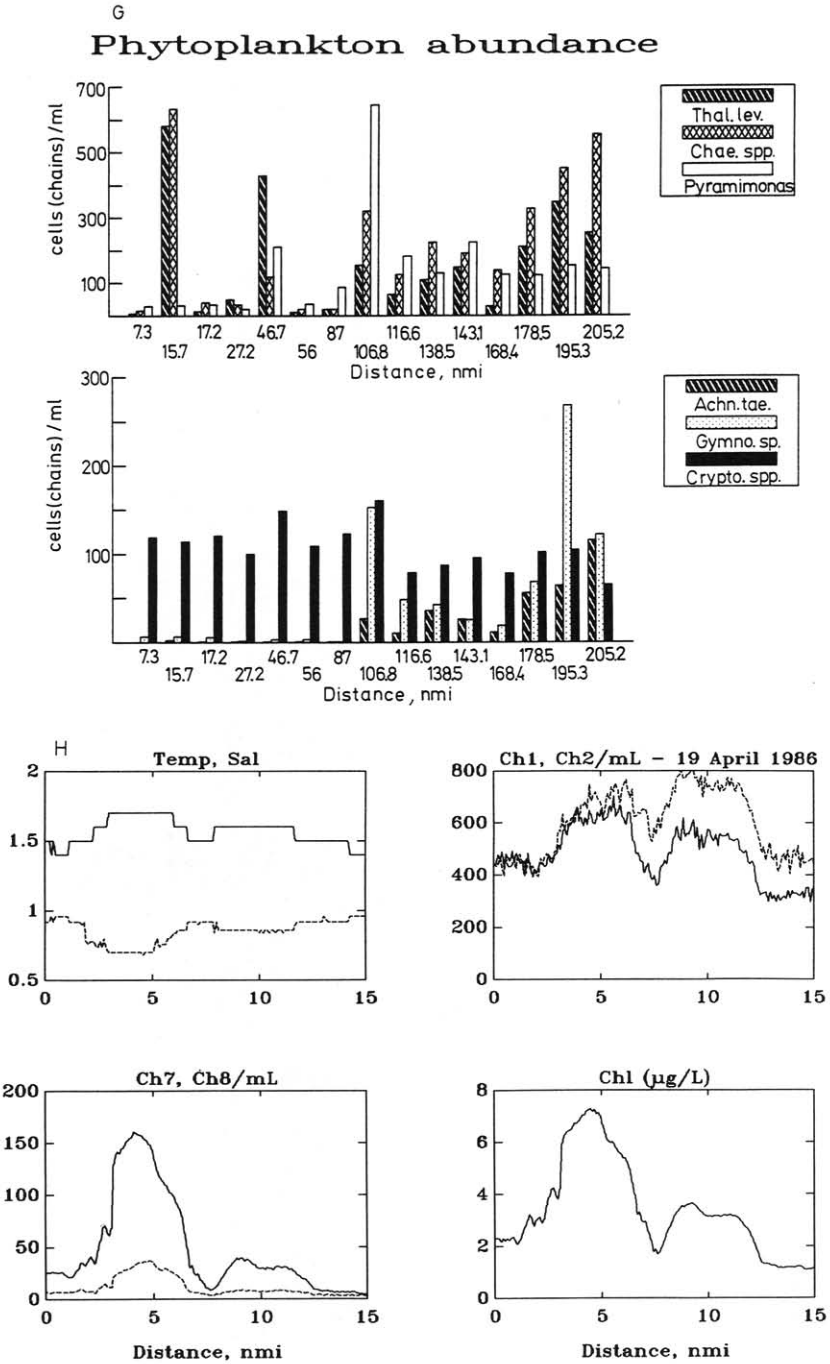
G
Phytoplankton abundance
cells (chains) /ml
700
500
300
100
Thal. lev.
Chae. spp.
Pyramimonas
7.3
15.7
17.2
27.2
46.7
56
87
106.8
116.6
138.5
143.1
168.4
178.5
195.3
205.2
Distance, nmi
cells(chains) / ml
300
200
100
Achn. tae.
Gymno. sp.
Crypto. spp.
7.3
15.7
17.2
27.2
46.7
56
87
106.8
116.6
138.5
143.1
168.4
178.5
195.3
205.2
Distance, nmi
H
Temp, Sal
2
1.5
1
0.5
0
5
10
15
Ch1, Ch2/mL – 19 April 1986
800
600
400
200
0
0
5
10
15
Ch7, Ch8/mL
200
150
100
50
0
0
5
10
15
Distance, nmi
Chl (µg/L)
8
6
4
2
0
0
5
10
15
Distance, nmi

Fig. 4G, H.

the increased plankton concentration is produced in the open sea after the formation of the filament, and how much originates from the transformed coastal water.

Example 3 is from the peak of the diatom abundance and is part of the PEX experiment (Fig. 5). The water temperature was close to the maximum density temperature and varied between 2.2 and 2.8°C. The phytoplankton patch with extremely sharp edges (between 15 and 23 nmi) had very high chlorophyll values, and corresponded to a mesoscale cyclonic eddy (J. ELKEN, personal communication). The very distinct minima of phytoplankton concentration on the eddy periphery were probably generated by a complicated vertical circulation pattern that did not allow the phytoplankton to stay in the euphotic layer. The effects of the thermal convection might have been involved as well (U. LASS, personal communication). The salinity transect (Fig. 5C) made simultaneously by a vertically undulating CTD-system ("Fish") confirms that the concentration minima at the eddy edges correspond to regions with nearly vertical isohalines, i.e. to frontal areas of intense vertical movements. As the water density at the time of the survey was predominantly determined by salinity, the salinity distribution is representative of the density distribution. During the diatom bloom the size fractions Ch7 and Ch8 are most closely related to the bulk of the phytoplankton biomass, as can be seen from their correlation with the simultaneously measured chlorophyll concentration (Fig. 5D). The correlation between chlorophyll and the small size fraction had disappeared. Microscopic examination showed that the phytoplankton assemblage was dominated by *Chaetoceros* spp. and *Thalassiosira levanderi.*

Example 4 is a section north from the Gdansk Bay on 27 April 1985 (Fig. 6) and demonstrates the influence of the fresh water discharge by the Wistula River on the commencement of the bloom. The bloom in the Gdansk Bay had probably started weeks before but the central Baltic could be considered as still in the prebloom phase. The plankton distributions were clearly related to the salinity and temperature distributions. As observed on several other occasions, the Ch2 fraction was a good indicator of the coastal water masses due to its negative correlation with salinity and positive correlation with temperature (Fig. 6D).

Space-averaged (mean) dynamics

A straightforward approach to get a general time curve of the bloom from spatially scattered data would be spatially averaging over each transect and pooling all the values

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Fig. 4. Distributions along a section across the northern and central Baltic on 17–19 April 1986. (A) Map of the section with the station numbers of the vertical cast (×). (B) Examples of vertical profiles of temperature, salinity and density (sigma-*t*) from different situations: open Baltic with stratification in the upper 40 m (Sta. 15), open Baltic with almost no stratification (Sta. 12), northern Baltic proper (Sta. 6) and the Gulf of Finland (Sta. 1) with strong thermohaline stratification. (C) Distribution of the upper mixed layer depth (MLD), mean chlorophyll *a* concentration in the mixed layer, assimilation number, and the sum of the nitrate and nitrite concentration in the mixed layer. The MLD is defined as the depth of 0.02 sigma-*t* difference from the surface 5-m depth value. (D) Temperature (°C) and salinity (relative units, dashed) vs distance from the southernmost point of the transect. (E) Ch7 (per 0.1 ml) and chlorophyll *a* (dashed). (F) Relative proportions of the Ch2 and Ch7 (dashed) size fractions in the total particle surface area. (G) Abundance of the characteristic phytoplankton species: *Thalassiosira levanderi, Chaetoceros* spp., *Pyramimonas* spp., *Achnanthes taeniata, Gymnodinium* sp. (20–30 μm), *Cryptomonas* spp. (7–15 μm) vs distance from the southern end of the transect. (H) Zoomed out portion of the section across the filament at 40 nmi showing the distributions of temperature (°C), salinity (dashed), Ch1, Ch2 (dashed), Ch7, Ch8 (dashed, particles per ml), and chlorophyll *a*.

