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PHYTOPLANKTON MODELS AND LIFE HISTORY STRATEGIES

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Phytoplankton models generally do not consider the initial phases of seed stocks and deal only with the vegetative growth phase, ignoring life history strategies. Some quantitatively important diatoms, such as species of *Chaetoceros* and *Skeletonema*, have special strategies with respect to the timing of the planktonic phase that cannot be explained purely on the basis of environmental clues. In Norwegian waters and elsewhere, the first *Chaetoceros* bloom of the growth season usually starts in mid March, initiated by *C. socialis*. Other *Chaetoceros* species appear in the water column later. Species of dinoflagellates like *Alexandrium* also bloom at certain times of the year. In many cases, phytoplankton inocula originate from resuspension of bottom-dwelling spores or cysts rather than from residual planktonic vegetative cells, and it is probable that, in some species, inoculation events are controlled by endogenous biological clocks. The sequential appearance of different *Chaetoceros* species may be related to day-length-regulated germination of spores. Most *Chaetoceros* species have few generations, but they appear at opportunistic times in the plankton. In contrast, *Skelelonema costatum* and *Scrippsiella trochoidea* appear at any time of the year. Some modelling results can be improved by including the dynamics of phytoplankton seed stocks in the sediments.

Ecosystem models are by definition simplifications of the real situation. Ecosystems are characterized by a high degree of complexity, spatial and functional heterogeneity, non-linearities, and important stochastic elements. Most phytoplankton production models consist of a physical model coupled to one or several biological submodels (Woods and Onken 1982, Wolf and Woods 1988, Slagstad and Støle-Hansen 1991, Hansen and Eilertsen 1995). The biological models that interact with the physical model are usually used to calculate changes in total phytoplankton vegetative biomass with time, when moved by the vertical mixing coefficient through gradients of irradiance and nutrients. Loss rates are affected by sinking and grazing, as well as by respiration. Such models respond with biomass increases whenever light and mixing conditions favour net growth, in accordance with Sverdrup's (1953) concept; thus biomass tracks the environment but it is not adapted to it in a Darwinian sense (Wyatt and Jenkinson 1987).

In many models, blooms are described as bulk increases in chlorophyll *a* or carbon, and the size and quantitative composition of the pre-bloom stocks that provide inocula are not taken into account. Yet, many diatoms and dinoflagellates form resting stages. Gran (1912) first proposed that diatom blooms are initiated after resuspension and germination of bottom-dwelling spores, a view that was later supported by Kashkin (1964), Garrison (1981, 1984), Kuznetsov (1992), Hansen and Eilertsen (1995) and Marcus and Boero (1998). The dynamics of benthic seed beds of dinoflagellate cysts may also regulate bloom dynamics (Wyatt and Jenkinson 1997, Eilertsen and Wyatt 1998). Germination of these dormant stages is probably regulated by endogenous biological clocks (Anderson and Keafer 1987, Eilertsen *et al.* 1995, McQuoid and Hobson 1995). During the vegetative phase, modulation of mixing rates and other environmental factors attributable to the algae themselves may affect growth (Jenkinson and Wyatt 1992, Wyatt and Jenkinson 1993). In addition, sexual processes are involved in many diatom and dinoflagellate life histories, and these can interrupt the momentum of vegetative growth. It is therefore suggested here that internally programmed life history strategies, as well as species-specific environmental requirements, should be taken into account when modelling phytoplankton population dynamics.

In this paper, the role of resting stages in the population dynamics of a spring bloom is investigated. The distributions of diatoms of the genus *Chaetoceros*, *Skeletonema costatum* and the dinoflagellate *Alexandrium tamarense* are first described in space and time. Then, the means whereby the magnitude of pelagic and benthic initial stocks can influence phytoplankton biomass and the amplitudes of blooms is examined by simulation. Only data from coastal and shallow habitats were used, because the significance of phytoplanktonic pelagic-benthic coupling in deep-water environments is unknown.

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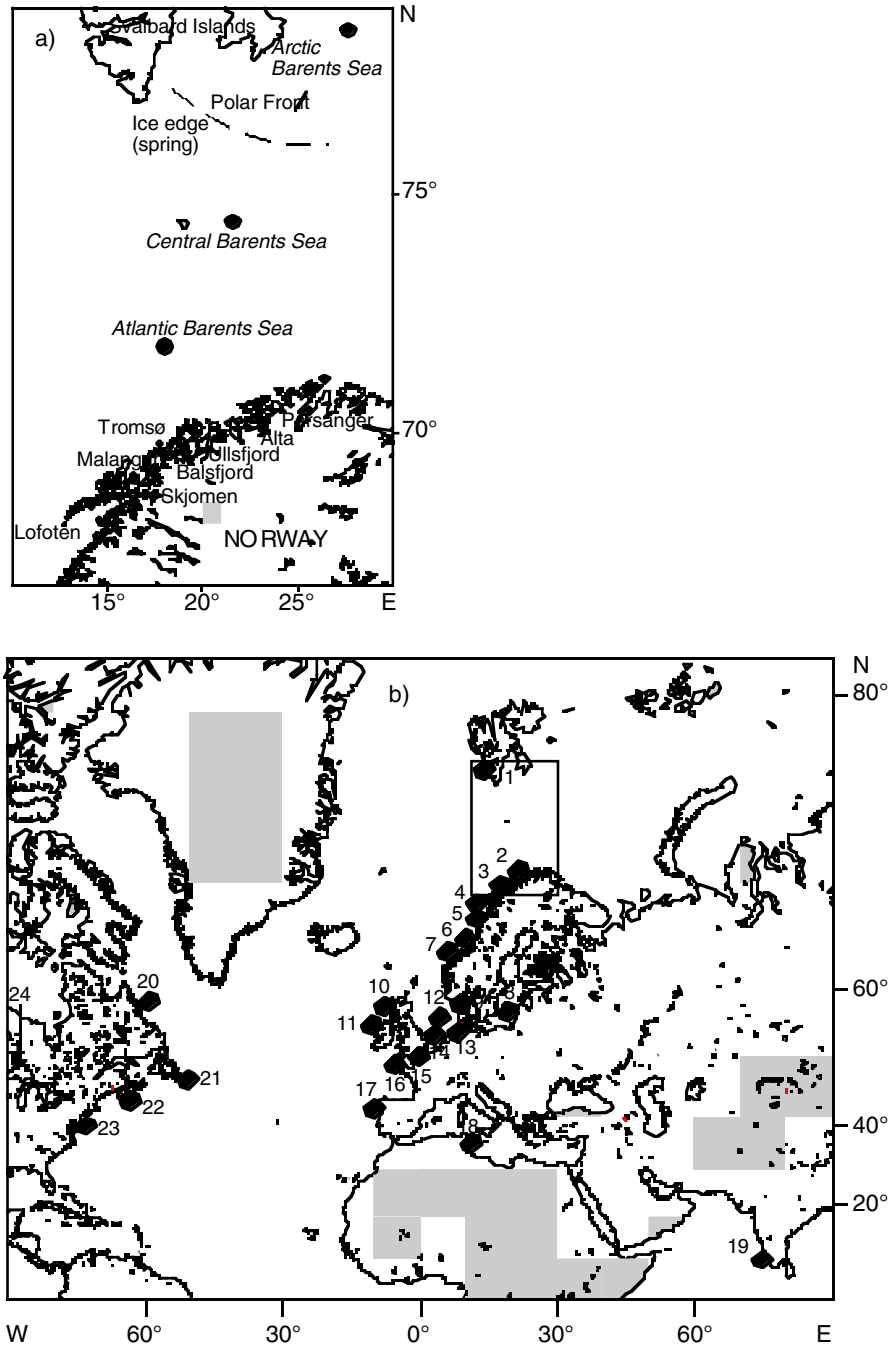

