

**Development and
dynamics of a coastal
sub-surface phytoplankton
bloom in the southwest
Kattegat, Baltic Sea***

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Abstract

The study was based on CTD-casts performed on 5 consecutive days at 7 positions along a shallow- to deep-water transect during the spring bloom in the southwest Kattegat. The development, dynamics and fate of the sub-surface chlorophyll maximum (SCM) are described. The SCM developed at a constant rate of $1.4 \text{ mg chl } a \text{ m}^{-3} \text{ d}^{-1}$, which is equal to a carbon fixation rate of $49.0 \text{ mg C m}^{-3} \text{ d}^{-1}$. The SCM developed at 6 m depth at low irradiance levels ($10\text{--}43.0 \mu\text{E m}^{-2} \text{ s}^{-1}$). Chl *a* concentrations reached up to $23 \text{ mg chl } a \text{ m}^{-3}$ in the centre of the SCM. Growth rates in the SCM were estimated at 0.82 d^{-1} . The water column was only weakly stratified, with nutrients in excess in the whole of the water column. The SCM was relocated vertically to depths below the photic zone by wind-induced advection between the bay and the outer Kattegat. There were indications of a horizontal relocation of the SCM by an internal standing wave. Application of high spatial and temporal resolution made it possible to estimate key SCM parameters, such as growth rates [$\text{mg chl } a \text{ m}^{-3} \text{ d}^{-1}$] and carbon fixation rate [$\text{mg C m}^{-3} \text{ d}^{-1}$], on the basis of chl *a* variations in time and space.

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1. Introduction

Part of biological oceanographic research centres on phytoplankton distributions and primary production. There has, in this respect, been focus on subsurface chlorophyll maxima (SCM) (Cullen 1982, Bjørnsen et al. 1993, Sharples et al. 2001), their dynamics (Kononen et al. 1998, 2003) and maintenance (Takahashi & Hori 1984, Banse 1987). SCM occur in brackish water (Kuosa 1990, Seppälä & Balode 1999), estuaries (Figuerias & Pazos 1991), in the coastal zone (Djurfeldt 1994), shelf areas (Sharples et al. 2001), and in open waters (Odate & Furuya 1998). SCM may contribute significantly to primary production, as shown for the North Sea (Richardson et al. 2000) and Århus Bay (Lund-Hansen et al. 2006). Development of SCM has been related to low light level adaptation (Anderson 1969), decrease in phytoplankton cell settling velocity (Takahashi & Hori 1984), grazing (Kononen et al. 1998), and diapycnal nutrient fluxes (Sharples et al. 2001). A 24-hour time-scale or less is generally applied in SCM studies at a fixed position with the tide as time-scaling factor (Sharples et al. 2001). The scale may be extended to several days (Cullen 1982, Kononen et al. 1998) when more positions are covered within a certain area.

The present study is based on repeated CTD-casts with fluorescence and optical parameters (once a day) for 5 consecutive days at 7 stations along a transect in an estuarine, temperate and shallow-water environment. Questions regarding the development, maintenance, fate and physical-biological interactions of SCM are addressed against this background.

2. Study area, material and methods

The study area is the semi-enclosed Århus Bay, southwest Kattegat, in the transition zone between the high (~ 35) saline North Sea and low (~ 10) saline Baltic Sea (Lund-Hansen et al. 1993, 1996) (Fig. 1). The average depth in the bay is about 14 m, and there are islands and shallow water areas along the southern boundary (Fig. 1). Seven positions located on a 16-km-long transect between deep (~ 45 m) and shallow (~ 12 m) water were chosen for CTD-casts and water sampling with a horizontal distance of 2.5 km between positions (Fig. 1). All positions were measured 5 times on 11, 12, 13, 14 and 15 March 2002, and CTD-casts were carried out between 10:00 and 14:00 hrs (local time). The GMI-CTD probe (Geological Marine Instrumentation – Denmark) measured conductivity (salinity), temperature, depth and fluorescence with a vertical resolution of 0.2 m. Depth and scalar irradiance were measured by a second CTD equipped with a LICOR (Li-193SA) sensor at depth intervals of 0.1 m. The water was sampled with a 5-litre Niskin bottle lowered to the sampling depth and released by