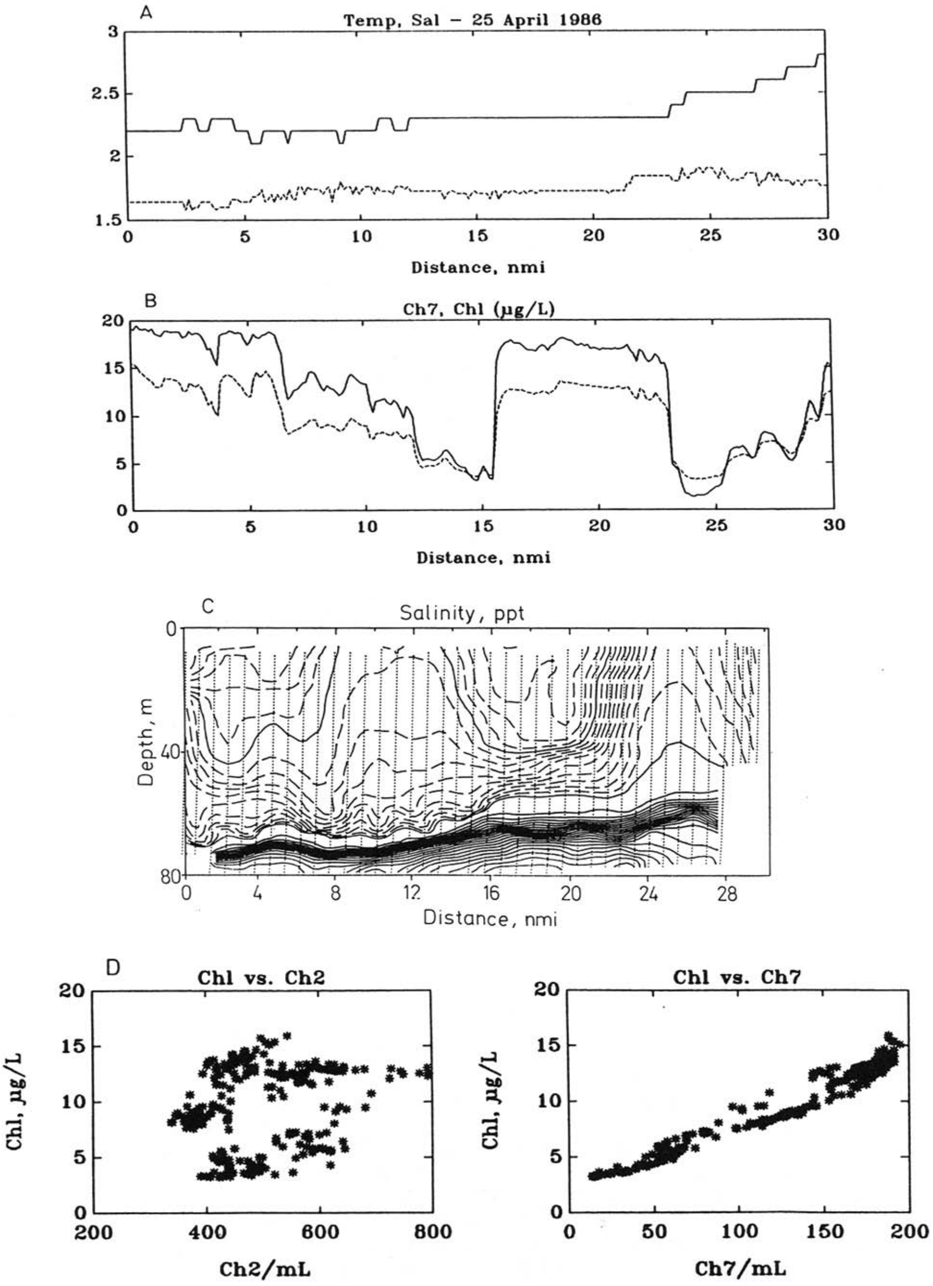


Fig. 5. A section of the PEX area on 25 April 1986. (A) Temperature (°C) and salinity (relative units, dashed). (B) Ch7 (particles per 0.1 ml) and chlorophyll *a* (dashed). (C) Vertical distribution of salinity between the depths of 0 and 80 m with the contours from 7.54 to 9.93 ppt. Contour interval is 0.1 ppt between continuous lines and 0.01 between dashed lines. The figure was kindly provided by M. Pajuste. (D) Relationships of chlorophyll *a* with Ch2 and Ch7.

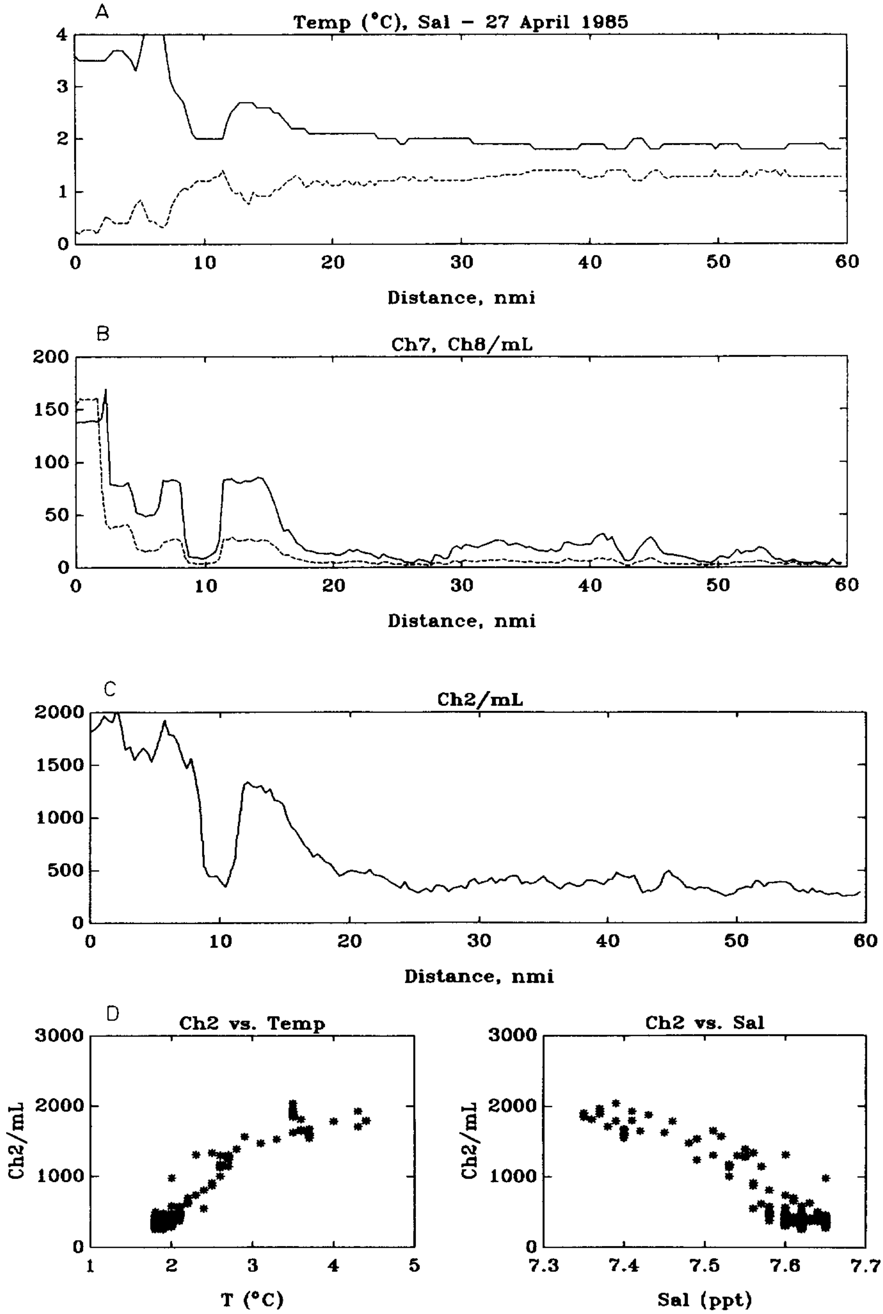


Fig. 6. Distributions along a section from the Bay of Gdansk (GD1 in Fig. 1) and Sta. BCS on 27 April 1985. (A) Temperature and salinity (relative units, dashed). (B) Ch7 and Ch8 (dashed). (C) Ch2. (D) Relationships of Ch2 with temperature and salinity.

