ORIGINAL PAPER

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Seasonal shifts in ice edge phytoplankton blooms in the Barents Sea related to the water column stability

Abstract The development of the phytoplankton bloom and its relation to water column stabilisation during the transition from early to high summer (of 1991) in the seasonally ice-covered zone of the Barents Sea were studied from a meridional transect of repeated hydrographic/biological stations. The water column stabilisation is described in detail with the aid of vertical profiles of the Brunt-Väisälä frequency squared (N^2). The contributions of seasonal warming and ice melting to stabilisation are elucidated by determining the effects of temperature and salinity on N^2. The spring bloom in 1991 migrated poleward from June to July by about 400 km, associated with the retreat of the ice edge. The spring bloom culminated with maximum chlorophyll concentrations in the mixed layer about 100–300 km north of the centre of the meltwater lens, at its northern edge, where the ice cover was still substantial. From the distribution of N^2 it becomes obvious that the bloom starts at the very beginning of stabilisation, which results solely from the release of meltwater. The increase in temperature due to the seasonal warming does not contribute to the onset of vernal blooming; temperature starts to contribute to the stratification later, when the spring bloom has ceased due to the exhaustion of nutrients in the mixed layer. By that time a deep chlorophyll maximum has formed in the seasonal pycnocline, 20–30 m below the base of the mixed layer. The effect of the seasonal ice cover on the mean areal new primary production is discussed.

Introduction

The timing of the phytoplankton spring bloom is one of the key factors determining the length of the growth season, the annual primary production, and how the phytoplankton blooming matches with the life-cycle of grazers. It is thus one of the key determinants of the flow of carbon through the marine food web. It may also influence the global climate via the drawdown of carbon from the atmosphere to the deep ocean and sea floor, which is mediated by the sedimentation of biogenic material. This study emphasises the role of haline and thermal stratification for vernal mixed-layer shallowing and their influence on the timing of the phytoplankton spring bloom in the seasonally ice-covered zone, by analysing measurements made in the Barents Sea.

Our observations will be interpreted in the framework of the following concept of the seasonal cycle of phytoplankton growth in the pelagial. The major temporal changes in the vertical distribution of new production[1] that are expected to occur during the course of the year are sketched in Fig. 1, based on first principles according to which production is most severely limited by shortages of light and nutrients.

Light limitation is strongly controlled by the depth of mixing, following Sverdrup's (1953) theory that is based on the assumption that photosynthesis decreases exponentially with depth related to the irradiance profile, whereas the loss of phytoplankton biomass is vertically constant. During winter no net primary production is possible where turbulence generated by wind forces and surface buoyancy fluxes maintains a mixed

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[1] New production denotes that fraction of the primary production that is available for export to higher trophic levels or to sedimentation (Eppley and Petersen 1979), and is defined as being based on the consumption of the macro-nutrient, nitrate (Dugdale and Goering 1967).

Fig. 1 Hypothetical annual cycle of phytoplankton growth, illustrated by the distribution of those areas (*stippled*) in the time-depth domain within which new production is possible. D_H indicates the top of the main thermocline that coincides with the depth of deepest winter mixing. The course of the mixed-layer depth, D_m, is suggested by results of a 1-dimensional model (Woods and Barkmann 1986). The courses of compensation depth, D_c, and critical depth, D_{cr}, are determined through seasonal changes of the climatological surface irradiance (at, however, temperate latitudes) and an attenuation coefficient that is assumed constant (no self shading effects). D_N indicates the depth above which nutrients are exhausted (from Strass and Woods 1991)
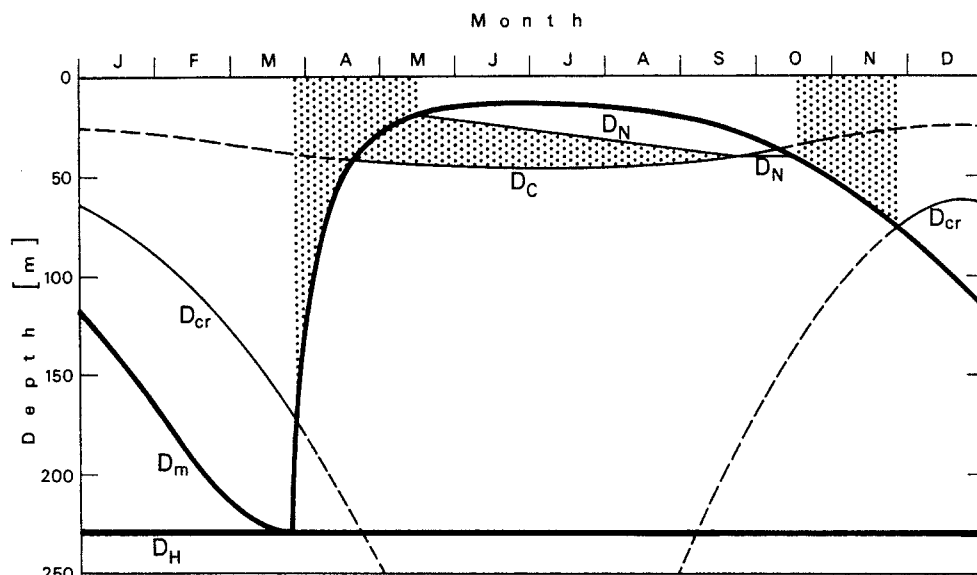
layer that extends so deep that phytoplankter circulating in it vertically receive an integrated amount of light that is less than would be required to compensate for losses of phytoplankton biomass. Winter, however, is the season when nutrients in the mixed-layer are replenished by entrainment from below. The growth season starts (according to Sverdrup 1953) in spring when the mixed-layer depth, D_m, becomes shallower than the critical depth, D_{cr}, which in counter-move deepens due to the seasonal increase of solar irradiance (Fig. 1). From then onward D_m defines the lower margin of the layer within which net production is possible, until it becomes shallower than the compensation depth, D_c. Thereafter the lower margin of the productive layer is marked by D_c, being located within the seasonal pycnocline; D_c defines that depth at which primary production and losses of phytoplankton biomass balance locally. The exhaustion of nutrients in the mixed layer through uptake by the growing phytoplankton marks the onset of seasonal oligotrophy and eventually terminates the spring bloom. During the course of the summer new production is only possible between the depth of the nutricline, D_n, and D_c. Before the annual growth season finally ceases an autumn bloom can occur if the relation between the vertical nutrient distribution, light availability and vertical mixing is such that $D_n \leq D_m \leq D_{cr}$ is satisfied. This condition may become satisfied as the result of strong wind events and lead to secondary blooms during summer (e.g. Sakshaug and Slagstad 1992).

The vernal shallowing of the mixed layer can be caused either by thermal stratification alone, which mainly results from solar heating, or by haline stratification arising from the release of light meltwater in regions that are seasonally ice covered. Whereas the warming due to the absorption of solar radiation is distributed over the water column following an ex-

ponential profile, the release of meltwater is confined to the top few metres, favouring the establishment of a shallower mixed layer. However, the seasonal warming cannot start before the ice has melted. It is therefore not obvious whether the melting of seasonal ice would accelerate or decelerate the vernal shallowing of the mixed layer.