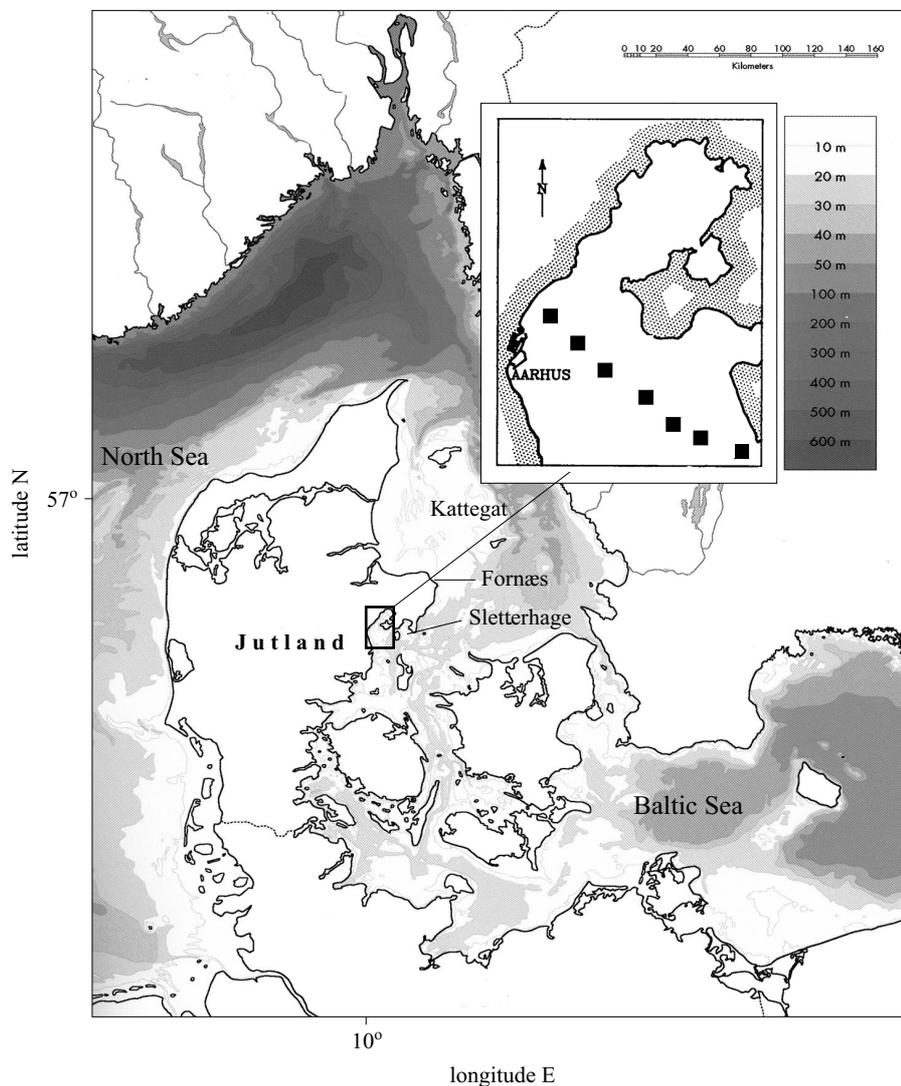


Fig. 1. Study area showing sampling positions

a messenger. *Chl a* concentrations were determined by filtering (Whatman GF/F) two litres of water onboard; the filters were stored in glass vials in 96% ethanol in the freezer. The samples were centrifuged in the laboratory and *chl a* concentrations were determined by spectrophotometer analyses following Strickland & Parsons (1972). The calibration between *chl a* concentrations [mg m^{-3}] and the CTD mounted fluorometer was highly positive and significant ($r^2 = 0.82$, $p < 0.001$). Photosynthetically active radiation (PAR) was measured with a LICOR (Li-191SA) sensor placed on a meteorological mast located about 4 km west of position 7 at Aarhus

University. Data on wind direction and speed were also obtained from the mast. Nutrient concentrations were sampled by the Århus County at the position 56°09.10'N, 10°19.20'E, about two kilometres northwest of position 5 in the present study area, and analyses were carried out following standard procedures (Grasshoff et al. 1999).