from a certain area. The time curves constructed this way for the central part of the eastern Gotland Basin from both 1985 and 1986 are shown in Fig. 7. Most of the data is from the area around the PrePEX and PEX areas. It must be noted that each point here is a result of spatial averaging over a transect of several tens of nautical miles. In case of drastic patchiness with a bimodal distribution (cf. Fig. 5B), the average might not be a typical value. The scatter of points corresponding to the same or close date is due to pooling the data from a comparatively large area encompassing different waters. In spite of the not-so-rigorous averaging (the length of each averaged transect is not exactly equal) and pooling of nearby but maybe different areas, we believe that Fig. 7 gives an approximation to the spatially averaged dynamics of the spring bloom in the eastern Gotland Basin. The time-curves for other areas are not shown as the sampling frequency was not adequate.

Comparing the two years, it is evident that the starting point of the near-surface water temperature in the PEX area was quite similar, i.e. 1.6 vs 1.5°C on 19 April 1985 and 1986, respectively. From that time on, however, the warming of the surface layer was significantly faster in 1986. This may be explained by the relatively calm weather and the associated low wind mixing in April/May 1986 compared to 1985. By the end of May the two curves both converge to about 6°C. Especially strong heating is evident in the period from 29 April to 2 May 1986 when the temperature curves for the 2 years strongly diverge. However, a significant diversion of the chlorophyll and Ch7–Ch8 time curves (Fig. 7B,D,E) had occurred even before that time (on 25–26 April) as the vigorous diatom spring bloom in 1986 had started already before the significant diversion of the temperature curves. It is again apparent that the water temperature is not determining the commencement of the spring bloom, and the restriction of vertical mixing is provided by the much stronger influence of the salinity stratification. The temperature difference between the 2 years on 26 April, when the differences in the phytoplankton abundance were the greatest, was only 0.5°C, i.e. 1.8°C in 1985 vs 2.3°C in 1986. It is obvious that the relationship between the water temperature and the stage of the bloom is not causal as both the commencement of the bloom and the warming of the upper layer are related to increased irradiance and decreased wind mixing. Statistically significant differences in the vertical salinity stratification between 1985 and 1986 are hard to prove because of strong effects of individual features (eddies, fronts), the influence of local topography etc.

The increase in the Ch7 concentration from the prebloom conditions (average concentration on 17–20 April 1985, 2.7 m l^{-1}) to the blooming maximum (average concentration during the maximum of 1985, 140 m l^{-1}) is over 50-fold. The peak values in 1986 were even higher and the maximum was attained 17–18 days earlier, i.e. 25–27 April 1986 vs 12–17 May 1985 (Fig. 7D). However, the extent of the delay has only a very general (spatially averaged) meaning due to the drastic differences in bloom development over mesoscale distances. The early high values of 1986 were directly related to the strong eddy field that may not have been representative of the whole central basin. The early peak of 1986 consisted mostly of the Ch7 and Ch8 size fractions, whereas the Ch3 and Ch4 fractions had their maxima about a week later on 3 May. Microscopic analysis of the phytoplankton (R. HANSEN and U. PASSOW, personal communication) showed that many of the *Chaetoceros* cells from the early peak of 1986 were already in very poor condition, indicative of declining population. Therefore, the peak production in 1986 had occurred even before 25 April.

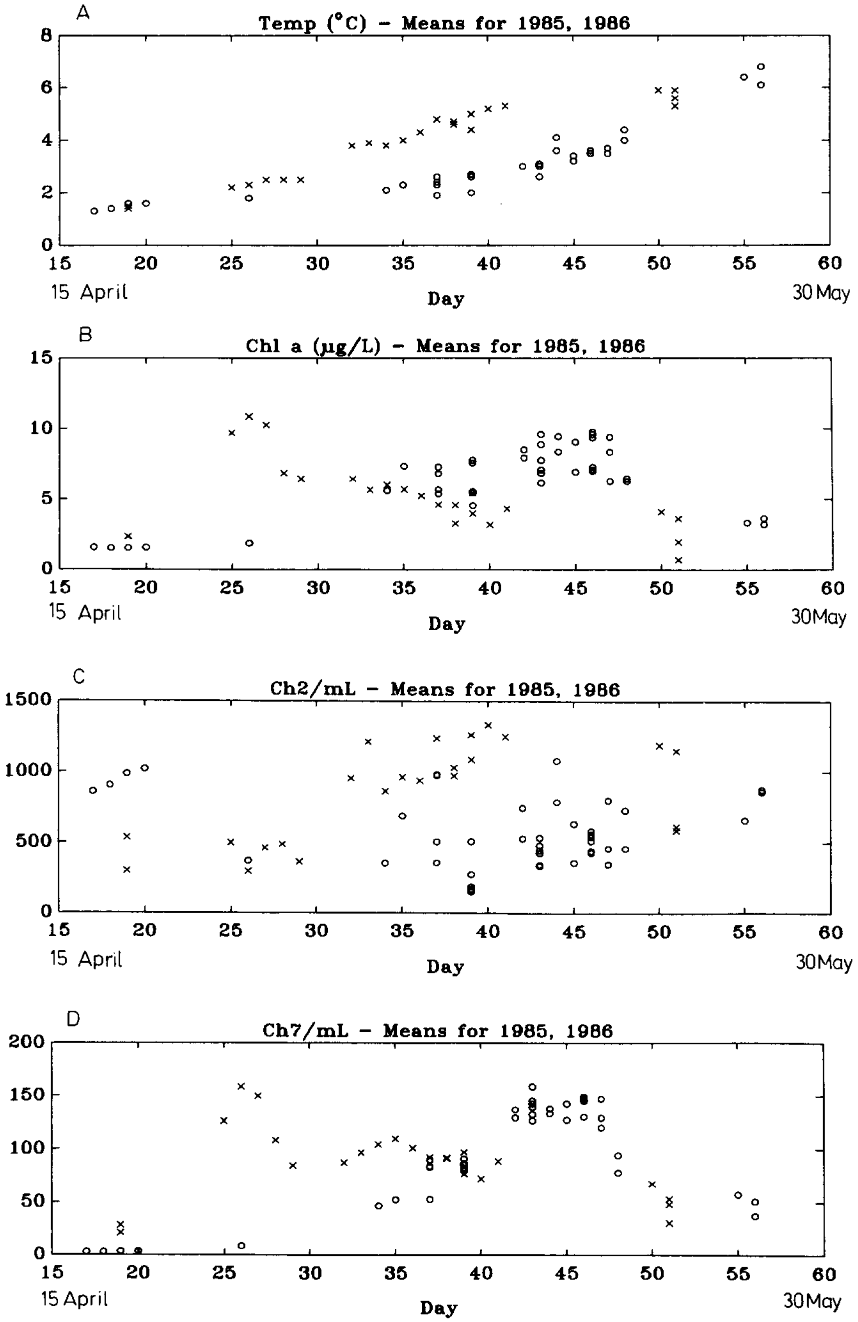

A
Temp (°C) - Means for 1985, 1986
0
2
4
6
8
15
20
25
30
35
40
45
50
55
60
15 April
Day
30 May
B
Chl a (µg/L) - Means for 1985, 1986
0
5
10
15
15
20
25
30
35
40
45
50
55
60
15 April
Day
30May
C
Ch2/mL - Means for 1985, 1986
0
500
1000
1500
15
20
25
30
35
40
45
50
55
60
15 April
Day
30May
D
Ch7/mL - Means for 1985, 1986
0
50
100
150
200
15
20
25
30
35
40
45
50
55
60
15 April
Day
30May

Fig. 7A, B, C, D.