Both processes of pycnocline formation can be observed in the Barents Sea (Loeng 1991). Related to the southward advance of the ice cover during the freezing season and its northward retreat during warming and melting, the southern boundary of the ice cover, the ice edge or marginal ice zone, sweeps over a large area (usually more than 0.5×10^6 km^2) of the Barents Sea (in total 1.4×10^6 km^2). By virtue of its influence on the penetration of light into the water and on the stratification of the water column, the seasonal change of the ice cover strongly influences the habitat of the phytoplankton.

Because the primary production in the Barents Sea supports, through the food chain, some of the world's richest commercial fisheries, it has attracted much scientific attention during the last decades. The most comprehensive investigations so far have been carried out between 1984 and 1989 during the Norwegian Pro Mare program (Sakshaug et al. 1991, and papers contained in that special volume of proceedings). The present study adds to this body of knowledge and related works (e.g. Rey and Loeng 1985, Rey et al. 1987; Skjoldal et al. 1987; Skjoldal and Rey 1989; Wassmann and Slagstad 1993) in that it is based on transects that extend further to the north and well into the ice, and that it includes a more detailed quantitative analysis of the relative roles of meltwater release and seasonal warming on stratification of the water column and the associated effects on the seasonal propagation of the spring bloom. It also contributes to our understanding

of the physical processes that make the marginal ice zones regions of elevated primary production (e.g. Smith 1987; Sakshaug and Skjoldal 1989) in general.

Materials and methods

At the beginning and the end of the Second European Polarstern Study (Arctic EPOS, Polarstern cruise ARK VIII/2), described by Rachor et al. (1992), RV "Polarstern" worked along an almost meridional track line across the Barents Sea, at roughly 32°E (Fig. 2). The first transect along that line covered the latitudes between 75°59′N and 77°27′N; the second covered the latitudes between 76°N and 80°42′N. The first transect was made in the period 22–26 June 1991 with the ship heading northwards, the second from 21–27 July 1991, with the ship heading southwards. The reoccupation of stations with about 1 month delay allows the study of temporal developments, during the transition from early to high summer.

At each station vertical profiles of temperature, salinity and pressure (depth) were obtained by lowering a CTD (Conductivity Temperature Depth sonde), type Neil Brown Mark III. A BACKSCAT fluorometer attached to the CTD made possible the continuous vertical profiling of the chlorophyll fluorescence in situ. The in situ fluorescence readings were later calibrated to give profiles of the chlorophyll a concentration (termed Chl in the following), using parallel bottle samples collected at 8–12 discrete depths down to 300 m with a General Oceanics rosette. The sample chlorophyll was extracted after filtering volumes of 0.5–1 l through Whatman GF/C filters with 90% acetone, and analysed on board with a Turner-Design fluorometer according to Evans and O'Reily (1987). Using the chlorophyll concentrations obtained from the bottle samples the in situ fluorescence calibration function was determined separately for each station. To allow for vertical variations of the calibration coefficient, the fluorescence yield (the ratio between the fluorescence reading and the chlorophyll concentration) was assumed to vary with depth following the shape of a Gaussian bell curve, determined as that analytical function best describing its observed vertical variations. This was made necessary because of the lack of irradiance measurements, which made it impossible to correct explicitly for the quenching of chlorophyll fluorescence due to ambient light (e.g. Strass 1990). The mean (rms, root mean square) error of the in situ fluorometric measurements of Chl was determined to be 0.14 mg m^{-3}. The errors in temperature, pressure, and salinity obtained from the CTD were estimated to 3 mK, 3 dbar, and $5*10^{-3}$ psu, respectively.

As a measure of the vertical stratification or static stability, the Brunt-Väisälä frequency squared, N^2, was derived from the vertical profiles of temperature and salinity following

$$N^2 = g \left[\beta \, \partial S / \partial z - \alpha \left(\partial T / \partial z - \Gamma_z \right) \right] \qquad \text{(Eq. 1)}.$$

where g is the acceleration due to gravity, T and S the temperature and salinity, α and β the thermal and haline expansion coefficients, respectively, and Γ_z the adiabatic lapse rate, with α, β, and Γ_z being dependents of T, S, and z. This Hesselberg-Sverdrup method (see Millard et al. 1990) allows for separating the individual effects of the thermal and haline vertical gradients. Accordingly, the contribution of temperature to the squared Brunt-Väisälä frequency is given by

$$N_T^2 = g \, \alpha \, (\Gamma_z - \partial T / \partial z) \qquad \text{(Eq. 2)}$$

and the contribution of salinity by:

$$N_S^2 = g \, \beta \, \partial S / \partial z \qquad \text{(Eq. 3)}.$$

Nutrient concentrations, determined from the discrete bottle samples by use of a Chemlab Continuos Flow Analyser, were provided by Luchetta et al. (1992).
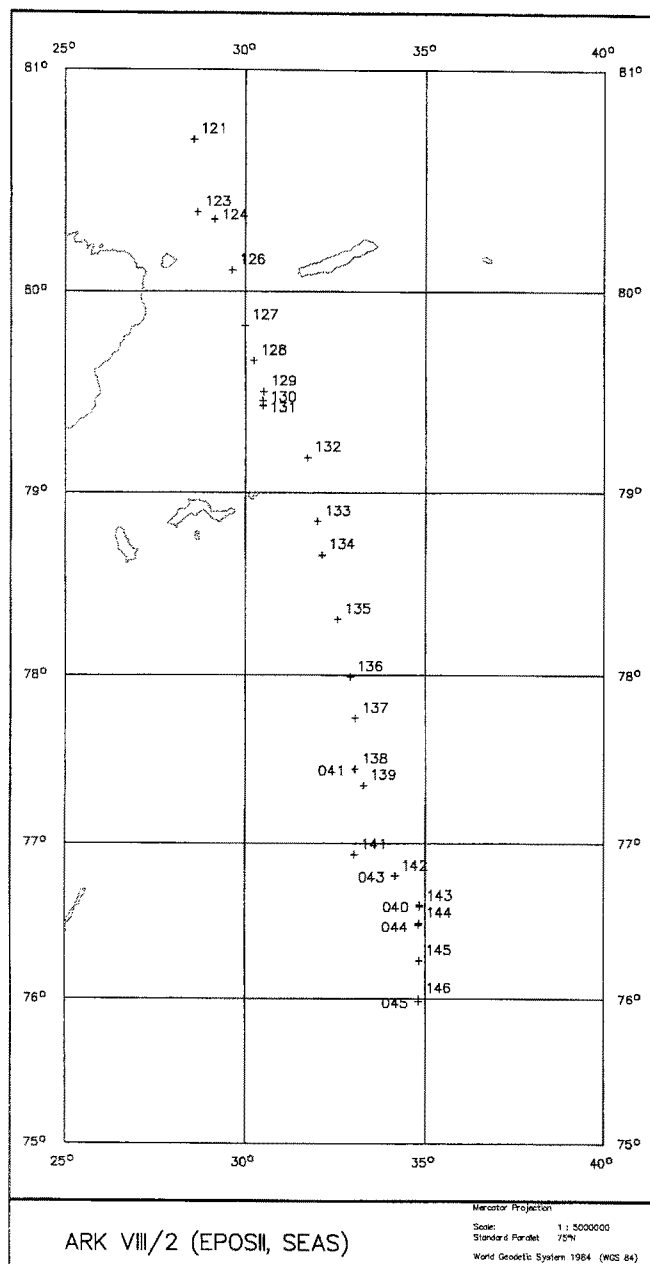

Fig. 2 Map of those stations made in the Barents Sea during Arctic EPOS that are used in this study. Stations 40–45 were occupied in the period 22–26 June 1991, stations 121–146 in the period 21–27 July 1991

Results

When the transect was visited the first time (22–26 June) the ice cover varied between zero and nine tenths, with the highest ice concentrations in the north (Fig. 3). During the revisit, about 1 month later, the ice cover in the same geographic range was drastically reduced to a maximum of one-tenth, and the ice edge (taken as the strongest gradient of ice cover) had propagated northward by 300–400 km.

