

SPRING PHYTOPLANKTON DEVELOPMENT AND ZOOPLANKTON REPRODUCTION IN THE CENTRAL BARENTS SEA IN THE PERIOD 1979-1984

By

Hein Rune Skjoldal, Arne Hassel, Francisco Rey and Harald Loeng
Institute of Marine Research
P.O. Box 1870 - Nordnes
5024 Bergen
Norway

ABSTRACT

Physical and biological conditions have been studied along a fixed transect across the polar front in the central Barents Sea in late spring or early summer in each year from 1979 to 1984. These data are analysed with respect to the spring bloom development and zooplankton reproduction and the influence of climatic conditions on these processes.

Of the six years analysed, 1979 and 1981 were particularly cold years with considerable melting of ice in Atlantic water south of the polar front. High stability due to the meltwater gave rise to spring blooms that culminated as much as 4-6 weeks earlier than in the warmer years when stability in the Atlantic water arose due to the atmospheric warming of the sea surface. Spawning of the dominant herbivore, Calanus finmarchicus, evidently occurred in early spring (late April - early May), as evidenced by dominance of copepodites in stages CI to CIV in June. The degree of copepodite development in the different years was related to the time of sampling, water column stability, and temperature. The timing of the copepodite development was less variable than, and showed no clear-cut relationship to, the timing of the spring bloom. This could reflect slower development of Calanus in cold years with early spring blooms. Reproduction of krill and Metridia longa occurred also in early spring.

Due to the more rapid development and early culmination of blooms in Atlantic water influenced by melting of ice, we expect the conversion efficiency of primary to pelagic secondary production to be generally lower in cold years than in warm years. Such a relationship is not evident, however, in the data for the period 1979-1984. The produced zooplankton biomass and numbers of Calanus copepodites were on the contrary extremely low in 1983 and 1984 which were warm years. Grazing by pelagic fish and advective transport of plankton are factors which need to be taken into consideration. The timing of inflow events of Atlantic water to the Barents Sea in relation to the seasonal vertical migration of Calanus finmarchicus in the Norwegian Sea could be of particular importance in this respect.

INTRODUCTION

The distribution and growth of capelin in the Barents Sea have been shown to be influenced by climatic changes (GJØSÆTER and LOENG 1984, 1987). The

annual individual growth of capelin has shown considerable variation between different years and between different regions of the capelin distribution area (GJØSÆTER 1985). It is possible that this variation partly reflects a direct effect of temperature variation on growth rate (GJØSÆTER and LOENG 1987). It is likely, however, that much of the effect is mediated through the feeding conditions of capelin, i.e. the plankton production.

In order to study the feeding conditions of capelin, the Institute of Marine Research has since 1979 carried out biological oceanographic investigations in the central and northern Barents Sea. These investigations have been conducted mainly during the summer season, with special emphasis on the receding ice edge. A working hypothesis has been that increased light and stability due to ice melt cause a phytoplankton bloom in the marginal ice zone area (LOENG 1987). This bloom, which follows the receding ice edge northwards during summer, provides an important food source for the development and production of zooplankton, which again is grazed upon by capelin on its northwards feeding migration. Data in support of this hypothesis have been presented by REY and LOENG (1985) and HASSEL (1986). The plankton development in the marginal ice zone area has also been subject of mathematical modelling (SLAGSTAD 1985). From 1984 these biological oceanographic investigations have been extended as a cooperation between our institute and the four Norwegian universities within the framework of the Norwegian Research Program for Marine Arctic Ecology (PRO MARE).

A good conceptual understanding and mathematical description of the feeding conditions of capelin requires detailed knowledge of the relationships between the physical conditions and phytoplankton growth on one hand and phytoplankton growth and zooplankton development and production on the other. This knowledge is a necessary requirement in order to provide realistic descriptions and assessments of the feeding conditions of capelin over its whole area of distribution, which is the scale where climatic changes exert their greatest effect (MIDTTUN and LOENG 1987, GJØSÆTER and LOENG 1987).

The Atlantic and Arctic water masses in the Barents Sea (LOENG 1987) are characterized by different plankton organisms. For instance, the copepod Calanus finmarchicus inhabits the Atlantic water whereas the somewhat larger Calanus glacialis is found in Arctic water (TANDE, HASSEL and SLAGSTAD 1985, HASSEL 1986). The polar front which separates these two major water masses, forms therefore a boundary between two different ecological regions. A third region is represented by mixed Atlantic and Arctic water which covers a considerable part of the eastern Barents Sea. The climatic and oceanographic changes are greatest in this area and local formation and exchange of heavy bottom water have been suggested as explanations for the great magnitude and apparent periodicity in these changes (MIDTTUN and LOENG 1987). Cooling of Atlantic water and mixing of Arctic and Atlantic water masses make the Barents Sea in many ways an extreme environment which may be sub-optimal for reproduction and development of zooplankton. Under such conditions it is possible that climatic changes are being magnified when it comes to their effects on zooplankton production and thereby on the feeding conditions of capelin.

The interrelationships between spring phytoplankton development and zooplankton reproduction and development are of central importance for our understanding of the production processes. Results from the North Sea, Kosterfjorden in Sweden, and Balsfjorden in northern Norway have indicated

a close correspondence between the timing of the spring phytoplankton bloom and reproduction of *Calanus finmarchicus* (KRAUSE and RADACH 1980, TANDE 1982, HOPKINS, TANDE and GRØNVIK 1984, BAMSTEDT 1985). Results from the Norwegian Sea on the other hand, suggest that reproduction and early development of *C. finmarchicus* can occur well before the spring diatom bloom (HALLDAL 1953, ØSTVEDT 1955). A similar pattern with spawning prior to the spring bloom has also been found for *Neocalanus* spp. and *C. marshallae* in the Bering Sea (SMITH and VIDAL 1984).

We have examined data on plankton development from a fixed section (Section I, Fig. 1) in the central Barents Sea covered during the late spring or mid-summer period, in each year from 1979 to 1984. In the present paper we have summarized and analysed these observations with emphasis on mechanisms for water column stabilization and the temporal aspects of plankton development. In an accompanying paper (REY, SKJOLDAL and SLAGSTAD 1987) we consider these results further with emphasis on quantitative and vertical aspects of production.

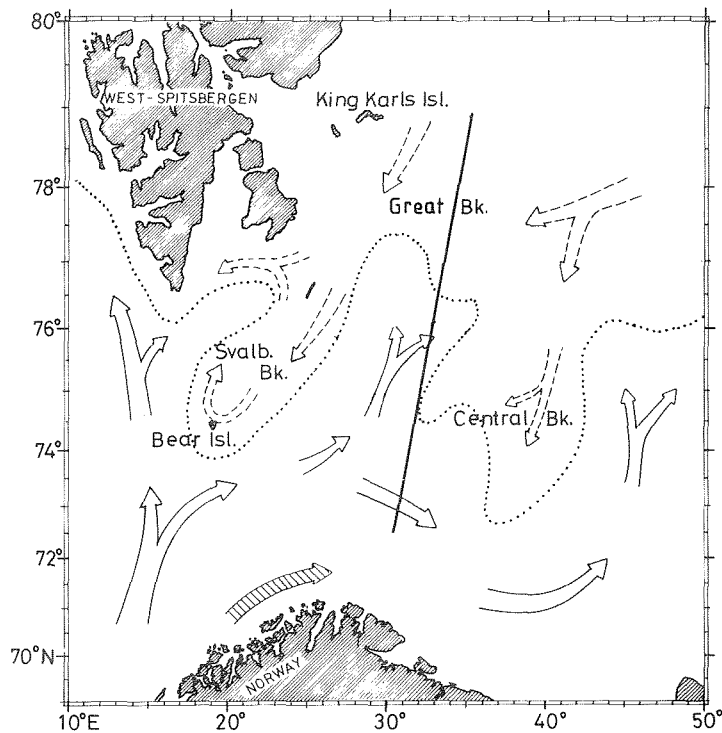


Fig. 1. Schematic picture of the currents in the Barents Sea. Solid line arrows: Atlantic water. Broken line arrows: Arctic water. Hatched arrows: Coastal water. The dotted line shows the position of the polar front. The thick straight line shows the position of the sampled transect, section I (from REY and LOENG 1985).

MATERIAL AND METHODS

An overview of the cruises covering section I (Fig. 1) is given in Table 1. R/V "G.O. Sars" has been used each year to cover the section from the ice edge and southwards. The ice-going vessel M/S "Lance" was used in addition to R/V "G.O. Sars" in 1983 to extend the section about 80 nautical miles into ice-covered waters.

Table 1. Overview of cruises covering section I in the central Barents Sea late spring or summer in the years 1979 to 1984.

Year	Vessel	Section I		
		Date	St. no.	Latitude
1979	R/V G.O.Sars	11-12 July	541-552	75°04'-76°52'
1980	R/V G.O.Sars	29-30 June	623-635	74°40'-76°36'
1981	R/V G.O.Sars	27-28 June	506-528	73°00'-75°59'
1982	R/V G.O.Sars	5-7 June	1145-1167	73°00'-76°21'
1983	R/V G.O.Sars M/S Lance	4-8 June	732-748	73°00'-78°04'
			128-145	
			158-164	
			173-174	
1984	R/V G.O.Sars	4-6 June	670-702	74°30'-77°10'

The time of coverage of the section has varied by approximately 5 weeks, from early June in 1982, 1983 and 1984, to late June in 1980 and 1981, and 11-12 July in 1979 (Table 1).

The part of the section covered has also varied due to the differences in time of coverage and ice conditions between the years. The part of the section between 75° and 76°N has been covered every year, whereas the northernmost station has varied from about 76°N in 1981 to 78°04'N in 1983 when M/S "Lance" was used. The section was covered south to 73°N in 1981 and 1982. In 1983 the section was continued as the Vardø-N section along 31°12'E south of 74°N to the coast of Finmark. We have in this paper included data from 73°N and northwards only.

The data used for the present analysis of the time series have been described previously in the following reports or publications: 1979 and 1980 (ELLERTSEN, LOENG, REY and TJELMELAND 1981, ELLERTSEN *et al.* 1982); 1981 (GJØSÆTER, HASSEL, LOENG and REY 1983a, REY and LOENG 1985, HASSEL 1986); 1982 (GJØSÆTER *et al.* 1983a); 1983 (GJØSÆTER *et al.* 1983b); 1984 (HASSEL, LOENG, REY and SKJOLDAL 1984a).

The methods of sampling and analyses have been described in the above reports and these should be consulted for details of the procedures. Here we limit ourselves to a brief outline of the methods, with emphasis on any changes in the procedures which need consideration when considering the data as a time series.

