

**Modelling the dynamics of harmful blooms of *Chattonella* sp. in
the Skagerrak and the Kattegat**

Kari Eilola^{a,*}, Elin Almroth^a, Lars Johan Naustvoll^b, Per Andersen^c and Bengt Karlson^a

^a *Swedish Meteorological and Hydrological Institute, SWEDEN*

^b *Institute of Marine Research, Flødevigen Marine Research Station, Norway*

^c *Bio/consult A/S, Denmark*

Abstract

The presentation shows observations, satellite images and model results describing the growth and spreading of *Chattonella* sp. flagellates in the Skagerrak and the Kattegat. *Chattonella* sp. is a harmful alga that may cause fish kills due to damage of the gills. Calm weather, stable water column stratification, and low turbulence may facilitate the onset of a *Chattonella* bloom. Results from the three-dimensional hydrodynamical model HIROMB (High Resolution Operational Model for the Baltic Sea) are used as forcing of a transport model that computes vertical and horizontal transports of chemical and biological compounds. A modified version of the Swedish Coastal and Ocean Biogeochemical model (SCOBI) is used to describe the temporal evolution of the phytoplankton spring blooms in the year 2001 when *Chattonella* was abundant and 2002 when only small amounts of *Chattonella* were observed. A comparison with satellite images and cell counts indicates that the model captures the main transport patterns of phytoplankton in the surface layers of the offshore areas. The *Chattonella* bloom of the model starts in the quite shallow parts of the western Kattegat and in the stratified coastal areas of the northern Skagerrak. The coastal waters near the river Göta Älv of Sweden also indicate a tendency of an increased occurrence of *Chattonella*. *Chattonella* is observed in the model during both years but the occurrence of *Chattonella* is more significant in the year 2001 than in 2002.

Keywords: Algal blooms; *Chattonella* sp.; Diatoms; HAB; Marine ecology; Modelling; North Sea; Skagerrak; Kattegat

*Contact author: Kari Eilola: Swedish Meteorological and Hydrological Institute,
Oceanografiska laboratoriet, Nya varvet 31, 426 71 VÄSTRA FRÖLUNDA, SWEDEN
[Tel.: +46 31 751 8963; fax: +46 31 751 8980; E-mail: kari.eilola@smhi.se]*

1. Introduction

The life cycles and dynamics of some harmful species of algae forming large scale high biomass blooms in some European waters were studied within the multidisciplinary EU-project HABILE (Harmful Algal Bloom Initiation and Prediction in Large European Marine Ecosystems). The chosen species of primary focus of the North Sea and the Skagerrak-Kattegat area (Fig. 1) was *Chattonella* sp. which formed large scale and high biomass blooms in the eastern North Sea in 1998 and 2000 and in the Kattegat in 2001. The blooms of 1998 and 2001 were observed also at the Swedish west coast and in the coastal waters of southern Norway where the blooms caused fish kills that led to economical losses within the aquaculture sector. The fish kills were likely caused by suffocation due to clogging of the gills. The phytoplankton genus *Chattonella* belongs to the class Raphidophyceae that is part of the division Heterokontophyta. In the genus *Chattonella* several species are able to form high biomass blooms and some species have caused large fish mortality of both wild and caged fish (Karlson and Andersson, 2003). For a long period, since about 1972, these problems have mainly been restricted to Japanese waters (Okaichi, 1989) but are now causing increasing problems also in other parts around the world (e.g. Marshall and Hallegraeff, 1999; Peperzak, 2003). Other important harmful algal bloom species that may cause nuisance in the North Sea-Skagerrak-Kattegat region are for instance algae that make shellfish toxic to humans (e.g. the genera *Alexandrium*, *Dinophysis* and *Pseudo-nitzschia*) and algae that are toxic to fish and other organisms (e.g. *Chrysochromulina polylepis*).

Chattonella has been observed in low concentrations at the Swedish west coast since 1993 (Mats Kuylenstierna, Kristineberg Marine Research Station, Sweden, pers. com.) though no harmful effects have been reported prior to 1998. *Chattonella* sp. has its main blooming period in the period March to May in the North Sea-Skagerrak-Kattegat region at salinities above 15 and at temperatures below 13 °C.

The *Chattonella*-bloom in 1998 was first observed in the North Sea at the Danish west coast, and later on in spring also in the Skagerrak and the Kattegat at the Swedish and Norwegian coasts. The *Chattonella*-bloom in 2000 was also first observed at the Danish west coast but this bloom did not appear in the Swedish or Norwegian waters (Karlson and Andersson, 2003; Andersen, 2004). The *Chattonella*-bloom in 2001 initiated in early March at quite low water temperatures (1-5 °C) before the ending of the primary diatom spring bloom, earlier than the previous blooms that started in April 1998 and 2000. The *Chattonella*-bloom in 2001 was first observed in the Kattegat and later on in spring also in the Skagerrak. At the Swedish coastal station Åstol (Fig. 1) *Chattonella* showed increasing concentrations (0-10m), from about 10^5

cells/l in the beginning of March to more than 10^6 cells/l at the end of March (Fig. 2). During this period the diatom bloom was interrupted while silicate concentrations still were rather high in the water. In autumn 2000 and winter-spring 2001 the precipitation of the catchment area of Lake Vänern was higher than normal. During spring 2001 the flow in the river Göta Älv, the major river on the Swedish west coast, was nearly three times higher than the average, indicating extreme conditions. In order to investigate possible effects on the marine environment, weekly sampling at four locations was performed by SMHI. The investigation presented by Karlson and Anderson (2003) concluded however that the effects of the flooding were less than expected and that no connection to the *Chattonella* bloom was detected from the measurements. The *Chattonella* was detected in Skagerrak and Kattegat also in 2002 but the concentrations were much lower than in 2001.