Fig. 1: Areas investigated in (a) the Barents Sea and along the coast of northern Norway and (b) at various localities in the northern hemisphere to 10°N. Note that Ramfjorden is close to Ullsfjord. Sampling procedures and locations are given in the Appendix

MATERIAL AND METHODS

Data from the Arctic, the central and Atlantic sectors of the Barents Sea, and the coastal waters of northern Norway were used in the analysis (Fig. 1). Details of the surveys conducted in those regions are presented in the Appendix.

Sediment samples containing diatom spores were collected at Tromsøysund (85 m depth) in the vicinity of Tromsø (Fig. 1) and stored in the dark at 5°C. Germination was induced in the cultures using f/20-autoclaved seawater (Guillard and Ryther 1962), under daylengths of 7 and 12 h specified by the use of daylight tubes. All cultures were provided with equal integrated irradiance.

The physical model

A modified 1D version of the 3D Blumberg-Mellor model was used (Mellor and Yamada 1982, Blumberg and Mellor 1987, Mellor 1991, Hansen and Eilertsen 1995). Input data to the model were meteorological parameters (air temperature, atmospheric visibility, humidity, cloud cover), sea surface temperatures, and tidally driven mixing values computed from data in Gjevik *et al*. (1990).

Surface heat flux components at the air-sea interface used as input to the model are described in Gill (1982). Sensible heat (Q_h) was modelled according to Brown (1990), latent heat (Q_h) as in Smith *et al*. (1983) and net long-wave radiation (Q_b) following Henderson-Sellers (1986).

Wind stress (r) was calculated using the formula $r = C_D \rho v^2$ (Gill 1982), where ρ is air pressure (from meteorological data), v is wind speed (meteorological data) and C_D is the drag coefficient ($C_D = 1.1 \times 10^{-3}$ for $v < 6$ m·s^{-1}, and $10^3 \times C_D = 0.61 + 0.063$ for 6 m·s$^{-1} < v < 22$ m·s^{-1}).

Visible short-wave solar irradiance (W·m^{-2}) for clear sky was computed following Frouin *et al*. (1989). After input of atmospheric visibility, regression coefficients for maritime atmospheres, the solar zenith angle was computed for each geographical position and time following Iqbal (1983). The irradiance model was calibrated against measurements collected during cruises conducted along the coast of northern Norway (Eilertsen and Holm-Hansen 2000). Conversion of measured irradiance (from quanta·m^{-2}·s^{-1} to W·m^{-2}), calculation of cloud cover corrected irradiance, diffuse attenuation coefficient (k), and albedo followed the regressions given in Eilertsen and Holm-Hansen (2000).

The biological model

The governing equation, ignoring advection, that describes the spatial and temporal evolution of phytoplankton biomass (biological model), is from Slagstad and Støle-Hansen (1991):

$$\frac{\partial B}{\partial t} = \frac{\partial}{\partial z}\left(K_H \frac{\partial B}{\partial z} \right) - w \frac{\partial B}{\partial z} + (P - \phi_r)\, B \quad , (1)$$

where B is phytoplankton concentration (mgChl a·m^{-3}) at depth z and time t, w is sinking velocity, P is growth rate and ϕ_r is loss rate. K_H is the coefficient of vertical eddy diffusion (m^{-2}·s^{-1}).

The functional relationship between light and photosynthesis used in the biomass equation is according to Webb *et al*. (1974):

$$P = \left(\frac{\text{Chl}}{C} \right) P^B \left(1 - e^{-aQ_{s(p)} / P^B}\right) \quad , \quad (2)$$

where P^B is maximum photosynthetic rate (mgC·mgChl a^{-1}·h^{-1}), α is photosynthetic efficiency (mgC·mgChl a^{-1}·h^{-1}·W·m^{-2}) and $Q_{s(p)}$ is PAR (W·m^{-2}) at depth z.

Model runs

The physical inputs for the Barents Sea simulations were hydrographic (sea temperature and wind: Blumberg-Mellor model) and meteorological parameters (air temperature: Blumberg-Mellor model; visibility, cloud cover, wind-irradiance model) collected during cruises and from the Norwegian Meteorological Institute. All irradiance and wind-mixing parameters were calculated in one-hour increments for the entire sampling period, and data for the periods between meteorological observations and measurements of sea temperatures were obtained by linear interpolation from adjacent points. Only one location in the central Barents Sea was modelled.

The biological input parameters used for the Barents Sea simulations were similar to those used by Hansen and Eilertsen (1995), i.e. $\alpha^B = 0.12$ mgC·mgChl a^{-1}·W·m^{-2}, $P^B = 1.7$ mgC·mgChl a^{-1}·h^{-1}, $\phi_r = 0.05$·day^{-1}, $w = 0$. The Chl : C ratio = 0.017 and $Z_0 = 0.01$ (bottom roughness parameter). The biological models were run with two pelagic (*Phaeocystis pouchetii* and diatoms) and one bottom compartment (diatom seed stock).

Because, in the Barents Sea, *P. pouchetii* and small quantities of *Thalassiosira* sp. are also present during the spring bloom, the relative contribution of diatom

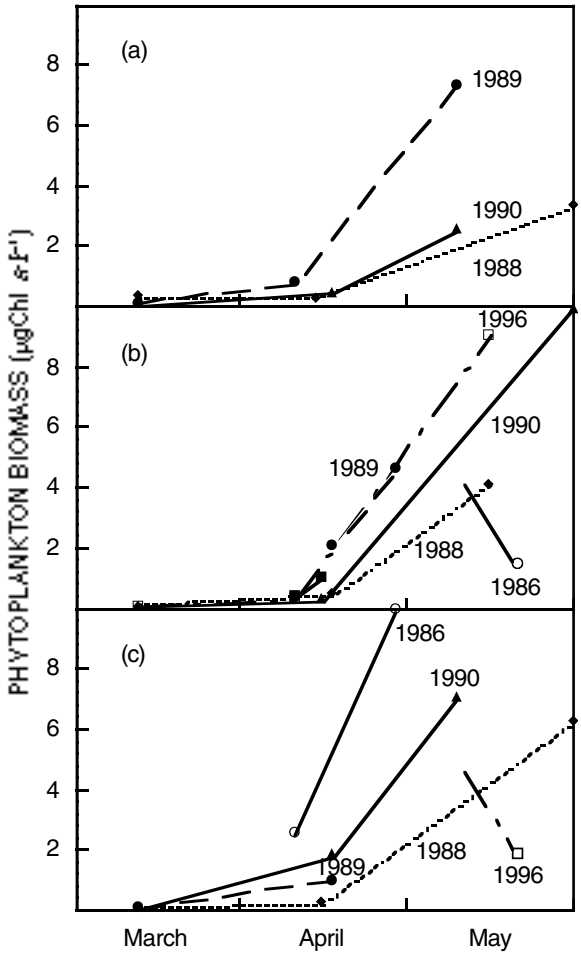

Fig. 2: Total phytoplankton biomass levels in (a) the Arctic, (b) the central and (c) Atlantic sectors of the Barents Sea in different years (see App. Table I). Note that sampling dates are indicated by symbols and that the lines between them are drawn for convenience