Standard hydrographic sampling was done with a Neil Brown Mk III CTD sonde. Water samples were collected with Niskin or Nansen bottles. Nutrients were determined with an autoanalyzer based on standard methods (FØYN, MAGNUSSEN and SEGLEM 1981). The samples in 1979 and 1980 were stored frozen and analysed at our institute after the cruises. In the subsequent years the samples were kept cold (+1°C) and in darkness for a maximum of about 12 h prior to analysis on board. Samples for phytoplankton pigments were filtered onto 0.45 µm membrane filters, and stored frozen before extraction with 90% acetone and fluorometric determination of chlorophyll a and phaeopigments (STRICKLAND and PARSONS 1972).

Zooplankton samples were taken by vertical hauls with a 36 cm diameter Juday

net. The mesh size of the net and the depth strata sampled have varied somewhat between the years (Table 2). A coarser mesh net, 375 μm , was used in 1981 and 1983 than in the remaining years when either 180 μm (1979, 1980, 1982) or 250 μm nets (1984) were used. The effect of this difference in mesh size is considered later in connection with data interpretation.

The sampling in 1979 was done from ca. 10 m above the bottom to the surface. In the subsequent years, sampling was done from the water column above 200 m depth. The uppermost 50 m was sampled with a separate haul to the surface. The deeper part of the water column was sampled either as a haul from 200 to 50 m or from 200 m to the surface (Table 2).

The zooplankton biomass was determined as displacement volume on formaldehyde-fixed samples (HASSEL 1986) and converted to wet weight assuming a density of 1 g per ml (see WIEBE, BOYD and COX 1975). This procedure was used for all samples from 1979 to 1982 and for the 200-0 m samples from 1983 and 1984. For the 50-0 m samples from these two years, biomass was determined as dry weight (Table 2). The wet weight biomass values have been converted to dry weight biomass, assuming a dry weight content of 19% of the wet weight (OMORI 1969; see also WIEBE *et al.* 1975, OMORI 1978, and BÄMSTEDT 1981).

Table 2. Overview of procedures for zooplankton sampling with 36-cm Juday net and biomass determination.

Year	Mesh size (μm)	Depth stratum (m)	Biomass
1979	180	Bottom ¹ - 0	Displacement volume
		40 - 0	" "
1980	180	200 - 50	Displacement volume
		50 - 0	" "
1981	375 (180 ²)	299 - 50	Displacement volume
		50 - 0	" "
1982	180	200 - 0	Displacement volume
		50 - 0	" "
1983 ³	375 ⁴	200 - 0	Displacement volume
		50 - 0	Dry weight
1984	250	200 - 0	Displacement volume
		50 - 0	Dry weight

1 From ca. 10 m above bottom.

2 180 μm used for the northernmost stations (st. no. 525 - 528).

3 Juday 80-cm used for the northernmost stations (st. no. 128 - 174)

4 180 μm used for the southernmost stations (st. no. 732 - 737).

CLIMATE AND OCEANOGRAPHIC CONDITIONS

Position of the polar front

The variation in the ocean climate is closely related to variations in the ice distribution in the Barents Sea (LOENG 1987, MIDTTUN and LOENG 1987). The position of the polar front in the area of section I is also apparently related to the climatic conditions. Fig. 2 shows a fairly strict relationship between the average temperature at 50-200 m in the Atlantic water mass at the Vardø-N section and the position of the polar front at section I. The position

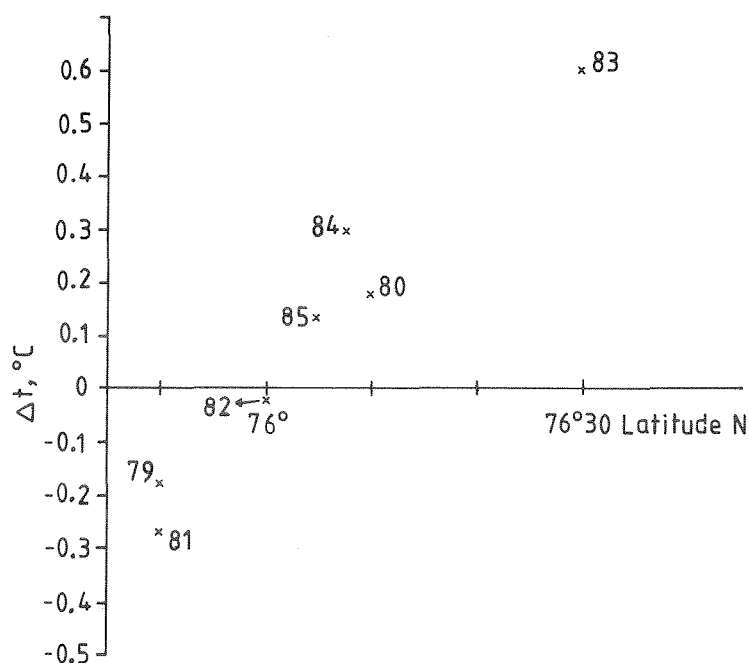


Fig. 2. Relationship between temperature anomaly for the Atlantic water of the Vardø-N section and position of the polar front in the late spring/early summer for the years 1979-1985.

of the polar front has been determined as the area of sharpest temperature gradient where the subsurface tongue of cold water meets the warmer Atlantic water (Figs 4-9).

The position of the polar front has varied by 40 nautical miles between the cold years of 1979 and 1981 and the warm year of 1983 (Fig. 2). This shift in position may reflect differences in the magnitude and strength of the inflow of Atlantic water to the Barents Sea, as suggested by the relationship with the temperature in the Vardø-N section (Fig. 2). It may also reflect differences in the ice conditions as the position of the polar front may be modified by ice melt or freezing during winter and spring.

Ice and hydrography

MIDTTUN and LOENG (1987) have described the ice and oceanographic conditions in the Barents Sea for the recent years. The ice conditions in the central Barents Sea from 1979 to 1985 have been summarized in Fig. 3, which shows the monthly mean positions for the southern ice border between 30 and 35°E. 1979 and 1981 distinguish themselves from the remaining years. In these two cold years the ice extended south of 75°N in April and May (Fig. 3).

The hydrographical results for section I for the years 1979-1984 are presented as isopleth diagrams in Figs 4-9, along with isopleth diagrams of the concentrations of nitrate and chlorophyll *a*. Reflecting the southerly distribution of ice, the upper layer of meltwater with reduced salinity extended far to the south in the cold years 1979 and 1981 (Figs 4 and 6). In the remaining years meltwater was not found south of approximately 76°N (Figs 5 and 7-9). A vertical temperature gradient existed in the water masses not influenced by ice, reflecting warming of the surface layer. This gradient was weakest in 1982 (Fig. 7) and strongest in 1980 (Fig. 5).

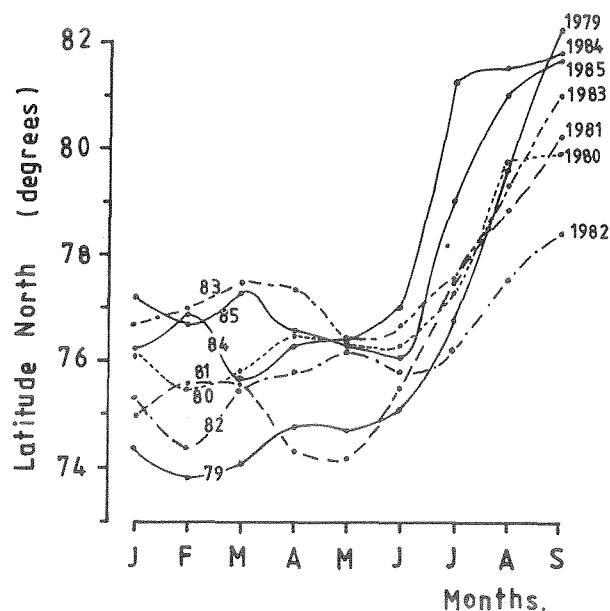


Fig. 3. Monthly mean position of the southern ice border between 30 and 35°E from January to September in the years 1979-1985.

STABILITY AND PHYTOPLANKTON SPRING BLOOM

Mechanisms for water column stabilization

Spring phytoplankton blooms are the result of increased incident light during the spring period and they are therefore, almost by definition, light limited. The average light intensity a phytoplankton cell experiences depends on the rate of vertical mixing. Although not absolutely mandatory (EVANS and PARSLOW 1985), water column stabilization exerts a very strong influence on the development of spring blooms (SVERDRUP 1953, REY 1981, SAMBROTTO, NIEBAUER, GOERING and IVERSON 1986).

Stability formation in the central and northern Barents Sea is caused by two major mechanisms: ice melt and warming. Melting of ice can again be separated into two categories depending on the source of energy: "warm" water or solar insolation. In cold years with heavy ice formation, ice can drift south of the polar front and start to melt due to the heat of the Atlantic water. This melting, which initially is more or less independent of atmospheric conditions, produces an upper layer with reduced salinity which is progressively being cooled by the melting process. Under cold atmospheric conditions, melting will therefore cease and new ice formation starts.

Melting of ice in Atlantic water south of the polar front evidently took place in 1979 and 1981. The section was not covered south of 75°N in 1979, but in 1981 meltwater was found south to about 73°45'N (Fig. 6).

In the absence of meltwater south of approximately 76°N in 1980 and 1982-1984, warming was here the principal cause of stability formation. The stability was low in 1982 (difference in σ_t in the upper 100 m: 0.01-0.08), somewhat higher in 1983 ($\Delta\sigma_t$: 0.05-0.10) and 1984 ($\Delta\sigma_t$: 0.10-0.15), and highest in 1980 ($\Delta\sigma_t$: ca 0.3). It should be noted, however, that the coverage in 1980 was about 3 weeks later than in 1982-1984 (Table 1).

