Zooplankton reproduction in the Barents Sea: Vertical distribution of eggs and nauplii of *Calanus finmarchicus* in relation to spring phytoplankton development

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Abstract

Variable influence of ice melting on water column stabilization causes a large variation in timing of the spring phytoplankton bloom in the central Barents Sea. During two cruises in April 1986 and May-June 1987 situations were encountered that ranged from early bloom stage in Atlantic water not influenced by ice to late bloom stage in meltwater regions. In the present paper we examine the reproduction of *Calanus finmarchicus* (Gunnerus) against the background of this large natural variation in the temporal and spatial distribution of phytoplankton food, with emphasis on the vertical distribution of spawning females, eggs, and nauplii.

The vertical distribution of the females indicated a shift from shallow spawning at the early bloom stations to deeper spawning in the pycnocline region at the late bloom stations. The females were generally concentrated in the layers with high concentrations of phytoplankton. The vertical distribution of eggs at the bloom and late bloom stations showed the same pattern as chlorophyll, either uniformly distributed in the upper mixed layer or concentrated as a sharp maximum in the region of the pycnocline and the deep chlorophyll maximum. The distribution of nauplii corresponded closely to the distribution of the eggs at these stations, suggesting little or no sinking of the eggs and hatching of the nauplii at depths with a rich food supply.

The eggs at the early bloom stations had a deeper distribution, although spawning apparently took place in the shallow part of the water column. This suggests a high rate of sinking of the eggs. Nauplii hatching from them probably encountered low food concentrations at great depths. The success of early spawning is probably limited through this.

The indicated high sinking rate at the early bloom stations in contrast to the low rate of sinking at the bloom and late bloom stations could reflect a difference in egg density owing to different feeding conditions. Increased water viscosity caused by mucus from phytoplankton could also have contributed to the lower sinking rate at high phytoplankton concentrations. Wind-induced vertical mixing did not play a major role in governing egg distributions.

Keywords : *Calanus*, sinking rate, vertical distribution, reproduction, phytoplankton.

Introduction

Differences in spawning strategies among copepod species in relation to the development of the phytoplankton spring bloom were reviewed by Heinrich (1962). Heavy spawning in *Calanus finmarchicus* has been found to be dependent on high phytoplankton concentrations associated with the phytoplankton spring bloom (Heinrich 1962, Hirche & Bohrer 1987, Melle *et al.* 1987, Skjoldal *et al.* 1987). In laboratory experiments, the spawning of *C. finmarchicus* has been shown to vary with the food supply and to stop after some time without food (Marshall & Orr 1972). Spawning at the right time relative to the spring bloom is essential to the new generation that is produced.

The phytoplankton cells are distributed mainly in the upper 50-80 m in the Barents Sea (Rey, Skjoldal & Hassel 1987, Skjoldal *et al.* 1987). The copepods need therefore not only to spawn at the right time, but also at the right depth. As for the right time, the right depth of spawning must provide sufficient food supply for the spawning females and later for the developing recruits. Besides the ability of active vertical migration in the older naupliar stages, match-mismatch between the depth distributions of food and the recruits depends on factors such as depth of spawning, sinking velocity of eggs and early naupliar stages, duration of egg incubation period, and influence of wind-induced turbulent vertical mixing.

The area of investigation in the Barents Sea includes both Atlantic water (warmer than 0 °C and salinity higher than 35.0 ‰) and Arctic water (less than 0 °C and salinity less than 35.0 ‰). The two types of water are separated by the polar front. During the investigation periods in April 1986 and May-June 1987, wide areas of both Atlantic and Arctic waters were covered by meltwater giving high stability to the water column.

The development of the spring phytoplankton bloom in these areas has been described by Marshall (1958), Rey & Loeng (1985), and Rey *et al.* (1987). The earliest bloom occurs in the meltwater region. The bloom is short and vigorous as a result of a shallow pycnocline which reduces the mixing of phytoplankton cells below the compensation depth. This results in an early culmination as the nutrients above the pycnocline soon become exhausted. In the late stage of bloom development a maximum in chlorophyll is found in or just below the pycnocline region. In homogeneous Atlantic water the bloom starts later, and owing to a weaker and deeper pycnocline, the bloom is less vigorous. The nutrients last longer and are to some extent renewed from the water below the pycnocline. This gives a prolonged period of high concentrations of phytoplankton in the upper water layers compared to the meltwater region.

