# PRIMARY PRODUCTION IN RELATION TO CLIMATIC CHANGES IN THE BARENTS SEA

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## ABSTRACT

The Barents Sea is characterized by extreme environmental conditions that have considerable influence on the biological development, especially during spring. Based on physical and biological observations obtained during a six years period and a mathematical model for phyto- and zooplankton, we have examined the biological development in relation to the climatic changes which occurred during this period. The main effect of climatic variations is in determining the timing of the phytoplankton spring bloom in the different water masses. Warm years are characterized by a delayed phytoplankton bloom and an earlier stage development of zooplankton in Atlantic waters, apparently resulting in a higher proportion of the spring bloom being grazed and channelized to higher pelagic trophic levels. Cold years, on the contrary, can result in earlier ice-edge spring bloom and late development of zooplankton, causing a significant portion of the primary production to be left ungrazed and to sediment out to the deeper water layers and the bottom.

# INTRODUCTION

The influence of ice and hydrographical conditions on the biological production of the Barents Sea has been described based both on field observations (MARSHALL 1957, REY and LOENG 1985) and on simulations with a mathematical phytoplankton model (SLAGSTAD 1985). The start of the spring phytoplankton bloom in the central part of the Barents Sea is closely related to water column stabilization, as described by SVERDRUP (1953). The timing of the bloom can be quite variable depending on the specific physical factors that are responsible for stabilization (REY and LOENG 1985). In waters that have been covered by ice, the necessary stability for the spring bloom is produced by melting of the ice. As a general rule, the bloom will take place earlier here than in more southern areas with Atlantic waters not covered by ice, where the vertical stability is due to warming of the upper layer (SKJOLDAL, HASSEL, REY and LOENG 1987).

As the ice recedes northwards, it is followed by a phytoplankton bloom at its edge. The marked pycnocline formed by the meltwater will effectively isolate the surface layer from the deeper water layers below it. Following nutrient depletion by the spring bloom, this upper layer can be characterized as oligotrophic water, where most of the biological production is supported by remineralization of nutrients, either through zooplankton grazing or bacterial activity.

Since the phytoplankton production processes are closely related to the physical environment, changes in hydrographical and ice conditions from year to year will undoubtedly have an effect on the temporal development of the spring bloom and possibly also on the overall production of the Barents Sea. Here we examine the possible effects of such climatic changes by using data obtained in late spring or early summer through 6 years, from 1979 to 1984. The basic data are presented in SKJOLDAL et al. (1987) and analysed there with respect to the timing of the bloom development and zooplankton reproduction and development. In the present paper, we analyse these data further, emphasizing the quantitative and vertical aspects of primary production. For this purpose we have also included results from a mathematical simulation model (SLAGSTAD 1981, 1982).

# MATERIAL AND METHODS

The present investigation is mainly based on observations made during late spring or early summer at a south-north section, section I, in the central Barents Sea (REY and LOENG 1985, SKJOLDAL et al. 1987) each year in the period 1979-1984. Sampling and analytical procedures have been previously described (ELLERTSEN, LOENG, REY and TJELMELAND 1981, ELLERTSEN et al. 1982, GJØSÆTER, HASSEL, LOENG and REY 1983a, GJØSÆTER et al. 1983b, HASSEL, LOENG, REY and SKJOLDAL 1984, REY and LOENG 1985). A short overview of the methods is also presented by SKJOLDAL et al. (1987).

A phytoplankton model was used to follow the dynamics of phytoplankton and nutrients as functions of the seasonal light intensity, vertical mixing, ice cover and zooplankton grazing (SLAGSTAD 1982). The equation describing the growth, sinking and turbulent mixing of phytoplankton is given by:

$$\frac{\delta P(t,z)}{\delta t} = -W \frac{\delta P}{\delta z} + \frac{\delta}{\delta z} (D_z \frac{\delta P}{\delta z}) + f \text{ biol}$$
(1)

where z is depth, t is time, and P(t,z) is the concentration of phytoplankton. The first term on the right hand side of the equation represents the vertical transport (sinking), whereas the second term represents the vertical turbulent mixing. The biological term, f biol, describes how respiration, light, nutrients and grazing affect the phytoplankton production:

f biol = 
$$P_{\text{max}} f_1(I_z)G_N P - \phi_r P - qI(P)$$
 (2)

The first term on the right hand side of the equation represents growth and the second term represents respiration and mortality of the phytoplankton. The last term gives the effect of the grazing pressure from zooplankton. P<sub>max</sub> is the maximum growth rate or uptake rate of nitrogen (which is assumed to be the limiting nutrient) and is a function of temperature.  $f_1(I_z)$  gives the effect of light on the growth rate (SLAGSTAD 1982).  $G_N$  is a Michaelis-Menten expression to account for reduced growth rate<sup>N</sup> when concentration of nitrogen is reduced (SLAGSTAD 1985).