A comprehensive guide to harmful marine microalgae is available from UNESCO (Hallegraeff et al., 2003) where the different species of harmful Raphidophyceae are described and discussed by Hallegraeff and Hara (2003). The specific environmental conditions favouring the bloom of *Chattonella* are qualitatively fairly well described by Andersen (2004). It is e.g. suggested that reduced grazing pressure on *Chattonella* may be a pre-requisite for the formation of high biomass blooms as compared to other smaller species of flagellates. It also seems that calm weather, stable water column stratification, and low turbulence may facilitate the onset of a *Chattonella* bloom.

The present paper presents some results from SMHI models, and from observations and satellite images contributed to the HABILE project (<http://www.nersc.no/HABILE>).

2. Material and Methods

2.1. The ecosystem model

A modified version of the Swedish Coastal and Ocean Biogeochemical model, SCOBI (Marmefelt et al., 2000) is used. The SCOBI module computes changes of the biogeochemical properties in the water and sediment in each grid point at each time step of the physical model. The SCOBI module was tested and used on a one-dimensional case at Släggö on the Swedish west coast and thereafter applied to the three dimensional case in the Skagerrak and the Kattegat without any changes of the set-up.

SCOBI is a process-oriented model that includes marine nitrogen, phosphorous and oxygen dynamics. It contains 9 prognostic pelagic variables: nitrate, ammonium, phosphate, autotrophs, zooplankton, detritus, and oxygen. For the present study we have divided the autotrophs into three variables representing the different characteristics of diatoms, summer

flagellates and *Chattonella* (Almroth and Eilola, 2004). Silicate was not included in the model at this stage since observations indicated that the *Chattonella* bloom in March 2001 started before silicate became the limiting nutrient of diatoms. The sediment layer in the model contains nutrients in the form of benthic nitrogen and phosphorus. The vertical light attenuation computed by the model depends on a background attenuation and attenuation due to varying concentrations of phytoplankton. Carbon (*C*) is used as the constituent representing detritus and zooplankton. Phytoplankton is represented by chlorophyll (*Chl*) according to a constant carbon to chlorophyll ratio *C:Chl*. Nitrogen (*N*) and phosphorus (*P*) content of phytoplankton, zooplankton and detritus are obtained from the Redfield molar ratio (*C:N:P=106:16:1*).

2.2. Plankton characteristics

The aim was to improve our understanding about *Chattonella* blooms in terms of physical and ecological processes found in our models and to keep the modification of the ecosystem model as simple as possible. The characteristics of diatoms, *Chattonella* and summer flagellates were added to the model in a similar way as in the original SCOBI model. The sinking speed of *Chattonella* and summer flagellates was assumed zero. Hence we neglected possible upward swimming performance of these plankton groups. The growth rate of diatoms and summer flagellates in the model obtained characteristics similar to the diatoms and flagellates described by Savchuk (2002). The maximum growth rate at 0 °C of the flagellates was modified to roughly describe characteristics of summer flagellates. Salinity and temperature dependence of the growth rate of *Chattonella* was taken from Yamaguchi et al. (1997). Since this formulae is valid only for temperatures higher than 5 °C, and no other information is available to the authors knowledge, we used a constant rate below 5 °C. The description of light limitation, mortality and grazing pressure was kept the same for all plankton groups in the experiments, but the nutrient limitation factors differs by their different half saturation constants. The specific characteristics of the different plankton groups used in the model are described in Table 1. The growth rate is in the model computed for continuous temperatures but is here only shown for discrete temperatures, 0°C, 10°C and 20°C.

Table 1: Characteristics of the modelled plankton

	Diatoms	Summer flagellates	Chattonella
Growth (day^{-1})	1.3/ 2.5/ 4.6	0.5/ 1.7/ 5.5	0.9/ 1.1/ 1.3
Temp= $0^\circ/ 10^\circ/ 20^\circ$			
Preferential grazing	0.3	0.3	0.3
Mortality (day^{-1})	0.05	0.05	0.05
Sinking (m day^{-1})	0.5	0.0	0.0
Half saturation constants PO ₄ /NO ₃ /NH ₄ (mmol m^{-3})	0.15/1.0/1.0	0.05/0.5/0.5	0.1/0.5/0.5

2.3. Three-dimensional model

The hydrodynamical model HIROMB (High Resolution Operational Model for the Baltic Sea) is a 3-dimensional baroclinic model with a fully coupled sea ice module of the North Sea and the Baltic Sea. For the application presented here, the system is set up on a nested grid, where a 12 nm grid covers the whole area, while the Skagerrak, the Kattegat, the Belt Sea and the Baltic Sea are covered with a 3 nm grid. Supplemented to the system is a storm surge model for the NE Atlantic. The vertical grid resolution of the surface layer of the HIROMB model is 4 m down to 12 m depth, and 6 m from 12 m to 30 m depth. The vertical grid resolution continues to grow coarser with increasing depth. A full description of the HIROMB model equations may be found in Kleine (1994) or Funkquist and Kleine (manuscript) and the parallelization of the HIROMB model is described by Wilhelmsson (2002).

In its updated version of HIROMB, the vertical eddy viscosity is computed using a buoyancy-extended k - ω model, in which conservation equations are solved for the turbulent kinetic energy (k) and the inverse time scale of the turbulence (ω), see Umlauf et al. (2003). The stability functions used by the turbulence model are those presented by Axell and Liungman (2001). Included in the turbulence model are parameterizations of internal wave energy and Langmuir circulations according to Axell (2002). Finally, the structure of the turbulence model is based on the GOTM model (general ocean turbulence model) (Burchard et al., 1999).

A data assimilation scheme has been implemented into the HIROMB ocean modelling system. The method is the so-called Method of Successive Corrections (SCM), described in e.g. Daley (1991). The model outcome has been compared with observational data from two buoy stations, one in the Kattegat and one in the Baltic, and from a hydrographic station in the Baltic (Andersson et al., 2004). The data used in the data assimilation scheme are vertical

profiles of salinity and temperature from the Swedish national database SHARK (Svenskt Havsarkiv). The database contain international oceanographic data, and data from Swedish research vessels which are available approximately every month at certain standard stations in the Baltic Sea, the Kattegat, and the Skagerrak.

