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SPAWNING AND DEVELOPMENT OF *CALANUS* SPP. IN THE BARENTS SEA

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ABSTRACT

From 1986 to 1988 eight cruises were conducted in the Barents Sea, covering Atlantic water in central parts of the Sea and meltwater and Arctic water in the Polar front region. During the cruises hydrography, nutrients, phytoplankton biomass and abundances of life stages of the three *Calanus* species; *C. finmarchicus, C. glacialis* and *C. hyperboreus*,were mapped. From this, development and spawning of the copepods in different water masses were related to the timing and progress of the phytoplankton spring bloom.

In central parts of the Atlantic water stabilization was caused by formation of a thermocline due to atmospheric warming and the process was time dependent. Phytoplankton spring bloom development was closely related to water column stability. Rates of egg production of the female populations of *C. finmarchicus* and *C. glacialis* showed strong correlations with chlorophyll content, indicating a functional relationship between spawning and food supply.

In the meltwater region water column stabilization was caused by ice melting, which is not purely a time dependent process. However, also in this region a close relationship between phytoplankton spring bloom development and spawning of *C. glacialis* was found. Spawning of *C. finmarchicus* was out of phase with the spring bloom and peaked during the post-bloom period. This was explained by a retarded development of the overwintered stock of *C. finmarchicus* in the meltwater region. In Arctic water development seemed to be slower for both species. Thus, mis-match between the phytoplankton bloom and spawning of *C. finmarchicus* due to retarded development is suggested as the main factor making this species an expatriate of the northern Barents Sea. In *C. glacialis* a two-year life cycle in the warmer parts of the Barents Sea, may result in a too long life span relative to the mortality rate of this area, and the species may be expatriated in the southern Barents Sea.

C. hyperboreus was found to spawn in January and February, or earlier, well before the spring bloom. The nauplii, however, did not develop beyond stage NIII which is the first feeding stage until the food concentrations increased during the spring bloom.

INTRODUCTION

The Barents Sea consists of three watermasses, each characterized by a distinct physical and chemical composition related to its origin. In the south Coastal water flows eastward along the Norwegian and Russian coasts as an extension of the Norwegian Coastal Current (Fig. 1). Atlantic water from the Norwegian Sea flows into the central parts of the Barents Sea. At the transition between Coastal and Atlantic water, the less saline Coastal water forms a narrowing lens of lighter surface water overlying the denser Atlantic water. The Polar front separates Atlantic water from Arctic water. In the western Barents Sea the front is a rather stable feature confined by bottom topography. In the east the position of the front fluctuates between a southern and northern position dependent on the climatic conditions. Arctic water north of the Polar front typically flows southward (Loeng 1991). At the polar front the Atlantic water dives under the lighter Arctic water. During spring and summer a low salinity surface layer formed by melting sea ice, covers extensive areas north of the Polar front. Stabilization of the water column by meltwater, vertical layering in the frontal areas, and heating of the Atlantic water south of the Polar front are important mechanisms for the initiation of the phytoplankton spring bloom of the Barents sea (Skjodal *et al.* 1987, Skjoldal & Rey 1989, Loeng 1991).

Three species of the copepod genus *Calanus* are common in the Barents Sea. *Calanus finmarchicus* dominates the zooplankton biomass in Atlantic and Coastal water (Manteufel 1938, Jaschnov 1970, Hassel 1986, Skjoldal *et al.* 1987, Hassel *et al.* 1991). The deeper parts of the North Atlantic, such as the Norwegian sea, are regarded as the main area of its reproduction and production (e.g. Jashnov 1970). In the Barents Sea *C. finmarchicus* is associated with the Atlantic water, being expatriated in the cold Arctic water (Jashnov 1958). The reverse pattern is the case for *Calanus glacialis* which dominates the zooplankton biomass of the Arctic watermass, and is regarded as an expatriate of Atlantic water (Jashnov 1970, Tande *et al.* 1985, Hassel 1986, Skjoldal *et al.* 1987, Hassel *et al.* 1991). Mixing of Atlantic and Arctic watermasses at the Polar front transports *Calanus finmarchicus* and *Calanus glacialis* across the front, although in relatively low numbers. The third species, *Calanus hyperboreus*, occurs generally in low numbers in all three watermasses of the Barents Sea (Hassel 1986, Melle *et al.* 1987, Skjoldal *et al.* 1987). This species appears to be most abundant in Polar waters of the Greenland Sea and in deeper Norwegian fjords (Digby 1954, Sømme 1934, Wiborg 1954, Matthews *et al.* 1978, Smith 1988, Hirche 1991).

Calanus finmarchicus in Atlantic and Coastal watermasses of the Barents Sea typically has a one-year life cycle (Tande *et al.* 1985, Skjoldal *et al.* 1987). Spawning of *C. finmarchicus* is dependent on an external food supply, as shown by both laboratory and field investigations (Marshall & Orr 1952, 1953, Runge 1985, Hirche 1990, Smith 1990, Diel & Tande 1992). Based on copepodite stage composition in summer it has been shown that the main spawning of *C. finmarchicus* in the Barents Sea at the early stage of spring

phytoplankton bloom (Skjoldal *et al.* 1987). This is supported by direct observation of high rates of egg production in the phytoplankton bloom period (Melle *et al.* 1987). In a North Norwegian fjord, under environmental conditions similar to those in the Barents Sea, a close relationship was found between spring bloom development and spawning of *C. finmarchicus* (Diel & Tande 1992). During summer the new generation develops into copepodite stages III, IV and predominantly V before overwintering (Hassel *et al.* 1984, 1986). Unlike the situation in the much deeper Norwegian Sea, a considerable portion of the population remains in the near surface water layers during winter (Hassel *et al.* 1986). The next spring *C. finmarchicus* starts the new growth season as mainly CIV, CV, and adults (Hassel 1986, Melle *et al.* 1987, Skjoldal *et al.* 1987).

Calanus glacialis in the Arctic watermass of the Barents Sea seem to have its main spawning in connection with the ice edge phytoplankton bloom (Melle *et al.* 1987, Tande *et al.* 1985), as it also does in the Polar water of the Greenland sea (Hirche & Bohrer 1987, Hirche 1989). Utilization of ice algae and internally stored lipids are also suggested as important sources of egg production, enabling significant spawning prior to the spring bloom of the planktonic algae (Smith 1990, Runge *et al.* 1991, Tourangeau and Runge 1991, Hirche & Kattner 1993). *C. glacialis* in the Arctic water of the Barents Sea probably has a predominant two-year life cycle with overwintering as mainly copepodite stages III and V (Tande *et al.* 1985).

The life cycle of *Calanus hyperboreus* in the Barents Sea is less known. Studies from the Norwegian Sea and North Norwegian fjords indicate that a one-year life cycle prevails (Sømme 1934, Wiborg 1954, Østvedt 1955, Conover 1988). However, as temperatures decrease towards north two- and possibly mult-year life cycles will probably dominate (Johnson 1963, Dawson 1978, Rudyakov 1983, Conover 1988). The main spawning of *C. hyperboreus* usually occurs in winter well before the phytoplankton bloom and is dependent on stored lipids (Sømme 1934, Wiborg 1954, Østvedt 1955, Heinrich 1962, Conover 1967, 1988, Smith 1990). Later spawning during spring and summer is also reported (Sømme 1934).

The main objective of this study was to reveal how spawning and early development of the *Calanus* spp. relate to the phytoplankton production cycle in various watermasses of the Barents sea. Similar studies have been done for many copepod species in different areas, using laboratory techniques or working in fjords and near shore sites. We attempted to obtain a time series of direct measurements of egg production in open sea. It is inherently difficult to obtain a high resolution time series from the open sea, which is the probable reason why such results do not exist already. The problems of infrequent sampling also influenced our results. We have tried to compensate for this by aggregating data from given watermasses from different cruises and years to produce a composite time series which reveal general features of seasonal development of *Calanus* reproduction in the Barents Sea.

There are many possible causes for expatriatism of *Calanus finmarchicus* and *Calanus hyperboreus* in the Barents Sea. As the inflowing Atlantic water to the Barents Sea is cooled *C. finmarchicus* have to endure temperatures several degrees lower than in the Norwegian Sea. Low temperatures may cause high mortality in developmental stages (Tande 1988) and slow rate of development may cause mis-match between phytoplankton bloom and *Calanus* spawning (Hassel *et al.* 1986). Preferred overwintering depth of *Calanus* spp. in the Norwegian Sea is below 600 m (Østvedt 1955), while bottom depth in the Barents Sea seldom exceeds 400 m. *C. hyperboreus* has its main distributional centre in the much deeper Greenland Sea. This may limit the possibility of the copepods to avoid predation from visual predators during overwintering. The mixing of Atlantic and Arctic watermasses at the Polar front, which brings *C. finmarchicus* into Arctic water and *C. glacialis* into Atlantic water, gives an opportunity to study what probably is extreme expatriatism since neither *C. finmarchicus* nor *C. glacialis* seem to persist for very long at the "wrong" side of the Polar front.

MATERIAL AND METHODS

Field sampling

Eight cruises over the years 1986 to 1988 covered the different water masses and phytoplankton bloom situations in the period from February to July in the Barents Sea. Two cruises in April 1986 were carried out with two ice going vessels from the Norwegian Coast Guard, the other cruises were limited to open sea. At all stations samples of eggs, larvae, and adult stages of zooplankton, chlorophyll, nutrients, and hydrography were obtained. From the cruise in June 1988 (M/S "Odin Finder"), however, samples of chlorophyll and nutrients are missing. The position of the stations are shown in the map of Fig. 1.

Eggs and nauplii were sampled with 30-L Niskin water bottles at about 8 depths from the surface to 100 or 150 m. The samples were sieved on 30 µm (1986) or 90 µm nets. On the cruise with R/V "Endre Dyrøy" eggs and larvae were sampled with a Juday net, 36 cm opening and 90 µm mesh. The net was hauled vertically from 150 m (or bottom) to the surface. Whether catch efficiency due to avoidance and clogging, differ between the net and water bottles is not known. However, the net was only used during pre- and early bloom situations when the abundance of algae was low, and clogging of the net was probably a minor problem. Copepodites were collected with a pump ("Hufsa"; Solemdal & Ellertsen 1984) as described in Melle & Skjoldal (1989), or with a WP-2 net, 52 cm opening and 180 µm mesh. The net was towed vertically from the bottom or 200 m to the surface. Zooplankton was fixed in seawater with 4% formaldehyde.

Sampling procedures for hydrography and chlorophyll are given by Melle &

Skjoldal (1989). Nutrients were usually taken from the whole water column, at intervals of 10 or 20 m down to 50 m, of 25 m between 50 and 100 m, and of 25 or 50 m below 100 m.

Laboratory and data analyses

Body size was used to identify the *Calanus* species for all stages except the egg stage. Details on the identification of species are given in Melle (1991). Size measurements were done on formaldehyde fixed animals. Egg size was measured as diameter. Nauplius stages 1 and 2 were measured as total length of the body, while nauplius stages 3 to 6, and copepodites were measured as length of cephalothorax. Eggs and nauplii were measured at 100x magnification, while copepodites were measured at 25 or 16x magnification under a stereo microscope. All eggs and nauplii in the water bottles were measured except on some rare occasions when the total number of one stage exceeded 100 specimens. In such cases a subsample of about 50 specimens was measured. The measurements of copepodites were usually done on subsamples, and the numbers measured of each stage at a station were usually less than 50.

Egg production of *Calanus finmarchicus* and *C. glacialis* was calculated as the ratio between number of eggs and females in the water column at each station. The ratio was normalized to eggs female^{-1} day^{-1} using temperature dependent embryonic duration (Corkett *et al.* 1986).

Samples for phytoplankton pigments (chlorophyll) were stored and analyzed as described by Rey & Loeng (1985). Nutrients were usually analyzed on-board using auto-analyzer according to the procedures described by Føyn *et al.* (1981). On the cruises with R/V "Endre Dyrøy" the nutrient samples were preserved with chloroform and kept in the dark in refrigerator until they were analyzed using an auto-analyzer shortly after the cruise (Hagebø & Rey 1984).

The stations were classified according to water mass and stage of phytoplankton bloom development. Methods and results are given in Melle (Fig.s 1-3; 1991). The categories used are given in Table 1. All the data were not used in both Melle (1991) and this study. The classification of water masses and bloom situations, however, was performed on the complete set of data and reported once in Melle (1991). Therefore, the data which were used in this study have been indicated in Table 1.

Table 1. Classification of water masses and stages of phytoplankton spring bloom development. See also Figure 1.

Water mass	**Stage of bloom**	**Data used**
Atlantic water	Pre-bloom	This study
Atlantic water	Early bloom	This study
Atlantic water	Bloom	This study
Atlantic water	Post-bloom	This study
Melt water (overl. Atl. water)	Pre- and early bloom	This study
Melt water (overl. Atl. water)	Bloom	This study
Melt water (overl. Atl. water)	Post-bloom	This study
Arctic water	Early bloom	This study
Coastal water	Pre-bloom	Melle (1991)
Coastal water	Early bloom	Melle (1991)
Coastal water	Post bloom	Melle (1991)

RESULTS

Atlantic water

Phytoplankton bloom development

Spring phytoplankton bloom development in Atlantic water was described by combining the stations sampled from early February to late July in 1986, 1987, and 1988 on a time axis (Fig. 2). The consumption of nitrate in the water column gives a cumulative measure of the development of the phytoplankton spring bloom, at least during the early phase of the bloom when remineralization is low. Stations from April 1986 follow the same temporal trend of the bloom in the Atlantic water mass as that described by the stations in 1987. A slight reduction in the concentration of nitrate in the upper part of the water column in late April in 1986 and 1987 (Fig. 2), indicated that the phytoplankton growth had started at that time. During May the bloom development accelerated, as evident by the rapid increase in nitrate consumption in late May (Fig. 2). The simultaneous increase of integrated content of chlorophyll confirms that the phytoplankton growth started by the end of April, and accelerated during the last part of May (Fig. 2). The limited number of stations available from Atlantic water in May made it difficult to describe more exactly the timing of the bloom.