3. Results

3.1. The spring bloom sub-surface chl *a* maximum

Density [kg m^{-3}] and chl *a* [mg m^{-3}] isopleths for each period (day) of CTD-casts were plotted (Fig. 2a); the vertical lines in the density isopleth indicate the measurement positions (Fig. 2f). Comparison of chl *a* isopleths shows that chl *a* concentrations gradually increase from about 5–7 to about 19–20 $\text{mg chl } a \text{ m}^{-3}$ at mid-depth between 11 and 13 March (Fig. 2a–e). The thick line (chl *a* isoline) in the chl *a* isopleths is the 16.0 $\text{mg chl } a \text{ m}^{-3}$ isoline (Fig. 2a–e). The chl *a* concentration reaches up to 22 $\text{mg chl } a \text{ m}^{-3}$ in the centre of the chl *a* patch. However, chl *a* concentrations were clearly lower above and below the area enclosed by the 16.0 $\text{mg chl } a \text{ m}^{-3}$ isoline, whereby a sub-surface chlorophyll maximum (SCM) is established (Cullen & Eppley 1981). The expansion of the 16.0 $\text{mg chl } a \text{ m}^{-3}$ chl *a* isoline is a strong indication of bloom development (Fig. 2a–e). The rate of change in chl *a* – $\partial C/\partial t$ – is constant at 1.4 $\text{mg chl } a \text{ m}^{-3} \text{ d}^{-1}$ between 11 and 14 March (Fig. 3). The figure shows the average chl *a* concentrations for all positions on each day of the study period. The surface area delineated by the 16.0 $\text{mg chl } a \text{ m}^{-3}$ chl *a* isoline increases from 2.2 on 13 March to 5.1 on 14 March; 12 March is taken to be unit 1. The increase in surface area is described by the exponential function $y = Ae^{0.82x}$ ($r^2 = 0.99$; $n = 4$), where 0.82 d^{-1} is here termed the SCM chl *a* patch growth rate. The rate takes account of diffusion, growth, grazing and settling related changes in chl *a* concentrations. Advection is not considered here: exchange between the Kattegat and the bay was restricted, as inferred from the very small changes in salinity between 11 and 14 March (see later). The time of year, the constant rate of increase in chl *a* concentrations, and the high chl *a* concentrations in combination indicated that it was a spring bloom. This statement is supported by Århus Bay monitoring data, which show that spring blooms are the most frequent in late February and early March (Århus County 2003).

3.2. Photosynthetically active radiation (PAR) and nutrients

The sky is quite clear on 12, 14 and 15 March, with maximum PAR values between 1000–1230 $\mu\text{E m}^{-2} \text{ s}^{-1}$ and partly overcast on 11 and 13