A mathematical model was also used to calculate production of zooplankton as a function of the concentration of phytoplankton and temperature. This model is described in detail by SLAGSTAD (1981) and only a brief outline is given here. The zooplankton biomass was assumed to be dominated by <u>Calanus finmarchicus</u> and the model parameters were adjusted accordingly. The zooplankton model is made up of three sub-models. The population sub-model calculates growth and reproduction rates as functions of the biological state. The biological state, which is calculated in the second sub-model, is again a dynamic function of the environment (available food concentration and temperature) and animal size. The third sub-model calculates the vertical migration of the animals as a function of the biological state, food concentration and light intensity.

The zooplankton model is coupled to the phytoplankton model in order to represent this dynamics as a function of physical conditions and grazing.

#### RESULTS

The position of the ice edge from January to September in the years 1979-1984 is shown in Fig. 1. It is seen that 1979 and 1981 were years when the ice was distributed south of  $75^{\circ}N$ . In contrast, in 1983 the ice edge barely extended south of  $77^{\circ}N$ .



Fig. 1. Monthly mean position of the ice border between 30 and  $35^{\circ}E$  from January to September in the years 1979-1985.

A summary of positions of the ice-edge and the melt water front at different times of the year is presented in Table 1. The ice recedes in general fairly slowly from April to June, whereas its receding speed increases markedly up to September when it usually reaches its northernmost extension. The melt water front, on the contrary, recedes northwards much less than the ice edge (Table 1). The recession of the melt water front is mainly the result of erosion by mixing with Atlantic water. As can be seen from Table 1, all the area north of about 76°30'N remains covered by melt water. The strong pycnocline associated with this layer effectively limits the input of nutrients to the upper mixed layer, resulting in an oligotrophic surface layer that remains throughout the summer. This is an important feature which influences the overall productivity of this region.

Year	Average ice edge position			Postition of melt water front		Extension of melt water area in September		
	Apri1	June	Sept.	June	Sept.	Eroded	Not eroded	
1981 1979 1982 1980 1984 1983	74 <sup>°</sup> 12'N 74 <sup>°</sup> 42'N 75 <sup>°</sup> 48'N 76 <sup>°</sup> 10'N 76 <sup>°</sup> 35'N 77 <sup>°</sup> 25'N	75 <sup>°</sup> 30'N 75 <sup>°</sup> 05'N 75 <sup>°</sup> 50'N 76 <sup>°</sup> 18'N 77 <sup>°</sup> 05'N 76 <sup>°</sup> 42'N	80 <sup>°</sup> 15'N 82 <sup>°</sup> 10'N 78 <sup>°</sup> 25'N 79 <sup>°</sup> 55'N 81 <sup>°</sup> 50'N 81 <sup>°</sup> 00'N	75 <sup>°</sup> 05'N 75 <sup>°</sup> 20'N 76 <sup>°</sup> 10'N 75 <sup>°</sup> 55'N 76 <sup>°</sup> 00'N 76 <sup>°</sup> 15'N	76 <sup>°</sup> 10'N 75 <sup>°</sup> 50'N 76 <sup>°</sup> 50'N 76 <sup>°</sup> 30'N 76 <sup>°</sup> 50'N 76 <sup>°</sup> 50'N	118 nm 68 nm 62 nm 20 nm 15 nm 8 nm	245 nm 380 nm 95 nm 205 nm 300 nm 250 nm	

Table 1. Positions of ice edge and melt water front and extension of the melt water area in the years 1979-1984.