This paper describes the vertical distributions of eggs, nauplii, and adult females of *Calanus finmarchicus* in relation to chlorophyll and physical conditions of the water column. Examples from early bloom, bloom, and late bloom situations are given representing homogeneous Atlantic water and meltwater regions.

Material and methods

The cruise in April 1986 was carried out with two of the Norwegian Coastguard vessels, KV *Senja* (2-13 April) and KV *Andenes* (14-23 April), covering the area between the Svalbard Bank and the Central Bank. The same area was again covered from 17 May to 9 June 1987 with RV *G.O.Sars* (Figure 1). An extensive program was carried out at selected daily stations. The research area in 1986 was partly in open sea and partly in close pack. The position of the ice border is indicated in Figure 1. In 1987 the whole cruise was in open sea, as we did not have an ice-going vessel.

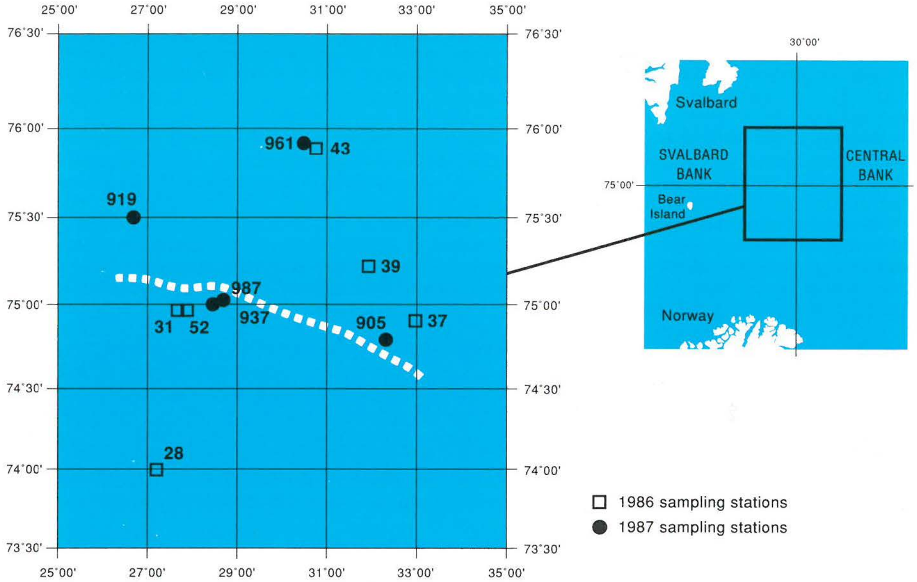

Figure 1.
Map showing major sampling stations within the investigation area in April 1986 and May-June 1987. Ice border from medio April 1986 shown as a dashed white line.

Standard hydrographic sampling was carried out with a Neil Brown MK III CTD sonde coupled together with a Rossette Sampler equipped with 5 l Niskin water bottles.

Samples for pigment analysis were filtered through 0.45 µm pore size membrane filters and stored frozen (–18 °C). Within a few days, the pigments were extracted with 90 % acetone for at least 16 hours in the dark. After centrifugation, the fluorescence of the extracts were measured before and after acidification, using a Turner Designs filter fluorometer.

Microzooplankton was collected with 30 l Niskin water bottles at 6-10 depths in the upper 100 or 150 m. The whole samples, or at a few stations half samples, were screened through 30 µm mesh in 1986 and 90 µm mesh in 1987 and preserved in 4 % formaldehyde. Copepod eggs and nauplii were sorted out under 25 times magnification using a stereo microscope, and identified under 100 times magnification. Eggs and nauplii were separated into genera/species according to size measurements and morphological characters given in the literature (Oberg 1906, Lebour 1916, Gibbons 1933, Sømme 1934, Wiborg 1948, Ogilvie 1953, Lovegrove 1956, Marshall & Orr 1972).