Spring bloom development in 1979-1984

During the relatively late coverage in 1979 (11-12 July), the bloom was over

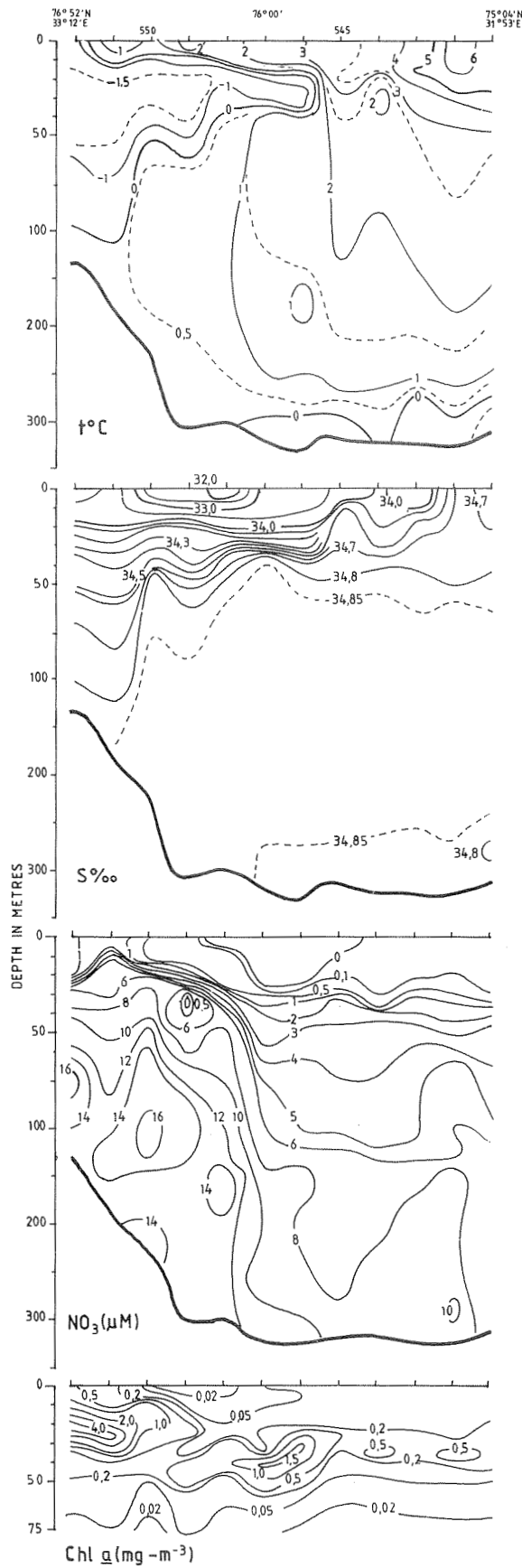


Fig. 4. Temperature, salinity, nitrate (μM) and chlorophyll a ($\mu\text{g}\cdot\text{l}^{-1}$) along section I, 11-12 July 1979.

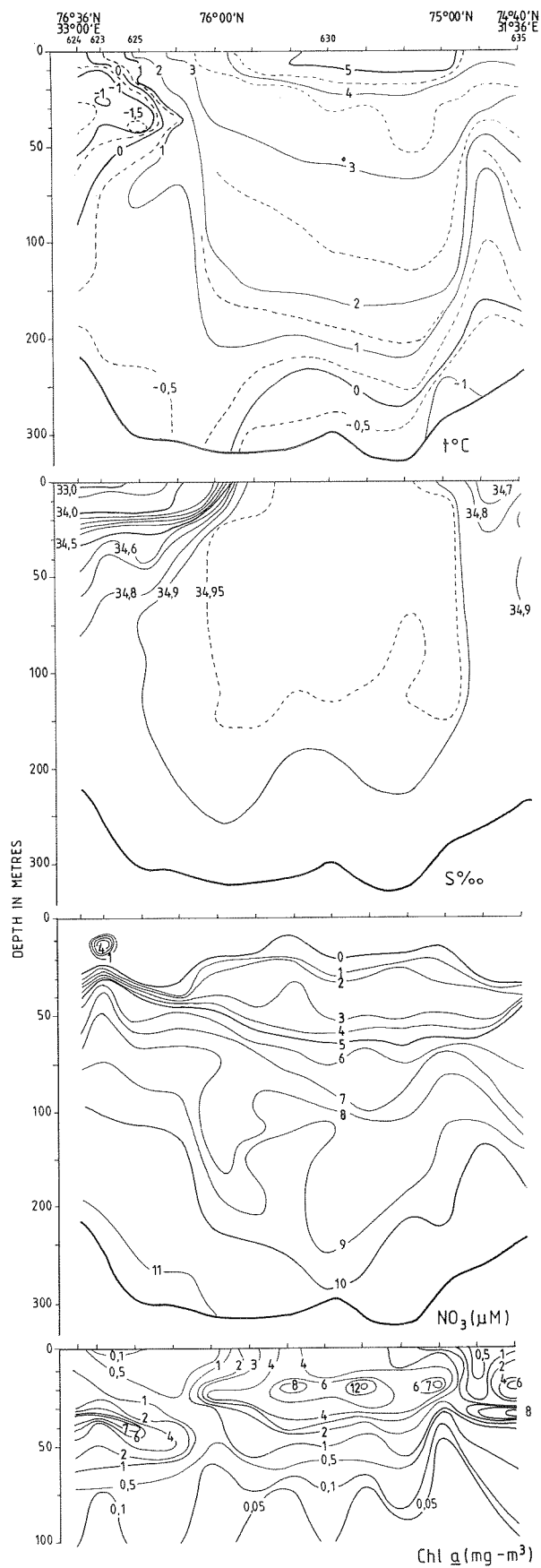


Fig. 5. Temperature, salinity, nitrate (μM) and chlorophyll *a* ($\mu\text{g}\cdot\text{l}^{-1}$) along section I, 29-30 June 1980.

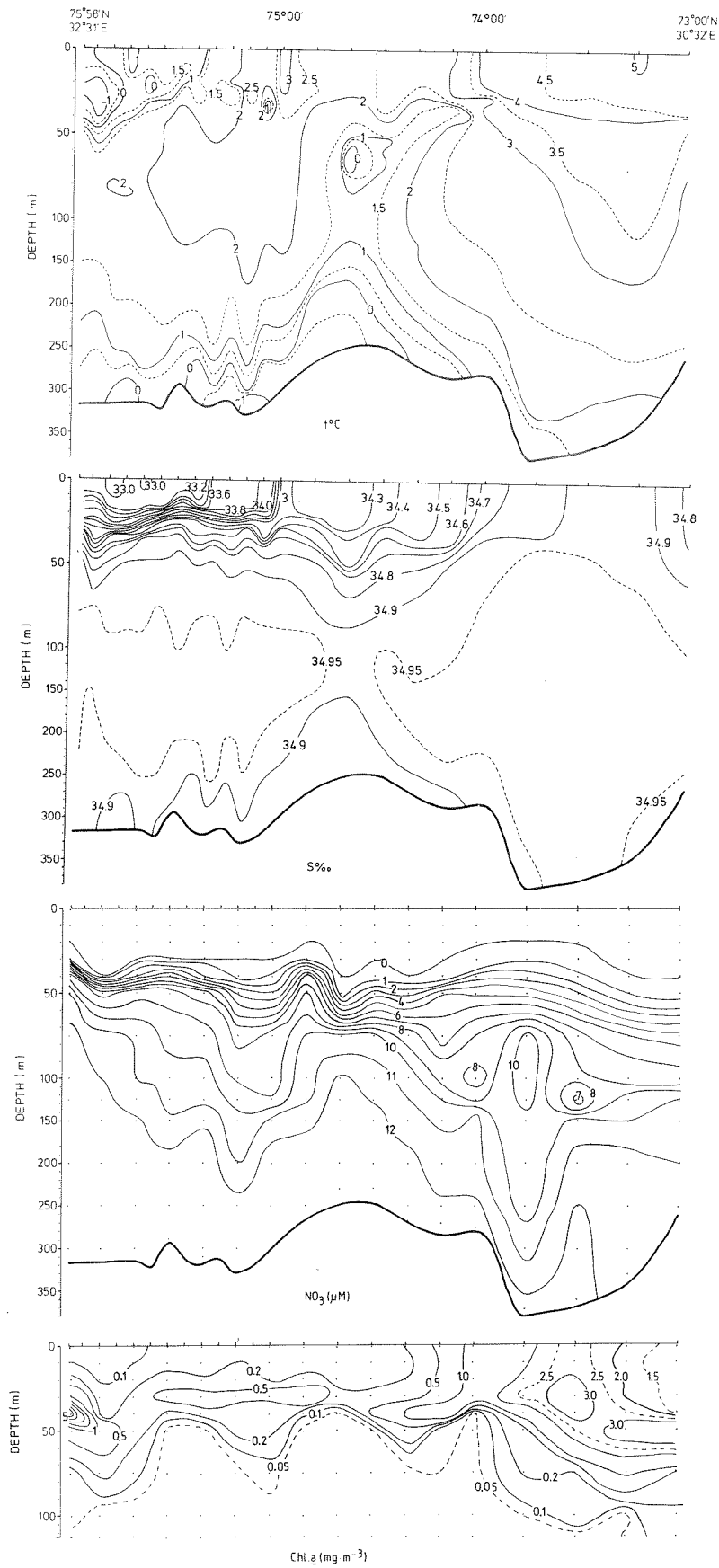


Fig. 6. Temperature, salinity, nitrate (μM) and chlorophyll *a* ($\mu\text{g}\cdot\text{l}^{-1}$) along section I, 27-28 June 1981.

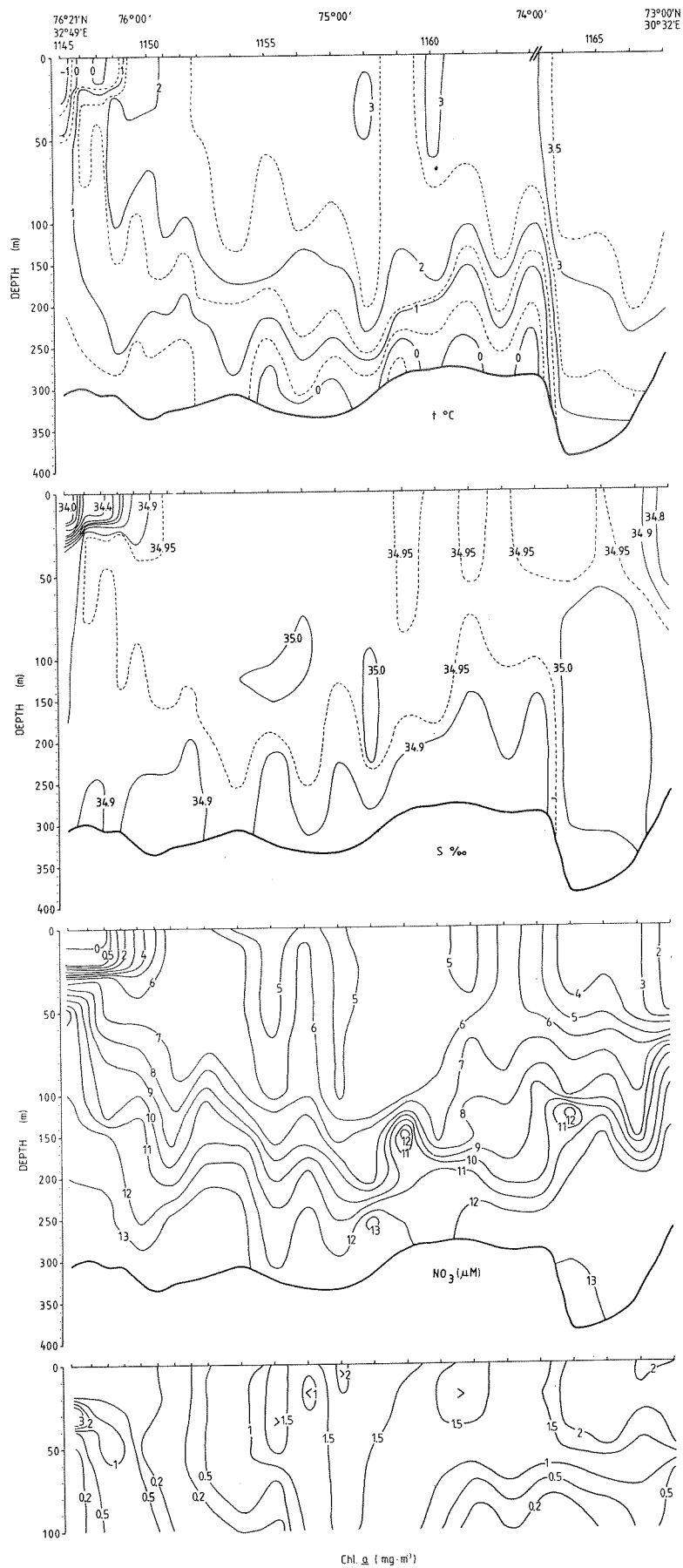


Fig. 7. Temperature, salinity, nitrate (μM) and chlorophyll a ($\mu\text{g}\cdot\text{l}^{-1}$) along section I, 5-7 June 1982.