Fig. 3 Distribution of ice cover along the quasi-meridional Barents Sea transect during its first and second occupation. The ice cover was determined by visual observations of the ship's officers, and is drawn versus distance, running southward from a reference position (close to the most northern point reached during the survey) of 81°50′N, 32°00′E at 0 km
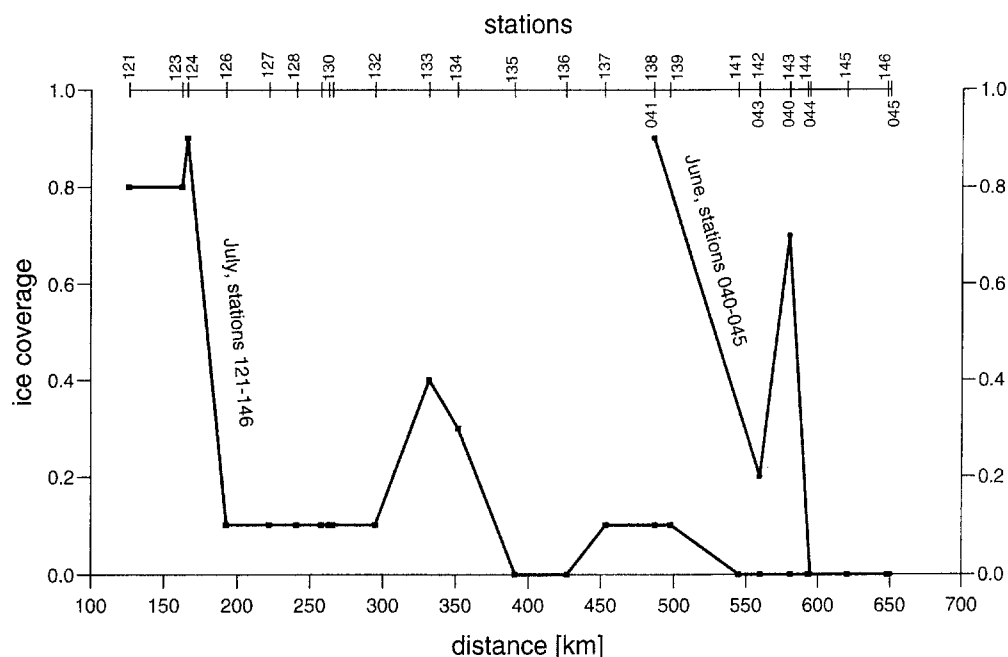
The June transect revealed enhanced chlorophyll concentrations in the mixed layer in the northern part, and a deep Chl maximum in the southern part (Fig. 4). The enhanced chlorophyll concentrations in the mixed layer provide evidence of a phytoplankton spring bloom, and the deep chlorophyll maximum, being associated with the nutricline (Luchetta et al. 1992), characterises a state of seasonal oligotrophy (referring to the concept of the phytoplankton seasonal cycle introduced with Fig. 1). The transition between the two regimes – spring bloom and seasonal oligotrophy – occurred between stations 041 and 043 (between 490 km and 550 km) where the ice coverage drastically decreased southward from nine-tenths to two-tenths (compare with Fig. 3). One month later, the surface bloom was replaced by a deep chlorophyll maximum everywhere along the line of repeated stations (Fig. 5c). Evidently, the mixed-layer bloom had propagated northward by about 300–400 km (Fig. 6c). Again, the transition from a mixed-layer bloom in the north to a deep chlorophyll maximum in the south (between stations 124 and 126) coincided with the strongest southward decrease of the ice coverage from nine-tenths to one-tenth. While the transition between the spring bloom and the oligotrophic regime coincided with the ice edge, the bloom itself occurred to the north of it, i.e. under the ice.

The northern limit of the bloom (defined by Chl $\geq 1\ \mathrm{mg\,m^{-3}}$) in July did not reach more than 50 km north of its southern flank. Further to the north the chlorophyll concentrations were low; at 11 of the 14 northernmost stations (not included in the sections shown here) Chl did not exceed $1\ \mathrm{mg\,m^{-3}}$ at any depth.

The narrow meridional extent of enhanced chlorophyll concentrations in the mixed layer (as observed in

July) suggests that the spring bloom is very short lived. A rough estimate of its duration may be obtained by relating its meridional extent of 50 km to the 300–400 km over which the bloom propagated poleward during the 1 month between June and July. This estimate indicates a duration of the spring bloom of about 3–5 days at a given locality. A comparable duration of the spring bloom is also suggested by the difference in the chlorophyll concentrations observed in the bloom maximum and in pre-bloom conditions (e.g. Fig. 6c). Assuming a phytoplankton growth rate of one doubling per day and starting with a pre-bloom Chl of $0.5\ \mathrm{mg\,m^{-3}}$, one ends up with $8\ \mathrm{mg\,m^{-3}}$ Chl after 4 days; one doubling every 2 days alternatively would yield a concentration of $4\ \mathrm{mg\,m^{-3}}$ after 6 days.

The spring bloom propagated poleward with the leading edge of the meltwater lens, approximately described by the northern outcrop of the 34.00 psu isohaline. The centre of the meltwater lens, located in, however, ice-free water south of the ice edge, propagated poleward somewhat slower than its leading edge: in June the minimum mixed-layer salinity was found around 600 km, and in July around 400 km (compare Figs. 4b and 6b). At the southern end of the section the fresh meltwater in the mixed layer to some extent was replaced by more saline water between June and July.

Fig. 4a–f Vertical distributions along the first Barents Sea transect ▶ of temperature **a**, salinity **b**, chlorophyll concentration **c**, squared Brunt-Väisälä frequency **d**, and the contributions of temperature **e** and salinity **f** to the squared Brunt-Väisälä frequency. The *distance coordinate* is the same as in Fig. 2. The station positions are indicated by the *upper x-axis*