species to total biomass was approximated, using 1.6 and 14 pg Chl *a*·cell^{-1} for *Chaetoceros* and *Thalassiosira* species respectively (Hegseth 1992). The initial pelagic stock was computed following the same procedure. Mean values of all vegetative diatom cell counts were for March (0.000048 µgChl $a\cdot\ell^{-1}$). The simulations were first performed with the initial pelagic stock evenly distributed. Runs were then performed in which the pelagic stock was retained and spores, represented by viable Chl *a* (as in the pelagic stock), were added to the lowest grid of the model as a sinusoidally time-varying influx of biomass from 1 March each year, regulated by site-specific tides (Gjevik *et al*. 1990). This influx was started each year with a value of 0.5 µgChl $a\cdot\ell^{-1}$ and increased in increments of 0.5–10 µgChl $a\cdot\ell^{-1}$. The maximum biomass influx to each simulation was set at a phase angle of 90°, corresponding to spring tides.

Alexandrium simulations were made for an area in the North Sea where toxic blooms of that genus are frequent (Wyatt and Saborido-Rey 1993). Wind speed and cloud cover were kept constant at 1 m·s^{-1} and 0.6 (cloud cover c.4.8 on 0–8 scale) respectively. Input temperatures were taken from Colebrook (1979). The biological coefficients used were α^B = 0.13 mgC·mgChl a^{-1}·W·m^{-2}, P^B = 3.5 mgC·mgChl a^{-1}·h^{-1}, ϕ = 0.05 day^{-1}, Chl : C ratio = 0.025 and Z_0 = 0.01 (Eilertsen and Wyatt 1998). The sinking rates (w) of diatoms and *Alexandrium* cysts at the start of each simulation were 0 and 0.1 m·day^{-1} respectively. All simulations started with initial diatom stocks (0.1 µgChl $a\cdot\ell^{-1}$), evenly distributed throughout the water column. At the start of the simulation, *Alexandrium* cyst stocks were set constant at 2.0 µgChl $a\cdot\ell^{-1}$ in the lowest grid of the model. The decline of the diatom bloom was simulated by increasing their sinking rate to 5 m·s^{-1} on 15 April. When the *Alexandrium* pelagic stock reached 6 µgChl $a\cdot\ell^{-1}$, equivalent to a cell concentration where gametogenesis and subsequent encystment begin (Wyatt and Jenkinson 1997), a sinking rate of 5 m·day^{-1} was assigned to *Alexandrium*, to simulate settlement of cysts to the sediments. The water column was inoculated from the cyst bed by site-specific tidal mixing, simulated as described above. In the simulations, if gametogenesis concentrations were reached, new cysts were added to the cyst bed stock; in some simulations the cyst bed was subjected to a specific annual loss rate, varying between 0 and 1. There was no functional nutrient limitation in the model runs, and a 20-year period (1970–1990), when data were available on *Alexandrium* toxicity, was modelled (Wyatt and Saborido-Rey 1993).

Critical depth calculations

The critical depth (D_{cr}) in the northern hemisphere at sites forming a north-south gradient was calculated following Sverdrup (1953). Cloud cover (0–6 on a 0–8 scale) and corrected subsurface irradiance was first calculated for the latitudes under study (75–l0°N, Fig. 1), with visibility = 75 km and humidity = 60%. Sverdrup's (1953) equation was then solved iteratively with respect to depth, with compensation light (I_c) set to a mean value of 1.0 W·m^{-2} (Platt *et al*. 199l).

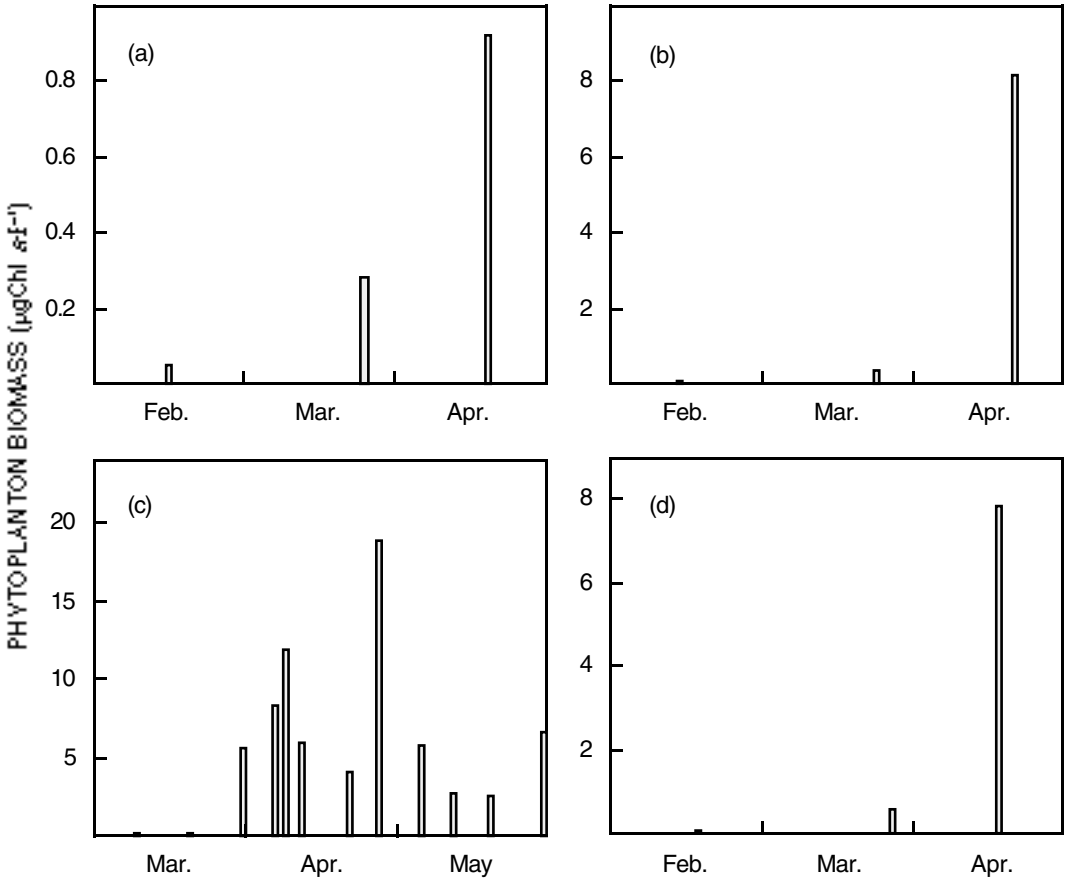

Fig. 3: Phytoplankton biomass in (a) Porsangerfjord, (b) Altafjord, (c) Tromsøysund and (d) Balsfjord during spring 1998 (note different y-axis values)

RESULTS

Pattern of the spring bloom

Owing to the absence of light, winter in the Barents Sea and northern Norwegian waters is characterized by very low or negligible phytoplankton concentrations, typically ranging between 0.01 and 0.05 µgChl $a \cdot \ell^{-1}$ (Evensen 1994, Hansen and Eilertsen 1995). The Barents Sea data show that biomass starts to increase at the latest around mid April (Fig. 2). For the Arctic sector, data from the open ocean were used. The patterns in the Arctic, central and Atlantic sectors of the Barents Sea were almost identical with respect to the timing of the spring bloom (Fig. 2). The rate of increase in biomass and maximum biomass levels varied between years. This could be attributed to variations in the numbers of different *Chaetoceros* species – numerically one of the most important genera in the region, after *P. pouchetti* (Evensen 1994) – which was more consistent during the years of study.