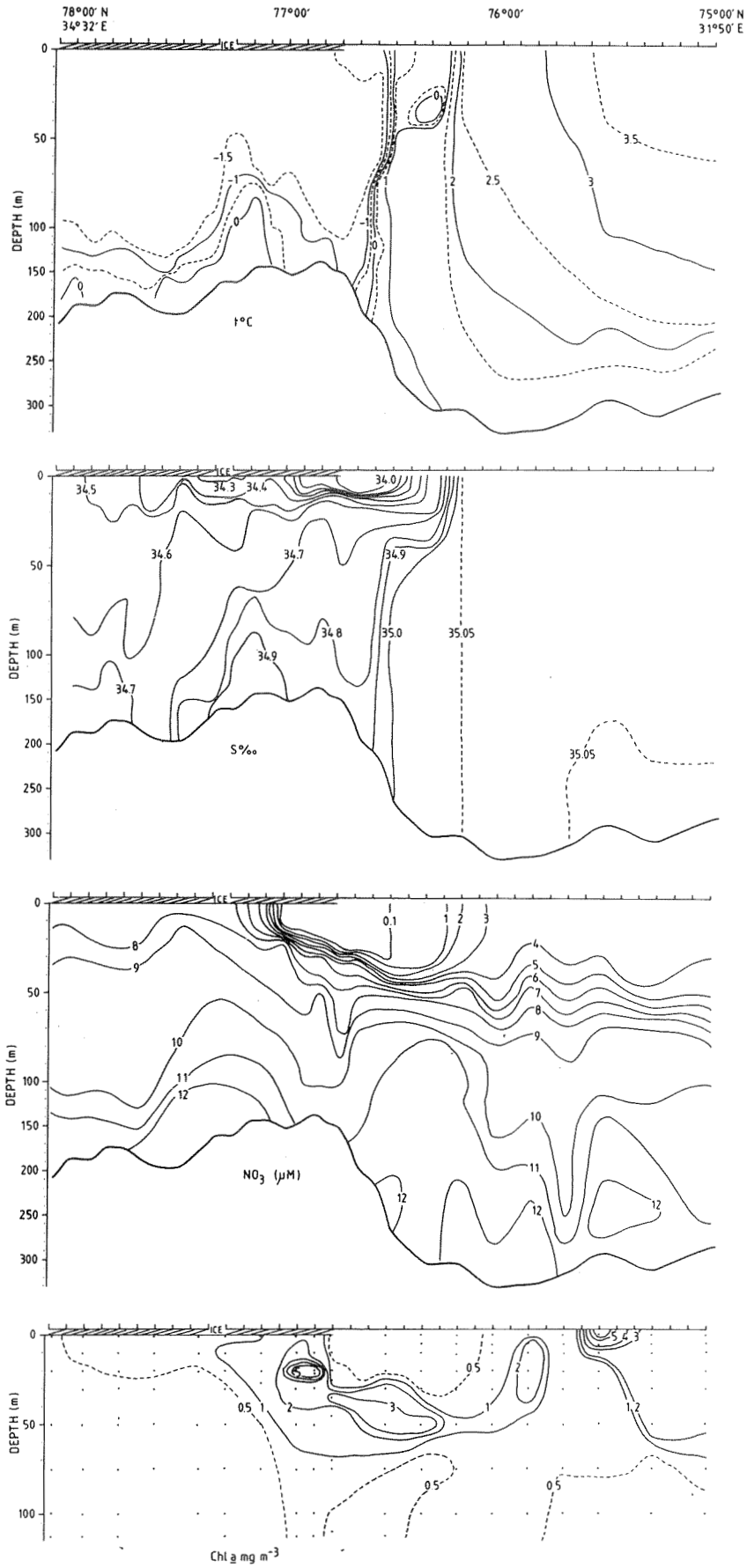


Fig. 8. Temperature, salinity, nitrate (μM) and chlorophyll a ($\mu\text{g}\cdot\text{l}^{-1}$) along section I, 4-8 June 1983.

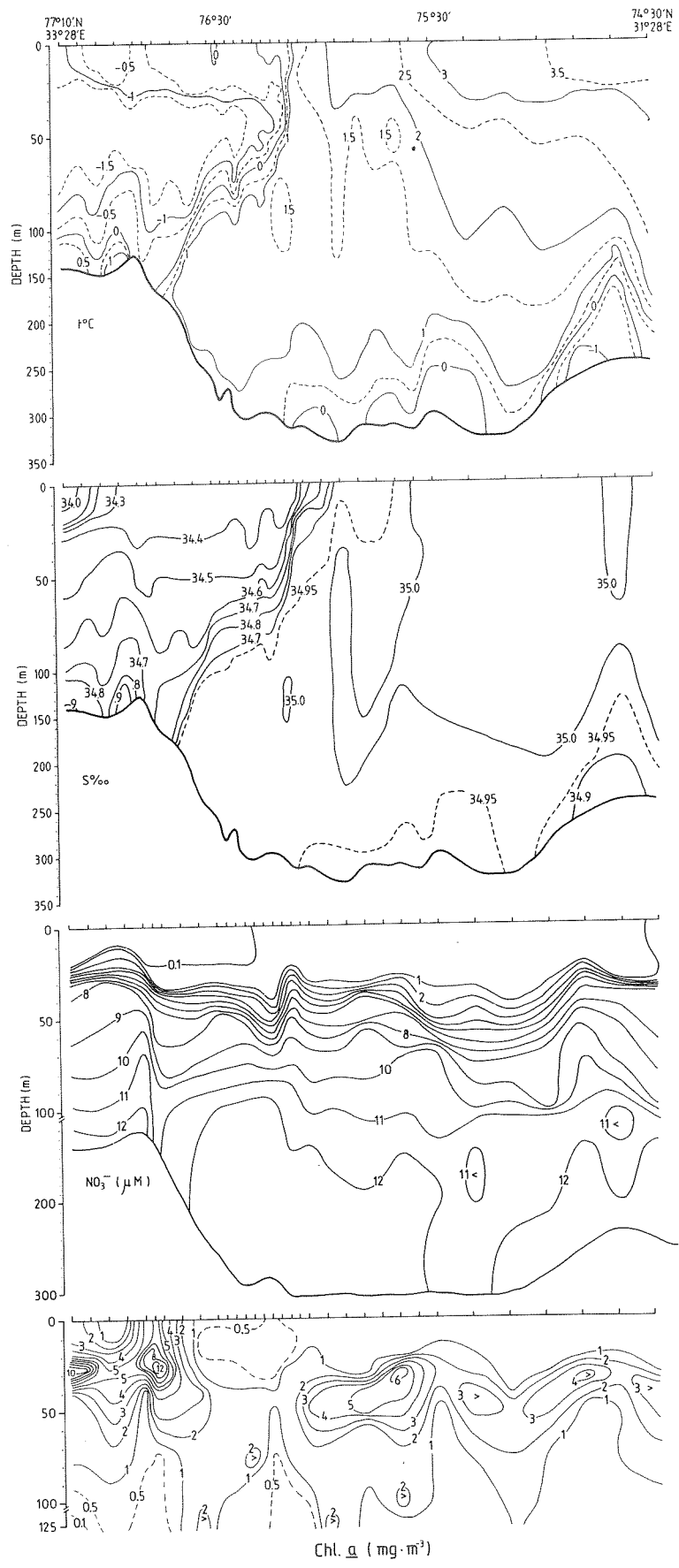


Fig. 9. Temperature, salinity, nitrate (μM) and chlorophyll a ($\mu\text{g}\cdot\text{l}^{-1}$) along section I, 4-6 June 1984.

except for the two northernmost stations close to the ice edge. The post-bloom situation at the stations south of $76^{\circ}30'N$ is seen from the low nitrate and chlorophyll *a* levels in the surface layer and the relatively low chlorophyll *a* level in the subsurface maximum located at the nitracline around 40 m depth (Fig. 4).

The situation in the second cold year with southerly ice, 1981, was fairly similar to that in 1979. North of $74^{\circ}N$, the spring bloom was over and a moderate subsurface chlorophyll maximum was developed (Fig. 6). The nitracline was very pronounced and located around 40 m. In contrast, the spring bloom was still found south of $74^{\circ}N$ in the Atlantic water not influenced by ice melting (Fig. 6). The section was covered during another cruise about $1\frac{1}{2}$ month earlier in 1981 (11-12 May). At this time the spring bloom at about its peak development was observed from about $74^{\circ}N$ and north to the ice edge at $74^{\circ}35'N$, whereas the bloom was just starting to develop in the homogenous Atlantic water at about $73^{\circ}30'N$ (REY and LOENG 1985).

In contrast to the cold years 1979 and 1981 with southerly ice (Fig. 3), bloom development south of $76^{\circ}N$ during the remaining years was influenced by thermal stabilization of the water column. By the end of June in 1980 (29-30 June), a bloom at about its peak development was found, as evidenced by fairly high concentrations of chlorophyll *a* in the nutrient depleted surface layer (Fig. 5). The nitrate gradient was less sharp under the thermally stratified conditions in 1980 than under the conditions influenced by meltwater in 1981 (Figs 5 and 6). The nitrate distribution in 1980 is indicative of low stability and deep mixing during the early part of the bloom development. Thus, the nitrate isolines dip further down into the deep water in the Atlantic water mass with homogenous salinity than they do in the meltwater region (Fig. 5). This situation can also be seen in the nitrate distributions in other years, e.g. 1982 (Fig. 7). The vertical distribution of nitrate in 1980 showed two steps in the gradient, one around 60 to 70 m depth and the other around 20 to 30 m depth (Fig. 5). The deeper step in the gradient probably reflected the early development of the bloom under conditions of low stability, whereas the shallower step probably reflected a recently formed temperature gradient in the upper layer (Fig. 5).