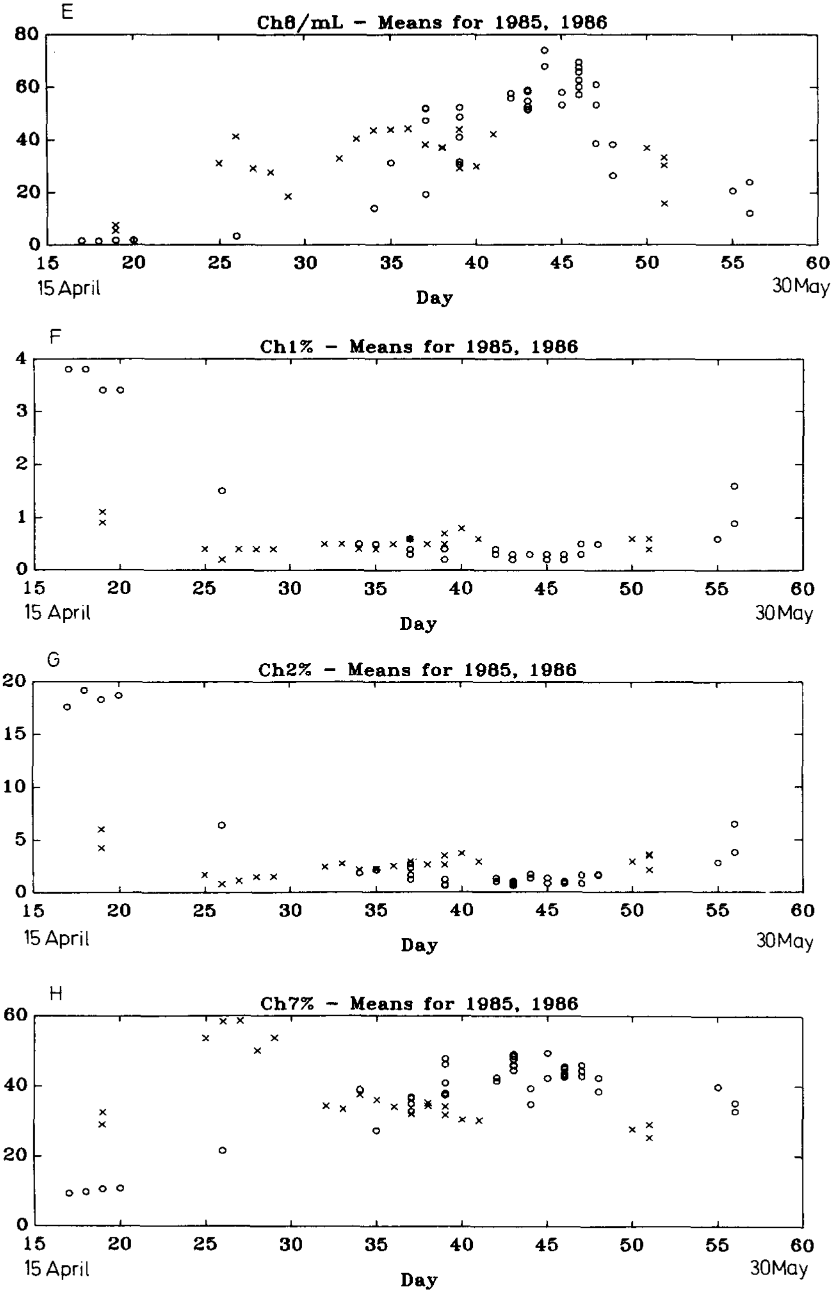

E
Ch8/mL - Means for 1985, 1986
80
60
40
20
0
15
20
25
30
35
40
45
50
55
60
15 April
Day
30May
F
Ch1% - Means for 1985, 1986
4
3
2
1
0
15
20
25
30
35
40
45
50
55
60
15 April
Day
30May
G
Ch2% - Means for 1985, 1986
20
15
10
5
0
15
20
25
30
35
40
45
50
55
60
15 April
Day
30May
H
Ch7% - Means for 1985, 1986
60
40
20
0
15
20
25
30
35
40
45
50
55
60
15 April
Day
30May

Fig. 7E, F, G, H.

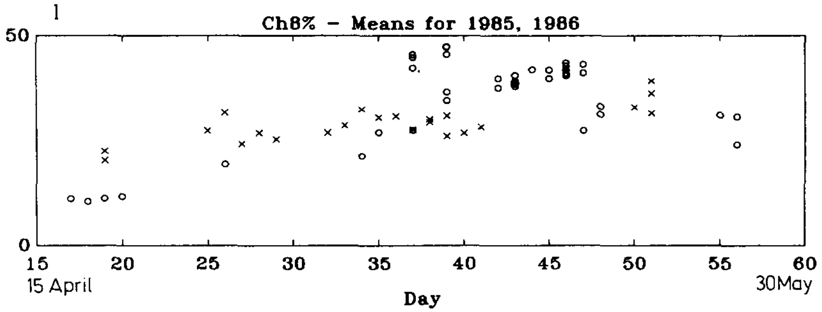


Fig. 7. Spatially averaged time dynamics of the spring bloom in the central part of the eastern Gotland Basin for 1985 (o) and 1986 (×). The days are counted from 1 April, e.g. 1 May is day number 31. (A) Temperature; (B) chlorophyll *a*; (C) Ch2; (D) Ch7; (E) Ch8. Relative surface areas of Ch1 (F), Ch2 (G), Ch7 (H), Ch8 (I).

The diatom blooms of the two consecutive years look similar in regard to the bulk absolute values. However, they differ in size structure. During the 1985 bloom the Ch8 fraction was more abundant, whereas in 1986 (especially during its first maximum on 25–27 April) the Ch7 fraction was clearly above the 1985 peak values. It appears as if the 1985 bloom consisted more of the bigger cells and/or chains. The difference in the Ch9 fraction is insignificant, whereas the large Ch10 fraction was, on the contrary, more abundant in 1986 and not in 1985. It is not clear which organisms made up this size fraction.