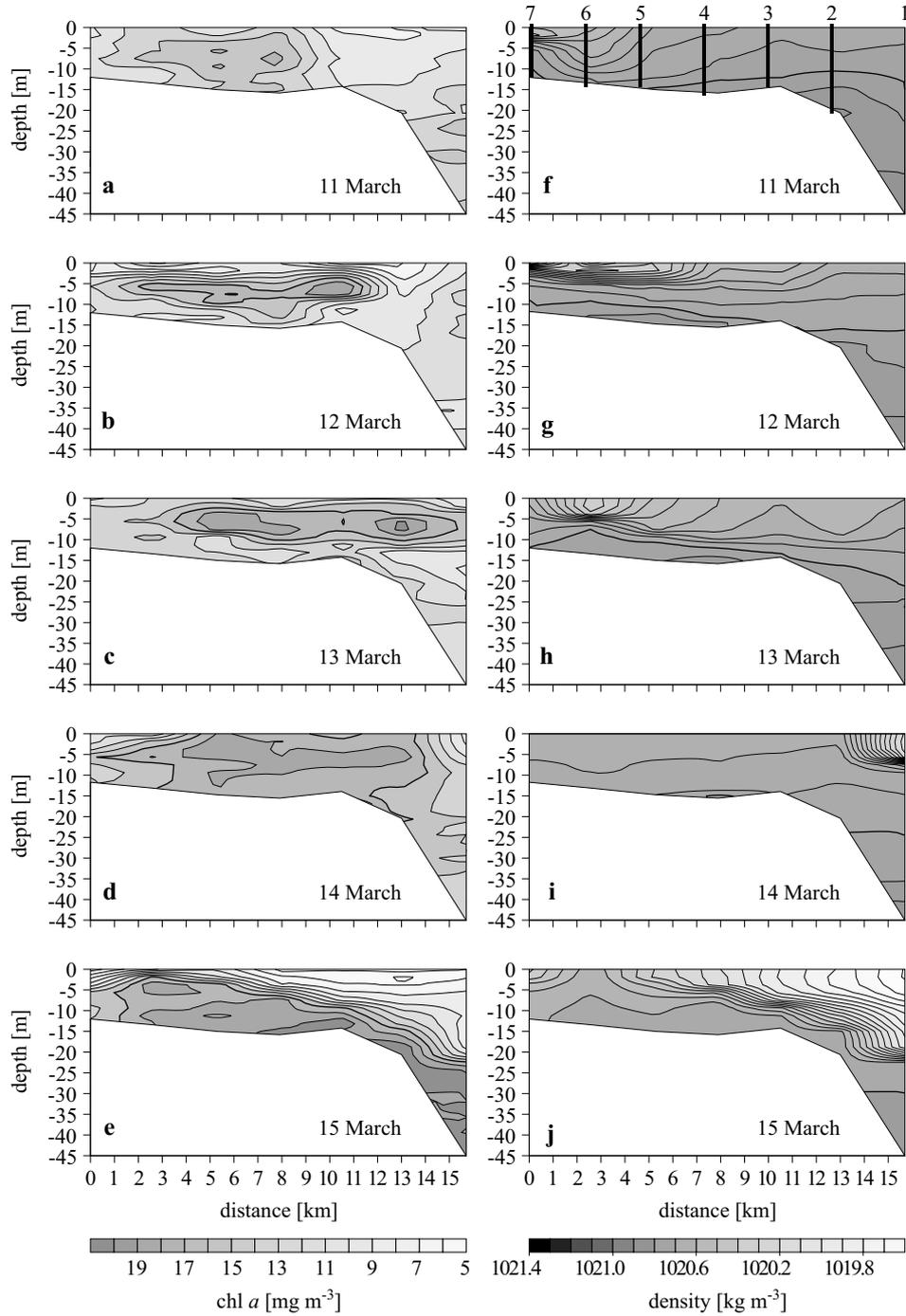


Fig. 2. Chl *a* [mg m^{-3}] and density [kg m^{-3}] isopleths: 11 (a-f), 12 (b-g), 13 (c-h), 14 (d-i) and 15 March (e-j)