The section was covered about 3 weeks earlier in 1982, 1983 and 1984 than in 1980 (Table 1). In 1982 the temperature gradient was slight and stability was low. The spring bloom was this year in its early development. The nitrate levels were still fairly high ($5-6 \mu M$) and chlorophyll *a* levels were moderate ($0.5-2 \mu g \cdot l^{-1}$) (Fig. 7). Both nitrate and chlorophyll *a* were fairly evenly distributed in the upper 100 m, and the sharpest nitrate gradient was located between 100 and 200 m. This shows that vertical mixing was fairly strong and extended deep in the water column during this early bloom period. At $73^{\circ}N$ the bloom development had progressed somewhat further due to the stability at the outer extension of the Norwegian coastal water (Fig. 7).

The spring bloom in the Atlantic water in 1983 had reached a similar or slightly more advanced development compared to 1982. Nitrate levels were $3-4 \mu M$ in the upper 30-40 m (Fig. 8). In contrast to the deep nitrate gradient in 1982, the gradient was located much higher in the water column (around 50 m) in 1983 (Figs 7 and 8). The bloom in Atlantic water in 1984 was in a more progressed stage of development than the blooms in 1982 and 1983. Nitrate was depleted from the upper 30 m and fairly high chlorophyll *a* levels were found in the lower part of the euphotic zone (Fig. 9). The nitrate gradient was found around 40-50 m.

In 1983 the coverage of the section extended about 80 nautical miles into the ice and this allowed a fairly complete description of the ice edge bloom. The peak of this bloom occurred 15-20 nautical miles into the drift ice from its edge. North of this bloom region, a prebloom situation was found with nitrate levels of 7-8 μM and chlorophyll a levels around $0.5 \mu\text{g} \cdot \text{l}^{-1}$ (Fig. 8). The transition from the prebloom to the bloom situation occurred fairly rapidly, as seen from the strong horizontal gradient in nitrate. In the meltwater region south of the ice edge a late stage of the bloom occurred, with a deep chlorophyll maximum at 40-50 m (Fig. 8).

Similar late stages of ice edge blooms were also found in the meltwater region north of 76°N in 1980, 1982 and 1984 (Figs 5, 7 and 9). The ice receded somewhat earlier in 1984 than in the other years (Fig. 3), and the section could therefore be covered further north (Table 1). Slightly earlier stages of bloom development was found at these northernmost stations in 1984, although the bloom had also here passed its peak (Fig. 9).

Generalizations and ranking of the investigated years

From the above descriptions of bloom development in the years 1979-1984 a few generalizations can be made. Stability formation due to melting of ice is generally more pronounced than that due to surface warming. Ice edge or meltwater blooms will therefore in general proceed more rapidly and last for a shorter while than do blooms in Atlantic water. They will also tend to start at an earlier date than the latter (REY and LOENG 1985).

Of the years considered here, 1979 and 1981 were different from the rest in that considerable ice melting took place in Atlantic water south of the polar front in these cold years. In the remaining years, ice did not extend much south of the polar front at about 76°N (Figs 2 and 3). Ice melting occurred therefore mainly due to solar and atmospheric heating in these years.

For comparison with the reproduction and development of zooplankton, it is of interest to compare the different years in terms of the timing of the spring bloom. Since bloom development needs to be considered as a temporal process with a variable and continually changing vertical structure, it is not a simple and straightforward task to fix dates of given stages of bloom development. We have attempted to do this, however, in a rather coarse and semiquantitative manner. In doing so, we use the following definitions for the start and peak of a bloom. The start of the bloom is defined as the time when $1 \mu\text{mol} \cdot \text{l}^{-1}$ of nitrate (about 10% of the winter level) has been utilized in the upper mixed layer. This corresponds to a production of about $0.5-1 \mu\text{g}$ chlorophyll a $\cdot \text{l}^{-1}$ (REY et al. 1987). The peak of the bloom is defined as the situation when the upper layer is nutrient depleted while the chlorophyll a level is still high and rather uniformly distributed. This situation corresponds usually to the maximum content of chlorophyll a per m^2 .

In attempting to date these two bloom events (to the nearest week) for the different years, we have had to extrapolate from the observations made during the few days coverage of the section each year (Table 1). In this, we have been guided by repeated coverages of the section in 1980 (ELLERTSEN et al. 1981, 1982) and 1981 (REY and LOENG 1985), as well as in April 1986 (SKJOLDAL 1986, REY and SKJOLDAL unpubl. results). Our estimates of the timing of the bloom events, which are to be regarded as educated guesses, are presented in Table 3.

During the coverage 11-12 May in 1981 the bloom was nearing its peak at

Table 3. Estimated times (week number) for the start and peak of the spring phytoplankton bloom, mean *Calanus* copepodite stage composition (stage index) by the time of coverage (see Table 2), and estimated dominant copepodite stage by mid-June at different latitudes along section I in each of the years 1979-1984. See the text for further details.

Year	Latitude (°N)	Estimated time of spring bloom (week no.)		Stage index	Dominant stage per 15 June
		Start	Peak		
1979	75	17	21	3.82	I
	76	19	22	3.37	I
1980	75	17	25	3.14	II
	76	18	24	2.64	I
1981	73	18	24	3.08	I
	74	16	20	3.39	I-II
	75	17	21	3.57	II
	76	19	22	2.91	I
1982	74	17	25	1.82	II
	75	18	26	1.58	II
	76	18	24	1.82	II
1983	74	17	24	3.27	IV
	75	17	24	2.90	IV
	76	18	25	2.64	IV
1984	75	15	22	2.06	II
	76	15	22	2.44	III

74°N (REY and LOENG 1985). We expect that the peak was reached about one week later (week 20). We have assumed a delay of one week for the peak bloom at 75°N (week 21) and two weeks at 76°N (week 22). As judged from the observations at 73°N in late June (Fig. 6) we expect that the peak bloom occurred two weeks earlier (week 24) (Table 3). Due to the fairly similar physical conditions, we have assumed similar timing of the bloom in 1979 as that in 1981.

During the coverage in late June 1980 the chlorophyll *a* distribution suggested that the bloom was just beyond its peak. We estimate that the peak occurred one week earlier at 75°N (week 25) and two weeks earlier at 76°N (week 24) where there was some influence of meltwater (Fig. 5). A bloom beyond its peak was also found during the coverage in early June 1984 (Fig. 9). We have assumed that the bloom at 75 and 76°N peaked about one week earlier (week 22).

During the early June coverages in 1982 and 1983 the blooms in the Atlantic

water had still not reached their peaks (Figs 7 and 8). We judge the bloom in 1983 to be more developed than in 1982, peaking one to two weeks after the coverage (week 24 at 74 and 75°N and week 25 at 76°N). Due to the lower stability and deeper mixed layer in 1982 (Fig. 7), we have assumed that the bloom this year needed an additional 1-2 weeks period to reach its peak (week 25 at 74°N and week 26 at 75°N). At 76°N the bloom seemed to be somewhat more progressed than further south due to the influence of meltwater (Fig. 7), and we estimate that the peak here occurred one week later (week 24).

The above analysis of the timing of the peak bloom indicates a variation of 3-4 weeks among the different years when considering only Atlantic water not influenced by meltwater (Table 3). Ice melting can lead to an earlier peak bloom, as exemplified by 1981, thus further extending the range of variation among years (Table 3).

Our estimates of the timing of the start of the blooms are generally more uncertain as they have required extensive extrapolations of our data. In 1986, when there was melting of ice in Atlantic water south to about 75°N, the bloom in this area apparently started in early April (SKJOLDAL 1986, REY and SKJOLDAL unpubl. results). Due to the more extensive ice coverages in 1979 and 1981, we have assumed that the blooms in these years started 1-2 weeks later than in 1986 (Table 3).

The part of the section around 73°30'N in 1981 was covered by Atlantic water not influenced by meltwater or coastal water. The bloom in this area seemed to have started just prior to the coverage 11-12 May and to have reached its peak just prior to the coverage 27-28 June (REY and LOENG 1985; Fig. 6). This gives an estimated duration of 7-8 weeks from start to peak bloom in Atlantic water in 1981. We have assumed this duration when estimating the timing of the start of the blooms in 1983 and 1984 and one week longer duration for the blooms in 1980 and 1982 (Table 3).

ZOOPLANKTON REPRODUCTION AND DEVELOPMENT

Calanus finmarchicus and *Calanus glacialis*

The two *Calanus* species, *C. finmarchicus* and *C. glacialis*, are inhabitants of the Atlantic and Arctic water masses south and north of the polar front, respectively (TANDE et al. 1985, HASSEL 1986). The two species are separated in routine analysis of samples according to differences in size. Where both species co-occur in mixed water masses, size spectra generally show two distinct peaks, the larger one corresponding to *C. glacialis* (RUNGE et al. 1985, HASSEL unpubl. results). There is some overlap of the peaks, however, which gives some uncertainty to this method of separating the species, especially where one of the species occurs in low abundance relative to the other. Using this method, the two species from copepodite stage II or III and upwards were separated in samples from 1979, 1980, 1982 and 1984 (Fig. 11).

The abundance of copepodites of *C. finmarchicus* and *C. glacialis* (not shown separately) showed dramatic variation among the years (Fig. 10). From a moderate abundance in 1979, the numbers of copepodites increased until 1982 when there was 1/4 - 1/2 million individuals m⁻². Between 1982 and 1983 there was an almost 100-fold reduction in abundance to 6-9000 copepodites m⁻². Low abundance was also found in 1984. The biomass of total zooplankton

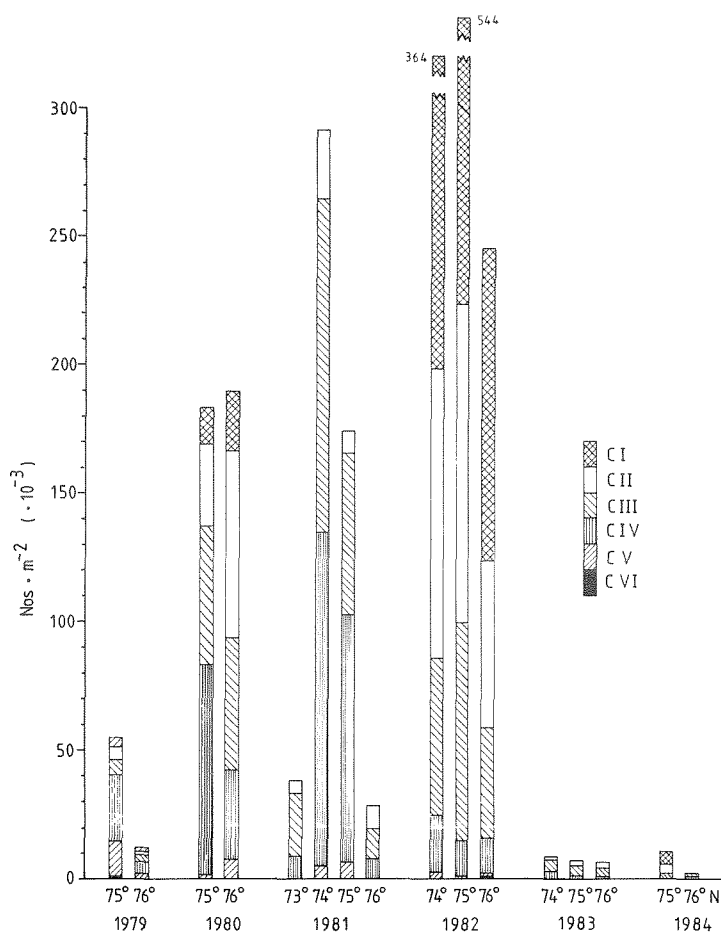


Fig. 10. Abundance (no. of individuals · m⁻²) of copepodites of *Calanus finmarchicus* plus *C. glacialis* (see Fig. 11) along section I in 1979-1984. The samples in 1980 were from 50-0 m; in the other years from bottom-0 m or 200-0 μm. 375 μm net was used in 1981 (except at 76° N) and 1983; 180 or 250 μm net was used the other years (Table 2).

also decreased, although more gradually, from about 20 g dry weight m⁻² in 1980 to about 2 g dry weight m⁻² in 1984 (REY et al. 1987).