Another aspect of the bloom development can be followed by the time curves of the percentage areas of the size fractions. Apart from the general increase–decrease of the phytoplankton biomass they give an indication of a changing community structure, i.e. its species composition (if different by size) or of the changing size of the diatom chains. The smallest size fractions (Fig. 7F,G) had especially high dominance in the middle of April 1985, before the occurrence of the massive diatom bloom. For example, on 18 April 1985 the size fraction 1–10 μm made up 62.2% of the total particle surface area in the range 1–1000 μm (the 1–20 μm range combined 70.9%). Examination of the relationships between the particle size fraction and chlorophyll concentration confirmed that the fraction 1–10 μm was well correlated with chlorophyll and, hence, represented small phytoplankton. In regard to most of the characteristics the water could still be classified as prebloom, winter water. However, the gradual increase in the concentration of the 2–4 μm fraction (Fig. 7C) during the four consecutive days of the PrePEX surveys as well as the distributions on individual transects (Figs 2 and 3) clearly distinguish this period as an initial growth phase of small chlorophyll-containing organisms. Microscopic examination of the samples showed that the Ch3–Ch5 fraction was dominated by the *Cryptomonas* and *Pyramimonas* species. The 1–4 μm phytoplankton organisms remained unidentified. In 1986 the initial bloom stage was again distinguished by increased ratio of the small phytoplankton fraction but both the relative abundances and the absolute concentrations remained below the respective values in 1985. However, values of picoplankton almost as high as in 1985 were found locally in patches of prebloom water north of the PEX area (Fig. 4F). It is probable that due to the earlier commencement of the bloom in 1986, the maximum of the small fraction was over by 19 April. In contrast to the massive diatom spring bloom, the growth phase of the picoplankton fraction is hard to detect. We distinguish this period from the prebloom, winter stage as a separate *initial* growth stage of the picoplankton that precedes the diatom bloom period.

Large-scale and mesoscale spatial patterns of the bloom

It has been generally accepted that the vernal phytoplankton bloom in the southern and central parts of the Baltic proper occurs in the second half of April; in the northern part of the Baltic proper and in the Gulf of Finland in early May (HÄLLFORS and NIEMI, 1981).

However, if we look at a section across the central and northern Baltic proper on 18–19 April 1986 (Fig. 4), we see that, quite on the contrary, bloom values covered the whole northern Baltic proper and the Gulf of Finland, and still prebloom winter values occurred locally in the central Baltic. Due to the shallow saline stratification, the bloom in the Gulf of Finland had started already below the ice, and the Chl *a* values exceeded 20 $\mu g\ l^{-1}$ (Fig. 4C). The conception that the bloom in the Baltic is progressing northwards is probably a misconception due to the scarcity of measurements during bloom period in the open sea.

In 1985 the first sections across the northern Baltic were made on 7–9 May (Fig. 8) when the bloom had already started even in the central Baltic. However, the size distributions show the more advanced stage of the bloom in the northern Baltic proper and the Gulf of Finland compared to the central Baltic. The inlet of the Gulf of Finland (near Osmussaar Island, about 23°E) was marked with a salinity drop (from around 7.33 to 6.85 ppt) associated with a drastic increase in the Ch9 size fraction. Whereas Ch7 gave most of the particulate biomass in the Baltic proper, Ch8% increased steadily northwards until both Ch7% and Ch8% dropped in the Gulf of Finland due to the drastic jump of Ch9. There the total particle surface area was made up almost exclusively by the Ch8 (45%), Ch9 (30%) and Ch7 (20%) size fractions. We have previously shown (KAHRU *et al.*, 1986) that the drastic change in the particle size structure across the front was caused by the increased size of the diatom *Achnanthes taeniata* chains. The increased chlorophyll concentration and the number of decaying cells of the cold-water species *Melosira arctica* and *Nitzschia frigida*, as well as the decreased assimilation number and bigger diatom chains on the fresher side of the front prove that the Gulf of Finland waters were in a more advanced stage of the spring bloom. Therefore, the earlier commencement of the spring bloom in the northern Baltic proper and especially in the Gulf of Finland was obvious in both years.

A very similar, drastic increase in the Ch9 fraction was evident in the eastern part of the Gulf of Finland about 3 weeks later (Fig. 9), by which time it had disappeared from the inlet of the Gulf. The change in the community structure was caused by drastically increased abundance of long *Gonyaulax catenata* chains, as well as cells of *Actinocyclus octonarius* and chains of *A. taeniata*. Massive nutrient loadings into the eastern Gulf of Finland probably sustain a high phytoplankton population there throughout the summer.

By the end phase of the spring bloom the concentration had declined significantly. However, as has been argued before (KAHRU *et al.*, 1982), the Baltic pelagic communities, perturbed by intermittent nutrient injections in fronts, eddies and filaments, never reach the so-called steady-state summer minimum when the single important source of nutrients is regeneration. For example, the front in the middle of the eastern Gotland Basin (Fig. 10) caused an abrupt increase in the phytoplankton concentration. The increase was most pronounced for the Ch9 size fraction (Fig. 10D) with 15-fold increase. As the anomalous frontal water was both warmer and fresher, the frontal effects could *not* have been due to frontal upwelling of nutrient-rich deep (colder) water. The warmer and fresher water probably represented a huge plume of transformed coastal water. The small size fractions were much more abundant in the warmer mass but Ch7–Ch9 clearly showed frontal effects that can be seen on the zoomed out Fig. 10E. The sharp maxima of Ch9 were clearly associated with locations of the front where the salinity was decreasing and temperature increasing northwards. This indicates a specific convergence–diver-

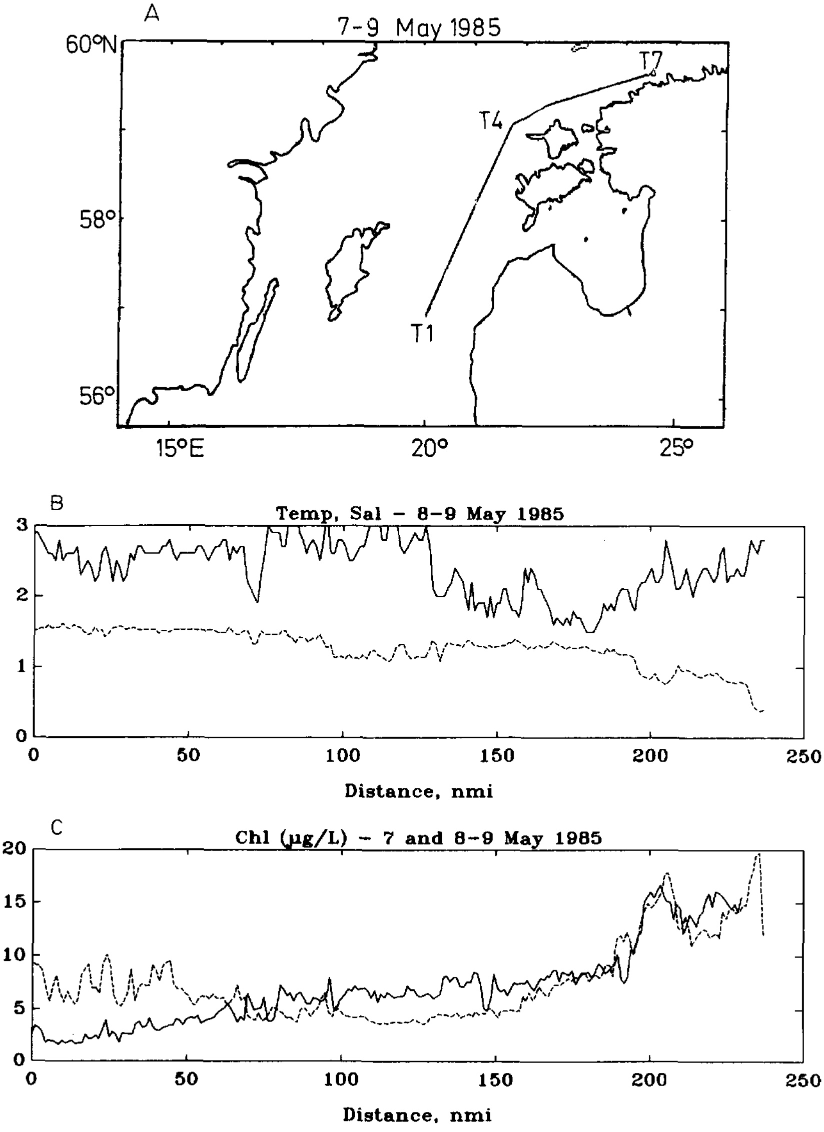


Fig. 8A, B, C.