2.4. Three-dimensional model forcing

The ECMWF (European Centre for Medium-Range Weather Forecasts) atmospheric model provides HIROMB with sea level pressure, wind at 10 m above surface, air temperature and specific humidity at 2 m above surface and total cloudiness. Climatological annual mean freshwater runoff was used for the HIROMB forcing. Initial conditions were derived from the SHARK database. Computed salinity, temperature, horizontal velocities and the turbulent vertical diffusion exchange coefficient were saved every 6-hour. Cloudiness was saved for the computation of solar radiation in SCOBİ. Air-sea exchange of oxygen is derived in the SCOBİ model from computed oxygen saturation concentrations and wind speed.

The long term average monthly nutrient supply from rivers and diffusive coastal nutrient supplies are mainly based on the data collected by Stålnacke (1996) (BED, Baltic Environmental Database). The organic fractions of phosphorus were added as detritus that implicitly adds organic nitrogen to the model in accordance with the Redfield ratio. The annual average atmospheric total (dry+wet) deposition of reduced and oxidised nitrogen for the year 2000 was taken from the EMEP (Co-operative programme for monitoring and evaluation of the long-range transmission of air pollutants in Europe, <http://www.emep.int>) database with the resolution 50x50 km. The annual average atmospheric deposition of phosphorus estimated by Areskoug (1993) was used. Average annual addition of nutrients from point sources was based on data from PLC4 (HELCOM, 2000). Initial conditions for the nutrients were taken from SHARK. The Skagerrak was initialised with vertically and horizontally homogenous values. The initial conditions of the Kattegat were divided into a homogenous surface layer above 15 m depth and a homogenous lower layer below, due to the large vertical gradient of nutrient concentrations across the halocline separating surface waters from the deeper layers. Primary producers were initialised with constant winter values. No-flux assumptions were used as boundary conditions at the Skagerrak-North Sea boundary, and at the Baltic Sea boundaries in the Belt Sea and the Sound, respectively.

2.5. The physical transport model

The SCOBIM model was run off-line using 6 hourly circulation, mixing and density fields from the HIROMB 3nm model for the years 2001 and 2002 obtained from the HIROMB 3 nm model. The physical transport model computes vertical and horizontal transports of chemical and biological compounds within selected sub-regions of the HIROMB model domain. The time step and the horizontal and vertical grid resolutions of the transport model are the same as used for the HIROMB model.

3. Results and discussion

3.1. Three dimensional model - year 2001

Maps of the results are presented in Fig. 3. The temporal evolution of the model results in general show relatively good agreement with the spatial distribution of chlorophyll as observed from satellite images. The modelled spring bloom starts in the western and southern parts of the Kattegat and continues northward along the Swedish and Norwegian coasts before its spread into the interior of the Skagerrak. A bloom is also initiated in the northern Skagerrak. Diatoms generally dominate the modelled spring bloom but the amount of *Chattonella* becomes significant in some parts of the model area.

The *Chattonella* blooms of the model start in February in the shallow parts of the western Kattegat and in the stratified coastal areas of the northern Skagerrak. The coastal waters near the river Göta Älv of Sweden also indicate a tendency of a *Chattonella* bloom. The major Kattegat bloom is transported into the interior of the Kattegat and to the Swedish coast from the Danish waters. The bloom continues to spread towards north during March. These results are in accordance with the observations from these areas (Fig. 4). The major bloom of the northern parts of the Skagerrak is transported along the Norwegian coast and spreads into the interior of the Skagerrak in February and March.

The temporal evolution of surface layer chlorophyll at four locations (Fig. 5) shows a varying degree of agreement with observations. It seems that the time of the onset of the phytoplankton bloom of the model is approximately a week or two too early at all locations. The cause of this is unclear at present but it is possible that the light attenuation is underestimated. The forcing derived from ECMWF and HIROMB results, as well as the simple initial and boundary conditions applied to the ecosystem model may also influence these results. The climatological freshwater forcing of HIROMB may also have an impact on the model results. The magnitude of the modelled chlorophyll concentrations in early spring is somewhat higher than observations from Anholt, Fladen and the Skagerrak. The chlorophyll concentrations of Åstol and Anholt are underestimated during most of the spring period. The

largest amounts of *Chattonella* chlorophyll are seen in the end of February at Åstol and in mid March in the central Skagerrak. Anholt and Fladen show an increased concentration of *Chattonella* in the end of February and in early March. Åstol also shows a second period of higher *Chattonella* concentrations in early April.

3.2. Three dimensional model - year 2002

Maps of the results are presented in Fig. 6. The temporal evolution of the model results in general show fairly good agreement with the spatial distribution of chlorophyll as observed from satellite images. The outcome from the year 2002 shows many similarities with the results from 2001. The modelled spring bloom starts in the western and southern parts of the Kattegat and continues northward along the Swedish and Norwegian coasts before its spread into the interior of the Skagerrak. A bloom is also initiated in the northern Skagerrak. Diatoms generally dominate the modelled spring bloom but the amount of *Chattonella* becomes rather significant in the western Kattegat and the northern Skagerrak. It seems however that the relative abundance of *Chattonella* is less than observed in the year 2001.

The *Chattonella* bloom of the model starts in February and is transported into the interior of the Kattegat and to the Swedish coast from the Danish waters. The bloom continues to spread towards north during March. The bloom of the northern parts of the Skagerrak is transported along the Norwegian coast and dispersed into the interior of the Skagerrak without creating a further bloom here. These results seem to be in fair accordance with available observations of *Chattonella* (Fig. 4).

The temporal evolution of surface layer chlorophyll at four locations (Fig. 7) indicates that the time of the onset of the phytoplankton bloom of the model seems a week or two too early. Comparison with data is difficult since the amount of data found at these locations from this year is low. All stations show an increased concentration of modelled *Chattonella* in February but no significant tendency towards a larger *Chattonella* bloom is detected.