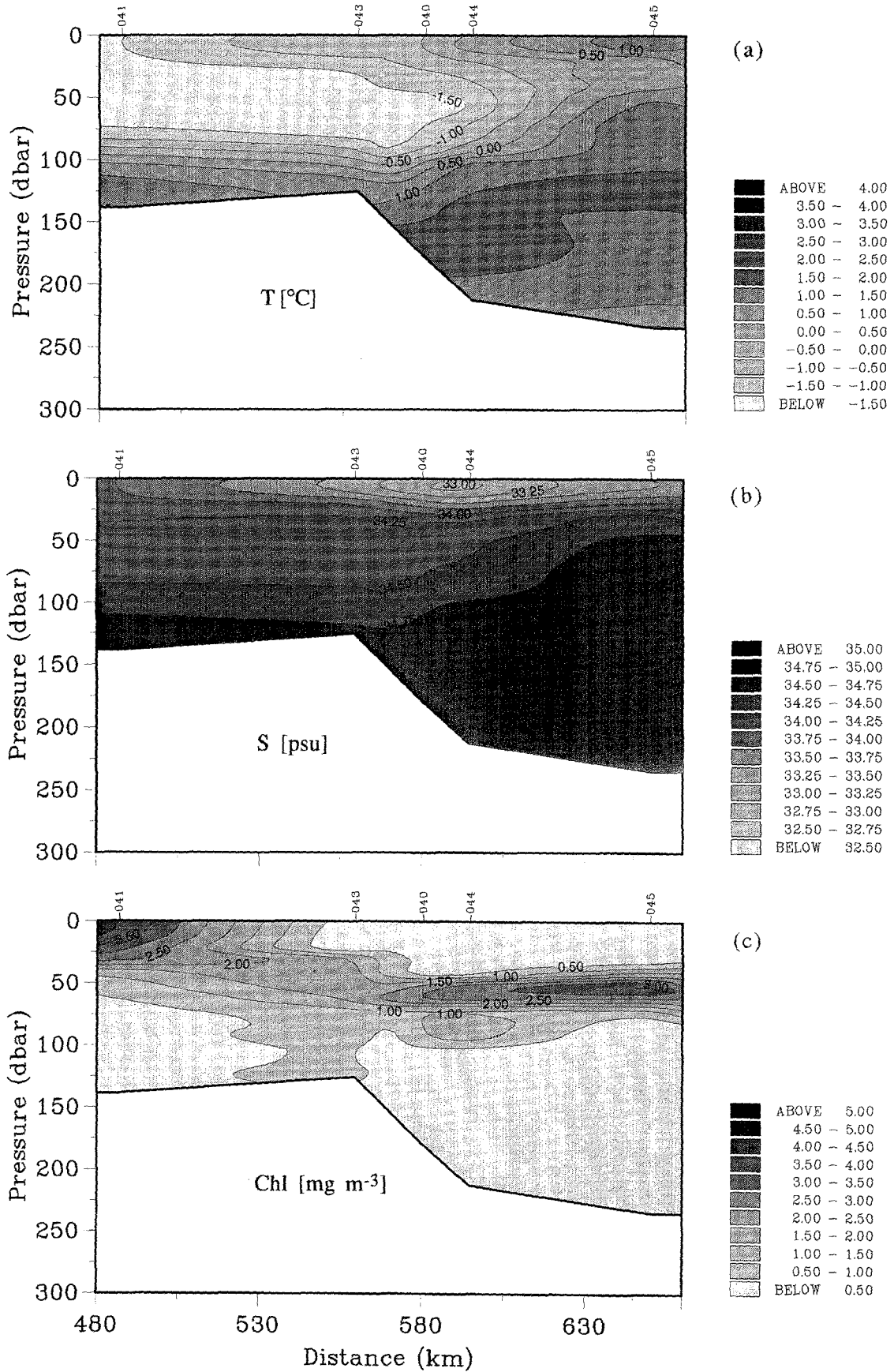# EPOSII: 1st Barents Sea Section

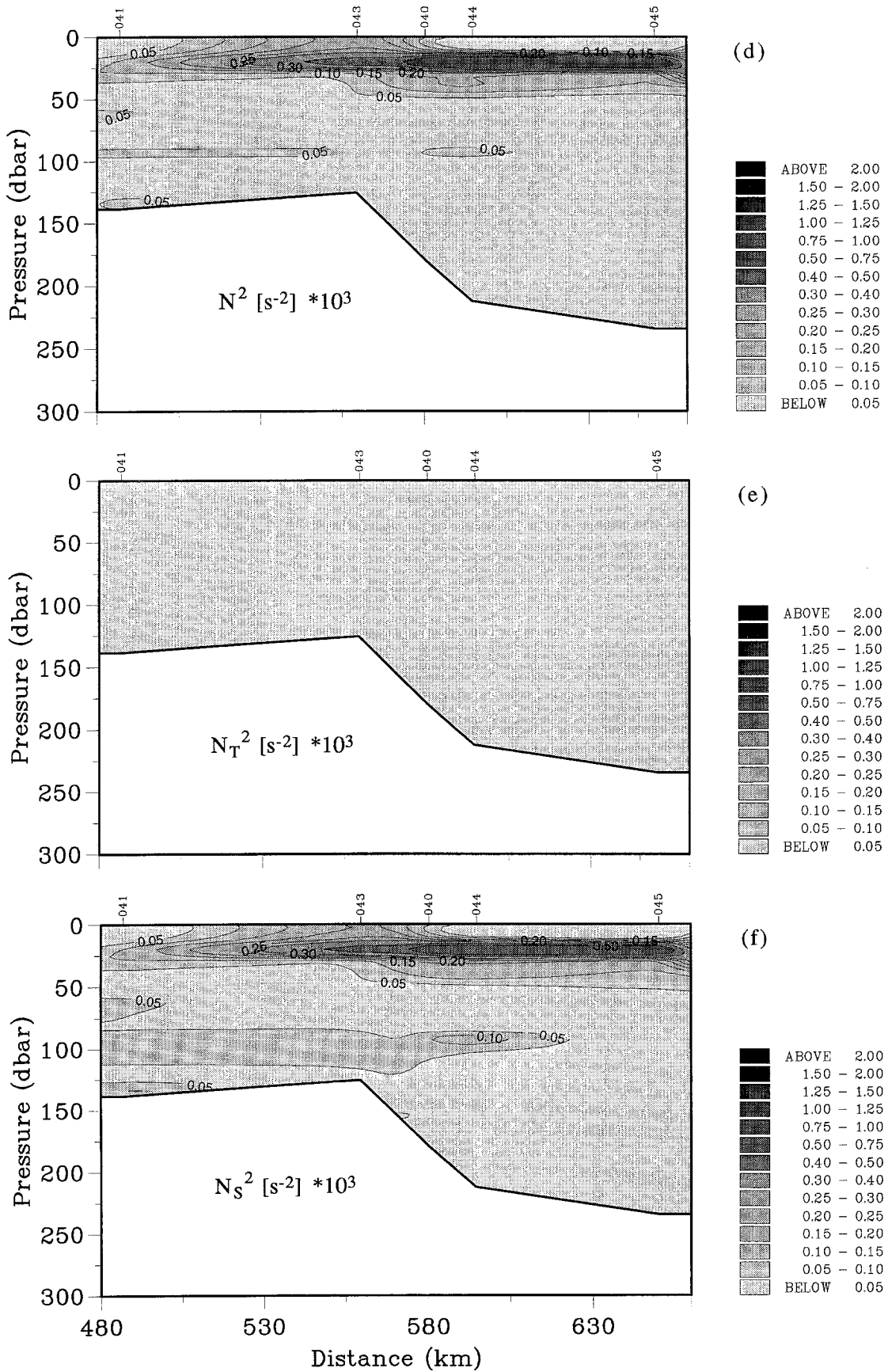Fig. 4a–c

EPOSII: 1st Barents Sea Section

Fig. 4d–f

The coincident poleward propagation of the spring bloom and the northern edge of the meltwater lens is explained by the immediate response of the phytoplankton to the onset of vernal stratification. The blooms both in June and in July occurred at the respective northern protrusions of the vertical maximum of the static stability N^2 (compare Figs. 4c and 6c with Figs. 4d and 6d). The vertical N^2 maximum near 25-m depth indicates the lower boundary of the summer mixed layer, or the top of the seasonal pycnocline, respectively; the northern protrusion of the stability maximum (where N^2 reaches values of about $0.1*10^{-3}$ s^{-2}) marks that position along the meridional line where the shallow summer mixed layer has most recently formed. Further north (north of 150 km; Fig. 6d) the stratification is vanishingly low and obviously not sufficient to suppress the vertical turbulent motion and the associated downward mixing of phytoplankton cells, and hence not sufficient to support a substantial growth, as indicated by the low chlorophyll concentration (Fig. 6c).