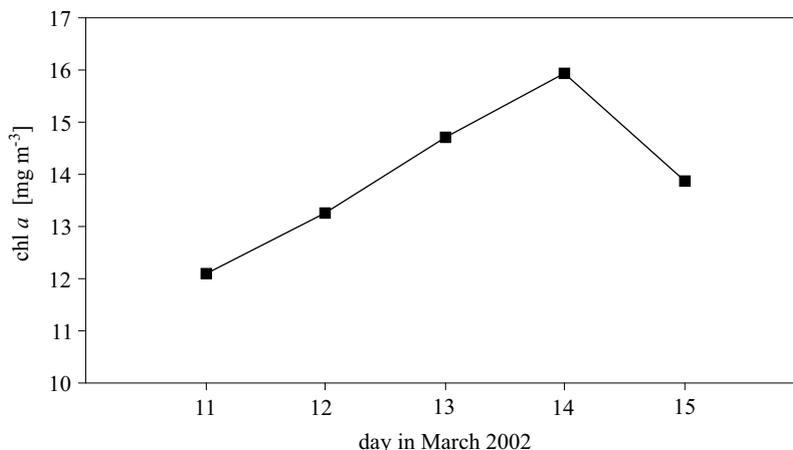


Fig. 3. Depth-averaged chl *a* [mg m⁻³] at all positions from 11 to 15 March

March, as shown by the PAR time-series (Fig. 4a), which are typical values for time of year and latitude (Walsby 1997). The constant increase in chl *a* concentrations (Fig. 3) demonstrates that PAR intensities are able to sustain SCM photosynthesis, although this maximum chl *a* concentration occurs around 6 m depth (Fig. 2). The average irradiance at 6 m depth for positions 3, 4, and 5 is $7.8\% \pm 4.0$ (SD) of surface values for 11–14 March. The 7.8% is equal to the absolute scalar irradiance 24.0 ± 11.0 (SD) $\mu\text{E m}^{-2} \text{s}^{-1}$ at an average irradiance just below the surface (~ 0.1 m) of $307.7 \mu\text{E m}^{-2} \text{s}^{-1}$. The combination of low irradiance levels at 6 m depth and high rates of changes in chl *a* indicates adaptation to low irradiance levels. The typical vertical distribution of chl *a* m⁻³ and scalar irradiance, given as a percentage of surface values, shows a clear chl *a* maximum at 6.5 m at position 3 on 12 March (Fig. 5). Passing clouds cause the irradiance signal to vary between the surface and 2 m during the cast. The average $K_0(\text{PAR})$ for all 7 positions on 13 March is 0.378 m^{-1} , with a maximum of 0.402 m^{-1} and a minimum of 0.351 m^{-1} . The scalar diffuse attenuation coefficient $K_0(\text{PAR})$ is calculated from $I = I_0 e^{-K_0(\text{PAR})z}$, where I_0 is the surface irradiance [$\mu\text{E m}^{-2} \text{s}^{-1}$] and I the irradiance at depth z [m] (Kirk 1994). $K_0(\text{PAR})$ increases by 55%, from 0.227 m^{-1} to 0.351 m^{-1} , between 11 and 13 March at position 3, which emphasizes the short time-scale of significant changes in optical conditions. This change is probably caused by an increase of $2.7 \text{ mg chl } a \text{ m}^{-3}$ in chl *a* concentrations between 11 and 13 March at this position.

Nutrients ($\text{NO}_2 + \text{NO}_3$, $\text{NH}_3 + \text{NH}_4$, PO_4 , SiO_2) were sampled concurrently with the 11 March CTD-casts, the first day of sampling: concentrations are very similar in the surface layer (1 m) and at the bottom (15 m) (Fig. 6). These mid-March concentrations are lower than the winter