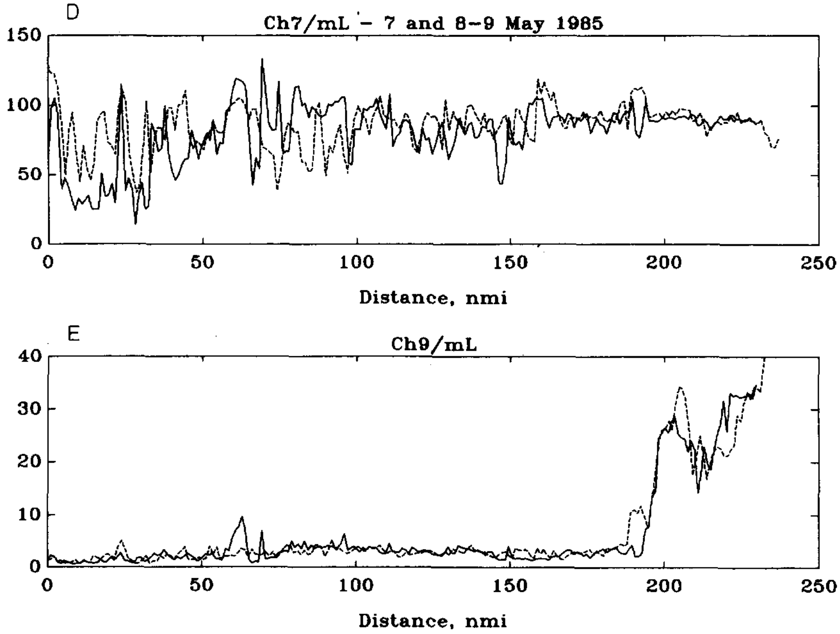


Fig. 8. Distributions along a repeated section in the northern Baltic on 7 May (to northeast) and 8–9 May 1985 (to southwest). The distance is measured from the southern end of the section. (A) Map of the section. (B) Temperature (°C) and salinity (relative unites, dashed). (C) Chlorophyll *a* (dashed on 8–9 May). (D) Ch7 (dashed on 8–9 May). (E) Ch9 (dashed on 8–9 May).

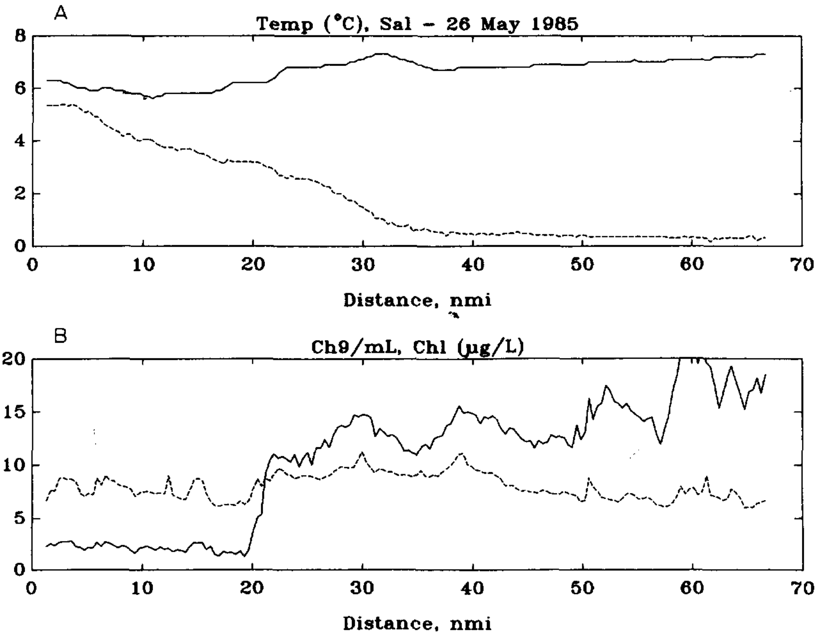


Fig. 9. Distributions along a section from Sta. T7 to T11 (see Fig. 1) in the Gulf of Finland. (A) Temperature and salinity (relative units, dashed). (B) Ch9 and chlorophyll *a* (dashed).

gence velocity pattern in the front. The broader maximum between 40 and 50 nmi seems to belong to an along-front, jet-like feature with the lowest salinity.

Progressing bloom wave

It has been frequently assumed that the phytoplankton spring bloom travels like a wave over the Baltic starting in the south and ending in the north (e.g. Jansson, 1978). On a very broad scale this is certainly true, but as shown in the previous section, on the scale of the eastern Gotland Basin it is not the north–south gradient but the different saline

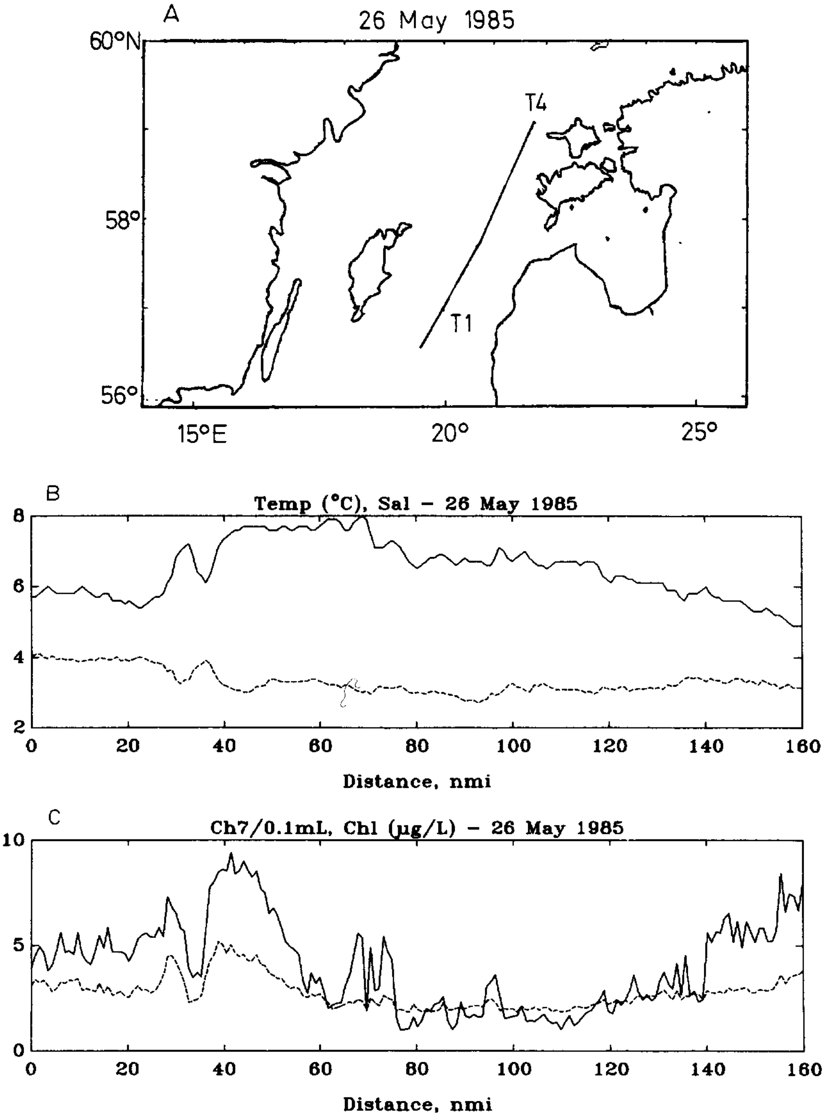
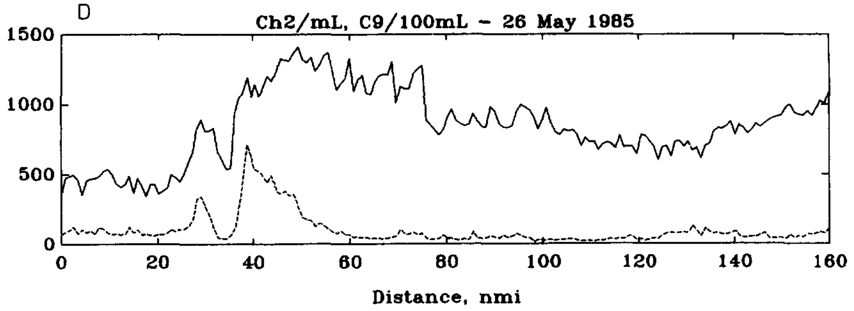


Fig. 10A, B, C.