4. Concluding remarks

The results of the investigations have suggested possible explanations of the onset and spreading of *Chattonella* blooms in the Kattegat and the Skagerrak area. It seems that the ecosystem model includes the major characteristics necessary to explain many of the features observed from the gathered *Chattonella* data. The *Chattonella* bloom of the model starts in the quite shallow parts of the western Kattegat and in the stratified coastal areas of the

northern Skagerrak. The coastal waters near the river Göta Älv of Sweden also indicate a tendency of an increased occurrence of *Chattonella*. *Chattonella* is observed in the model during both years but the occurrence of *Chattonella* is more significant in the year 2001 than in 2002. This might be explained by the weather conditions in February and March which were more favourable for a *Chattonella* bloom in 2001 than in 2002. A period of low winds and strong irradiance induced the diatom spring bloom in the beginning of March in 2001, and from mid March to the end of March an unusually long period with low winds and strong irradiance prevailed (Karlson and Andersson, 2003). This period coincided with the maximum of the *Chattonella* bloom.

The water circulation and transport patterns of the Skagerrak and the Kattegat are important for the spreading of harmful blooms in the area.

There are of course still details that are not well captured by the model and that need to be further investigated to obtain an even better agreement with observations but the results obtained from the investigations done within the HABILE-project are still encouraging for the future modelling work.

The future work will include an extension of the ecological model domain to the North Sea. The plankton characteristics used in the model presented here were based on values found from the literature. Including silicate and using the specific characteristics of species from Skagerrak and Kattegat that were investigated during the HABILE project will also be incorporated to the future work. Using model results and data from a large number of years together with an objective and quantitative evaluation to study the correlation of the model results with observations could give more information about what is well reproduced and what problems the model is still facing. Further investigations using the extensive data sets collected within the HABILE project might be done to study the impact of stratification on the phytoplankton dynamics.

5. Acknowledgement

SMHI and the EU-project HABILE (contract no. EVK3-2001-00087) financed this work. We want to very much acknowledge Lars Edler (SMHI) and Mats Kuylenstierna (Kristineberg Marine Research Station, Sweden) who together with Lars Johan Nausvall and Per Andersen gathered the *Chattonella* data in 2001 and 2002, and Pia Anderson, SMHI for data management and map production, Satellite images copyright NASA SeaWiFS project Team/Orbital imaging Corp processed by the Remote Sensing Group, the Plymouth Marine

Laboratory (PML), United Kingdom. Thanks to Per Pemberton, Lars Axell and Lennart Funkqvist at SMHI for their support during the development of the transport module.

6. References

- Almroth, E., and K. Eilola, 2004, One-dimensional (1-D) algal cycle modelling, HABILE report, contribution to work package 3 (WP3).
- Andersen, P., 2004. HAB dynamics and life cycles. HABILE report, contribution to WP2.
- Andersson, P., Axell, L., Borenäs, K. and Karlsson B., 2004. Data assimilation in the HIROMB model. HABILE report, contribution to WP6.
- Areskoug, H., 1993. Nedfall av kväve och fosfor till Sverige, Östersjön och Västerhavet. Naturvårdsverket, Rapport 4148 (in Swedish).
- Axell, L.B., and Liungman, O., 2001. A one-equation turbulence model for geophysical applications: Comparison with data and the $k-\varepsilon$ model. *Environmental Fluid Mechanics* 1: 71-106.
- Axell, L.B., 2002. Wind-driven internal waves and Langmuir circulations in a numerical ocean model of the southern Baltic Sea. *J. Geophys. Res.*, 107(C11): 3204.
- Burchard, H., Bolding, K. and Villareal, M.R., 1999. GOTM, a general ocean turbulence model. Theory, implementation and test cases. European Commission, Report EUR 18745.
- Daley, R., 1991. *Atmospheric Data Analysis*. Cambridge Atmospheric and Space Science Series, Cambridge University Press, Cambridge.
- Funkquist, L., and E. Kleine, manuscript, An introduction to HIROMB, an operational baroclinic model for the Baltic Sea.
- Hallegraeff, G.M., Anderson, D.M. and Cembella A.D., 2003. *Manual on Harmful Marine Microalgae*. UNESCO, Paris.
- Hallegraeff, G.M., and Hara Y., 2003, Taxonomy of harmful marine raphidophytes. In: Hallegraeff, G.M., Anderson, D.M. and Cembella, A.D., (Eds.), *Manual on Harmful Marine Microalgae*. UNESCO, Paris, pp. 511-522.
- HELCOM, 2000. The fourth Baltic Sea pollution load compilation (PLC-4). *Balt. Sea environ. Proc.*, 93.
- Karlson, B., and Andersson, L., 2003. The *Chattonella*-bloom in year 2001 and effects of high freshwater input from river Göta Älv to the Kattegat-Skagerrak area. *SMHI Reports Oceanography*, No 32.
- Kleine, E., 1994. *Das operationelle Modell des BSH für Nordsee und Ostsee, Konzeption und Übersicht*. Bundesamt für Seeschifffahrt und Hydrographie, Hamburg (in German).