The stage of development of the hydrographical and biological conditions at the time of coverage of section I in each of the years 1979-1984 can be observed in Figs 2 to 4 which show the vertical stability of the water column, the chlorophyll a concentration, and nitrate utilized, respectively. The stability in the upper 100 m was always higher in the area that had been covered by ice than in the Atlantic water not influenced by ice (Fig. 2). The stability in the melt water area was mainly the result of a decrease in salinity, while in the southern part of the section it was due to an increase in temperature. The vertical stability of the water column south of the melt water front was lowest in 1982, higher in 1983 and 1984 and highest in 1980. The position of the meltwater front, which at this time of the year reflects quite well the southernmost extension of the ice-edge, also indicates that 1979 and 1981 were cold years.

The time of coverage has varied somewhat, and this must be taken into account when comparing the bloom developments in the different years. The section was covered on 11-12 July in 1979, in late June in 1980 and 1981, and in early June in 1982, 1983 and 1984 (SKJOLDAL et al. 1987). In the cold years 1979 and 1981, the low concentrations of chlorophyll a north of the melt water front both in the upper mixed and deeper layers, together with the high nitrate utilization, indicate that long time had elapsed since the spring phytoplankton bloom at the ice edge. However, in the Atlantic water not covered by ice in 1981, relatively high average concentrations of chlorophyll a in the upper layer indicate that the spring bloom had taken place more recently.

The high chlorophyll a concentrations found during late June in 1980, especially south of the melt water front, indicate that the spring phytoplankton bloom took place much later than in 1979 and 1981 (Fig. 3). The average nitrate utilization in the upper layer in these three years varied from about 10 to 12 µM nitrate, indicating nitrate depletion of the upper layer by phytoplankton (Fig. 4). The relatively high nitrate utilization below the upper mixed layer is due mainly to the conspicuous chlorophyll a maximum that develops below the pycnocline towards the end of the spring bloom (REY and LOENG 1985). A trend of lower nitrate utilization towards the north can also be observed; this could reflect a trend in the spring phytoplankton bloom development, with the youngest stage of the bloom to the north. The same trend can be observed in the depth stratum from 100 to 200 m, although the decrease in nitrate concentration in this layer reflects upwards transport by vertical mixing and subsequent utilization in the euphotic zone.



Fig. 2. Density ( $\Delta \sigma t$ ), salinity ( $\Delta S^{\circ}/oo$ ) and temperature ( $\Delta t^{\circ}C$ ) gradients in the upper 100 meter water column at different latitudes in the main section during 1979–1984.



Fig. 3. Average chlorophyll  $\underline{a}$  at different depth layers and depth of the mixed layer at different latitudes in the main section during 1979-1984.



Fig. 4. Average nitrate utilization at different depth layers and at different latitudes in the main section during 1979-1984.

In 1982, the phytoplankton bloom had already taken place at the ice edge. In the Atlantic water that had not been covered by ice, the low vertical stability of the water column (Fig. 2) had delayed the spring bloom, although a noticeable phytoplankton growth could be observed (Fig. 3). The upper mixed layer was very deep, up to 200 m, which resulted in a fairly large consumption of nitrate in the 100 to 200 m layer (Fig. 4). In the southernmost part of the section which was influenced by the Norwegian Coastal Current, the upper mixed layer was about 50 m deep, and the spring bloom was more progressed than in the homogenous Atlantic water further north. In 1983, the situation was more or less similar to that in 1982, but slightly higher vertical stability in the Atlantic water had resulted in a somewhat earlier spring bloom (Figs 2 and 3). In this year, sampling was extended to ice covered regions and this allowed a more complete description of the spring bloom in the marginal ice edge zone (Figs 3 and 4). Some growth, indicative of a prebloom phase, was observed further into the ice to the north. In 1984, a marked spring bloom was observed near the ice edge, but in the remaining part of the melt water areas the bloom was already over. The higher vertical stability in the Atlantic water in 1984 (Fig. 2) caused the spring bloom to take place earlier than in 1982 and 1983, and most of the chlorophyll a was found below the pycnocline (Fig. 3).