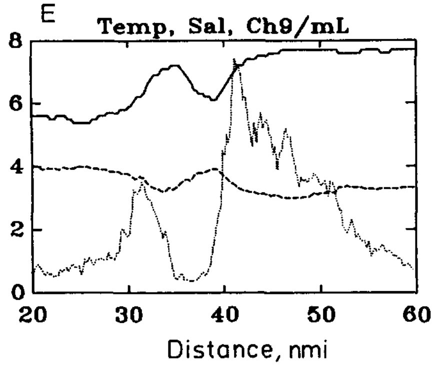


Fig. 10. Distributions along a section in the central Baltic on 26 May 1985. The distance is measured from the southern end of the section. (A) Map of the section. (B) Temperature and salinity (relative scale, dashed). (C) Ch7 (per 0.1 ml) and chlorophyll *a* (dashed). (D) Ch2 and Ch9 (dashed). (E) Zoomed out portion of the front showing the adherence of Ch9 (dotted) maxima to the areas of declining salinity (dashed) and increasing temperature (continuous line).

stratification that is causing the uneven commencement of the bloom. Evidence for a wave-like propulsion of the spring bloom was still gained from a 86-mile long transect between the Bornholm and the eastern Gotland basins (Stas BY5 and BCS) that was covered four times during the bloom in 1985 (Fig. 11). The transect follows roughly the Stolpe Furrow connecting the deeps of the Bornholm and Gotland basins. As the transect is far from the influence of the lower-salinity coastal water, it should be representative of the open southern Baltic.

On 27 April, the bloom had started in the Bornholm Basin but had not reached the open southern Gotland Basin. The edge of the bloom is clearly visible in the middle of the transect (Fig. 11C). The surface temperature did not reveal any front-like structure associated with the edge of the spring bloom. On 4 May the bloom was all over the transect, whereas on 18 May it was at its peak in the eastern end and had already declined in the Bornholm Basin. On 25 May the post-bloom stage had been reached on both basins. On all the transects both the surface temperature and salinity were very much homogeneous over the whole area. Striking and quasi-periodic fine-scale variability was evident in the Ch9 size fraction on 27 April (Fig. 11B). The mechanisms for the generation of the variability that is specific to a certain phytoplankton size fraction is not known.

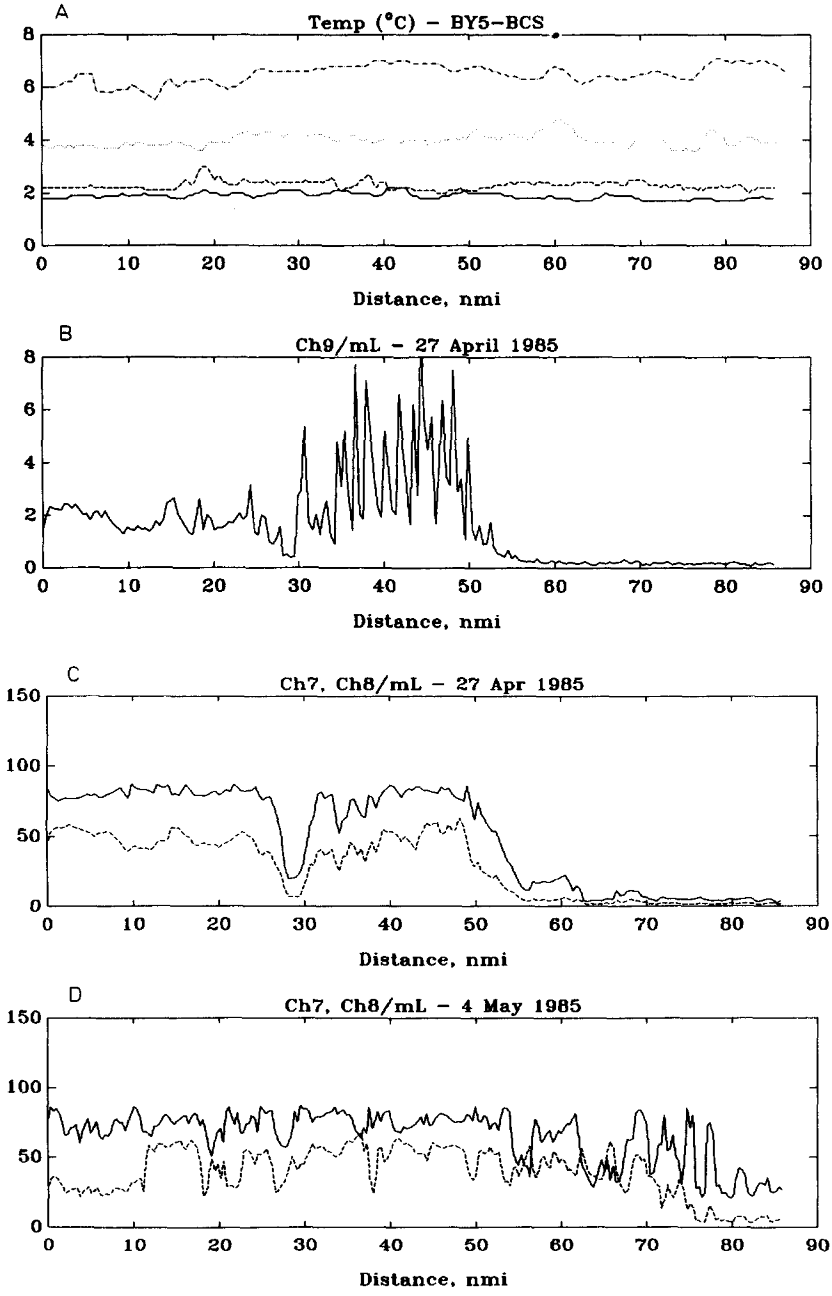

A
Temp (°C) – BY5–BCS
8
6
4
2
0
0 10 20 30 40 50 60 70 80 90
Distance, nmi
B
Ch9/mL – 27 April 1985
8
6
4
2
0
0 10 20 30 40 50 60 70 80 90
Distance, nmi
C
Ch7, Ch8/mL – 27 Apr 1985
150
100
50
0
0 10 20 30 40 50 60 70 80 90
Distance, nmi
D
Ch7, Ch8/mL – 4 May 1985
150
100
50
0
0 10 20 30 40 50 60 70 80 90
Distance, nmi

Fig. 11A, B, C, D.