Net growth of the phytoplankton stock is dependent of a minimum theoretical residence time of the phytoplankton cells above the compensation depth by reduced mixing below the critical depth (Sverdrup 1953). An index

of water column stability, $\Delta sigma_t$; which was the difference in water density between 5 and 100 m, was used for comparison with the development of the phytoplankton bloom. Fig. 2 shows that the bloom started before the large increase in the index of water column stability by the end of June. However, a closer inspection of the physical, chemical, and biological properties of the water column at the stations in May and early June with a well developed bloom showed that a clear stratification existed, although the change in density within the water column from 5 to 100 m depth was rather small, <0.05 $sigma_t$ units (Fig 3, station 987).

The degree of stratification at pre-bloom stations in April was similar to that found at bloom stations in May and June, when measured as $sigma_t$. However, density increased gradually with depth at the former stations while a more sharp pycnocline characterized the latter. Therefore another measure of water column stability which reflected changes in density over smaller depth intervals was introduced. We chose the maximum change in temperature over 5 m depth intervals in the water column. Temperature was used instead of density because salinity data lacked at some stations. However, since stabilization in the Atlantic water mass is related to the formation of a thermocline, temperature seemed to be a good variable. Maximum change in temperature over 5 m in the water column showed a significant linear relationship (after log-log transformation) with nitrate consumption (Fig. 4). This indicated that even in the early phase of the spring bloom a close relationship exists between stability of the water column and bloom development.

In July 1988 the integrated chlorophyll content was low, showing that the bloom was over. The nitrate concentrations were close to zero above the pycnocline and the nitrate consumption indices high (Fig. 2).

Vertical profiles of temperature, salinity, density, chlorophyll, and nutrients are shown for selected stations from the composite time series in Fig. 2 (Fig. 3). St. 102 was from a typical winter pre-bloom situation in Atlantic water with little stratification of the water column, low values of chlorophyll, and only minor reductions in nutrients.

At st. 876 in the middle of May, lower salinity (≈35.08) in the upper 75 m gave a weak reduction in density and therefore some stability to the water column. Lowered nitrate concentration was found in this upper layer due to some phytoplankton production, which also was seen as a slight increase in chlorophyll content. However, by the middle of May there still was no strong phytoplankton bloom (Fig. 3).

St. 987 was from early June during the spring bloom (Fig. 2, 3). At this station there was a rather deep and sharp pycnocline, although $\Delta sigma_t$ was not higher than at earlier stations. However, due to the sharp pycnocline there was a significant increase in the index of maximum temperature change (Fig. 4). The temperature were about 1.7 ^0C and salinity about 35.03 $^0/_{00}$ above the pycnocline. Below the pycnocline temperature and salinity gradually

decreased with depth from 1.6 ^{0}C and 35.07 $^0/_{00}$, respectively.

Calanus finmarchicus

The progress in the rate of spawning (eggs · female^{-1} · day^{-1}, Material and Methods) of *Calanus finmarchicus* was closely related to the integrated water column chlorophyll content, indicating a link between food supply and spawning (Fig. 5). The stage ratio index between the number of CVI females and CV's (CVI females-CV's/CVI females+CV's; Diel & Tande 1992) of *Calanus finmarchicus* showed an increasing trend from only CV's (-1) in February to almost exclusively females (1) in early May (Fig. 5). After the initiation of heavy spawning in May the relative number of females dropped, and in July the CV's dominated at most stations. Development from CV's into CVI's from February to May did not seem to be related to the chlorophyll content.

Abundances of all developmental stages for the stations included in Fig. 5 are given in Fig. 6. A general decrease in the abundance of CV's from February to June seems to reflect the molting into CVI females. After the start of heavy spawning in late May, a reduction in the abundance of females relative to CV's followed. This reduction was not related to the recruitment of CV's from the new generation as this generation had only reached stage NVI to CII at that time (Fig. 6). Therefore, a higher rate of mortality of CVI females seemed to coincide with increased rate of spawning. There were hardly any CVI males during the sampling period, probably due to the general tendency of *Calanus finmarchicus* to mate in deep waters earlier in the winter (e.g. Conover 1988). The high abundance of CV's in July probably represented the new generation. At most stations the CV's did not yet seem to be molting into CVI's, and CVI males were only observed at the latest and southernmost station. Therefore, the population seems not to be reproducing more than once a year.

The new generation first occurred as eggs and young nauplius stages in late March and early April (Fig. 6). These are recruits from the pre-bloom spawning. The numbers of eggs and young nauplii peaked in late May and early June, and generally low numbers were found in July. The older nauplius stages first occurred in high numbers in late May and early June after the increase in spawning rate. Relatively low numbers were found in July, except at the easternmost station (at day 200), which seemed to have a less developed population of *Calanus finmarchicus* compared to the western stations (Fig. 6). Copepodites in high numbers were not found until July, although the two youngest copepodite stages occurred at some stations in June. As already mentioned some individuals of the new generation had developed into stage CV in July.

Calanus glacialis and *C. hyperboreus*

The spawning rate of *Calanus glacialis* changed over time in much the same

manner as for *Calanus finmarchicus* (Fig. 7). There was a close relationship between the amount of chlorophyll in the water column and number of eggs spawned. There was also a reduction in number of females relative to the number of CV's at the start of heavy spawning in May. In contrast to *Calanus finmarchicus,* there were no CV's of *C. glacialis* in February to April (stage ratio = 1.0). The fall in the ratio when the spawning at a high rate started could have been due to an increased mortality of CVI females, but could also involve development of overwintered CIV's into CV's.

The spawning of *Calanus hyperboreus* could not be characterized by spawning rate and stage ratio, because CV's and CVI females were hardly caught in the analyzed net hauls. A plot of the number of eggs versus time shows that spawning, unlike for the other *Calanus* species, occurred through out the sampling period from February to July (Fig. 8). Maximum number of eggs, however, occurred during the bloom period in May and June.

The eggs of *Calanus hyperboreus* and *Calanus glacialis* could be easily recognized by the spiny outer membrane of the latter and the bigger size relative to *Calanus finmarchicus* of the former. Due to overlap in size, the nauplii of the two species could not be separated from each other based on measurements of body length of the stages. However, on the basis of the occurrences of eggs and copepodites of the two species and a higher fat content of the nauplii found in February and March, giving them a black color after fixation in formalin, some assumptions about the occurrences of the nauplii of the two species were done. During February and March, hardly any eggs of *Calanus glacialis* were found. We assume that the nauplii with a high fat content were of *Calanus hyperboreus.* Therefore, the nauplii during this period were most likely of *Calanus hyperboreus* (Fig. 8). Even though spawning had been going on since February, and possibly earlier, no nauplii older than stage 3 were found. The first stage NIV nauplii occurred in the middle of April, at the time of the first weak increase in chlorophyll content. This may indicate that NIII is the first-feeding-stage where development stops until sufficient food is available. Although the spawning starts earlier the new generation of *Calanus hyperboreus* did not seem to develop into copepodites earlier than the other two *Calanus* species (Fig. 8).

The nauplii in May and June were probably of *Calanus glacialis,* at least the older ones, since high numbers of CI and CII of this species were found (Fig. 9). Therefore, *Calanus glacialis* seemed to have a spawning and development in Atlantic water very similar to that of *Calanus finmarchicus,* with very low spawning rate during the pre-bloom situation until the middle of May, then increased spawning and rapid development of the nauplii population in May and June, followed by relaxed spawning and development into copepodites by July.

The stage distribution of the overwintering population of *C. glacialis* in February, March, and April is in agreement with the proposed two-year life cycle of this species (e.g. Tande *et al.* 1985, Fig. 9). The individuals overwintering for the first time are in stage CIII and CIV in late winter and

spring, while after the second overwintering all are in stage CVI and in February no CVI males are left. In contrast to *C. finmarchicus*, the spawning generation of *C. glacialis* do not emerge after the overwintering as CV's or younger stages.

Meltwater

Phytoplankton bloom development

In the meltwater region phytoplankton spring bloom development was less related to time than in Atlantic water. This was expected since the start of the bloom in the meltwater region is dependent of stabilization by formation of a low salinity surface water layer from melting ice. This process is less time dependent than the formation of a thermocline in Atlantic water, and in general a gradient in stages of the bloom is found related to distance from the retreating ice edge (e.g. Skjoldal *et al.* 1987). Therefore, areas ranging from typical pre-bloom to post-bloom situations can be observed through out spring and summer in the meltwater region.

To be able to make general conclusions about spawning and development of copepods relative to the bloom development, we needed an index, other than time, that would reflect the bloom development of this region. Neither nitrate consumption nor water column stability alone were able to describe bloom development very well. The start and development of the spring phytoplankton bloom are, as already commented on, dependent on physical and chemical properties of the water column, light, and weather conditions. To get a better model of the bloom development we therefore included different measures of the physical and chemical conditions of the water column representing some of the requirements for a bloom together with some of the parameters we meant were results of the bloom (nitrate consumption and chlorophyll content). The parameters are described in Table 1. After a correlation analysis redundant parameters were removed from groups of highly correlated parameters. The rest were included in a Principal Component Analysis (PCA) and we found that the first axis represented a gradient in salinity and nitrate concentration (Fig. 10). Therefore the stations score along the first PCA-axis was taken as an index of bloom development, however, it was not a causal gradient.

A plot of nitrate consumption and chlorophyll content at the sampled stations versus this new index showed that nitrate increased towards an asymptote during and that chlorophyll content increased towards a maximum in the same region and thereafter decreased towards zero at the late bloom stations (Fig. 11). Since the stations now seemed to be arranged along an axis of bloom development we proceeded with the analysis of spawning and development of the copepods relative to the spring phytoplankton bloom.

Examples of vertical profiles of physical, chemical and biological properties of

the water column during early bloom, bloom and post-bloom (Fig. 11) are given in Fig (12).

Calanus finmarchicus

Intermediate rates of spawning (>10 eggs · female^{-1} · day^{-1}) of *Calanus finmarchicus* were observed in the middle of April when high levels of chlorophyll content were found (Fig. 13). This indicated an earlier increase of spawning in the meltwater region compared to the Atlantic water mass. Maximum spawning rates were observed at stations in a late bloom situation, sampled in July 1988 in areas covered with ice earlier in the spring.

Unlike the situation in Atlantic water, the stage ratio did not reach high values before spawning (Fig. 13). The ratio was rather low for the rest of the sampling period as well. This may indicate that spawning in the meltwater region starts before the major part of the CV's have developed into CVI's, and that after the start of spawning a reduction in the number of females, as suggested for Atlantic water, prevents the ratio from building up toward 1.0.

Eggs of *C. finmarchicus* were found at all stations in the meltwater region. The first nauplii occurred in late April. The maximum numbers of eggs and nauplii were found at the stations sampled in May 1987 (Fig. 14). In July 1988 the new generation of copepodites occurred in high numbers (CI, CII, CIII). At the stations in April and May the new generation occurred at only one station in May. Thus, spawning did not seem to be later in the Meltwater region compared to Atlantic water, and there was no clear evidence of delayed development of the new generation. The relatively high number of CIV and CV's from the over-wintering generation throughout the sampling period, however, indicated that development of the overwintered population was slowed down compared to what was found in Atlantic water.

Calanus glacialis and Calanus hyperboreus

The rate of spawning of *Calanus glacialis* in the meltwater region peaked at nearly 80 eggs · female^{-1} · day^{-1} in the middle of April, while the spawning rate was lower in May and July (Fig. 15). A close relationship was found between the rate of spawning and the chlorophyll content. The stage ratio showed that the overwintering generation that was to spawn, was made up of CVI females only. The low values of the ratio in May 1987 and July 1988 were probably due to CIV's of the first overwintering generation molting into CV's (see Atlantic water).

Unlike the situation described for *C. finmarchicus*, the eggs of *C. glacialis* had developed into nauplii at the stations with the least developed spring bloom in April (Fig. 16). Towards late April and at the stations from May and July an increasing proportion of the new generation occurred as late naupliar stages, and as copepodite stages CI, CII and CIII. The new generation of *Calanus glacialis* in the meltwater region did not seem to develop markedly faster

than that of *Calanus finmarchicus*, except for a possible faster development of the eggs at the very early stations. The copepodites of the new generation of *Calanus glacialis* first occurred in May both in Atlantic water and in the meltwater region indicating that the rate of development was not very different in the two water masses. The two overwintering generations of *C. glacialis* were in stages CII to CIV (the youngest) and CVI (the oldest) after the overwintering. The youngest generation, now about one year old, started to developed into CV's in May, and were then ready for the next over-wintering. The last individuals in stage CIII of this generation developed into CIV's at the same time. At the post-bloom station in July there were not any individuals of the spawning generation left.

Eggs of the third Calanus species, *C. hyperboreus*, were found in low densities during most of the sampling period in the meltwater region. We therefore assume that the nauplii of the largest size group were mainly nauplii of *C. glacialis*.

Arctic water

This is an area covered with meltwater during spring and summer, like the area earlier described as the meltwater region. However, in that region the meltwater overlies Atlantic water, while here we are on the arctic side of the Polar front and the meltwater overlies Arctic water.