The distribution of zooplankton biomass along the section during the six years is shown in Fig. 5. In 1979 to 1981 zooplankton biomass values were quite high at the middle of the section and decreased towards the ice edge. In 1982 the zooplankton biomass was lower than in the previous years, but it was still relatively high. The grazing pressure on phytoplankton combined with the low stability and the deep mixed layer could together have been responsible for the delayed phytoplankton bloom in the Atlantic water in 1982. In 1983 and 1984 the zooplankton biomass decreased drastically along the whole section. Reduced grazing pressure could have resulted in more massive sinking of phytoplankton from the euphotic zone due to nutrient depletion and explain the relatively large concentrations of chlorophyll <u>a</u> found below the upper mixed layer down to 100 m depth (Fig. 3).

Looking at the investigated period as a whole, relatively large variations in the development of the spring phytoplankton bloom were observed, depending mainly on the degree of vertical stability of the water column. The peak and culmination of the bloom varied by as much as 4-5 weeks in the period 1979-1984 in a given area. An attempt to date the timing of the spring bloom development is given in an accompanying paper (SKJOLDAL et al. 1987).

Fig. 6 shows the integrated content of chlorophyll a in the upper 100 m plotted against the vertical stability of the same layer. In the Atlantic water where the stability is regulated by the warming of the upper layer, the integrated content of chlorophyll a increased with increasing values of the vertical stability (Fig. 6A). In the areas covered by melt water where the stability is stronger and mainly due to a decrease in salinity, the relationship was not so obvious because of the wide range in seasonal phytoplankton development. The highest chlorophyll a contents were found at moderately high stability values (Fig. 6B). The chlorophyll content decreased as the stability increased further, reflecting the culmination of the bloom and disappearance of chlorophyll from the water column.

The degree of vertical stability is important in determining the extension of vertical mixing and consequently the magnitude of input of nutrients from the deeper layers to the euphotic zone. This can be illustrated by Fig. 7 where

the decrease in nitrate concentration in the 100 to 200 m depth layer has been plotted against the degree of vertical stability in the upper 100 m. Low stability resulted in a large decrease in nitrate in this layer due to deep mixing. The degree of apparent nitrate utilization decreased rapidly with increasing stability.

Nitrate is the main nitrogen source for phytoplankton growth during the spring bloom. One way to compare the nitrate utilization is to relate it to a



Fig. 5. Zooplankton biomass at different latitudes in the main section during 1979-1984.



Fig. 6. Integrated chlorophyll  $\underline{a}$  as a function of the degree of vertical stability in the upper 100 meters for A) stations that have not been covered by ice and B) stations with a melt water upper layer.

biomass parameter such as chlorophyll a. This has been done for the whole investigated period, separating the values for the upper mixed layer from those from the deeper layer down to 100 m depth (Fig. 8). The main disadvantage with such a comparison is that chlorophyll a in late phases of the spring bloom can be removed from a certain layer by grazing, sinking or natural degradation, and will therefore not be representative of the biomass produced during the bloom.



Fig. 7. Average nitrate utilization between 100 and 200 meter depth as a function of the degree of vertical stability in the upper 100 meters.

The solid line in Fig. 8 corresponds to 0.84 mg chlorophyll a m<sup>-3</sup> per  $1 \mu M$ nitrate. This can be taken as an estimate of the amount of chlorophyll produced per unit nitrate consumed, in the absence of any losses of chlorophyll. The data points closest to this line are from 1984 and 1983, which were the years when the zooplankton biomass and assumedly also the grazing pressure were lowest (Fig. 5). If we assume a mean weight ratio of chlorophyll a/phytoplankton carbon of 0.017 (n=46) (REY, unpublished observations) for phytoplankton during the spring bloom both at the ice edge and in Atlantic waters, then 1  $\mu$ M nitrate should result in a biomass of about 50 mg C  $\cdot$  m<sup>-3</sup>. Since the mean particulate atomic N/C ratio of the same samples was 0.189, it seems that most of the phytoplankton nitrogen (78% or more) originated from winter nitrate. Taking 10 and  $11.5 \mu M$  as winter concentrations of nitrate for ice-covered and not ice-covered waters, respectively, then 635 and 730 mg C  $\cdot$  m<sup>-3</sup> would be produced until the upper mixed layer became depleted of nitrate. In the Arctic waters when a shallow melt water layer became depleted of infrate. In the Arctic waters when a shahow melt water layer is formed (about 20 m), the total amount of carbon produced will be approximately 13 g C  $\cdot$  m<sup>-2</sup>. In Atlantic water with an upper mixed layer 30-40 m deep, the carbon produced will be between 22 and 29 g C  $\cdot$  m<sup>-2</sup>. It has been shown that nitrate can become depleted well below the pycnocline LOENG 1985) and that a reduction in nitrate (REY and concentration can be observed as deep as to 200 m (Figs 4 and 7). Usually, a noticable reduction in nitrate occurs down to about 100 m. From the nitrate utilization values for the upper 100 m shown in Fig. 4, the total production can be calculated to be on the average 49 and 54 g C  $\cdot$  m<sup>-2</sup> for the Arctic and Atlantic waters, respectively.