The weak stratification, setting off the spring bloom results from a salinity decrease in the mixed layer (Figs. 4b, 6b) from about 34.25 to 34.00. Such a decrease would be explained by the melting of 0.2 m of sea ice (of an assumed salinity of 3). The drop in salinity in the centre of the meltwater lens down to 32.5 (at stations 136 and 137 of the July transect, Fig. 6b) could have been achieved by the melting of 1.5 m of sea ice, which roughly corresponds to the mean ice thickness of 1.4 m observed in the area in June (Inall and Parker 1992).

Once the ice has completely melted and the highest stability is reached (e.g. in the lens of low-salinity meltwater between stations 044 and 045 in June, Fig. 4b, d, or between stations 135 and 138 in July, Fig. 6b, d), the spring bloom in the mixed layer is already over and the phytoplankton is concentrated in a deep maximum (Figs. 4c, 6c). Hence, static stability and mixed-layer Chl are positively correlated in time during the beginning of the vernal pycnocline formation and the onset of the spring bloom, but are negatively correlated after the peak of the spring bloom when stratification is still strengthening. Correlation again becomes positive later in summer, when the trend of stratification also reverses towards a weakening, associated with the disappearance of the meltwater lens.

Closer examination of the effects of temperature and salinity on the static stability confirms that stratification during the vernal development of the pycnocline in the seasonally ice-covered zone is largely dominated by the ice melt, with only a minor contribution by the seasonal warming of the water column (Figs. 4, 5, 6; panels d, e, f). Also, the stratification maxima induced by either temperature or salinity are decoupled in space and time: at a given time, the respective stratification maxima are separated by almost 200 km (Fig. 6e, f). At a given position, the thermal vertical gradient starts to significantly contribute to the stratification not before the haline vertical gradient has already weakened

(Figs. 4e, f, 5e, f). Related to the seasonal development of the phytoplankton, the thermal stratification is established after the nutrients in the mixed layer are already exhausted, i.e. too late to be of importance for triggering the onset of the spring bloom. At the time the thermal gradient is established it may even be disadvantageous for the growth of phytoplankton because it hinders the turbulent diffusive processes that otherwise could support a more substantial upward flow of nutrients into the impoverished euphotic zone.

The deep chlorophyll maximum (DCM), formed after exhaustion of nutrients in the mixed layer, is situated well below (up to 40 m; Figs. 4c, 5c, 6c) the base of the mixed layer as indicated by the vertical N^2 maximum (Figs. 4d, 5d, 6d). The DCM slopes down meridionally from north to south, from a depth of about 30 m just south of the spring bloom to about 50 m at the southern stations (Fig. 6c). The DCM also slopes down relative to the depth of the N^2 maximum (Fig. 6c, d). It is, however, closely linked to the depth of the nutricline, especially that for nitrate (Fig. 7).

Discussion

The finding that the deep chlorophyll maximum (DCM) is clearly separated from the depth of strongest stratification but is correlated with the depth of the strongest vertical nutrient gradient, confirms the hypothesis that the DCM is formed by new production at the depth of the nutricline (e.g. Wolf and Woods 1988; Strass and Woods 1991), leading to mutual deepening of the DCM and nutricline during summer. In accordance with that view, the meridional slope of the DCM is explained by the superposition of the poleward propagation of seasonal oligotrophy and a local deepening of the DCM and the nutricline when the nutrients in the mixed layer are exhausted. Due to random vertical displacements by the omnipresent internal waves, the local deepening of the DCM is, however, hard to extract from direct comparison of the few stations repeated with only 1-month delay between the first and second occupation of the Barents Sea transect.

The poleward propagation of the transition between the spring bloom and the DCM is clearly documented in our data set, whereas the poleward advance of the onset of the spring bloom unfortunately is not, as only the second transect extends far enough into the ice and beyond the northern edge of the bloom. However, the transition to seasonal oligotrophy lags the onset of the spring bloom by the time it takes to exhaust the nutrients in the mixed layer. We may therefore conclude that the onset of the spring bloom propagates poleward at about the same rate as the transition to

Fig. 5a–f Same as Fig. 4, but based on data recorded about ▶ 1 month later, between 25 and 27 July 1991
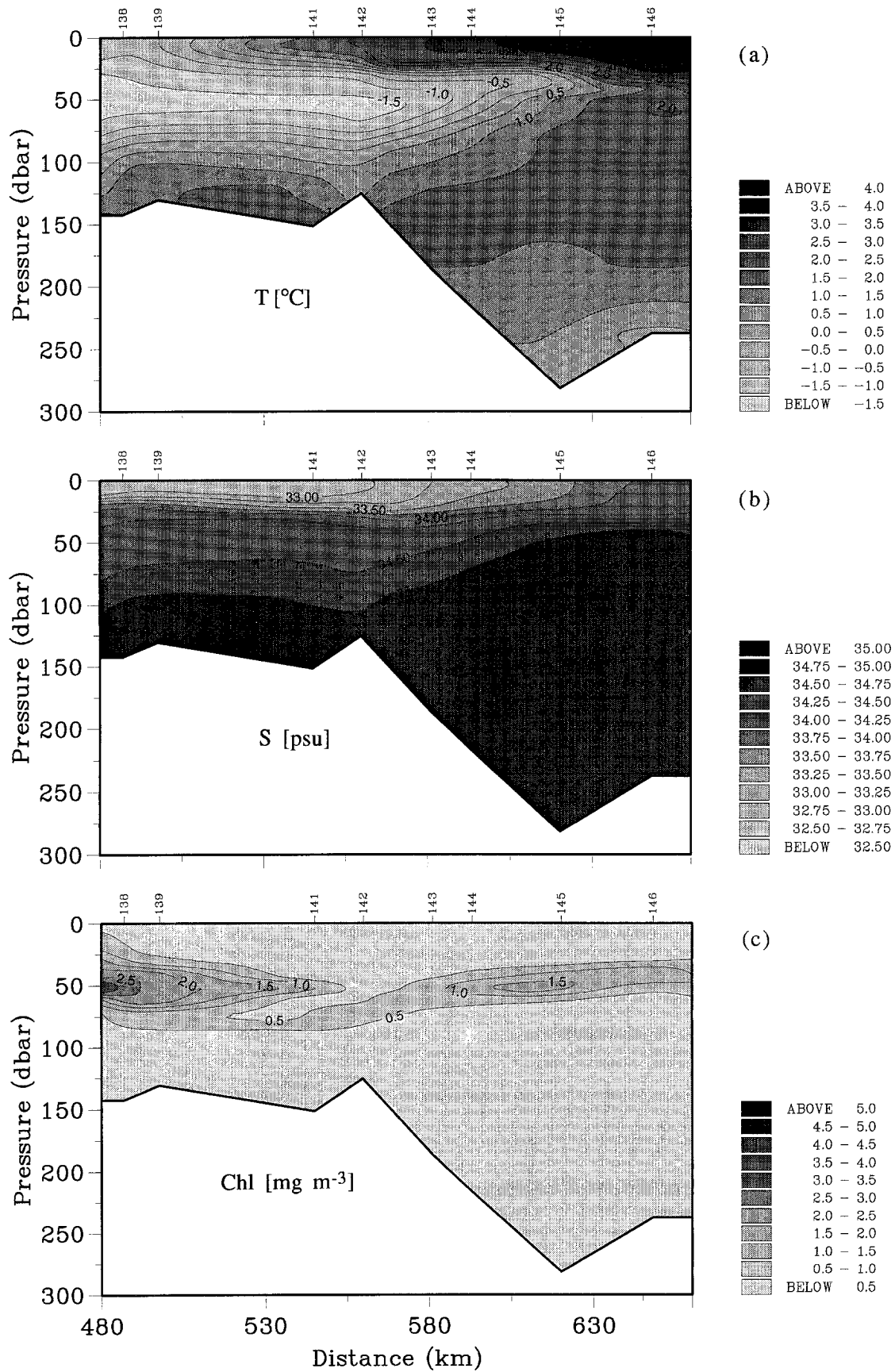
EPOSII: 2nd Barents Sea Section