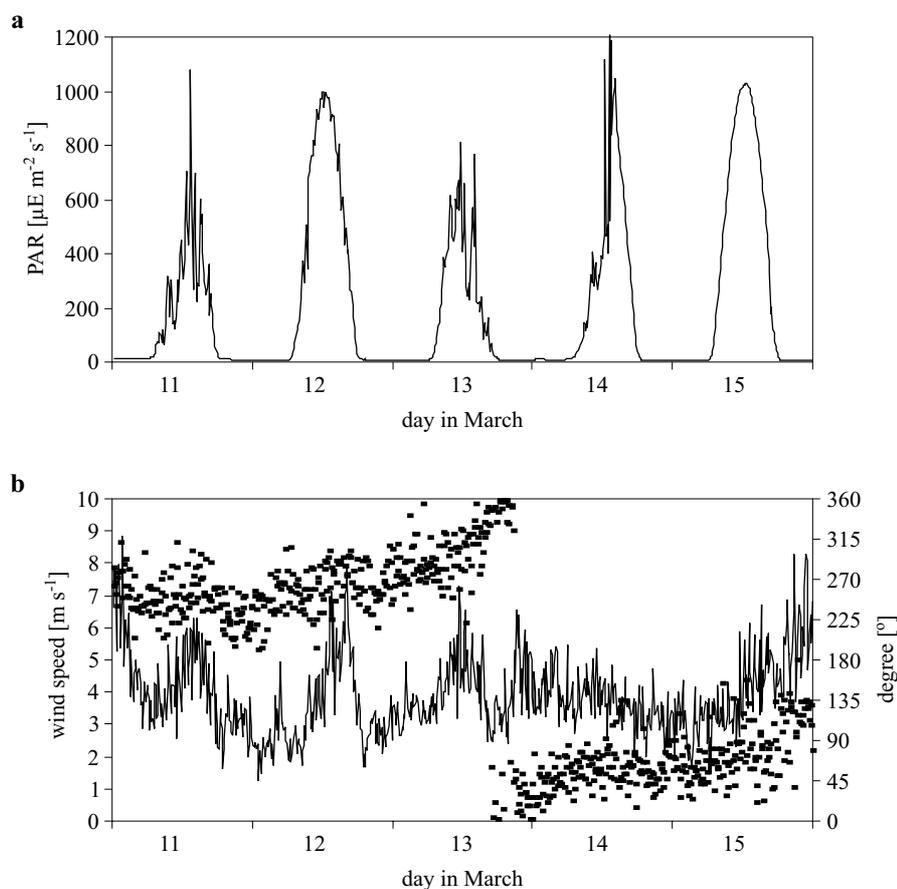


Fig. 4. PAR [$\mu\text{E m}^{-2} \text{s}^{-1}$] from 11 to 15 March (a), and wind speed [m s^{-1}] (solid line) and direction (black square) (b)

concentrations ($\sim 10 \mu\text{M NO}_2 + \text{NO}_3$) and higher than the summer concentrations ($\sim 1\text{--}0.5 \mu\text{M NO}_2 + \text{NO}_3$) in the surface waters (Århus County 2003). This is a strong indication that nutrients were in excess at the beginning of the study period.

3.3. Displacements of the SCM – internal standing wave and advection

The SCM patch is displaced about 2–3 km horizontally on 13 March as compared to 12 and 14 March, when the patch is located on the shelf (Fig. 2b–d). The density field shows, in comparison, an upward displacement of the 1021.3 kg m^{-3} isopycnal (thick line), which commenced on 11 March and continued through 12 and 13 March (Fig. 2f–j). The isopycnal displacement is presumably an oscillation, with 11–13 March

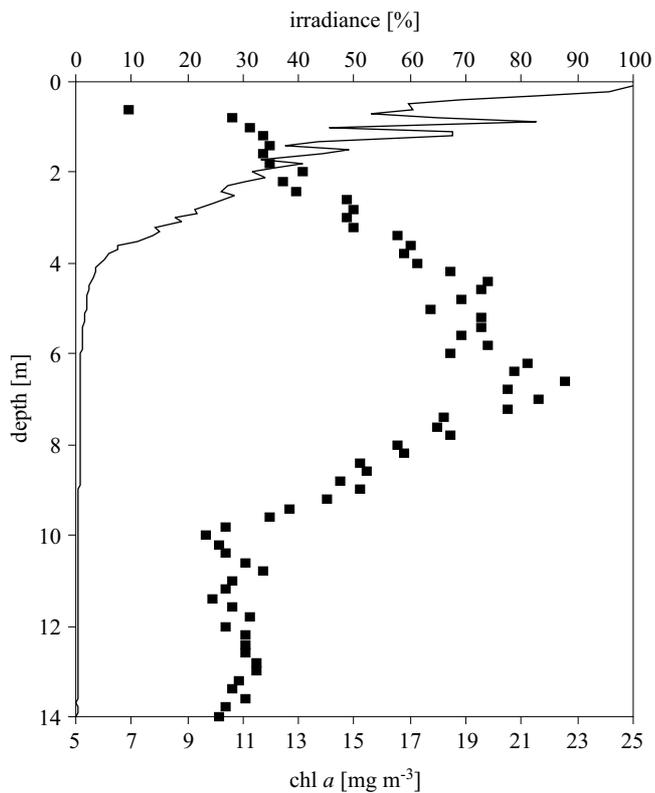


Fig. 5. Vertical distribution of irradiance [%] and chl *a* [mg m^{-3}] at position 3 on 12 March