Fig. 8. Average chlorophyll  $\underline{a}$  as a function of average nitrate utilization at the upper mixed layer (open symbols) and below the upper layer and down to 100 meter depth (filled symbols).

These values compare quite well with estimates of the primary production of the spring bloom based on measurements of radiocarbon uptake (REY, unpublished data). During the prebloom situation, when chlorophyll a levels are about  $0.5 \text{ mg} \cdot \text{m}^{-3}$ , the primary production ranges from 100 to 400 mg  $C \cdot m^{-2} \cdot day^{-1}$  and then rapidly increases in the spring bloom to values usually about 2 g C  $\cdot m^{-2} \cdot day^{-1}$ . This period of the bloom with very high production rates is short-lived, since later on the large amount of organic material produced effectively reduces the penetration of light, limiting high production rates only to the surface layers. So, primary production rates decrease rapidly again to more stable and moderate rates during summer. The culmination of the bloom is usually reached when nutrients become depleted, and thereafter most of the phytoplankton growth is based on remineralized nutrients. The biological conditions during summer are more stable in the sense of phytoplankton growth, and average primary production rates are in the range of 400 to 600 mg C  $\cdot$  m<sup>-2</sup>  $\cdot$  day<sup>-1</sup> in June-July, decreasing gradually to between 200 and 250 mg C  $\cdot$  m<sup>-2</sup>  $\cdot$  day<sup>-1</sup> in August. Fig. 9 shows the development of the primary production from spring to autumn based on average values of measurements taken at different seasons during the period 1979-1984, thus representing an "average" year. The amount of carbon produced during the bloom and until 1 June is 39 g C  $\cdot$  m<sup>-2</sup>, a value that is fairly similar to the estimates based on nitrate utilization. The annual production is 69 g C  $\cdot$  m<sup>-2</sup>  $\cdot$  year<sup>-1</sup>.

The dynamics of the phytoplankton development for an average year have also been reproduced using the phytoplankton model. The vertical turbulent mixing in the model is given by the parameter Dz i equation (1). The representation of the mathematical model given by equation (1) in a digital computer makes it necessary to divide the water column into discrete layers of a certain depth. Each layer is considered to be well mixed whereas Dz gives





the degree of mixing between the layers. The variation of Dz with depth is given by four parameters (Fig. 10):

Dmix : vertical mixing in the upper layer Dpycn: vertical mixing through the pycnocline Ddeep: vertical mixing below the pycnocline Zp : depth of the pycnocline

In the simulation runs the depth of the mixed layer for the case of Atlantic water with no influence of melt water was considered to be 75 m until 1 May, decreasing to 40 m during May. The coefficients of mixing were 150, 0.5 and  $2 \text{ cm}^2 \cdot \text{s}^{-1}$  for Dmix, Dpycn and Ddeep, respectively. Fig. 11 shows the resulting vertical profiles of nitrate at different dates. The total phytoplankton production during the simulation period (1 March to 31 August) was 77 g C  $\cdot \text{m}^{-2}$  and the average nitrate utilization in the upper 100 m was  $8.1 \,\mu\text{M}$ .





Fig. 10. Variations of the coefficient of vertical mixing with depth

Fig. 11. Simulated nitrate vertical profiles at different dates for Atlantic waters that have not been covered by ice.

In a second case, representing Atlantic water covered by ice, the depth of the mixed layer was considered to be 50 m until 1 May, decreasing to 20 m at the beginning of June. The coefficients of mixing for Dmix, Dpycn and Ddeep were 150, 0.2 and  $2 \text{ cm}^2 \cdot \text{s}^{-1}$ , respectively. Vertical distributions of nitrate at different dates are shown in Fig. 12. The total production during the simulation period was 70 g C  $\cdot \text{m}^{-2}$  and the average nitrate utilization in the upper 100 m was 7.9  $\mu$ M.