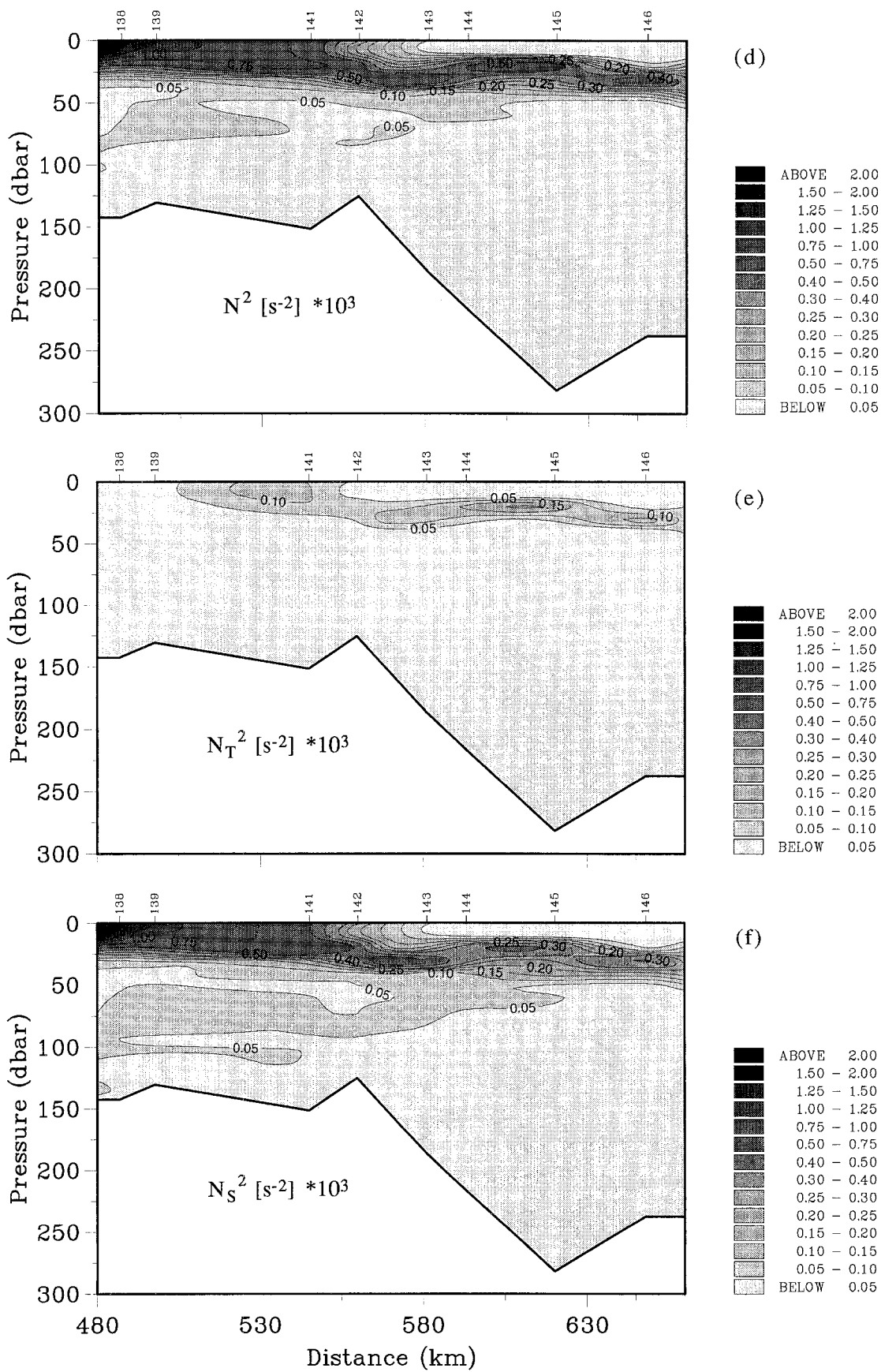

Fig. 5a–c

EPOSII: 2nd Barents Sea Section

Fig. 5d–f
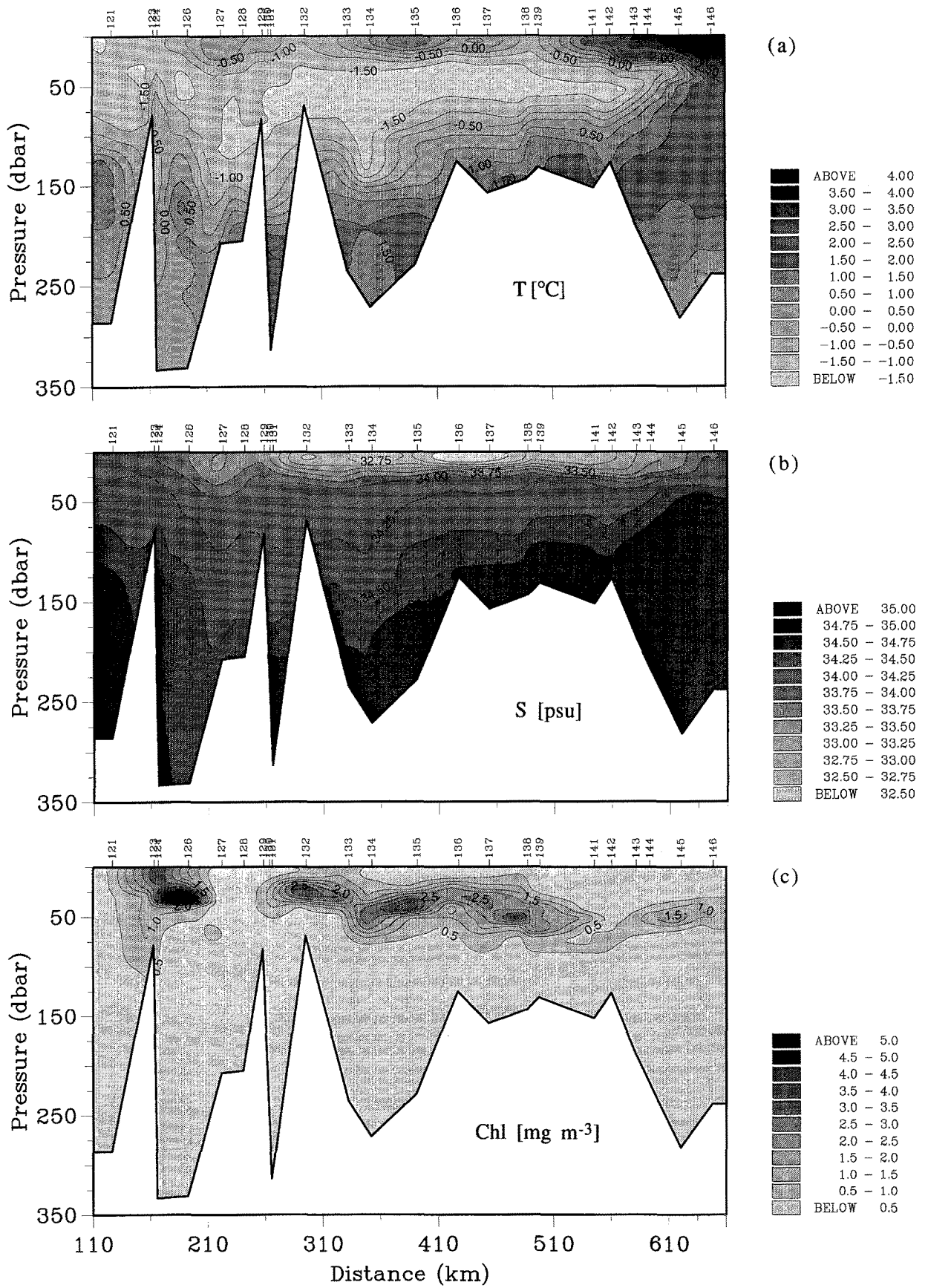
EPOSII: Long N–S Section

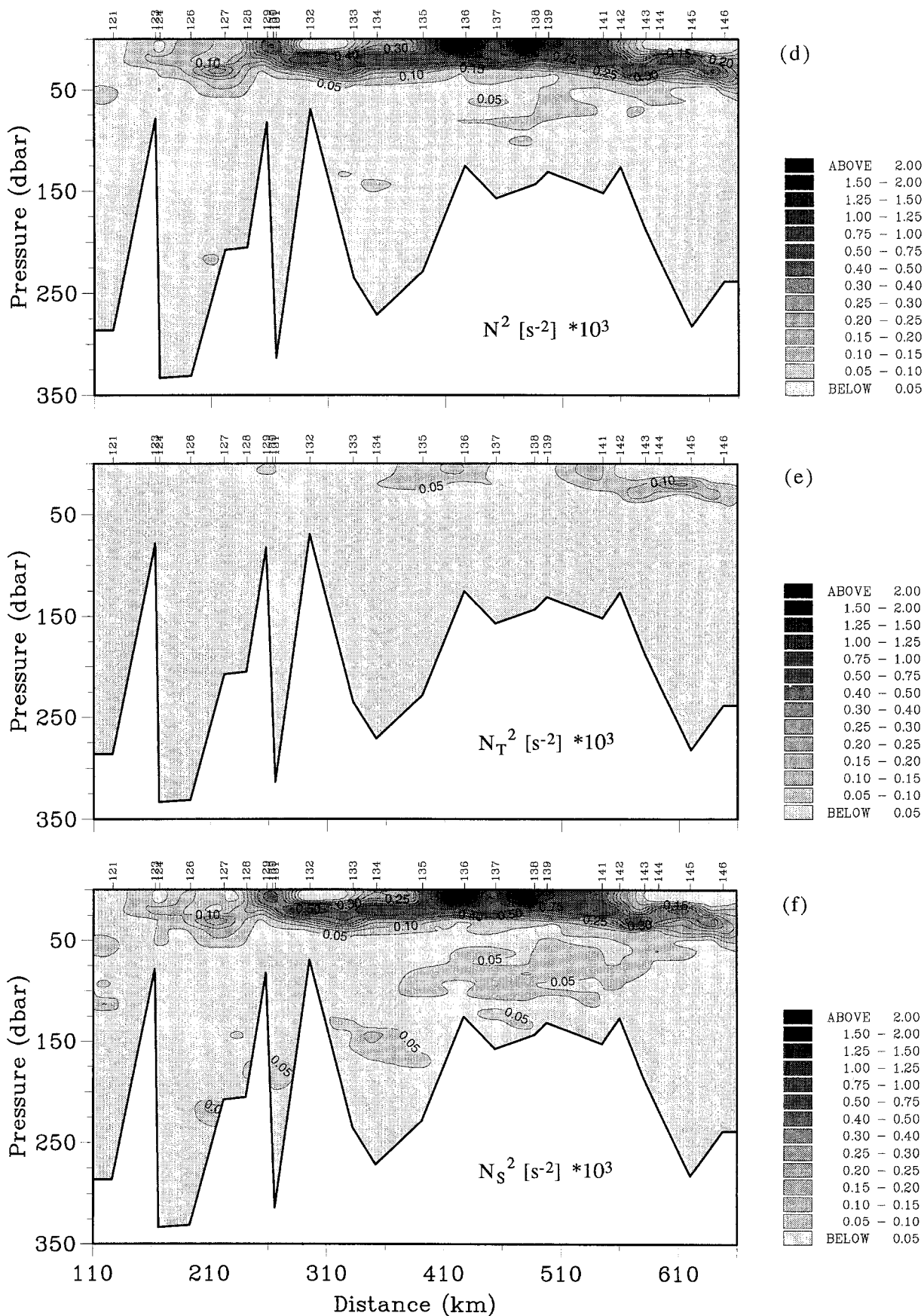Fig. 6a–c

EPOSII: Long N–S Section

Fig. 6d–f

◀ **Fig. 6a–f** Same as Fig. 5, but also including the more northern stations that were occupied during the second long north-south transect, but not during the first Barents Sea transect

oligotrophy, assuming a uniform initial concentration and uptake rate of the nutrients.

There is, nevertheless, evidence of a discontinuous poleward advance of the spring bloom. The low chlorophyll concentrations seen at stations 127 and 128 (Fig. 6c) between the mixed-layer bloom to the north and the deep Chl maximum to the south might indicate that the bloom develops earlier at a more northern position than at a more southern one on horizontal scales of about 100 km. Indeed, nitrate, at stations 127 and 128, was not completely exhausted in the mixed layer (Fig. 7). The apparent delay of the bloom at this location may be related to a somewhat deeper mixed layer than to the north and south (Fig. 6d), associated with an eddy-shape downward displacement of the isotherms and isohalines (Fig. 6a, b).