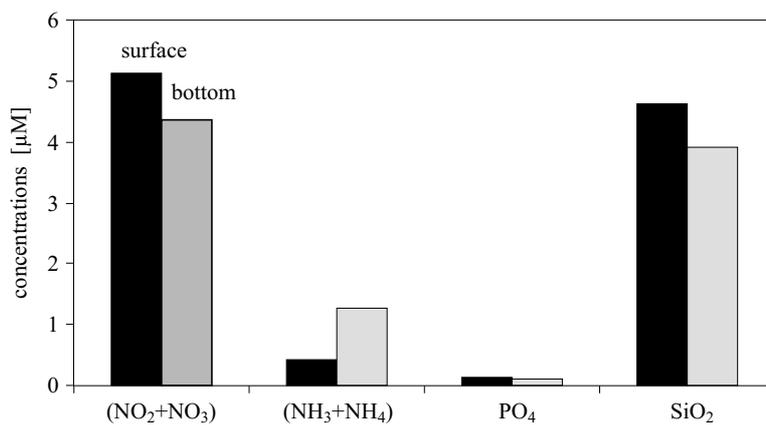


Fig. 6. Surface (1 m) (black) and bottom (~15 m) (grey) nutrient concentrations [μM] on 11 March

constituting about half a period, whereby one period is equal to about 4 days. This corresponds approximately to a calculated period of $T = 3.3$ days, which is the time-scale or period T of an internal standing wave:

$$T = 2L/\sqrt{(\delta_2 - \delta_1)/\delta_2} g (h_1 \times h_2)/(h_1 + h_2), \quad (1)$$

where δ_1 and h_1 are the density [kg m^{-3}] and thickness [m] of the upper (1) and lower (2) layers, g is the acceleration due to gravity [m s^{-2}], and L is the basin width [m] (Pedersen 1986). The 12 March layer depths and densities were applied in (1). The second incidence of relocation was an inflow of low saline surface waters on 15 March that actually commenced on 14 March; it was observed as a change in the surface water density field (Fig. 2i). The surface inflow is balanced by an outflow of dense bottom water, whereby the SCM is replaced by advection (Fig. 2e). It is, on the other hand, unknown whether the entire SCM was replaced or if some part of it remained inside the bay, as there are no CTD-data for the following day. However, the major part of the SCM is relocated to larger depths below the photic zone of about 14 m, where photosynthesis could no longer be maintained. Concentrations of chl *a* in the replacement water were around 6 mg chl *a* m^{-3} , a reduction of about 200% (Fig. 2e). The extended advection is related to the change in dominant wind direction from west to northeast during 13 March (Fig. 4b). This direction enhances the outflow of low saline surface waters from the Baltic Sea (Lund-Hansen et al. 1996, Gustafsson 2000). This tallies with the reduction in surface salinity of about 2 PSU at position 1 between 14 and 15 March (Fig. 2 i-j).

4. Discussion

4.1. Development of the subsurface chlorophyll maximum (SCM)

An SCM is defined as a maximum of chl *a* (i.e. phytoplankton biomass) at a certain depth below the surface (Cullen 1982) and develops by in situ photosynthesis or by intrusion of water with intermediate density and high phytoplankton concentrations. An intrusion has recently been observed in the Little Belt (southwest Kattegat), where peak concentrations reached up to 40 mg chl *a* m^{-3} (Lund-Hansen & Vang 2004). However, development of the present SCM was clearly related to in situ photosynthesis, as there were no significant changes in salinity, temperature or density structure around mid-depths between 11 and 14 March (Fig. 2a-i). The constant increase in chl *a* excludes the possibility that the development of the SCM was related to grazing or accumulation of phytoplankton cells in the pycnocline (Takahashi & Hori 1984) in the absence of a strong pycnocline. The obtained SCM path growth rate of 0.82 d^{-1} is comparable to a net phytoplankton growth