The vertical distribution of mesozooplankton was obtained with an *in situ* pump similar to that described by Solemdal & Ellertsen (1984). Pumping times were 3 or 6 min, and in most cases a flowmeter was attached to the pump. The samples for species determination were preserved in 4 % formaldehyde. To reduce the sample size before counting, the samples were divided with a plankton divider usually to 1/2 or 1/4, while in some cases to 1/32. Copepods were determined to species and stage. *Calanus* was identified to *C. finmarchicus*, *C. glacialis* or *C. hyperboreus* depending on size of cephalothorax. Only results for *C. finmarchicus* are presented here.

Results

At the stations with an early stage of phytoplankton bloom, the vertical distribution of the eggs of *Calanus finmarchicus* showed no clear relation to the vertical distribution of chlorophyll (Figure 2). These stations were taken in April 1986 and had different physical conditions. Stations 28 and 37 were in Atlantic water and in ice-covered Arctic water on the Central Bank, respectively, and had little vertical stratification. Stations 39 and 43 were in ice-covered water and had a pycnocline separating Arctic meltwater overlying Atlantic water (Figure 2, lower panel). A stratified water column may influence the vertical distribution of the eggs both through sinking velocity of the eggs and vertical turbulent mixing. The sinking velocity of *C. finmarchicus* eggs as calculated from Stokes equation (see Discussion) are plotted for each station in Figures 2-5, lower panel. At stations 28 and 37 the number of eggs showed a general increase with depth in the upper 100 m. At station 43 the eggs were found in the layer above the pycnocline at about 80 m, while at station 39 the eggs were abundant both above and below the more shallow pycnocline at about 25 m depth (Figure 2).

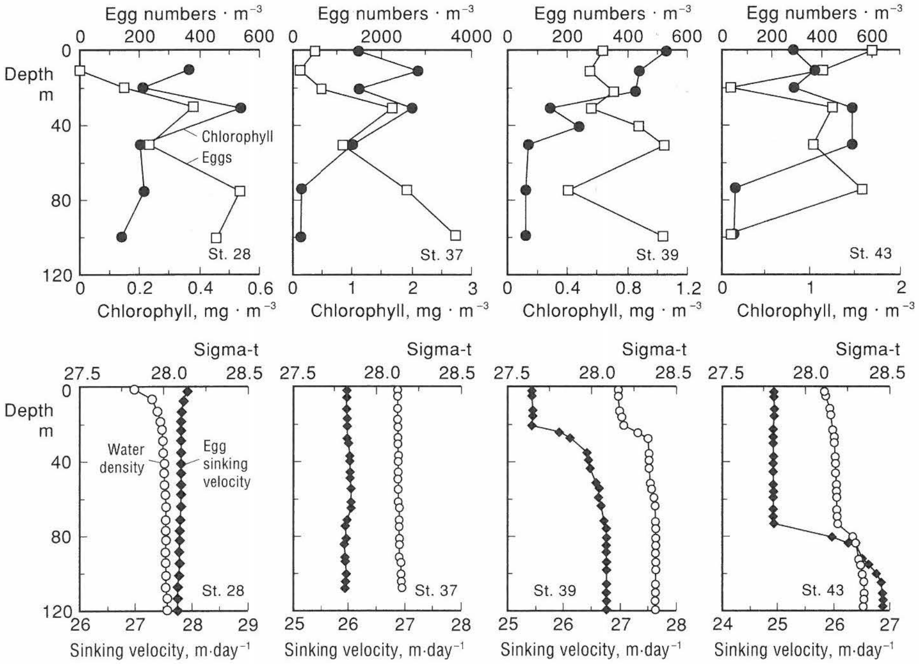

Figure 2.
Vertical distribution of eggs of *C. finmarchicus*, chlorophyll-*a*, water density (sigma-t), and egg sinking velocity at early bloom stations.