In addition to *Chaetoceros* species, small quantities of *P. pouchetii* were observed in April in the Arctic sector of the Barents Sea, and *Thalassiosira* spp. were present from May onwards. Along the coast of northern Norway, blooms can begin as early as the end of March (Fig. 3). The blooms there are initiated with *C. socialis* mixed with *P. pouchetii*.

Negligible winter stocks as well as late March or early April spring blooms, initiated with *Chaetoceros* and *Phaeocystis*, are also characteristic of other northern

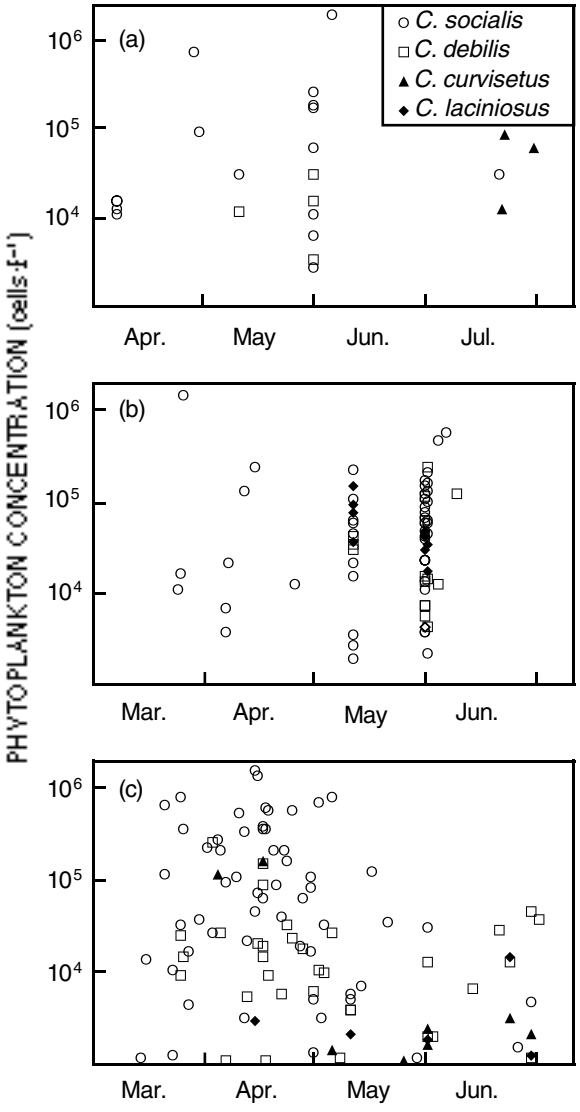

Fig. 4: Concentrations of *Chaetoceros* during spring and early summer in (a) the Arctic sector of the Barents Sea, (b) in the central and Atlantic sectors of the Barents Sea and (c) along the coast of northern Norway (see App. Table I). Note logarithmic y-axis

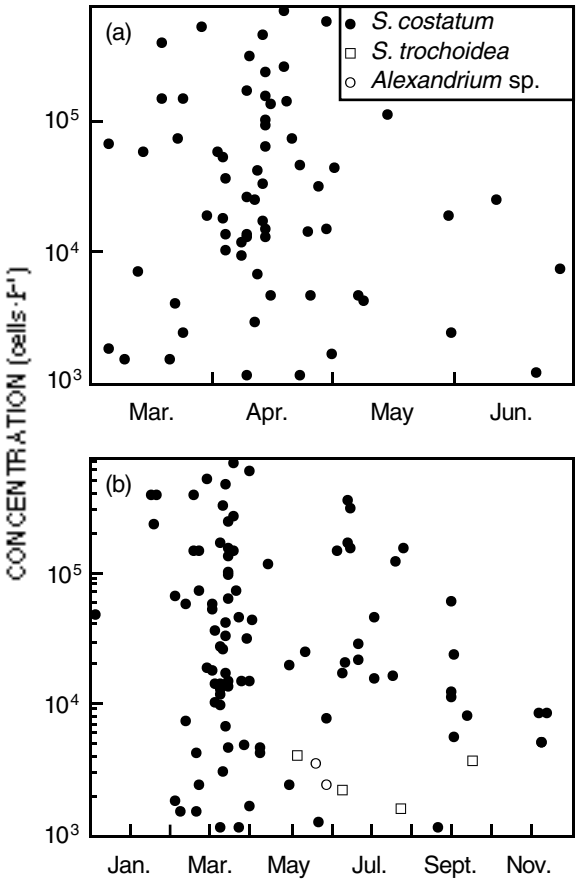

Fig. 5: Monthly changes in the concentration of time-series of *S. costatum*, *S trochoidea* and *Alexandrium* sp. in (a) the central Atlantic Barents Sea and (b) along the coast of northern Norway

localities, e.g. Ullsfjorden, Trondjord, Ramfjorden, Malangen, Skjomen and Vestfjorden (Føyn 1929, Gaarder 1938, Heimdal 1974, Schei 1974, Beck 1980, Pedersen *et al*. 1989). In more southerly regions south of Oslofjorden and the Baltic, spring blooms sometimes start earlier, usually initiated by *S. costatum*, but *Chaetoceros* spp. appear at the same time as those in the north. In Trondheimsfjord, *S. costatum* may bloom as early as March, whereas in Korsfjord and Oslofjord the species may bloom as early as late January (Hasle and Smayda 1960, Dahl *et al*. 1974, Sakshaug 1972, Erga and Heimdal 1984). Farther south, where light intensities are higher and days are longer, phytoplankton growth can continue throughout the entire winter season. For example, in Narragansett Bay there may be large midwinter blooms of *S. costatum* (Smayda 1983). It is also typical in these southern localities for considerable numbers of viable cells to be present in winter, potentially initiating new blooms. However, there are no pronounced increases in phytoplankton biomass there at such times.