- Marmefelt, E., Håkansson, B., Erichsen, A.C. and Sehestad-Hanses, I., 2000. Development of an Ecological Model System for the Kattegat and the Southern Baltic. Final Report to the Nordic Councils of Ministers, SMHI Reports Oceanography, No. 29.
- Marshall, J.A., and Hallegraeff, G. M., 1999. Comparative ecophysiology of the harmful alga *Chattonella marina* (Raphidophyceae) from South Australian and Japanese waters. *J. Plankton Res.*, 21 (10): 1809-1822.
- Peperzak, L., 2003. Climate change and harmful algal blooms in the North Sea. *Acta Oecol.*, 24: 139-144.
- Okaichi, T., 1989. Red tides: Biology, environmental science, and toxicology. In: Okaichi, T., Anderson, D.M., and Nemoto, T. (Eds.), *Red tide problems in the Seto Inland Sea, Japan*. Elsevier, New York, pp. 137-142.
- Savchuk, O., 2002. Nutrient biogeochemical cycles in the Gulf of Riga: Scaling up field studies with a mathematical model. *J. Mar. Syst.* 32: 253-280.
- Stålnacke, P., 1996. Nutrient loads to the Baltic Sea. Ph.D Thesis, ISBN 91-7871-829-5, Dept. of water and environmental studies, Linköping University, Sweden.
- Umlauf, L., Burchard, H., and Hutter, K., 2003. Extending the $k-\omega$ turbulence model towards oceanic applications. *Ocean Modelling*, 5: 195-218.
- Wilhelmsson, T., 2002. Parallelization of the HIROMB ocean model. Liceantiate thesis, ISBN 91-7283-296-7, Royal institute of technology, Stockholm, Sweden.
- Yamaguchi, M., Itagukura, S., Nagasaki, K., Matsuyama, Y., Uchida, T., and Imai, I., 1997. Effects of temperature and salinity on the growth of the red tide flagellates *Heterocapsa c.* (Dinophyceae) and *Chattonella v.* (Raphidophyceae). *J. Plankton Res.*, 19 (8): 1167-1174.

7. Figures

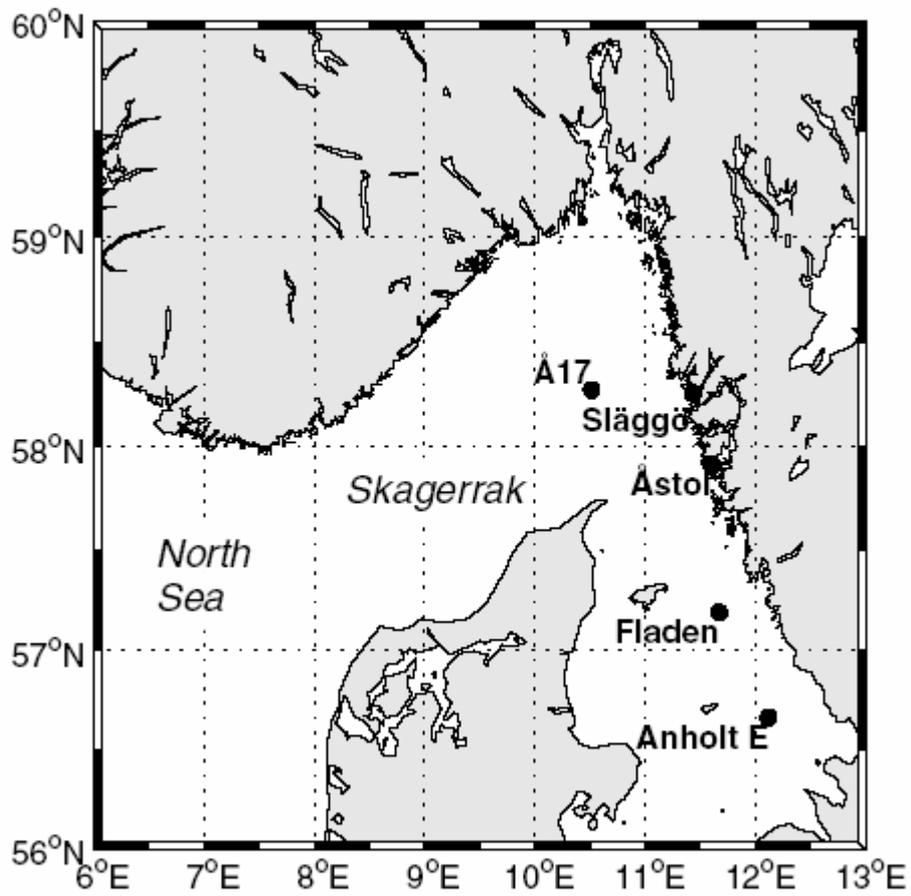


Fig. 1. Map of the Kattegat and the Skagerrak area including sampling stations used for model evaluation.

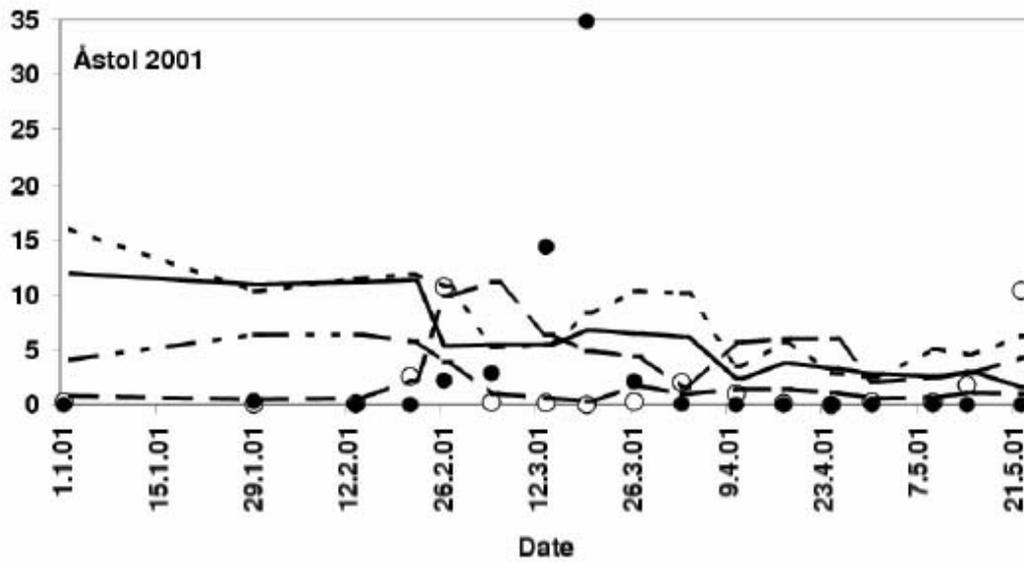


Fig. 2. Observations from Åstol in spring 2001. Black dots indicate *Chattonella* ($10^5 \text{ cells l}^{-1}$, 0-10 m) and open circles diatoms ($10^5 \text{ cells l}^{-1}$, 0-10 m). The long-dashed line indicates total surface chlorophyll a (mg m^{-3}). The solid, dotted and the dot-dashed lines indicates surface silicate, nitrate and phosphate (x10), respectively (mmol m^{-3}).