Stations 31 and 52 were taken in open pack and open water just south of the ice, respectively, in April 1986. A phytoplankton bloom close to its peak was found at these stations which had a high and evenly distributed chlorophyll content above the pycnocline (Figure 3). At station 52 the salinity data are missing, and the temperature profile is included in Figure 3 to indicate the depth of the pycnocline. The vertical distributions of *Calanus finmarchicus* eggs were closely related to the profiles of chlorophyll, and high densities of eggs were found above the pycnocline (Figure 3).

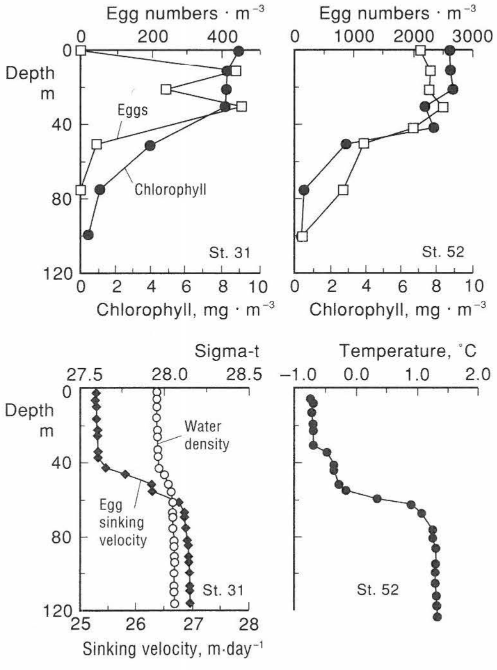

Figure 3.
Vertical distribution of eggs of *C. finmarchicus*, chlorophyll-*a*, water density (sigma-t), and egg sinking velocity at bloom stations. At st. 52 temperature is shown (see text).

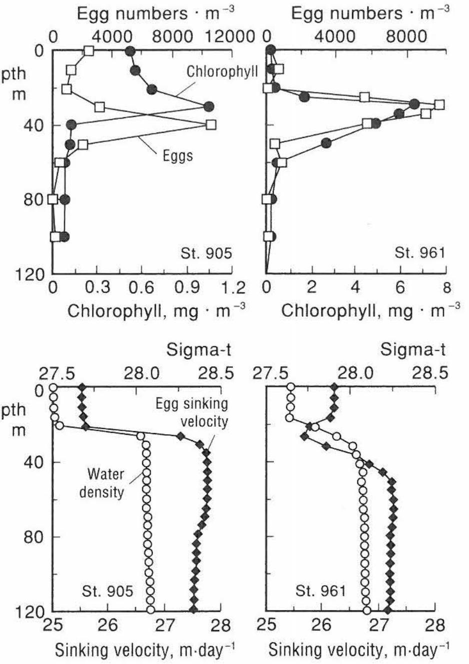

Figure 4.
Vertical distribution of eggs of *C. finmarchicus*, chlorophyll-*a*, water density (sigma-t), and egg sinking velocity at late bloom stations with strong pycnocline.

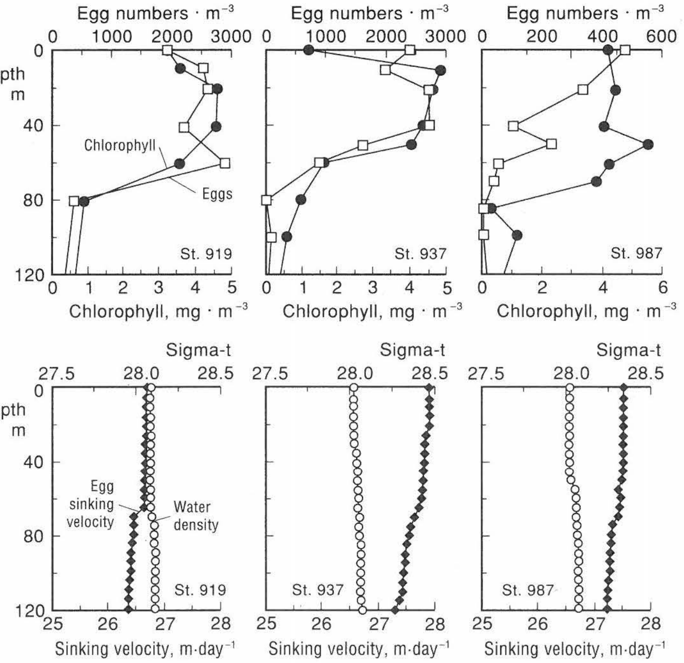

Figure 5.
Vertical distribution of eggs of *C. finmarchicus*, chlorophyll-*a*, water density (sigma-t), and egg sinking velocity at bloom stations in Atlantic water.