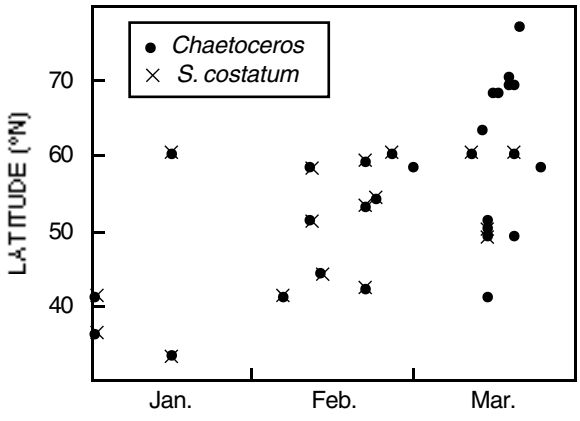

Fig. 6: Time of onset of spring blooms of *Chaetoceros* and *S. costatum* at various latitudes. Data from sources listed in App. Tables I and II

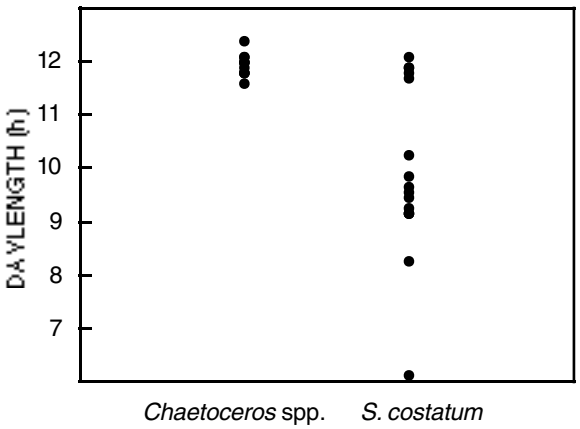

Fig. 7: Daylength at time of onset of spring blooms of *Chaetoceros* and *Skeletonema.* Dots represent locations referred to in App. Table II

This contrasts with northern Norwegian waters and the Barents Sea, where winter phytoplankton concentrations are close to or at zero (Gaarder 1938, Hegseth *et al.* 1995).

Succession in *Chaetoceros, Skeletonema, Scrippsiella* and *Alexandrium*

In all northern areas investigated here (and even as far south as Tunisia – see Kefi 1993), succession begins with *C. socialis*, followed by *C. debilis* and later by *C. laciniosus* and *C. curvisetus* (Figs 4, 5; Table I). If blooms of *S. costatum* are excluded, the spring diatom increase is initiated within a short period of time (between 14 and 22 March) at all latitudes considered here.

S. costatum was present throughout the sampling period in the northern areas. It was also present along the coast of northern Norway for brief periods in December and early January, in short chains of vegetative cells up to 10^3 cells·ℓ^{-1} (data not shown). *Scrippsiella trochoidea* was found off northern Norway from May to October. *Alexandrium* occurred in low concentrations in June (Fig. 5). Blooms before mid March were south of 60°N and consisted of *S. costatum* (Fig. 6), whereas *Chaetoceros*-dominated blooms began from mid March, when daylength approaches 12 h (Fig. 7).

Environmental variables from north to south

With initial phytoplankton stocks of 0.1–1.0 µgChl $a\cdot\ell^{-1}$ and cloud cover ranging between 0 and 4, the computed critical depths increased monotonically from north to south (Fig. 8). The shallowest critical depths are north, in generally unstratified water masses where water temperatures are lowest (i.e. -1.5°C at Spitzbergen, 78°N) v. 30°C at 10°N (Fig. 9).

Model run for the Barents Sea diatom blooms

Model runs with the initial low pelagic diatom stock (bottom stock = 0) in the central Barents Sea showed that the diatom biomass varied around the low (0.000048 µgChl $a\cdot\ell^{-1}$) initial stock, and that there

Table I: Summary of data from Figs 3 and 4. The starting date of the bloom is defined as the date when chlorophyll *a* values rose above 0.1 µg·ℓ^{-1}

Area	Starting date of bloom	Species rank
Arctic Barents Sea	11 April	*C. socialis*, *C. debilis*, *C. curvisetus*
Central – Atlantic Barents Sea	22 March	*C. socialis*, *C. debilis*, *C. laciniosus*
Coast of north Norway	20 March	*C. socialis*, *C. debilis*, *C. laciniosus*, *C. curvisetus*

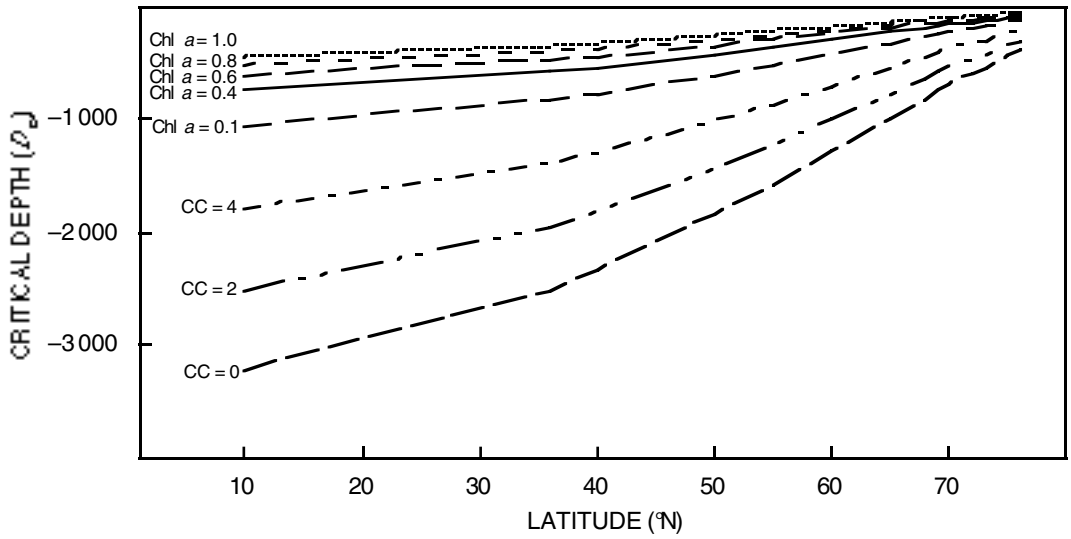

Fig. 8: Theoretical critical depths along a north-south axis on 15 March. The five uppermost curves were computed with a cloud cover value of 6 and initial phytoplankton biomasses ranging from 0. 1–1.0 µgChl $a{\cdot}\ell^{-1}$. The three lower curves were computed with a phytoplankton biomass value of 0.1 µgChl $a{\cdot}\ell^{-1}$ and cloud cover (CC) values ranging from 0–4

was no increase during the run period March–May (data not shown). The increase in biomass (Fig. 2) peaked in late April/early May (1–4 µgChl $a{\cdot}\ell^{-1}$). In order of ranking, the earliest bloom was in 1996, followed by 1986, 1989 and 1990, all with similar timing, and the latest bloom was in 1988. It should be noted that, although the central Barents Sea was chosen to be modelled, samples from there showed similar timing and species composition as those from the open water Arctic and Atlantic sectors.

When diatoms were fed into the deepest grid of the model at different concentrations (0–10 µgChl $a{\cdot}\ell^{-1}$) for each run, it was possible to simulate blooms that reached realistic densities (Fig. 10). At a constant bottom concentration of 5 µgChl $a{\cdot}\ell^{-1}$, the simulated years approximated the observed ranking (Fig. 10). Blooms started in unstratified water masses, permitting simulated spore biomass to reach the upper water layers. Vertical mixing decreased during the run period as a result of decreasing winds from March to May. There was increased heat input and slight stratification from mid to late April onwards.