The Arctic water mass north of the Polar front was sampled only three times in April 1986, when an ice going vessel was used. The stations were in an early bloom situation. The rates of spawning of *Calanus finmarchicus* and *C. glacialis* were high at the two stations with most reduced nitrate content (Fig. 17). The spawning rate did not seem to be different from that measured at the stations in April in the Meltwater region. Spawning rate of both species covaried with the chlorophyll content. The ratio between CVI females and CV's of *C. finmarchicus* seemed to be similar to that in the Meltwater region at the same time, indicating a similar reduction in developmental rate. The stage ratio of *C. glacialis* was equal to 1 except for station 37, where 40 CV's m^{-2} were found. These were the only CV's of *C. glacialis* found in April at all during this investigation, indicating that a reduction in development of the over-wintering population may take place in the coldest regions, and that the complete development into CVI's after the second over wintering may be a feature typical for populations of *C. glacialis* living in the warmer outskirts of its distributional area.

In spite of the high number of eggs of *C. glacialis* and *C. finmarchicus* the number of nauplii were relatively low for both species (Fig. 18; conf. early stations of Meltwater region). This may be related to a resent start of the spawning in combination with prolonged developmental time due to low temperatures (between -1.2 and -1.9^{0}C) causing accumulation of individuals in the egg stage. At the time of sampling no individuals of the new generation had developed into copepodites yet (Fig. 18). The relatively high numbers of CIII, CIV and CV's of *C. finmarchicus* indicate that development

is slow during the over wintering.

DISCUSSION

Phytoplankton spring bloom development

In Atlantic water a significant relationship was found between maximum change in temperature over 5 m in the water column, a measure related to water column stability, and the consumption of nitrate, a measure of cumulative growth of the phytoplankton (Fig. 4). From early spring on (April), when changes in temperature associated with the build-up of a thermocline were small, a significant relationship was found. This agrees well with the classic theory of water column stabilization and the initiation of phytoplankton spring blooms (Sverdrup 1953, Sambrotto *et al.* 1986). When stability of the water column increased from late May to early June, the most marked growth in phytoplankton, as measured by chlorophyll concentrations and use of nitrate, occurred simultaneously. Thus, the phytoplankton spring bloom in Atlantic water of the Barents Sea was initiated when water column stability was still low, but not in a homogenous water column as suggested by Tande (1991). A high resolution of the density or temperature profiles is needed to reveal the weak thermoclines described here. When these variables are presented on coarser temporal or spatial scales the small variations will not be visible. In the Norwegian Sea a situation is described during spring where a thermocline is formed several times and broken down by storms before the final stabilization in May (Halldal 1953). Just after a storm a situation with low stability and a significant use of nitrate and intermediate chlorophyll concentrations probably can be observed.

In the meltwater region a layer of fresher meltwater on top of Atlantic water stabilized the water column in April. At the same time the bloom was initiated and peaked. On a transect North-South across the ice edge one typically will find pre-bloom situation in the ice-covered water, bloom siyuations close to the ice edge, and post-bloom situations farther away from the ice edge (Skjoldal *et al.* 1987). Therefore, a multivariate axis, ordering the stations according to stage of bloom development, was used in stead of a time axis like in Atlantic water (Fig. 10, 11). This was not a causal axis, but it was acceptable for our purpose which was to relate the spawning of the *Calanus*-species to the phytoplankton spring development.

Spawning and development of Calanus

The pre-bloom phase

In situ spawning rates (Fig. 5, 7) showed that pre-bloom spawning of *Calanus finmarchicus* and *C. glacialis* in Atlantic water started in late February. In the meltwater region the pre-bloom phase was not sampled until the middle of April, however, both species spawned at low rates at the 2-3 stations available (Fig. 13, 15). By back-calculations from first occurrence of CI's, using

temperature dependent developmental rates according to Corkett *et al.* (1986), the start of the spawning for both *C. finmarchicus* and *C. glacialis* was estimated to late March in Atlantic water and early April in meltwater. Pre-bloom spawning may have been some what delayed in the meltwater region compared to the situation in Atlantic water, however, better sampling of the pre-bloom period of the meltwater region is needed before a firm conclusion can be drawn. A later start of spawning in Atlantic water estimated by back-calculations compared to direct observations of spawning may indicate a lower survival rate of the early spawned recruits, as suggested by Melle & Skjoldal (1989) based on observations of rates of sinking of the early spawned eggs.

Pre-bloom spawning rates of *Calanus finmarchicus* were <1-8 and ~3 eggs female^{-1} day^{-1} and of *Calanus glacialis* <1-6 and 7-37 eggs female^{-1} day^{-1} in Atlantic water and meltwater, respectively. The rates generally increased towards the end of the pre-bloom phase. Interpretation of these spawning rates is complicated since sampling from February to April with M/V «Endre Dyrøy» was limited to the upper 150 m, at a time when part of the overwintered female population was still distributed below 150 m. Thus, the spawning rate for the whole population may have been over estimated during this time period. On the other hand, in the Barents Sea *C. finmarchicus* and *C. glacialis* are known to overwinter more evenly distributed throughout the water column, and the bias introduced by restricted sampling depth may not be as important as one would expect for other areas, e.g. the Norwegian Sea.

Information about batch size or rate of egg production by the portion of females that is spawning are frequently found in the literature. Egg production rate of the whole female population, however, is not very often reported. Neither is population spawning rate combined with information about the state of phytoplankton bloom development. In Atlantic water of the Greenland Sea, females of *C. finmarchicus* incubated in the laboratory in natural sea water immediately after capture spawned a mean number of 13.7 eggs female^{-1} day^{-1}. The females were collected at stations in a pre-bloom phase (Hirche 1990). Using the same method Diel & Tande (1992) measured a pre-bloom spawning rate of <10 eggs female^{-1} day^{-1} in the *C.finmarchicus* population of a North Norwegian fjord. Pre-bloom spawning rate of *C. glacialis* in the Greenland Sea was less than 2.5 eggs female^{-1} day^{-1} (Hirche 1990). Measured by the egg ratio method (Runge 1984), mean pre-bloom spawning rate of *C. glacialis* was 2.2 eggs female^{-1} day^{-1} in the Hudson Bay (Tourangeau & Runge 1991), a spawning possibly supported by feeding on ice algae. Taking our results as maximum estimates of pre-bloom spawning rates, they fall within the range of earlier reported spawning rates.

Eggs of *C. hyperboreus* were found regularly from the first day of sampling in February (Fig. 8), which showed that this species spawned actively during winter, a spawning strategy well known from previous investigations of *C. hyperboreus* (Sømme 1934, Østvedt 1955, Conover 1988). Spawning rates could not be calculated, however, since females were seldom caught. As the

females of *C. hyperboreus* may spawn prior to or during the migration towards the surface layers in December to May (Sømme 1934, Wiborg 1954, Østvedt 1955, Conover 1988), our catches of eggs in the upper 100-150 m may have under-estimated the egg numbers. The main spawning in the Norwegian Sea occur in February and March (Østvedt 1955). A secondary possibly more shallow spawning takes place during the phytoplankton bloom (Sømme 1934). This investigation did not cover the period before February so the spawning in the Barents Sea may have started earlier than February. Within the sampling period spawning was continuous, with increased densities of eggs during the spring bloom. The increase of egg densities during the bloom could have been due to higher spawning rates as a result of improved feeding conditions. However, a more shallow spawning or maturation of a new population of more actively spawning females may also have been reasons for this. The eggs of *C. hyperboreus* may be buoyant during the first part of the spawning and heavier than sea water when spawned during the feeding period in the productive near surface waters (Conover 1988). We have, however, found that eggs of *C. hyperboreus*, spawned during experiments for metabolic rate measurements in the Barents Sea in January, were heavier than sea water (unpubl. results).

Pre-bloom spawning seems to be common among the *Calanus spp.* of the Barents Sea. Central questions are how this early spawning is initiated, what the energy resources on which it is based are, and what advantages gained by the early spawning individuals and their recruits there may be? In *C. hyperboreus* spawning in winter and early spring based on energy from lipids stored from the previous growth season, is regarded as the most important spawning strategy (Conover 1988). Field observation have demonstrated a close relationship between rate of spawning of *Calanus finmarchicus* and chlorophyll concentrations or diatom numbers. In laboratory studies pre-bloom spawning rates are enhanced when the females are fed. This suggests that spawning in*C. finmarchicus* is depent on an external food source (Marshall & Orr 1953, Runge 1985, Hirche 1990, Diel & Tande 1992). Before the bloom rates of spawning are low (Diel & Tande 1992, Hirche 1990, Smith 1990). In studies of pre-bloom spawning of *C. glacialis* one has arrived at various conclusions. In the Greenland Sea and in the Hudson Bay, pre-bloom spawning occurs at a low rate, the pre-bloom spawning in Hudson Bay being partly sustained by grazing on ice algae by the females. It has been concluded that *C. glacialis* has a spawning strategy similar to that of *C. finmarchicus* (Hirche & Bohrer 1987, Hirche 1989, Tourangeau & Runge 1991). In other studies from the Greenland Sea and the Barents Sea, high individual spawning rates were observed before the bloom. The conclusion drawn in these studies was that pre-bloom spawning is an important part of the spawning strategy of *Calanus glacialis*, and that internal reserves of lipids are used as an energy source like in *C. hyperboreus* (Smith 1990, Hirche & Kattner 1993). This is supported by unpublished observations of *C. glacialis* spawning under 2 m of ice in the central Canadian Arctic when chlorophyll content was less than 0.1 $\mu g\ l^{-1}$ (Conover 1988). In the above cited investigations, where female gonad maturation was recorded, it was found that the gonads of both *C. finmarchicus* and *C. glacialis* matured during the

pre-bloom phase, and it was concluded that the energy source was internal stored lipids, probably supported by feeding on ice alga in Hudson Bay. During the pre-bloom phase in the Barents Sea a low density of algae and heterotrophic microplankton suitable for food for females of *C. finmarchicus* and *C. glacialis* are found, and gut analyses have shown that feeding at a low rate starts in January in Atlantic water (Nejstgaard and Skjoldal 1991). Although no quantitative measures of pre-bloom feeding in *C. finmarchicus* and *C. glacialis* are given, pre-bloom spawning in the Barents Sea may be initiated and supported by low pre-bloom food concentrations.

Early spawning may improve the overall recruitment success of the population. First, development through the non-feeding egg- and nauplius-stages NI and NII before the bloom may be advantageous for exploiting short lasting food resources during the bloom. Secondly, the chances of completing the life cycle within one year in the cold environment of the Barents Sea, may be enhanced by an early spawning. The spawning strategy of *Calanus hyperboreus* seems to be of the first type, since the nauplii developed to stage three, but not further (Fig. 8), until the bloom started, indicating that to be in the first feeding stage at the start of the bloom may be advantageous to the nauplii. Conover (1967) found that NIII was the first feeding stage in *C. hyperboreus*, and observed irregular development at this stage in the laboratory.

In Atlantic water a continuous development of the overwintering populations of *C. finmarchicus* and *C. glacialis*, as characterized by the ratio between CVI females and CV's, was observed in spite of low food concentrations (Fig. 5, 7). This indicates that development was more related to internal factors and, possibly, sea temperature. The steady increase of the CVI females to CV's ratio in *C. finmarchicus*, without a simultaneous increase in spawning rate, indicates that a major portion of the population is ready to spawn at a time when the actual spawning rate is low due to food limitation. It is not clear whether the final maturation of the gonads or the spawning activity itself are food limited (conf. Diel & Tande 1992).

The bloom and post-bloom periods

With the increase in phytoplankton biomass by the end of May and early June in Atlantic water, spawning rates of *Calanus finmarchicus* and *C. glacialis* increased simultaneously (Figs 2, 5, 7). This was probably in response to the increased supply of food. The close relationship between the main spawning of *Calanus finmarchicus* and the phytoplankton spring bloom is in accordance with results from the weather ship M in the Norwegian Sea (Halldal 1953, Østvedt 1955). Results from fjords in Northern Norway have also shown a close relationship between spawning and state of the phytoplankton bloom (Marshall and Orr 1952, 1953, Diel & Tande 1992). It was suggested by Melle *et al.* (1987) and Diel & Tande (1992) that the main spawning by *Calanus finmarchicus* is related to increased food supply at the time of the phytoplankton spring bloom, while the start of the pre-bloom

spawning might be related to internal maturation or external factors such as light or temperature change. Our results of low spawning rate in the pre-bloom situation followed by a high spawning rate in the bloom situation, together with the observation of feeding in *Calanus finmarchicus* females at pre-bloom food concentrations (Nejstgaard & Skjoldal 1991), suggest that spawning of *Calanus finmarchicus* is a simple function of food supply. A similar relationship between spawning activity of *C. glacialis* and bloom development suggests that food supply govern the spawning of this species as well.

Development in the overwintering populations of *C. finmarchicus* and *C. glacialis* in Atlantic water, as characterized by the increasing ratio between CVI females and CV's, were ahead of the increase in spawning activity. Development into females was completed before or when (*C. glacialis* and *C. finmarchicus*, respectively) food supply started to increase in connection with the phytoplankton spring bloom (Fig. 5, 7). Therefore, development during the last phase of overwintering seems to depend on internal energy stores, probably adjusted by sea temperature and possibly enhanced by a low winter supply of food. The total dominans of CVI females before the bloom started, shows that *Calanus finmarchicus* and *C. glacialis* are able to complete their life cycles within one and two years, respectively, in Atlantic water of the Barents Sea.