Late bloom situations in meltwater regions were observed at stations 905 and 961 in June 1987. They were characterized by a shallow and strong pycnocline and a marked subsurface chlorophyll maximum in the pycnocline region. The water above the pycnocline showed low chlorophyll concentrations. The vertical distributions of eggs were very similar to the chlorophyll profiles, although displaced somewhat deeper at station 905 (Figure 4).

Bloom or late bloom situations were encountered in June 1987 in Atlantic water with a weak pycnocline resulting from a relatively deep thermocline (stations 919, 937, and 987; Figure 5). The concentration of chlorophyll was relatively high above the pycnocline, as the nutrients were not yet completely exhausted. The vertical distribution of eggs of *Calanus finmarchicus* showed a general resemblance to that of chlorophyll at these stations as well. The eggs were rather evenly distributed above the pycnocline at stations 919 and 937, while they showed a general decrease from the surface at station 987 (Figure 5).

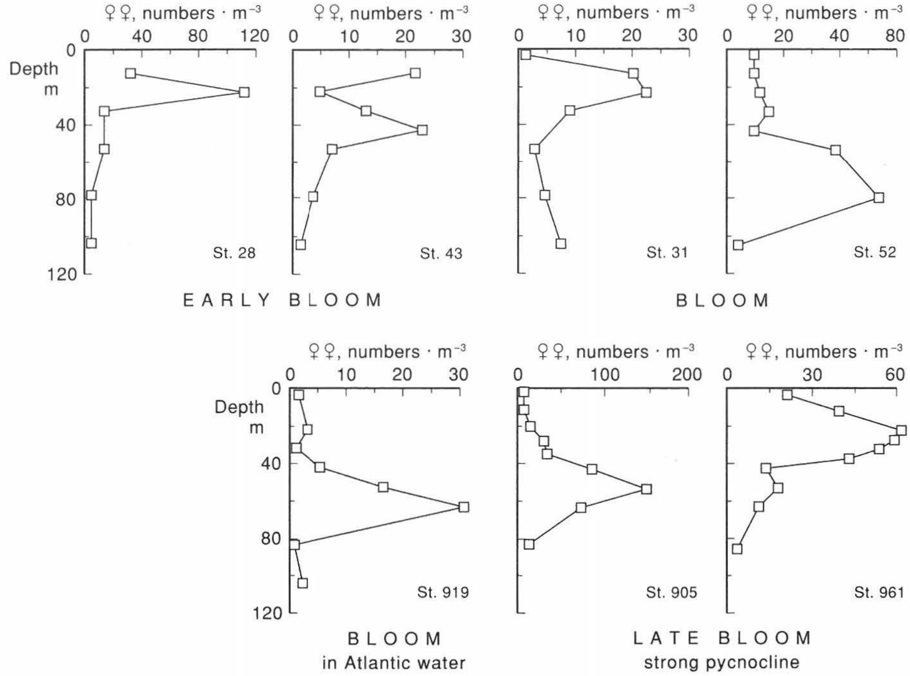

Figure 6.
Vertical distribution of females of *C. finmarchicus.*

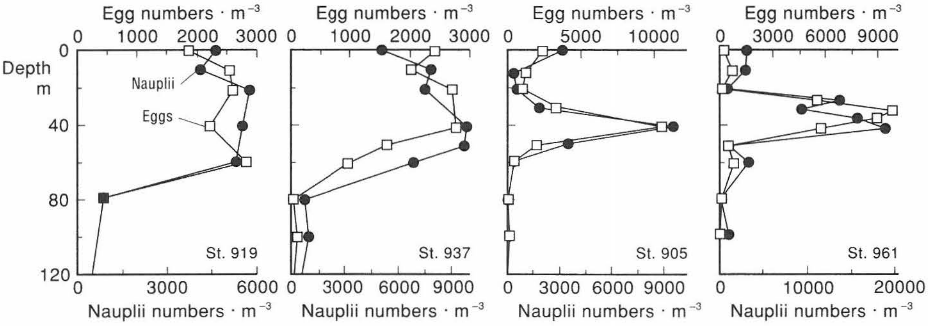

Figure 7.
Vertical distribution of eggs and nauplii of *C. finmarchicus.*

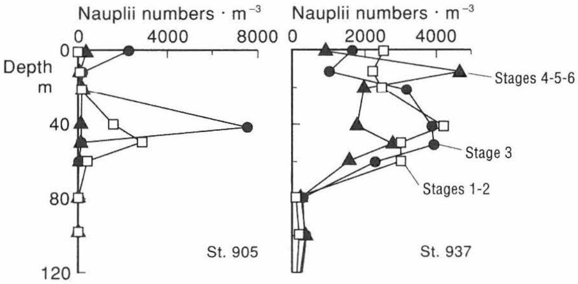

Figure 8.
Vertical distribution of naupliar stages 1-6 of *C. finmarchicus.*

The vertical distribution of adult females may provide information on spawning depth. The females were found in highest abundance above 50 m at the early bloom stations. At the more advanced bloom and late bloom stations both shallow and deep distributions were found (Figure 6). In many cases the females seemed to concentrate in the deeper part of the chlorophyll distribution at or just below the pycnocline.

A comparison of the vertical distributions of eggs and nauplii of *Calanus finmarchicus* are of special interest in relation to the magnitude and importance of sinking of eggs. The vertical distributions of the nauplii corresponded closely to those of the eggs (Figure 7). The older naupliar stages may have had a more shallow distribution than the younger, but because of variability and low numbers of the older stages this tendency of vertical ontogenetic migration is not clear (Figure 8).

Discussion