The abundance of diatoms, and not *P. pouchetti*, varied substantially with time, and they contributed most to the biomass. Therefore, diatoms were the "true" regulator of bloom timing. It should also be noted that, because bottom stock was kept constant in all years (Fig. 10), the irradiance and vertical turbulence (created by tides, cooling and wind) generated by the model caused the timing of blooms to vary between years.

Model run for the North Sea *Alexandrium* bloom

When *Alexandrium* is modelled, together with a normal diatom bloom (data not shown) in April in the North Sea, with a dynamic bottom stock and no loss or accumulation of cysts from one year to the next, it was not possible to reproduce the observed interannual variations of toxicity (Eilertsen and Wyatt 1998). These simulations generate blooms every year with peaks of approximately similar magnitude after the spring diatom bloom is over, whereas cyst abundance increases to eight times the original value (= 1) after 20 years (Wyatt and Saborido-Rey 1993).

The onset and peaks of blooms varied between 3 and 4 days. Timing of the relevant lunar events indicates that bloom timing is controlled by high tides at full or new moon, i.e. peaks in the flushing of cysts from the bottom. When the loss rate from the cyst bed was allowed to vary at a rate of $0.3{\cdot}\text{year}^{-1}$, it was possible to discriminate between bloom and non-bloom years with some degree of confidence (Fig. 11).

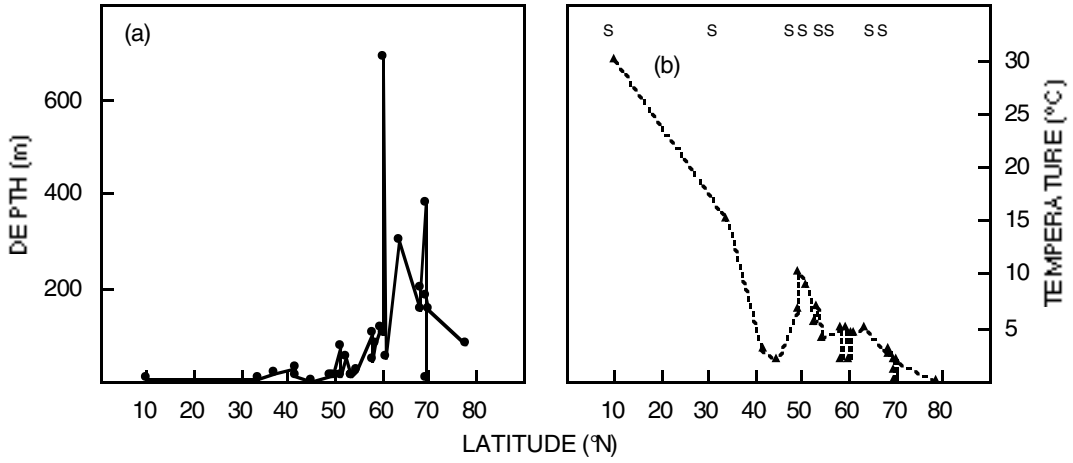

Fig. 9: Environmental variables at the onset of spring blooms along a north-south axis – (a) depth at location (see App. Table II) and (b) temperature and recorded positive stability in the surface layer (S)

DISCUSSION

Data from the central and Atlantic sectors of the Barents Sea and along the coast of northern Norway were consistent in that *Chaetoceros* species, which initiate spring blooms, increase from mid March onwards (Fig 4). A similar pattern was found in a shallow lagoon in Tunisia (36.8°N), where *C. socialis* blooms peak in March (Kefi 1993).

The onset of a phytoplankton spring bloom has traditionally been explained by Sverdrup's paradigm (Sverdrup 1953), i.e. for a bloom to occur, the mixed depth must be equal to or shallower than the critical depth. The present data indicate that this situation does not hold for blooms in March north of the polar circle, where winter darkness prevails for up to three months. There, the formation of surface stability, as a consequence of increased air temperature and radiation and/or freshwater run-off, does not start until the spring bloom is well under way, or has already ended (Gaarder 1938, Heimdal 1974, Eilertsen *et al*. 1989). Therefore, blooms in March in the polar circle generally occur in unstratified water (Eilertsen 1993), as has been reported for areas farther south (Townsend *et al*. 1992, Perry *et al*. 1989). If the critical depth in the Barents Sea is sufficiently deep to initiate blooms in March, the photosynthetic coefficients and weather conditions must be optimal and the water should be extremely clear. The diatom blooms observed later in the Arctic sector of the Barents Sea could therefore be attributed to a shallowing of the critical depth (Figs 2, 8, 9), caused by low irradiance levels and ice cover at these latitudes (north of 75°N), and to the spring bloom following the retreat of the ice edge (Syvertsen 1991).

Arctic and northerly spring blooms usually start in waters with very low phytoplankton concentrations (<0.05 µgChl $a \cdot \ell^{-1}$) and an almost complete absence of phytoplankton stocks (Khromov and Salakhutdinov 1985, Hansen and Eilertsen 1995). In the northern part of the study area, diatom blooms start in the deepest and coldest waters with the highest rates of cooling (Fig. 9), at the shallowest critical depths (Fig. 8) and from small pelagic stocks. There is no nutrient limitation in the central Barents Sea and the increase in biomass is a function of stock size (Kristiansen *et al*. 1994). Farther south, blooms sometimes start earlier when day length is <12 h, i.e. before the vernal equinox. The feature common to these winter-spring blooms is that they are usually dominated by *S. costatum* (Figs 6, 7). The presence of blooms in unstratified waters have been explained in several ways, including the possible absorption of sunlight by phytoplankton cells, leading to increased thermal stratification (Stramska and Dickey 1993), or reduced grazing (Smayda 1983, Koseff *et al*. 1993). There are no indications that such regulatory mechanisms operated in the present study area. It is therefore concluded here that the diatom blooms in the region do not originate from pelagic stocks that are regulated by surface mixing and light, as in Sverdrup's model, but that some other regulatory factor(s) must be involved.

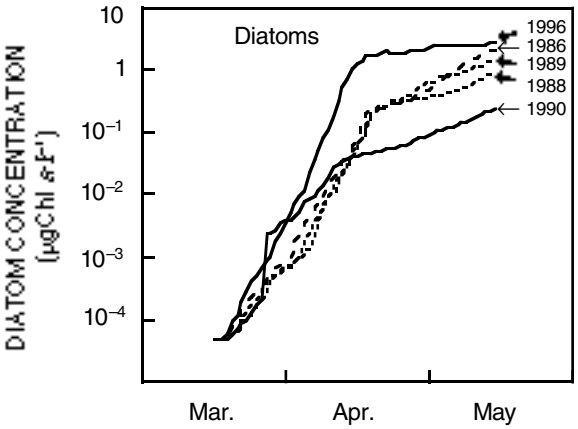

Fig. 10: Diatom stock in the central Barents Sea (200 m), modelled with a bottom stock of 5 µgChl $a \cdot \ell^{-1}$ from 15 March

Gran (1912) suggested that phytoplankton blooms are seeded by bottom-dwelling stages. Even small quantities of bottom sediments are able to produce dense populations of spring bloom species, after short periods of time (Itakura *et al*. 1997). Table II shows that incubated bottom sediment samples without vegetative cells (diluted 5 000 times) reached concentrations of >25 and $>59 \times 10^6$ cells$\cdot\ell^{-1}$ of *C. socialis* and *C. furcellatus* respectively after only 11 days. The possibility that spores may seed diatom blooms has been reported from several other areas: Karnag Sea (Zgurovskaya and Yakhno 1979), Hiroshima Bay (Itakura *et al*. 1997), the Benguela upwelling system (Pitcher 1986, 1990) and Monterey Bay (Garrison 1981). Levasseur *et al*. (1998) attributed delayed diatom blooms in the St Lawrence Estuary in Canada to early stratification, which created a barrier to the upward transport of diatom spores.