In a third case, representing Arctic waters, the water column was assumed to be well mixed down to 50 m during the winter. The coefficient of mixing was assumed to be less than in open Atlantic water due to the presence of ice. The pycnocline at 50 m was assumed to be strong, and we used 0.05  $cm^2 \cdot s^{-1}$  as the value for Dpycn. When the ice starts melting, the low salinity creates a strong pycnocline at 10-15 m. The mixing coefficient through this pycnocline was assumed equal to 0.03 cm<sup>2</sup>  $\cdot s^{-1}$ . Below the pycnocline the mixing was set as 2.0 cm<sup>2</sup>  $\cdot s^{-1}$ . This situation was assumed to remain for the rest of the simulation period. The date when the ice starts melting is probably variable from year to year. During the simulation the ice cover was assumed to be 7/10 in March and April. The ice was almost gone for a few days in early May. After this the water was covered by 5/10 of ice until 1 June, when the ice disappeared. Temperature was -1.8°C in the whole water column until 1 June, after which there was a gradual increase in temperature in the upper 20 m to 5°C in late August. Simulated vertical distributions of nitrate is shown in Fig. 13. The total production during the simulation period was 47 g C  $\cdot$  m<sup>-2</sup> and the average utilization of nitrate in the upper 100 m was 6.2 µM.





Fig. 12. Simulated nitrate vertical profiles at different dates for Atlantic waters that have been covered by ice.

Fig. 13. Simulated nitrate vertical profiles at different dates for Arctic waters.

In all the simulation runs the N/C ratio for phytoplankton was 0.143. Using an N/C ratio of 0.189, as found in the spring bloom, the primary production in Atlantic water with no ice would be about  $58 \text{ g C} \cdot \text{m}^{-2}$  as compared to 77 g C  $\cdot \text{m}^{-2}$  estimated by the model.

According to the zooplankton simulation model (SLAGSTAD 1981), secondary production is very sensitive to variations in the overwintering stock of adult



Fig. 14. Simulated production of zooplankton biomass as a function of the overwintering stock of <u>C</u>. finmarchicus females.

	Numb 500	er of 1000	overwi 2000	nterin 4000	g indi 6000	viduals 8000
Primary production (g C • m <sup>2</sup> )	71	73	77	81	79	77
Secondary production (g C • m <sup>-2</sup> )	8.2	10.0	14.0	18.0	18.0	17.0
Utilization efficiency (%)	12	14	18	22	23	22

Table 2. Variations in primary and secondary production in relation to the overwintering stock of <u>Calanus fin</u>-marchicus.

females (Fig. 14). This can also have an effect on the overall primary production. Table 2 shows the results of simulation runs using different overwintering stocks. As can be seen, the maximum variation in primary production due to differences in the overwintering zooplankton stock was 14%, while the secondary production varied by as much as 120%.

The zooplankton production along the main section has been simulated for each year in the period 1981-1984, based on temperature and ice data for those years. The stock of overwintering females was taken to be 2000 ind.  $\cdot m^{-2}$ . The simulation results show fairly similar and high production in each year (Fig. 15). The low zooplankton biomass values observed in 1983 and 1984 (Fig. 5) can apparently not be related to unfavourable growth conditions in these years, as indicated by the high production potential revealed by the simulation results.

Assuming a growth efficiency of 20-30%, the simulated secondary production of Calanus finmarchicus indicates an efficient potential conversion from primary to pelagic secondary production (Table 2). The high zooplankton biomass values in 1979–1981 (about 20 g dry weight  $\cdot m^{-2}$ ; Fig. 5), the majority of



Fig. 15. Simulated production of zooplankton biomass along the main section for 1981-1984.

which represented biomass produced during the spring season (HASSEL 1986, SKJOLDAL et al. 1987), is evidence that this potential can be achieved in some years.