The observed differences in vertical distributions of eggs, nauplii, and females of *Calanus finmarchicus* seem to be coupled to the development of the spring phytoplankton bloom, which in turn depends on the degree of stability in the water column (Rey *et al.* 1987, Skjoldal *et al.* 1987). Vertical migration among the developmental stages of *C. finmarchicus* may obscure their relationship to the phytoplankton vertical distributions. However, in Arctic areas in summer with relatively small variations in light between day and night, diurnal vertical migration is usually not observed in zooplankton (Longhurst, Sameoto & Herman 1984, Smith 1988). Vertical migration in *C. finmarchicus* was probably therefore of minor importance for the observed vertical distributions in the Barents Sea, both for females and the naupliar stages.

Laboratory measurements have shown a high specific density of eggs of *Calanus finmarchicus* (Salzen 1956). This gives a sinking rate of 25 to 28 $\text{m}\cdot\text{day}^{-1}$ (Figures 2-5) as calculated from Stokes equation, expressing the terminal sinking velocity (w) of eggs (Sundby 1983):

$$w = 18^{-1}\cdot g\cdot d^{2}\cdot \Delta\rho\cdot v^{-1},$$

where

g = gravity acceleration,
d = egg diameter,
$\Delta\rho$ = density difference (between egg and water), and
v = molecular viscosity.

The calculated sinking velocities based on the density measurements of Salzen (1956) is not far from the directly measured sinking velocities obtained by Gross & Raymont (1942). The density of krill eggs, however, varies with changes in osmotic pressure, and therefore a density gradient column should not be used to measure densities (Marschall 1983). Salzen (1956) used a density gradient column when measuring the densities of *Calanus finmarchicus* eggs, while Gross & Raymont (1942) did not have the possibility to acclimatize the eggs to the medium used in their experiments. This raises some doubt as to the validity of their results. However, the densities are similar to those measured for krill eggs (Marschall 1983) as well as adult planktonic crustaceans (Aleev & Khvorov 1985). Further, the changes in density of krill eggs were a result partly of water uptake by the embryo and partly shrinking of the egg shell, giving changes in the volume of the perivitelline space (Marschall 1983). As the eggs of *C. finmarchicus* have a very small perivitelline space the effect is probably of less importance in this species. New experiments are needed, though, where egg densities of *C. finmarchicus* are measured under different osmotic pressures.