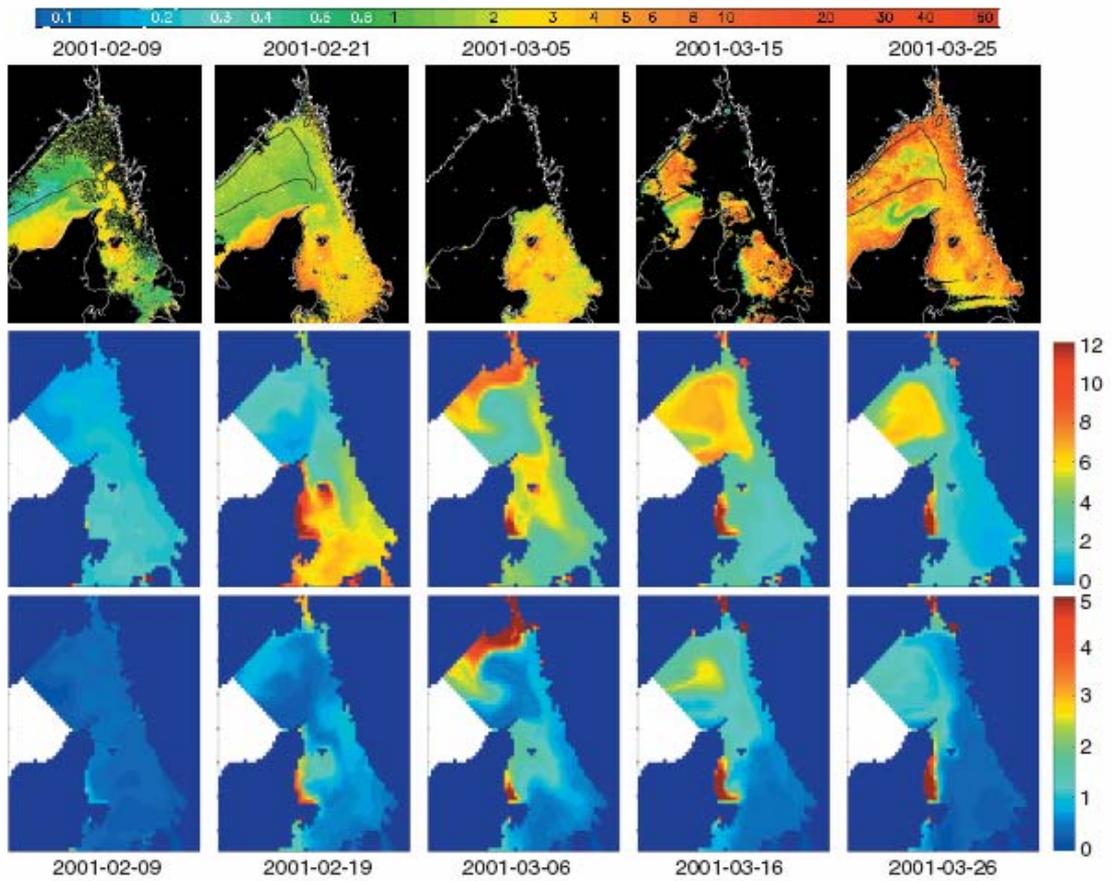


Fig. 3. Surface chlorophyll (mg m^{-3}) in February and March 2001. Satellite images on the upper panel are processed by the Plymouth Marine Laboratory (PML) Remote Sensing Group. Satellite image colour bar and dates above figure. Model results of total chlorophyll and *Chattonella* chlorophyll concentrations (0-4 m depth) are shown in the middle and lower panels, respectively. Corresponding colour bars to the right.