C. glacialis is here assumed to have a two-year life cycle in Atlantic water due to the total lack of CV's in the population in late winter and spring which indicates that two cohorts were present at the same time (Figs 7, 23). Tande *et al.* (1985) came to the same conclusion, however, did not find *C. glacialis* on the Atlantic side of the Polar front. In other studies a bimodal or wide stage distribution have been considered to reflect a prolonged spawning season (Grainger 1961, McLellan 1967, Conover 1988). However, when no CV's are present at all like in our results, there must have been a long lasting arrestment of the development in stage CIV. This we have taken as a proof of a two-year life cycle. The view that this is a mechanism that ensures synchronization of late and early spawners can not be rejected, but a second post-bloom spawning which could produce a population similar in size to the population spawned during the bloom was not observed at the post-bloom stations in July 1988.

The continuous increase of the stage ratio of *C. finmarchicus* from January to May indicates that synchronization of the population by arrested development in diapause stages had not taken place during the winter in Atlantic water (Fig. 5). Rather heavy spawning limited to the time of the phytoplankton bloom seem to serve as a synchronizing mechanism in *Calanus finmarchicus* populations, as suggested by Diel & Tande (1992).

Winter temperatures of the Atlantic watermass are several degrees lower in the Barents Sea than in the Norwegian Sea, about 3 and 8^{0}C, respectively (Loeng 1991, Melle *et al.* 1993). *Calanus finmarchicus* overwinter more or less evenly distributed in the water column in the central Barents Sea. In the

Norwegian Sea this species overwinters in Norwegian Sea water below Atlantic water, and there experiences water temperatures below -1^{0}C. Thus, with respect to temperature, development during overwintering in the Barents Sea is expected to be at least as fast as in the Norwegian Sea. The phytoplankton spring bloom in Atlantic water of the Barents Sea and the Norwegian Sea, depends on the formation of a thermocline, and seems to occur somewhat earlier in the Norwegian Sea than in the Barents Sea (Halldal 1953, this study). The main spawning of *C. finmarchicus* seem to co-occur with the bloom in both seas (Østvedt 1955, this study). If we compare stage distributions within the population about to spawn of *C. finmarchicus* when the spawning starts in the Barents Sea with the results from Østvedt (1955) from the Norwegian Sea, 60% females and 20% CV's were found in the Norwegian Sea, while the population consisted of females only in the Barents Sea. Even a month earlier a copepod ratio close to one was found in the Barents Sea. Thus, *C. finmarchicus* in Atlantic water of the Barents Sea completes its life cycle within one year, and compared to the population in the Norwegian Sea, a higher percentage of the population may have been ready to spawn when the phytoplankton bloomed.

In the meltwater region there were clear signs of a mismatch between spawning of *Calanus finmarchicus* and the phytoplankton bloom. Maximum spawning rate was not found at the stations with the highest chlorophyll concentrations, but rather at post-bloom stations, and the spawning rate during the bloom was much lower than in Atlantic water (Fig. 5, 13). The lower rate of spawning in the meltwater region did not seem to be due to food limitation, since concentrations of chlorophyll were higher during the bloom in the meltwater than in Atlantic water (Fig. 5, 13). On the other hand the ratio between CVI females and CV's never exceeded 0.5 during the pre-bloom and bloom periods. This indicates that development during winter or the previous growth season was slower in the meltwater region than in Atlantic water. A generally lower sea temperature towards north may be the reason for this. If spawning in the meltwater region is triggered by the phytoplankton bloom before development of the overwintering population into CVI females is completed, the synchronizing effect described in Atlantic water is not achieved, and parts of the population will not be able to take advantage of spawning in connection with the enhanced food supply during the short bloom (see the high spawning rates at post-bloom stations; Fig. 13). This may be an important mechanism making *Calanus finmarchicus* an expatriate outside the Atlantic watermass.

While there seemed to be a mismatch between spawning of *Calanus finmarchicus* and the bloom in the meltwater region, *Calanus glacialis* spawned at a maximum rate during the spring bloom (Fig. 15). It seems reasonable to conclude that this was due to the 2-year life cycle which ensured that most females were ready to spawn at the time of the bloom as indicated by a total dominans of CVI females over CV's in the spawning population (Fig. 15).

In Arctic water only three stations were sampled, one over the Svalbard Bank

and the other two near the Central Bank. The two stations near the Central Bank were in an early bloom stage. Here the index of the ratio of CVI females to CV's of *C. finmarchicus* were low (-0.2 - -0.5), and lower than at early bloom stations in both Atlantic and meltwater (0-1). This indicates that development in the Arctic watermass is even slower than that observed in the meltwater region, potentially causing severe mis-match between spawning and phytoplankton bloom. We assume this to be the major factor making *Calanus finmarchicus* an expatriate in Arctic water. However, the answer to whether low developmental rate is caused by low temperatures or bad food conditions must await further investigations.

Diel & Tande (1992) suggested that reduction in the ratio between CVI females and CV's immediately after the main spawning in connection with the bloom, could be used as an indicator of the spawning event in *C. finmarchicus*. This is supported by our results from Atlantic water (Fig. 5). In the meltwater, however, a corresponding reduction in the copepodite ratio did not take place, since the CVI females were not completely dominating before spawning, and CVI females were continuously arising from a pool of CV's (Fig. 13). The reduction in the ratio of CVI females to CV's were by Melle *et al.* (1987) and Diel & Tande (1992) interpreted as the combined effect of increased mortality of the spawning females (relative to late CV's developing into CVI's) and later on contribution of CV's from the new generation. However, it is clear from Fig. 6 that the first CV's of the new generation do not appear before July. Therefore, the reduction in the copepodite ratio must be due to an increased mortality among the spawning or the spent females.

For *C. glacialis* in Atlantic water the period of intensified spawning during the bloom coincided with a reduction in the copepodite ratio, followed by a secondary increase possibly related to late spawners (Fig. 7). The reduction in the ratio at the time of maximum spawning can in addition to increased mortality among the spawning females also reflect individuals of the youngest overwintering generation (CIII and CIV) molting into CV's at this time.

During the bloom in Atlantic water *C. finmarchicus* and *C. glacialis* produced eggs at a rate of 24-44 and 15-99 eggs female^{-1} day^{-1}, respectively (Figs 5, 7). Post-bloom spawning rates of the species were <4 and <1 eggs female^{-1} day^{-1}.In the meltwater region during the bloom spawning rates of *C. finmarchicus* were less than 15 eggs female^{-1} day^{-1} at all stations (Fig. 13). Spawning rate of *C. glacialis* varied between 20 and 80 eggs female^{-1} day^{-1} during the bloom in meltwater (Fig. 15). Unlike the situation in Atlantic water the rates of spawning of *C. finmarchicus* and *C. glacialis* were occasionally high after the bloom as well, up to 20 and 40 eggs female^{-1} day^{-1}, respectively.

By the egg production method the population spawning rate of *C. finmarchicus* during the bloom in a North Norwegian fjord was found to be 20-30 eggs female^{-1} day^{-1} (Diel & Tande 1992), which is some what lower than

spawning rates during the bloom in Atlantic water reported here. *In situ* rates of spawning measured by us during the bloom in the Barents Sea were similar to maximum spawning rates of females incubated under high food concentrations in the laboratory (Runge 1985, Hirche 1990), and similar to or higher than batch size of fed females (Marshall & Orr 1953, 1972). Judged from the high rates of spawning nearly 100% of the females in Atlantic water must have taken part in the spawning during the bloom.

To our knowledge the spawning rate of *C. glacialis* in Atlantic water, or comparable environments outside its arctic habitat, have not been measured earlier. Population spawning rates of *C. glacialis* during the bloom in Hudson Bay at -1^{0}C were 4-16 eggs female^{-1} day^{-1} (Tourangeau & Runge 1991). In the Greenland Sea at temperatures less than 0^{0}C the population spawning rate was 15-45 eggs female^{-1} day^{-1} (Hirche & Bohrer 1987). These spawning rates are similar to or lower than the spawning rates observed by us both in Atlantic water and the meltwater region of the Barents Sea. The population rate of spawning of *C. glacialis*, was similar to spawning rates of fed females in the laboratory and egg production of single individuals excluding non-spawners (Hirche 1989, Runge *et al.* 1991, Hirche & Kattner 1993). Spawning in Hudson Bay and the Greenland Sea took place under conditions that was very different from those in Atlantic water. The meltwater region was comparable to the Greenland Sea and Hudson Bay with respect to temperature during the bloom (-1.8-0^{0}C), while the concentrations of chlorophyll were very different; 299-447 mg m^{-2} in the meltwater region compared to <80 and <25 mg m^{-2} in the Greenland Sea and Hudson Bay, respectively (Hirche & Bohrer 1987, Tourangeau & Runge 1991). Thus, different levels of food supply may be the cause of the observed differences in spawning rates. Additional factors possibly regulating spawning rates could be linked to the developmental state of the populations, as discussed earlier.

At the early bloom stations in Arctic water *C. finmarchicus* and *C. glacialis* produced eggs at moderate rates; 13-18 and 36-42 eggs female^{-1} day^{-1}, respectively (Fig. 17). Hirche (1990) concluded that inability of *C. finmarchicus* to spawn was not the factor that excluded the species from the Polar waters of the Greenland Sea. Our observations of *C. finmarchicus* spawning at a high rate during an early bloom situation in Arctic water indicates that other factors are more important making *C. finmarchicus* an expatriate in Arctic water (conf. earlier discussions of development during overwintering).

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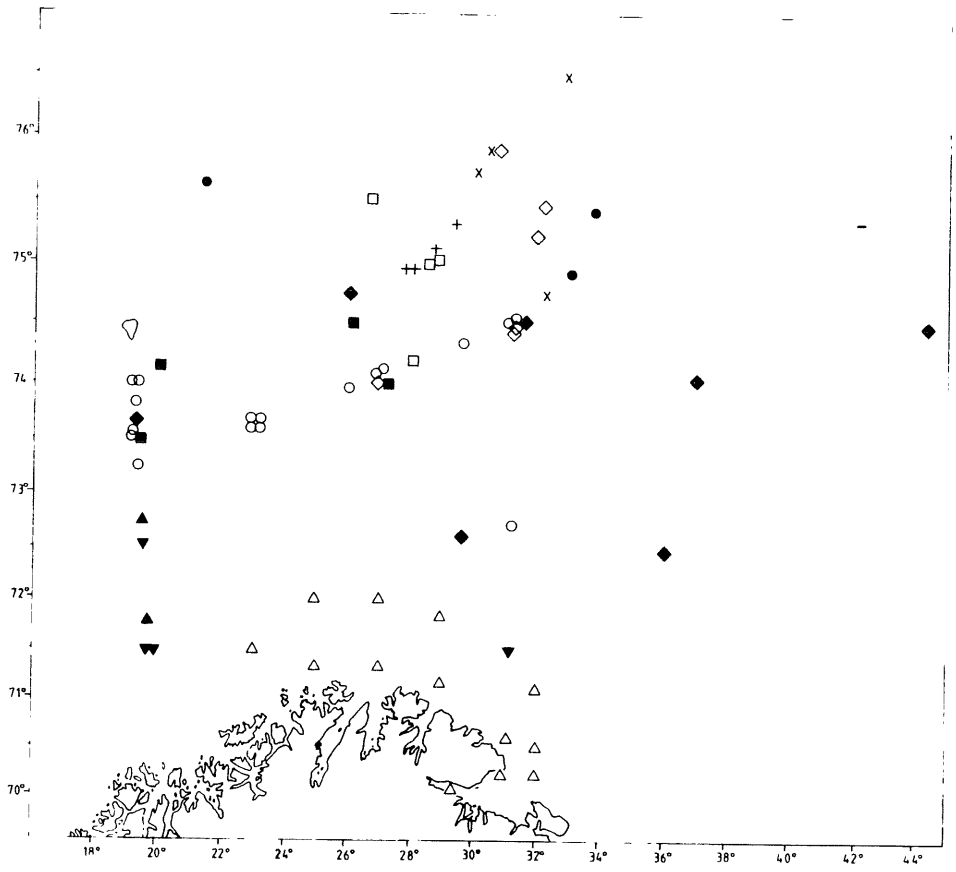

Fig. 1. Map of sampling stations. Symbols in the map refer to classification of water masses and stages of phytoplankton bloom development (Melle 1991). ● Arctic early bloom, ○ Atlantic pre-bloom, ■ Atlantic early bloom, □ Atlantic bloom, ♦ Atlantic post-bloom, ◊ meltwater pre- and early bloom, + meltwater bloom, X meltwater post-bloom, ∇ coastal pre-bloom, Δ coastal early bloom, Δ coastal post-bloom. Stations from the coastal current are not used here (conf. Melle 1991).