The relative composition of the copepodite stages of *C. finmarchicus* and *C. glacialis* in the different years is shown in Fig. 11. This (as well as Fig. 10) is based on samples from the upper 200 m or the whole water column (Table 2), except for 1980 where samples from the upper 50 m were used. The biomass distribution in 1980 revealed, however, that most of the zooplankton occurred in the upper 50 m (REY et al. 1987).

Before we discuss the results in Fig. 11, the effects of variable mesh size and the uncertainty in species separation should be considered. The coarse mesh size of the net used in 1981 and 1983 (375 μm, Table 2) may have resulted in incomplete sampling of the youngest copepodite stages. MATTHEWS, HESTAD and BAKKE (1978) considered a net with 500 μm mesh unsuitable for catching stages I and II of *C. finmarchicus*, with considerable undersampling also of stages III and IV. According to WIBORG (1954), copepodite stages I-III of *C. finmarchicus* would all be retained by 366 μm mesh net (silk no. 2). Using preserved samples collected with 180 μm net, we tested the retention of *C. finmarchicus* copepodites on a 375 μm mesh screen.

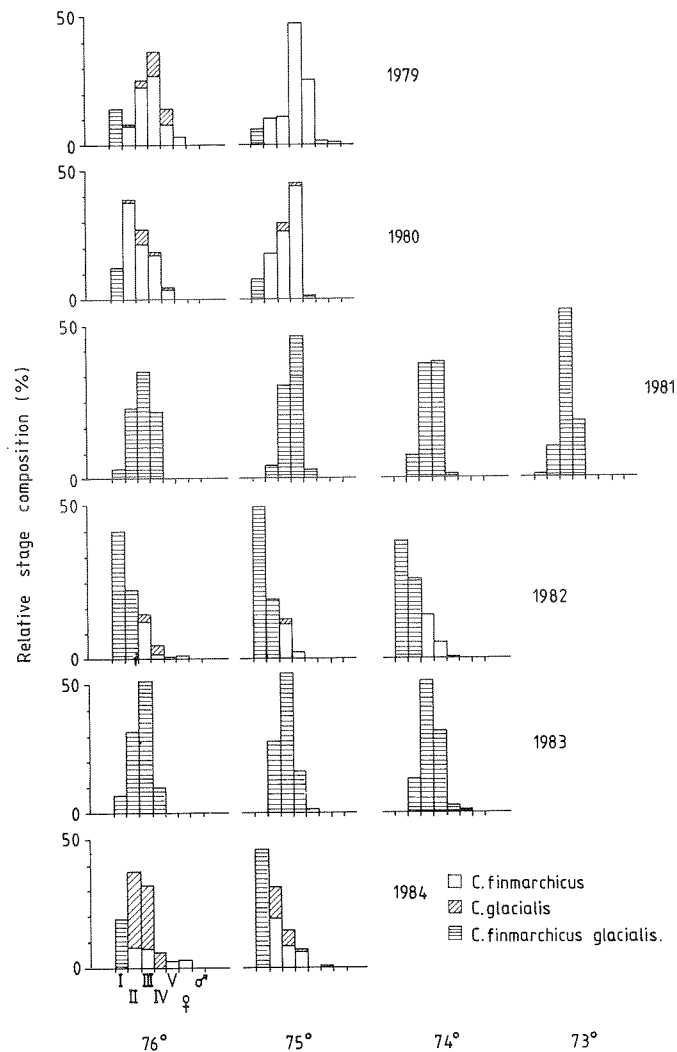


Fig. 11. Relative (%) copepodite stage composition for *Calanus finmarchicus* and *C. glacialis* at section I in 1979-1984. The two species were not separated in 1981 and 1983 as were neither stage CI in the remaining years and stage CII in 1982. See legend to Fig. 10 for details concerning sampling.

Almost half the number of stage I was found to wash through the screen (44%). Almost all stage II individuals, however, were retained on the screen (98%). It is therefore probable that stage I copepodites were undersampled in 1981 and 1983, whereas stages II and older apparently were not. In calculating values for the average stage composition (see below), we have multiplied the observed numbers of stage I obtained with the 375 μ m net by a factor 2.

Stage compositions of *C. glacialis* observed in the northern Barents Sea and in the Canadian Arctic have suggested a two years life cycle (LONGHURST, SAMEOTO and HERMAN 1984, TANDE *et al.* 1985). In ice-covered waters north of the polar front there was a clear predominance of stage IV copepodites and adult females in late May - early June 1983 (GJØSÆTER *et al.* 1983b). In January 1985 there was predominance of stages III and IV and adult females of *C. glacialis* in samples both from Storfjordrenna and from the Southeastern Basin (HASSEL, LOENG and SKJOLDAL 1986). These results are consistent with a two years life cycle for *C. glacialis*.

The apparent contribution of C. glacialis to the stock of Calanus copepodites varied among the years as well as with latitude (Fig. 11). It was in general higher at 76°N close to the polar front than further south, and it was highest in 1984 when the total abundance was low (Fig. 10). This high relative contribution of C. glacialis in the Atlantic water in the "warm" year 1984 is surprising and may reflect difficulties in the method used to separate the species. This need not be the case, however, since C. glacialis may have been contained in the cold bottom water (Fig. 9) and migrated upwards to co-occur with the low-abundance stock of C. finmarchicus.

In the following analysis of copepodite development in each year we have not separated between the species. This is mainly due to the lack of separation of the species in 1981 and 1983 and of stage CI the other years. Apart from the sample from 76°N in 1984, C. finmarchicus constituted the majority of the copepodites (Fig. 11). The copepodite stage composition for C. finmarchicus is not drastically altered by including C. glacialis for the samples where the two species were separated (Fig. 11). We therefore assume that the stage composition for both species combined is largely representative for the development of C. finmarchicus.

The Calanus stage composition was generally dominated by the younger copepodite stages (Fig. 11). Adult males were rarely found, as were adult females except in 1979 and 1982 when they occurred with about 500 individuals per m² (Figs 10 and 11). These results show that spawning had occurred fairly early in the spring, and that the new generation of C. finmarchicus had already gone through a considerable part of its development.

As an index of the Calanus stage development we have calculated the mean stage for each of the distributions in Fig. 11 (Table 3). The highest index values were observed during the relatively late coverages in the cold years 1979 and 1981. CIV was the dominant stage 11-12 July 1979, as it also was at 74° and 75°N in late June 1981 (Fig. 11). The copepodite stage composition indicated a somewhat delayed development at 76°N than further south in both years. Also at the southern end of the section (73°N) in 1981, at the outer extension of coastal water (Fig. 6), the development was apparently somewhat retarded in 1981. The sample from 76°N in 1981 was taken with a 180 µm net, and the low proportion of stage CI here indicates that the lack of CI further south was real and not a sampling artefact, due to the coarser mesh net used there (Table 2).

Compared to 1981 the samples from the same time (late June) in 1980 showed a less advanced development, with stage CII as the dominant one at 76°N (Fig. 11). More advanced development in the meltwater front at 76°N than in the Atlantic water at 75°N was found in 1982 and 1984, but not in 1980. In 1983 the meltwater front was located north of 76°N (Fig. 8). The copepodite stage composition indicated a slightly more advanced development at 74°N than at 75°N both in 1982 and 1983 (Fig. 11).

The general pattern which emerges from the results in Fig. 11 is that the copepodite development started first in the southern part of the meltwater region. In the Atlantic water south of the meltwater region, copepodite development was progressively delayed with increasing latitude, as it also was in the meltwater region in the cold years 1979 and 1981.

The copepodite development was least advanced in early June 1982 when CI₂ was the predominant stage (Fig. 11). The total number of copepodites per m² was highest this year and even though the relative stage composition was

dominated by CI and CII, the absolute numbers of stages CIII and CIV were also generally high (Fig. 10). Compared to 1982 the copepodite development in early June in the two following years were more advanced, especially in 1983 when stage CIII predominated (Fig. 11).

The stage compositions in Fig. 11 and the calculated stage index values (Table 3) are from a time span of 5 weeks, from early June in 1982-1984 to 11-12 July in 1979 (Table 1). Although there is a general correspondence between stage distribution and time of coverage, the results from the last 3 years show that some variation from year to year occurs. We have attempted to normalize the results by extrapolating them to a common date, mid-June, each year. This gives only an approximate description of the real situation since recruitment to CI from nauplii is ignored. However, except for 1982, the relative stage distributions indicates that the peak in recruitment to CI was over. This suggests that any distortions of the data by extrapolation would be small.

Extrapolation requires knowledge of the rate of development of the copepodites. This can be strongly dependent on temperature (RUNGE *et al.* 1985). Some estimates of stage durations of *C. finmarchicus* from field observations or laboratory experiments are summarized in Table 4. These suggest durations of about 1 week for the youngest copepodite stages, with a general increase in stage duration with increasing stage number and size of the copepodites. We have assumed 1 week stage durations for CI, CII and CIII in our extrapolations.

Table 4. Durations of copepodite development for stages CI, CII and CIII of *Calanus finmarchicus* estimated from the development of field populations or, in the case of RUNGE *et al.* (1985), from laboratory rearing or molting rate determination.

Area				
Norwegian Sea	<1wk	1wk	2wk	ØSTVEDT 1955
North Sea	5d	5d	10d	KRAUSE and RADACH 1980
Korsfjorden, W.Norway	-	-	6d	MATTHEWS <i>et al.</i> 1978
NW Atlantic (off Nova Scotia)	-	-	3-5d	RUNGE <i>et al.</i> 1985

The estimated dominant stage by mid-June varied from stage CI in 1979 to stage CIV in 1983 (Table 3). This represents a variation of about 3-4 weeks in the time of maximum copepodite recruitment.