The present results, and the observation that northern Norwegian waters may contain large numbers of spores prior to the spring bloom (Eilertsen *et al*. 1995, Hansen and Eilertsen 1995), indicate that resuspended spores must be considered a possible alternative inoculum to vegetative cells. McQuoid and Hobson (1995) suggested that increased temperatures leads to higher rates of germination, but northern surface waters are considerably colder than the bottom layers (Eilertsen *et al*. 1981). Experiments similar to those summarized in Table II, in which temperature was varied between 2.5 and 6°C, showed no relationship between germination rates and temperature (Ljungfeldt 2000). This mechanism is therefore rejected at this stage.

Contrary to diatoms, dinoflagellate blooms can be seeded from bottom-dwelling cysts without the requirement for resumuspension (e.g. Giacobbe *et al*. 1996, Ishikawa and Taniguchi 1996). Blooms of *Alexandrium tamarense* peak in late May or early June in many areas, including the North Sea (Wyatt and Jenkinson 1997), western Mediterranean (Forteza *et al*. 1998), the Gulf of St Lawrence (Levasseur *et al*. 1998), the Gulf of Maine (Franks and Anderson 1992) and off northern Norway (Fig. 5). *Scrippsiella trochoidea*, on the other hand, is widespread in time and space and has cysts that germinate year-round (Ishikawa and Taniguchi 1994), in accordance with the present data (Fig. 7).

Table II: Numbers of vegetative cells of selected species in cultures started from 0.04 mℓ bottom sediment diluted in 200 mℓ f/200 medium (Guillard and Ryther 1962). Sediment with spores was collected from Tromsøysund on dates indicated and stored in the dark at 5°C prior to starting the experiments. Cultures were exposed to daylengths of either 12 or 7 h at 5°C and similar integrated daily irradiance. Experiments lasted 11 days

Sediment sampled	Number of vegetative cells (cells$\cdot$mℓ^{-1})			
	12 h		7 h	
	1 Mar. 1993	15 Nov. 1995	1 Mar. 1993	15 Nov. 1995
C. compressus	240	620		
C. constrictus		80		
C. curvisetus		80		
C. debilis	580	820		
C. gracilis	440			
C. furcellatus	6 300	59 320	61	3
C. socialis	14 720	25 720		
C. subsecundus	280			
C. gracilis	4	7	1.2	14
C. costatum	120	1 860	880	1 020

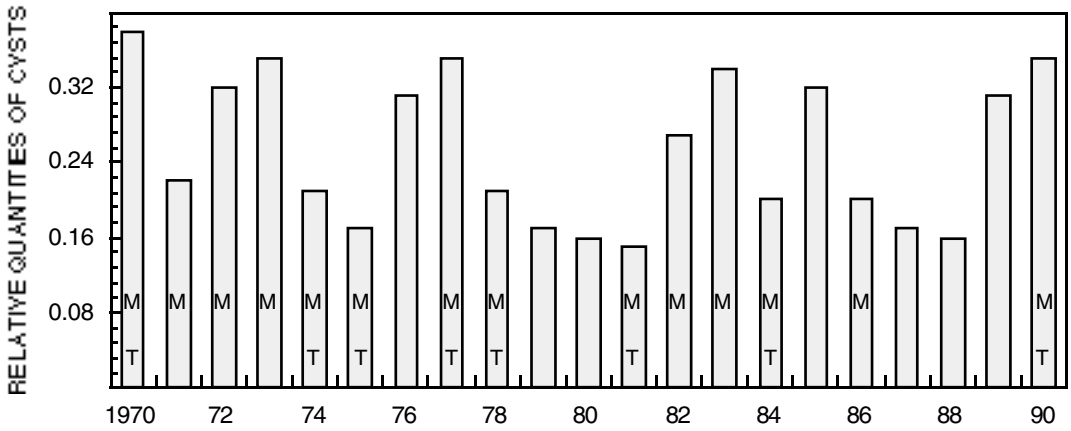

Fig. 11: Relative quantities of *Alexandrium* cysts in seed bed at a specific loss rate of 0.3·year^{-1} (y-axis). M indicates bloom modelled successfully (reached 6 µgChl *a*·ℓ^{-1} = gametogenesis). Years when toxicity levels exceeded 1 000 STX equivalent·100 g^{-1} mussel meat are denoted by T. Modelled blooms took place 19–37 days after observed blooms

The simulations that most successfully depict blooms are those in which seed stocks are fed in from bottom waters. Implicit in this theory is that, during the onset phase of blooms, a vertically unstable water column (mixed by the wind) is favourable for bloom initiation. Thus, the inoculation of the water column by germination and resuspension of dormant stages appears to be more of a contributing factor in the initiation of the spring bloom than conventional environmental parameters. It is concluded that inoculation strategies are an important component of the population dynamics of phytoplankton, especially in determining seasonality and trends in biomass. Some species, such as the larger species of *Chaetoceros* and *Alexandrium*, appear in the plankton in well defined and narrow time windows – the "staggered germination times" expressed by McQuoid and Hobson (1995) – and have few "generations" each year. Other species, such as *S. costatum* and *S. trochoidea*, may be present throughout most of the year and therefore have a multitude of generations each year. However, these observations apply to coastal, shelf and shallow-water systems; once blooms are initiated they are regulated by combinations of water stability and grazing.

In summary, the present analysis suggests that the timing and amplitude of the spring bloom are controlled both by the classical mechanisms outlined in Sverdrup's (1953) model and by the internal dynamics of phytoplankton life history strategies. Variations in the timing of the bloom, viewed as a bulk phenomenon, are generated in the model described here by the inoculation of species with and without precise daylength requirements for spore or cyst germination, as well as the existence, in some cases, of residual populations of vegetative cells. Variations in the amplitude of the spring bloom depend on classical forcing by mixing rates and light availability.

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APPENDIX

The datasets from the Barents Sea and the coastal waters of northern Norway (Fig. 1) were collected during cruises on R.V. *G. O. Sars*, *Lance*, *Endre Dyrøy*, *Johan Ruud* and *Jan Mayen* (App. Table I). Samples were collected with Niskin and Hydrobios 5–l bottle at depths of 0, 10, 20, 30 and 50 m. During cruises to the Barents Sea in March 1989, March and April 1990, April and May 1996, and along the coast of northern Norway in 1994–1996 and 1998 (App. Table I), samples were also taken at 50 m intervals to the bottom.