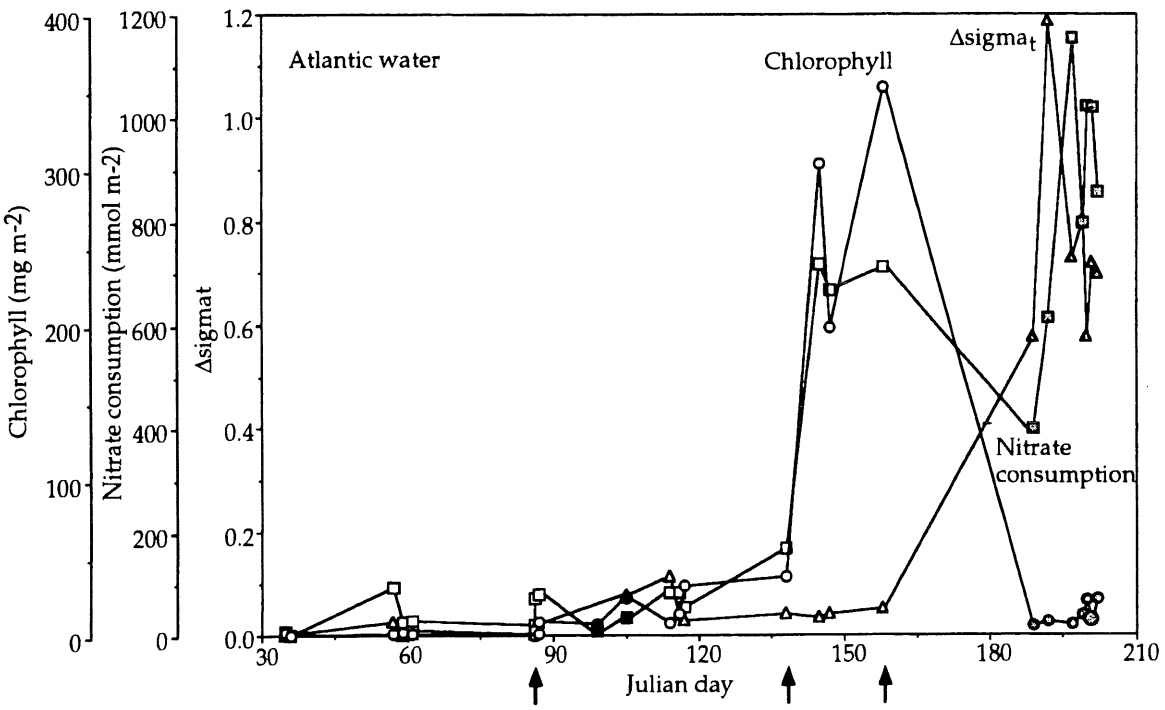

Fig. 2. Integrated chlorophyll concentrations, nitrate consumption (winter concentration of nitrate minus integrated nitrate concentration), $\Delta sigma_t$ (water density at 100 m depth minus density at 5 m) vs. day number (Julian day). Open symbols; 1987, symbols filled with black; 1986, symbols filled with gray; 1988. Arrows below x-axis denotes stations from which vertical profiles are presented in Fig. 3.

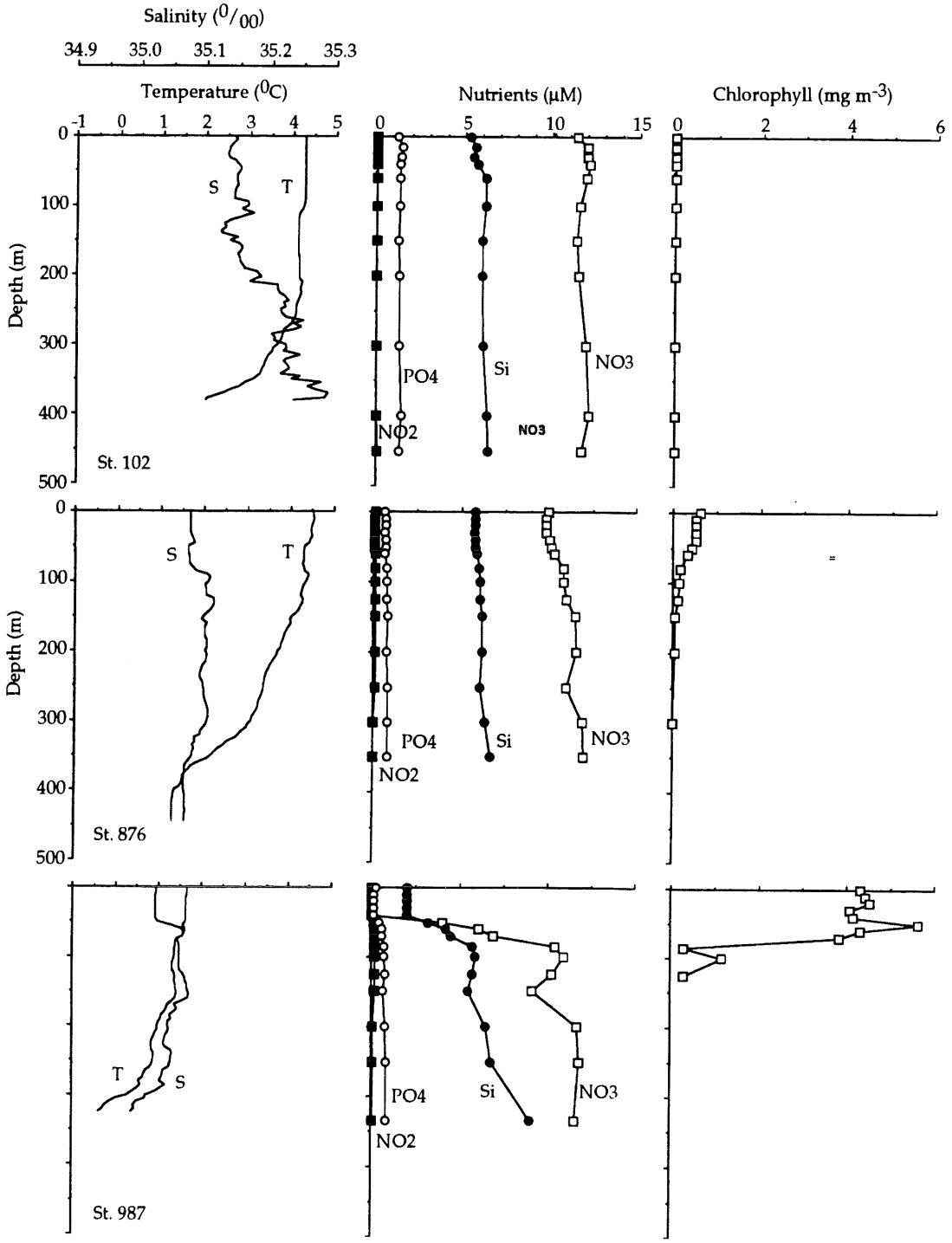

Fig. 3. Vertical profiles of hydrography, nutrients and chlorophyll at pre-bloom, early bloom and bloom stations in Atlantic water (see Fig. 2).

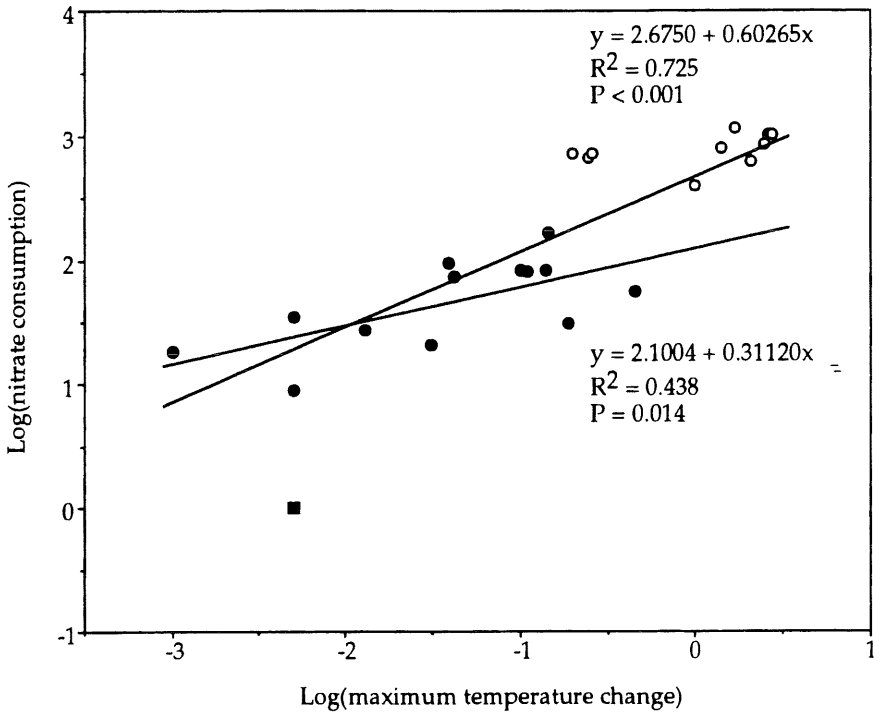

Fig. 4. Relationship between bloom development and water column stability represented by linear regression analysis of log-transformed nitrate consumption and log-transformed maximum temperature change over 5 m in the water column (see text). Upper equation and statistics refer to the regression of the total dataset (except the station marked with a filled square which was defined as an outlier). The lower equation refer to the regression including the pre-bloom and early bloom stations (filled circles), excluding the bloom and postbloom stations (open circles).

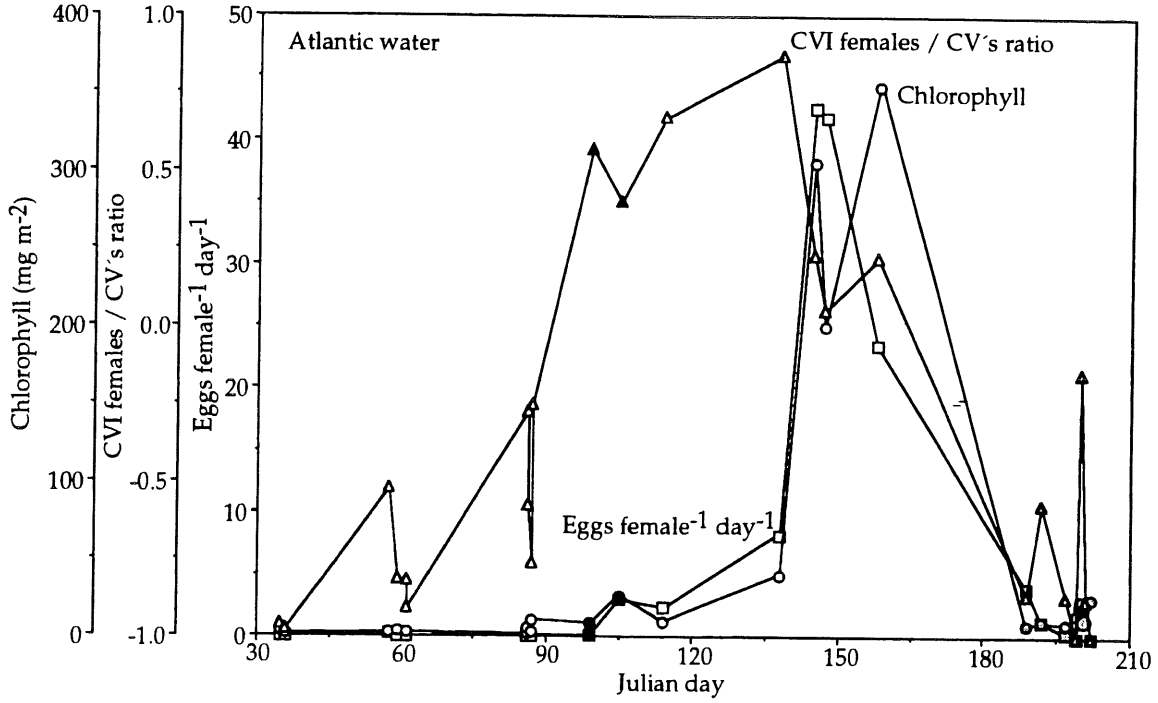

Fig. 5. Egg production and stage ratio index (see text) of *Calanus finmarchicus* in relation to chlorophyll concentrations vs. day number (Julian day).

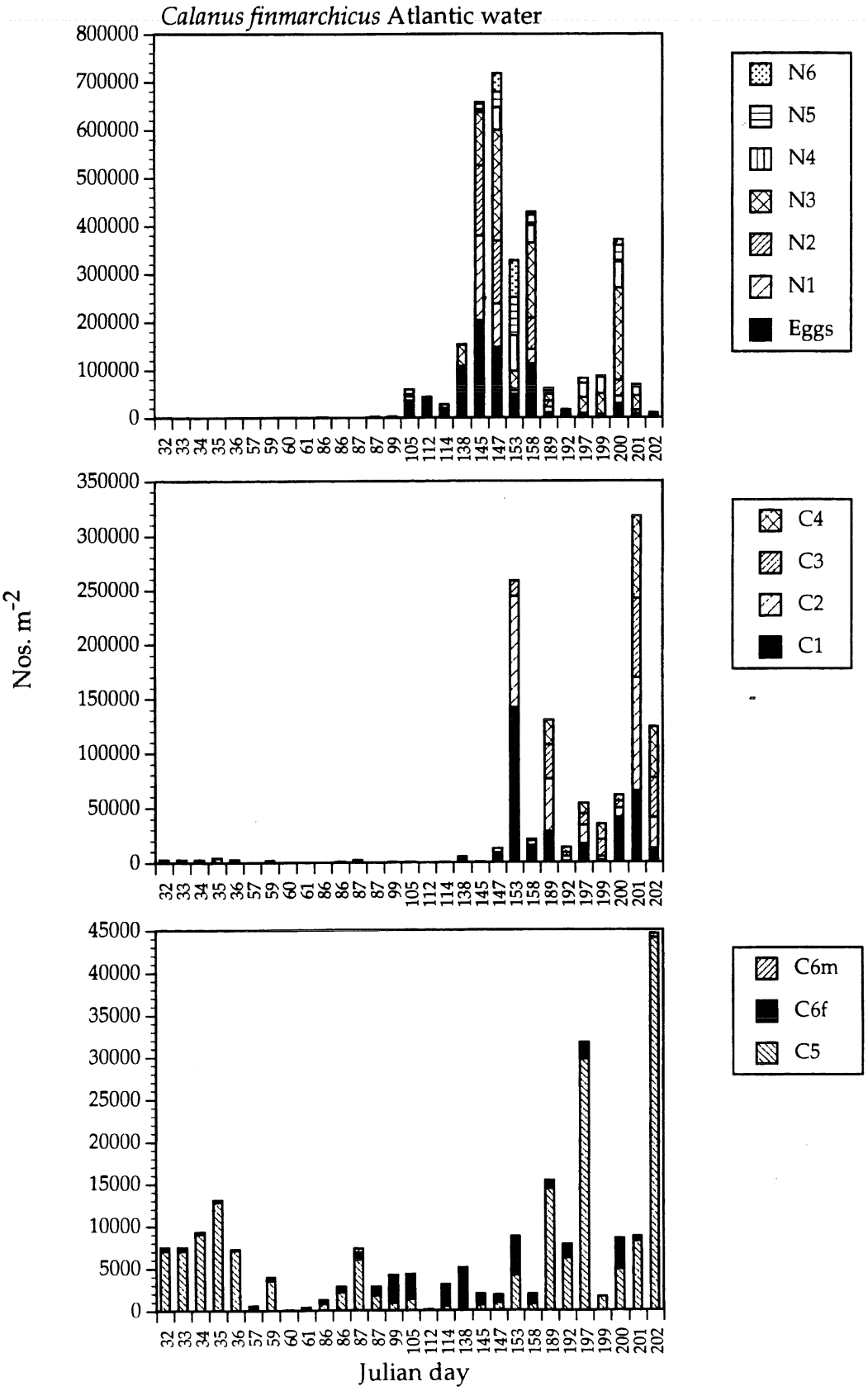

Fig. 6. Numbers of eggs, nauplii, copepodites and adults m^{-2} vs. day number (Julian day).