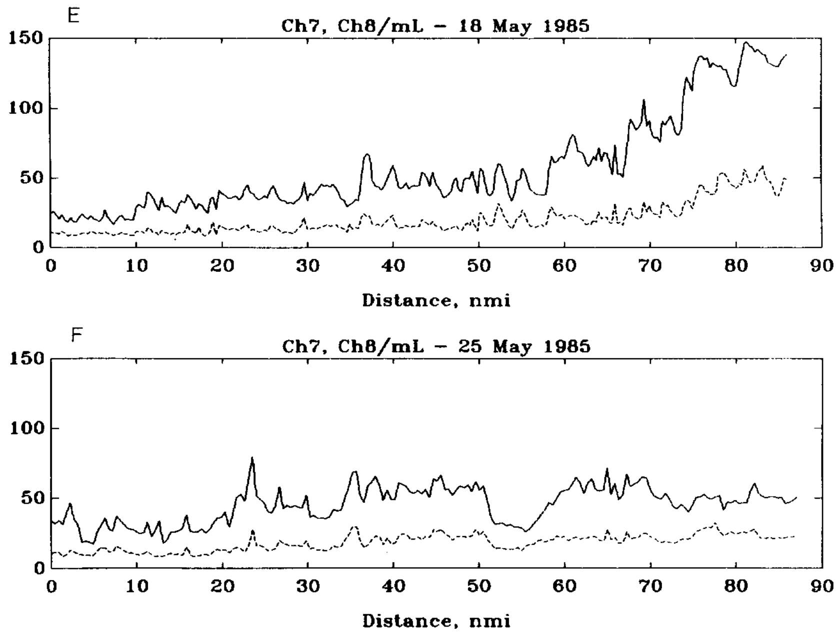


Fig. 11. Demonstration of the wave-like progression of the spring bloom between the Bornholm and southern eastern Gotland basins (from Sta. BY5 to BCS, see Fig. 1) in the spring of 1985. (A) Temperature, the four curves with increasing values are from 27 April, 4 May, 18 May and 25 May, respectively. (B) Ch9 on 27 April. Ch7 and Ch8 (dashed) on 27 April (C), 4 May (D), 18 May (E), 25 May (F).

DISCUSSION

Although the phytoplankton spring bloom has been extensively studied all over the world ocean, including the Baltic Sea, many important questions have still remained uncertain. Whereas Kaiser and Schulz (1978) argued that the thermal stratification in the deeper parts of the Baltic Sea is essential for the commencement of the spring bloom, Bodungen *et al.* (1981) conclude that the spring bloom in the Bornholm Basin can commence in calm weather before the thermal stratification is established. The importance of the synoptic scale eddies and the associated shallowing and deepening of the halocline for the phytoplankton spring bloom in the Baltic was shown by Kahru *et al.* (1982), who observed the highest variability in the phytoplankton biomass during the spring bloom. To explain the drastic variability, they conjectured that most of the bloom-time mesoscale spatial variability was due to the differences in the time of the commencement of the bloom.

In 1986 the bloom was very early, compared to the data of Kaiser and Schulz (1978). However, in the case of monthly or even less frequent measurements, the start of the bloom as well as the peak values are easily missed, and the apparent maxima are far from the real maxima. The magnitudes of the blooms in 1985 and in 1986 were quite comparable, although there were differences in the particle size structure that implies differences in the phytoplankton assemblage. Hobro (1979) has observed differences in the year-to-year species composition of the spring bloom in a coastal area in the northern Baltic.

That many offshore plankton blooms initially start at the coast as water packages of high nutrients and become conspicuous first far from land was conjectured by JANSSON (1978) for the late-summer blue-green algal blooms. We have shown that the spring bloom in the offshore Baltic starts in filaments and eddies providing vertical stability. Filaments in the upwelling and shelf-break regions have been observed in many different areas, e.g. the California Current (ABBOTT and ZION, 1985) and the Mediterranean Sea (WANG *et al.*, 1988).

CONCLUSIONS

The phytoplankton spring bloom in the Baltic is triggered by the saline stratification and light rather than by the establishment of the thermal stratification. The bloom starts before the maximum density temperature has been reached.

The bloom progresses from the more stratified areas towards the less stratified central areas.

The saline density stratification in the photic layer of the offshore areas is affected by synoptic scale eddies, and by filaments with salinity deficiency. The filaments probably originate from the transformed coastal water.

The massive diatom spring bloom is preceded by an initial growth phase of unidentified picoplankton (1–4 µm) and small monads of the *Cryptomonas* and *Pyramimonas* species.

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REFERENCES

ABBOTT M. R. and P. M. ZION (1985) Satellite observations of phytoplankton variability during an upwelling event. *Continental Shelf Research*, **4**, 661–680.

ACKEFORS H. and O. LINDAHL (1975) Investigations on primary phytoplankton production in the Baltic in 1974. *Meddelande fran Havsfiskelaboratoriet, Lysekil*, **195**, 14 pp.

BODUNGEN B. v., K. v. BRÖCKEL, V. SMETACEK and B. ZEITZSCHEL (1981) Growth and sedimentation of the phytoplankton spring bloom in the Bornholm Sea (Baltic Sea). *Kieler Meeresforschunge*, **5**, 49–60.

DIETRICH G. and K. KALLE (1957) *Allgemeine Meereskunde*, Bornträger, Berlin, 492 pp.

EDLER L. (1979) Recommendations for marine biological studies in the Baltic Sea. *The Baltic Marine Biologists*, **5**, 38 pp.

GRAN H. H. and T. BRAARUD (1935) A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine. *Journal of the Biological Board of Canada*, **1**, 219–467.

HÄLLFORS G. and A. NIEMI (1981) Vegetation and primary production. In: *The Baltic Sea*, A. VOIPIO, editor, Elsevier, Amsterdam, pp. 220–237.

HOBRO R. (1979) Annual phytoplankton successions in a coastal area in the northern Baltic. In: *Cyclic phenomena in marine plants and animals*, E. NAYLOR and R. G. HARTNOLL, editors, Pergamon, Oxford, pp. 3–10.

HORSTMANN U., H. VAN DER PIEPEN and K. W. BARROT (1986) The influence of river water on the southeastern Baltic Sea as observed by Nimbus 7/CZCS imagery. *Ambio*, **15**, 286–289.

ICES (1989) The Baltic Sea Patchiness Experiment: General Report, Vols 1–2. Cooperative Research Report, No. 163. 100 + 156 pp.

JANSSON B.-O. (1978) The Baltic—a systems analysis of a semi-enclosed sea. In: *Advances in oceanography*, H. CHARNOCK and G. DEACON, editors, Plenum, New York, pp. 131–183.

KAHRU M., A. AITSAM and J. ELKEN (1982) Spatio-temporal dynamics of chlorophyll in the open Baltic Sea. *Journal of Plankton Research*, **4**, 779–790.

KAHRU M., S. NÕMMANN, M. SIMM and K. VILBASTE (1986) Plankton distributions and processes in the Baltic boundary zones. In: *Marine interfaces ecohydrodynamics*, J. C. J. NIHOUL, editor, Elsevier, Amsterdam, pp. 273–293.

KAISER W. and S. SCHULZ (1978) On the causes for the differences in space and time of the commencement of the phytoplankton bloom in the Baltic. *Kieler Meeresforschungen*, **4**, 161–170.

LARSSON U., R. HOBRO and F. WULFF (1986) Dynamics of a phytoplankton spring bloom in a coastal area of the northern Baltic proper. *Contributions from the Askö Laboratory*, **30**, 3–32.

PLATT T. and K. L. DENMAN (1978) The structure of pelagic marine ecosystems. *Rapport et Procès-verbaux des Réunions. Conseil Permanent International pour l'Exploration de la Mer*, **178**, 24–27.

PUGH P. R. (1978) The application of particle counting to an understanding of the small-scale distribution of plankton. In: *Spatial pattern in plankton communities*, J. H. STEELE, editor, Plenum, New York, pp. 111–129.

RILEY G. A. (1942) The relationship of vertical turbulence and spring diatom flowerings. *Journal of Marine Research*, **5**, 67–87.

SJÖBERG S. and W. WILMOT (1977) Systems analysis of a spring phytoplankton bloom in the Baltic. *Contributions from the Askö Laboratory*, **25**, 1–99.

WANG D.-P., M. E. C. VIEIRA, J. SALAT, J. TINTORE and P. E. LA VIOLETTE (1988) A shelf/slope filament off the northeast Spanish coast. *Continental Shelf Research*, **46**, 321–332.