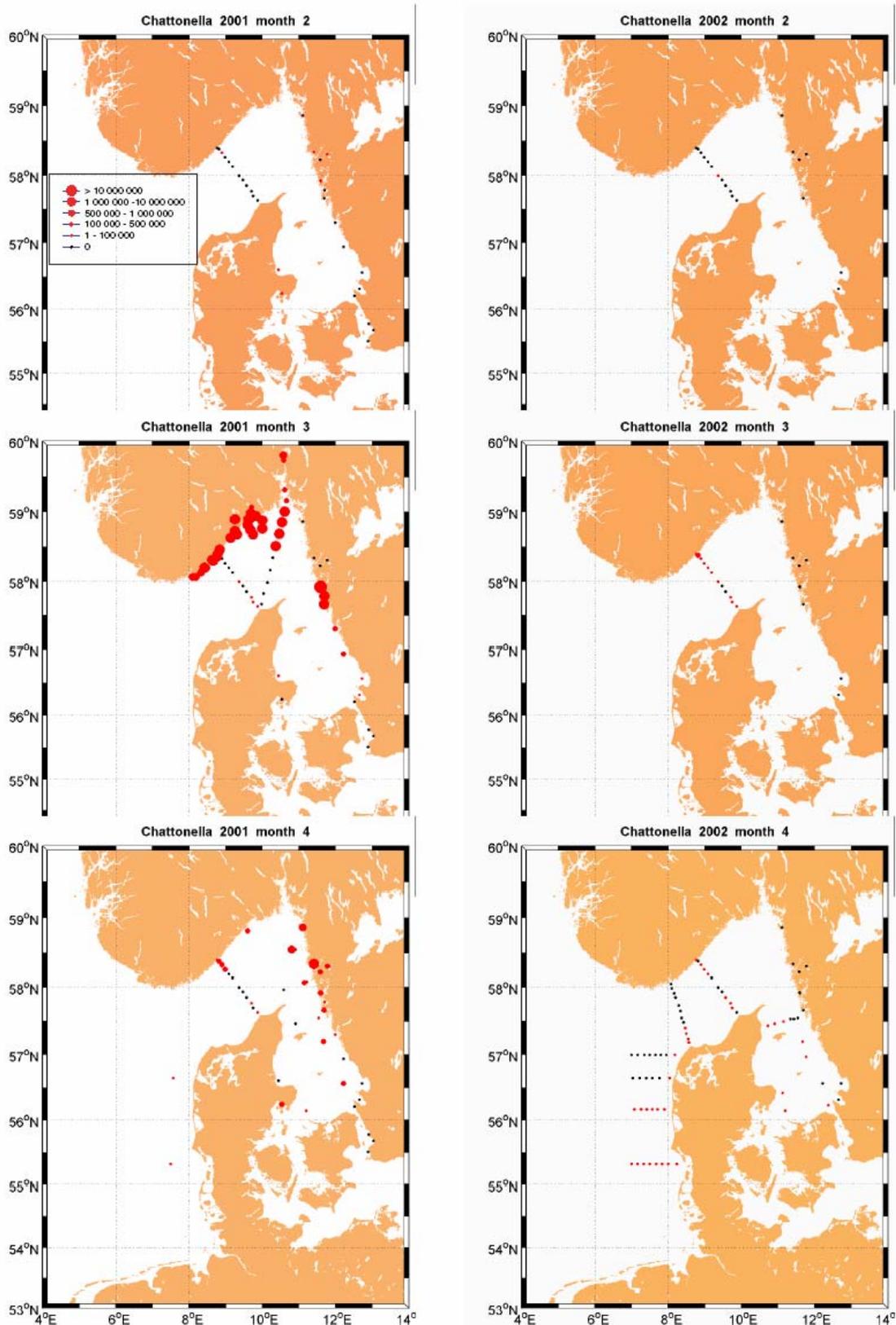


Fig. 4. Observed abundance cells l^{-1} (max. concentration registered in each month) of *Chattonella* sp. at Danish, Swedish and Norwegian monitoring stations (dots) during the period February-April 2001 and 2002. Size of red dots relates to the number of *Chattonella* according to the legend in the upper left panel. Maps by Pia Anderson, SMHI.

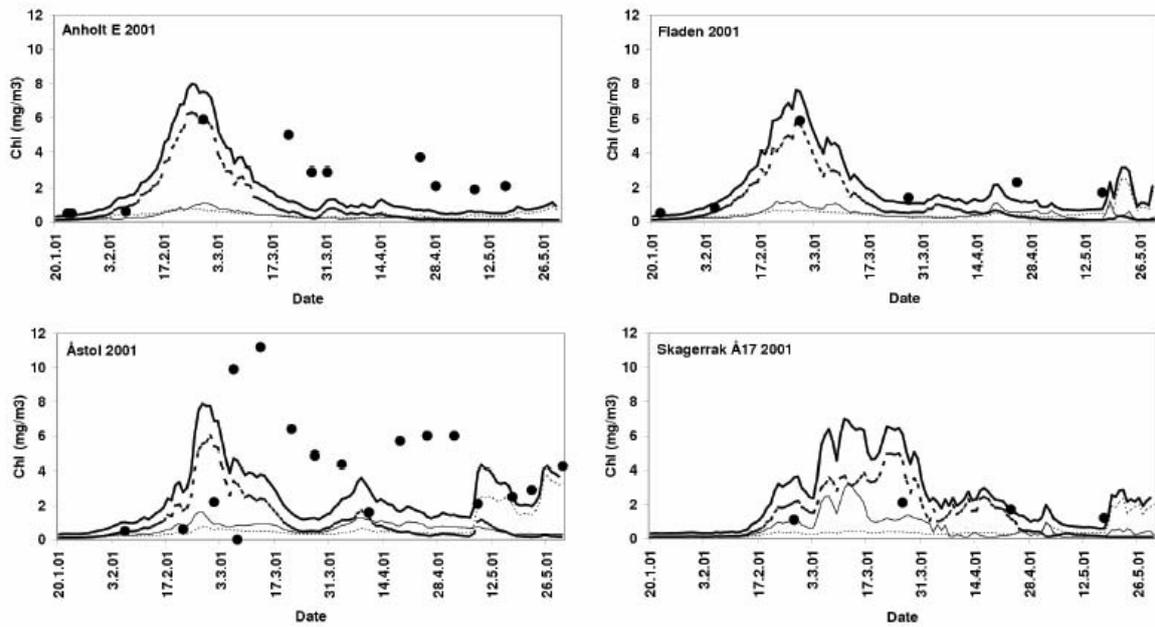


Fig. 5. Time plot 2001 of modelled surface layer (0-4 m) chlorophyll at Anholt (upper left), Fladen (upper right), Åstol (lower left) and central Skagerrak (lower right). Total chlorophyll, diatoms, *Chattonella* and summer flagellates are indicated by the thick solid, thick dashed, thin solid and thin dotted lines, respectively. Dots show chlorophyll observations from the surface layer (0 m). See Fig. 1 for the positions of sampling stations.