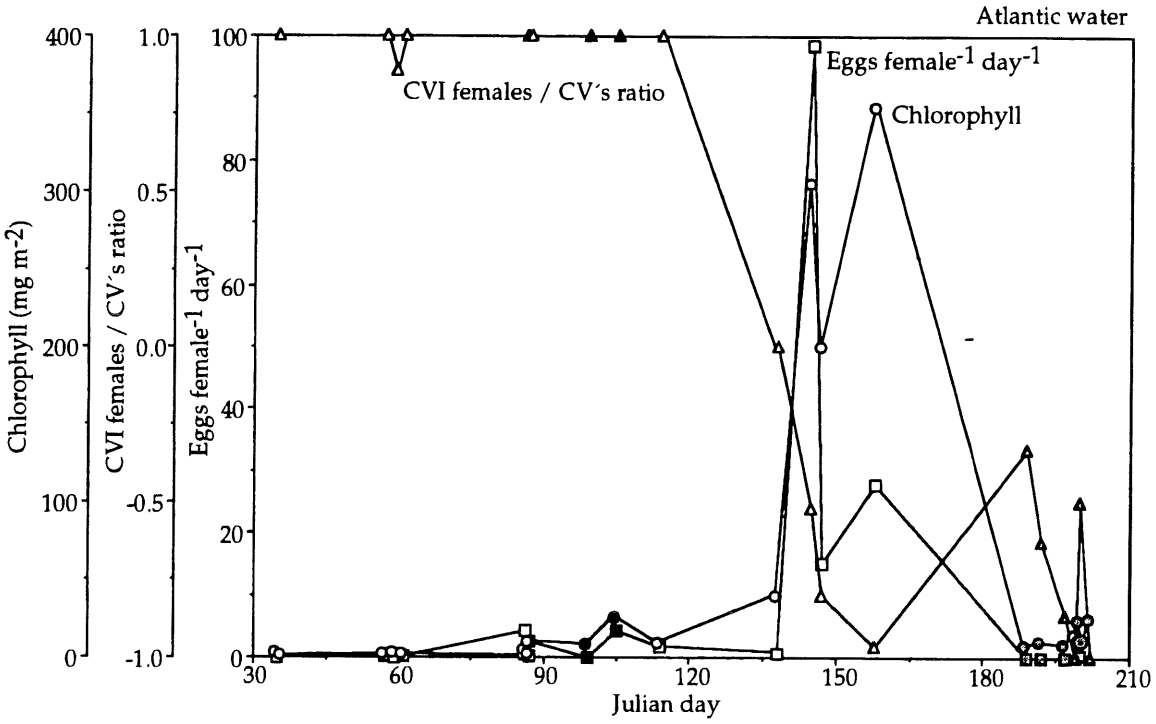

Fig. 7. Egg production and stage ratio index (see text) of *Calanus glacialis* in relation to chlorophyll concentrations vs. day number (Julian day).

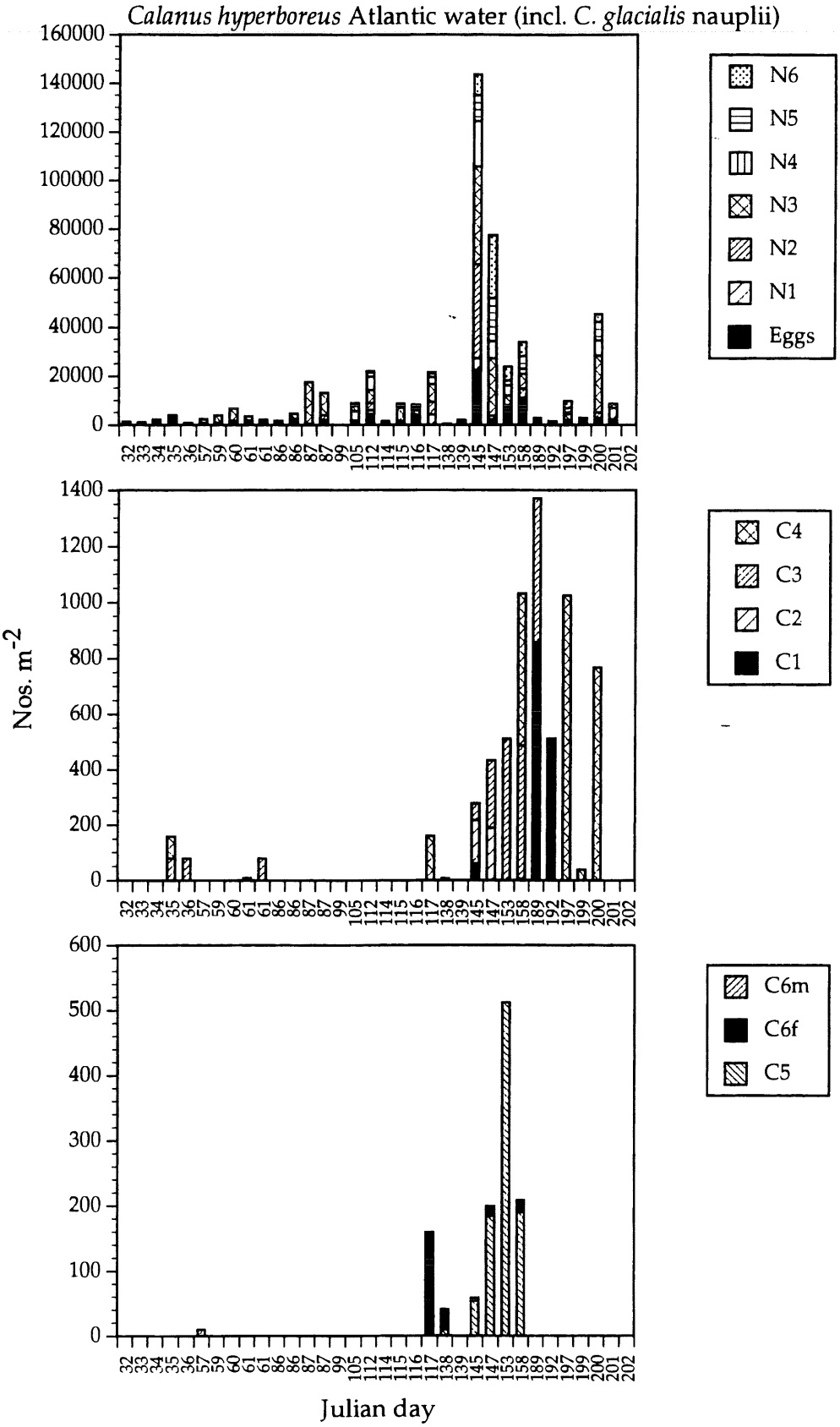

Fig. 8. Numbers of eggs, nauplii, copepodites and adults m^{-2} vs. day number (Julian day). Nauplii of *C. hyperboreus* could not be separated from nauplii of *C. glacialis* based on body size measurements, therefore, nauplii presented here are of both species (see text).

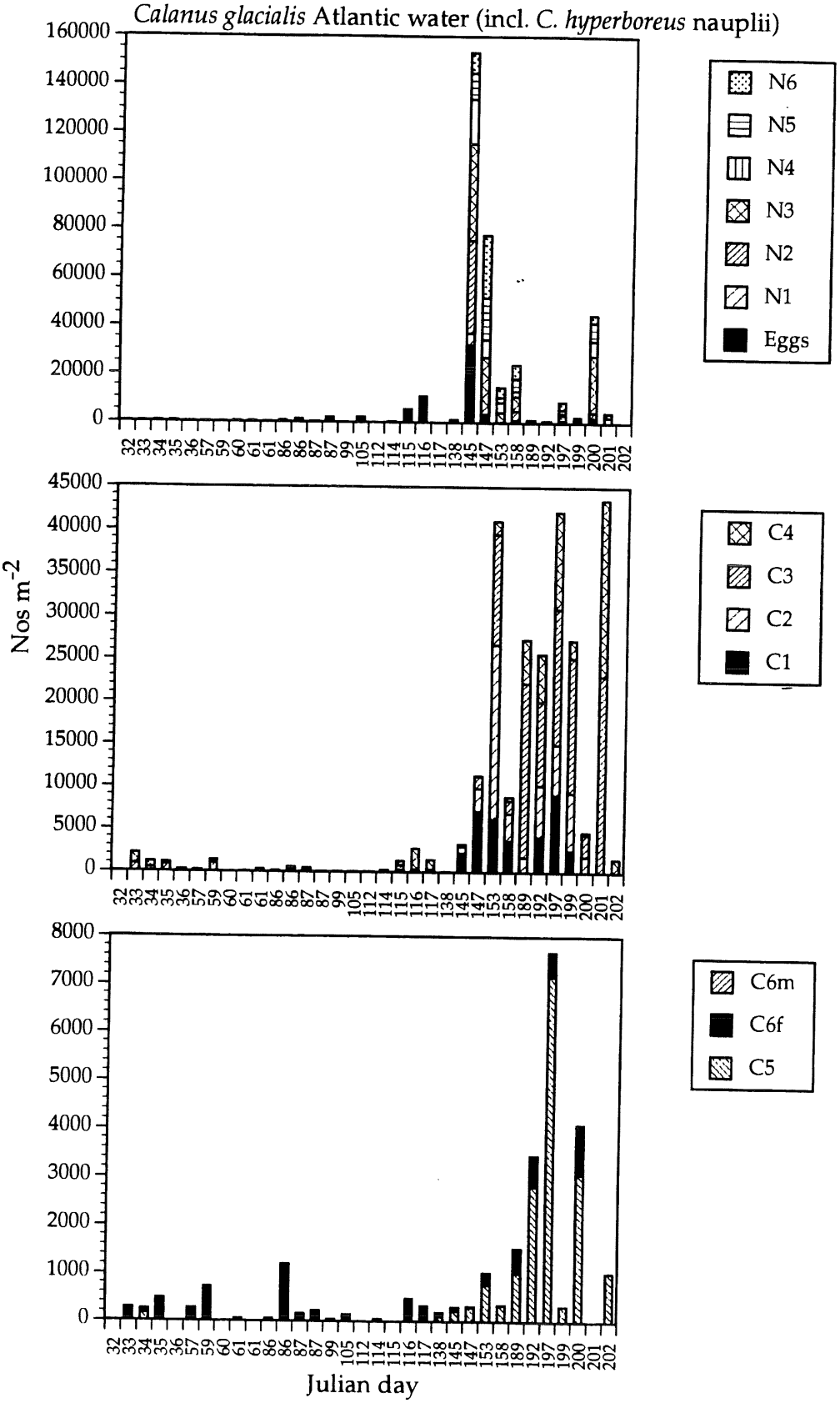

Fig. 9. Numbers of eggs, nauplii, copepodites and adults m^{-2} vs. day number (Julian day). Nauplii of *C. hyperboreus* and *C. glacialis* are presented both in Fig. 8 and here (see text).

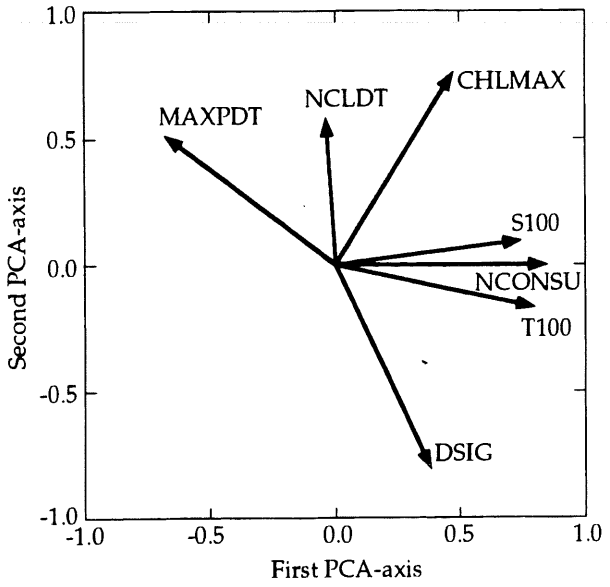

Fig. 10. Principal component analysis of selected physical, chemical and biological variables from stations in the meltwater region (see text).