Calanus hyperboreus

The largest of the *Calanus* species, *C. hyperboreus*, occurred in fairly low numbers (1000 copepodites m^{-2} or less; Table 5). The abundance was usually higher at 76°N than further south. Adults were never found, and the dominant stages were usually CIII and CIV (Table 5). *C. hyperboreus* was not separated from *C. finmarchicus* and *C. glacialis* in stage CI.

C. hyperboreus has an annual life cycle and reproduces in late winter or early spring (ØSTVEDT 1955, MATTHEWS *et al.* 1978, RUDYAKOV 1983). There is some uncertainty as to whether it reaches maturity after 1 or 2

Table 5. Calanus hyperboreus. Abundance (individuals·m⁻²) of copepodites in samples from section I in 1979-1984. The samples in 1980 were from the upper 50 m; in all other years from bottom-0 m or 200-0 m.

Stage	1979		1980		1981				1982			1983			1984		
	75°	76°	75°	76°	73°	74°	75°	76°	74°	75°	76°	74°	75°	76°	75°	76°	
CII	0	20	0	80	0	0	0	0	0	0	0	0	0	0	0	0	
CIII	0	40	0	0	0	0	0	0	0	160	40	160	0	0	20	0	768
CIV	80	800	0	0	0	0	0	0	820	240	0	240	0	80	20	24	16
CV	0	140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8

years and whether it reproduces successfully in Arctic regions (RUDYAKOV 1983). In Korsfjorden, western Norway, C. hyperboreus was found to develop rapidly after spawning in late winter to reach stage CIV in May (MATTHEWS et al. 1978). The stage compositions in Table 5 are consistent with such an early development. Although based on fairly low numbers, the copepodite development seemed to be somewhat more progressed in the cold years 1979 and 1981 than in 1982 and 1984 (Table 5). This trend is similar to that found for C. finmarchicus (Fig. 11).

Pseudocalanus sp. and Metridia longa

Pseudocalanus sp. and Metridia longa were the most abundant herbivorous copepods in the samples from the Barents Sea after the Calanus spp. Their numerical abundances varied considerably among the years, being generally low in 1983 and 1984 (Fig. 12), as was the case also for C. finmarchicus (Fig. 10).

During sample analysis, stages were grouped as CI to CIII and CIV to CV and not further discriminated. This makes a detailed analysis of the development in the separate years more difficult than for C. finmarchicus. The use of 375 µm net in 1981 and 1983 (Table 2) also complicates the interpretation, especially for the smaller Pseudocalanus sp. A considerable proportion of stages CI-III could have passed through this net. The similarity between the sample from 76°N in 1981 taken with 180 µm net and the samples from 74° and 75°N taken with 375 µm net, may indicate, however, that the majority of copepodites had by then developed into larger stages that were more representatively sampled. A screening test with Metridia longa gave as result that 25% of stage CI passed 375 µm mesh. In contrast to the case for Pseudocalanus sp., the use of 375 µm net should therefore not have caused any substantial influence on the results for this species.

The dominant stages of Pseudocalanus were CIV-V except in 1980 when stages I-III were equally or slightly more abundant. At Weathership M in the Norwegian Sea ØSTVEDT (1955) found P. minutus to develop through to stage IV by early June. The stage distributions in Fig. 12a could therefore reflect that the development through stages CI-III was in general completed by the time the cruises were conducted. However, results from a later cruise in 1981 (8-19 August) showed a pronounced increase in stages CI-III as well as in CIV-V (HASSEL 1986). A similar pronounced increase in the younger copepodite stages was also observed in August 1984 (HASSEL, LOENG, REY and SOLBERG 1984b). This late summer increase in the number of copepodites

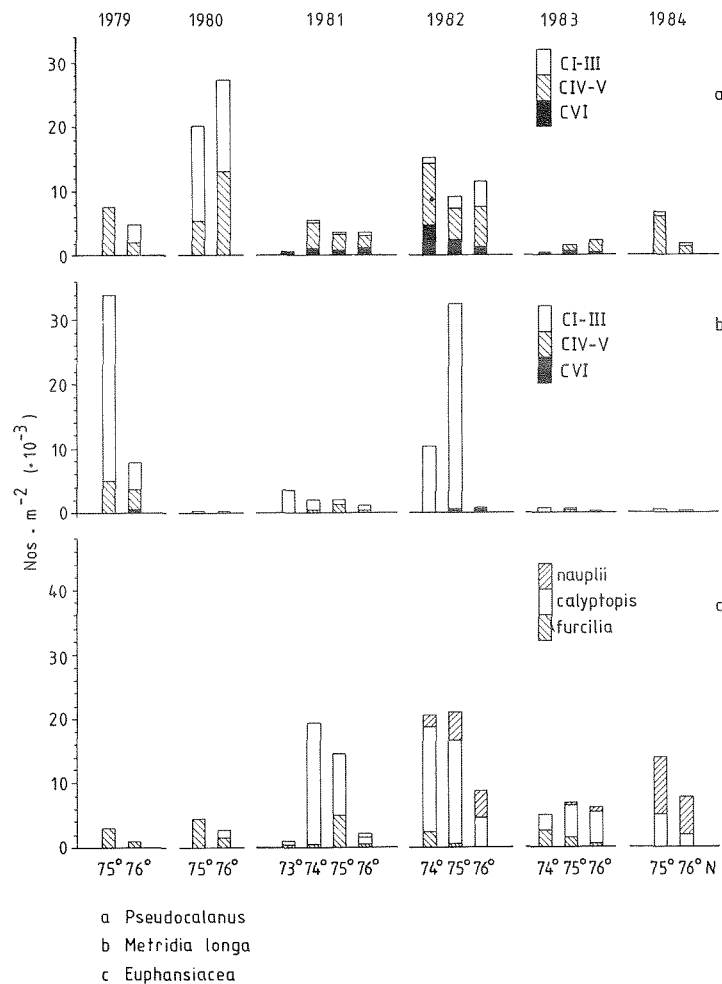


Fig. 12. Abundance (no. of individuals·m⁻²) of copepodites of Pseudocalanus sp. (a) and Metridia longa (b) and larval stages of krill (c). See legend to Fig. 10 for details concerning sampling.

may represent a second generation of Pseudocalanus sp. However, ØSTVEDT (1955) observed only a single spawning period for P. minutus in the Norwegian Sea. If this is also the case in the Barents Sea, the stage compositions in Fig. 12a are indicative of a fairly late spawning and development for Pseudocalanus.

Assuming a single generation per year, we interpret the large proportion of adults in 1982 as indicative of late spawning this year (Fig. 12a), which also was the year with the least developed Calanus population (Fig. 11). 1980 seemed to be the year with the earliest development of Pseudocalanus sp. (Fig. 12a).

Metridia longa occurred in very low numbers in 1980, 1983 and 1984 (Fig. 12b). The development was apparently more progressed in 1979 than in 1982, which were the only years when the species occurred in moderately high abundance. Metridia longa was found to spawn and develop somewhat later than Calanus finmarchicus in Balsfjorden in northern Norway (HOPKINS et al. 1984). This seems also to be the case in the Barents Sea (Figs 11 og 12b).

Krill

Only the juvenile stages of krill are sampled properly with the Juday net.

Thysanoessa inermis was usually the dominant krill species, but T. raschii also occurred.

During the coverage 11-12 May 1981 krill eggs and nauplii were predominant and few calyptopis or furcilia stages were observed (HASSEL 1986). By the end of June 1981, nauplii were no longer found except for low numbers at 76°N. Calyptopis and, to a lesser degree, furcilia were the dominant stages (Fig. 12c). Reproduction of Thysanoessa spp. in the Barents Sea therefore occurs in early spring as it does also in Balsfjorden (HOPKINS et al. 1984).

The abundance of juvenile krill showed a 10-fold range of variation, from a low in 1979 to highest values in 1981 and 1982 (Fig. 12c). The recruitment of krill was least developed in early June 1984 as indicated by the high proportion of nauplii and absence of the furcilia stage (Fig. 12c). The development seemed to be progressively more advanced in early June 1982 and 1983, late June 1981 and 1980, and early July 1979 (Fig. 12c).

ZOOPLANKTON REPRODUCTION IN RELATION TO SPRING BLOOM DEVELOPMENT

The foregoing analysis of spring bloom and zooplankton developments in the years 1979-1984 have revealed a variation of about one month in both these processes among the different years (Table 3). We now address the questions of how the variation in zooplankton development relates to the differences in spring bloom development, and how these variations relate to the differences in ocean climate.

Besides the differences in estimated times for the blooms to peak (Table 3), there were other qualitative differences in the bloom developments with regard to water column stabilization and pycnocline strength and depth. The degree of stability, expressed as the difference in σ_t between 100 m and the surface, explained much of the variability in bloom development among the years (REY et al. 1987). Stability also explained part of the variation in copepodite development of Calanus (Fig. 13). Thus the greatest proportion of older stages was generally found when stability was high due to meltwater. Exceptions to this pattern occurred. The stage index values were higher in 1983 than in 1984 (Fig. 13), despite the greater stability and further developed bloom in the latter year (Figs 8 and 9).

The nitrate utilization in the upper 100 m can be used as a measure of bloom development, integrating both the temporal and vertical aspects (REY et al. 1987). A plot of Calanus stage index values versus amount of nitrate utilized shows, however, only a weak relationship (Fig. 14). If one removes the high values for 1979 and 1981 there is no relationship for the remaining data points. Also there seems to be no clearcut relationship between the normalized Calanus stage composition, expressed as the dominant copepodite stage in mid-June, and the estimated time for peak bloom (Table 3). Thus, the stage development was further advanced during the rather late bloom in 1983 than during the earlier bloom in 1984.

Any strict relationship between Calanus development and the spring bloom remains elusive and is not easily demonstrated by any single measure of bloom development. A relationship could nevertheless exist, being dependent on a more complex representation of the blooms. To examine this any further would require more extensive extrapolation and reconstruction of the various phases of bloom development.

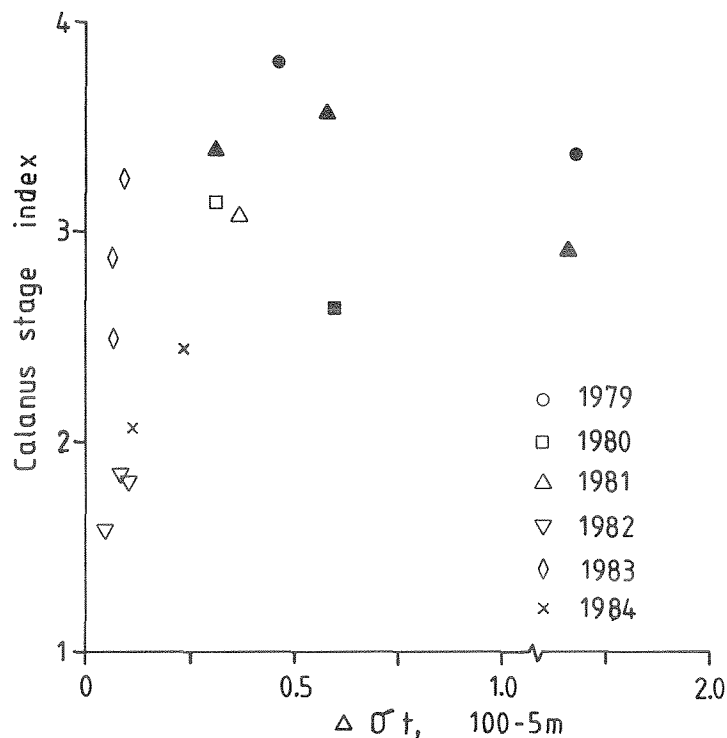


Fig. 13. Relationship between average copepodite stage index) of *Calanus finmarchicus* plus *C. glacialis* and water column stability expressed as difference in temperature between 100 m and the surface for stations along section I in 1979-1984. Filled symbols: meltwater. Open symbols: thermal stability. Half-filled symbol: outer extension of coastal water.