The reason for the apparently low zooplankton biomass produced in 1983 and 1984 could be due either to low standing stock of overwintering females (Fig. 14) or to heavy grazing by fish and other predators. Grazing could be a major factor in regulating the number of spawning females of Calanus finmarchicus, thereby potentially influencing the food supply for the predators in the following season. We have no data on the number of overwintering females for the years under consideration. In January 1985 the numbers of overwintering Calanus finmarchicus were about 5000 and 10 000 ind.  $\cdot m^{-2}$  in Storfjordrenna and the Southeast Basin, respectively (HASSEL et al. 1986). Many of those were in stage CIII or CIV, particularly in the Southeast Basin, and the number of females developing to spawn the following spring is probably lower and may be in the sensitive region for production (Fig. 14).

## DISCUSSION

The physical oceanographic conditions play a central role in the development of phytoplankton in the Barents Sea (REY and LOENG 1985). The formation of a stable upper mixed layer and the strength of the pycnocline, indispensable factors for the phytoplankton spring bloom to take place, varied significantly at the different main water masses present in the Barents Sea. The physical factors responsible for the formation of the upper mixed layer are the ice melting in ice covered water masses, either they are Arctic water or Atlantic water and the warming up due to an increase in atmospheric temperature and solar insolation in the water masses that have not been covered by ice, usually the Atlantic water. Climatic changes will, without doubt, have a key role in determining the magnitude of these two physical factors and the extension of the area affected by them. According to LOENG (1979) the winter extension of the sea ice is mainly controlled by the oceanographic conditions, in the sense that most of the ice in the Barents Sea is one year-old ice and its formation is strongly influenced by the water temperature. When the water temperature is low it will result in more ice. Warm years, characterized by high inflow of Atlantic water with high temperature into the Barents Sea, generally results in little ice, if any, south of the Polarfront, while cold years result in a more southern extension of the ice, some times well into the Atlantic waters. In warm years, since the ice reaches only to the polar front it does not come in contact with the Atlantic waters and its melting is mainly caused by solar or atmospheric heating, and will therefore be very dependent on local meteorological conditions. Cold north winds, for example, can effectively delay the ice melting. Usually, ice melting in the Arctic waters occurs during May. On the other hand, warm years are also characterized by a strong influx of warm Atlantic waters of very low vertical stability and quite often with not stability at all down to the bottom. In both cases the phytoplankton spring bloom will take place later than in cold years, but also the bloom in the Atlantic water will be delayed with respect to that at the ice edge. The development of the thermocline in the Atlantic waters will be slow, and the overall phytoplankton growth will be reduced due to the removal of it from the euphotic zone by vertical turbulence. However, the deep and weak thermocline permits the advective input of nutrients from layers below the thermocline and this can probably support a higher total primary production. Also the higher temperatures of the Atlantic water are favourable for an earlier development of Calanus finmarchicus to an stage where it can efficiently graze on the delayed

phytoplankton bloom. This would lead to a major fraction of the primary production during spring being channelized to higher pelagic trophic food levels.

In cold years, when the ice extends south of the polar front into Atlantic waters, the melting will take place much earlier than in warm years and a strong pycnocline will be formed given place to an intense but short-lived spring bloom. The lower water temperatures will retard the stage development of <u>Calanus finmarchicus</u> in such a way that a great portion of the early bloom at the ice edge will remain ungrazed and will sink to deeper layers or to the bottom. In the areas that have not been covered by ice, the pycnocline will develop later than at the ice-edge, but somewhat earlier than in similar areas during warm years, so it is probably that a portion of the spring bloom will also end in the deeper layers.

With respect to the total primary production, it seems that in a given area only small variations in the yearly primary production occurs from year to year, since the amount of nitrate being removed from the upper 100 meters does not presented large changes during the investigated period. However, generally somewhat higher production would be expected from the Atlantic water than from the Arctic waters, because the deeper upper mixed layer will involve the utilization of larger amounts of nutrients. Also a south-north gradient in the total primary production in Arctic waters seems to be a general trend. This is due to the time-lag in the spring bloom produced by the receding of the ice. Observations of a ice edge bloom as far north as 79°N during August have been made (REY and LOENG 1985).

Summarizing, we can say that climatic changes will not cause very much impact on the total primary production of the Barents Sea, but it will have pronounced effects on the development in time of the spring bloom, especially in Atlantic waters and at the ice edge at the polar front or south of it. In warm years the primary production from the spring bloom available for zooplankton will be larger than in cold years and most of it will be channelized to the pelagic ecosystem. In cold years, on the contrary, the primary production available for secondary production will be lower as a part of it sinks to deeper layers in the water column or to the bottom.