Wind-induced vertical turbulent mixing is known to keep sinking particles suspended in the upper mixed layer (Smayda 1970, Alldredge, Gotschalk & MacIntyre 1987, Lande & Wood 1987). The suspension time in the mixed layer of particles with low sinking velocity depends mainly on the degree of vertical mixing (Lande & Wood 1987). For particles with high sinking velocity, however, the time it takes to sink through the mixed layer makes up a larger fraction of the total suspension time and the influence of vertical mixing is less. The total suspension time depends mainly on the sinking velocity of the particles in the pycnocline, as this determines the probability that the particles will be resuspended into the mixed layer (Lande & Wood 1987). At the pycnocline and below, the suspension time of particles depends in general mainly on their sinking velocity as vertical mixing is much reduced (Sundby 1983, Lande & Wood 1987, Westgård 1988).

Alldredge *et al.* (1987) analysed the effect of wind-induced vertical turbulent mixing on suspension time of fecal pellets. Following their argumentation, the suspension time of copepod eggs with a sinking velocity of 28 $\text{m}\cdot\text{day}^{-1}$ is mainly governed by sinking and not by vertical mixing at wind speeds less than 10 $\text{m}\cdot\text{s}^{-1}$. At higher wind speeds the effect of mixing increases, but even at 20 $\text{m}\cdot\text{s}^{-1}$ the effect of vertical mixing is moderate.

The pycnoclines encountered in the bloom and late bloom situations in the meltwater region of the Barents Sea were quite pronounced, with water density increasing by about 0.5 units across the pycnocline at stations 905 and 961 (Figure 4). Despite this, the pycnocline had only a modest effect on the calculated high sinking velocities. Contrary to the usual situation in a thermocline, the sinking velocities of the eggs increased in the meltwater pycnocline (Figures 2-4). This was a result of reduced viscosity in the warmer water underlying the cold surface layer of meltwater, which had a stronger effect on the sinking velocity than the change in water density.

The vertical distributions of eggs of *Calanus finmarchicus* at the early bloom stations (Figure 2) were in general compatible with a high sinking rate. The majority of females was found in the upper 30-50 m at stations 28 and 43 (Figure 6), indicating that spawning took place in the surface layer. Assuming an incubation period before hatching of at least 4 and 7 days at 2 and –1 °C (Melle, unpubl. results), respectively, a majority of the eggs should reach 100-200 m before hatching if they were spawned in the upper 50 m. The maximum egg concentrations were found fairly deep in the water column, at 80 or 100 m, which was the deepest depth sampled. The vertical distributions of eggs at stations 28 and 37 provide the clearest support for the high egg density and sinking velocity measured by Salzen (1956) and Gross & Raymont (1942). At station 43 most of the eggs were found above the deep pycnocline at about 80 m, whereas at station 39 the eggs were abundant both above and below the more shallow pycnocline located at about 30 m. These profiles provide less clear evidence for high sinking rate of the eggs than the previous two stations.

In contrast to the early bloom stations, the eggs of *Calanus finmarchicus* at the bloom and late bloom stations (Figures 3-5) did apparently not sink at a high rate. This apparent discrepancy was not because of the difference in water density as this was rather similar between the early bloom, bloom and late bloom stations (Figures 2-5). The uniform concentrations of eggs in the upper mixed layer at the bloom stations indicate that wind-induced vertical mixing was retaining the eggs above the pycnocline (Figures 3 and 5). At the late bloom stations with a strong pycnocline the eggs were apparently retained within and just below the pycnocline where vertical mixing is much reduced (Figure 4). These vertical distributions suggest that the eggs did not sink or sank at a low rate.