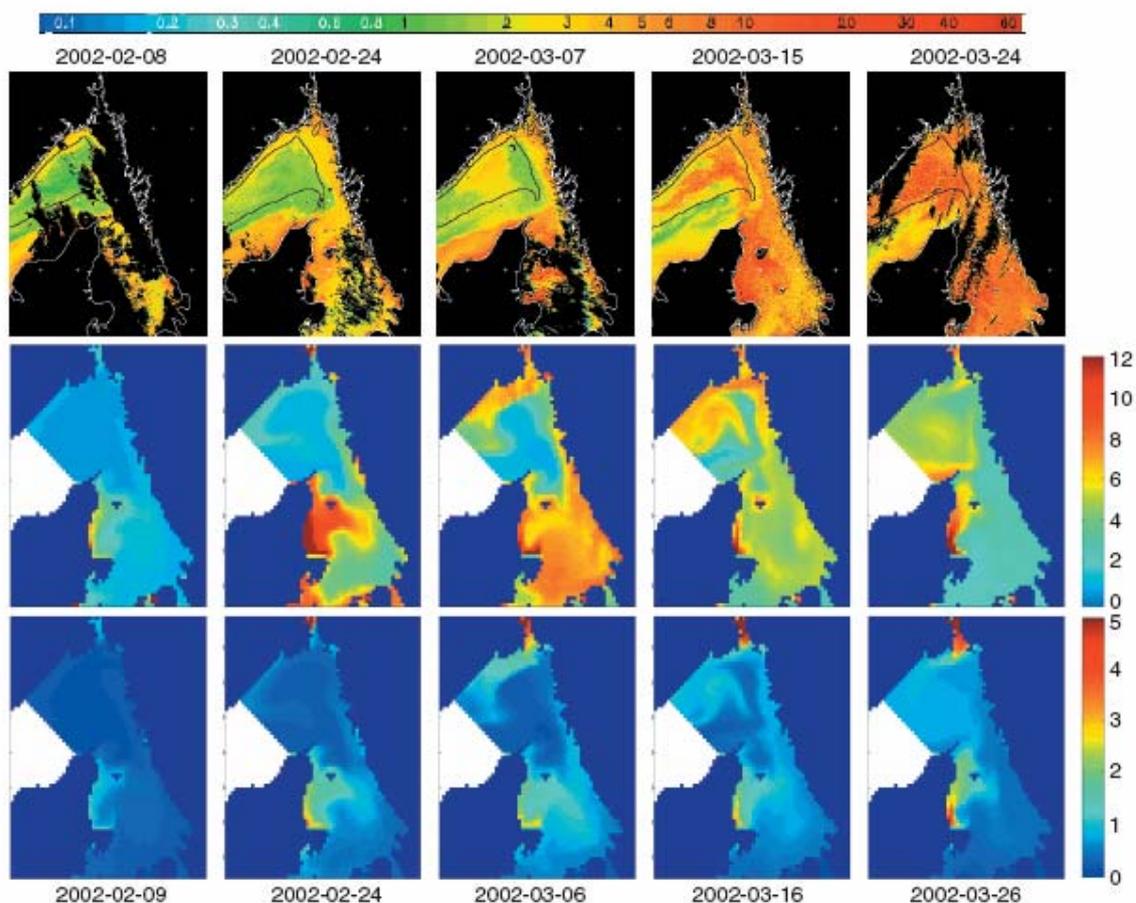


Fig. 6. Surface chlorophyll (mg m^{-3}) in February and March 2002. Satellite images on the upper panel are processed by the Plymouth Marine Laboratory (PML) Remote Sensing Group. Satellite image colour bar and dates above figure. Model results of total chlorophyll and *Chattonella* chlorophyll concentrations (0-4 m depth) are shown in the middle and lower panels, respectively. Corresponding colour bars to the right.

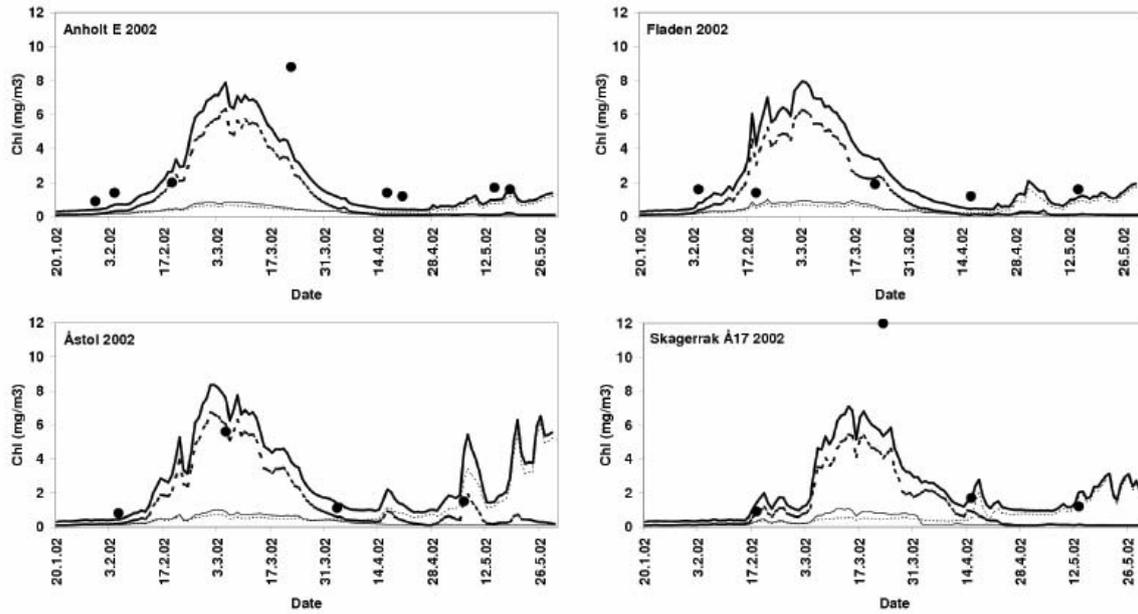


Fig. 7. Time plot 2002 of modelled surface layer (0-4 m) chlorophyll at Anholt (upper left), Fladen (upper right), Åstol (lower left) and central Skagerrak (lower right). Total chlorophyll, diatoms, *Chattonella* and summer flagellates are indicated by the thick solid, thick dashed, thin solid and thin dotted lines, respectively. Dots show chlorophyll observations from the surface layer (0 m). See Fig. 1 for the positions of sampling stations.