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# REFERENCES

- ELLERTSEN, B., LOENG, H., REY, F. and TJELMELAND, S. 1981. The feeding conditions of capelin during summer. Field observations in 1979 and 1980. <u>Fisken Hav., 1981</u> (3): 1-68 (In Norwegian, English Abstract).
- ELLERTSEN, B., HASSEL, A., LOENG, H., REY, F., TJELMELAND, S. and SLAGSTAD, D. 1982. Ecological investigations in the marginal ice zone in the Barents Sea the summers 1979 and 1980. <u>Fisken Hav.</u>, 1982 (3): 31-83 (In Norwegian, English Abstract).
- GJØSÆTER, H., HASSEL, A., LOENG, H. and REY, F. 1983a. Marinøkologiske undersøkelser nær iskanten i Barentshavet somrene

1979-1982. Sluttrapport for prosjektet "Lodda på sommerbeite". Havforskningsinstituttet Rapport Nr. FO 8309, 59 s. (In Norwegian).

- GJØSÆTER, H., HASSEL, A., LOENG, H., REY, F. and SKJOLDAL, H.R. 1983b. Preliminære resultater fra tokt i Barentshavet med M/S "Lance" Sars" F/F "G.O. og i mai-juni 1983. Havforskningsinstituttet 21 s. Rapport Nr. FO 8301, (In Norwegian).
- HASSEL, A., LOENG, H., REY, F. and SKJOLDAL, H.R. 1984. Preliminære resultater fra tokt med F/F "G.O. Sars" i Barentshavet, 28.5.-18.6.1984. <u>Havforskningsinstituttet Rapport nr. FO 8409</u>, 34 s. + 7 App. (In Norwegian).
- HASSEL, A. 1986. Seasonal changes in zooplankton composition in the Barents Sea, with special attention to <u>Calanus</u> spp. (Copepoda). J. Plankt. Res., 8 (2): 329-339.
- HASSEL, A., LOENG, H. and SKJOLDAL, H.R. 1986. Marinøkologiske undersøkelser i Barentshavet i januar 1985. <u>Havforskningsinstituttet</u> Rapport Nr. FO 8604, 33 s., 4 App. (In Norwegian).
- LOENG, H. 1979. A review of the sea ice conditions of the Barents Sea and the area west off Spitsbergen. Fisken Hav., 1979 (2): 29-75.
- MARSHALL, P.T. 1957. Primary production in the Arctic. J. Cons. perm. int. Explor. Mer, 23, 173-177.
- REY, F. and LOENG, H. 1985. The influence of ice and hydrographic conditions on the development of phytoplankton in the Barents Sea. p. 49-63 In Gray, J.S. and Christiansen, M.E. (eds) Marine Biology of Polar regions and Effects of Stress on Marine Organisms. J. Wiley & Sons Ltd.
- SLAGSTAD, D. 1981. Modelling and simulation of physiology and population dynamics of copepods. Effects of physical and biological parameters. Model. Identif. Control, 2: 119-162.
- SLAGSTAD, D. 1982. A model of phytoplankton growth-effect of vertical mixing and adaptation to light. <u>Model.</u>, <u>Identif.</u> <u>Control</u>, <u>3</u>: 111-130.
- SLAGSTAD, D. 1985. A model of phytoplankton in the marginal sea-ice zone of the Barents Sea. p. 35-48 in Gray, J.S. and Christiansen, M.E. (eds) Marine Biology of Polar Regions and Effects of Stress on Marine Organisms. J. Wiley & Sons Ltd.
- SKJOLDAL, H.R., HASSEL, A., REY, F. and LOENG, H. 1987. Spring phytoplankton development and zooplankton reproduction in the central Barents Sea in the period 1979-1984. p. 59-90 in Loeng, H. (ed.) The effect of oceanographic conditions on distribution and population dynamics of commercial fish stocks in the Barents Sea. Proceeding of the third Soviet-Norwegian Symposium (This volume).
- SVERDRUP, H.U. 1953. On conditions for the vernal blooming of phytoplankton. J. Cons. perm. int. Explor. Mer, 18: 287-295.