What remains clear is that the reproduction of the dominant herbivores occurs early in the spring, in general well in advance of the spring bloom. This is similar to the pattern described for *C. finmarchicus* from the Norwegian Sea (ØSTVEDT 1955, HALLDAL 1953). It is possible that spawning is influenced by phytoplankton growth in an early phase of the bloom development and that this to a certain degree fixes the further timing of copepodite development. There is no clear relationship between the copepodite stage development and our estimates of time for the start of the blooms (Table 3). This could, however, reflect the uncertain nature of these estimates.

Another source of variation is the temperature dependency of the rates of development of nauplii and copepodite stages (RUNGE et al. 1985). According to an equation for this dependency based on laboratory rearings of *C. finmarchicus* (RUNGE et al. 1985), the time from hatching to stage CIII would be 78 days at 0°C, 55 days at 2°C, and 35 days at 5°C. Field observations have indicated times for this development to CIII as approximately one month in the North Sea (KRAUSE and RADACH 1980) and in Korsfjorden (MATTHEWS et al. 1978) at temperatures of 5-10°C, and 1½ to 2 months in Balsfjorden at about 3°C (TANDE 1982, HOPKINS et al. 1984). It has been suggested that the success of development is reduced at temperatures below 2°C due to high mortality rate (TANDE pers. comm.).

Temperature explained part of the variation in *Calanus* stage development in our data (Fig. 15). The temperature values used were those of the upper mixed layer at the time of the cruises. This gives only a very approximate representation of the temperature conditions during the early development. A

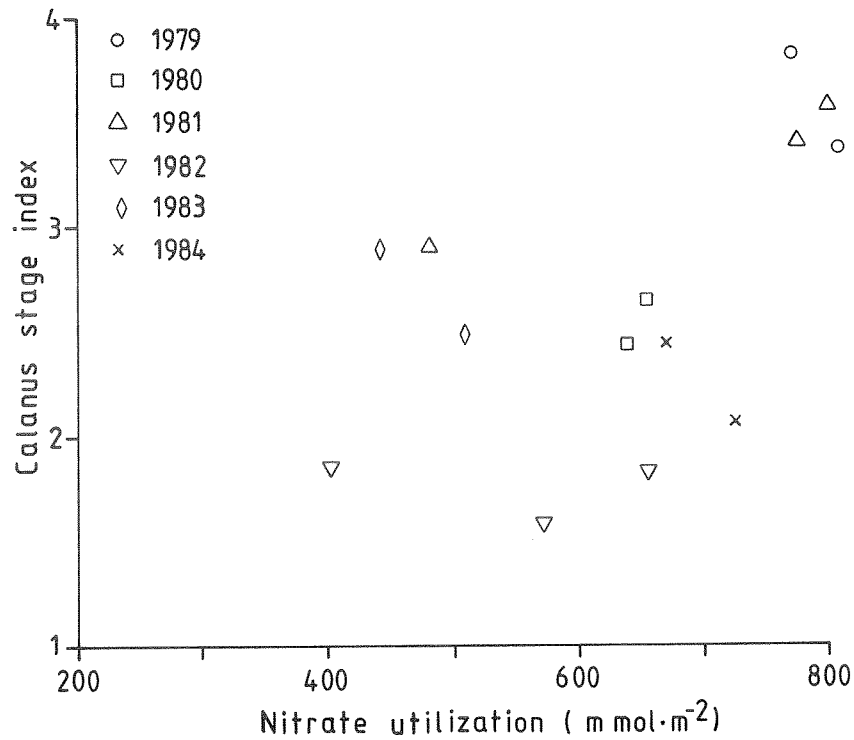


Fig. 14. Average copepodite stage number (stage index) of *Calanus finmarchicus* plus *C. glacialis* plotted against nitrate utilization (0-100 m) by the spring phytoplankton bloom in 1979-1984.

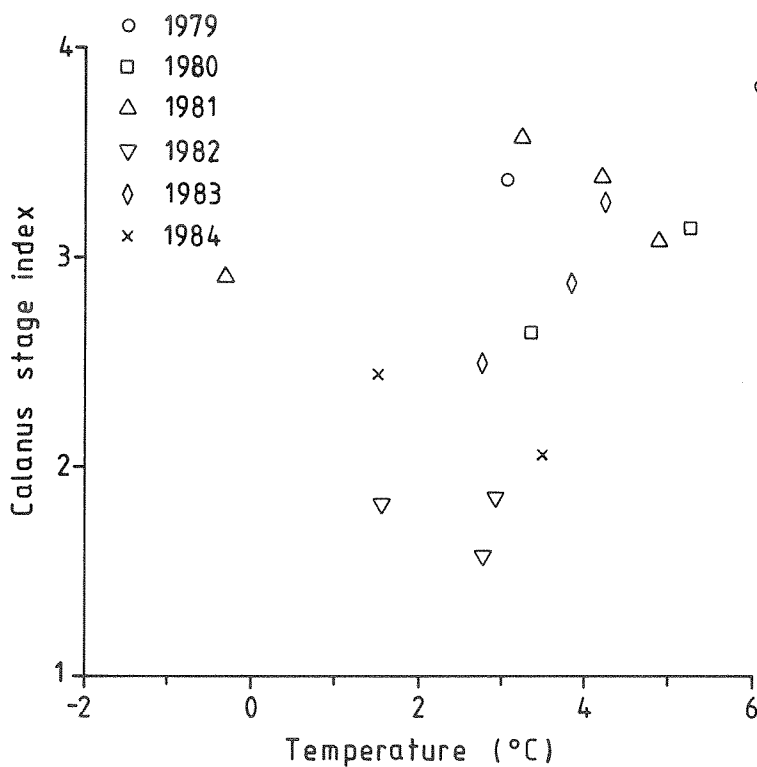


Fig. 15. Relationship between average copepodite stage number (stage index) of *Calanus finmarchicus* plus *C. glacialis* and temperature of the upper mixed layer at the time of coverage of section I (Table 1) in 1979-1984.

further difficulty in interpreting the relationship in Fig. 15 lies in the interdependency between temperature on one hand and time, stability formation and bloom development on the other. The data point for 76°N in 1981 is exceptional and noteworthy. The copepodite development here was fairly advanced with CIII as the predominant stage (Fig. 11), despite temperature below 0°C (Fig. 6). This suggests that development of C. finmarchicus can take place at very low temperatures, although the abundance of copepodites was considerably lower here than at higher temperatures further south (Fig. 10). C. finmarchicus was not separated from C. glacialis, however, and it is therefore possible that the latter species contributed to the high stage index value found at 76°N.

The temperature isopleth diagrams (Figs 4-9) suggest that the early development of Calanus in Atlantic water not influenced by meltwater has mainly occurred at temperatures of 2-4°C. With the influence of ice melting, such as in 1979 and 1981, the temperature conditions were assumedly more variable, being very low in the early phase of development. Such low temperatures could retard the hatching and development of nauplii, thus countering the possible effect of earlier spring bloom development under such conditions. This could be one reason for the fairly similar level of development reached in mid-June in each year. Except for 1983, the dominant stage by that time was estimated to be stage CI or CII (Table 3). There was in fact a weak tendency of slightly less advanced development in the cold years 1979 and 1981 than in the warmer years (1980, 1982-1984).

The phytoplankton spring bloom is to a great extent influenced by the physical oceanographic conditions and thereby also by the climatic conditions. In cold years with extensive ice melting in Atlantic water south of the polar front, stability formation is mainly due to meltwater. This is exemplified by the years 1979 and 1981. Such stability formation is usually more pronounced and occurs earlier than stability formation due to warming of the upper layer. The spring bloom is therefore expected to start earlier in the cold years and to culminate a month or more prior to the culmination of the blooms in Atlantic water in warmer years (Table 3). One might ask which of these conditions are more favourable for the development and production of herbivores such as Calanus finmarchicus. The early blooms in cold years might be advantageous for maturation and spawning and possibly also for the development of the nauplii. However, the copepodites may not reach a size which allows them to fully utilize the bloom prior to its culmination. In contrast, the slower bloom development in warmer years may be more favourable for copepodite development. Assuming that the Norwegian Sea is the true home area of Calanus finmarchicus where its ecological properties have been molded through evolution, one would intuitively believe the development in warmer years to be the more favourable for this species.

One can envisage an alteration from a closely coupled and efficient pelagic system in warm years to a system where a greater fraction of the spring bloom is left ungrazed to sediment out to the deeper water or benthos in cold years. This generalization applies mainly to the area immediately south of the polar front where the variable influence of ice melt is taking place. If we turn to our data for Calanus abundance (Fig. 10), they provide no clear-cut support for this hypothesis. Thus the recruitment of Calanus seemed to be successful in the cold year 1981, although the highest zooplankton biomass (REY et al. 1987) and copepodite numbers occurred in the warmer years 1980 and 1982, respectively. The copepodite numbers were, on the other hand, very low in the warm years 1983 and 1984.

Zooplankton abundance and biomass depend perhaps as much on predation as on growth and production. Grazing by capelin and other predators is no doubt a factor to be reckoned with in order to fully explain variations in zooplankton as influenced by climatic conditions.

Advective transport of plankton is another process which is potentially very important. The inflow of Atlantic water from the Norwegian Sea is possibly related to climatic phenomena within the Barents Sea and may occur in pulses rather than as a steady flow (MIDTTUN and LOENG 1987). The population of *C. finmarchicus* in the Norwegian Sea overwinters mainly below 600 m (ØSTVEDT 1955, HASSEL et al. 1986). Its ascent to the surface layer takes place in February-March (ØSTVEDT 1955). Inflow to the Barents Sea prior to this ascent could introduce water practically devoid of *C. finmarchicus*. Computer simulations have shown the number of overwintering females to be important for the total production (SLAGSTAD 1981, REY et al. 1987). The timing of major inflow events in relation to the seasonal vertical distribution of *C. finmarchicus* could therefore be of great ecological significance for the Barents Sea.

ACKNOWLEDGEMENT

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