Sampling frequencies ranged from one to four weeks. In the Barents Sea, 12 stations were sampled within the areas marked on Figure 1 (Atlantic, Central and Arctic sectors of the Barents Sea). The following parameters were sampled at each station: temperature and salinity (Neil Brown sonde systems), surface and subsurface scalar irradiance (Lambda Instruments Model Li 185 quantum meter, 400–700 nm, and from 1996 PUV 500/510, Biospherical Instruments, UVR in $W \cdot m^{-2}$ and PAR, 400–700 nm, quanta), and chlorophyll *a* (Turner mod. 111 or Turner Designs fluorometer). Meteorological data were obtained from the Norwegian Meteorological Institute (2–4 day intervals) in addition to meteorological observations made on board during the cruises.

For phytoplankton analysis, 100 mℓ water samples were preserved in 4 mℓ 20% formaldehyde, neutralized with hexamine. Subsamples were counted in 2 mℓ and occasionally in 50 mℓ sedimenting chambers using an inverted microscope. Cell counts were then compiled in a database. For each sampling date and station, the highest cell number from 50 m and above were extracted for the *Chaetoceros* species, *Skeletonema costatum* and dinoflagellates. Cell numbers was used in the subsequent analysis, together with the environmental variables (sampling time, depth, temperature, salinity). Cell numbers were plotted against time of year.

App. Table I: Barents Sea and northern Norway datasets used in the present investigation (Fig. 1)

Sampling period and area in the Barents Sea	Time period, area (latitude °N, depth, m) off northern Norway
28 May–15 Jun. 1984; II, III 18 Jul.–15 Aug. 1984; II, III	8 Apr.–9 Oct. 1992, 6 Jan.–30 Sep. 1998, Porsangerfjord (70.5, 180) 7 Apr.–10 Oct. 1992, 29 Sep. 1997, 16 Feb.–28 Sep. 1998, Altafjord (70.2, 180)
1 Apr.–28 Apr. 1986; II	21 Mar.–25 Sep. 1963, 14 Apr. 1964, 12 Oct. 1995, 22 Mar. 1996, 14 Jul.–30 Sep. 1998, Ullsfjord[7] (70.0, 150)
15 Jul.–23 Jul. 1987; II	3 Mar.–20 Oct. 1980, Tromsøysund[5] (69.4, 30) 19 Sep.–7 Dec. 1997, 23 Mar.–30 Sep. 1998, Tromsøysund (69.4, 30)
14 Mar.–20 Mar. 1988 8 Apr.–17 Apr. 1988 27 May–1 Jun. 1988; I, II, III[1]	20 Mar.–20 Oct. 1980, Ramfjord[5] (69.3, 120)
13 Mar–20 Mar. 1989	3 May–8 Dec. 1930, 14 Jan.–25 Apr. 1931, Balsfjord[4] (69.5, 180) 13 Apr.–12 May 1976, 23 Mar.–31 Aug. 1977, 4 Apr.–10 Aug. 1978, Balsfjord[6] (69.5, 180) 12 Apr.–20 Aug. 1992, 6 Mar.–22 Apr. 1993, 8 Jan.–13 Jul. 1998, Balsfjord (69.5, 180)
8 May–13 May 1989; I, II, III[1]	
12 Mar.–18 Mar. 1990 17 Apr.–29 Apr. 1990 10 May–16 May 1990; I, II, III	24 Mar.–22 Apr. 1922, 21 Mar.–24 Apr. 1923, 21 Mar.–11 Apr. 1924, 30 Mar.–8 May 1926, Lofoten[3] (68.3, 200) 9 Apr.–13 Apr. 1996, Lofoten (68.3, 200)
23 Apr.–29 Apr. 1996 15 May–25 May 1996; II, III	16 Mar–23 May 1977, 13 Mar.–7 May 1978, 30 Mar.–14 May 1979m Skjomen (68.2, 150) 14 Mar.–26 May 1970, 10 Mar.–6 May 1971, 21 Mar.–3 May 1972, Skjomen[2] (68.2, 150)
30 Sep. 1998; I	

[1]Evensen (1994), [2]Schei (1974), [3]Føyn (1929), [4]Gaarder (1938), [5]Beck (1980), [6]Eilertsen *et al.* (1981), [7]Heimdal (1974), [8]Kefi (1993)
I = Atlantic (71.5–73.0°N, mean depth 220 m)
II = Central (73.0–74.5°N, mean depth 330 m)
III = Arctic (74.5–76.0°N, mean depth 400 m)

App. Table II: Locations referred to in Figure 1. The sources listed provide information on the north-south gradients in species composition, timing of spring bloom and environmental variables (note that all refer to inshore localities)

Reference number (see Fig. 1)	Location	Years investigated	Source
1	Svalbard	1985,1986	Eilertsen *et al.* (1989)
2	Ullsfjord	1963, 1964	Heimdal (1974)
3	Trondjord-lagoon	1987	Pedersen *et al.* (1989)
	Balsfjord	1930,1931	Gaarder (1938)
	Balsfjord	1976–1978	Eilertsen *et al.* (1981)
	Malangen	1930, 1931	Gaarder (1938)
4	Vestfjorden	1922–1927	Føyn (1929)
	Skjomen	1970, 1971	Schei (1974)
5	Trondheimsfjord	1963–1966	Sakshaug (1972)
6	Lindåspollen	1975	Lännergren and Skjoldal (1975)
	Korsfjord	1977	Erga and Heimdal (1984)
	Boknafjorden	1981	Erga (1989)
7	Hardangerfjord	1955, 1966	Braarud *et al.* (1974)
8	Baltic	1967–1969	Bagge and Niemi (1971)
	Baltic	1973–1976	Ackerfors and Lindahl (1975)
			Edler (1979)
9	Oslofjord	1957, 1958	Hasle and Smayda (1960)
	Oslofjord	1973	Dahl *et al.* (1974)
10	Loch Etive	1970, 1971	Wood *et al.* (1973)
11	Irish West Coast	1971	Dooley (1973)
12	Celtic Sea	1975	Pingree *et al.* (1976)
13	Kiel Bight	1972	Von Bodungen *et al.* (1975)
	Kiel Bight		Smayda (1983)
14	Dutch Coast	1973	Kat (1977)
	Galway Bay, Wadden Sea	1969–1985	Cadée (1986)
	Eastern Scheldt	1971	Bakker and Vegter (1978)
15	English Channel	1975–1976	Holligan and Harbour (1977)
16	English Channel	1978, 1979	Gros and Ryckaert (1983)
17	Ría de Vigo	1955	Margalef (1958)
18	Bou Grara (Tunisia)	1991	Kefi (1993)
19	Cochin Backwater	1969	Smayda (1983)
20	Auke Bay	1985–1989	Ziemann *et al.* (1991)
21	Monterey Bay	1976, 1977	Garrison (1981)
22	Nova Scotia	1977	Conover and Mayzaud (1984)
23	Narragansett Bay	1976, 1977	Smayda (1983)
	Narragansett Bay	1982	Rines and Hargraves (1987)
24	Vancouver Harbour	1976, 1977	Stockner and Cliff (1979)