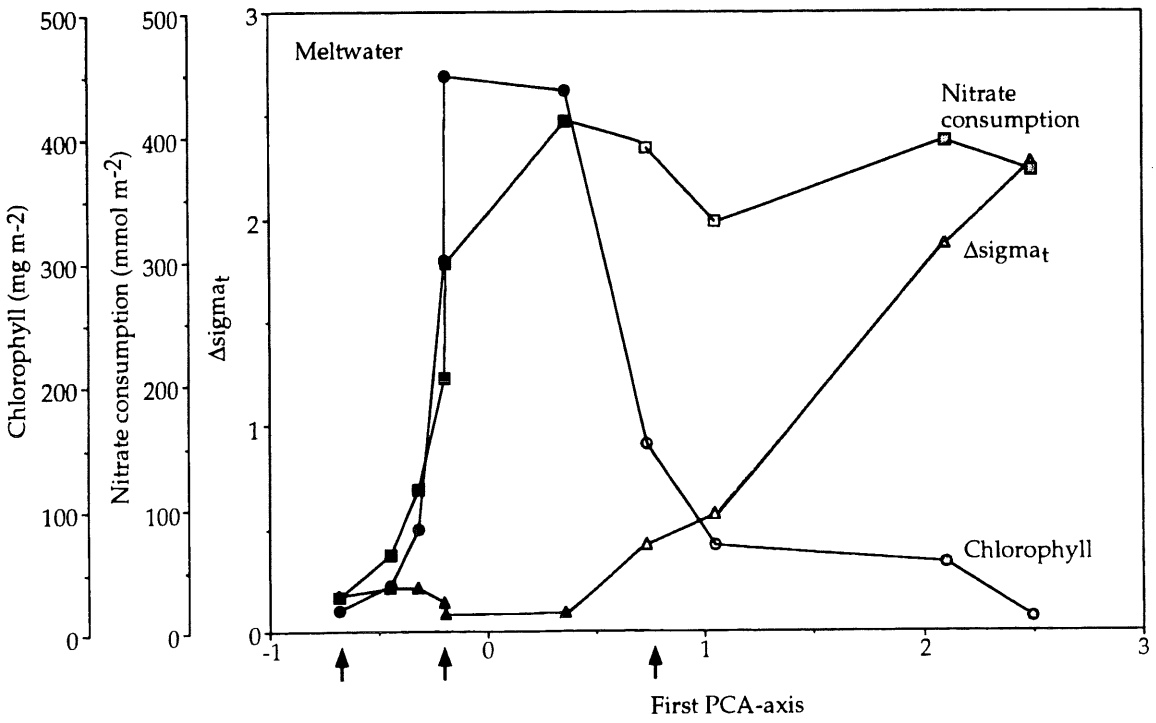

Fig. 11. Integrated chlorophyll concentrations, nitrate consumption (winter concentration of nitrate minus integrated nitrate concentration), $\Delta sigma_t$ (water density at 100 m depth minus density at 5 m) vs. first PCA-axis in Fig. 10. Open symbols; 1987, symbols filled with black; 1986, symbols filled with gray; 1988. Arrows below x-axis denotes stations from which vertical profiles are presented in Fig. 12.

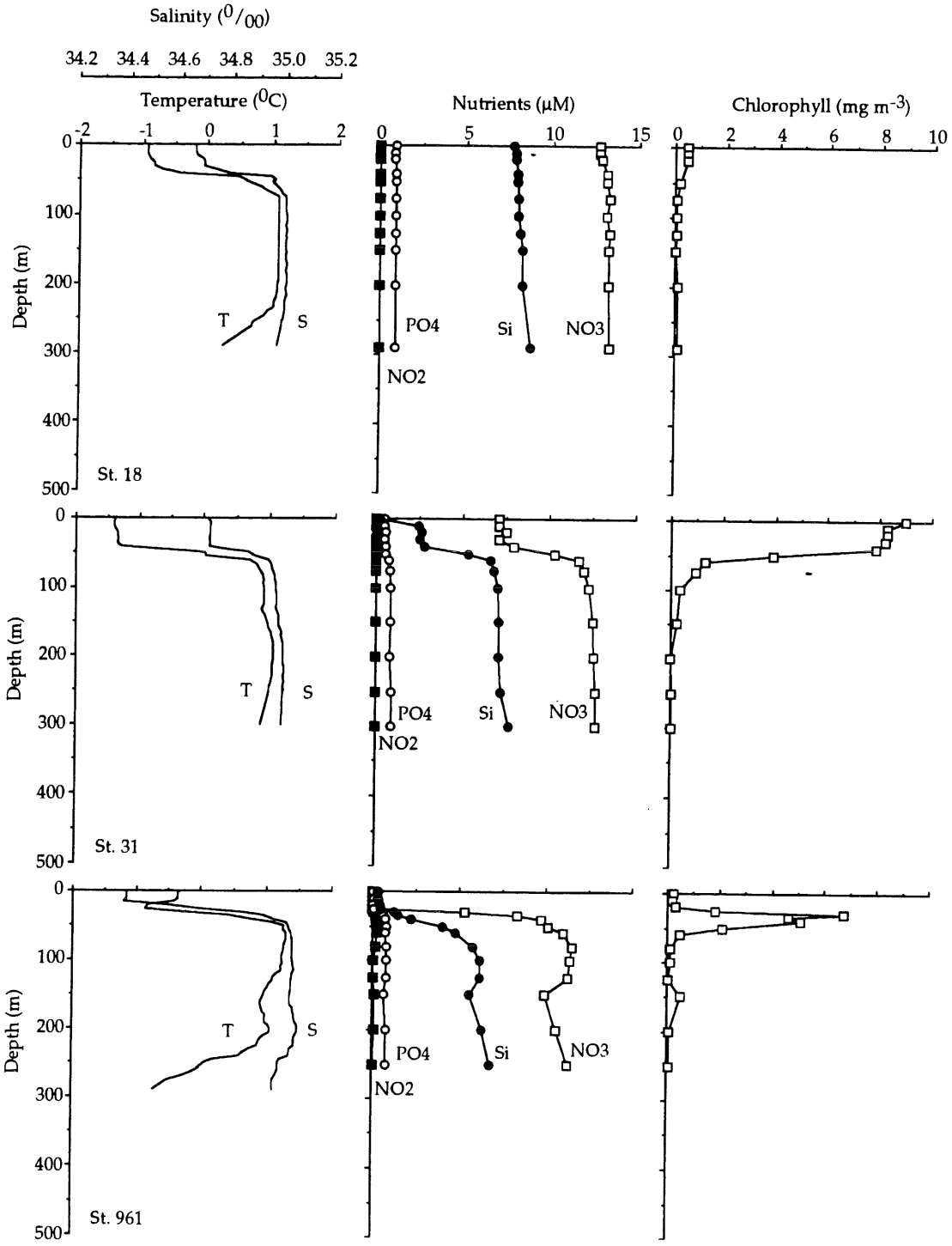

Fig. 12. Vertical profiles of hydrography, nutrients and chlorophyll at early bloom, bloom and post-bloom stations in the meltwater region (see Fig. 11).

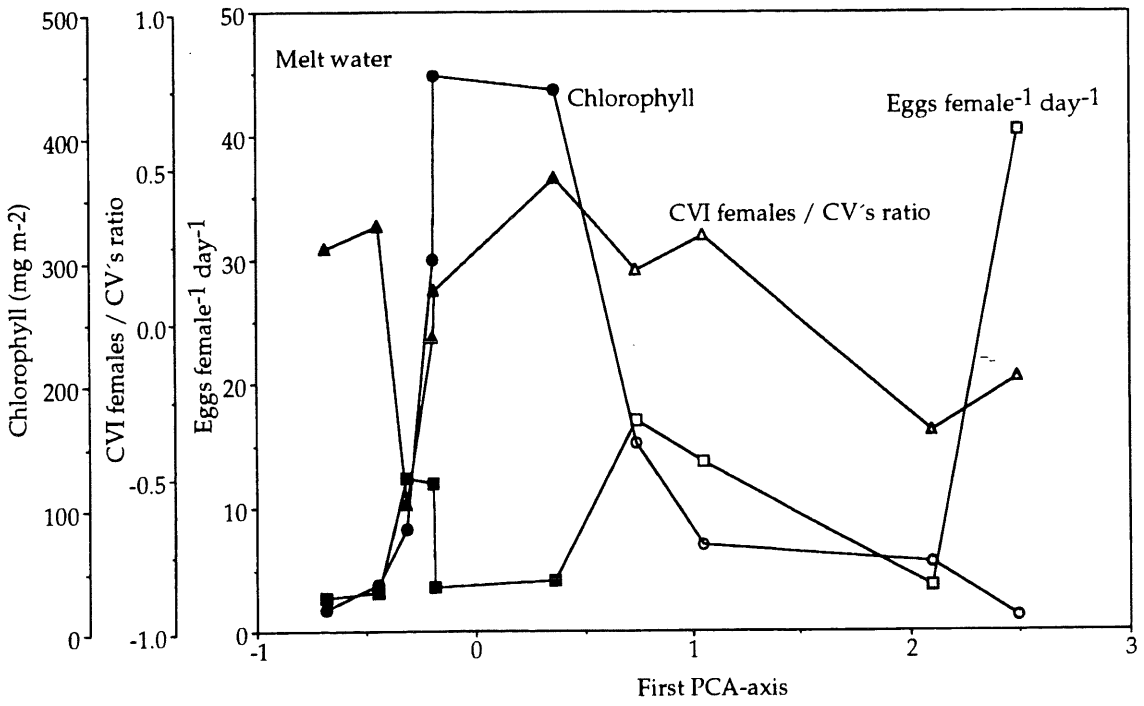

Fig. 13. Egg production and stage ratio index (see text) of *Calanus finmarchicus* in relation to chlorophyll concentrations vs. first PCA-axis (see 12).

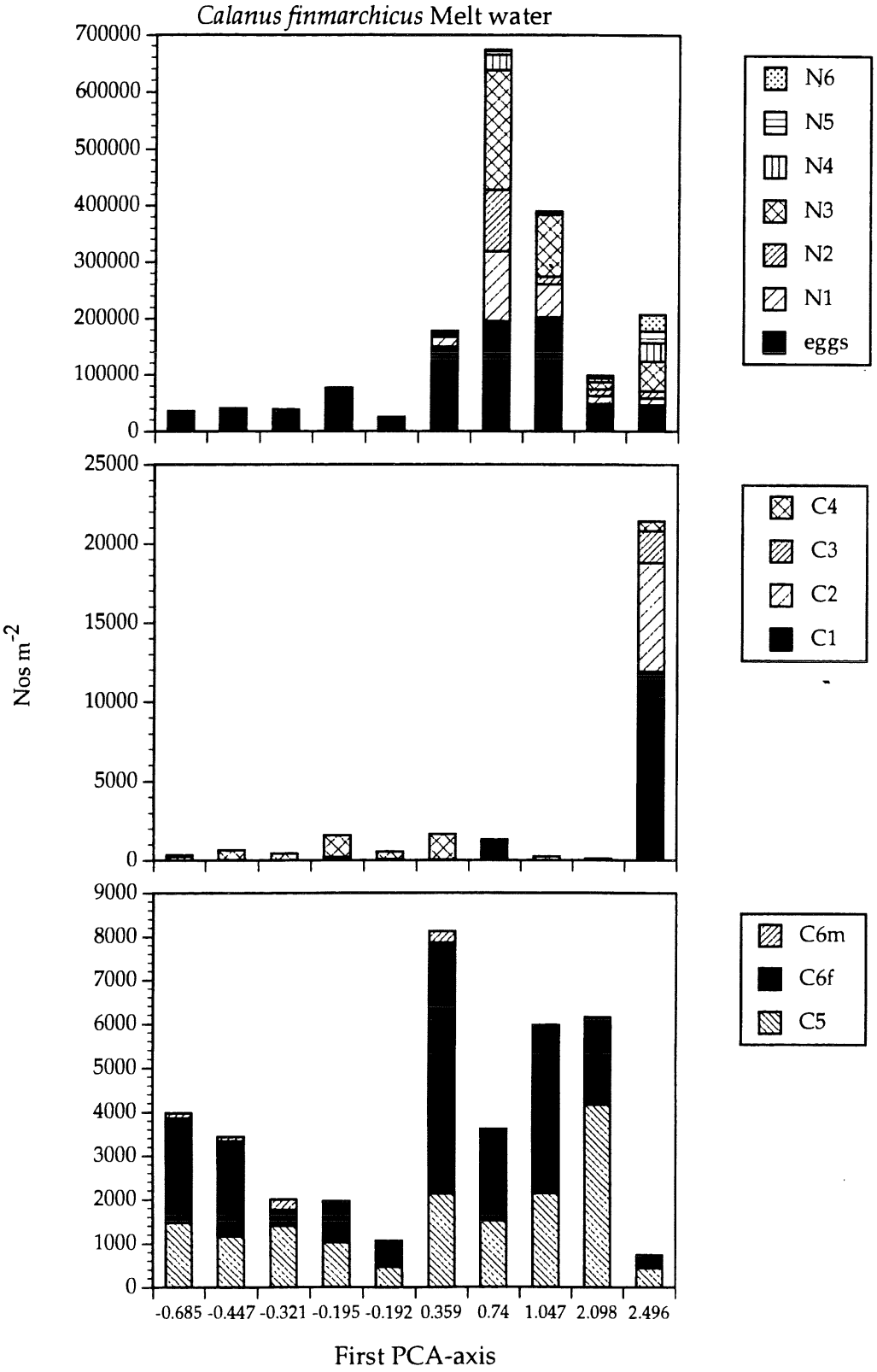

Fig. 14. Numbers of eggs, nauplii, copepodites and adults m^{-2} vs. first PCA-axis (see Fig. 12).