Although we have described the seasonal propagation of the spring bloom in relation to the retreating ice edge, it must be stressed that the bloom occurred underneath an almost closed ice cover, the thickness of which, however, decreased by melting. Phytoplankton growth underneath the ice is possible when the ice is transparent enough, this being to a large extent inversely related to the thickness of the snow cover on top. A transparent ice cover during the phase of melting can be very favourable for the pelagic phytoplankton because it supports the rapid formation of a shallow pycnocline by hampering downward wind-mixing of the meltwater.

A central question to be directed to the possible mean effect of the ice edge retreat on the areal production is: will the mean areal production increase or decrease if the physical conditions of a region change climatically from being seasonally ice covered to permanently open, or vice versa?

Certainly, where the seasonal melting starts late and becomes vanishingly small at the position of maximum poleward ice retreat marking the transition to a permanent ice cover, the annual growth season for the pelagic phytoplankton will be short and annual production will be low. In regions, however, where the seasonal ice is present for only a short time in winter, the situation may be quite different.

Our study has demonstrated that the water column stabilisation resulting from the release of meltwater precedes the thermal stratification. The effect is that the spring bloom peaks earlier at a particular place if it was covered by seasonal ice during the preceding winter, and later if it was permanently open during a warm winter (Rey et al. 1987; Skjoldal et al. 1987; Mitchell et al. 1991). From a regional point of view, the spring bloom in the zone of maximum seasonal ice extent starts earlier than in the more southern part of the Barents Sea, which is more directly influenced by the inflow of warmer Atlantic water and hence is permanently open (Rey and Loeng 1985; Rey et al. 1987; Sakshaug and Skjoldal 1989; Slagstad and Støle-Hansen 1991). The spring bloom in the seasonally ice covered zone may even precede by one month or more the spring bloom in the open central North Atlantic, 20° of latitude further south (Strass and Woods 1991).

Ignoring other control mechanisms of the algal blooming like grazing by herbivorous zooplankton, the above may indicate a prolongation of the growth season due to the existence of a seasonal ice cover, and an associated increase in the annual production. A prerequisite for a prolongation of the growth season, however, is that primary production continues after the end of the spring bloom in the deep chlorophyll maximum that forms subsequently. A continuation of new production during summer in the deep chlorophyll maximum has already been discovered in the open North Atlantic where it contributes a significant

Fig. 7 Vertical distribution of the concentration of nitrate (μmol l^{-1}) along the whole second, north-south Barents Sea transect (same section as shown in Fig. 6); figure kindly provided by A. Luchetta and G. Civitarese

NITRATE (μM)
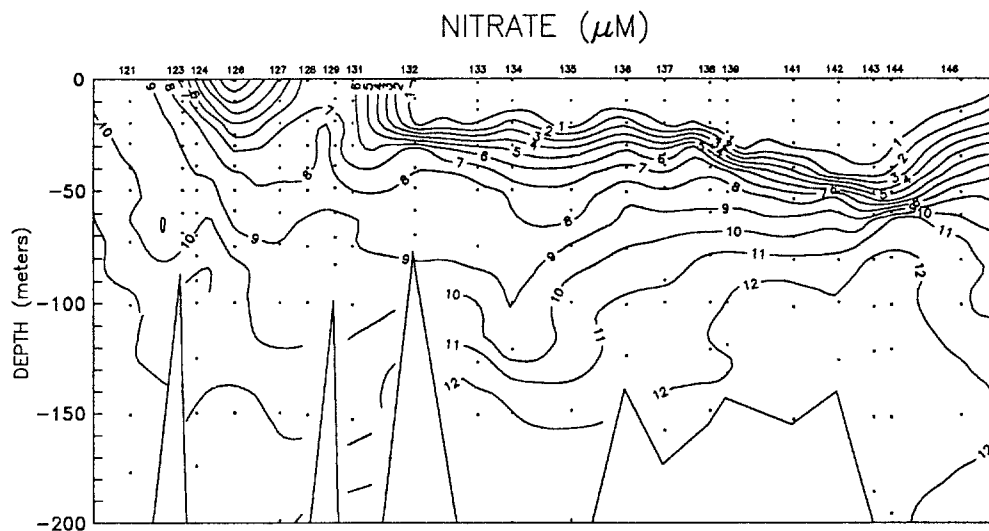
fraction to the annual new production (Strass and Woods 1991). The meridional slope of the DCM and nutricline as well as the local deepening of both documented by our data support the view that new production also continues in the Barents Sea.

An estimate of the new production may be obtained by vertically integrating the nitrate consumption, defined as the difference between the initial late-winter concentration and that nitrate concentration actually observed at a particular time of the growth season, and converting nitrate-nitrogen into carbon using the Redfield ratio of 106/16 (Redfield et al. 1963). Assuming an initial late-winter nitrate concentration in the mixed layer of 10 µM (which is implied by concentrations found at greater depth in summer, Fig. 7, and is also suggested by the valuation of Glover and Brewer 1988) and using the measured nitrate concentrations of Luchetta et al. (1992), new productions of 32 g C m^{-2} until June and 42 g C m^{-2} until July at the location of stations 043 and 142 are suggested. That pair of stations has been selected for this estimation because of the almost exact coincidence of the station positions, and because station 043 is the northernmost station of the first transect with a distinct deep Chl maximum already formed. The difference of 10 g C m^{-2} between July and June can be attributed to new production that is associated with the deepening of the DCM during that 1 month. It is reasonable to assume that new production associated with the DCM will continue, albeit at a somewhat reduced rate, until the end of the growth season. A reasonable estimate for the annual new production at this location might be 50 g C m^{-2}, probably being composed of about equal amounts of production from the short-lived but intense spring bloom and of the longer-lasting production in the deep Chl maximum. The 50 g C m^{-2} annual new production is also in general agreement with an earlier estimate based on nitrate consumption (Rey et al. 1987) and with model results (Wassmann and Slagstad 1993) for the central Barents Sea.

The nitrate concentrations observed in July (Fig. 7) indicate a nitrate consumption and hence an integral new production that is highest at the southernmost extension of the seasonal ice cover (Fig. 2), which, incidentally, coincided with the position of the Polar Front (revealed by the strongest inclination of isotherms and isohalines; Figs. 4a, b, 6a, b; see also Loeng 1991), where the spring bloom started earliest. Integral new production as evidenced by the depth of the nutricline decreases as much to the north, associated with the delayed onset of the bloom, as to the south where the nutricline is less well formed as the result of a different vernal establishment of the seasonal pycnocline, which lacks the early formation of a shallow mixed layer associated with the meltwater release.

The apparent decline of new production to the south of the Polar Front does not corroborate the results of existing model studies (Slagstad and Støle-Hansen 1991; Wassmann and Slagstad 1993), which suggest an annual primary production about twice as high in the Atlantic sector of the Barents Sea as in the seasonally ice-covered zone, with the extra of the annual amount either being ascribed to production that takes place before the formation of a distinct bloom or to secondary peaks of production associated with wind events (Sakshaug and Slagstad 1992). Indeed, our data reveal substantial phytoplankton biomass and new primary production in the more northern, seasonally ice-covered part of the Barents Sea where measurements have been sparse and the related models (Slagstad and Støle-Hansen 1991; Wassmann and Slagstad 1993; Sakshaug and Slagstad 1992) predict a vanishingly low production.

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