rate of 1.08 d^{-1} applied in the modelling of SCM (Sharples & Tett 1994), and to the phytoplankton doubling rates of 0.85 d^{-1} observed in some SCM (Cullen & Epply 1981). The rate of change in chl *a* concentrations reached an average of $1.4 \text{ mg chl } a \text{ m}^{-3} \text{ d}^{-1}$ covering all positions between 11 and 14 March (Fig. 3). This rate is equal to a carbon fixation rate of $49.0 \text{ mg C m}^{-3} \text{ d}^{-1}$ with a C:Chl *a* ratio of 35 (Bjørnsen et al. 1993), which is comparable to primary production rates measured in the Kattegat (Nielsen et al. 1994). The average chl *a* rate of change of $1.4 \text{ mg chl } a \text{ m}^{-3} \text{ d}^{-1}$ during 11–14 March was about twice the average rate obtained in a Gulf of Finland SCM (Kononen et al. 1998), which most likely reflects the time of year, i.e. the spring bloom in March in Århus Bay and late summer (July–August) conditions in the Gulf of Finland. Nevertheless, maximum chl *a* concentrations at the SCM centre of $23 \text{ mg chl } a \text{ m}^{-3}$ are comparable to chl *a* SCM figures obtained in similar estuarine environments, such as the Gulf of Riga (Seppälä & Balode 1999), San Francisco Bay (Huzzey & Cloern 1990), and Spanish rias (Figueiras & Pazos 1991). The present SCM maximum chl *a* concentrations of $23 \text{ mg chl } a \text{ m}^{-3}$ is higher than the average chl *a* concentrations in the bay of $5 \text{ mg chl } a \text{ m}^{-3}$ by a factor of about 6 (Århus County 2003). This indicates that the frequency of such high chl *a* concentrations in the bay is low.

Several studies have shown that SCM occur in the vicinity of a strong pycnocline, and hence also of a strong nutricline, with surface waters depleted of nutrients and high concentrations in the waters below, where the diapycnal transport of nutrients maintains the SCM (e.g. Bjørnsen et al. 1993, Kononen et al. 1998, 2003, Sharples et al. 2001). However, nutrients were initially in excess in both the upper and lower part of the water column in the present study, but the SCM still developed at a low (24.0 ± 11.0 (SD)) $\mu\text{E m}^{-2} \text{ s}^{-1}$ irradiance level at 6 m depth in the weakly stratified water column. The occurrence of SCM at low ($< 50 \mu\text{E m}^{-2} \text{ s}^{-1}$) irradiance levels has been observed in several studies (e.g. Cox et al. 1982, Cullen 1982, Vandeveldt et al. 1987, Furuya 1990). The present irradiance level ($\sim 24.0 \mu\text{E m}^{-2} \text{ s}^{-1}$) is about 10 times lower than the 200–300 $\mu\text{E m}^{-2} \text{ s}^{-1}$ obtained as P_{max} in recent (March 2005) C-14 incubations in the bay (L. C. Lund-Hansen, unpublished data). It has been shown that photosynthesis can be maintained even at $16 \mu\text{E m}^{-2} \text{ s}^{-1}$ (Alpine & Cloern 1988), but the fact that SCM actually developed at the observed low irradiance levels in a weakly stratified water column calls for further studies. However, it is emphasized that the isopleths (Fig. 2) are still only a two-dimensional representation of the SCM, which is a three-dimensional feature; the design of new sampling programmes will have to take this into consideration.

4.2. Physical and biological interactions

There was a clear displacement of the SCM by advection and indications of horizontal SCM displacement by an internal standing wave. Only the first instance was expected to have any biological effects, as relocation of the SCM to a depth below the photic zone would inhibit any photosynthesis in the first place. Secondly, a large part of the organic matter produced in the water column is thereby no longer available for the cycling of particulate bound nutrients in the bay (Jørgensen 1996, Lund-Hansen 2004). The loss of organic matter from the bay might, on the other hand, also reduce the periods of anoxia related to the oxygen-consuming degradation of this matter frequently observed in the bay (Jørgensen 1996). Advection between the bay and the Kattegat was indicated by a change in surface salinities and thus densities (Fig. 2g). The high salinity range of about 12 in the surface waters and about 10 in the bottom waters demonstrates that advection between the Kattegat and the bay is considerable (Lund-Hansen et al. 1993, 1996). The importance of advection in the bay was emphasized in a study showing that oxygen-depleted bottom water was replaced by oxygen-rich water by simple advection (Skyum et al. 1992). However, the relocation also emphasized that the fate of a bloom is not ultimately linked to the simple settling of the organic matter below its site of production (Olesen & Lundsgaard 1993, Høgländer et al. 2004), but that advection may play a fundamental role in the cycling of elements and substances.

Acknowledgements

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