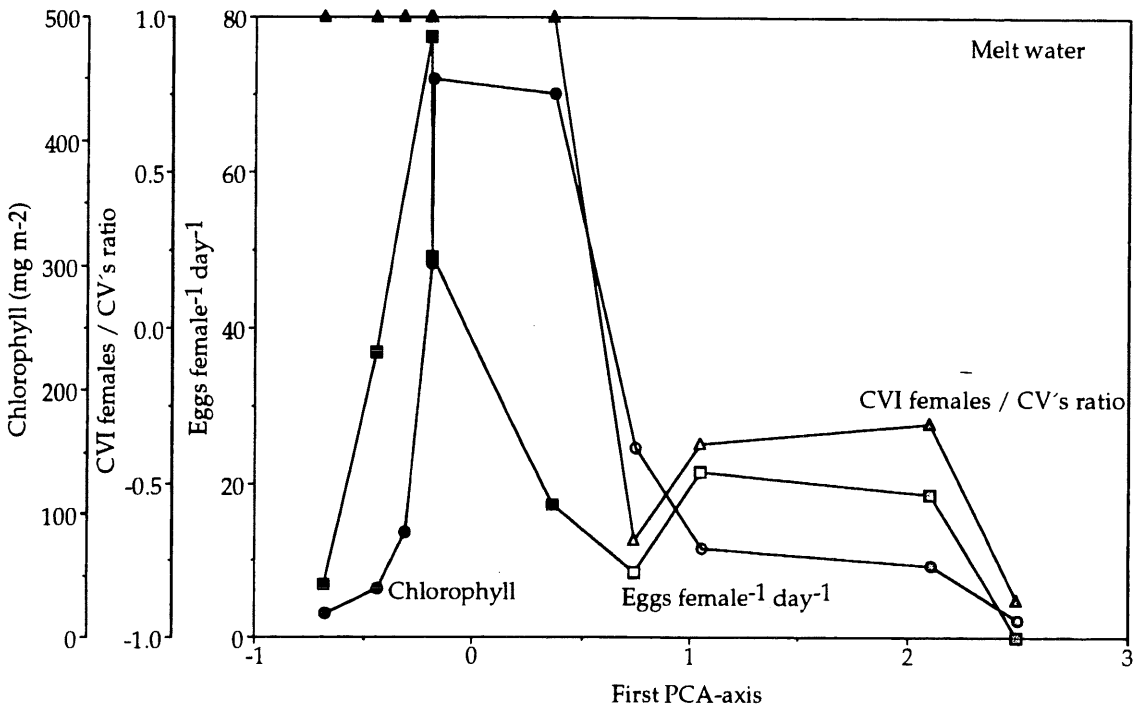

Fig. 15. Egg production and stage ratio index (see text) of *Calanus glacialis* in relation to chlorophyll concentrations vs. first PCA-axis (see 12).

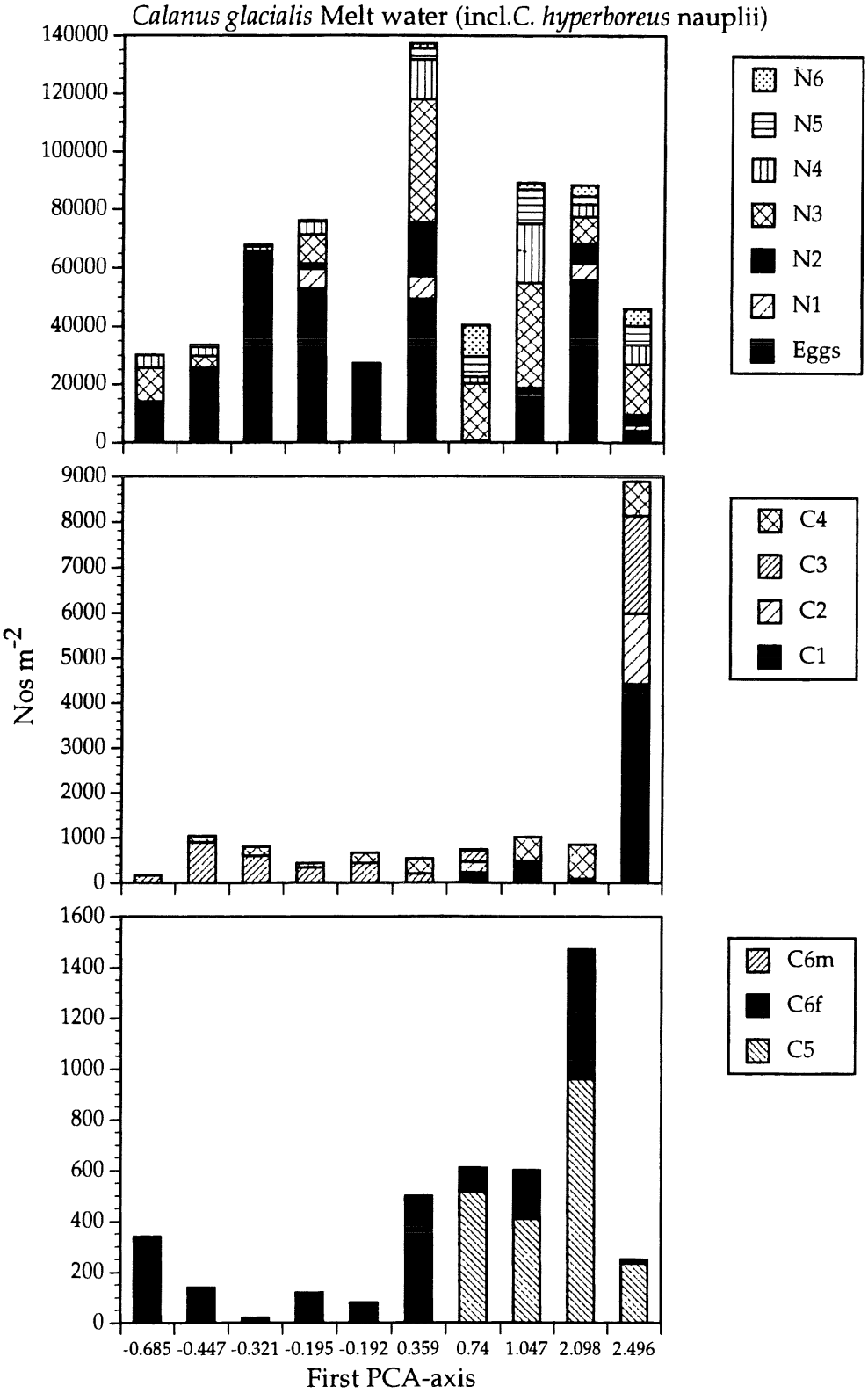

Fig. 16. Numbers of eggs, nauplii, copepodites and adults m^{-2} vs. first PCA-axis (see Fig. 12). Nauplii of both *C. hyperboreus* and *C. glacialis* are presented here (see Fig. 8).

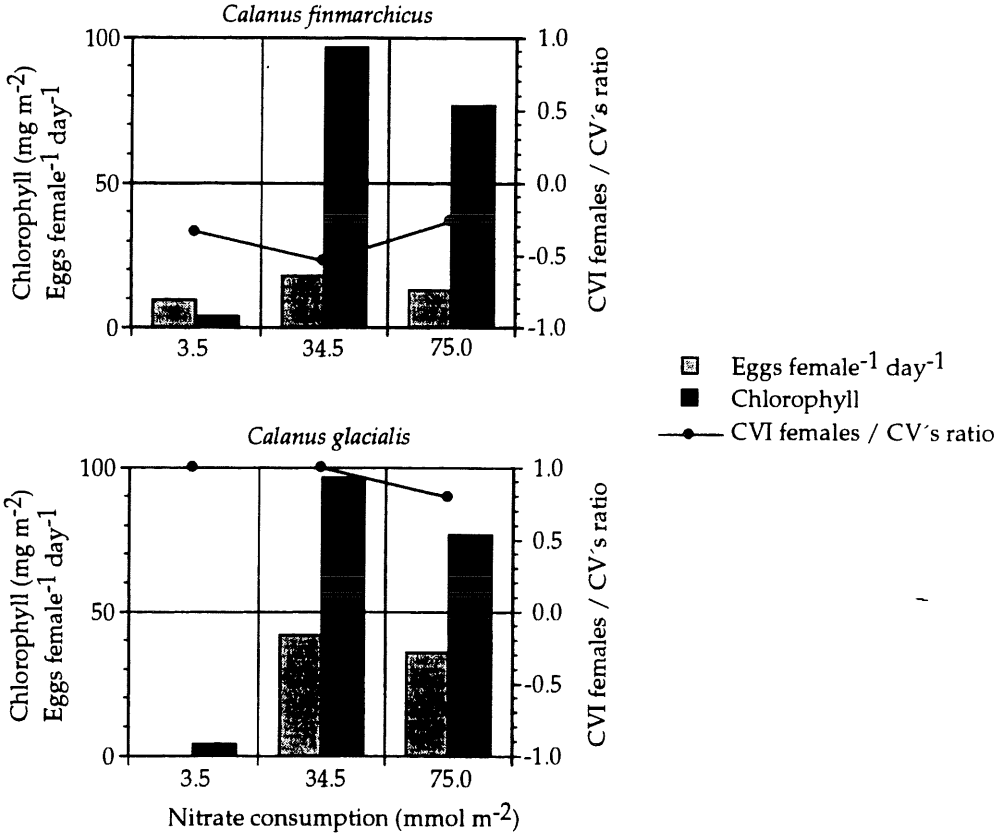

Fig. 17. Egg production and stage ratio index (see text) of *Calanus finmarchicus* and *C. glacialis* in relation to chlorophyll concentrations vs. nitrate consumption at three stations in Arctic water.

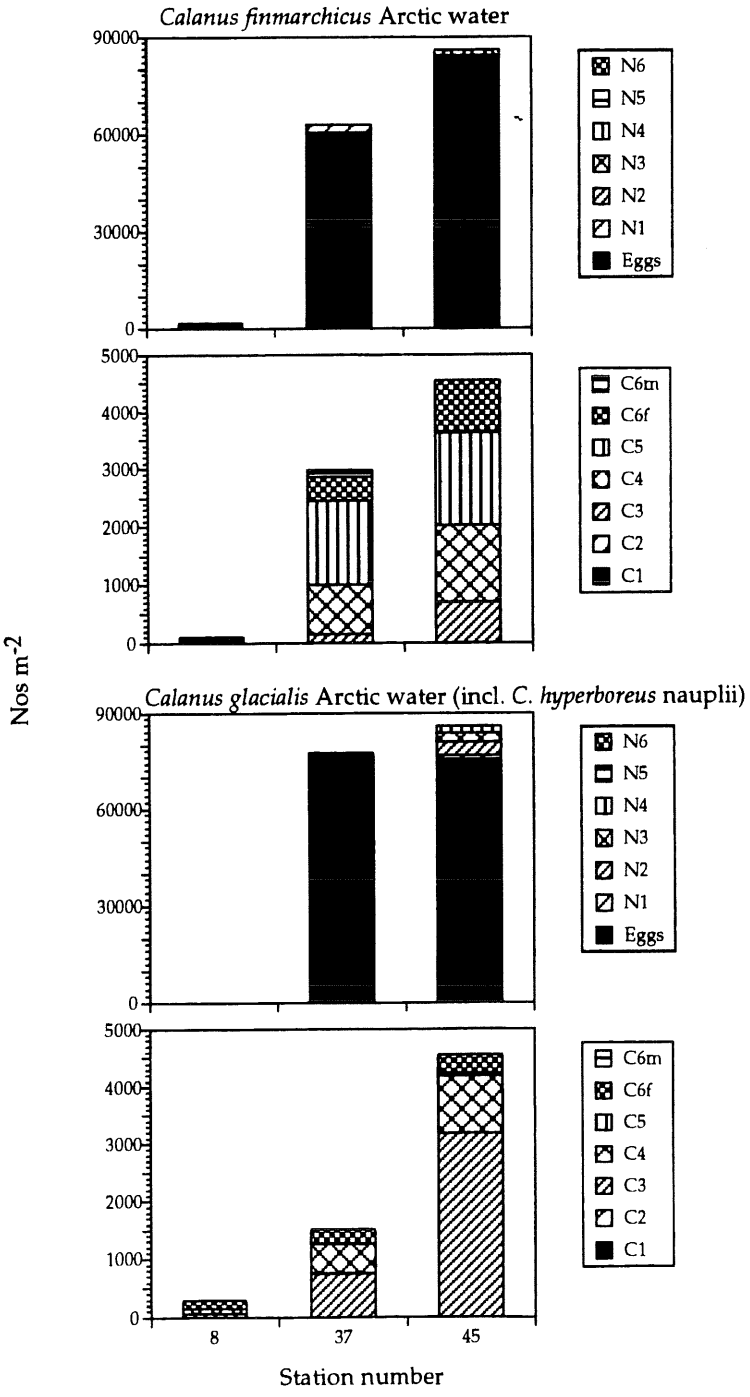

Fig. 18. Numbers of eggs, nauplii, copepodites and adults m^{-2} vs. station number. Nauplii of both *C. hyperboreus* and *C. glacialis* are presented here (see Fig. 8).