The apparent discrepancy in sinking rate between early bloom and bloom and late bloom stations could reflect a difference in the density of the eggs. Different contents of lipid and water may change the buoyancy of the eggs. The females that spawn in early spring rely perhaps more on their internal body reserves for egg production than do females which spawn later when an abundant phytoplankton food resource is available. This could possibly result in less lipid deposition and denser eggs in the former case. To our knowledge there are no measurements on copepod egg buoyancy or composition to evaluate this suggestion.

Marshall & Orr (1972) proposed increased viscosity, as a result of mucus production by phytoplankton cells, as an explanation for the apparent discrepancies between laboratory measured and *in situ* sinking rates of copepod eggs. The possible effect of phytoplankton mucus on the viscosity of sea water was also discussed by Smayda (1970), but no conclusions were drawn. An influence of higher viscosity of water with high phytoplankton concentrations is consistent with the observed egg distributions, which suggest high sinking rate at the early bloom stations with low phytoplankton concentration and low sinking rate at the bloom and late bloom stations with high phytoplankton concentrations.

The vertical distributions of eggs and nauplii reflect dynamic processes such as depth-specific rates of production, development and mortality, sinking rate, vertical mixing, and for nauplii, ability of vertical migration. The close correspondence between the vertical distributions of eggs and nauplii at the bloom and late bloom stations (Figure 7) gives a more static impression, however, suggesting that the nauplii hatched in the same layers as the maximum egg concentrations were found. There seemed to be no or limited ontogenetic upwards migration by the nauplii (Figure 8).

If the sinking rate of eggs really was high, this would imply that most of the eggs at the bloom and late bloom stations were newly spawned. Even by assuming that all females in the water column were spawning at the time of sampling, the number of eggs spawned per female (55-92 at stations 905 and 961) exceeds the spawning intensity (20-60 eggs) in laboratory experiments using well fed females (Marshall & Orr 1972). Assuming that the eggs do not sink and thus represent the total amount of eggs spawned over the last seven days, and also assuming a daily instantaneous mortality rate of 0.1, gives an estimate of spawning intensity of 10-18 eggs$\cdot$female$^{-1}\cdot$day^{-1}. This is in the range of values reported for *Calanus finmarchicus* and related *Calanus* species (Peterson 1988).

The very low egg concentrations below the egg maximum at the late bloom stations are also inconsistent with a high sinking rate unless the egg concentrations are very quickly reduced owing to dispersal or high mortality. However, reductions in concentration from about 10 000 eggs$\cdot$m^{-3} in the maximum at stations 905 and 961 to near zero 10-20 m below is very unlikely considering the high concentrations of nauplii found.

Choosing the simplest explanation for the observed vertical distributions we conclude that the eggs at the bloom and late bloom stations did not sink or sank at a low rate. As the eggs at the late bloom stations were found within and below the pycnocline this low rate of sinking could not be a result of vertical mixing. Vertical wind-induced mixing probably played a minor role in keeping the eggs of *Calanus finmarchicus* suspended in the water column.

The depth of spawning and the sinking rate of the eggs will affect the feeding conditions of the nauplii and therefore possibly the reproductive success. At the early bloom stations with low phytoplankton concentrations the eggs apparently had a high sinking rate, resulting in a deep distribution. The majority of the nauplii presumably hatch well below the euphotic zone. This could possibly reduce the reproductive success of early spawners of *Calanus finmarchicus*, although upwards vertical migration of the non-feeding first naupliar stages might to some extent counteract the great depth of hatching. The abundance of nauplii at the early bloom stations was low, which prevents further analysis of this point.

At the bloom and late bloom stations the females of *Calanus finmarchicus* seemed to adjust their spawning according to the chlorophyll distribution which changed from uniformly high concentrations in the upper mixed layer to a narrow deep chlorophyll maximum layer. By spawning where the high chlorophyll concentrations are, the females reduce the chances of mismatch between the recruits and their food. A dependency of egg production on the food supply for the females is probably a mechanism which contributes to this spatial match. Reduced rate of sinking is a further mechanism which ensures that the nauplii hatch at these favourable depths. The reason for this reduced rate of sinking is still unknown. There is an intriguing possibility, however, of a feed-back effect from the phytoplankton on the sinking rate of the eggs, either through the content and composition of lipids or through increased viscosity of the water.

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